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Cover illustration: Cryptic Geometridae larvae (unidentified species). This species resembles a modified trichome on liverwort *Monoclea gottschei* Lindb. This species of liverwort is encountered in cloud forests of Veracruz state, Mexico. Image courtesy of Fernando Hernández-Baz. See paper on page 81.

BARLEY CULTIVARS AFFECTING NUTRITIONAL PERFORMANCE AND DIGESTIVE ENZYMATIC ACTIVITIES OF *EPHESTIA KUEHNIELLA* ZELLER (PYRALIDAE)

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ABSTRACT. The eggs and larvae of the Mediterranean flour moth, *Ephestia kuehniella* Zeller are routinely utilized as a substitute host for the rearing of parasitoids and predators required for biological control. Nutritional performance, digestive enzymatic activities and growth indices of the fifth instar larvae of *E. kuehniella* were evaluated on flour of seven barley (Fajr 30, Reihan 03, 5 Shoor, Dasht, Sahra, Khorram and EH-83-7) and two wheat (Bam and Sepahan) cultivars at $25\pm1°C$, $65\pm5\%$ R.H., and a photoperiod of 16:8 (L: D) h. The results show that the highest larval growth index was observed when larvae were fed barley cultivar Reihan03. The highest and lowest values of larval weight gain were on barley cultivars EH-83-7 and Sahra, respectively. The highest value of efficiency of conversion of ingested food was in larvae reared on barley cultivar EH-83-7, whereas the lowest value was on barley cultivar Sahra. Moreover, the highest relative growth rate was detected on barley cultivar EH-83-7. The highest and lowest levels of amylolytic activity were on wheat cultivar Bam and barley cultivar Khorram, respectively. The highest proteolytic activity was observed in larvae reared on barley cultivar Fajr 30, whereas the lowest activity was on barley cultivars Dasht, Khorram and wheat cultivar Bam. Finally, barley cultivars EH-83-7 and Reihan 03 can be suggested as the most suitable cultivars for laboratory rearing of *E. kuehniella*.

Additional key words: Mediterranean flour moth, feeding performance, amylolytic activity, proteolytic activity, barley cultivars

In insects, the efficiency of conversion of digested food into body biomass depends on the activity of digestive enzymes in their midgut (Lazarevic et al. 2004). Also, the activity of key digestive enzymes like proteases and α-amylases depends on the nature of the food sources (Slansky 1982, Mendiola-Olaya et al. 2000). It is generally accepted that a change in food quality can significantly change the growth rate of arthropods (Waldbauer 1968). Carbohydrate is one of the important sources of energy for most insects, especially for stored-product pest species. These insects require digestive α-amylase to hydrolyze and utilize the starch in their diet (Valencia-Jiménenz et al. 2008). For example, the Mediterranean flour moth, *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae), which is known as one of the major pests of stored-grain products particularly flour or other powdered cereals (Sedlacek et al. 1996, Hill 2002, Rees 2003), needs a carbohydrate source to reach maturity (Chapman 1998). Additionally, it was reported that a diet with flours deprived of protein fractions delays *E. kuehniella* development and increases the pupal mortality (Nawrot et al. 1985). Therefore, like in most insects, balance of nutrients is crucial for growth (Thomas et al. 1999).

In addition to the importance of *E. kuehniella* as a target stored product pest, its eggs and larvae are routinely used as a substitute host for mass rearing of some parasitoids and predators, because of its availability and low-cost of rearing (Iranipour et al. 2009, Jokar & Golmohammadi 2012, Jokar & Zarabi 2012, Sighinolfi et al. 2013).

Hitherto, several researches have been done on the effect of various diets on the biology and digestive enzymatic activity of *E. kuehniella* (Locatelli et al. 2008, Pytelkova et al. 2009, Madboni & Pour Abad 2012, Jafarlu et al. 2012). Abdi et al.(2014) recently considered the nutritional indices and digestive enzymatic activity of *E. kuehniella* on the flour of different wheat, *Triticum aestivum* L., cultivars. Although barley, *Hordeum vulgare* L., may be more susceptible to stored-product insects than other grains (Baker, 1988), and it generally has a low price compared to wheat (Akar et al. 2004), no published information exists on the nutritional and digestive physiology of *E. kuehniella* in response to feeding on the flour of various barley cultivars.

Since the nutritional value of barley cultivars tested in this research can compete with the nutritional value of wheat for *E. kuehniella* (Rees 2003, Akar et al. 2004), two wheat cultivars along with barley cultivars were used to compare the results. This study hypothesized that larvae fed on flour of some barley cultivars will accumulate biomass more efficiently than those fed on the wheat cultivars examined. The objective of this study, therefore, was to evaluate the nutritional performance, digestive enzymatic activity and growth indices of *E. kuehniella* on flour of various barley cultivars and to select the most suitable cultivar for laboratory rearing of *E. kuehniella* in order to optimize its mass rearing as a host for natural enemies released for biological control.

MATERIALS AND METHODS

Barley and wheat cultivars. In this research, seven barley cultivars (Fajr 30, Reihan 03, Shoor, Dasht, Sahra, Khorram and EH-83-7) and two wheat cultivars (Bam and Sepahan) were obtained from the Agricultural and Natural Resources Research Center of Isfahan, Iran (ANRRC). Whole grain of barley and wheat cultivars was milled and used for larval feeding.

Rearing of insects. The strain of *E. kuehniella* was obtained from a laboratory colony of the ANRRC. The larvae of *E. kuehniella* were reared on flour of seven barley and two wheat cultivars in a growth chamber at a temperature of 25 ± 1°C, a relative humidity of 65 ± 5% and a 16:8 h light:dark photoperiod. Nine separate stock cultures were maintained, for two generations, on various barley and wheat cultivars before being used in the experiments.

Growth indices. Larval growth index (LGI), standardized insect-growth index (SII) and fitness index (FI) of *E. kuehniella* were calculated for different tested cultivars using the formulae (Itoyama et al. 1999):

$$LGI = l_x/L$$
$$SII = Pw/L$$
$$FI = (P \times P_w)/(L + P_d)$$

Where, lx = survival rate of larvae, L = larval period, P = percentage of pupation, P_d = pupal period, and P_w = pupal weight.

Larval nutritional performance. To start the experiment, 1 g of newly laid eggs was added to 750 g of barley and wheat flour of each examined cultivar into plastic containers (diameter 20 cm, depth 8 cm) with a hole covered by a mesh net for aeration. Fifth instar larvae were collected from the containers and separated into five replicates (10 larvae in each) and transferred into a plastic Petri-dish (diameter 8 cm, depth 1 cm), containing 1 g of flour of each examined cultivar (Abdi et al. 2014). Nutritional performance was quantified using the fifth instar larvae after 12 h starvation, as they were easier to measure than the earlier instars. The larvae were weighed daily, and the quantity of food consumed was calculated by subtracting the diet remaining at the end of each experiment from the total weight of food given. To obtain the dry weights of the foods and larvae, 100 g of barley and wheat flour of the examined cultivars and 20 larvae reared on each cultivar were weighed, oven-dried (48 h at 60°C) and then re-weighed to establish a percentage of their dry weight. Nutritional performance was calculated based on dry weight, as suggested by Waldbauer (1968) to calculate consumption index (CI), efficiency of conversion of ingested food (ECI), relative consumption rate (RCR) and relative growth rate (RGR):

$$CI = \frac{E}{A}$$
$$ECI = \frac{P}{E}$$
$$RCR = \frac{E}{A*T}$$
$$RGR = \frac{P}{A*T}$$

where A is the mean dry weight of insect over unit time (mg), E is the dry weight of food consumed (mg), P is dry weight gain of insect (mg) and T is duration of feeding period (d).

Chemicals. Digestive enzymes substrate (azocasein and starch), Bradford reagent, the dinitrosalicylic acid (DNS) and maltose were bought from Sigma Chemical Co., St Louis, USA. Bovine serum albumin (BSA) and potassium iodine (KI) were respectively obtained from Roche Co., and Merck Co., Germany, whereas Iodine (I_2) was purchased from Maarssen Co., Netherlands.

Preparation of digestive enzymes. After 12 h starvation, the fifth instar larvae of *E. kuehniella* fed for 24 h on the flours of various barley and wheat cultivars were immobilized on ice for several minutes and quickly dissected under a stereo-microscope. The midguts were cleaned by removal of unwanted tissues, collected into a known volume of distilled water and homogenized with a handheld glass grinder on ice. The homogenates were then centrifuged at 16000 × g for 10 min at 4°C and the resulting supernatants were collected into new micro tubes, stored at -20°C in aliquots for further use.

Protein quantification of larvae. Protein concentrations in *E. kuehniella* fifth instar larvae were determined by Bradford's method (Bradford 1976) using BSA as a standard.

Amylolytic activity assay. Dinitrosalicylic acid (DNS) procedure (Bernfeld 1955), with 1% soluble starch as substrate at the optimal pH (pH 10), was used to assay the digestive amylolytic activity of the fifth instar larvae of *E. kuehniella* fed with various barley and wheat cultivars. Briefly, the enzyme extract (20 µL) was incubated with soluble starch (40 µL) in 10 mM universal buffer (500 µL) at pH 10 and at 37 °C for 30 min. The reaction was stopped by adding 100 µL DNS and heating in boiling water for 10 min. The absorbance was read at 540 nm (spectrophotometer JENWAY 6705 UV/Vis, USA) after cooling on ice. One amylase unit was expressed as the amount of enzyme required to release 1 mg of maltose equivalent per minute under the above conditions. All experiments were carried out in triplicates (with three different supernatants).

Proteolytic activity assay. The general proteolytic activity of *E. kuehniella* fifth instar larvae was determined using the azocasein digestion method. The universal buffer system (50 mM sodium phosphate borate) was used to assay the optimal pH of proteolytic activity (Elpidina et al. 2001). To evaluate the azocaseinolytic activity, the reaction mixture containing 80 µL of 1.5% azocasein solution in 50 mM universal buffer (pH 12 as an optimal pH) and 50 µL of crude enzyme was incubated at 37 °C for 50 min. The enzyme activity was stopped by adding 100 µl 30% trichloroacetic acid (TCA), continued by cooling at 4 °C for 30 min and centrifugation at 16000 × g for 10 min. The supernatant (100 µl) was added to 100 µL of 2 M NaOH and the absorbance was read at 440 nm (Microplate reader anthos 2020, England). Appropriate blanks, which TCA had been added prior to the substrate, were prepared for each treatment. One protease activity unit was defined as an increase in optical density mg^{-1} protein of the tissue min^{-1} due to azocasein proteolysis (Elpidina et al. 2001). All experiments were done in triplicates (with three different supernatants).

Starch and protein determination of flour of barley and wheat cultivars. The starch content of barley and wheat cultivars flour was evaluated by the method of Bernfeld (1955), with some modifications, using starch as standard. A quantity of each cultivar flour (200 mg) was homogenized in distilled water (35 ml),heated to boiling point, and centrifuged at 13000 × g for 10 min. One-hundred microliters of each sample was added to 2.5 ml of iodine reagent (0.02% I$_2$ and 0.2% KI) and absorbance was read at 580 nm (Bouayad et al. 2008).

The protein content of flour of barley and wheat cultivars was quantified using BSA as a standard according to Bradford (1976) with minor modifications. A quantity of flour of each cultivar (200 mg) was homogenized in distilled water (10 ml), centrifuged at 13000 × g for 10 min, and then 100 µl of the homogenate was added to 3 ml of Bradford reagent. The samples were incubated in darkness at 37°C, and absorbance was read at 595 nm (Bouayad et al. 2008).

Data analysis. The nutritional performance and digestive enzymatic activity of *E. kuehniella* reared on the flours of various barley and wheat cultivars were analyzed using one-way analysis of variance (ANOVA) followed by comparison of the means with LSD test at α = 0.05, using statistical software Minitab 16.0. All data were checked for normality prior to analysis.

RESULTS

Growth indices. The results show that the larval growth index of *E. kuehniella* ranged from 1.527 when larvae were fed with the barley cultivar Khorram, to 2.214 when they were fed with the barley cultivar Reihan 03. The standardized insect-growth index (F= 13.40, df= 200, *P*<0.01) and fitness index (F= 25.57, df=

TABLE 1. Nutritional performance of fifth instar larvae *Ephestia kuehniella* on flour of barley and wheat cultivars

	Index (mean ± SE)						
Host (cultivar)	P[a] (mg)	A[b] (mg)	FC[c] (mg/larva)	CI[d]	ECI[e] (%)	RCR[f] (mg/mg/day)	RGR[g] (mg/mg/day)
Barley (Fajr)	39.65±7.28bcd	245.90±2.21c	22.168±0.99ab	1.352±0.057bc	12.09±2.39bcd	0.243±0.010b	0.030±0.006bcd
Barley (Reihan)	43.15±7.01abcd	227.98±7.39d	17.49±2.92bc	1.127±0.167bc	18.87± 4.67ab	0.211±0.033bc	0.036±0.006bc
Barley (Shour)	55.35±0.88ab	247.92±0.36c	21.12±1.03b	1.305±0.086bc	15.14±2.61abc	0.242± 0.017b	0.043±0.001ab
Barley (Dasht)	21.67±7.04cde	185.77±2.68e	26.48±2.16a	2.133±0.156a	6.06± 2.24de	0.438±0.060a	0.022±0.006cd
Barley (Sahra)	4.91±0.34e	188.66±4.10e	17.51±0.97bc	1.395±0.083b	1.93± 0.06e	0.231±0.009b	0.004±0.000e
Barley (Khorram)	19.00±4.25de	182.68±3.63e	15.96±1.92c	1.324±0.184bc	8.03± 1.70cde	0.217±0.032bc	0.017±0.004de
Barley (EH-83-7)	66.60±6.30a	237.41±4.55cd	20.38±1.53bc	1.284±0.080bc	21.79±0.99a	0.250±0.018b	0.055±0.005a
Wheat (Bam)	44.30±14.80abc	404.93±6.94a	20.35±1.16bc	0.757±0.051d	13.88±4.40abcd	0.135±0.011c	0.021±0.007cd
Wheat (Sepahan)	26.15±8.52cde	273.56±6.66b	19.47±1.32bc	1.076±0.093c	8.56±2.23cde	0.190±0.020bc	0.018±0.007de

Means followed by different letters in the same column are significantly different (LSD, *P*<0.01).

[a] Dry weight gain of insect
[c] Dry weight of food consumed
[e] Efficiency of conversion of ingested food
[g] Relative growth rate

[b]Mean dry weight of insect over unit time
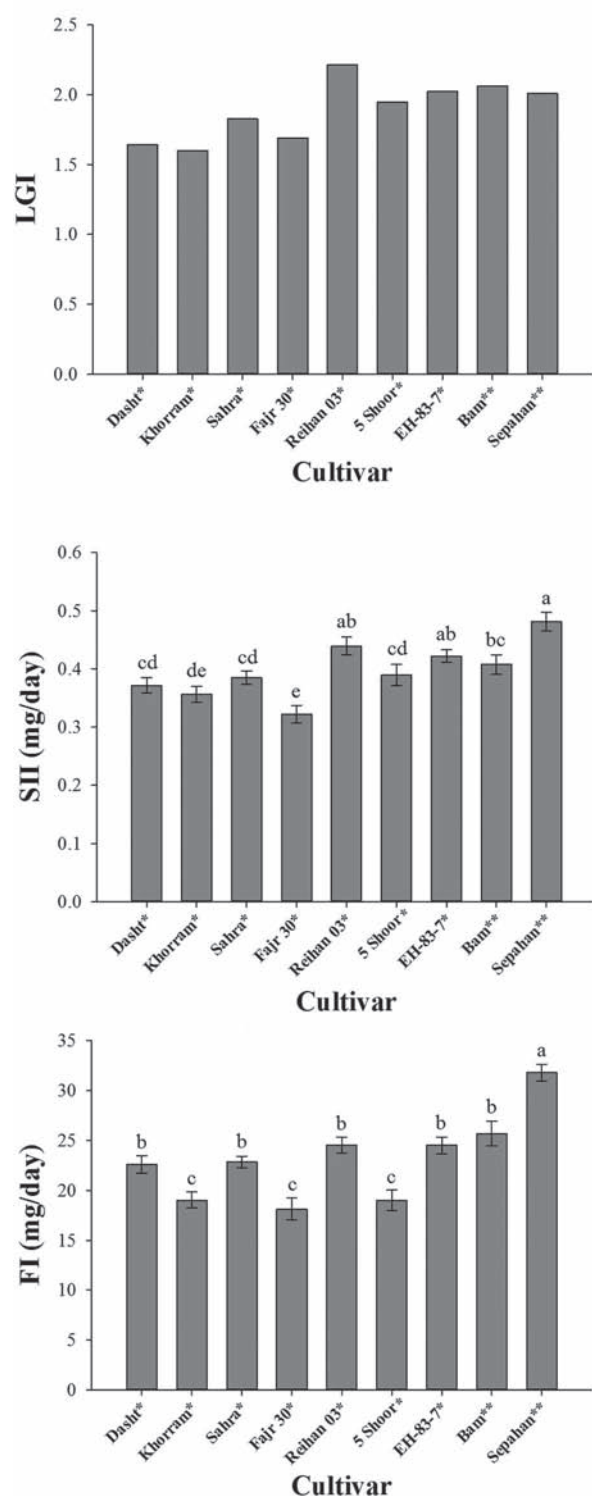[d] Consumption index
[f] Relative consumption rate

FIG. 1. Mean (±SE) larval growth index (LGI), standardized-insect growth index (SII) and fitness index (FI) of *Ephestia kuehniella* on different barley and wheat cultivars. Means followed by different letters are significantly different (LSD, P < 0.01). *Barley cultivars; **Wheat cultivars

142, *P*<0.01) of *E. kuehniella* showed significant difference, being highest on wheat cultivar Sepahan (Fig. 1).

Larval nutritional performance. The results of the nutritional performance of the fifth instar larvae are shown in Table 1. Significant differences were found for larval weight gain (F= 4.80; df = 8, 36; *P*<0.01). The highest and lowest values of larval weight gain were on the barley cultivars EH-83-7 (66.60 ± 6.30 mg) and Sahra (4.91 ± 0.34 mg). Significant differences in mean larval weight were found (F= 174.94; df = 8, 37; *P*<0.01). Mean larval weight was heaviest on wheat cultivar Bam (404.93 ± 6.94 mg) and lightest on barley cultivars Khorram (182.68 ± 3.63 mg), Dasht (185.77 ± 2.68 mg) and Sahra (188.66 ± 4.10 mg). The highest food consumption (F= 3.00; df = 8, 38; *P*<0.01) was detected in larvae fed on the barley cultivar Dasht (26.48 ± 2.16 mg/larva), while the lowest was recorded for the larvae reared on the barley cultivar Khorram (15.96 ± 1.92 mg/larva) (Table 1).

The fifth instar larvae reared on barley cultivar Dasht (2.133 ± 0.156) and wheat cultivar Bam (0.757 ± 0.051) show the highest and lowest values of consumption index (F=9.79; df = 8, 38; *P*<0.01), respectively. The highest value of efficiency of conversion of ingested food (F= 4.09; df = 8, 37; *P*<0.01) was in larvae reared on barley cultivar EH-83-7 (21.79 ± 0.99%), whereas the lowest value was on barley cultivar Sahra (1.93± 0.06%). Moreover, the larvae fed on the barley cultivar Dasht (0.438 ± 0.060 mg/mg/day) and wheat cultivar Bam (0.135 ± 0.011 mg/mg/day) had the highest and lowest values of relative consumption rate (F= 8.57; df = 8, 38; *P*<0.01). The highest value for relative growth rate (F= 6.20; df = 8, 36; *P*<0.01) was recorded for the fifth instar larvae reared on barley cultivar EH-83-7 (0.055 ± 0.005 mg/mg/day), while the lowest value was for those fed on the barley cultivar Sahra (0.004 ± 0.000 mg/mg/day) (Table 1).

