

Immature stages of *Ebusus ebusus ebusus* (Cramer, 1780) in the Peruvian Amazon (Lepidoptera: Hesperiiidae: Hesperiiinae)

Rodrigo Ccahuana^{1,2}, Rafael Tejeira^{1,2}, Thalia Hurtado^{1,3}, Shinichi Nakahara^{4,5}, Maryzender Rodríguez-Melgarejo⁵, Riley J. Gott⁴, Joseph See¹ and Geoffrey Gallice^{1,4}

1. Alliance for a Sustainable Amazon, Hanover, MD 21076, USA; 2. Universidad Nacional de San Antonio Abad del Cusco, Av. de La Cultura 773, Cusco 08000, Perú; 3. Facultad de Ciencias Naturales y Matemática, Universidad Nacional Federico Villarreal, Jr. Río Chepén, El Agustino, Lima, Perú; 4. McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA; 5. Departamento de Entomología, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Apartado 14-0434 Lima-14, Perú;

*Correspondence: info@sustainableamazon.org

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Abstract: We here report for the first time the complete immature life cycle of a Neotropical skipper butterfly, *Ebusus ebusus ebusus* (Cramer, 1780), with a report of a new natural hostplant based on a single individual reared at Finca Las Piedras (Madre de Dios, Peru). An egg obtained in nature passed through four larval instars and reached the adult stage, feeding on a palm species identified as *Mauritia flexuosa* L.f. (Arecaceae: Calamoideae). We provide images of each life stage including illustrations of head capsules and larval shelter structures, as well as information on the duration of the stages.

Resumen: Aquí reportamos por primera vez el ciclo de vida completo de una mariposa hespérida Neotropical, *Ebusus ebusus ebusus* (Cramer, 1780) y el registro de una nueva planta hospedera basado en un solo individuo criado en Finca Las Piedras (Madre de Dios, Perú). El huevo colectado en su hábitat natural pasó por cuatro estadios larvales y alcanzó la etapa adulta alimentándose de una especie de palma identificada como *Mauritia flexuosa* L.f. (Arecaceae: Calamoideae). Proveemos imágenes de cada etapa de vida, incluyendo ilustraciones de las cápsulas de la cabeza y de las estructuras de los refugios para larvas, así como información sobre la duración de los estadios larvales.

Key Words: Finca Las Piedras, life history, lowland rainforest, Madre de Dios, skipper.

INTRODUCTION

The family Hesperiiidae has remained one of the most poorly understood groups of butterflies (Papilionoidea) in the Neotropics in terms of its species diversity and systematics. However, with the wide availability of high-throughput sequencing techniques, well-resolved and strongly supported higher-level phylogenetic hypotheses are consistently being generated for this family, and thus our understanding of higher-level skipper systematics is steadily improving (e.g., Cong *et al.*, 2019; Li *et al.*, 2019; Zhang *et al.*, 2019a,b). Advances in molecular techniques have also contributed to our understanding of the species richness of Neotropical skippers, including discoveries of cryptic species (e.g., Hebert *et al.*, 2004; Bertrand *et al.*, 2014). Nevertheless, despite our improving knowledge of the group's systematics, only scarce information exists for the early stage biology of skippers, a situation similar to a number of other butterfly groups in the tropics, with moderately detailed immature stage information and reliable natural hostplant data available for only a small fraction of Neotropical species (e.g., Moss, 1949; Burns & Janzen, 1999, 2001; Cock, 2003, 2005, 2006, 2008, 2009; Greeney & Jones, 2003; Greeney & Warren, 2004, 2009a, b, 2011; Greeney *et al.*, 2010; Bächtold *et al.*, 2012;

Moraes *et al.*, 2012; Lepesqueur *et al.*, 2017; Freitas, 2018, 2020). Nevertheless, documenting immature stage morphology of a diverse group in the Neotropics can be extremely valuable, for example, in terms of its comparative information, even at the species level (e.g., Hill *et al.*, 2011).

