

Synopsis of *Athis thysanete* (Dyar, 1912) (Castniidae: Castniinae) populations, courtship behavior and other observations on its biology

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Date of issue online: 29 October 2022

Electronic copies (ISSN 2575-9256) in PDF format at: <https://journals.flvc.org/tropolep>; <https://zenodo.org>; archived by the Institutional Repository at the University of Florida (IR@UF), <http://ufdc.ufl.edu/ufir>; DOI: 10.5281/zenodo.7246181

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Abstract: *Athis thysanete* (Dyar, 1912) is one of the Mexican endemic species of Castniidae distributed in the Tehuacán-Cuicatlán Valley. Based on collected material and field studies carried out in recent years, biological aspects and distribution of the species are clarified, and previously unknown bionomic details are provided. The species is recorded for the first time in the state of Oaxaca. Its intrapopulation variability and the phenotypic variation between the Puebla and Oaxaca populations are analyzed.

Key words: bionomics, endemism, Lepidoptera, Mexico, Oaxaca, Puebla, Tehuacán-Cuicatlán Valley, *Tillandsia*, variability.

Resumen: *Athis thysanete* (Dyar, 1912) es una de las especies de Castniidae endémicas de México que se distribuye en el Valle de Tehuacán-Cuicatlán. A partir de la obtención de material y estudios de campo realizados en los últimos años, se aclaran aspectos biológicos de la especie junto con su distribución y se proporcionan detalles bionómicos previamente desconocidos. Se registra la especie por primera vez en el estado de Oaxaca. De igual manera, se analiza su variabilidad intrapoblacional y variación fenotípica entre las poblaciones de Puebla y Oaxaca.

Palabras clave: aspectos bionómicos, endemismo, Lepidoptera, México, Oaxaca, Puebla, *Tillandsia*, Valle de Tehuacán-Cuicatlán, variabilidad.

INTRODUCTION

Castniidae is a pantropical family with records in the Malayan Peninsula, Australia and in the American continent (Miller, 2000; González & Hernández-Baz, 2012). The majority of species are found in the Americas, and are distributed from Mexico to Argentina, including the Caribbean (Miller, 1986; González & Cock, 2004; López-Godínez & Porion, 2012; García-Díaz *et al.*, 2020). Despite being a family that is poorly represented in entomological collections worldwide (Vinciguerra *et al.*, 2011; Moraes & Duarte, 2014; Worthy *et al.*, 2017; González & Domagała, 2019), interest in Castniidae on the part of Mexican researchers and collectors has increased considerably in the last two decades (García-Díaz *et al.*, 2019; García-Díaz & Turrent-Carriles, 2022). Following Vinciguerra *et al.* (2011), López-Godínez & Porion (2012), Moraes & Duarte (2014), Worthy *et al.* (2019) and González *et al.* (2021), *Athis* Hübner, [1819] is the most speciose genus within the Neotropical Castniidae, comprising 17 species of which seven are distributed in Mexico. The descriptions of *Athis pirrelloii* Vinciguerra, 2011 and *A. jaliscana* López-Godínez & Porion, 2012, as well as the re-establishment of *A. miastagma* (Dyar, 1925) as a valid species, have increased the number of known species in the genus. To date, there are eight known castniid species endemic to Mexico. Within the Gulf slope only three species are endemic to the country. Among them is *Athis thysanete* (Dyar, 1912), which is regarded as one of the ‘rarest’

and least known members of the genus (De la Maza-Elvira, 2001; Vinciguerra, 2011; Vinciguerra & González, 2011; Vinciguerra *et al.*, 2011). The species was described by Harrison Gray Dyar based on a female collected in June 1910 by Roberto Müller (Dyar, 1912), who was the first to collect and carry out field studies in the Tehuacán Valley, Puebla, Mexico (Hoffmann, 1932; De la Maza-Elvira *et al.*, 2017; García-Díaz *et al.*, 2021).

In the past few years I have been able to study the habits of *A. thysanete* in the vicinity of Tehuacán, specifically in the La Lobera area, located northeast of the city. Observations have also been made in Santiago Miahuatlán, Puebla, and in Puerto Mixteco, Tepelmeme Villa de Morelos municipality, Oaxaca. Males as well as females were observed, but only once was a copulation witnessed. On two occasions females were observed ovipositing on their host plant. The present work is based not only on recent observations but on prior knowledge from consulted collectors and a revision of numerous specimens and appropriate references.

MATERIALS AND METHODS

For ten years, between the months of May and August, weekly or fortnightly excursions were made with the purpose of studying the habits and behavior of *A. thysanete* in La Lobera, Tehuacán, Puebla. On two occasions, sites within the municipality of Tepelmeme Villa de Morelos, Oaxaca, were visited. During May 2021, a small population of the species

was discovered in Santiago Miahuatlán, Puebla.

To examine specimens of the species, the following collections, both institutional and private, were consulted: Private collection of José de Jesús García-Díaz, Tehuacán, Puebla, Mexico (JJGD); Private collection of the Hagenbeck Family, Tehuacán, Puebla, Mexico (CFH); Private collection of the De la Maza Family, Mexico City, Mexico (CDM); Private collection of Bernardo López-Godínez, Guadalajara, Mexico (BLG); Private collection of the Turrent Family, Mexico City, Mexico (CFT); Private collection of the Villarreal Family, Oaxaca, Oaxaca, Mexico (CFV); Private collection of Robert Worthy, Caterham, Surrey, U.K. (RW); Private collection of Dirk Casteleyn, Brugge, West Flanders, Belgium (DC); Private collection of Daniel J. Curoe, Mexico City, Mexico (DJCC); Colección Entomológica del Instituto de Biología de la Universidad Nacional Autónoma de México, Mexico City, Mexico (IBUNAM); Museo de Historia Natural de la Ciudad de México, Mexico City, Mexico (MHNCM); Colección Entomológica de la Facultad de Ciencias Agronómicas de la Universidad Autónoma de Chiapas, Villaflores, Chiapas, Mexico (UNACH); Yale Peabody Museum of Natural History, New Haven, USA (YPM); Museum für Naturkunde, Berlin, Germany (ex-ZMHB: Zoologisches Museum der Humboldt Universität zu Berlin, Germany) (MfNB); American Museum of Natural History, New York, USA (AMNH); Natural History Museum, London, U.K. (NHMUK).