Amylolytic activity. Significant differences in the digestive amylolytic activity for the fifth instar larvae reared on flour of various barley and wheat cultivars were found (F =4.46; df = 8, 18; *P*<0.01) (Table 2). Larvae fed on the wheat cultivar Bam (0.0262 ± 0.0016 mU mg^{-1}) showed the highest levels of amylolytic activity, while the lowest activity was in larvae fed on the barley cultivar Khorram (0.0146 ± 0.0014 mU mg^{-1}).

General proteolytic activity. General proteolytic activity data (*P*<0.01) from *E. kuehniella* fifth instar larvae reared on flour of various barley and wheat cultivars are shown in Table 2. The highest proteolytic activity was for the larvae reared on the barley cultivar Fajr 30 (F = 5.10; df = 8, 18; *P*<0.01) (3.256 ± 0.250 U mg^{-1}), whereas the lowest activity was recorded for larvae

fed on the barley cultivars Dasht (2.301 ± 0.095 U mg^{-1}) and Khorram (2.249 ± 0.210 U mg^{-1}) as well as wheat cultivar Bam (2.253 ± 0.152 U mg^{-1}).

Starch and protein determination of flour of barley and wheat cultivars. Statistical tests indicated significant differences in the content of starch and protein among the flours of the various barley and wheat cultivars tested ($P<0.01$) (Table 3). The highest starch content was found in the flour of the wheat cultivar Sepahan (F = 78.71; df = 8, 18; $P<0.01$) (11.375 ± 0.240 mg mL^{-1}), while the lowest content was in the flour of the barley cultivars EH-83-7 (4.287 ± 0.324 mg mL^{-1}), Khorram (4.456 ± 0.213 mg ml^{-1}) and Reihan 03 (4.471 ± 0.153 mg mL^{-1}). The highest content of protein was in the wheat cultivar Sepahan (F =9.20; df = 8, 18; $P<0.01$) (0.0343 ± 0.0032 mg ml^{-1}) and barley cultivar Dasht (0.0341 ± 0.0044 mg ml^{-1}), however, the lowest content was in the barley cultivar Fajr 30 (0.0085 ± 0.0011 mg ml^{-1}).

DISCUSSION

This study shows that different barley cultivars and two wheat cultivars had a significant effect not only on the nutritional indices of *E. kuehniella*, but also on the enzymatic activities, as well as growth indices of this insect.

Although the highest standardized insect-growth index was observed when larvae were fed wheat cultivar Sepahan, however, no significant difference was detected between this cultivar and the barley cultivars Reihan 03 and EH-83-7, suggesting that Sepahan, Reihan 03 and EH-83-7 are suitable nutritious cultivars for the feeding and growth of *E. kuehniella*. Also, the results indicate that the highest larval growth index was on cultivar Reihan 03, showing that the larvae fed on this cultivar had a higher survivorship compared to larvae reared on other cultivars tested.

The significant differences in nutritional performance of the fifth instar larvae of *E. kuehniella* on the flour of barley and wheat cultivars indicate that the cultivars tested had different nutritional values. The results show that the highest and lowest values of larval weight gain were on the barley cultivars EH-83-7 and Sahra, respectively, suggesting that these cultivars are a high and low-nutritious diet for this insect (Che Salmah 2010). The highest larval weight gain on barley cultivar EH-83-7 is higher than that reported by Abdi et al. (2014) for *E. kuehniella* on the wheat cultivar Pishtaz (a suitable host) (4.77 ± 0.69 mg). The inconsistency can be due to differences in the calculation method, host cultivar or variations in the strains of *E. kuehniella*. The highest mean larval weight was in the larvae fed on the wheat cultivar Bam, while the lowest CI was detected on this cultivar, indicating that cultivar Bam can be a proper diet for *E. kuehniella* larvae.

In insects, the amount of food consumed (FC) is one of the main characteristics that can influence the enzymatic activity, responsible for supplying energy (Sivakumar et al. 2006). It is noticeable that the ingested nutrients must meet requirements for growth and other metabolic processes. In this study, the larvae reared on barley cultivar Khorram recorded the lowest FC value, showing that the larvae fed on this cultivar had low weight gain and digestive enzymatic activity. Moreover, the highest rate of food consumed by the larvae of *E. kuehniella* was on the barley cultivar Dasht, which may be correlated with relatively low soluble starch content in this cultivar. In parallel of food consumption, the highest consumption index and relative consumption rate by larvae was recorded on the barley cultivar Dasht.

TABLE 2. Mean (± SE) amylolytic and proteolytic activities of midgut extracts from fifth instar larvae of *Ephestia kuehniella* on flour of barley and wheat cultivars

Host (cultivar)	Amylolytic activity (mU mg^{-1})	Proteolytic activity (U mg^{-1})
Barley (Fajr)	0.0156±0.0018ef	3.256 ± 0.250a
Barley (Reihan)	0.0206±0.0023bcde	2.568 ± 0.189cd
Barley (Shour)	0.0162±0.0018def	2.931 ± 0.187abc
Barley (Dasht)	0.0226±0.0003ab	2.301 ± 0.095d
Barley (Sahra)	0.0216±0.0011abcd	2.659± 0.073cd
Barley (Khorram)	0.0146±0.0014f	2.249 ± 0.210d
Barley (EH-83-7)	0.0218± 0.0012abc	2.738 ± 0.108bcd
Wheat (Bam)	0.0262±0.0016a	2.253 ± 0.152d
Wheat (Sepahan)	0.0168±0.0035cdef	3.225 ± 0.206ab

Means followed by different letters in the same column are significantly different (LSD,P <0.01)

TABLE 3. Mean (± SE) starch and protein contents of flour of barley and wheat cultivars used for *Ephestia kuehniella* feeding

Host (cultivar)	Starch content (mg mL^{-1})	Protein content (mg mL^{-1})
Barley (Fajr)	7.755±0.699b	0.0085 ± 0.0011c
Barley (Reihan)	4.471±0.153d	0.02219 ± 0.0007b
Barley (Shour)	7.111±0.174b	0.0201 ± 0.0022b
Barley (Dasht)	5.820±0.274c	0.0341 ± 0.0044a
Barley (Sahra)	1.954±0.104e	0.0192± 0.0011b
Barley (Khorram)	4.456±0.213d	0.0223 ± 0.0043b
Barley (EH-83-7)	4.287± 0.324d	0.0189 ± 0.0004b
Wheat (Bam)	7.241±0.058b	0.0190 ± 0.0024b
Wheat (Sepahan)	11.375±0.240a	0.0343 ± 0.0032a

Means followed by different letters in the same column are significantly different (LSD, *P* <0.01).

Insects consume less of a special diet simply because they are able to transfer it more efficiently into body growth. Furthermore, when the larvae consume less, the diet will tend to pass through their gut slowly, and it can be efficiently converted into their body biomass (Soo Hoo & Fraenkel 1966).

It is useful to note that, among the nutritional indices, ECI is a feeding index that can be different due to variations in food digestibility and the proportion of digestible food converted to insect body matter and metabolized to obtain energy (Abdel-Rahman & Al-Mozini 2007). Moreover, this index indicates an insect's ability to incorporate food into growth (Nathan et al. 2005). The ECI value increased when larvae was fed flour of the barley cultivar EH-83-7, suggesting that it was more efficient at the conversion of ingested food to biomass, evident as weight gain by the larvae (Koul et al. 2003). Also, the larvae fed with the wheat cultivar Bam had the lowest RCR value, most likely because of appropriate nutrient content.

With regards to the results of this study, the lowest RGR was recorded on the barley cultivar Sahra, which may be because of a decrease in ECI. Also, the highest RGR was recorded on the barley cultivar EH-83-7, indicating its high quality and suitability as a diet for the larvae of the Mediterranean flour moth. According to the obtained results, the flour of barley and wheat cultivars considerably influenced the digestive enzymatic activity of the *E. kuehniella* fifth instar larvae. Since the variations of starch content in the barley and wheat cultivars may lead to differences in the amylolytic activity (Lwalaba et al. 2010) of the Mediterranean flour moth, the highest amylolytic activity was detected in the larvae reared on the wheat cultivar Bam, which is

attributed to the high starch content of this cultivar. In addition, the larvae fed with the barley cultivar Khorram had the lowest level of amylolytic activity, which was approximately 2-fold lower than the wheat cultivar Bam. It can be concluded that the amylolytic activity of this insect on the above-mentioned cultivars was directly proportional to the starch content. The amylolytic activity of the Mediterranean flour moth on flour of the wheat cultivar Bam is lower than the amylolytic activity reported by Abdi et al. (2014) for *E. kuehniella* on the wheat cultivar Bam (0.90 ± 0.13 mU mg-1). According to the study of Abdi et al. (2014), *E. kuehniella* whole extract body (instead of midgut extract) was used to assess the digestive enzymatic activity, and the possible reason for this discrepancy can be due to variations in experimental methods.

The fifth instar larvae of *E. kuehniella* fed on the barley cultivar Fajr 30 showed the highest proteolytic activity, while the protein content was lowest in this cultivar. Previously, it was reported that the insects release less of the enzymes for nutrients present in excess, while maintaining or increasing levels of enzymes for nutrients in shortage (Kotkar et al. 2009, Lwalaba et al. 2010). Also, because protein ingestion takes place totally during the larval stages (Sorge et al. 2000), thus, the larvae can allow no dietary protein to pass undigested through the gut.

The highest starch content was detected in the flour of the wheat cultivar Sepahan, while the larvae fed on this cultivar showed low level of amylolytic activity, which can be correlated to the presence of some amylase inhibitors. The soluble protein evaluations of the flour of barley and wheat cultivars suggest that the wheat cultivar Sepahan and barley cultivar Dasht had

the highest protein content. Although the highest protein content was detected in these cultivars, the larvae fed with them had low weight gain and ECI value, indicating the unsuitability of these diets for *E. kuehniella*. Moreover, since low dietary protein can cause an increase in consumption rate (Slansky 1993), this study observed a high food consumption by the fifth instar larvae fed with the barely cultivar Fajr 30.

In conclusion, the highest larval weight gain, efficiency of conversion of ingested food and relative growth rate as well as more regulated amylolytic activity were obtained when larvae were fed with the barley cultivar EH-83-7. Also, standardized insect-growth index and larval growth index were higher when larvae were fed with the cultivar Reihan 03, therefore, it can be suggested that EH-83-7 and Reihan 03 are the most suitable cultivars for the laboratory rearing of *E. kuehniella*.

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UPDATED DISTRIBUTIONAL DATA FOR *CITHERONIA SEPULCRALIS* GROTE & ROBINSON, 1865 (SATURNIIDAE: CERATOCAMPINAE), WITH A NEW HOST PLANT RECORD

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ABSTRACT. The distribution of *Citheronia sepulcralis* (Saturniidae: Ceratocampinae) is updated. Compared to previous literature, a much more extensive inland distribution in the eastern United States is provided, including a new state report from Delaware. A recent photographic voucher from the Bahamas is reported and discussed. A new natural host plant, *Pinus clausa* (Pinaceae), is mentioned.

Additional key words: Bahamas, biogeography, insect-host plant association, pine devil, *Pinus*

Citheronia sepulcralis Grote & Robinson, 1865 (Saturniidae: Ceratocampinae), also known as the pine devil, is a moderately sized (wingspan: male: 67–85 mm; female: 68–95 mm), obscurely marked moth, found in pine and mixed forests throughout the eastern United States (Ferguson 1971, Lemaire 1988, Tuskes et al. 1996). The cryptic, horned, larvae of *C. sepulcralis* feed exclusively on various species of *Pinus* (Pinaceae). While reports in nature of this species are sparse, *C. sepulcralis* can be quite common in the correct habitats.

Citheronia sepulcralis is the only species of Ceratocampinae obligate on *Pinus*, and one of only a few Ceratocampinae that will feed on this genus of trees. The other ceratocampine known to feed on pine, *Eacles imperialis imperialis* (Drury, 1773) and *E. i. pini* Michener, 1950 are not obligate on *Pinus*. The former is polyphagous; with *Pinus* being just one of many host genera, and the latter is reported to feed on spruce (*Picea*) and broadleaved plants in addition to *Pinus* (Ferguson 1971, Stone 1991, Tuskes et al. 1996).

Historically, *C. sepulcralis* was encountered along the Atlantic coast in areas with an abundance of pines, from southern Maine south to the Florida Keys, and in all of the Gulf Coast states with the exception of Texas. Its occurrence inland is represented by scattered reports throughout the northern portions of the Gulf Coast states and northeast through the Appalachians.

This paper aims to present a more inclusive distribution map of *C. sepulcralis*, providing a clear pictorial representation of a range that, while limited, is more expansive than previously reported, potentially even reaching outside of the United States. Additionally, some hypotheses are proposed in an attempt to understand the distribution boundaries of this species, and why it is absent in some locations where *Pinus* is common.

MATERIALS AND METHODS

The following institutions were either visited or contacted by the author to examine or request *C. sepulcralis* data:

AMNH American Museum of Natural History, New York, New York, USA

CGCM Collection of Carlos G. C. Mielke, Curitiba, Paraná, Brazil

CMNH Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA

CNC Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Ontario, Canada

CUIC Cornell University Insect Collection, Ithaca, New York, USA

FSCA Florida State Collection of Arthropods, Gainesville, Florida, USA

MEM Mississippi Entomological Museum, Mississippi State, Mississippi, USA

MGCL McGuire Center for Lepidoptera & Biodiversity, Gainesville, Florida, USA

NHM The Natural History Museum, formerly British Museum (Natural History), London, U.K.

TAMU Texas A&M University, College Station, Texas, USA

UCMS University of Connecticut, Storrs, Connecticut, USA

UGCA Collection of Arthropods, Georgia Museum of Natural History, Athens, Georgia, USA

USNM National Museum of Natural History, formerly United States National Museum, Washington, D.C., USA

YPNM The Yale Peabody Natural History Museum, New Haven, Connecticut, USA

Additional distributional data were gathered from the literature, personal communications, and online databases, such as the Butterflies and Moths of North America, BugGuide, and the Lepidopterists' Society Season Summary.

Natural larval host plant data was gathered from Geddes (1903), Packard (1905), Forsyth (1933), and Ferguson (1971) in order to confirm the new host plant record reported below. Records, particularly those included in Stone (1991) that list *Pinus* species not native to the distribution of *C. sepulcralis*, or those that do not explicitly state the collection of larvae from a given species of pine, were not considered "natural hosts."

The map was created with SimpleMappr (Shorthouse 2010) and edited with CS4 (Adobe 2008). All geographical coordinates are approximate, and are based on the localities provided on specimen labels. GPS data were acquired with Google Earth.

RESULTS

The accompanying map (Fig. 2) illustrates a number of inland records, which extend the traditional, largely coastal distribution of *C. sepulcralis*. New peripheral reports come from central and western Tennessee (K. Childs pers. com.; B. Reynolds pers. com.; CUIC), as well as from northern Alabama (B. Reynolds; MEM) and central Mississippi (AMNH), displaying an inland extent of distribution from the Gulf of Mexico that was not presented by Lemaire (1988), Opler (1995), or Tuskes et al. (1996). In addition to numerous new county records for all states, *C. sepulcralis* is reported here for the first time from Delaware (MGCL) and Washington D.C. (CNC).

A single photographic voucher of *C. sepulcralis* from Grand Bahama, Bahamas, from February 2009 provides the first evidence of this species being found outside of the United States.

No additional natural host plant records have been reported since those consolidated in Ferguson (1971). The single *C. sepulcralis* larva that I have found in nature was feeding on *Pinus clausa* Chapman (Vasey) near Ocala, Florida, which is a new host record, reported here for the first time.

DISCUSSION

Pine trees are the only known natural host of *C. sepulcralis*, and thus its distribution very clearly follows the range of various pines in the eastern United States. Natural host records exist only for *Pinus strobus* L. (Packard 1905), *P. rigida* Mill (Packard 1905), and *P. caribaea* Morelet (Forsyth 1933) (all cited by Ferguson 1971). Other *Pinus* species reported in literature refer to host plants probably used in captivity, as evident by the various European *Pinus* species listed by Stone (1991).

Apparently the distribution of *C. sepulcralis* does not merely follow the distribution of pine, but more

FIG. 1. *Citheronia sepulcralis* found on February 21, 2009, Grand Bahama Island, Bahamas. Photo credit: Larry Manfredi, used with permission.

specifically, that of the *Australes* subsection (Gernandt et al. 2005). These pines comprise the familiar hard pines of the southeastern United States with some species ranging more northward, such as the pitch pine, *P. rigida*. This association with southern pines certainly provides some explanation as to the relationship of *C. sepulcralis* with pitch pine in the Northeast, which is the only *Australes* pine present in New England and most of New York (Critchfield & Little 1966). Similarly, the distribution of *C. sepulcralis* is restricted in other states where *Australes* pines are not widespread. For example, in Ohio and Kentucky, *C. sepulcralis* is present only in the portions of these states where *Australes* pines are found (Critchfield & Little 1966, Metzler & Horn 2009, Covell 1999).

Although there is a clear association between *C. sepulcralis* and *Australes* pines in the Northeast, records do exist for *C. sepulcralis* feeding on white pine, *P. strobus*, which is not a member of the *Australes* subsection (Packard 1905, Gernandt et al. 2005). However, when reared on white pine, *C. sepulcralis* does not attain large size or maintain good health. More specifically, I have reared *C. sepulcralis* on white pine on two occasions and on pitch pine three times. The first time that I reared *C. sepulcralis* on white pine, indoors, resulted in a 40% pupation rate out of 10 larvae. The second time that I reared this species, sleeved outdoors, on white pine, resulted in complete mortality of about a dozen larvae, potentially from disease and malnutrition. Siblings from this second white pine batch were also sleeved outdoors on pitch pine with only minimal mortality. Similar low, to zero,
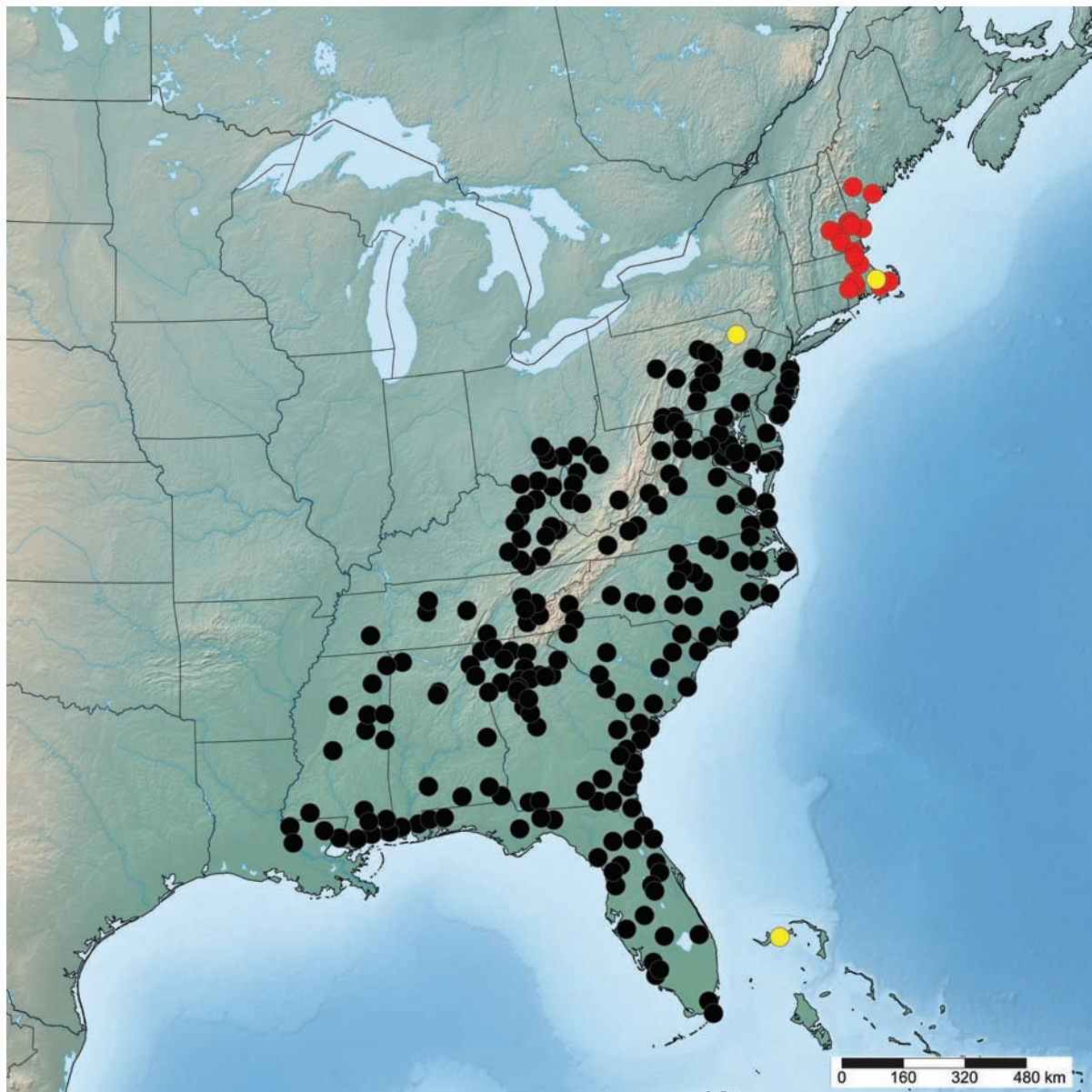
FIG. 2. The distribution of *Citheronia sepulcralis* in the United States and the Bahamas. Red circles represent localities of extirpation; black circles represent records from localities where *C. sepulcralis* is still considered extant; yellow circles represent potential populations that have not yet been confirmed or may now be extirpated.

mortality was seen each additional time when *C. sepulcralis* was reared on pitch pine. Geddes (1903) reported trouble rearing *C. sepulcralis* on white pine, and had better results on pitch pine as well. This same author also mentioned *P. mitis* (=*P. echinata*) as a possible host but did not state that larvae were found on this species. Perhaps if *C. sepulcralis* had adapted to feeding on white pine, the distribution northward could have been much more extensive, considering the distribution of white pine in New England relative to pitch pine (Critchfield & Little 1966). Thus the

northern extent of the historical distribution of *C. sepulcralis* in southern Maine and New Hampshire mirrors the northeastern distribution of pitch pine. Similarly, the westernmost distribution of *C. sepulcralis*, to be discussed further below, parallels the distributions of all southeastern *Australes* subsection pines, at least as far west as the Mississippi River Valley (Critchfield & Little 1966).