Ebusus ebusus ebusus (Cramer, 1780) is a taxon currently placed in the skipper tribe Calpodini (Mielke, 2004, 2005), although recent molecular data suggests its placement in the subtribe Carystina (Hesperiiini) may be warranted (Cong *et al.*, 2019). As currently conceived (but see discussion below), this species ranges from southern Mexico throughout Central America, the Guianas, Trinidad, the Amazon basin, and into southeastern Brazil (Evans, 1955; Miller, 1985; Cock, 2005). Miller (1985) recognized the population from southern Mexico to represent a taxon different from the nominate subspecies, and at least three additional species-group names are associated with this specific epithet (Mielke, 2004, 2005). *Papilio ebusus* Cramer, 1780 was described by Pieter Cramer in his *De Uitlandsche Kapellen* series (work completed by Caspar Stoll) based on an unspecified number of specimen(s) from Suriname (Cramer, 1780: 20). Although the syntype(s) of *P. ebusus* has not been located to our knowledge (B. Hermier and H. Gernaat, pers. comm.), the illustrations associated

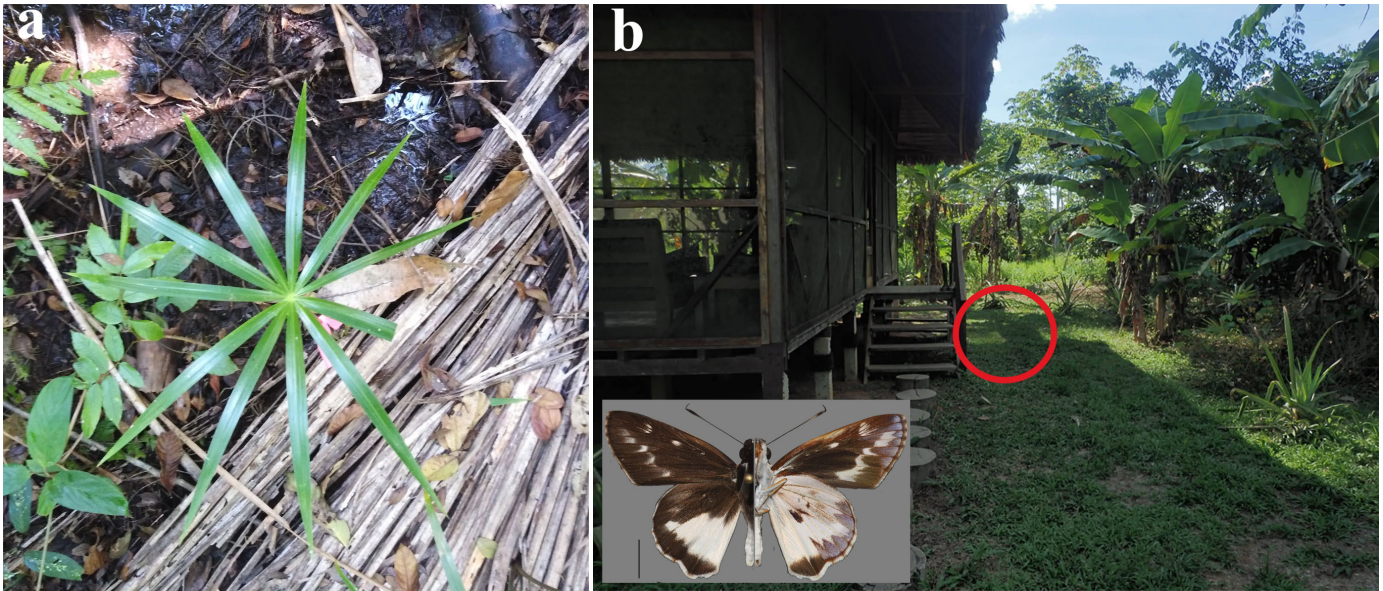


Figure 1. Habitat and hostplant of *Ebusus ebusus ebusus* (*Mauritia flexuosa*): a) close-up view of *Mauritia flexuosa* of a similar size; b) general view of the habitat where the hostplant on which the female oviposited was located (location circled but the plant no longer exists, photographed in December 2020) with adult in the left corner (scale = 10 mm).