All photos, except for those of the predators of *Athis thysanete* illustrated in Fig. 2, were taken with a Fujifilm FinePix HS20EXR camera. The distribution map of *A. thysanete* was prepared using SimpleMappr (Shorthouse, 2010). Georeferencing of localities was done by means of Google Earth. Adobe Photoshop 2020 was used for editing figures.

RESULTS

Habitat. The Tehuacán-Cuicatlán Valley, located in the states of Puebla and Oaxaca (Fig. 1), corresponds to the southernmost, smallest, and most isolated arid region in North America (Rzedowski, 1973, 1978; Canseco-Márquez & Gutiérrez-Mayen, 2010; Rojas *et al.*, 2013; García-Díaz & Turrent-Carriles, 2020; García-Díaz *et al.*, 2020; García-Díaz *et al.*, 2021; González *et al.*, 2021). Predominant vegetation consists of xerophilous scrub in the northern part, and subdeciduous dry tropical forest in the south. The valley is of considerable biological interest as it harbors great numbers of endemic species of flora and fauna. Regarding vegetation, the predominant species belong to the families Cactaceae, Bromeliaceae, Asparagaceae and Fabaceae, among others. García-Díaz & Turrent-Carriles (2019a, 2019b, 2020) listed species present within the study area. The species of Bromeliaceae that are mainly distributed in the localities where *A. thysanete* has been observed are: *Hechtia aquamarina* I. Ramírez & C. F. Jiménez, *H. tehuacana* B. L. Rob., *H. roseana* L. B. Sm., *H. bracteata* Mez, *H. caulescens* López-Ferr., Espejo & Mart. C., *H. sphaeroblasta* B. L. Rob., *Tillandsia tehuacana* Ramírez & Carnevali, and *T. inopinata* Espejo, López-Ferrari & Till (López-Ferrari & Espejo-Serna, 2014).

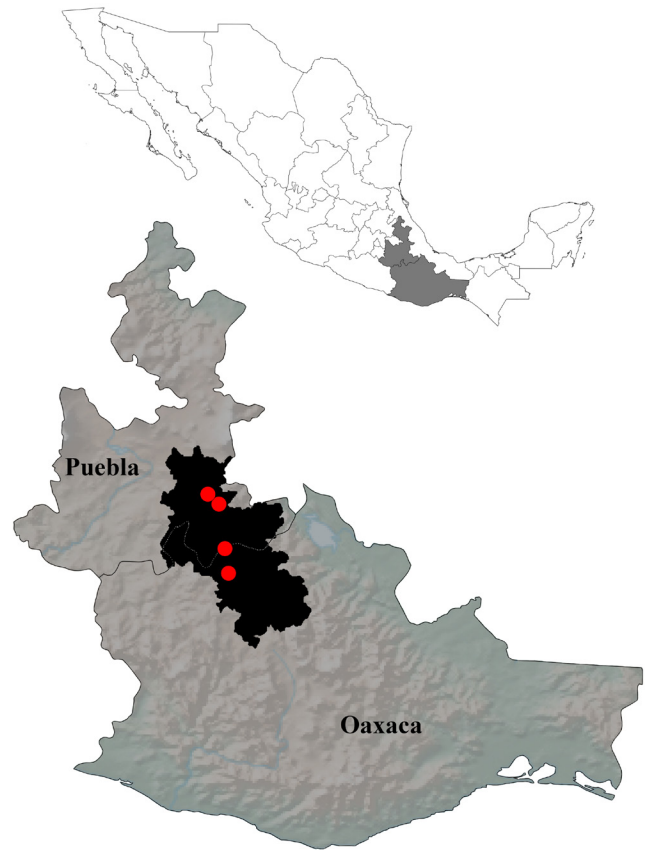


Figure 1. Geographic distribution of *Athis thysanete* in the Tehuacán-Cuicatlán Valley.

Ecology and behavior. *Athis thysanete* coexists with *A. hechtiae* (Dyar, 1910) at various localities in the dry region of the valley between 1200 and 2000 masl and with an abundance of Bromeliaceae, mainly in the genera *Hechtia* Klotzsch, 1835 and *Tillandsia* L., 1753 (González *et al.*, 2021). In two localities it is sympatric with *Escalantiana chelone mendozai* García-Díaz & Turrent-Carriles, 2022. Records for *A. thysanete* range from mid-May to early August, depending on the beginning and duration of the rainy season as well as the population's locality, since each locality has particular environmental conditions (Table 1). Unlike *A. hechtiae*, it often flies in ravines and small canyons, where its host plant, *Tillandsia inopinata* Espejo, López-Ferrari & Till (Fig. 2C), is found mainly on cliff walls or medium-sized to large trees (3-5 m).

Generally, males eclose 10-15 days before females. Males and females begin to fly between 10:30-11:00 on sunny days with temperatures between 20-25 °C, and between 11:00-12:00 on cloudy days with temperatures between 16-20 °C. At all times males are more frequently observed than females, especially during the first hours of flight activity, between 10:30-12:00. As the temperature increases (26-35 °C, between 12:30-13:30), the number of individuals increases and between 4 and 7 males can be observed in a ravine at the same time; these become more active at higher temperatures. On two occasions males were observed during light drizzle, yet no changes in their daily habits were observed. Neither males nor females fly during rain. Unlike *A. hechtiae*, females of *A. thysanete* are less frequently observed and are much scarcer.

