



## Research paper

## Oviposition in the bird parasitic fly *Philornis torquans* (Nielsen, 1913) (Diptera: Muscidae) and eggs' adaptations to dry environments



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## ABSTRACT

The larvae of Neotropical muscid genus *Philornis* (Meinert, 1980) are parasites of a wide range of bird species. For a long time *Philornis* reproductive biology was associated with larviposition due to the low number of empirical data and studies on the life cycle of these parasitic flies. We document oviposition of a subcutaneous species, *Philornis torquans* (Nielsen, 1913), for first time. We provide for the first time a complete morphological description of eggs with Scanning Electric Microscopy (SEM) images and highlight some adaptations to dry environments. We found that the respiratory structure (a kind of plastron) at the anterior pole is reduced in size. This suggests that *P. torquans* eggs could be adapted to birds' nests dry environment.

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### 1. Introduction

The genus *Philornis* (Meinert, 1890) contains 50 species, predominantly distributed in the Neotropics (Carvalho et al., 2005). An important characteristic of this muscid genus is that their larvae are parasites of a wide range of bird species (Löwenberg-Neto, 2008). *Philornis torquans* (Nielsen, 1913) is one of the four *Philornis* species that are considered valid for Argentina (Couri et al., 2009; Silvestri et al., 2011); and their larvae are subcutaneous blood feeders (Dudaniec and Kleindorfer, 2006). After penetrating into the host integument, the larvae become established between the dermis and the superficial muscles where undergo a period of development and growth (Teixeira, 1999).

*Philornis torquans* was first observed by Nielsen (1911) in the Zoological Museum of Copenhagen, in samples collected from bird nests in Argentina by Mr. Mogensen. In this work, Nielsen did not observe eggshells, so he supposed that this species placed larvae over birds' skin. Later, several authors also considered *P. torquans*

as larviparous (Skidmore, 1985) or multilarviparous (Meier et al., 1999). However, there is controversy about the viviparity-oviparity of *Philornis* species. Some authors (Arendt, 1985; Couri, 1999) suggested that eggs or already-hatched larvae are laid in nest material and larvae then seek for their hosts. So far, oviparity was observed only for the free living coprophagous larvae of *Philornis rufoscutellaris* (Couri, 1983) and for two species with free living semi-hematophagous larvae: *Philornis downsi* (Dodge and Aitken, 1968) (Lincango and Causton, 2008) and *Philornis falsificus* (Dodge and Aitken, 1968).

Morphological studies on immature stages of *Philornis* centred mainly on the third instar larvae and pupae (Couri et al., 2005, 2007a; Dodge and Aitken, 1968; Skidmore, 1985). Only a brief description of eggs of *P. falsificus* (Dodge and Aitken, 1968) and *P. rufoscutellaris* (Couri, 1983) are known. In addition, a single Scanning Electric Microscopy (SEM) image of part of the egg of *Philornis* sp. without a description was presented in a technical report (Arendt, 2006). However, no full descriptions of eggs of any species of *Philornis* have been published so far.

To expand knowledge of the immature stages of *P. torquans* we provide information not only morphological structures that may be of help to the identification of this species, but also about its biolog-

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ical significance as adaptations to the environment, parasites, etc. This is especially true when using SEM images, since such technique provides comprehensive and detailed pictures of some structures not visible under the light microscope (Hinton, 1981).

The aim of this work is to document oviposition and adaptations of eggs of *P. torquans* to dry environments and to provide a complete morphological description of the eggs with SEM images.

## 2. Materials and methods

As part of a *P. torquans* research program, since 2013, we collected larvae from infested broods in a native forest of central Argentina (Santa Fe Province – 60° 55' 0''W; 31° 23' 08''S). Fully developed larvae were carefully removed from hosts with fine lab tweezers and then kept individually in 25 cm<sup>3</sup> plastic containers lined with tissue paper. Larvae were delivered to the laboratory within a few hours after removal. Pupation occurred at a temperature of 26 ± 1 °C and a humidity of 65 ± 15%. After emergence, and under described room conditions, pairs consisting of one male and one female were placed in a plastic container (250 cm<sup>3</sup>) to explore their reproductive biology and behaviour. Each recipient was checked daily to feed adults as well to register their activity and survival. Food provided was a mixture of natural juice, sugar water and proteins placed into a 1.5 ml vial; diet that proved to be effective for other *Philornis*' species (Lahuatue et al., 2016). After death, some adult specimens were preserved in 70% ethanol while others were kept dry.