with Cramer's original description (pl. CCC [300], figs C, D) do reasonably match what we currently conceive as this widespread species, thus we apply this specific epithet herein, in accordance with a number of previous studies such as Miller (1985) and Cock (2005). Furthermore, there has been a great confusion surrounding the dates of publication and authorship regarding nomenclatural acts in the four volumes (in 34 parts) of *De Uitlandsche Kapellen* (see Dos Passos, 1958; ICZN, 1958; Chainey, 2003), resulting in *P. ebusus* erroneously being attributed to Stoll in many earlier studies such as Evans (1955), Miller (1985) and Cock (2005). We therefore follow Chainey's (2005) justification as to applying the dates of publication and authorship for *P. ebusus*, and attribute this specific epithet to Cramer, not Stoll. Subsequently, Evans (1955) proposed the monospecific genus *Ebusus* Evans, 1955 to harbor this taxon, which classification has been followed by subsequent authors (e.g., Mielke, 2004, 2005).

We here describe for the first time the complete immature life cycle and report a new natural hostplant record for *Ebusus ebusus ebusus* in the Peruvian Amazon, to contribute to our knowledge of Neotropical skipper life histories. This article is part of an ongoing series of publications resulting from rearing of butterfly immature stages at Finca Las Piedras (FLP) (Madre de Dios, Peru) (following See *et al.*, 2018; Baine *et al.*, 2019; Nakahara *et al.*, 2020; Tejeira *et al.*, in press).

STUDY SITE AND METHODS

The present study is based at Finca Las Piedras (FLP), a 54 ha biological research station located approximately 48 km north of Puerto Maldonado in Madre de Dios, Peru (-12.22789, -69.11119; ca. 240 m elevation). For further information regarding FLP, see Baine *et al.* (2019) and See *et al.* (2018). Field work was conducted between April and July 2020 by RC and RT. Eggs collected in the field were taken into the laboratory to observe growth and for photography. The immatures were kept

in a 1 L plastic container marked with a unique code (provided below), covered by a nylon mesh fabric fastened with an elastic band. The larva received fresh leaves from its hostplant and the leaves were kept hydrated using floral tubes filled with water. The immatures were photographed and the container was cleaned daily. Observations of the head capsules were done using a Leica LED2500 stereomicroscope with magnification ranging from 10x to 160x. The head capsule drawings were made with Adobe illustrator CC 2015 by MRM. Terminology for immatures largely follows Stehr (1987) and Minno (1994). All morphological examinations were conducted at Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM) by MRM, and voucher material will be deposited at the Alliance for a Sustainable Amazon collection, Puerto Maldonado, Peru (ASA).

RESULTS

Two eggs were collected on *Mauritia flexuosa* L.f. (Arecaceae: Calamoideae) on 23 May 2020, and vouchered as 2020_FLP_IMM_0173 and 0174 (see below for more details); 2020_FLP_IMM_0174 did not hatch, thus the following data is based solely on 2020_FLP_IMM_0173. Egg hatch was recorded on 1 June 2020; L1 to L2 on 6 June 2020; L2 to L3 on 11 June 2020; L3 to L4 on 17 June 2020; pupation on 27 June 2020; and adult eclosion on 17 July 2020.

Hostplant and Behavior

The hostplant was identified as *Mauritia flexuosa* L.f. (Arecaceae: Calamoideae) (Fig.1a), one of two species in this palm genus. *Mauritia flexuosa* is widely distributed throughout the Amazon basin, in addition to lower elevations of the eastern Andes and other parts of tropical South America (Henderson *et al.*, 1995). In Peru, *M. flexuosa* is commonly known as "aguaje" and this palm species is commercially important (Henderson *et al.*, 1995, pers. obs.). The hostplant was growing as an