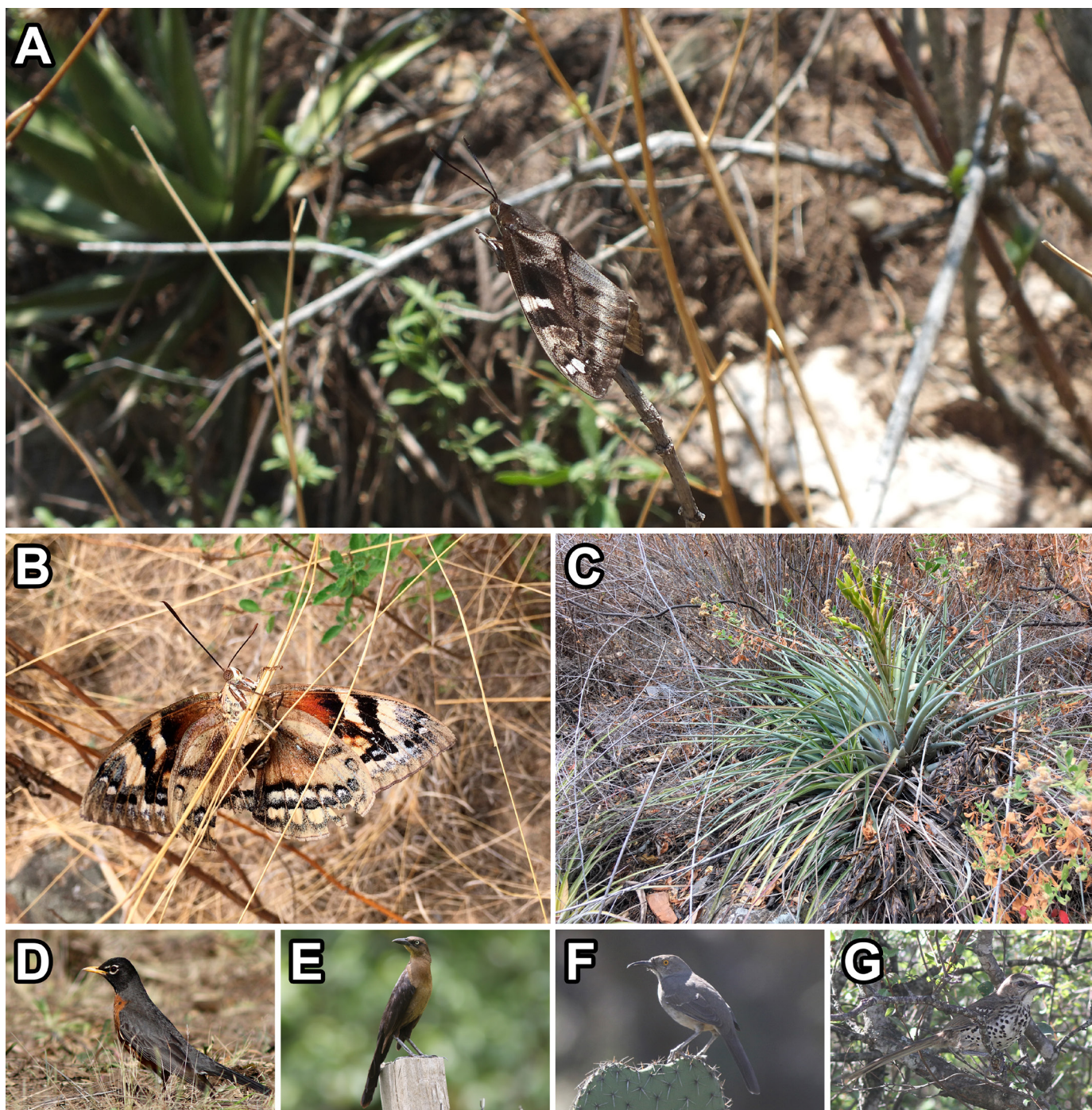


Figure 2. A) Lateral view of a male *Athis thysanete* camouflaged against its surroundings (La Lobera, Tehuacán, Puebla, 23-V-2021); B) male *A. thysanete* without abdomen, after bird attack (La Lobera, Tehuacán, Puebla, 02-VI-2019); C) *Tillandsia inopinata*, host plant of the species (La Lobera, Tehuacán, Puebla, 01-II-2020); D) *Turdus migratorius phillipsi*, predator of *A. thysanete* (Centro Recreativo El Conejo, Perote, Veracruz, 03-IV-2020, photograph: Amy E. McAndrews); E) *Quiscalus mexicanus mexicanus*, predator of *A. thysanete* (El Triunfo, Ángel Albino Corzo, Chiapas, 01-V-2018, photograph: Amy E. McAndrews); F) *Toxostoma curvirostre curvirostre*, predator of *A. thysanete* (Laguna Alchichica, Tepic, Jalisco, 23-XI-2019, photograph: Amy E. McAndrews); G) *Toxostoma ocellatum villai*, predator of *A. thysanete* (Azumbilla, Nicolás Bravo, Puebla, 10-VIII-2014, photograph: Amy E. McAndrews).

Males fly rapidly (though slower than *A. hechtiae*) in an erratic, up-and-down zigzag pattern, down to a height between 1.5 and 3.5 m above ground level. Females exhibit a similar flight pattern, though slower and heavier. They often fly in the middle of a ravine, in search of a male to copulate with. Similarly, they fly up to 5 m high with the purpose of finding

a *Tillandsia* on which to oviposit. Males perch like other *Athis* species in Mexico, that is, with forewings covering most the hindwings, in a stegopterous position (Miller, 1986; Ríos & González, 2011; Vinciguerra *et al.*, 2011; García-Díaz *et al.*, 2020; González *et al.*, 2021) (Figs. 2A, 3). They tend to perch on dry twigs or on shrubs with dry flowers; their cryptic

Table 1. Comparison of climatological data between Tehuacán (Station No. 21083) and Tepelmeme Villa de Morelos (Station No. 20157). Information obtained and calculated from CONAGUA (2021). Annual averages, monthly maximums and minimums are in bold.