With a clearer representation of the inland and westernmost distribution of *C. sepulcralis*, (Fig. 2), it now becomes possible to elucidate the western

terminus of the geographic range of this species. Data gathered in the present work shows that this species has not been reported west of the Mississippi River Valley, although one record that reports otherwise must be noted. The *C. sepulcralis* figured by D'Abrera (1995) was labeled as being from Texas, without further information. I was able to locate a short series of specimens at the NHM labeled "Texas", including the male figured by D'Abrera. But these obviously very old specimens, without much wear; appear to have been reared—perhaps in Texas, especially considering that an uncommonly collected female was included. Lemaire (1988) mentioned Texas as part of the distribution and Tuskes et al. (1996) hesitantly repeated this record. The specimens at the NHM appear to be the origin of these reports. Additionally, there are no recent records of this species from Texas despite intensive collecting in the state (E. Knudson pers. com.). However, it is important to mention that *Australes* pines are distributed in eastern Texas (Critchfield & Little 1966) and so it is not impossible for *C. sepulcralis* to exist there. Similarly, there are no records from southern Arkansas, northern Louisiana, or northwest Mississippi, despite appropriate hosts (Critchfield & Little 1966). The lack of records from otherwise seemingly appropriate habitat in this region suggests that there is a natural barrier limiting the western edge of distribution to just east of the Mississippi River. The three species of *Australes* pines that range in this region, *P. palustris* Mill, *P. taeda* L., and *P. echinata*, are all absent immediately along the Mississippi River. There is a roughly 80 km gap between the distributions of these pines in the southeastern United States east of the Mississippi, which includes much of the known southeastern distribution of *C. sepulcralis*, and their reappearance in western Louisiana, eastern Texas, and northwards to Arkansas (Critchfield & Little 1966). The lack of naturally occurring *Australes* pines in the Mississippi River Valley offers an explanation as to why *C. sepulcralis* is apparently not found in the pine forests west of southeastern Louisiana, where they have been commonly collected for decades (Brou 1997).

The distribution presented in Figure 2 not only provides some insight as to the edge of the distribution of *C. sepulcralis*, but also provides an opportunity to publish some records from within the known range that were previously unreported and to allow the invalidation of numerous questionable records. The only states within the known area of distribution that apparently lack published records are Delaware and Connecticut. I have only seen a single, old specimen from Delaware (MGCL), and I consider this a state record. Unfortunately, it lacks specific data, but the male specimen appears to have been collected in May. *Citheronia sepulcralis* likely occurs in the loblolly pine forests in the southern part of the state, especially considering the number of records from the Delmarva Peninsula from nearby Maryland and Virginia, thus its presence in Delaware is not surprising. For Connecticut, one specimen from Tolland County in the Yale Peabody Museum "collected" in 1954 bears a label reading "probably reared from Georgia specimens", and thus is a doubtful, but not impossible record. Furthermore, records have not been published from Washington D.C. A handful of very old specimens at the CNC are labeled as originating from Washington D.C. Numerous reports from adjacent Maryland and Virginia (see Fig. 2) corroborate the likelihood of *C. sepulcralis* occurring in D.C., either historically or currently.

Questionable records of *C. sepulcralis* have persisted in the literature from Illinois and New York. The often-reported outlier record from Illinois is incorrect. Cashatt & Godfrey labeled this record erroneous as early as 1990, when they said the following in a footnote: "A dubious state record. *Citheronia sepulcralis* apparently was reared in Normal, McLean County, where there are no native *Pinus* species prior to the relocation of the Illinois Natural History Survey to Urbana in 1885." Unfortunately this reference was overlooked for many years and the record has been perpetuated in later literature (Bouseman & Sternburg 2002), and subsequently in online databases (R. A. St. Laurent pers. obs.). New York similarly has dubious records, with some old, obscure, literature references to specimens coming from Albany (T. McCabe pers. com.). One specimen from 1938 at the AMNH bears an Albany label with an explanation that it was reared stock received from A. E. Brower (potentially originating from Maine), and thus this particular specimen could signify the sole NY literature record. Also, the New York Natural Heritage Program mentions a specimen from Montauk in Suffolk County, known from "a pupa" collected in 1984, which is a very bizarre record indeed, as subterranean ceratocampine pupae are the least likely life stage to be encountered, let alone identified to species. According to T. McCabe (pers. com.), the Montauk *C. sepulcralis* is incorrectly reported in the online database, and is in fact *E. imperialis*. To further invalidate *C. sepulcralis* reports from otherwise seemingly ideal habitat on Long Island, H. McGuinness has not encountered this species in the Long Island pine barrens despite extensive sampling (H. D. McGuinness pers. com.). Furthermore, the CUIC lacks any specimens of *C. sepulcralis* from Long Island despite the presence of numerous large series of other Ceratocampinae collected there by R. Latham. Packard

(1905), reported *C. sepulcralis* from New York City, citing both Grote and Edwards, but this is questionable as well, because I have been unable to trace the source of this locality information in Packard's cited sources. Forbes (1923) also mentioned *C. sepulcralis* as occurring in New York, but did not give specific information or a citation. While *C. sepulcralis* is well represented from New England (Massachusetts, Maine, New Hampshire, and Rhode Island) by pre-1950s specimens, Connecticut and New York form a distinct gap between the current northernmost distribution in Pennsylvania and New Jersey and the historical distribution in New England. Whether or not *C. sepulcralis* was widely distributed in these intervening states is not clear.

Of all records to be reported in this current work, perhaps the most interesting is one from Grand Bahama, Bahamas. Larry Manfredi posted a picture to his website (Manfredi 2009) of a relatively fresh individual photographed during the day, on the side of a restaurant on the coast of the island (Fig. 1). Saturniidae are nearly absent throughout the Caribbean Islands, except for *Automeris io* (Fabricius, 1775), thus this report of *C. sepulcralis* is particularly surprising (T. McCabe & J. Miller pers. com.). The topic of island colonization by Saturniidae has only been briefly mentioned in literature, and thus our understanding of this family in the Bahamas is not well investigated (Rougerie & Herbin 2006, Goldstein 2010). This evidence suggests that the individual may have arrived at Grand Bahama due to some human assistance. However, if there is a population of *C. sepulcralis* on the island, it surly represents only one of a few instances of Saturniidae colonizing a Caribbean island, human assisted or otherwise. The possibility that this recent record represents a natural population is not improbable however, especially considering the short distance between Florida and Grand Bahama. More importantly, Caribbean pine, *P. caribaea*, is present on Grand Bahama and other Bahama islands (Critchfield & Little 1966). *Pinus caribaea* is a member of the *Australes* subsection (Gernandt et al. 2005) and one of the few *Pinus* species that actually has been recorded as a host of *C. sepulcralis* (Forsyth 1933). Regardless of its origin, the Grand Bahama record is certainly a country record for *C. sepulcralis*.

Forsyth (1933) was the last to publish a new, natural host plant for *C. sepulcralis* until this present work. This is not surprising considering the crypsis of the larvae. I have, for example, searched for many seasons targeting *C. sepulcralis* larvae in Pennsylvania, West Virginia, and Florida, only to reveal a single larva on *P. clausa*, a species of pine on which *C. sepulcralis* had not been previously reported. It is probable that further targeted searches will reveal larvae on additional species of *Australes* pines found within the natural distribution of *C. sepulcralis*.

Although the distribution of *C. sepulcralis* is not restricted, this species has seen serious declines in parts of its range. *Citheronia sepulcralis* is one of the Saturniidae and other large moths that declined from the northeastern United States around the 1950s–1960 due to various debated factors, such as the introduced parasitoid *Compsilura concinnata* (Meigen, 1824) and DDT spraying (Goldstein 2010, Schweitzer et al. 2011, Wagner 2012). Schweitzer et al. (2011) reported the last records of *C. sepulcralis* from New England as 1952 and mentioned a record from the Myles Standish State Forest in Plymouth, Massachusetts, from 2010. I attempted to confirm this contemporary record and set out to this location with M. Nelson of the Massachusetts Natural Heritage with a number of reared *C. sepulcralis* females in tow in order to utilize them in an attempt to attract wild males. Despite numerous nights spent in the state forest and other pine barren habitats in Massachusetts and Rhode Island with reared females emitting pheromones in June and July of 2011, 2012, and 2014, no males were attracted. Therefore, it is possible that the 2010 record may have been an introduction, or potentially a serendipitous discovery of an apparently very low or transitory natural population. A recent sighting of *C. regalis* (Fabricius, 1793) from central New York may signal repopulation of the northeastern states by this other previously extirpated, large ceratocampine (Lepidopterists' Society Season Summary 2014). Therefore, sightings of the congeneric *C. sepulcralis* in the Northeast may increase in frequency in coming years assuming that the declines of both species were caused by similar factors.

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LARVAL KEY AND LIFE HISTORIES FOR FOUR NORTH AMERICAN *RIFARGIA* SPECIES (NOTODONTIDAE: HETEROCAMPINAE)

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ABSTRACT. The genus *Rifargia* includes four North American species: *R. benitensis* (Blanchard), *R. ditta* (Barnes and McDunnough), *R. subrotata* (Harvey), and a new species, which is the western sister taxon of the latter. All are hackberry (*Celtis*) specialists. We provide images for each species, a larval key, and brief descriptions of the five instars for both of the eastern species (*R. benitensis* and *R. subrotata*).

**Additional key words:** Life history, *Celtis*, Spiny Hackberry

The heterocampine notodontid genus *Rifargia* Walker 1862, as recently re-circumscribed by Becker (2014), includes 11 described species which range from Argentina to New York State. Four species are found north of Mexico: *R. benitensis* (Blanchard), *R. ditta* (Barnes and McDunnough), and *R. subrotata* (Harvey), as well as an undescribed species sister to *subrotata* from Arizona (Miller et al. in prep.). The first two of these form a pair of sister species, with *ditta* being, so far as known, endemic to Arizona and adjacent parts of Mexico; likewise the latter also form a pair of sister species with the n. sp. known from Arizona only. The life history of only one of these, *subrotata* (Wagner 2005), was known prior to our work. Here we provide life history notes, images, and a key to the last instars of the four North American *Rifargia*. More detailed treatments are supplied for the two eastern species, *benitensis* and *subrotata*: all five instars are figured and their life histories briefly compared. While we focus on the eastern pair of taxa, we suspect that our images (Figs. 9–18) could be used gainfully to distinguish early and middle instars of the two Arizonan *Rifargia*, i.e., *subrotata* (Figs. 9, 11, 13, and 15) will closely approximate those for *R*. n. sp., and our images for *benitensis* (Figs. 10, 12, 14, and 16) will closely approximate those for *R. ditta*.

All four *Rifargia* species have closely similar life histories and larvae. The eggs—bright green, smooth, shiny, and hemispherical—are laid singly on the underside of young growth. There are five larval instars and the pupal stage is believed to overwinter below ground or in duff. The first instars have enormous antler-like scoli on the prothorax, and smaller, less branched scoli on A1–A6, A8, and A10 (Figs. 9, 10). The scoli get

progressively smaller with each molt and are largely absent by the penultimate instar. It is noteworthy that the two eastern species are most easily distinguished in the early instars, and become increasingly similar in later instars, showing the importance of studying the entire life history.

In the last instar all have a lime green ground color and corrugated texture that is most obvious along the dorsal midline (especially in profile); the small head is retracted partway into the prothorax (Figs. 1–8). There is a prominent white middorsal stripe, edged with red, that splits toward the posterior of A6, with the arms carrying to the anal prolegs. The small anal prolegs are held elevated above the substrate in all instars. The trunk is speckled with pale bluish dots which form rings in *subrotata* (Fig. 2) and the n. sp. (Fig. 4), but are more randomly distributed in *ditta* (Fig. 6) and *benitensis* (Fig. 8). There are faint, yellowish, oblique lines that extend from the subdorsum downward toward the prolegs. Primary setae are small and inconspicuous; they do not exude clear defensive secretions as in many heterocampine genera (e.g., *Hyparpax* Hübner, *Oligocentria* Herrich-Schäffer, and *Schizura* Doubleday). The orange spiracles are relatively small.

All four of our species are specialists on *Celtis* and parse out by species group. *R. benitensis* and *R. ditta*, so far as known, feed only on spiny hackberry (*C. pallida*) in the wild; while *R. subrotata* and *R*. n. sp. feed on sugarberries (*C. laevigata*, *C. reticulata*, and related species). At least southward, they are facultatively multivoltine, with generations continuing as long as conditions are favorable for the growth of hackberries, especially in more arid regions. In southeastern Arizona, *R. ditta* can be essentially univoltine, with activity tied to
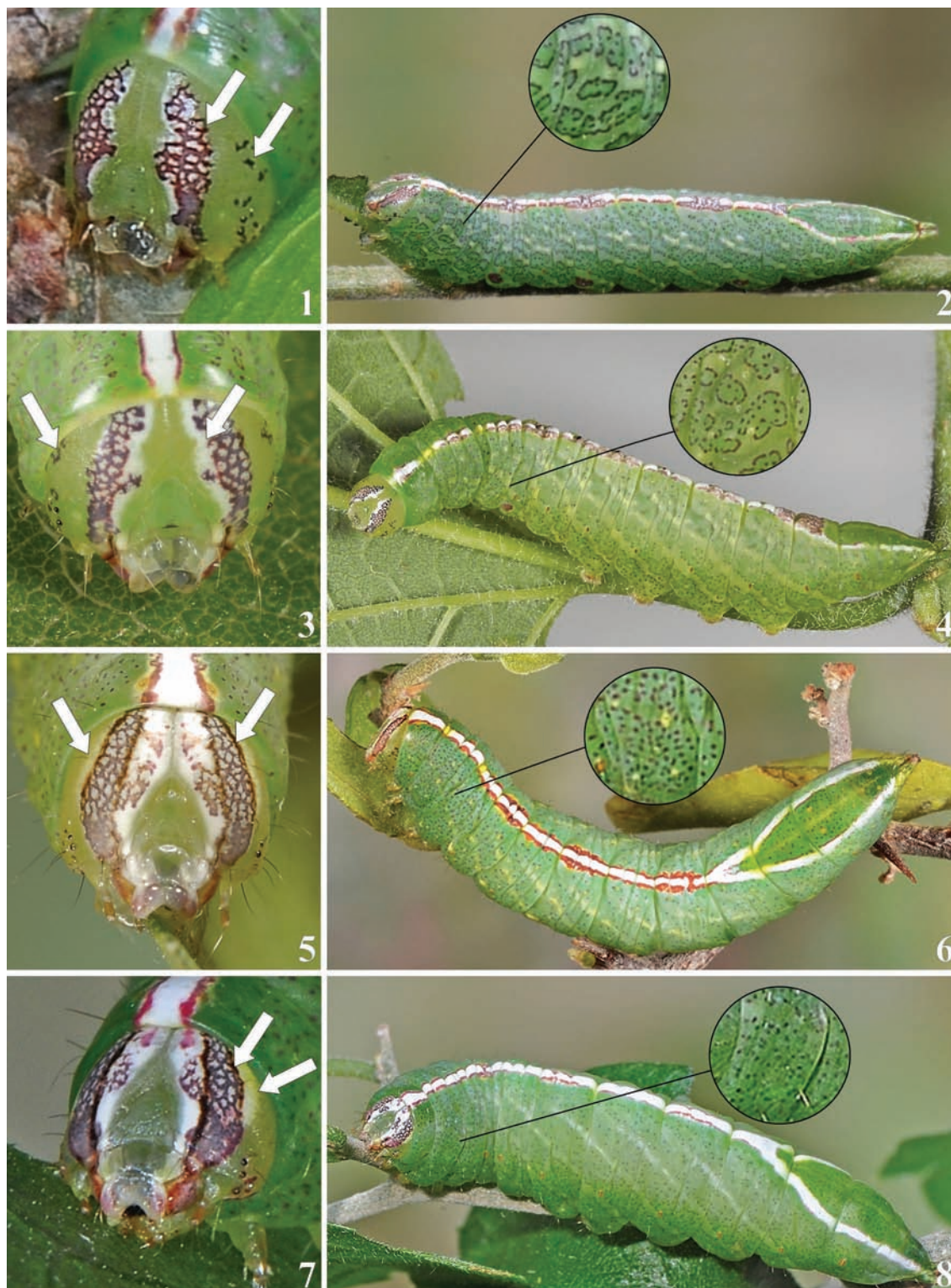
FIGS. 1–8. Visual key to fifth instar *Rifargia*. **1**. *R. subrotata* head, unlined vertical band and spotted gena emphasized; **2**. *R. subrotata* dorsolateral, inset: blue spots form irregular circles; **3**. *R.* n. sp. head, spotted gena and generous white edging emphasized; **4**. *R.* n. sp. dorsolateral, inset: blue spots form irregular circles (inset from different individual); **5**. *R. ditta* head, elongate creamy spot and edging of red band emphasized; **6**. *R. ditta* dorsolateral, inset: simple blue spots; **7**. *R. benitensis* head, edging of red band and elongate creamy spot highlighted; **8**. *R. benitensis* dorsolateral, inset: simple blue spots.
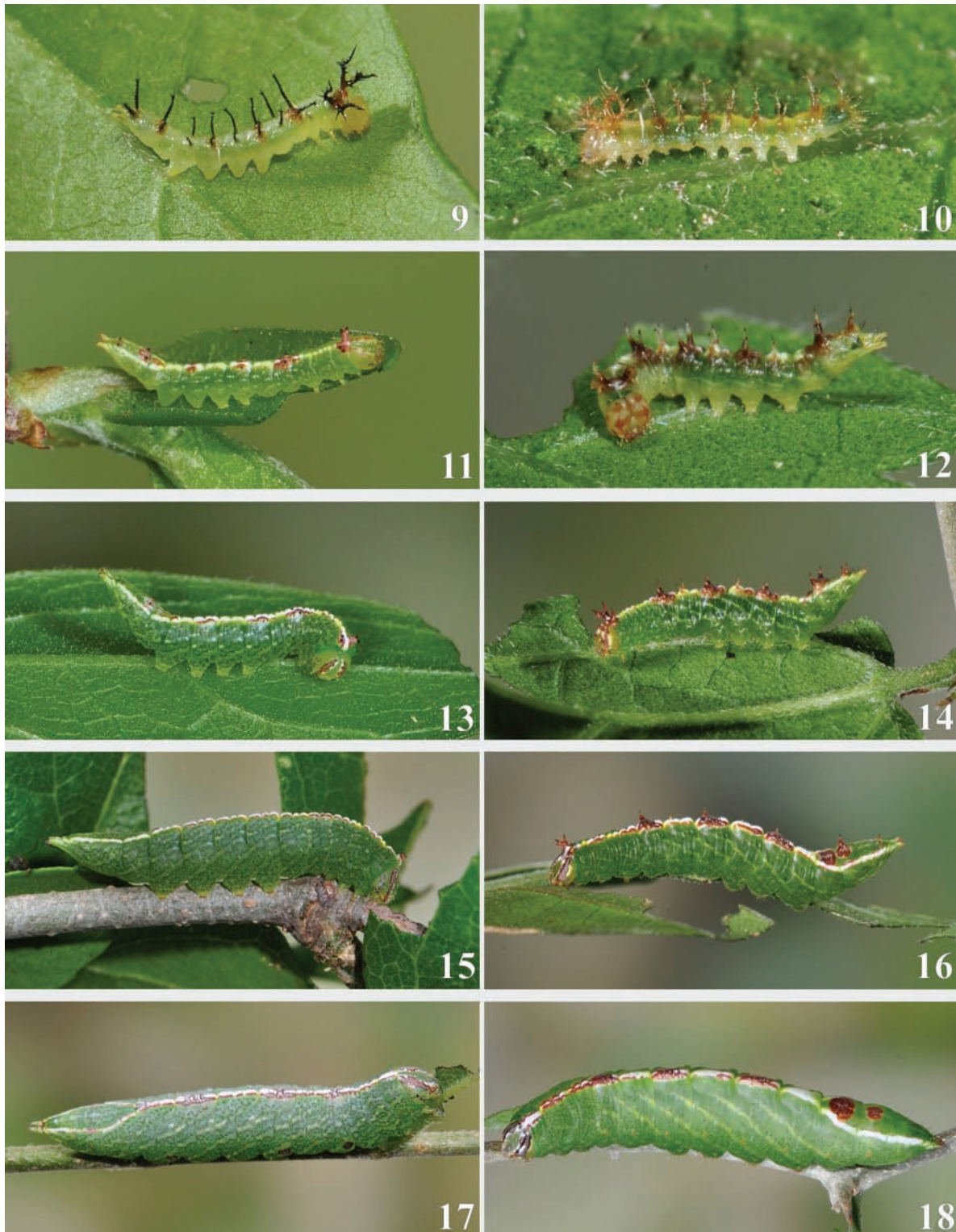
FIGS. 9–18. *Rifargia subrotata* (left column) and *Rifargia benitensis* (right column). **9**. *R. subrotata* first instar; **10**. *R. benitensis* first instar; **11**. *R. subrotata* second instar; **12**. *R. benitensis* second instar; **13**. *R. subrotata* third instar; **14**. *R. benitensis* third instar; **15**. *R. subrotata* fourth instar; **16**. *R. benitensis* fourth instar; **17**. *R. subrotata* fifth instar; **18**. *R. benitensis* fifth instar.