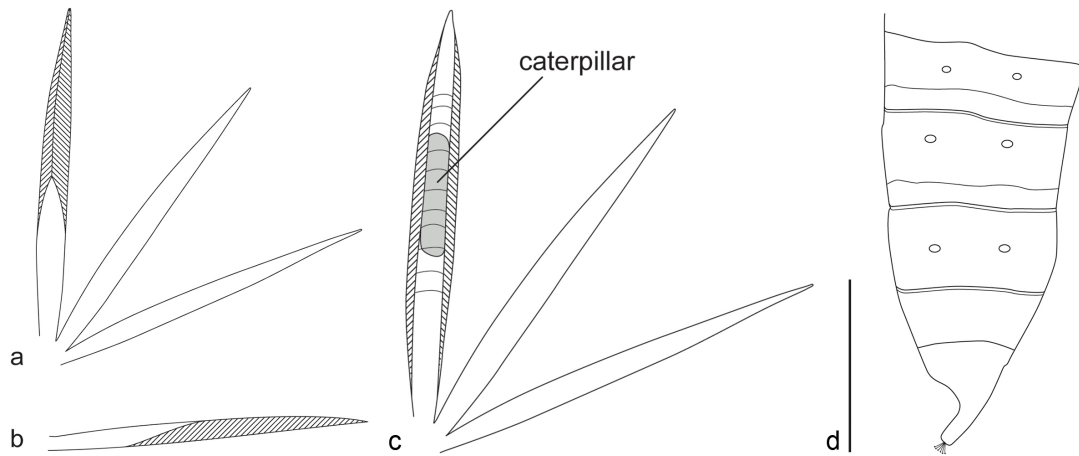


Figure 2. Shelter structure and terminal abdominal segments of pupa: a) shelter structure in dorsal view, for first and second instar; b) shelter structure in lateral view, for first and second instar; c) shelter structure in dorsal view, for third and fourth instar; d) terminal abdominal segments of pupa (cremaster) in dorsal view. Scale bar = 5 mm.