Month	A) Mean Monthly Temperature (°C)			B) Mean Monthly Precipitation (mm)		
	Tehuacán	Tepelmeme	Difference	Tehuacán	Tepelmeme	Difference
January	14.4	12.9	1.5	6.2	3.1	3.1
February	16.0	13.9	2.1	5.6	2.8	2.8
March	18.5	16.1	2.4	9.3	9.3	0.0
April	20.5	17.7	2.8	21.0	27.0	6.0
May	21.2	18.0	3.2	58.9	68.2	9.3
June	20.5	17.6	2.9	105.0	111.0	6.0
July	19.0	16.0	2.8	65.1	58.9	6.2
August	19.4	16.6	2.8	71.3	55.8	15.5
September	19.3	16.5	2.8	87.0	90.0	3.0
October	17.8	14.9	2.9	31.0	34.1	3.1
November	16.0	13.2	2.8	9.0	6.0	3.0
December	15.0	12.5	2.5	3.1	6.2	3.1
Annual Average	18.1	15.5	2.6	472.5	472.4	0.1

coloration blends in with the environment at that time of the year (Fig. 2A). Usually, males end their flights by landing on the upper half of a dry twig (Fig. 3). Following this, they walk slowly toward the tip, with the middle pair of legs moving in a rapid ‘shuffling’ manner. After reaching the tip, they remain there until they fly off again. Just after landing, or when they perceive a sudden movement nearby, males adopt an alert position (Fig. 3B); after perching for more than a minute, they change to a resting position (Fig. 3A). Males are territorial and get startled if another male flies close to the twig on which they are perching, or if a predator or small bird is close by. This species, unlike *A. hechtiae*, is not easily startled by small butterflies flying by. During the day, males often fight with other territorial butterfly species such as *Achalarus tehuacana* (Draudt, 1922) and *Codatractus arizonensis* (Skinner, 1905) (Hesperiidae) by chasing them along the length of the ravine in order to expel them from their perching zones. Males are frequently observed fighting for possession of a particular twig or for part of the ravine. When this occurs, they will fly together up to 15-20 m high. Once the fight is over, the winning male remains in its zone while the loser flies away until it disappears. Sometimes, losing males return and resume the fight, attempting to seize the desired perching zone. This can repeat itself several times during the day. On three occasions males were observed attacking people. When this occurs, they whirl intensely around the victim, hitting the person’s body with its wings.

Sometimes, while 10-20 American barn swallows (*Hirundo rustica erythrogaster* Boddaert, 1783 (Passeriformes)) are in a flock in a ravine, close to where a male *A. thysanete* is perched, the castniid will often chase them to defend its territory, flying several meters towards the swallows and attempting to scare them away. The castniid then returns to its perch, and thereupon resumes the confrontation. Pursuing flights can last several minutes and can take place up to 20 m from the ground. This has been observed most frequently with large male *A. thysanete* individuals. These small swallows, measuring 13-17 cm in length, were never seen attacking male *A. thysanete* and do not

seem to be predators of this moth species.

Their main predators seem to be larger birds reaching 30 cm in length, such as *Quiscalus mexicanus mexicanus* (Gmelin, 1788), *Toxostoma ocellatum villai* Phillips, 1986, *Toxostoma curvirostre curvirostre* (Swainson, 1827) and *Turdus migratorius phillipsi* Bangs, 1915 (Passeriformes) (Figs. 2D, 2E, 2F, 2G). On various occasions, individuals of those bird species have been observed preying on *A. thysanete* males while the latter were flying unguardedly along a ravine or engaged in a fight at great height, where they appear to be more vulnerable. Sometimes, the predatory birds catch male *A. thysanete* by the abdomen and even though some harmed moths managed to escape without their abdomen, they died shortly thereafter (Fig. 2B).

The only female that was observed perching behaved much like the males, however, it did not walk toward the tip of a dry twig with the middle legs moving in a rapid ‘shuffling’ manner but instead remained totally motionless. Two males flew close to the perching female but did not startle it. Following that, in the same area, one of the males chased the female and both were flying together in irregular trajectories where they suddenly changed height, going from 1 to 10 m up and down; they repeated the pattern several times for about five minutes until they finally perched on the twig where the female was originally and began to copulate. During copulation, the male remained on the lower part of the twig while the female was on the upper part. Their heads pointing in opposite directions, as seen in *A. hechtiae* (García-Díaz *et al.*, 2020). The copulation lasted about 10 minutes, until the male flew off while the female remained perching for a few more minutes. The two females that were observed ovipositing did so on the lower middle part of the host plants, which were 5 m off the ground. Apparently, they deposited only one egg per plant. Neither eggs, nor larvae, nor pupae of the species were observed. As far as I know, *Athis thysanete* adults have never been observed feeding on flowers, mud or decomposing fruits.