the monsoon. Below we provide a key and images for the four North American species of *Rifargia*

KEY TO LAST INSTAR NORTH AMERICAN *RIFARGIA*

1a Blue spots along sides of thorax forming irregular circles (Figs. 2, 4); vertical red bands on head not edged outwardly with black (Figs. 1, 3); no elongate creamy crescent-shaped spot outside the vertical red band above the eyes; gena with numerous black spots (Figs. 1, 3); on sugarberry and related deciduous hackberries ....…………. 2

1b Blue spots along sides of thorax not forming irregular circles (Figs. 6, 8); vertical red bands on head distinctly edged outwardly with black (Figs. 5, 7); elongate creamy spot outside the vertical red band above the eyes (Fig. 7); gena with or without numerous black spots; on spiny or desert hackberry ....………………. 3

2a Vertical red bands on head not edged inwardly with white or with little white above frons (Fig. 1); known from Rio Grande Valley and Hill Country of South-Central Texas eastward and northward ...……… *Rifargia subrotata*

2b Vertical red bands on head generously edged inwardly with white above the frons (Fig. 3); known only from southeastern Arizona ....………….............……….*Rifargia* n. sp.

3a Small yellow spot anterior to spiracle on A1–A3 (just visible in Fig. 6); elongate creamy spot outside the vertical red band above the eyes inconspicuous (Fig. 5); gena sometimes with numerous black spots; southeastern Arizona only ...………….….……….....................…… *Rifargia ditta*

3a No small yellow spot anterior to spiracle on A1–A3; elongate creamy spot outside the vertical red band above the eyes more conspicuous (Fig. 7); gena without numerous black spots; extreme southern Texas from San Patricio County to Brownsville …..…................ *Rifargia benitensis*

Rifargia benitensis was described from specimens collected in San Benito, Texas, by Andre Blanchard in 1971. This species occurs from San Patricio County (Corpus Christi area) south through Hidalgo and Cameron Counties, into northeastern Mexico. We have been unable to confirm reports of the species from the Hill Country in the vicinity of Austin and San Antonio, southward to Edwards County (specimens from these more inland sites have so far proven to be *R. subrotata*) (Miller et al. in prep.). At times the species is common in the Sabal Palm Sanctuary in Brownsville. It has not yet been collected from south of the Rio Grande (Miller et al. in prep.). We only know it from scrub and palm forests; we have not yet seen it from desert and otherwise more open xeric associations. The moth has a long flight season, from March to at least November, with adult numbers peaking in the fall wet season, from September into October. We found six wild *Rifargia* larvae in the Sabal Palm Sanctuary on hackberry in November 2014. Three *R. benitensis* came from spiny hackberry (*Celtis pallida*), while the three remaining larvae from sugarberry (*Celtis laevigata*) proved to be *R. subrotata*. Ex ova larvae of *benitensis* offered both

species of *Celtis* accepted both. Its sister species, *R. ditta*, is believed to be a strict spiny hackberry specialist.

Larval Description for *Rifargia subrotata*.
First instar (Fig. 9). Head light tan. Body of neonate cream, becoming pale green after feeding. Cream middorsal stripe. On T1, very large antler-like black scoli with primary fork at roughly one-quarter length from body; each branch with irregular bends and sparse secondary spines. Unbranched spinulose black scoli on A1–A6, A8, and A10, terminating in 3 rami, height of abdominal scoli exceeding thickness of body.

Second instar (Fig. 11). Head olive green with green-white vertical bands partly overlaid by mottled red-brown pattern. Body green with sparse dark spots, especially below dorsum; additional pale streaks in subdorsal area where oblique lines appear in later instars. Pale middorsal stripe, occasionally edged with yellow. T1 scoli reduced to short, thick, smooth purplish spines, bifurcated and blackened at tip. Abdominal scoli reduced to purplish setal bumps on A1, A3, A5, A8, and A10.

Third instar (Fig. 13). Head olive green with white vertical bands partly overlaid by mottled purple pattern; dark spots on gena. Body green with small dark spots forming irregular circles. Oblique abdominal lines from subdorsum downward across 2–3 segments to subventer. Dorsum corrugated; white middorsal stripe occasionally broken by yellow or purple spots. T1 spines short, reddish purple, bifurcate, blackened at their apices. Pairs of setal bumps on A1, A3, and A8.

Fourth instar (Fig. 15). Head olive green with white vertical bands partly overlaid by mottled purple pattern; dark spots on gena. Body green with small dark spots forming irregular circles (Fig. 2). Oblique abdominal lines from subdorsum downward across 2–3 segments to subventer. T1 spines nearly absent, red. Dorsum corrugated; sections of white middorsal stripe interrupted with yellow or reddish-purple. Spotting on face and body stronger than previous instar.

Fifth instar (Fig. 17). Head as previous instar. No setal bumps on T1. Body slightly thickened through A2–A6; green, tinted with blue above spiracles; spotting purplish. Occasional irregular large purple spots on body. White dorsal stripe occasionally interrupted by reddish-purple spots, especially on A1, A3, A5, and A7. Larva to 30 mm.

Larval Description for *Rifargia* benitensis.
First instar (Fig. 10). Head pale; occasionally with slightly darker horizontal band across middle. Body of neonate cream; after feeding, dorsum green, occasionally with brown about scoli. On T1, enormous antler-like tan scoli with primary fork at roughly one-

quarter length; each branch serpentine with numerous, long, secondary spines. Unbranched spinulose scoli on A1–A6, A8, and A10, terminating in 3 rami; height of abdominal scoli exceeding thickness of body. Bases and scoli proximally tan; distally clear with dark tips.

Second instar (Fig. 12). Head light tan-green; red-brown splotches yield checkered appearance. Body light green, somewhat darker green dorsally. Abdominal scoli in same positions as first instar, shorter (about half thickness of body) with no rami. T1 scoli shorter, forked, with fewer apical spines. Much-broken pale middorsal stripe broken by reddish-brown scoli on A1, A3, A5, A8, and A10; alternating with paler scoli on A2, A4, and A6.

Third instar (Fig. 14). Head yellowish-green; creamy splotches above frons crossed by vertical reddish-purple bands. Body green with oblique pale yellow abdominal lines from subdorsum downward across 2–3 segments to or through spiracles. Sparse small dark green spots on thorax and in ventral area of abdomen. Scoli in same positions as previous instars, but shorter without rami. T1 scoli antlerlike with three dorsal spines. White and yellow middorsal stripe broken by reddish-brown scoli on A1, A3, A5, A8, and A10. Dorsum corrugated; sections of white middorsal stripe interrupted with, yellow or reddish purple markings.

Fourth instar (Fig. 16). Head yellowish green; white splotches above frons crossed by mottled reddish purple vertical stripes, edged inwardly and outwardly with black. Body green with oblique pale abdominal lines from subdorsum downward across 2–3 segments to or through spiracles. Numerous small dark blue-green spots, most evident on thorax and subventer of abdomen. Scoli in same positions as previous instars, but shorter without rami, and that over A10 much reduced. T1 scoli with three dorsal spines. White middorsal stripe broken by reddish-brown scoli on A1, A3, A5, A8, and A10. Dorsum corrugated; sections of white middorsal stripe interrupted with, yellow or reddish-purple.

Fifth instar (Fig. 18). Head as previous instar but vertical band with purple and black edging more conspicuous (Fig. 7). Body slightly thickened through A2–A6; oblique pale abdominal lines more conspicuous, running downward across 3 segments to or through spiracles; purplish spotting, largely absent from dorsum of abdominal segments, not forming rings along sides of thorax (Fig. 8) (as in *subrotata*, Fig. 2). No raised scoli. White dorsal stripe often interrupted by reddish-purple spots, especially on A1, A3, A5, and A7. Larva to 32 mm.

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A REEVALUATION OF *PAPILIO PEGALA* F. AND *PAPILIO ALOPE* F., WITH A LECTOTYPE DESIGNATION AND A REVIEW OF *CERCYONIS PEGALA* (NYMPHALIDAE: SATYRINAE) IN EASTERN NORTH AMERICA

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ABSTRACT. A review of the available evidence related to the descriptions of *Papilio pegala* F. and *Papilio alope* F. (now generally recognized as *Cercyonis p. pegala* and *C. pegala alope*, respectively) reveals that the suggested type localities of these nominal taxa are untenable for the reasons originally given. The vicinity of Charleston, South Carolina, is retained for *P. pegala*, but for different reasons than those first proposed. Based on an eighteenth century illustration in "Jones' Icones," the Georgia type locality for *P. alope* is revised to the vicinity of New York, New York, and a lectotype is designated. Additional nominal taxa are discussed, including *Satyrus alope* var. *maritima* W. H. Edwards, *Satyrus nephele* var. *olympus* W. H. Edwards, *Cercyonis pegala* race *borealis* F. Chermock, *Cercyonis alope carolina* F. Chermock & R. Chermock, *Cercyonis alope ochracea* F. Chermock & R. Chermock, *Cercyonis pegala abbottii* F. Brown, and *Cercyonis pegala agawamensis* Arey & Grkovich. The holotypes of *C. p. borealis*, *C. a. carolina*, and *C. a. ochracea* are figured for the first time. Perceived morphological trends within *C. pegala* in eastern North America are mapped, revealing a broad clinal blend zone in the southeast and an extensive contact zone northward, which partly exhibits characteristics of a mosaic hybrid zone. Evidence suggests that temperature may influence phenotypic expression in *C. pegala*. Based strictly on wing pattern, an arrangement is proposed that recognizes four subspecies of *C. pegala* in eastern North America.

Additional key words: John Abbot, distribution, Alexander Garden, William Jones, "Jones' Icones," subspecies

The recent description of a new subspecies of the butterfly *Cercyonis pegala* (F.) by Arey and Grkovich (2014) emphasizes the need to reconsider the proposed type localities of *Papilio pegala* F. and *Papilio alope* F., which are commonly recognized as the subspecies *C. p. pegala* and *C. pegala alope*, respectively. These taxa were described during the eighteenth century and both lacked definitive type localities. Attempting to rectify this deficiency, Brown ([1966a]) proposed a type locality for each, but based his conclusions on meagre evidence. As a result, the type locality of *P. alope* shifted the traditional concept of this taxon from the northeastern United States to the southeastern coastal plain, in proximity to the proposed type locality of *P. pegala*. My own examination of the available evidence, much of which was not previously considered, refutes the conclusions of Brown ([1966a]). *Papilio alope* serves as the type-species of the genus *Cercyonis* Scudder, increasing the importance of stabilizing its nomenclature.

Cercyonis pegala exhibits a dizzying array of phenotypes across its broad North American range, fostering an ongoing debate about the validity of various described forms and subspecies. Klots (1951) mentioned five eastern subspecies of *C. pegala*, but thought it was perhaps best to "lump" them into a single clinal subspecies. Emmel (1969, 1975) recognized four eastern subspecies and four forms. Like Klots (1951), Miller and Brown (1981, 1983) listed five eastern subspecies. Sourakov (1995) conducted a more comprehensive investigation and concluded that *C.*

pegala is highly clinal. He suggested that only the nominotypical subspecies be recognized in the east, with two major wing-pattern forms ("*alope*" and "*nephele*") defining most populations. Despite this recommendation, up to seven subspecies are currently recognized in eastern North America, though interpretations vary (Pelham 2008, 2014, Arey & Grkovich 2014). The treatment of western populations is even more complicated (Austin 1992). Based on my own investigation involving thousands of specimens, including recently rediscovered type material, I propose an alternative treatment that recognizes four subspecies in eastern North America.

Methods

The original descriptions of *Papilio pegala* and *P. alope* were translated from Latin and compared. The conclusions of Brown ([1966a]) were studied. The following museums were searched for relevant historical specimens, many of which were photographed by me or staff of those institutions: Alabama Museum of Natural History, Univ. of Alabama (Tuscaloosa; UANH), Carnegie Museum of Natural History (Pittsburgh, Pennsylvania; CMNH), Hope Entomological Collections, Oxford University Museum of Natural History (Oxford, UK; OUMNH), Hunterian Museum, University of Glasgow (Glasgow, UK; HMUG); L. C. Bates Museum (Hinckley, Maine; LCBM), Linnean Society of London (London, UK; LSL); Macleay Museum, University of Sydney (Sydney, Australia; MAMU); Museum of Comparative Zoology, Harvard

University (Cambridge, Massachusetts; MCZ); Natural History Museum, London (London, UK; BMNH); National Museum of Natural History, Smithsonian Institution (Washington, D.C.; USNM); and Übersee-Museum Bremen (Bremen, Germany; UMB). In addition to the numerous *C. pegala* in some of the collections above, several thousand additional specimens were examined in the collection of the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History (Gainesville, Florida; MGCL) and my personal collection. Hundreds of photographs of living and preserved *C. pegala* were reviewed, including those available in the online databases of The Academy of Natural Sciences of Philadelphia (Philadelphia, Pennsylvania; ANSP), Peabody Museum of Natural History, Yale University (New Haven, Connecticut; PMNH), and MCZ. Many regional publications on butterflies were consulted, as well as various unpublished manuscripts, including the personal journals and correspondence of William H. Edwards (Charles C. Wise, Jr. Library, West Virginia State Archives, West Virginia University, Morgantown; WVSA) (photocopies in the MGCL archives).

<div align="center">RESULTS</div>

Original descriptions. In 1775, the Danish zoologist Johan (Johann) C. Fabricius (1745–1808) described a number of new North American insects in his treatise entitled *Systema Entomologiae* (Fabricius 1775). Among them was a new butterfly named *Papilio pegala*, which he vaguely attributed to "America." Fabricius (1781, 1787) subsequently published abbreviated versions of this description, followed by the entire description with slight alterations in Fabricius (1793). The original Latin description of *P. pegala* and English translation are as follows. The last line indicates that Fabricius based his description on more than one specimen.

> **Pegala.** 223. P. N. G. *alis dentatis, fuscis: anticus fascia rufa ocelloque unico, posticis supra ocello, subtus sex.*
>> Habitat in America. Mus. D. Hunter.
>> *Magnitudo P. Semele. Corpus fuscum. Alae anticae fuscae, fascia lata rufa, quae tamen margines haud attingit. Ocellus utrinque unicus, pupilla alba. Posticae supra fuscae ocello atro, iride fulva pupillaque alba, subtus variegatae, ocellis sex atris, iride ferruginea pupillaque albida, Tres e his ocellis ad margenem tenuiorem connati, quintus maximus.*
>> *Variat interdum ocello primo et quarto obsoletis*

English translation:

Pegala. 223. Genus *Papilio* [butterflies], division *Nymphales* [with scalloped wings], subdivision *Gemmati* [with eyespots]. Wings scalloped, brown: forewing with ruddy band with one eyespot, hindwing with eyespot above, six below.

Inhabits America. [From the] Museum of Dr. Hunter.

Size of *Papilio semele*. Body brown. Forewings brown with wide ruddy band that does not reach the margin. Both sides [above and below] have one eyespot with a white pupil. Hindwing above brown with dark eyespot, ringed in reddish-yellow with white pupil. Variegated below with six dark eyespots ringed by rust with white pupil. Three of these eyespots are joined near the margin, the fifth is the largest.

The first and fourth eyespots are sometimes absent.

Nearly twenty years after naming *P. pegala*, Fabricius described *Papilio alope* within the third volume of another important systematic work, *Entomologia Systematica* (Fabricius 1793), and stated that the butterfly inhabited "India." The original Latin description of *P. alope* and English translation are as follows. There is no indication from this description that Fabricius consulted multiple specimens.

> ***Alope*** 715. *P. S. alis dentatis fuscis: anticis utrinque fascia flava; ocellis duobus, posticis ocello supra unico subtus sex.*
> *Papilio Alope. Jon. fig. pict. 4 tab. 12 fig. I.*
> *Habitat in India Dom. Francillon.*
> *Corpus medium, fuscum. Alae anticae concolores, fuscae fascia lata, abbreviata, flava & in hac ocelli duo atri pupilla alba strigaque postica atra. Subtus obscurae, fusco irroratae ocellis sex pupilla alba.*

English translation:

Alope 715. Genus *Papilio* [butterflies], division *Satyri* [hindwing inner margin grooved to accommodate the abdomen]. Wings dark brown and scalloped: both sides [above and below] of forewings with yellow band; two eyespots. One eyespot on the hindwing above, six below.