First eggs of *P. torquans* were found on December of 2013 inside of recipients and some of them were immediately preserved in 70% alcohol. Adult females that laid eggs were identified as *P. torquans* using taxonomic key and descriptions provided by Dodge (1968) and Couri et al. (2009). Terminology of eggs description follows Hinton (1981), Skidmore (1985), and Grzywacz et al. (2012) for terms “hatching pleats” and “hatching line”.

Eggs used for the SEM were collected and preserved the same day that they were laid. A total of 10 eggs were dehydrated through 80, 90, and 99.5% ethanol; critical point dried in CO<sub>2</sub> and coated with gold-palladium in a Thermo VG Scientific SC 7620 sputter coater. Images were taken with a Philips XL30 TMP SEM at the MACN. Digital photographs of eggs (n = 3) with stereoscopic microscopy were taken using an Olympus DP 25 digital camera mounted on an Olympus SZX 16 stereomicroscope. Measurements (n = 10) were digitally obtained with the software Leica Application Suite EZ Version 2.1.0. We used the software Olympus cellSens Standard and Combine ZM for image processing.

Voucher specimens were deposited in the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN), Buenos Aires, Argentina, and in the Laboratorio de Ecología de Enfermedades (LECEN- ICIVET), Santa Fe, Argentina.

## 3. Results

### 3.1. Oviposition

In late December 2013 first eggs laid by *P. torquans* were found on the inside surface of recipients. From there a total of 1836 eggs laid by 41 females were collected. Eggs were laid individually, having been found indistinctly on containers' surface, on food containers and on food.

### 3.2. Egg

Length: 1049.09 ± 22.97 μm, width 250.00 ± 34.54 μm.

Colour brown with irregular white spots, elongated, rounded at posterior pole (Fig. 1). Dorsal surface is flat, with a broad median

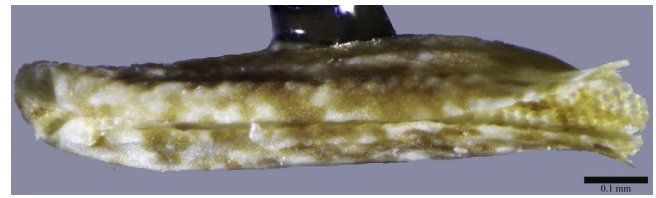


Fig. 1. Egg of *Philornis torquans*, dorsal view. The large brown item at the upper side of the image is the pin used to hold the egg.

area and two development pleats. Hatching pleats are parallel and extending outwards with regard to the media area. The pleats diverge from the median area towards the anterior and posterior poles (Fig. 2A).

The reticulated pattern of median area presented elevated and thick ridges extending to posterior pole (Figs. 2A, D; 3C). Also this reticulated pattern presented two thick longitudinal ridges that connect with the hatching pleats (Fig. 2A). Inner surface of hatching pleats presents a hexagonal pattern, more conspicuous towards the hatching line (Fig. 2C). On the other hand, the outer surface of hatching pleats has a hexagonal pattern with little depressions (not pores) and with elevated ridges that reduce towards hatching line (Fig. 3A, B). We observed two perforations or orifices covered by the reticulated ridges pattern that extend from the median area to the posterior pole (Fig. 3C).

At the anterior pole a respiratory structure (a kind of plastron) is present. This structure is of reduced size and is only present close to the hatching line (Fig. 2B). The inner surface of hatching pleats shows an external hexagonal pattern of few perforations (Fig. 4A) and internal papillae (Fig. 4B). The outer surface of the hatching pleats presents some type of island pattern (Fig. 4A), that would be interacting with the papillae of the inner surface of hatching pleats to form a kind of plastron.