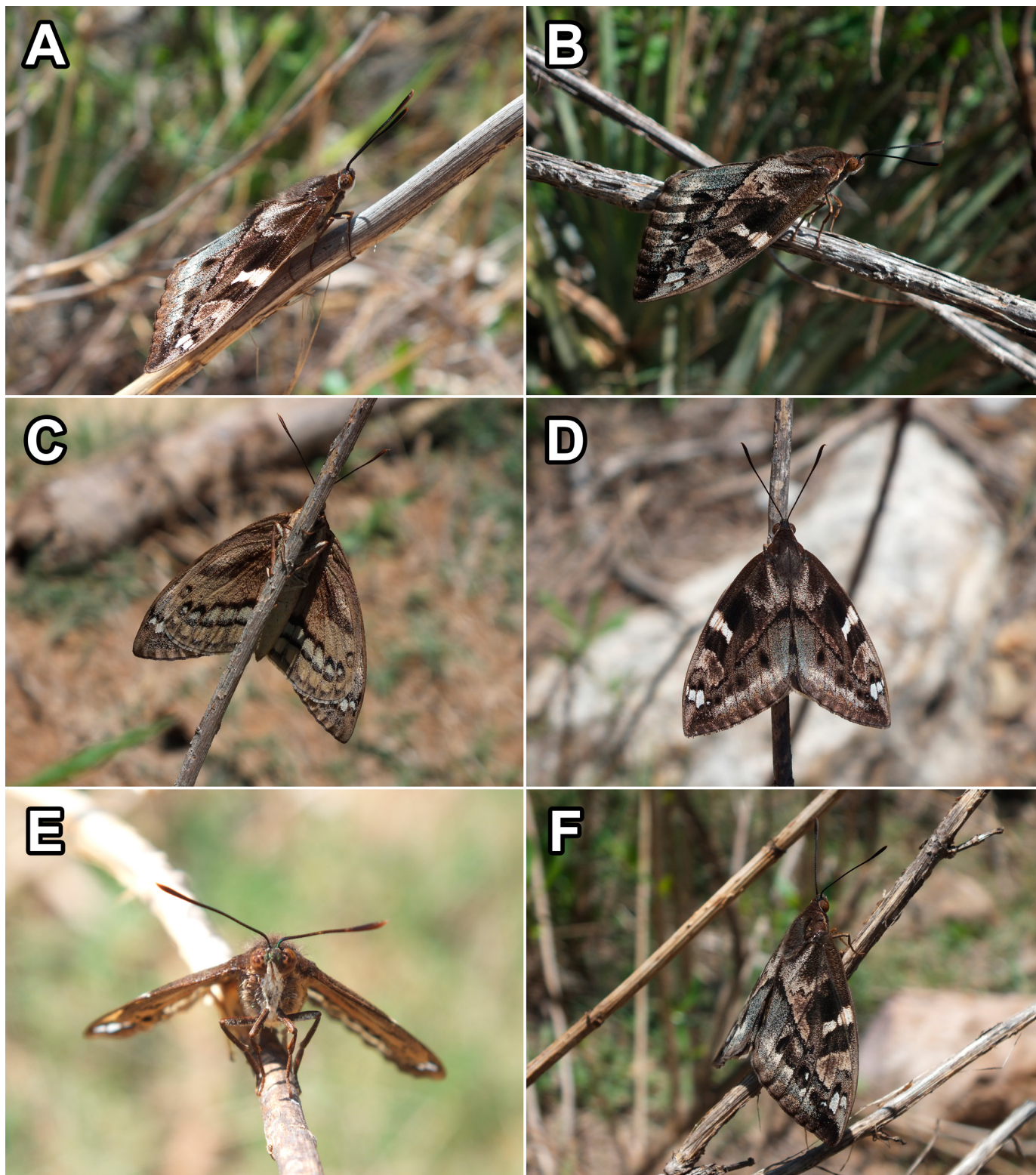


Figure 3. *Athis thysanete* males perching in stegopterous position in La Lobera, Tehuacán, Puebla, 23-V-2021. (A) In resting state, lateral view; (B) in alert state, lateral view; (C) ventral view; (D) dorsal view; (E) frontal view; (F) lateral view.

Material examined. As a result of the examination of various collections, a total of 107 specimens (95♂♂, 12♀♀) were recorded: **Oaxaca:** 2♂♂, 1♀, Tepelmeme Villa de Morelos, Arroyo El Aguacate, 21-VI-1997, *leg.* J. de la Maza E. (CDM); 2♂♂, Tepelmeme Villa de Morelos, Arroyo El Aguacate, 29-VI-1997, *leg.* J. de la Maza E. (CDM); 3♂♂, Tepelmeme Villa de Morelos, Arroyo El Aguacate, 20-VI-1998, *leg.* J. de la Maza E. (CDM); 1♂, Tepelmeme Villa de Morelos, Arroyo El Aguacate, 01-VII-1998, *leg.* J. de la Maza E.

(CDM); 2♂♂, 1♀, Tepelmeme Villa de Morelos, Tepelmeme, 24-V-2016, *leg.* J. J. García D. (JJGD); 4♂♂, Tepelmeme Villa de Morelos, Tepelmeme, 24-V-2016, *leg.* J. J. García D. (BLG); 1♂, Tepelmeme Villa de Morelos, Tepelmeme, 05-VIII-2020, *leg.* J. P. Martínez Z. (CFT); 2♂♂, II-1979 (RW) [The date for these specimens does not coincide with typical collecting dates for the species, therefore their validity is doubtful]; **Puebla:** 1♂, Tehuacán, La Lobera, 21-V-2006, *leg.* F. G. Hagenbeck F. (CFH); 1♂, Tehuacán, La