Given as *Papilio alope* in Jones' drawings, volume 4, plate 12, figure 1.

Inhabits India. Owned by Francillon.

Body brown and of average size. Forewings the same brown color with wide, narrowed, yellow band containing two dark eyespots with white pupils, dark streak at bottom [of hindwings]. Obscure pattern below, marked with six darkened eyespots with white pupils.

After its description, *P. pegala* was largely misunderstood and mostly treated as a form of *P. alope*. The majority of known specimens that matched the description of *P. pegala* were in European collections and unseen by American lepidopterists. The concept of this taxon was essentially lost until the mid-nineteenth century (Edwards 1865). Meanwhile, the identity of *P. alope* was variously interpreted in the literature.

"Jones' Icones." As part of his description of *Papilio alope*, Fabricius (1793) cited an illustration of this butterfly by William Jones (1745–1818), a wine merchant and naturalist from Chelsea, now an affluent area of central London. During the early1780s, Jones began rendering life-sized watercolor drawings of Lepidoptera specimens that were contained in notable collections around London. He continued to work on his illustrations for over a decade, adding new drawings and inserting handwritten identifications for those he had previously rendered. When Jones illustrated an undescribed species, he left enough space around the figures to add its name and other details at a later date. Once the description of that species appeared in print, Jones inserted its name and cited a publication for reference. He also copied a portion of the species' Latin diagnosis as it appeared in the works of Linnaeus or Fabricius, regardless if these authors were responsible for the original description. Many of the species that Jones depicted were described decades after his death, demonstrating the great amount of material that remained unrecognized in British collections during his lifetime. Jones ultimately filled seven volumes with about 1500 figures. These drawings, long ago nicknamed "Jones' Icones," are currently bound into six volumes and are preserved at the Hope Library of Entomology (OUMNH) (see Calhoun 2009, Vane-Wright 2010). Images of all these drawings were recently made available online (OUMNH 2014). Surprisingly, Brown ([1966a]) did not consult Jones' drawings as part of his research concerning *P. alope*.

Plate 12 of volume 3 (cited by Fabricius as vol. 4) of "Jones' Icones" portrays dorsal and ventral aspects of a male specimen of *Cercyonis*, identified as *"Alope,"* which Jones credited to "Francillon" (Fig. 1). John Francillon (1744–1816) was a prominent jeweler and natural history dealer who owned a shop on Norfolk Street, along the Strand in central London (Cowan 1986). As the authority for the name *alope*, Jones cited "Fabricius ES 715," meaning species no. 715 in *Entomologia Systematica* (Fabricius 1793), the publication in which it was originally described. Below the figures, Jones transcribed a portion of Fabricius' description. The figures portray a medium-sized, dark brown male butterfly. On the forewing is an ochre-yellow postdiscal patch (band), slightly narrowed at vein M_2, containing two nearly equal-sized eyespots. The ventral hindwing bears a row of six small postdiscal eyespots. The length of the forewing (base to apex) measures 26 mm. The figures portray a North American butterfly that is now generally recognized as the subspecies *Cercyonis pegala alope*. Possibly as an oversight, or because he disagreed with Fabricius' reference to India, Jones did not indicate the published "habitat" (purported region of occurrence) on his drawing.

Within the same volume of illustrations, on Plate 49, Jones figured a larger *Cercyonis* under the name *"Pegala"* (Fig. 2). As the authority for this name, he cited "Fabricius N° 338," a reference to species no. 338 in *Species Insectorum* (Fabricius 1781), though *P. pegala* was actually described in Fabricius (1775). As in Fabricius' original description, Jones attributed the origin of his figured specimen to "Dr. Hunter." The figures portray a large, cocoa-brown male butterfly with pointed forewings that possess broad reddish-orange forewing patches containing single eyespots. The ventral hindwing displays a row of six prominent postdiscal eyespots. The length of the forewing (base to apex) measures 31 mm. The figures portray a butterfly from southeastern North America, which is now generally recognized as the subspecies *Cercyonis pegala pegala*. Written faintly in pencil on the right side of the drawing, probably by a later researcher, is "Conf [*confer* in Latin] 12," a suggestion to compare these figures with those of *P. alope* on Plate 12. Based on a reassessment of its origin (see below), and the completion date of Fabricius (1775), the figured specimen of *"Pegala"* was most likely collected between 1755 and 1773.

In a letter to the English physician and botanist Sir James E. Smith (1759–1828), dated August 1787, William Jones remarked, "Fabricius is in London…he is going thro' my drawings to correct amend and add to a Mantissa that he has now in hand, yet I have more than he will be able to accomplish in the time he has limited to stay" (Linnean Society of London; Smith 1832). This visit preceded the publication of Fabricius' *Mantissa Insectorum*, published in December of that year (Fabricius 1787). By the time Fabricius visited Jones, however, the *Mantissa* was already in press and he was working towards the publication of the multi-volume systematic work, *Entomologia Systematica*, in which *P. alope* would appear in the first part of the third volume (Fabricius 1793).

Fabricius (1792) listed Jones ("Jones Londoni") among the naturalists that he visited during his travels. On the other hand, Fabricius (1781, 1792) did not name Francillon among those that he called upon in England.
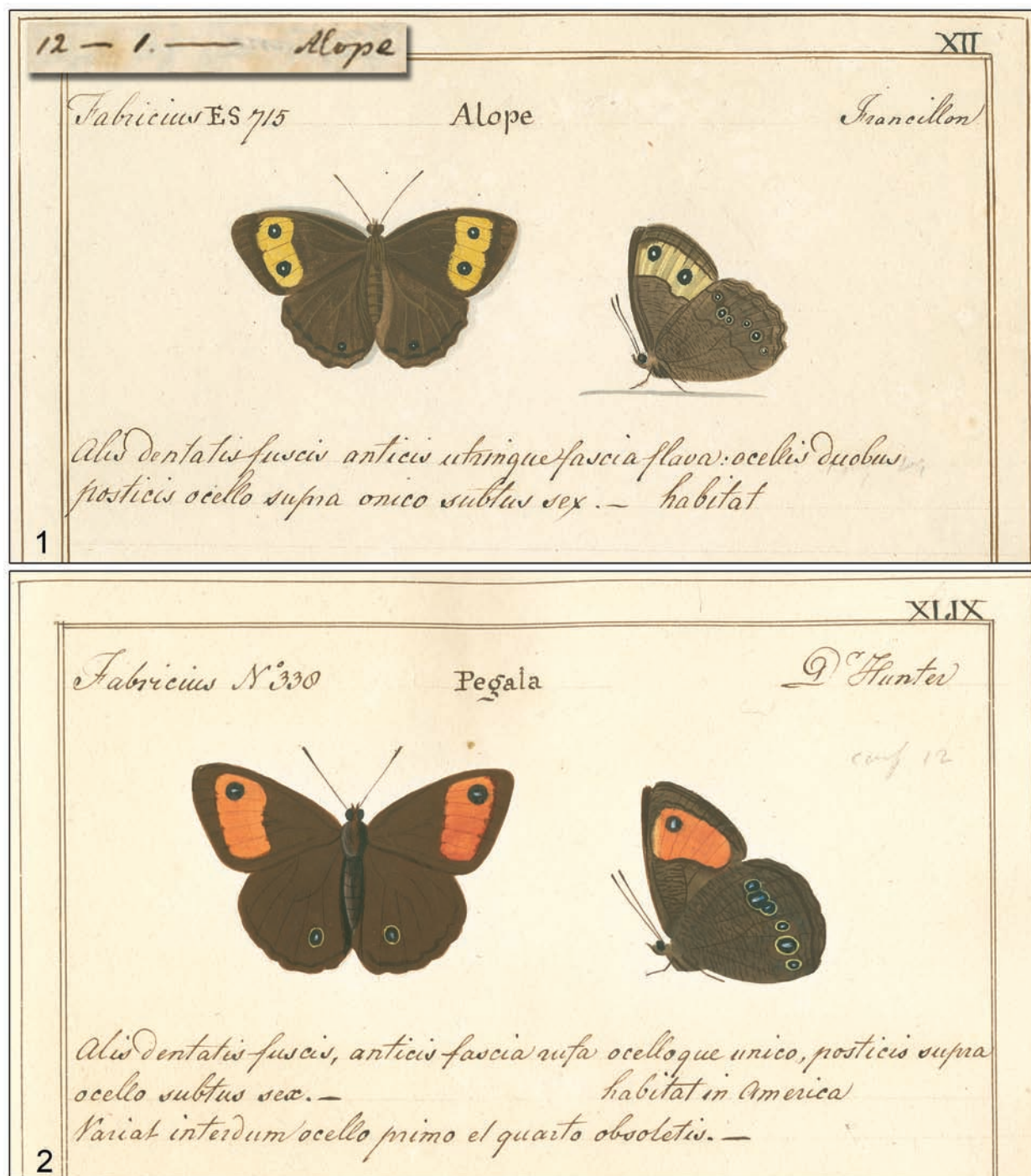
FIGS. 1, 2. Figures from "Jones' Icones." **1**, "*Alope*," consulted by J. C. Fabricius to describe *Papilio alope*. Inset is Fabricius' hand-written identification of the figures (enhanced). **2**, "*Pegala*," possibly depicting the lectotype of *Papilio pegala*. (images © Oxford University Museum of Natural History).

This suggests that Fabricius' description of *Papilio alope* was derived entirely from Jones' figures, not a physical specimen in Francillon's collection. James E. Smith, a friend of Jones, confirmed that many of Jones' drawings were "themselves the original authority for many of Professor Fabricius's recently published *Papiliones*, which were actually described from thence alone" (Smith & Abbot 1797). Smith was alluding to the publication of *Entomologia Systematica*, which had appeared four years earlier and included the description of *P. alope*. In a separate handwritten list, preserved with the third volume of "Jones' Icones," Fabricius identified the figures on Plate 12 as "*Alope*" (Fig. 1, inset), thus confirming that he personally consulted this illustration. Because there is no clear indication that Fabricius visited Jones more than once, he presumably conceived the name *alope* in 1787, six years before publishing its description. Fabricius did not include the name *pegala* on his list because Jones had already identified that illustration based on Fabricius (1781). This implies that Fabricius agreed with Jones' determination, reinforcing the concept of nominotypical *pegala* as we recognize it today.

Brown's analysis. In his original description, Fabricius (1775) attributed the type material of *P. pegala* to "Dr. Hunter." While studying nomenclatural aspects of *Cercyonis*, the American lepidopterist F. Martin Brown wrote to Ella Zimsen, the former Conservator of Insects at the Zoologisk Museum in Copenhagen, who had just published a treatise on Fabrician types. In early 1965, Zimsen informed Brown about the existence of two specimens identified as *Papilio pegala* at the University of Glasgow, which were from the collection of "Mr. Hunter." Brown was unaware that Kerr (1910) had previously listed these specimens as the types of *P. pegala*. Brown obtained photographs of the specimens and designated one of them as the lectotype of *P. pegala* (Brown [1966a]) (Fig. 5). Deposited at HMUG, these specimens are accompanied by a large cabinet label which identifies them as "*Pap. Pegala*" (Fig. 5, inset). This label includes the citation "Fabr. pag 76 Nº 338," referring to the entry for *pegala* in Fabricius (1781), rather than the original description in Fabricius (1775). This is not unusual, as the cabinet labels for all the butterflies in Hunter's collection cite entries in Fabricius (1781), regardless if they were described previously. They were prepared between 1783 and 1785 by Hunter's nephew, Matthew H. Baillie (Hancock et al. 2015).

Brown ([1966a]) associated "Dr. Hunter" with the celebrated Scottish surgeon and comparative anatomist John Hunter (1728–1793). Brown also claimed that Hunter had visited America during the 1750s while serving in the British Navy. Because Charleston, South Carolina, served as an important British port during the mid-eighteenth century, and the lectotype of *P. pegala* resembles butterflies from that area, Brown ([1966a]) concluded that the appropriate type locality of *P. pegala* is "the vicinity of Charleston, South Carolina."

Unfortunately, Brown's ([1966a]) investigation of *P. pegala* is flawed for several reasons. Not only was John Hunter not in the British Navy (he served as a surgeon in the British Army), the "Dr. Hunter" cited by Fabricius (1775) was actually John's older brother, William Hunter (1718–1783). William was a prominent obstetrician and "Physician Extraordinary" to Queen Charlotte, the wife of King George III (Liston 2013, Hancock et al. 2015). He assembled large and diverse natural history collections, including over 7,600 insects, which were bequeathed to the University of Glasgow, where they were received in 1807 (Keppie 2010, Brown et al. 2011). Fabricius spent entire days curating William's insects during several visits to London between the years 1767 and 1787 (Armitage 1958, Hancock 2004, Hancock et al. 2015). Fabricius (1775) based many descriptions on William's specimens (Kerr 1910, Zimsen 1964, Brock 1980, Douglas & Hancock 2007). Fabricius last visited William's collection in 1782, just months before William's death. *Species Insectorum* (Fabricius 1781) was then the standard of reference, explaining why Matthew Baillie subsequently cited only this publication on William's labels, presumably following Fabricius' suggested identifications.

In addition to his misidentification of "Dr. Hunter," Brown was also mistaken about Hunter's presence in America. In truth, neither of the Hunter brothers ever visited America (Simmins 1783, Bynum & Porter 1985, Keppie 2010). The central premise for Brown's suggested type locality of *P. pegala* is therefore invalid.

Brown's ([1966a]) study of *P. alope* is equally problematic. He reviewed the original description and concluded that it was consistent with "the characteristic form [of *C. pegala*] from the North Atlantic states." Ignoring this observation, he ultimately argued that the description of *P. alope* was likely based upon specimens collected by the English naturalist John Abbot (1751–c.1840), who lived in Georgia from 1776 until his death. It is widely known that John Francillon, who owned the specimen of *alope* portrayed by Jones, received many butterflies from Abbot. Brown therefore suggested a type locality for *P. alope* of "Burke-Screven-Bulloch counties region of Georgia," where Abbot is known to have lived. Miller and Brown (1981) later restricted this to "Screven County, Georgia," presumably at the insistence of Brown, who was primarily responsible for the arrangement of *Cercyonis*

in that publication (see Sourakov 1995). The Georgia type localities for *P. alope* are all the more surprising given that they are situated within the southeastern coastal plain, relatively near Brown's ([1966a]) proposed type locality for *P. pegala*. This action was perhaps Brown's way of reinforcing his opinion about the status of these taxa. In a 1963 letter, Brown wrote, "I tend to think of *pegala* as a species distinct from *alope*" (Knudson & Post 1963). His placement of these type localities in such close proximity was possibly intended to encourage this treatment. Brown apparently changed his mind, however, as Miller and Brown (1981, 1983) listed *alope* as a subspecies of *pegala*, just as dos Passos (1964) had done. The connection of *P. alope* to John Abbot is often cited as an example of the scientific significance of Abbot's work (e.g. Rogers-Price 1983). Regrettably, this correlation is unfounded, as Abbot's involvement is not supported by available evidence.

John Abbot's illustrations and specimens. Based on my previous studies of John Abbot's contributions, I realized that his illustrations and specimens of *C. pegala* did not agree with *P. alope* as portrayed in "Jones' Icones." An accomplished artist, Abbot illustrated *C. pegala* at least eleven times, even incorporating a female into an ornithological watercolor (Fig. 3, inset). I have examined all these renderings, including two duplicate compositions preserved at the Alexander Turnbull Library, Wellington, New Zealand (Calhoun 2007a) (Fig. 3) and the Hargrett Rare Book and Manuscript Library, University of Georgia (Calhoun 2007b). A portion of yet another duplicate of this composition was used to portray the hostplant and early stages of "*Satyrus Alope*" on Plate 59 in Boisduval and Le Conte (1829–[1837]) (Fig. 4). To accommodate the smaller size of that published plate, the engraver rearranged Abbot's figures of the larva and pupa, and also modified the leaves of the hostplant. Although Abbot's original drawing for this plate is missing, his accompanying notes are deposited at the Houghton Library, Harvard University. The entry for this drawing reads, "Great Meadow brown Butterfly. Feeds on the grass figured, and other grasses. Tyed up 19th June changed 20th bred 5th July. Frequents the pine woods etc. is not common" (Calhoun 2004). This is nearly identical to the notes that Abbot wrote to accompany his two other duplicate drawings (Calhoun 2007a, 2007b). These three drawings were completed between 1816 and 1825.

The specimens figured by Boisduval and Le Conte (1829–[1837]), as well as those portrayed in Abbot's two duplicate compositions, represent the southeastern coastal plain phenotype of *C. pegala*. Strecker (1878) was the first to correctly associate these figures with Fabricius' concept of *pegala*, followed by Edwards

(1880). All the males of *C. pegala* in Abbot's drawings lack the lower eyespot on the forewing (Fig. 3). Although this is a variable trait, a large percentage of southeastern males lack this eyespot, including the lectotype and paralectotype of *Papilio pegala* at HMUG (Fig. 5).

None of Abbot's addtional illustrations of *C. pegala* include early stages or hostplants, and only one other is accompanied by written notes. Abbot's earliest known illustration of this species is included in a series of drawings that were completed c. 1790–1805 for John Francillon. These and many other natural history illustrations by Abbot are preserved at the Natural History Museum, London (BMNH). Accompanying a rendering of a large female *C. pegala* is the caption "Female, the Male has one spot or Eye in the upper wing. Taken in Oak Woods and the Pine Woods near Savannah River, the Male was taken 25th June, the Female which don't come out till after the Males, was taken 12th July, not common." These observations were transcribed by Francillon from Abbot's handwritten notes, which were apparently discarded. Abbot collected insects in Georgia along the Savannah River from Burke County (where he lived when this particular drawing was rendered), southeastward to Chatham County. Due to his lack of familiarity with southeastern *C. pegala*, Brown (1969) associated these coastal populations with sedge marsh habitats. Abbot actually collected these butterflies in upland oak and pine woods, which is the typical habitat of this butterfly in the region.

I examined eight museum specimens of *C. pegala* that were collected during the twentieth century in and around Screven County, Georgia: five males and one female from Screven County (MGCL and UANH) (Fig. 14); one female from Bullock County (also included within the type locality suggested by Brown [1966a]) (UANH); and a male from nearby Emanuel County (MGCL). A female from Screven County was also figured by Ehrlich and Ehrlich (1961, fig. 160). Like Abbot's illustrations, all of these specimens represent the large southeastern coastal phenotype. None resemble the figures in "Jones' Icones," which were consulted by Fabricius for his description of *P. alope* (Fig. 1). This agrees with previous authors (e.g. Richards 1931), who ascribed specimens from that portion of Georgia to the coastal phenotype. Although this evidence is extremely persuasive, it is also important to consider specimens that were likely collected by Abbot.