Ventral surface is convex with a longitudinal corrugated (Fig. 4C); the hexagonal pattern with elevated ridges looks stronger towards the anterior pole (Fig. 4E). The micropylar plate has a well-defined dorsally wall (Fig. 4C). The hexagonal pattern surrounding the micropyle is different from the polygonal patterns observed in other areas of this egg (Fig. 4D).

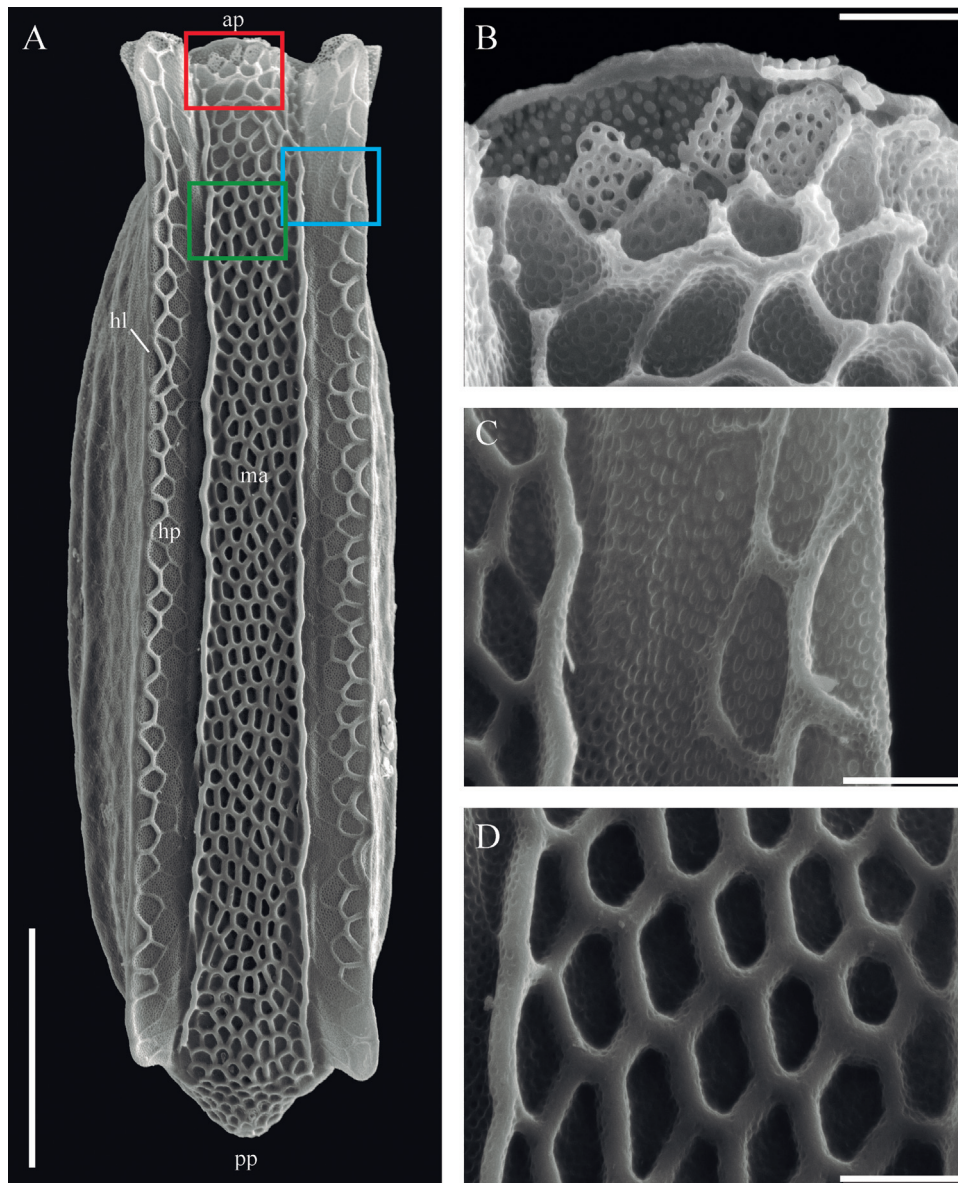
## 4. Discussion

For a long time scientists have speculated on *Philornis* reproductive biology, due to the low number of empirical data and studies on the life cycle of these parasitic flies. The present contribution represents the first time the oviposition of a subcutaneous *Philornis* species is documented.