Lobera, 10-VI-2006, leg. F. G. Haghenbeck F. (CFH); 4♂♂, Tehuacán, La Lobera, 20-V-2007, leg. F. G. Haghenbeck F. (CFH); 3♂♂, Tehuacán, La Lobera, 25-V-2007, leg. L. Haghenbeck C. (CFH); 2♂♂, Tehuacán, La Lobera, 25-VI-2007, leg. L. Haghenbeck C. (CFH); 1♂, Tehuacán, La Lobera, 30-V-2009, leg. F. G. Haghenbeck F. (CFH); 4♂♂, Tehuacán, La Lobera, 08-VI-2010, leg. L. Haghenbeck C. (CFH); 2♂♂, Tehuacán, La Lobera, 01-VII-2010, leg. F. G. Haghenbeck F. (CFH); 1♂, Tehuacán, La Lobera, 01-VIII-2010, leg. F. G. Haghenbeck F. (CFH); 2♂♂, Tehuacán, La Lobera, 05-VII-2011, leg. F. G. Haghenbeck F. (CFH); 2♂♂, Tehuacán, La Lobera, 30-V-2012, leg. L. Haghenbeck C. (CFH); 1♀, Tehuacán, La Lobera, 15-VI-2012, leg. L. Haghenbeck C. (CFH); 1♂, Tehuacán, La Lobera, 01-VI-2011, leg. F. G. Haghenbeck F. (BLG); 1♀, Tehuacán, La Lobera, 15-VI-2011, leg. J. J. García D. (JJGD); 1 Tehuacán, La Lobera, 23-V-2012, leg. F. G. Haghenbeck F. (BLG); 1♂, Tehuacán, La Lobera, 26-V-2012, leg. F. G. Haghenbeck F. (BLG); 1♂, Tehuacán, La Lobera, 26-V-2013, leg. F. G. Haghenbeck F. (BLG); 1♂, Tehuacán, La Lobera, 25-V-2014, leg. J. J. García D. (JJGD); 1♀, Tehuacán, La Lobera, 22-V-2015, leg. J. J. García D. (JJGD); 3♂, 1♀, Tehuacán, La Lobera, 07-VI-2015, leg. J. J. García D. (JJGD); 1♀, Tehuacán, La Lobera, 10-VI-2015, leg. J. J. García D. (JJGD); 1♂, Tehuacán, La Lobera, 29-V-2016, leg. F. G. Haghenbeck F. (BLG); 1♀, Tehuacán, La Lobera, 01-VI-2016, leg. J. J. García D. (JJGD); 1♀, Tehuacán, La Lobera, 09-VI-2016, leg. J. J. García D. (JJGD); 1♂, Tehuacán, La Lobera, 15-VI-2016, leg. J. J. García D. (JJGD); 1♂, Tehuacán, La Lobera, 27-V-2017, leg. J. J. García D. (JJGD); 7♂♂, Tehuacán, La Lobera, 07-VI-2017, leg. J. J. García D. (JJGD); 1♂, Tehuacán, La Lobera, 10-VI-2017, leg. J. J. García D. (JJGD); 4♂♂, Tehuacán, La Lobera, 14-VI-2017, leg. J. J. García D. (JJGD); 2♂♂, Tehuacán, La Lobera, 21-VI-2017, leg. J. J. García D. (JJGD); 2♂♂, Tehuacán, 20-V-2010 (DC); 1♂, Tehuacán, 18-V-2010 (DC); 1♀, Tehuacán, VI-2012 (DC); 2♂♂, Tehuacán, La Lobera, 03-VI-2013, leg. J. J. García D. (CFV); 2♂♂, Santiago Miahuatlán, Santiago Miahuatlán, 30-V-2021, leg. J. J. García D. (JJGD); 1♂, Tehuacán, VI-2013 (RW); 2♂♂, Tehuacán, 29-V-2011, leg. P. Rodríguez (RW); 1♂, Tehuacán, 1800 m, 20-V-2010, leg. B. López (RW); 1♂, 1♀, Tehuacán, 1800 m, VIII-2010, leg. B. López (RW); 1♀, Tehuacán, 1700 m, 20-V-2015 (RW); 3♂♂, Tehuacán, La Lobera, 20-V-2016, leg. A. Turrent C. (CFT); 1♂, Tehuacán, La Lobera, 21-V-2016, leg. A. Turrent C. (CFT); 1♂, Tehuacán, La Lobera, 17-VII-2016, leg. J. J. García D. (CFT); 1♂, Tehuacán, La Lobera, 22-V-2016, leg. J. J. García D. (CFT); 1♂, Tehuacán, La Lobera, VI-2015, leg. L. Haghenbeck C. (CFT); 1♂, Tehuacán, 30-V-2009, leg. Francisco Haghenbeck (IBUNAM); 2♂♂, Tehuacán, La Lobera, VI-2015, leg. L. Haghenbeck C. (CDM); 1♂, No. 2712, Tehuacán, VI, leg. R. Müller (MHNCM); 1♂, No. 2713, Tehuacán, VI, leg. R. Müller (MHNCM); **Veracruz:** 1♂, Orizaba, Río Blanco, VI-2016, leg. B. López (DC) [Bernardo López (pers. comm.) points out that this *A. thysanete* specimen was, without doubt, erroneously labeled 'Río Blanco, Orizaba, Veracruz', since it was collected in Tehuacán]; 1♂, Type, No. 478, 20.31, Coatepec, Joicey Bequest. Brit. Mus. 1934-120 (NHMUK) [Vinciguerra *et al.* (2011) indicate that this specimen corresponds to a female; however, after examining the specimen it can be seen that it is in fact a male (Robert Worthy, pers. comm.). Moreover, the specimen's locality is doubtful, since the host plant of *A. thysanete* is not present in that ecosystem, which is completely different to that of the Tehuacán-Cuicatlán Valley; see discussion below].

Variability. *Athis thysanete* is one of the most variable Mexican castniids; this is due to the presence of various colors on its wings, mainly in dorsal view (Fig. 4). Dorsally, the number and size of the black spots on the forewings' postdiscal region is variable. Their white, brown and gray tones, as well as the white subapical spots and the white costal patches vary in most specimens. On the hindwings, the length and width of the red discal band, as well as the size and number of yellow postdiscal spots and the yellow submarginal band are variable. Ventrally, on the forewings, the reddish coloration between the base and the discal region, as well as the gray, brown and cream tones vary in each specimen. The number and size of the white postdiscal and subapical spots is variable. On the hindwings, the base coloration, size and internal coloration of the postdiscal spots vary in each specimen. Vinciguerra *et al.* (2011) illustrate the dorsal variability of the Tehuacán, Puebla population.

This castniid species exhibits little sexual dimorphism.

Concerning wing pattern, there are no exclusive characters that differentiate males from females. Nevertheless, females generally have a greater wingspan and a more rounded forewing apex; the abdomen is wider and more voluminous. In males, the base-apex distance varies between 3.0-5.1 cm. In females, the red band tends to be narrower.

Specimens from the known populations from studied localities in the states of Puebla (Tehuacán municipality: El Riego, La Lobera, San Diego Chalma and Santiago Miahuatlán municipality: Santiago Miahuatlán) and Oaxaca (Tepelmeme Villa de Morelos municipality: Arroyo El Aguacate, Puerto Mixteco, Tepelmeme) appear to show interpopulation variability. However, between the populations in both states, some differences can be observed between the population of La Lobera (Puebla) and that of Tepelmeme (Oaxaca), especially among males (Fig. 4), while the population from Arroyo El Aguacate, located between the above-mentioned localities, exhibits characteristics present in both localities. On the forewings (dorsal view), the specimens from Tepelmeme tend to exhibit more extensive and whiter areas than in the Tehuacán populations; while on the hindwings the reddish discal band and the submarginal band are wider; the postdiscal spots are smaller and tend to be white instead of yellow. Ventrally, the forewings of the Oaxaca specimens tend to have more reddish coloration; while on the hindwings, the postdiscal row of spots becomes progressively narrower toward the costa (Fig. 4).

DISCUSSION

Athis thysanete is scarce in collections worldwide (Vinciguerra *et al.*, 2011), and De la Maza-Elvira (2001) notes that until May 1997, fewer than 10 specimens were known. However, observations and collecting records of the species have increased considerably since then.