A close examination of the figures of "*Alope*" on Plate 59 in Boisduval and Le Conte (1829–[1837]) reveals that the wing veins are more accurate than those in Abbot's duplicate compositions, and the eyespot configurations
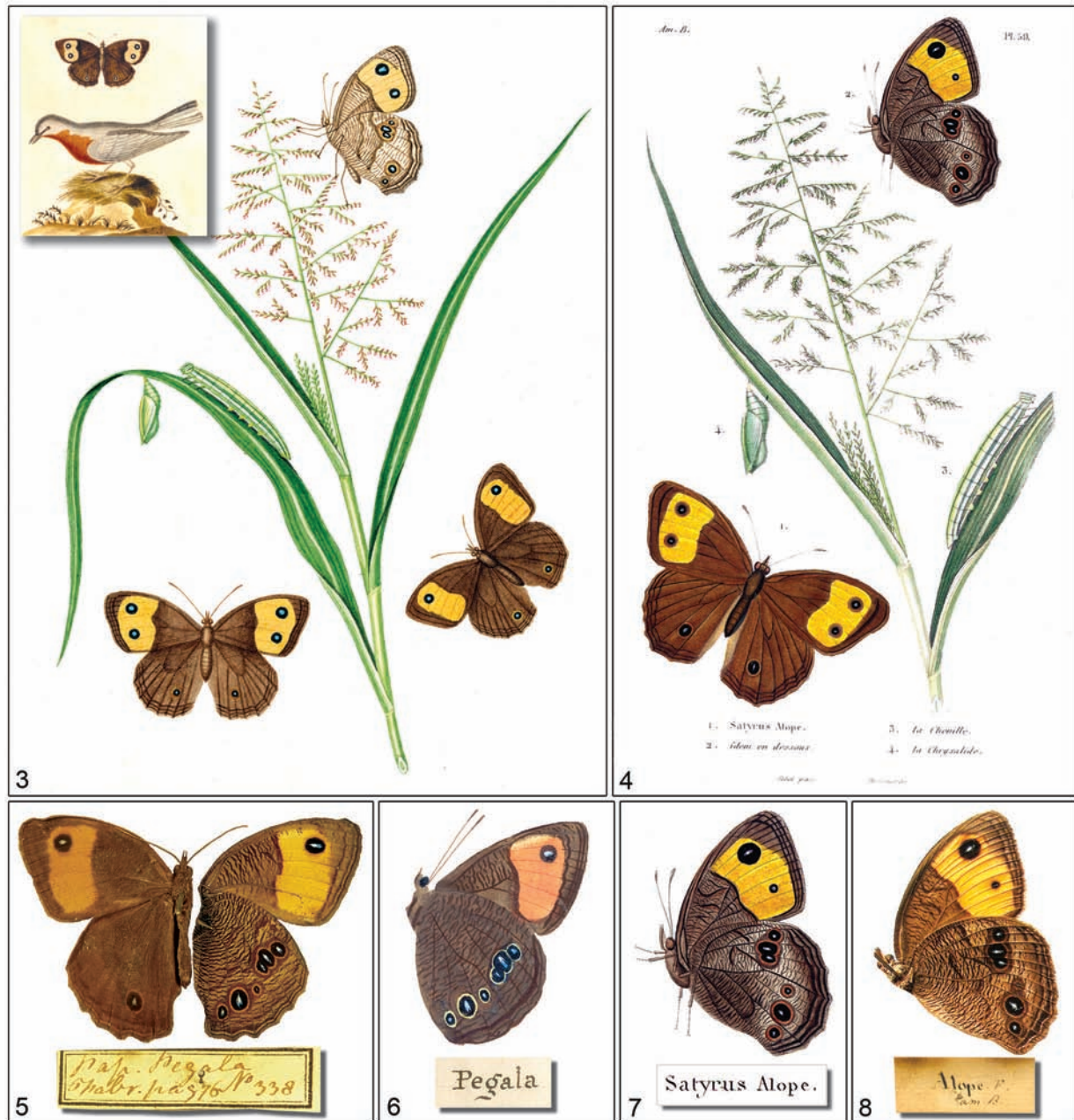
Figs. 3–8. Illustrations and specimens of C. *P. pegala*. **3**, J. Abbot drawing, ca. 1816–1818 (Alexander Turnbull Library). Inset is drawing of "Blue Warbler" by Abbot, including a female *C. pegala*, ca. 1825 (private collection). **4**, Plate 59 of "*Satyrus alope*" in Boisduval & Le Conte (1829–[1837]). **5**, male lecotype of *Papilio pegala* (dorsal/ventral) (HMUG), with Baillie's cabinet label. **6**, ventral figure of "*Pegala*" from Pl. 49 of "Jones' Icones," possibly depicting the lectotype, with the name as written by Jones. **7**, ventral figure in Boisduval & Le Conte (1829–[1837]), with the name as published. **8**, male, probably ex J. Abbot, used as the model for the ventral figure in Boisduval & Le Conte (1829–[1837]) (USNM), with Boisduval's cabinet label.

differ. Many of Boisduval's specimens are now deposited at USNM (Calhoun 2004, 2006b). Among them are three specimens of *C. pegala*, two males and one female. The female (Fig. 9), and a male with a greatly reduced lower eyespot on the forewing (Fig. 8), doubtless served as models for the adult figures on the published plate. The dark striations on the ventral wings of the male, like a fingerprint in this species, are equivalent (Figs. 7, 8). The ventral pattern is unlike that of Abbot's illustrations, which include fewer eyespots on the hindwing and a larger lower eyespot on the forewing (Fig. 3). Labels associated with these two specimens of *C. pegala* at USNM indicate that they were identified in Boisduval's collection as "*Alope*" (Fig. 8, inset). The remaining male from Boisduval's collection, with a single eyespot on the forewing (Fig. 10), was identified as "*Pegala*," reflecting his opinion that *pegala* represents a form of *alope* with a single forewing eyespot (Boisduval & Le Conte 1829–[1837]). All three of these specimens were almost certainly collected by Abbot. In preparation for their book, J. E. Le Conte visited Boisduval in Paris in 1825, bringing with him a large number of Abbot's butterfly specimens and drawings (Calhoun 2006a).

The American entomologist Thaddeus W. Harris (1795–1856) received many insects from Abbot. Harris' collection, which is deposited at MCZ, contains six specimens of *C. pegala*. His accompanying handwritten collection catalog (also at MCZ) records that he received four "*Hipparchia Alope*" from Georgia: two from Abbot and two from Abbot's friend, Augustus G. Oemler (1770–1854). One large male *C. pegala* in Harris' collection, without lower eyespots on the forewings, is labeled "Georg^{a}" in Harris' hand (Fig. 11). A female is labeled "Geo" in Harris' hand. These specimens, representing southeastern coastal *C. pegala*, were possibly received from Abbot. Harris' letters (MCZ) imply that he received Abbot's specimens between 1834 and 1836, when Abbot was residing in Bulloch County, Georgia. Another large, unlabeled southeastern male *C. pegala* in the collection, surely from Georgia, bears very small lower eyespots on the forewings. The fourth specimen from Georgia is missing. The three remaining specimens of *C. pegala* in Harris' collection (two females and one male) were apparently collected in Massachusetts and are consistent with phenotypes from that area. Beyond the four Georgia specimens, Harris' collection catalogue lists several from Massachusetts, but none from any other localities. Among Harris' other documents at MCZ is a handwritten manuscript entitled "North American Diurnal Lepidoptera in the Cabinet of T.W.H. 1837." Like his collection catalog, it also lists "*Alope*" only from Massachusetts and Georgia. At no time did Harris refer to any specimens by the name *pegala*, which is consistent with the usage of that era.

In the collection of the Linnean Society of London (LSL) are two old specimens of *C. pegala*, male and female. They were received by the Society in 1829 from James E. Smith, who in 1784 purchased the prized collection of Carl Linnaeus (Carl von Linné) (Gage & Stearn 1988, Fitton & Harman 2007). Smith published a series of Abbot's watercolors in the magnificent work *The Natural History of the Rarer Lepidopterous Insects of Georgia* (Smith & Abbot 1797). Based on their labels, the two *C. pegala* at LSL are from Smith's personal collection. The male, labeled "Georgia" (Fig. 12), was received from another English botanist, Sir William J. Hooker (1785–1865), from whom Smith obtained a large number of insects, including over 20 butterflies labeled "Georgia" (Fig. 12, inset). Several of these butterflies are dated 1806, which is probably when Smith acquired them. The female *C. pegala* from Smith's collection lacks locality data and was received from the amateur horticulturalist Mary Watson-Wentworth, Marchioness of Rockingham (1735–1804), who met Smith during the 1780s and remained his good friend until her death (Smith 1832). Both specimens of *C. pegala* at LSL are consistent with the southeastern coastal phenotype and were likely collected by Abbot, whose insects circulated widely among English naturalists of the period. Other specimens of Lepidoptera at LSL are labeled "Georgia - Abbot" in Smith's handwriting. All such specimens were probably acquired via John Francillon.

John Francillon served as Abbot's agent by selling his drawings and specimens to other naturalists in Europe. After his death, Francillon's collection was auctioned in two segments. The catalogs for these auctions (King 1817, 1818) list at least seven specimens of "*Alope*," but only one entry includes a locality: "Georgia." Numerous other unidentified Lepidoptera specimens were listed from "America" without specific localities. About 1200 of Francillon's specimens were purchased by the English naturalist Alexander Macleay (1767–1848), who moved to Australia in 1825 (Holland 1988, Stacey & Hay 2007). Macleay's collection serves as the core of the Macleay Museum (MAMU). A number of North American insects at MAMU are labeled "Georgia," and all were probably collected by Abbot. Within this collection are seven specimens of *C. pegala* from eastern North America: five males and two females. One male bears a dubious label reading "Boston New Engl." All represent the large phenotype found in coastal Georgia. One male lacks a lower eyespot on the forewing like those in Abbot's illustrations (Fig. 13), whereas others have reduced lower eyespots. It is

conceivable that all of these specimens were collected by Abbot, including the male labeled "Boston New Engl."

Alexander Macleay's son, William S. Macleay (1792–1865), also collected insects. On his return to London from Cuba in early 1836, William visited Philadelphia and arranged to acquire quantities of American specimens via exchange (Holland 1988, Horning 1988). While in Philadelphia he met the esteemed naturalists Titian R. Peale (1799–1885) and Charles Pickering (1805–1878) (Macleay 1838). Pickering was a close friend of the Massachusetts entomologist T. W. Harris. Probably at the urging of Pickering, Macleay wrote to Harris on 4 June 1836 asking if he was interested in exchanging insects. Harris responded on 16 June that he was pleased to offer Macleay whatever interesting insects he considered "most singular" or "least common or unknown in Europe" (Harris correspondence, MCZ). With this letter Harris sent 156 specimens of various insect orders, but no Lepidoptera. Although this shipment did not include butterflies, it demonstrates that Harris was acquainted with Macleay and they exchanged specimens. The specimen labeled "Boston N. Engl." may be the missing Georgia specimen of *C. pegala* from Harris' collection. Because Harris' specimens typically lack data, Macleay possibly assumed it was collected in the Boston area, or simply cited the city from which it was received. William immigrated to Australia in 1839, taking with him "what he may have collected or obtained by exchange or gift in Cuba, or at Philadelphia and the other ports of call on the outward and homeward voyages; and what he may have acquired in England, after his return, by exchange or otherwise" (Fletcher 1920). In 1848, William inherited his father's insect collection. Upon William's own death, the joint collection of 480 cabinet drawers was bequeathed to his cousin, Sir William J. Macleay (1820–1891), who added additional material. Sir William donated the entire collection, contained in 936 drawers, to the University of Sydney, where it was transferred into the newly constructed Macleay Museum in 1888.

Abbot also sent insects to the English artist and natural history dealer Thomas Martyn (fl.1760–1816), who was one of Abbot's benefactors when he emigrated to America. From 1797 until about 1802, Martyn issued parts of a book of illustrations under the title *Psyche, Figures of Non descript Lepidopterous Insects* (Martyn 1797–[c. 1802]). Included among the life-sized figures in this book are specimens from "New Georgia," which were undoubtedly collected by Abbot. Portrayed on Plate 23 is a female identified as "*Papilio Macularia*" from "Brazils" (Fig. 15). The origin of this specimen was apparently forgotten and Martyn believed it was from tropical America. Again, Abbot is the most likely source of this specimen, which represents the same phenotype found in coastal Georgia.

From 1776 to 1840, John Abbot lived in Bulloch, Burke, Chatham, and Screven Counties of Georgia. For nearly 50 years he collected butterflies extensively throughout the region, but there is no evidence that he ever encountered any *C. pegala* like that figured as "*Alope*" by Jones. The Georgia type localities suggested by Brown ([1966a]) and Miller and Brown (1981) are therefore untenable. When the Georgia type localities are rejected, and Jones' figures are considered, it becomes obvious that the concept of *Papilio alope* applies to a phenotype of *C. pegala* that occurs in the northeastern United States.

Discussion

The type locality of *Papilio pegala*. The type localities of *Papilio pegala* as suggested by Brown ([1966a]) and Miller and Brown (1981) cannot be accepted on the principle that the type specimens were personally collected by John Hunter in the vicinity of Charleston, South Carolina. However, this type locality can be retained if we consider a more likely source: Alexander Garden (1730–1791). Garden was a Scottish physician and naturalist who lived in Charleston from 1752 to 1783, when the city was known as Charles Town. Although he was most interested in botany, Garden was a prominent naturalist who collected a wide variety of natural history specimens, many of which he sent back to Europe (Berkeley & Berkeley 1969). A proponent of the Linnaean classification system, Garden provided numerous specimens, including insects, to Linnaeus for description (Finger 2010). He maintained an active correspondence with the London merchant and naturalist John Ellis (c.1710–1776), who, as a Fellow of the Royal Society of London, was among the natural history elite of that city and received many of Garden's shipments (Sanders & Anderson 1999). Linnaeus referred to Ellis as "the main support of natural history in England" (Stearn 1981). Among the shipments to Ellis were butterflies, as Garden indicated in a letter dated 25 March 1755: "I have sent you some butterflies. . . If these will be agreeable, I can send you any number of them . . ." (Smith 1821). Zoological specimens from Garden are preserved at LSL (Jackson 1913), including some Lepidoptera labeled "Carolina." Garden's insects were also introduced to London collections through other contacts, such as Henry Baker (1698–1774), another Fellow of the Royal Society who received natural history specimens from Garden from the 1750s to the 1770s (Berkeley & Berkeley 1969). From these
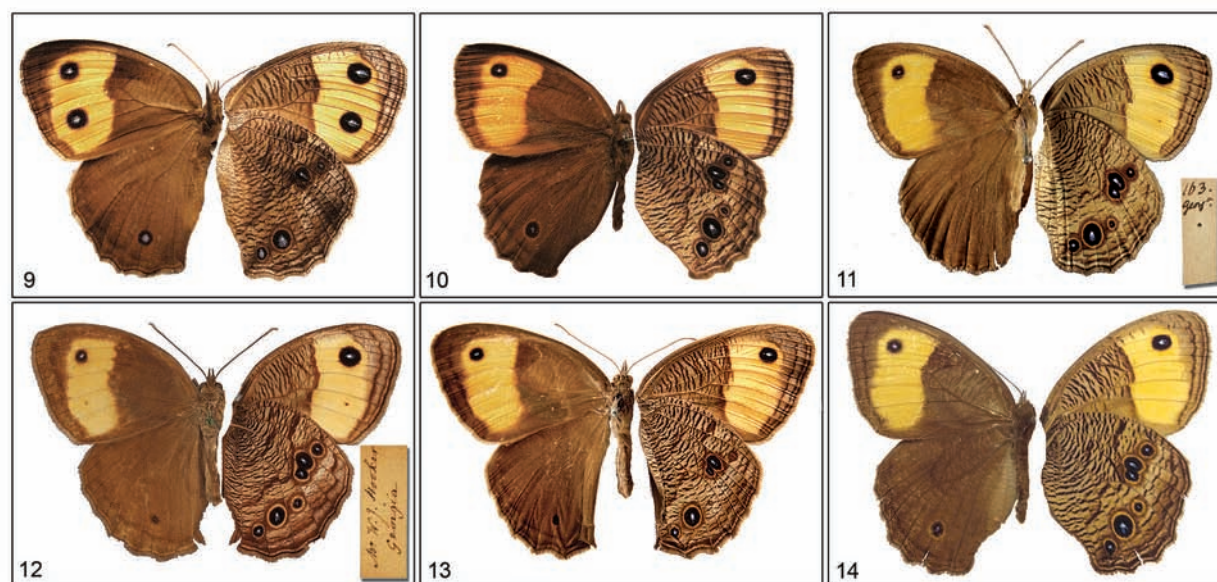
Figs. 9–14. *Cercyonis p. pegala* (dorsal/ventral) likely ex. John Abbot, with a more recent specimen from Georgia. **9**, female, [pre-1825], used as the model for the dorsal figure in Boisduval & Le Conte (1829–[1837]) (USNM). **10**, male, [pre-1825] (USNM). **11**, male, [c. 1834–1836], "Georga" (MCZ-ENT213251), with original label. **12**, male, [c. 1806], "Georgia" (LSL), with original label (cropped). **13**, male, [pre-1817], (MAMU). **14**, male, 9.vii.1946, Screven Co., GA, Leg. A. K. Wyatt (UANH).

primary recipients, Garden's specimens were evidently dispersed to additional naturalists. A worn female *Antheraea polyphemus* (Cramer) at LSL bears J. E. Smith's label attributing it to "South Carolina, Dr. Garden." Like Baker and the Hunter brothers, Garden was a Fellow of the Royal Society. John Hunter examined an electric eel and other specimens that Garden sent to London (Finger 2010). In a letter to Ellis, written in 1768, Garden referred to John Hunter: "If you could introduce my brother to Mr. Hunter, it would be a great favour done him, and it might give rise to an acquaintance between them" (Smith 1821). Garden was clearly familiar with the Hunters and was undoubtedly aware of William's collections. Garden returned to England in 1783, when he was expelled from South Carolina for being a British sympathizer during the American Revolution.

During the mid-eighteenth century there were very few collectors in southeastern North America who sent butterflies to England. John Abbot arrived in America in 1773, but he first lived in eastern Virginia, where *C. pegala* somewhat differs from the types of *P. pegala* (see below). Although the types of *P. pegala* agree with populations of this species in coastal Georgia, Abbot did not move there until 1776, the year after this taxon was described. Although William Hunter received numerous American insects from some of his former

medical students who visited there (Keppie 2010, Hancock et al. 2015), Alexander Garden is a plausible source of the *P. pegala* types, which are consistent with the phenotype of *C. pegala* found in the Charleston area (see below).

The shifting concept of *Papilio alope*. Holland (1915) defined the range of *Satyrus alope* as "Atlantic seaboard from New Jersey to New Hampshire, and westward to the Mississippi." Macy and Shepard (1941) gave the northern limits of *Minois alope* as "southern New England westward to the Middle West." Klots (1951) stated that the subspecies *C. p. alope* is found from "Virginia (mountains) and New Jersey n. to Maine and Quebec (coastal plain) and New York (inland)." These authors identified populations within the southeastern coastal plain and Piedmont as a separate form or subspecies named *pegala*. Due to a poor understanding of eastern *C. pegala*, and the omission of Jones' figures from evidence, Brown ([1966a]) and Miller and Brown (1981) proposed Georgia type localities for *P. alope* based exclusively on the relationship between John Abbot and John Francillon. Screven County, Georgia, is located only about 137 km (85 mi) west of the proposed type locality of *P. pegala* and within the same physiographic region (southeastern coastal plain). The proposed Georgia type localities for *P. alope* encouraged a shift in the long-held concept of

this taxon, from populations in the northeastern United States to those in the southeastern coastal plain, where nominotypical *pegala* also occurs.

Based on Brown's ([1966a]) conclusions, Harris (1972) identified populations within the upper coastal plain and Piedmont of Georgia as the subspecies *C. p. alope*. Gatrelle (1985, 1992) also accepted the Georgia type locality and considered typical *alope* to represent populations that are intermediate between the southeastern coastal phenotype (i.e. *C. p. pegala*) and those of the southern Appalachians, which he identified as the subspecies *C. p. carolina* F. Chermock & R. Chermock. The name *carolina* is often used to identify pale-patched phenotypes that occur sporadically within the southern Appalachian Mountains and Piedmont. Although Klots (1951) popularized the notion of *carolina* as a weak subspecies of *C. pegala*, all subsequent North American checklists and catalogs (e.g. dos Passos 1964, Miller & Brown 1981, 1983, Pelham 2008, 2014) listed *carolina* as a form or synonym of the subspecies *C. p. alope* (for more on the status of *carolina* see Distributional Analysis, below).