However oviposition (instead of larviposition) seems to be usual in other nestling birds' parasites as those of the non Neotropical genera *Passeromyia* (Rodhain and Villeneuve, 1915) (Muscidae) and *Protocalliphora* (de N Hough, 1899) (Calliphoridae). Observations of oviposition behaviour in *Passeromyia* show that the eggs are laid in masses (12–17) in the nest or under host's wings (*Passeromyia heterochaeta* (Villeneuve, 1915) – Skidmore, 1985 and *Passeromyia indecora* (Walker, 1853) – Pont, 1974; respectively). In a similar way, oviposition is present in species of *Protocalliphora*. Zumpt (1965) stated that it is not known if *Protocalliphora* is oviparous or larviparous. However, later observations showed that these flies are oviparous (Bennett and Whitworth, 1991; Sabrosky et al., 1989).

Unlike species of *Passeromyia*, it is too hard to find *Philornis*' eggs in the wild. Their small size and the nest colour make difficult to find them on nests or on the nestlings. Particularly, we observed that *P. torquans* lays egg individually in laboratory.

An additional observation argues that *P. torquans* oviposit. As opposed to a reduction of the telescoping female terminalia asso-



**Fig. 2.** SEM micrographs of the egg of *Philornis torquans*. (A) Dorsal view, red square: detailed in Fig. 2B, blue square: detailed in Fig. 2C, green square: detailed in Fig. 2D. (B) Detailed image of the anterior pole with plastron. (C) Detailed picture of the reticular pattern of the inner surface of hatching pleats. (D) Detailed image of the reticular pattern of the median area. Ap, anterior pole; hl, hatching line; hp, hatching pleat; pp, posterior pole. Scale bars = (A) 200  $\mu\text{m}$ ; (B–D) 20  $\mu\text{m}$ . (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

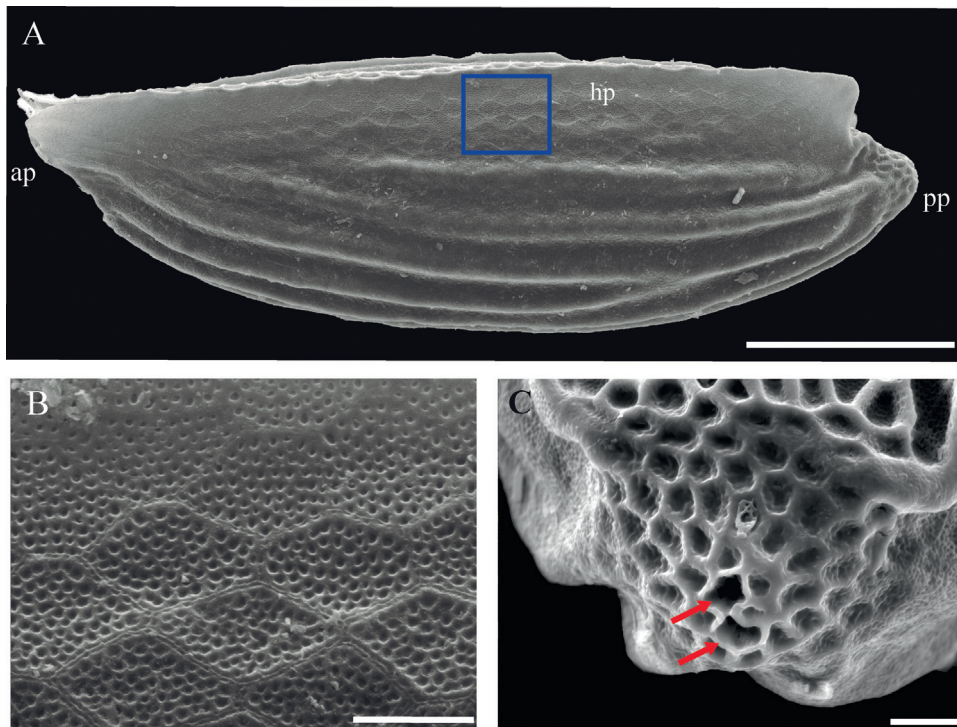
ciated with larviparous habit (Meier et al., 1999), we observed (information not published) a long telescoping female terminalia. This observation matches with a general pattern observed for species of this genus (Couri et al., 2007b).