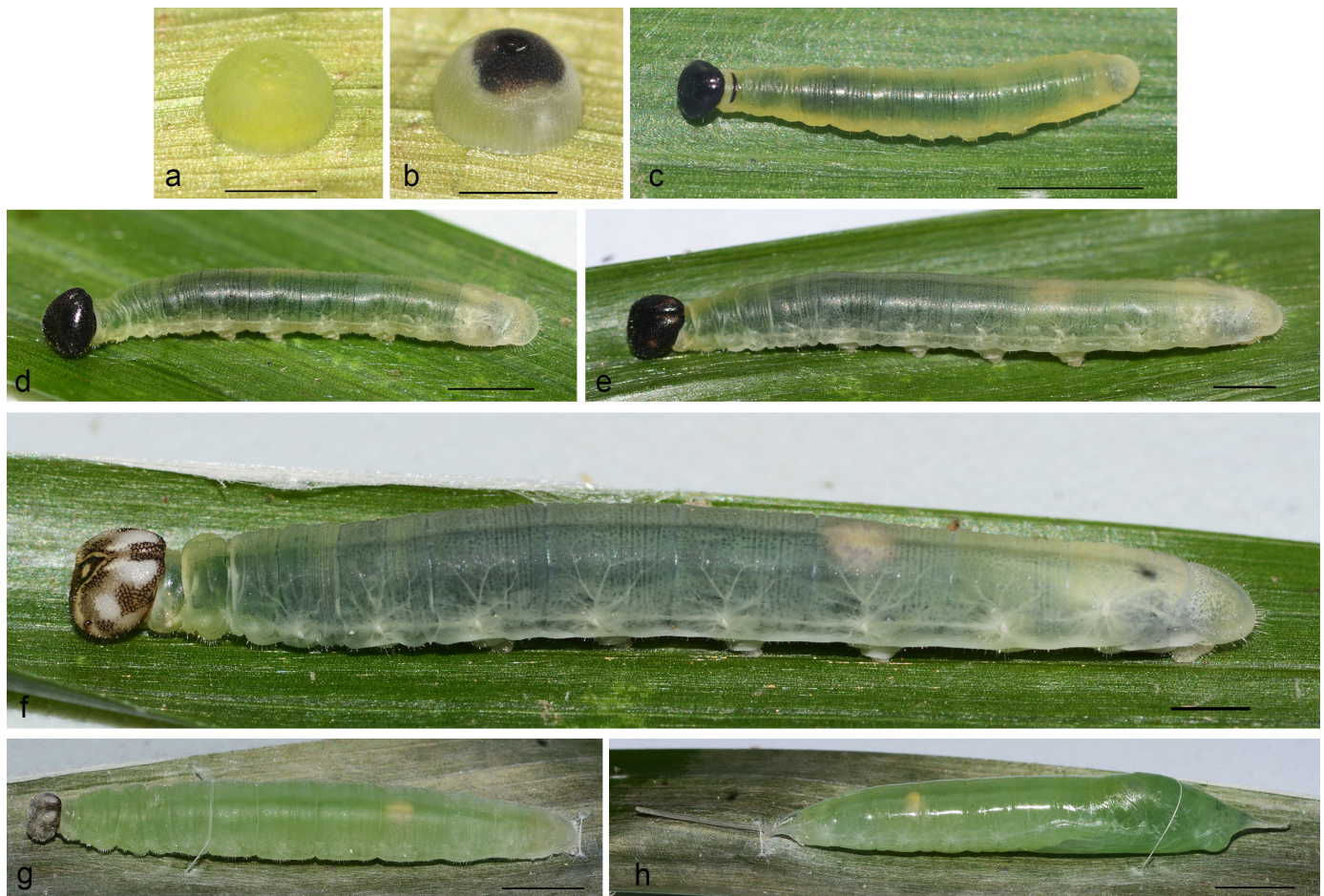


Figure 3. Immature stages of *Ebusus ebusus ebusus*: a) egg; b) egg with visible head capsule; c) first instar in dorsal view; d) second instar in dorso-lateral view; e) third instar in dorso-lateral view; f) fourth instar in lateral view; g) prepupa in dorso-lateral view and h) pupa in dorso-lateral view. All images are based on 2020_FLP_IMM_0173. Scale bar = 1 mm.

ornamental on the grounds of FLP, which is situated within an agricultural matrix of abandoned and active agricultural fields dominated by *Brachiaria* sp. grass (Poaceae) and regenerating forest less than three years old (Fig.1b). The edge of a large intact forest begins approximately 200 m away from this location and multiple swamps dominated by *M. flexuosa* are

found nearby. At the time of egg collection, the plant was less than 50 cm in height. The adult female was encountered by RC, on 23 May 2020 around 14:30 (recorded temperature of the day was 16°C, with a minimum of 14.5°C and maximum of 19°C). When observed, this individual was flying rapidly for several minutes over the aforementioned small “aguaje” plant,

attempting to land several times on the leaves until it landed on the underside of one of the leaves where it remained for 5 to 6 seconds before laying two eggs on the ventral surface of the leaf. During the first and second instar, a shelter was built by joining two ends of the leaflet to form a “tube” that completely covered the larva (Fig. 2a, b), and the larva emerged only to feed. In the third and fourth instar, as well as the pupal stage, a similar tube was built, although the shelter did not fully cover the caterpillar during these instars and was easily visible inside the shelter (Fig. 2c). These refuges are considered Type II shelters based on Greeney *et al.* (2010). The larva fed mostly at night and in order to photograph it during the day the shelter was broken to visualize it, but it was later re-built by the larva. When the larva was inside the shelter, RC observed the feces being launched with a strong force from the shelter, reaching a distance of about 20 cm away from the shelter.

Description of the immature stages (n=1 throughout)

Egg (Fig. 3a-b). Hemispherical, translucent yellowish, with radial vertical ribs all over surface; diameter: 1.4 mm. Duration: 9 days.

First instar (Figs. 3c, 4a). Black head capsule, epicranial notch minute, vertex rounded, without projections or scolum, with pitted sculpturing, frons and clypeus fused (= frontoclypeus), frontoclypeus dark brown, primary setae F1, C1, C2, A1, A2, S1, S2, S3, P1, P2, and L1 present, 5 setae present on one side of labrum, stemmata 1-4, 6 equal in size, stemma 5 slightly larger and closer to stemma 6 than stemma 4. Head capsule width: 0.8 mm, height: 0.8 mm. Smooth body, translucent integument, white before feeding, green after feeding, black prothoracic plate present, anal plate undifferentiated from integument. Maximum body length: ~7 mm. Duration: 5 days.