Because of its Georgia type locality, Gatrelle (1985) believed that the name *alope* would have to be "dropped into the synonymy of *pegala*" and that the name *carolina* would then be used to represent the "eastern 'yellow' subspecies of *pegala*." Gatrelle (2004) later wrote, "*Alope* does not exist as a taxon—it is described from the edge of the range of nominate *pegala* . . . So, *alope* is not a valid 'subspecies' and thus does not occur anywhere as such." This opinion persuaded Scott (2008a) to identify all patched populations in the northeastern United States as the subspecies *C. p. maritima* (W. H. Edwards), explaining, "R. Gartrelle found that topotypical *alope* is a syn. of ssp. *pegala* (in the blend zone *pegala×carolina*), thus *maritima* replaces the usual usage of *alope*." Scott (2008b) omitted the subspecies *C. p. alope* and instead listed only *C. p. maritima*, maintaining that the name *alope* applies to "a form in blend zone of *pegala-carolina*, according to Ronald Gatrelle." Following this scheme, *alope* was recently defined as "an essentially highly variable southern Piedmont group of populations" (Arey & Grkovich 2014). In spite of this approach—instigated by Brown ([1966a])—most authors associated the name *alope* with patched populations in the northeast, as either a form or a subspecies (e.g. Fales 1974, Shapiro 1974, Shull 1987, Iftner et al. 1992, Nielsen 1999, Webster & DeMaynadier 2005, Belth 2013).

The type locality of *Papilio alope*. During the eighteenth century, European naturalists sustained a network of contacts in foreign lands from which they received countless specimens. As expected, most insects

from America were obtained from collectors who visited or resided in states located immediately along the Atlantic seaboard. To determine a more appropriate type locality for *Papilio alope*, I compared Jones' figures with thousands of specimens of *C. pegala*, mostly at MGCL. Concentrating on coastal material from central Florida northward to southern Maine, it was immediately apparent that these populations are extremely clinal in nature, with size and pattern complexity decreasing northward. Individual butterflies within any given area also vary in size, coloration, and pattern. Regardless of this variability, populations exhibit morphological trends that are helpful in determining the most likely geographical origin of the male figured by Jones. As observed by Remington (1985), females of *C. pegala* are extremely variable across the species' range, while males are more geographically diagnostic. The measurements below denote approximate male forewing lengths, base to apex.

In Florida, adults are medium brown and large (32 mm) (Fig. 36, bottom center). The forewing of the male is rather pointed. Both sexes have a broad postdiscal forewing patch, which varies in color from cream (rarely) to reddish-orange (usually paler in females). Males have one eyespot on the forewing, though the presence of two full eyespots or a diminished lower spot is not uncommon. Females usually possess two eyespots, though many bear only one. The ventral wings are pale brownish-gray with a complex pattern of bold, dark transverse striations. The ventral hindwing ground color is often paler beyond the median, imparting a two-toned effect. The eyespots on the ventral hindwing are large and usually five or six in number; the three located towards the apex are typically oval and often conjoined. Populations in extreme northeastern Florida, southeastern Georgia, and southeastern South Carolina (including the type locality of *P. pegala*) are like those found farther south, but adults average slightly smaller in size (29 mm) (Figs. 5, 8, 9–15).

From northeastern South Carolina into coastal North Carolina and extreme southeastern Virginia, individuals are duskier brown and the ventral striations are less defined (Fig. 36, center, second from bottom). Males average somewhat smaller (27 mm) and the forewing is more rounded. Northward in this region, males more often possess two forewing eyespots. The eyespots on the ventral hindwing are smaller on average and usually more rounded. Klots (1951, Pl. 7, fig. 6) figured a male from Currituck Co., North Carolina, to represent the nominotypical subspecies.

Populations in the vicinity of Baltimore, Maryland, eastward to Delaware and southern New Jersey, express
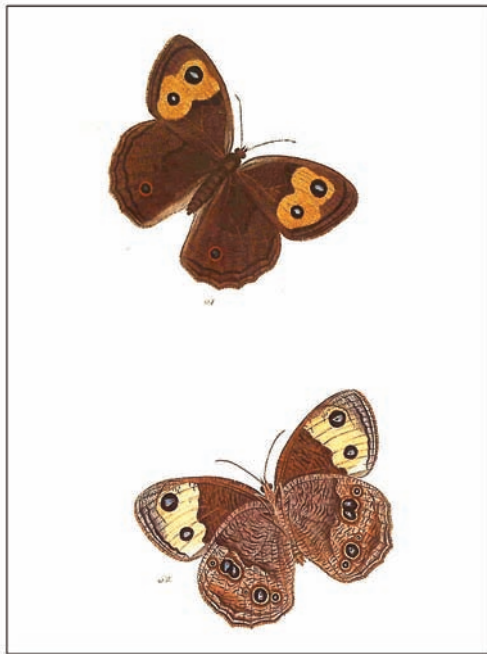
Fig. 15. Illustration of *"Papilio Macularia"* from Martyn (1797–[c.1802]), portraying a female *C. p. pegala*, probably ex J. Abbot.

a wide range of variation in overall size and eyespot development. Although most males have two forewing eyespots, occasional individuals possess a single forewing eyespot or a greatly reduced lower eyespot (Fig. 36, middle center). The color of the forewing patch varies from ochre-yellow to orange. This geographical area lies at the narrow eastern edge of a significant blend zone, where populations transition to smaller, less well-marked phenotypes. These populations are the basis of reports of southeastern phenotypes (i.e. *C. p. pegala*) occurring as far north as Maryland and New Jersey (e.g. Edwards 1880, Smith 1884, 1890, Muller 1968, Simmons & Andersen 1971). Figures of a specimen from southern New Jersey in Edwards (1890, Pl. *Satyrus* I, figs. 6, 7) mislead Brown (1969) into believing (erroneously) that these populations represent the same phenotype of *C. pegala* that occurs at the type locality of Charleston, South Carolina, prompting him to describe the subspecies *C. p. abbottii* to differentiate populations in southern Georgia and northern Florida.

From southeastern Pennsylvania and northern New Jersey, northward into southeastern Maine, occur variable populations of smaller (25 mm), darker adults (Fig. 36, center, second from top). The eyespots on the ventral hindwing are reduced and they are often entirely lacking in females. The forewing patch varies from yellow to dark orange. Males typically have two eyespots

on the forewing, but they sometimes possess a reduced lower eyespot, especially southward. Towards the north/northwest, populations show the effects of introgression from patchless phenotypes, resulting in individuals with absent or greatly diminished forewing patches (e.g. Figs. 20; 36, top center). Patchless northeastern phenotypes are often identified as the subspecies *C. p. nephele* (W. Kirby).

Although butterflies associated with the name *alope* are nearly always described in the literature as having a "yellow" forewing patch, this diagnosis overlooks a wide range of variation. Harris (1862) described the patch as "ochre-yellow." Scudder (1888–1889) characterized the patches of males as "pale dull orange" and Weed (1917) referred to the patch as "yellowish brown." Klots (1951) called the patch "orange" and "yellow orange," while Allen (1997) said it ranged from "yellow to orange." Color illustrations of butterflies identified as *alope* in popular books portray decidedly orange-hued patches (Maynard 1886, Scudder 1888–1889, Holland 1898, 1915, 1931, Comstock & Comstock 1904, Klots 1951, Howe 1975). My analysis revealed that the majority of patched males in eastern North America exhibit some degree of orange coloration, ranging from ochre-yellow to dark pumpkin. The patches of females can be considerably paler, sometimes nearly white, even within populations that produce richly-hued males.

Originally intended to distinguish dark, diminutive butterflies with "reddish-yellow" forewing patches, *Satyrus alope* var. *maritima* W. H. Edwards was described from specimens collected on the islands of Martha's Vineyard (Dukes Co.) and Nantucket (Nantucket Co.), Massachusetts (Edwards 1880). However, *maritima* has since become a confusing and nebulous concept that lacks a consistent definition. Some authors (e.g. Maynard 1891, Forbes 1960, Shapiro 1966, 1974) claimed that the forewing patch of *maritima* is more poorly defined than in *alope*. Conversely, Holland (1931), who was familiar with the type series of *maritima* from the collection of W. H. Edwards, described the forewing patch of these populations as "bright and sharply defined." While Klots (1951) considered lowland coastal populations from Maryland to Maine to represent the subspecies *C. p. maritima*, some authors (e.g. Brimley 1938) applied the name to montane Appalachian butterflies. Clark and Clark (1951) observed that the first adults of *C. pegala* to emerge in the Piedmont of Virginia resembled *maritima*, while later adults resembled *alope*. Contrary to most accounts, Arey and Grkovich (2014) assigned coastal populations to *C. P. alope* and more inland populations to *C. p. maritima*, which they believed to range "west along the northern limits of the lighter

(yellowish) eye-patched southeastern populations of *C. pegala* at least to western Pennsylvania . . . also into Ohio and southern Michigan and perhaps as far west as Illinois." Arey and Grkovich (2014) also remarked that populations of *C. P. alope* and *C. p. maritima* appear to be "rather poorly differentiated" in southern and central New England. Like Edwards (1880), most authors considered *maritima* to be a form of *alope*, including Jones and Kimball (1943), who collected specimens on Martha's Vineyard and Nantucket. Klots (1951) was the first to treat *maritima* as a subspecies, but most subsequent authors (e.g. dos Passos 1964, Emmel 1969, Miller & Brown 1981, Pelham 2008, 2014) listed it as a synonym of either *C. p. pegala* or *C. p. alope*. Although *maritima* is supposedly distinguished from *alope* by a more richly colored forewing patch, the interpretation of this trait is extremely subjective and inconsistently applied. Even Edwards' (1880) interpretation of the patch color in the original description of *maritima* was somewhat exaggerated.

I examined ten male specimens of *C. pegala* from Martha's Vineyard, Massachusetts, including images of the lectotype (Figs. 18, 35a) and four paralectotypes of *S. a.* var. *maritima* from Edwards' collection at CMNH. One of the paralectotypes likely served as the model for the specimen figured by Edwards (1882, Pl. *Satyrus* II, figs. 6) (Fig. 17). Although Edwards (1880) described the forewing patches of *maritima* as "reddish-yellow," the patches of all the specimens examined from the type locality are yellow-orange, without any reddish hue. Holland (1898) fittingly described the patch of *maritima* as "orange-yellow." The patch color of more recent specimens of *maritima* from Martha's Vineyard figured by Arey and Grkovich (2014) are similarly colored.

It is fairly easy to understand why Edwards (1880) described *S. a.* var. *maritima.* Soon after publishing his description of *maritima*, Edwards (1882, Pl. *Satyrus* II, fig. 6) illustrated his concept of this taxon alongside a pair (male and female) with yellow patches (Pl. *Satyrus* II, figs. 1–4), which he identified as "*alope*" (Figs. 16, 17). In a letter to the Massachusetts entomologist Samuel H. Scudder, Edwards referred to his figures of *alope* as "typical" (5.iii.1881, Museum of Science, Boston, Massachusetts). He noted that the patches of *alope* were originally described as "*flava*" (yellow), thus he defined the forewing patch of *alope* as "pale yellow in both sexes" (Edwards 1880, 1882). Specimens of *C. pegala* from Edwards' collection at CMNH infer that his figured male *alope* (Fig. 16) most likely originated from the foothills around his home in Coalburgh, Kanawha County, West Virginia, where he rarely encountered this species (Edwards' Journal H, WVSA). The figured female *alope* is from Hunter, New York (Edwards 1882).

Edwards' experience with yellow-patched butterflies encouraged him to describe the orange-tinted (as "reddish-yellow") *maritima* as an island variety, not realizing that such phenotypes are frequent throughout the northeast. Shortly after the description of *maritima* was published, the Chicago lepidopterist Charles E. Worthington (1851–1926) informed Edwards that he had an example of *maritima* from Connecticut (Edwards' Journal I, WVSA). Afterward, Edwards supposed that *maritima* "must be fd [found] about the coast for a ways inland" (24.iii.1880, Scudder corresp., MCZ). The Massachusetts entomologist Samuel H. Scudder, who was more familiar with *C. pegala* in New England, never mentioned *maritima* in his own publications. Edwards was unaware that specimens from as far west as Indiana can closely agree with the type series of *maritima*.

Chermock and Chermock (1942) examined 32 specimens from Rhode Island and western Pennsylvania, which they described as having an "ochraceous replacement of the yellow in the patch of the limbal area of the primaries." They concluded that these specimens did not agree with the types of *maritima* at CMNH (Fig. 18), nor other specimens identified as *maritima* by W. H. Edwards. The Chermocks therefore described these specimens as "*Cercyonis alope ochracea* New Form," which they also called a subspecies in the same publication. The Code (ICZN 1999) dictates that the use of the term "form" prior to 1961 refers to a subspecific name unless "its author also expressly gave it infrasubspecific rank, or the content of the work unambiguously reveals that the name was proposed for an infrasubspecific entity." Pelham (2008, 2014) considered *ochracea* to be infrasubspecific, stating "The text clearly indicates that this taxon was described as an individual variant."

The butterfly collection of Franklin (Frank) H. Chermock (1906–1967) is deposited at MGCL (ex. Allyn Museum of Entomology 1980; see Miller 1983). The collection of his brother, Ralph L. Chermock (1917–1977) is deposited at UANH (Calhoun 2015). Within these two collections I located all but one of the 32 specimens from the type series of *C. a. ochracea*. Missing for decades, I found the holotype within R. H. Chermock's collection at UANH and it is herein figured for the first time (Fig. 19). It is a male from Washington Park, Rhode Island, dated 18 July 1935, with a red holotype label signed "F. H. & R. L. Chermock" (Fig. 35b). A paratype male at MGCL bears the same data, revealing that the collection year of 1933 reported by Chermock and Chermock (1942) is in error. Both of these specimens exhibit a full yellow-orange forewing patch, which agrees with the original description of

ochracea ("ochraceous replacement of the yellow in the patch of the limbal area of the primaries"). Despite the claim by Chermock and Chermock (1942) that specimens of *ochracea* do not agree with the types of *maritima*, the primary types of these taxa represent analogous phenotypes (Figs. 18, 19). The remaining paratypes of *ochracea* (23 males and six females) possess patches ranging from yellow to orange in color, which are suffused to varying degrees; in some cases the forewing patch is lacking and the eyespots are merely surrounded by yellow scales (Fig. 20). The original description mentioned such variants: "As in the normal *alope*, the amount of ochraceous varies from a large patch to a fairly small one" (Chermock & Chermock 1942). Only twenty of these darker paratypes bear locality labels and all are from counties in western Pennsylvania (Fig. 35c).

The great variation in the type series makes it extremely difficult to understand the Chermock's concept of *ochracea*. The Chermock's confusing taxonomic notions sometimes resulted in friction with other lepidopterists. The prominent writer and lepidopterist Vladimir Nabokov charged F. H. Chermock with creating subspecific names for "chance series and morphological intergrades," arguing that Chermock was merely interested in "giving names to things" (Boyd & Pyle 2000). Some of F. H. Chermock's concepts and descriptions are certainly debatable (Masters 1968). His brother, Ralph, had a special interest in Satyridae. As early as 1947, while still a graduate student at Cornell University, Ralph planned to publish an extensive study of the genus *Cercyonis* (Chermock 1947, Brown 1954). Although this project was never realized, Ralph was regarded as an "expert" on this group of butterflies (Mather 1952).

Although I do not agree with Pelham (2008, 2014) that the original description of *ochracea* unambiguously reveals infrasubspecific rank, the Chermock's use of the term "form" for *ochracea*, as opposed to "race" for *C. a. carolina* (which they described in the same publication), certainly suggests this intention. Unfortunately, the Chermocks seemingly employed the terms "form," "race," and "subspecies" interchangeably, thus it is probably best to defer to the Code and treat *ochracea* as a subspecific name. Scott (2008a) curiously characterized *ochracea* as "an infrasubspecific *pegala×carolina* intergrade." Emmel (1975) mistakenly cited the type locality of *ochracea* as "Ohio," which was reiterated by other authors (e.g. Hess 1977).

The subspecies *C. p. agawamensis* was recently described by Arey and Grkovich (2014) from a few coastal salt marshes and estuarine habitats in Massachusetts, New Hampshire, and Maine (TL Newbury, Massachusetts). In late 2014, Alex Grkovich generously donated to MGCL five males and two females identified as *agawamensis*, as well as one comparative female from Massachusetts identified as *C. p. maritima*. All seven of these *agawamensis* were collected on 5 August 2007 in Rockingham County, New Hampshire, where 17 paratypes of *agawamensis* originated (Arey & Grkovich 2014). Also, I had the opportunity on 23 July 2015 to visit the type locality of *C. p. agawamensis* in Essex Co., Massachusetts, where I observed numerous adults and vouchered specimens from the salt marshes and nearby upland habitats. On 31 July 2015, I located a previously undocumented population of *C. pegala* in a salt marsh in York Co., Maine, within the range of *agawamensis* as defined by Arey and Grkovich (2015).

In common with other northeastern populations of *C. pegala*, individuals from salt marsh habitats exhibit a great deal of variation in size, ground color, forewing patch coloration, patch size, and eyespot configuration (Figs. 21, 22). One New Hampshire male received from Grkovich has a greatly restricted orange forewing patch, similar to the male from Sagadahoc Co., Maine in Figure 36 (top center). Most males (Fig. 21) closely resemble the lectotype of *maritima* from Massachusetts (Fig. 18) and the holotype of *ochracea* from Rhode Island (Fig. 19).

The seven specimens identified as agawamensis from Grkovich, as well as the specimens that I collected in salt marshes in 2015, reveal inconsistencies in the published definition of *C. p. agawamensis*. Although the original description indicated that male *agawamensis* are "somewhat larger" and females are "significantly larger" than individuals identified as *C. p. maritima* (Arey & Grkovich 2014), the forewing lengths of the specimens that I examined are consistent with other northeastern *C. pegala*. For example, the two female *agawamensis* at MGCL measure 29 and 30 mm, while Grokovich's female "*maritima*" measures 29 mm. These dimensions agree with the specimens that I collected in Massachusetts and Maine. Arey and Grkovich (2014) also stated that the anal eyespot on the dorsal hindwing of female *agawamensis* is "always well-defined and circled in orange," whereas "*maritima* females typically lack this eyespot altogether." This eyespot, however, is absent on one of the two female *agawamensis* from Grkovich (Fig. 23), and is very poorly developed and not ringed with orange on the other. This spot is likewise very small and not ringed with orange on two females that I collected in salt marshes in Massachusetts and Maine. Conversely, the "*maritima*" female received from Grokovich, and a number of females that I collected in upland habitats in Massachusetts and

FIGS. 16–35. *Cercyonis pegala* phenotypes (dorsal/ventral unless otherwise indicated). **16**, male (dorsal), fig. 1 from Pl. *Satyrus* II of Edwards (1882). **17**, male (dorsal), *Satyrus alope* var. *maritima*, fig. 6 from Pl. *Satyrus* II of Edwards (1882). **18**, male, lectotype of *S. alope* var. *maritima*, [July 1877], [Oak Bluffs], Martha's Vineyard [Dukes Co.], MA (CMNH). **19**, male, holotype of *Cercyonis alope* var. *ochracea*, 18.vii.1935, Washington Park [Providence Co.], RI (UANH). **20**, male (partial dorsal), paratype of *C. a. ochracea*, Big Run Base, Foltz Hill, Butler Co., PA (UANH). **21**, male, identified as *C. pegala agawamensis*, 5.viii.2007, Rt. 286, Hampton, Rockingham Co., NH (images reversed) (MGCL). **22**, male, identified as *C. p. agawamensis*, same data (MGCL). **23**, female, identified as *C. p. agawamensis*, same data (MGCL). **24**, female (dorsal), 13.vii.1985, Hwy 27, Southampton Twp., Suffolk Co., Long Island, NY (MGCL). **25**, female (ventral), same data (MGCL). **26**, male, from Pl. 12 of "Jones' Icones;" specimen herein designated the lectotype of *Papilio alope*. **27**, male, 28.viii.1941, Bedford [Westchester Co.], NY (MGCL). **28**, male, 16.vii.1924, Trenton [Mercer Co.], NJ (MGCL). **29**, male (ventral), Mt. Kisco [Westchester Co.], NY (MGCL). **30**, male (dorsal), no data (HMUG); specimen that R. Gatrelle intended to designate as the lectotype of *P. alope*. **31**, male forewings, both 14.vii.1974, Kingston [Bartow Co.], GA. **32**, male, holotype of *C. alope carolina*, Conestee [sic Connestee] Falls near Brevard [Transylvania Co.], NC (UANH). **33**, female, holotype of *C. pegala* race *borealis*, 10.vii.1920, Trumbull Co., OH (MGCL). **34**, male (ventral), lectotype of *S. alope* var. *texana*, Bastrop [Bastrop Co.], TX (CMNH) (side mounted specimen). **35**, original labels from type specimens (enlarged): **a**, lectotype of *S. a.* var. *maritima*; **b**, holotype of *C. a. ochracea*; **c**, paratype of *C. a. ochracea* (see Fig. 20); **d**, holotype of *C. a. carolina*; **e**, holotype of *C. pegala* race *borealis*; **f**, lectotype of *S. alope* var. *texana*.