Morphological descriptions of eggs of Muscidae were summarized by Skidmore (1985). In this work, Skidmore compiled the bibliographic information and proposed a classification considering the hatching pleats and chorionic structure. On the basis to the brief description of hatching pleats of the egg of *P. falsificus* presented by Dodge and Aitken (1968), Skidmore included *Philornis* in the *Phaonia*-type egg. The eggs of a second species of this genus, *P. rufoscutellaris* were presented through an illustration (Couri, 1983), and showed a similar hatching pleats as described to *P. falsificus*. The eggs of *P. torquans* have well developed hatching pleats that slightly project towards the anterior pole; features that allowed us to include this specie as with a *Phaonia*-type egg.

Two differences were observed between the eggs of *P. rufoscutellaris* and *P. torquans*. The hexagonal pattern of the median area

reaches the posterior pole in *P. torquans*, while in *P. rufoscutellaris* the hatching pleats are jointed before posterior pole, close to the median area. Also, Couri (1983) showed two different hexagonal patterns in *P. rufoscutellaris* egg, while *P. torquans* presents a unique one. The partial egg SEM image of *Philornis* sp. presented by Arendt (2006) could not be herein compared as the specie is not identified and the part of the egg photographed is not specified.

As previously stated, the use of SEM provides comprehensive and detailed studies of eggs' morphology. The interpretation of these structures can contribute to improve the knowledge of the biology of the species. The work presented by Hinton (1981) is considered the first step for such kind of studies. Later, some few studies presented descriptions of muscid eggs by using SEM, mainly using species of medical (Alencar and Leite, 1992) or forensic relevance (Cortinhas et al., 2016; Grzywacz and Pape, 2010; Mendonça et al., 2008). Some of these species, as *Muscina levida* (Harris, 1780) (Liu and Greenberg, 1989), *Muscina stabulans* (Fallén, 1817) and *Synthesiomyia nudiseta* (Van Der Wulp, 1883) (Alencar and Leite,



**Fig. 3.** SEM micrographs of the egg of *Philornis torquans*. (A) Lateral view, blue square: detailed in Fig. 3B. (B) Detailed image of the reticular pattern of the outer surface of hatching pleats. (C) Detailed picture of the posterior pole with two orifices (red arrows). Ap, anterior pole; hp, hatching pleat; pp, posterior pole. Scale bars = (A) 200  $\mu\text{m}$ ; (B–C) 20  $\mu\text{m}$ . (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

1992), that are phylogenetically close to *Philornis* (Haseyama et al., 2015), show similar hatching pleats. Pictures of eggs of *M. stabulans*, *M. levida* (Greenberg and Kunich, 2002), and *S. nudiseta* (Alencar and Leite, 1992) showed hatching pleats that extend outwards from the median area; similar those observed in *P. torquans*. When comparing the polygonal pattern of the median area of *P. torquans* with *M. stabulans* and *S. nudiseta*, we observed several differences. On one hand, *P. torquans* presented elevated and thick ridges and two thick longitudinal ridges that connected the median area with the hatching pleats, while *M. stabulans* and *S. nudiseta* showed only open and thin ridges in the median area without any longitudinal ridge. Also, *P. torquans* lacks the pits or perforations on the median area present in *M. stabulans* and *S. nudiseta*.