Vinciguerra *et al.* (2011) mention two records of *Athis thysanete* from outside the Tehuacán-Cuicatlán Valley, from the states of Michoacán (Coahuayana) and Veracruz (Coatepec). They correspond, respectively, to records in the former Tarcisio Escalante Collection (currently incorporated to the McGuire Center for Lepidoptera and Biodiversity, MGCL) and the NHMUK (Vinciguerra *et al.*, 2011). These represent the only known records for the species outside the states of Puebla and Oaxaca, which raises doubts about the veracity of their origins. Coatepec is a town with nearby cloud forests, located about 14 km from Xalapa, the capital of Veracruz, on the Gulf of Mexico slope. Coahuayana de Hidalgo is a city situated on the Pacific slope of Mexico, 6.5 km from the sea and close the Colima state border. These localities present unfavorable ecosystems for *Athis thysanete* in several respects: (1) they are in high humidity areas, lack xerophilous scrub vegetation and are not within the distribution area of *Tillandsia inopinata*, *A. thysanete*'s food plant, which is endemic to the Gulf of Mexico slope and broadly distributed in the states of Guanajuato, Hidalgo, Oaxaca, Puebla, Querétaro, San Luis Potosí and Tamaulipas (Espejo-Serna *et al.*, 2008; López-Ferrari & Espejo-Serna, 2014); (2) Coahuayana de Hidalgo is located at sea level on the Pacific coastal plain, near the Sierra Madre del Sur central subprovince, a region characterized by fauna that is endemic

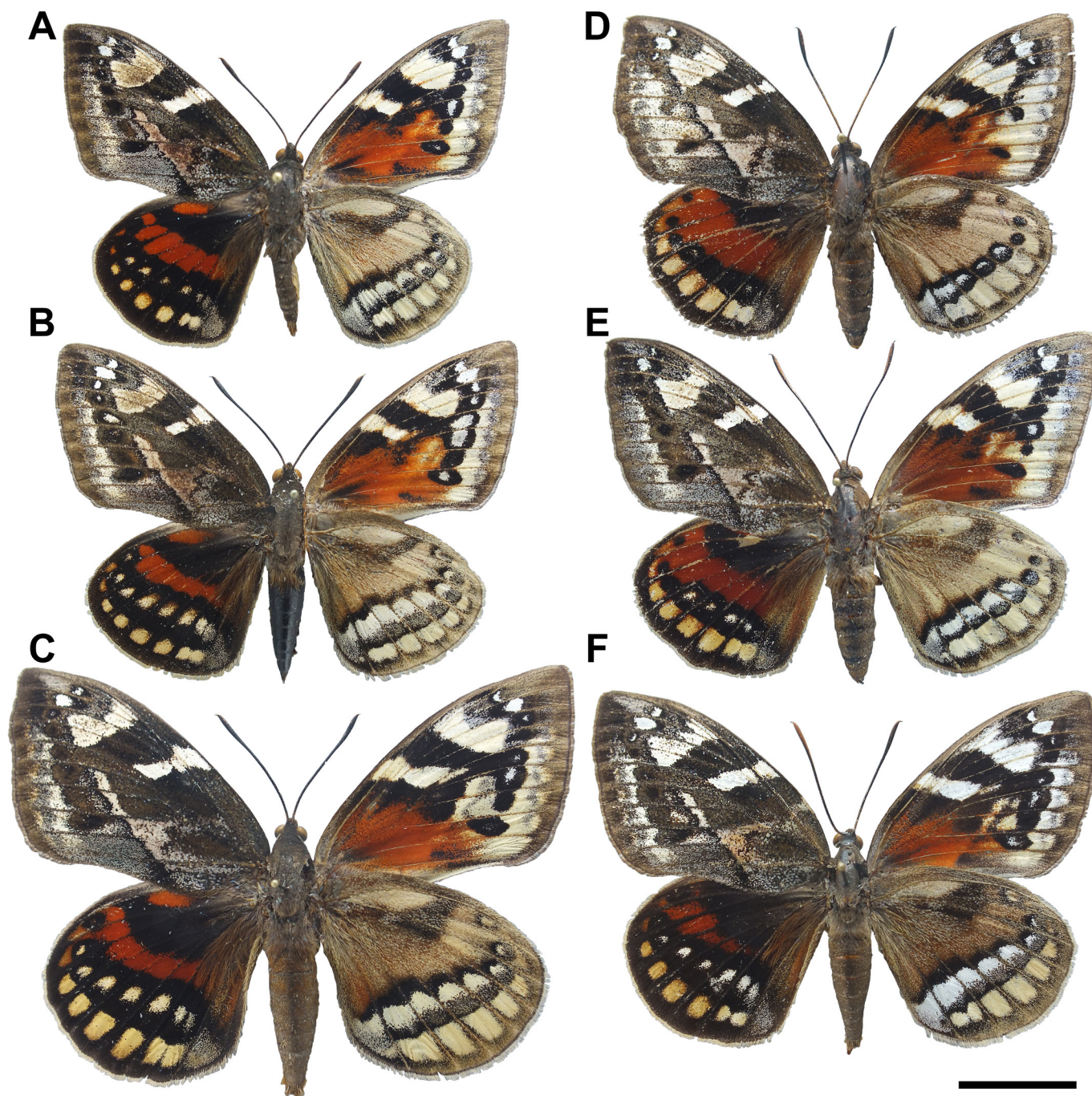


Figure 4. Dorsal and ventral comparison of *Athis thysanete* specimens from the states of Puebla (A-C) and Oaxaca (D-F). A) Male from Puebla, Tehuacán, La Lobera, 07-VI-2017, leg. J. J. García D. (JJGD); B) male from Puebla, Tehuacán, La Lobera, 10-VI-2017, leg. J. J. García D. (JJGD); C) female from Puebla, Tehuacán, La Lobera, 10-VI-2015, leg. J. J. García D. (JJGD); D) male from Oaxaca, Tepelmeme Villa de Morelos, Tepelmeme, 24-V-2016, leg. J. J. García D. (JJGD); E) male from Oaxaca, Tepelmeme Villa de Morelos, Tepelmeme, 24-V-2016, leg. J. J. García D. (JJGD); F) female from Oaxaca, Tepelmeme Villa de Morelos, Tepelmeme, 24-V-2016, leg. J. J. García D. (JJGD). Scale bar = 2cm.