Second instar (Fig. 3d). Head capsule similar to previous instar except head sculpturing ‘pebbly’ instead of pitted, secondary setae obscure primary setae. Head capsule width: 1.56 mm, height: 1.77 mm. Smooth body, with translucent integument, becoming white and opaque in last three abdominal segments, intestinal contents dark green, white tracheal system forming a lateral line in spiracles, prothoracic plate undifferentiated from surrounding integument, anal plate undifferentiated from integument. Maximum body length: ~13 mm. Duration: 5 days.

Third instar (Fig. 3e). Dark brown head capsule, epicranial notch slightly deeper than in previous instars, vertex rounded, irregular light brown spots on sides of epicranial suture, from epicranial zone to ocelli, with pitted sculpturing. Head capsule width: 2.19 mm, height: 2.31 mm. Smooth body, translucent gray integument, with a rounded yellow spot on dorsal area of A5; dark green intestinal contents; white tracheal system forming a lateral line at spiracles. Maximum body length: 23 mm. Duration: 6 days.

Fourth (last) instar (Figs. 3f-g, 4b). Dark brown head capsule, two pairs of rounded white markings nearly conjoined on epicrania, one pair near epicranial notch, one pair medially, an irregular cream-colored band that spans from adfrontal area to base of ocelli, single cream-colored spot posteriad of ocelli following break in irregular cream-colored band, single cream-colored spot on dark brown frontoclypeus, pebbly sculpturing present, numerous secondary setae, stemmata 1-4, 6 equal in size, stemma 5 slightly larger and closer to stemma 6 than stemma 4. Head capsule width: 2.75 mm, height: 3.36 mm. Smooth body similar to previous stage, with a more noticeable yellow spot on dorsal area in A5 and white tracheal system that forms a lateral line on spiracles similar to previous stage. Maximum body length: 35 mm. Duration: 10 days.

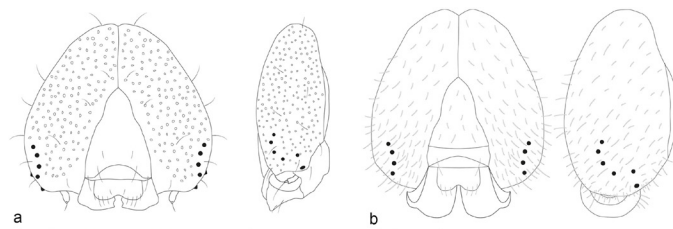


Figure 4. Head capsule illustrations: a) first instar (in frontal and lateral view); b) fourth instar (in frontal and lateral view). Scale bar = 1 mm.

Pupa (Figs. 2d, 3h). Elongated, thin, light green; proboscis sheath longer than body length, abdominal and cremaster dorsal ridges not observed, cremaster with numerous setae with posterior tips curled. Attached to blade by two bands of silk crossing cremaster and thoracic region. Maximum length: 37 mm. Duration: 20 days.

DISCUSSION

Despite there being some information on the early stage biology of *E. ebusus ebusus* (Cock, 2005; Moss, 1949), the present study is arguably the most comprehensive to date by providing data for the complete immature life cycle, illustrating morphological characters not figured previously, and identifying a natural hostplant resulting in a new host record for this taxon. Moss (1949: 74) reported “Assahy and Pachiúba palms” as hostplants for *E. ebusus ebusus* (as *Carystus ebusus*) based on his rearing in southern Brazil. According to Cock (2005), the former palm species is *Euterpe oleracea* Mart. (Arecaceae), while the latter is *Socratea exorrhiza* (Mart.) H. Wendl. (Arecaceae), a fact reflected in Beccaloni *et al.*'s (2008) checklist. Cock (2005) also provided hostplant records for this species as “unidentified palm” and *Bactris major* Jacq. (Arecaceae) from Trinidad, although the latter species is indicated as an accepted plant in captivity, not a natural hostplant. Janzen & Hallwachs (2018) reported three palm species as natural hostplants for this taxon in Costa Rica, namely *Socratea exorrhiza*, *Reinhardtia latisepta* and *Iriartea deltoidea* (all Arecaceae). Our record (feeding on *Mauritia flexuosa*) thus represents a new hostplant record for *E. ebusus ebusus*, also being consistent with other records by being a palm species in the family Arecaceae.