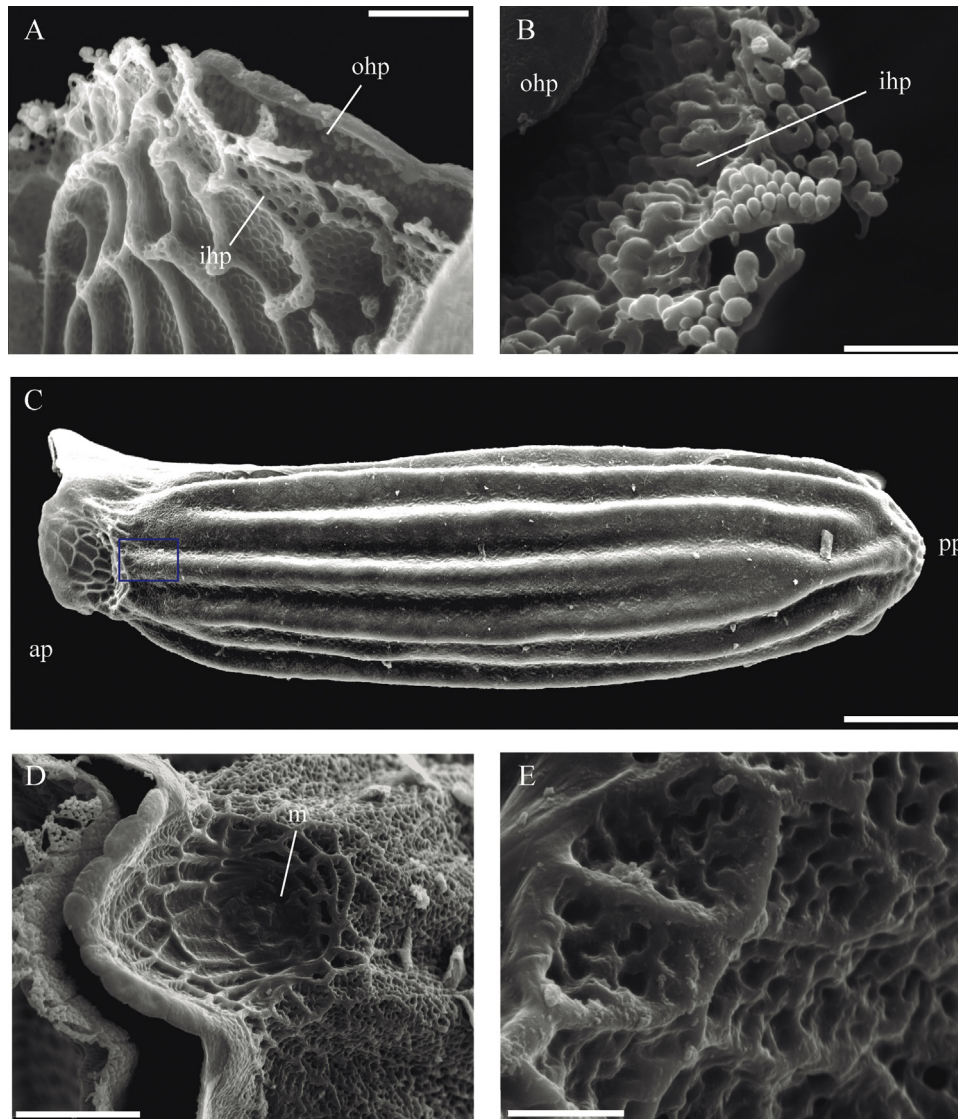
In Muscidae eggs, the micropyle is a single pore through which spermatozoa enter into the egg and is located at the anterior pole surrounded by a micropylar plate. *Philornis torquans* presented a well-defined micropylar plate and a polygonal pattern surrounding the micropyle; similarly found in *M. levida*, *M. stabulans* (Greenberg and Kunich, 2002), and *Ophyra aenescens* (Wiedemann, 1830) (Cortinhas et al., 2016). In the later three species the polygonal pattern is close to the micropyle, while in *S. nudiseta* such structure extends to the ventral surface of the egg (Alencar and Leite, 1992). We also observed a unique structure of *P. torquans* micropyle plate: the presence of a well-defined dorsal wall.