to that slope (Morrone, 2017; Rocha-Méndez *et al.*, 2019); (3) in the Coatepec area, the temperatures are low for much of the year and the region is located between the boundaries of the Trans-Mexican Volcanic Belt and the Sierra Madre Oriental (Llorente-Bousquets *et al.*, 1986; Hernández-Baz, 1993); both regions support well defined fauna and flora (Luna-Vega *et al.*, 2016). These aspects might indicate that the locality records for those specimens are possibly erroneous. Additionally, it is difficult to formulate the hypothesis that those specimens were

found at the aforementioned localities because high elevation mountain barriers stand between the two putative populations and the Tehuacán-Cuicatlán Valley. There is the possibility that those two specimens were collected in Oaxaca or Puebla and were erroneously placed with material from Michoacán and Veracruz, respectively. De la Maza-Elvira *et al.* (2017) point out that Tarcisio Escalante relied on collectors who often mixed material from several localities, a practice which has complicated various studies on the distribution of Mexican

Lepidoptera. Based on the above-mentioned statements, we should consider *A. thysanete* endemic to the Tehuacán-Cuicatlán Valley (Fig. 1).

Athis thysanete, *A. flavimaculata* and *A. inca* belong to the same complex of species (Miller 1972, 2000) and are allopatrically distributed in Mexico: *flavimaculata* on the Pacific slope, *inca* in the rainforests and cloud forests along the Gulf slope, and *thysanete* in the Tehuacán-Cuicatlán Valley. The isolation of *thysanete* in the xerophilous Tehuacán-Cuicatlán Valley was possibly caused by the formation of the Trans-Mexican Volcanic Belt, an event that partitioned the Oaxaquia microcontinent in two, thus separating the Tehuacán-Cuicatlán valley from Metztlán (Centeno-García *et al.*, 2008; De la Maza-Elvira & De la Maza Elvira, 2019; González *et al.*, 2021; García-Díaz & Turrent-Carriles, 2022). I concur with Roberto de la Maza (pers. comm.) who hypothesizes that its isolation process possibly began in the late Miocene.

Vinciguerra *et al.* (2011) point out that *Yucca periculosa* Baker could be the host plant of *A. thysanete*, which seems to be doubtful because after ten years of field work, neither males nor females have been observed perching on the leaves of those plants. Luis Haghenbeck (pers. comm.) also indicates that in 30 years of expeditions in the Tehuacán-Cuicatlán Valley, he has never observed this castniid species perching on leaves of any *Yucca* species. Additionally, it is well known that Mexican *Athis* species are closely associated with Bromeliaceae (García-Díaz *et al.*, 2019; García-Díaz *et al.*, 2020; González *et al.*, 2021). According to López-Ferrari & Espejo-Serna (2014), *T. inopinata* is a Mexican endemic bromeliad with wide distribution north of the Trans-Mexican Volcanic Belt; nevertheless, south of the Trans-Mexican Volcanic Belt it has only been recorded within the Tehuacán-Cuicatlán Valley, in the states of Oaxaca and Puebla. The distribution of the host plant of *A. thysanete* supports the isolation of the castniid species in the xerophilous region south of the Trans-Mexican Volcanic Belt. Likewise, it is possible that *A. inca* has *T. inopinata* as a host plant in certain localities in Hidalgo, Querétaro, San Luis Potosí, or Tamaulipas.

The recent discovery of *A. thysanete* in Santiago-Miahuatlán could indicate that the species has more than one host plant, because *T. inopinata* has not been observed in that locality and was not recorded by López-Ferrari & Espejo-Serna (2014). However, more field work is required to confirm this hypothesis.

Athis thysanete has been observed at 1650 masl in the Tehuacán municipality and at 2000 masl in the Tepelmeme Villa de Morelos municipality. During every month of the year, the monthly mean temperature is higher in Tehuacán; the average annual temperature is 2.6 °C higher than in Tepelmeme (Table 1). On the other hand, the annual average precipitation is similar in both localities, though in Oaxaca precipitation peaks during April, May and June (Table 1). This explains the delay in the last eclosions of the species in Tepelmeme, which can be observed up until the first days of August.

In the eastern part of the Tepelmeme region there is oak forest; consequently, it is inhabited by some Lepidoptera species that have not been observed in other parts of the valley. These ecosystem differences between this place and other localities in

the valley, to a large extent, might explain part of the phenotypic variation seen between *Athis thysanete* specimens from the two regions within the Tehuacán-Cuicatlán Valley (Fig. 4).

Athis hechtiae as well as *A. thysanete* are Tehuacán-Cuicatlán Valley endemic species, with highly local and restricted distributions. For this reason, they are more vulnerable than other lepidoptera within the region. Their ecosystems in the Tehuacán-Cuicatlán Biosphere Reserve (RBTC) and the Cerro Colorado Protected Natural Area (ANPCC) must continue to be protected.

ACKNOWLEDGMENTS

The following individuals and families are thanked: Nicolás García, Bernardo López and Roberto de la Maza for their comments and revision of the manuscript; the Haghenbeck, De la Maza and Turrent families and Robert Worthy, Dick Casteleyn, Omar Villareal, Daniel J. Curoe, and Bernardo López for allowing access to their collections; Luis Haghenbeck and Javier de la Maza for their comments on *A. thysanete*, and Geoff Martin and Nicola Lowndes for photographing the specimen deposited at NHMUK; Cristina Mayorga, Ivonne Garzón, Alejandro Zaldívar and Adolfo Ibarra for assistance with examination of specimens in the Entomological Collection of the IBUNAM; María Eugenia Díaz-Batres for allowing the consultation of the MHNCM collection; Lawrence Gall for his help with the consultation of the collection at the YPM; Suzanne Rab Green and David Grimaldi for their help with the consultation of the collection at the AMNH; Viola Richter and Théo Lédger for their help with the consultation of the collection at the MfNB; Ana Rosa López Ferrari for her support in the identification of this castniid's host plant; Amy McAndrews and Jorge Montejo for their comments and photographs of the predatory birds of *A. thysanete*; Daniel J. Curoe for his comments and support in the revision of the manuscript in English; and Jorge M. González, Robert Worthy and Shinichi Nakahara for their careful reviews and thoughtful comments that improved this manuscript.

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