Hostplants reported for hesperiids in the Neotropics are primarily monocots, with host preference for monocots or dicots being associated with phylogenetic relationships. Generally, taxa in the subfamilies Heteropterinae and Hesperinae feed on monocots, with few exceptions, most notably Afrotropical hesperiines as discussed by Cock & Congdon (2013), while taxa in the other subfamilies are primarily associated with dicots (Sahoo *et al.*, 2017). All reported hostplants for *Ebusus ebusus* belong to Arecaceae, being a common hostplant family for members in the subtribe Carystina, including *Carystus* spp., *Daron seron* (Godman, [1901]), and *Tromba xanthura* (Godman, 1901), while members of the subtribe Calpodina, including *Panoquina* spp., *Saliana* spp. and *Calpodius ethlius* (Stoll, 1782) are reported to feed on a variety of other plant families, such as Cannaceae, Poaceae (Gramineae), Heliconiaceae, Marantaceae, and Zingiberaceae (Beccaloni *et al.*, 2008). Although the hostplants of *E. ebusus* are in the same family as many species in the subtribe Carystina, *E. ebusus* shares a commonality with Calpodina larvae by being thin-bodied and feeding on hostplants with thin and hard leaves, as discussed by Freitas (2018). The importance of this character for phylogenetic analyses is not fully understood, but additional information from future rearing will clarify its usefulness.

The “aguaje”, *Mauritia flexuosa*, is a palm that inhabits swampy areas with poor drainage (Henderson *et al.*, 1995), where it is typically a dominant canopy species. One hostplant reported for *E. ebusus ebusus* from Brazil, *Euterpe oleracea* Mart., is also found in lowland alluvial floodplains as well as areas dominated by *Mauritia flexuosa*, and can reach 20

m in height (Henderson *et al.*, 1995). *Mauritia flexuosa* and *E. oleracea* can be differentiated by the former being a palm with a large solitary stem that reaches a height of 25 m with orange-red fruits, while the latter has comparatively smaller dark purple fruits at maturity and a smaller-diameter stem (Henderson *et al.*, 1995). Use of hostplants near water sources might be important functionally as a means of eliminating feces from underneath larval shelters, potentially removing olfactory and visual cues for predators and/or parasitoids (Weiss, 2003; Greeney & Warren, 2009). As an additional means to potentially reduce olfactory cues, we observed that *E. ebusus* expels feces from its refuge with great force. Weiss (2003) suggested this action could reduce parasitism, maintain hygiene to avoid pathogens, and could prevent overcrowding within the larval shelter, and this observation is consistent with other reared species. In addition, Moraes *et al.* (2012) indicated that expulsion of frass can potentially help avoid predators, since that study showed that ants can be attracted to feces.

Whether *Ebusus* should be regarded as monospecific remains to be clarified, once multiple kinds of evidence are available for specimens spanning its range from both sides of the tropical Andes, in order to assess the taxonomic status of populations. The Andes mountains serve as a barrier to separate the Transandean and Amazonian regions (Brown, 1982), and indeed, a number of lowland butterfly taxa are restricted in their distribution to just one side of the tropical Andes, with the Andean split separating a number of sister butterfly species (e.g., *Euptychia meta* Weymer, 1911 and *E. favonius* Nakahara, Vega & Willmott, 2016; Nakahara *et al.*, 2016). Evaluation of hostplant associations and other ecological characters along with future molecular studies will contribute to understanding the relationships of taxa in Calpodina and Carystina, in addition to delimiting species. As mentioned above, Cong *et al.* (2019) found *E. ebusus* to be a member of the subtribe Carystina based on genomic data, although no morphological characters were discussed in that study to support its placement. Nevertheless, morphological characters remain essential for identifying organisms and diagnosing taxa, which is an important process for any kind of biodiversity-related research. Furthermore, morphological features based on immature stages have proven to be informative in several broad phylogenetic studies of insects (e.g., Willmott & Freitas, 2006; Archangelsky *et al.*, 2020). Thus, accumulating such data for a pair of sister species or a group of closely related taxa could be extremely valuable not only because of the phylogenetic signals they contain, but also since the information will allow us to identify which of these morphological characters are informative in species-level classification (e.g., Hill *et al.*, 2011) in a highly diverse group such as Neotropical skippers.

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