At the posterior end we observed, for *P. torquans*, two pores or orifices without an associated function. Unlike the two pores observed for *O. aenescens* (Cortinhas et al., 2016) and one pore described for *S. nudiseta* (Alencar and Leite, 1992; El-Alfy, 1994), pores present in *P. torquans* were covered by the reticular pattern.

Different types of respiratory systems have evolved in order to satisfy oxygen demands and avoid dehydration (Hinton, 1981). Some muscid species as *O. aenescens* (Cortinhas et al., 2016) or *S. nudiseta* (Alencar and Leite, 1992), showed a plastron-bearing area with a “holes and islands” pattern extending over the whole median area. Females of these species lay eggs in a wet envi-

ronment (on moist organic matter) to prevent drying (Hinton, 1960). Other Muscidae shows horns with a plastron that may be an adaptation of eggs to survival under water or in wet or waterlogged habitats (Grzywacz and Pape 2010; Hinton, 1981; Merritt and Wotton, 1988). In this situation, the respiratory horn of eggs of *Musca autumnalis* (De Geer, 1776), projects slightly above the organic matter (dung) where are deposited. The outer surface of these eggs, apart from the area between the hatching lines, is not an open network (as *O. aenescens*) but it is a continuous sheet of chorion which would serve to avoid dehydration (Hinton, 1960). In a similar way, *Limnophora riparia* (Fallén, 1824) laid eggs in the exposed or partially submerged moss, so the horns and the reticulated pattern of median area could be adaptations to the wet environment (Merritt and Wotton, 1988). An interesting observation for *P. torquans* is related to the presence of a very small respiratory structure (a kind of plastron) found on the anterior pole. Accordingly, species laying eggs into a relatively dry environment should be characterized by a smaller proportion of the egg surface that functions as a plastron (Grzywacz et al., 2012). Erzinçlioglu (1988) described eggs of calliphorid's species like *Protophthora azurea* (Fallén, 1817), whose larvae are hematophagous parasites on nests birds as *Philornis* (Sabrosky et al., 1989). Those eggs (Erzinçlioglu, 1988), in contrast with the pattern of “holes and islands” observed for carrion-breeding flies, presented a reduced median area with perforations or pores that may be an adaptation to the relatively warm dry environment of a bird's nest. Also, a similar respiratory structure was observed in a Rhinophoridae species (Draber-Mońko, 1997). The reduced respiratory structure found in *P. torquans* is consistent with the observations for species whose eggs are deposited in dry environments suggesting that it could be an adaptation of the eggs to the environment of birds' nests.

As shown before, morphological studies provide information on environmental features that may be critical for the development of the egg (i.e. humidity). Also, can be used for species identification and phylogenetic purposes (Meier and Hilger, 2000; Pape, 2001).



**Fig. 4.** SEM micrographs of the egg of *Philornis torquans*. (A) Detailed image of the external surface of plastron. (B) Detailed picture of the internal surface of plastron. (C) Ventral view, blue square: detailed in Fig. 4E. (D) Micropylar plate. (E) Detailed image of the reticular pattern of the ventral surface. Ap, anterior pole; ihp, inner surface of the hatching pleat; m, micropyle; ohp, outer surface of the hatching pleat, pp, posterior pole. Scale bars = (A) 20  $\mu\text{m}$ ; (B) 10  $\mu\text{m}$ ; (C) 200  $\mu\text{m}$ ; (D) 50  $\mu\text{m}$ ; (E) 10  $\mu\text{m}$ . (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

This study represents the first full description of a *Philornis* egg by using SEM, information that will shed some light on the intricate taxonomy of this genus of flies.

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