Maine, bear a small anal eyespot. Some female *C. pegala* at MGCL are very similar in appearance to those identified as *agawamensis* by Grokovich, but they were collected in more upland habitats, including mixed forest openings (Figs. 24, 25).

Behavioral traits associated with *C. p. agawamensis* are also shared with other populations of *C. pegala.* Although Arey and Grkovich (2014) claimed that nectaring behavior in *agawamensis* was "unlike almost all other populations of *C. pegala*," it is well-documented in other populations across North America, including coastal Massachusetts (Scudder 1888–1889, Saunders 1932, Allen 1987, Iftner et al. 1992, Bouseman & Sternburg 2001, Pyle 2002, Mellow & Hansen 2004, Leahy 2006, Patterson 2006, Scott 2014). I have personally observed patched *C. pegala* nectaring in upland habitats in Maine. I agree with Tveten and Tveten (1996), who remarked that nectar habits in *C. pegala* "undoubtedly vary with individual populations and with the resources available."

Arey and Grkovich (2014) mentioned supposed "intergrades" between what they identified as *C. p. agawamensis* and *C. p. alope*, suggesting that salt marsh and upland populations interact. Indeed, I observed adults of *C. pegala* freely moving between the salt marshes and adjacent upland habitats, and some were seen resting in trees at the edges of the marshes during the day. At the type locality, I watched a number of butterflies purposefully flying from the salt marshes into adjacent trees in the late afternoon, presumably to roost for the night. Although I detected no obvious differences in the condition of the adults that I found in salt marshes versus those of upland habitats, Arey and Grkovich (2014) reported a slight disparity in the phenology of these populations. If present, this may be the result of microclimatic differences of the cooler, more humid lowland marshes. More research is clearly needed to confirm the status of *C. p. agawamensis*.

Based on this review of Atlantic coast *C. pegala*, the specimen of "*Alope*" illustrated by Jones most closely agrees with a patched northeastern phenotype (Figs. 26–29). I therefore propose the vicinity of New York, New York, as the revised type locality for *Papilio alope*. This conclusion is supported by the following: 1) the City of New York was occupied by the British until 1783 and served as an important military and political base of operations; 2) many insect specimens were received from New York by British naturalists during the second half of the eighteen century; 3) this area is located roughly midway between Pennsylvania and Maine where these phenotypes occur; 4) populations of *C. pegala* in this area have been associated with the name *alope* for over a century (e.g. Beutenmüller 1893); 5) the

popular concept of the subspecies *C. p. alope* was forged when Klots (1951, Pl. 7, fig. 5) figured a male by that name from Bedford, Westchester Co., New York; 6) individuals of *C. pegala* from this area agree with the specimen portrayed by Jones (Figs. 26, 27, 29).

Lectotype of *Papilio alope*. A few weeks before his untimely death, R. R. Gatrelle announced that he had rediscovered "the types of *Cercyonis pegala alope*" and believed that this taxon was not described from Georgia, but rather from "up north" (Gatrelle 2005). Gatrelle posted images of one of these specimens on the webpage of the International Lepidoptera Survey (TILS) with the caption, "This is the lectotype [in press] of *Cercyonis pegala alope.* Type locality: northeastern US [in press], USA." Although Gatrelle was unable to complete his planned publication, the images he posted on the TILS webpage (TILS 2013) could still be viewed at the time of this writing.

In 2009, I was asked by E. G. Hancock of HMUG to identify images of North American butterflies in William Hunter's collection. During the course of this project, I recognized Gatrelle's intended lectotype as one of two unlabeled males of *C. pegala* at HMUG. The intended lectotype is the larger of the two (28 mm) with poorly developed yellow-orange forewing patches (Fig. 30). The second specimen is small (25 mm) and worn, with a well-developed forewing patch of faded ochre-yellow, typical of an old individual. Both are identified on the Hunterian Museum webpage (HMAG 2006) as candidates for lectotype designation on the assumption that Fabricius, having worked with Hunter's collection, was familiar with these specimens when he described *Papilio alope*. These specimens are not identified like other butterflies in Hunter's collection, as Fabricius did not publish the description of *P. alope* until 1793, a decade or more after M. H. Baillie created the cabinet labels. Images of these specimens on the HMUG webpage are captioned as "probably collected in Pennsylvania" on the authority of "Ron Gatrelle, pers. comm., July 2005" (HMAG 2006). This locality was possibly based on information from the museum that a former student of Hunter's named William Wood (fl. 1770s–1780s) collected insects around Philadelphia during the late 1770s when he was serving as a surgeon in the British Army (Hunter correspondence, Univ. of Glasgow; Brown et al. 2011). Regardless of its origin, the specimen that Gatrelle intended to designate as the lectotype is inconsistent with the concept of *Papilio alope* as described by Fabricius (1793) and illustrated by Jones (Fig. 26). Contrary to the original description, it lacks a wide yellow forewing patch and bears only five spots on the ventral hindwing, not six. Although the second specimen at HMUG has a more defined yellow
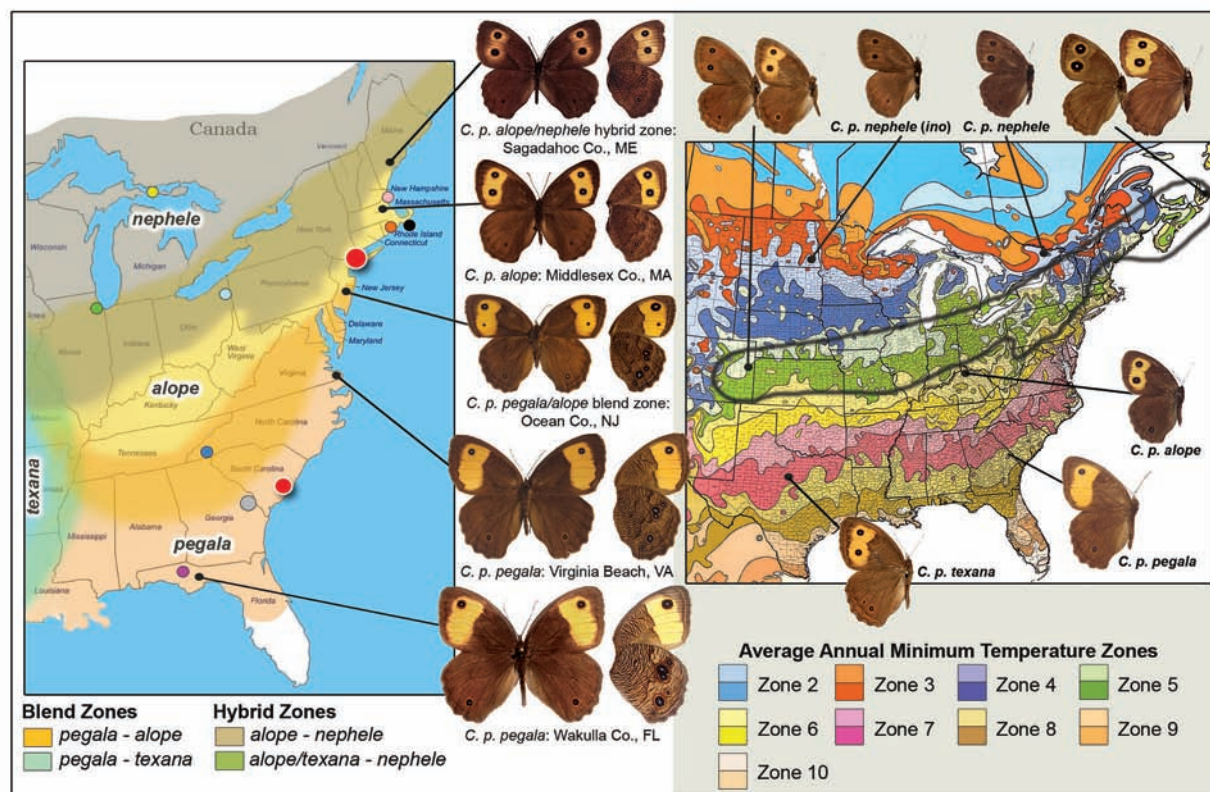
FIG. 36. Maps and phenotypes of *C. pegala*. Left map: eastern North America showing perceived blend zones and hybrid zones, with examples of patched butterflies that occur along the Atlantic coast (center). Type localities: *Papilio pegala* (vicinity of Charleston, SC), small red dot; *Papilio alope* (previously proposed; Screven Co., GA), gray dot; *Papilio alope* (newly proposed; vic. New York, NY), large red dot; *Cercyonis p. abbottii* (Chipley FL), purple dot; *Cercyonis alope carolina* (Connestee Falls, NC), dark blue dot; *Satyrus nephele* var. *olympus* (Chicago, IL), green dot; *Hipparchia nephele* (possibly Little Manitou Island, Ontario, Canada), yellow dot; *Cercyonis pegala* race *borealis* (Trumbull Co., OH), pale blue dot; *Satyrus alope* var. *maritima* (Oak Bluffs, Martha's Vineyard, MA), black dot; *Cercyonis p. agawamensis* (Newbury, MA), pink dot; *Cercyonis alope ochracea* (Providence, Rhode Island) orange dot. Right map: average annual minimum temperatures across much of North America (USDA 1990). Dark gray outline is the approximate boundary of the hybrid zone between patched and patchless *C. pegala*. Also shown are examples of *C. pegala* found at different points across the region.

forewing patch, it too has only five spots on the ventral hindwing. Despite these discrepancies, it could be argued that Fabricius examined these specimens and they contributed to his concept of *P. alope*, even though he did not publish the description of *alope* until many years after he may have seen them, nor did he refer to any such specimens in Hunter's collection (ICZN 1999, Art. 72.4.1.1). This underscores the need for a more suitable lectotype of *Papilio alope*.

Jones' illustration (Fig. 26) likely served as the basis of the description of *Papilio alope* Fabricius, 1793, thus the specimen it portrays is hereby designated as the **lectotype** of this nominal taxon in accordance with Article 74 of the Code (ICZN 1999). Although the fate of this specimen is a mystery, the designation of such "lost" specimens is permissible under the Code (Article

74.4). Jones' figures are accurate enough to represent the objective standard of reference whereby the application of the name *Papilio alope* can be determined.

Distributional analysis. Now that a type locality has been suggested for *P. alope*, and a lectotype designated, this nominal taxon must be considered within the concept of *C. pegala*. In other words, we must ask the question, "Where does *alope* occur within the range of *C. pegala* in relation to other nominal taxa?" Although variation is considerable, local populations of *C. pegala* tend to engender a principal phenotype. The interpretation of these phenotypes across eastern North America has led to the description of ten subspecies, whose recognition is as erratic and confusing as the phenotypes themselves. In addition, there are

aberrations and other pattern variants which occur throughout the species' range. Such variants sometimes possess characteristics that are evocative of distant populations, but they may have no direct genetic connection. The distributions of the various phenotypes of *C. pegala* in eastern North America are the result of postglacial expansion and more recent human influences. A detailed review of these processes is far beyond the scope of the present study, which focuses on perceived present-day ranges and their connection to described nominal taxa.

From the midst of this seeming chaos, I have attempted to map morphological trends within *C. pegala* across much of the eastern United States and Canada using established subspecies nomenclature. Based on a review of thousands of specimens, photographs, and other information, this map (Fig. 36, left) illustrates the approximate boundaries of these trends (or perceived "morphological averages"). It is not known how the distributions of the various phenotypes have changed over time, particularly in response to human alterations to the landscape. The map is based primarily on specimens and photographs dating from 1930 to the present. This analysis may help to locate appropriate areas from which to obtain DNA samples for future comparative studies.

As mentioned by other authors, transitional areas are extensive and serve as the basis of ongoing disagreements over the number of subspecies of *C. pegala* in eastern North America. However, equally extensive regions occur where phenotypes essentially stabilize into variable, yet distinguishable entities (i.e. subspecies). Nominotypical *pegala* is distributed entirely within the Lower Austral life zone, southeast of the fall line (boundary between the coastal plain and Piedmont), from Louisiana to southeastern Virginia (Fig. 36, left map). Although adults of *C. p. pegala* become somewhat smaller and darker northward along the southeastern coastal plain, they remain consistent with the concept of this taxon as originally described and defined by its lectotype. Larger adults found in northern Florida and southern Georgia were described by Brown (1969) as the subspecies *C. p. abbottii*, but the cline is so smooth between Florida and southeastern Virginia that any boundary used to segregate these populations would be arbitrary. Populations in Virginia and Florida represent the northern and southern extremes of *C. p. pegala*, whose type specimens from Charleston, South Carolina, convey the "average" expression of this taxon.

Phenotypes consistent with the concept of the subspecies *C. p. alope* are distributed from western Kentucky and northern Tennessee, eastward in a narrow belt to the coast, then northward into extreme southern Maine (Fig. 36, left map). This includes populations sometimes considered to represent the subspecies *C. p. maritima*. Pending additional research, the miniscule northeastern range of *C. p. agawamensis* is also included within *C. p. alope*.

A broad swath of populations that are intermediate between *C. p. pegala* and *C. p. alope* extends from the lower Mississippi Valley (within the Gulf Coastal Plain region of western Tennessee and southeastern Missouri), across the southern Appalachians and Piedmont, into southern New Jersey (Fig. 36, left map). This area represents a blend zone wherein populations cline northward from larger *C. p. pegala* to smaller *C. p. alope*. Such populations in and around Georgia were considered by Gatrelle (1985) and Scott (2008b) to represent typical *alope*, intermediate between *C. p. pegala* and the putative subspecies *C. p. carolina*.

The name *carolina* is often used to identify butterflies with white to pale yellow forewing patches that are found within the blend zone of the southern Appalachians and Piedmont. Usually uncommon, such pale-patched butterflies are often found in the company of darker-patched individuals (Harris [1950], 1972, Clark & Clark 1951). The original description defined *carolina* as a lighter brown butterfly with a white forewing patch. The description also indicated that the lower eyespot on the forewing of the male is reduced, and the eyespots on the ventral hindwing "suggest an approach toward *pegala*" (Chermock & Chermock 1942). Because patch scales in living *C. pegala* are easily lost, older individuals from any patched population can resemble the pale *carolina* phenotype. Among the thousands of *C. pegala* specimens at MGCL and UANH, I found relatively few fresh individuals with pale patches, and most are females. Most of these pale-patched butterflies originated from the mountains and Piedmont of North Carolina and Georgia, while others were collected in the mountains of eastern Tennessee, West Virginia, and the upper Piedmont of North Carolina. Two cream-patched males were collected in Alachua County, Florida. A few specimens from elsewhere in the southeastern coastal plain possess equally pale patches. In nearly all instances where multiple specimens were collected at a given locality, pale-patched individuals are accompanied by those with conspicuously yellow or orange-yellow patches (Fig. 31).

I recently located the "lost" holotype of *Cercyonis alope carolina* in the R. L. Chermock collection at UANH (Calhoun 2015) and it is herein figured for the first time (Fig. 32). Although the right wings are detached and the antennae are missing, it is otherwise in good condition. From Connestee Falls, Transylvania County, North Carolina, it is a relatively small male

bearing a red holotype label signed "F. H. & R. L. Chermock" (Fig. 35d). Reminiscent of *C. p. pegala*, the lower eyespot on the forewing is greatly reduced, the eyespots on the ventral hindwing are large, and the dark ventral striations are distinct. Although the original description indicated that *carolina* is "lighter brown in color than typical *alope*" (Chermock & Chermock 1942), the ground color of the holotype is quite dark (Fig. 32). The damaged female "allotype," also from the mountains of North Carolina, is deposited at UANH. Like the male, it is evocative of *C. p. pegala*, with contrasting ventral wings and larger ventral eyespots. Although lighter brown in color, it is a worn individual that was collected very late in the season (22.ix.1937). Miller and Brown (1981) and Pelham (2008, 2014) cited the existence of paratypes of *carolina* at MGCL (ex Allyn Museum), but I was unable to locate any of the remaining seven paratypes mentioned by Chermock and Chermock (1942). However, two specimens at MGCL, labeled in F. H. Chermock's hand, are from "Monteagle Tenn," which is a paratype locality (reported as "Mt. Eagle, Tennessee"). In addition, R. L. Chermock identified as *C. a. carolina* eight specimens in his collection from Madras, Coweta County, Georgia, which is located within the Piedmont.

I was surprised to learn that very few Chermock specimens identified as *carolina* possess white forewing patches as defined in the original description; those with the palest patches are worn females that lack patch scales. Even the patch of the holotype is slightly cream-colored (Fig. 32). Two males and a female from the F. H. Chermock collection at MGCL, collected in 1939 near the type locality, possess cream-colored patches. The patches of the remaining specimens of "*carolina*" in R. L. Chermock's collection vary from cream to yellow-orange. Like the Chermock's description of *C. a. ochracea*, it is extremely difficult to comprehend their concept of *C. a. carolina*. Because their specimens from Monteagle, Tennessee (a location within the type series) possess yellow patches, the Chermocks were undoubtedly aware that individuals with colored patches occurred alongside their white-patched concept of *C. a. carolina*. Moreover, R. L. Chermock identified specimens with yellow and yellow-orange patches as *carolina*.

I found no evidence of the alleged blend zone that Gatrelle (1985) recognized between pale-patched montane phenotypes and orange-patched butterflies of the coastal plain. Rather, pale-patched individuals occur in small numbers within the coastal plain (even rarely in Florida), northward into the southern Appalachian Mountains, where they are more frequent, but not exclusive. In overall appearance, pale-patched adults

from North Carolina southward most closely resemble nominotypical *pegala* (often larger size, larger ventral hindwing spots, and the lower eyespot on the male forewing is often greatly reduced or wanting) (Figs. 31, 32). Individuals at higher elevations tend to be smaller and sometimes have reduced forewing patches, but they generally resemble *C. p. pegala*. Although cream-colored and pale yellow patched phenotypes also occur sporadically from West Virginia northward into Maryland and southern New Jersey, they more closely resemble *C. p. alope* (Fig. 16). The putative subspecies *Cercyonis alope carolina*, as originally described, is better recognized as an extreme form (i.e. "form *carolina*") that occurs with variable frequency in southeastern populations, particularly at higher elevations within the blend zone between *C. p. pegala* and *C. p. alope*.

Butterflies that are essentially recognizable as *C. p. alope* arise from the northern fringe of the blend zone within the Appalachian Plateau, and along the northern edge of the Piedmont in Maryland, Pennsylvania and New Jersey (Fig. 36, left map). Northward, *C. p. alope* shares a broad contact zone with patchless phenotypes commonly recognized as the subspecies *C. p. nephele* and/or *C. p. olympus* (W. H. Edwards) (Fig. 36, left map). A portion of this region corresponds to the area recognized by Remington (1968) as the "Northeastern—Central Suture-Zone," where multiple groups of otherwise allopatric taxa, including subspecies, meet and hybridize in northeastern North America. In fact, Remington (1968) included the pair "*Cercyonis pegala nephele* group" and "*C. p. alope* group" within this suture zone and considered the amount of crossing to be "Intense." Populations of *C. pegala* within this region do not gradually cline from south to north as they do in the southeast, but broadly overlap and intermingle. Phenotypes resembling either parental subspecies, along with presumed "intermediates," seem to haphazardly occur across the region. Edwards (1880) termed this region the "belt of dimorphism," where both patched and patchless *C. pegala* are found. Adults exhibit a wide range of variation across this region, even within the same populations. A series of 42 specimens at LCBM, collected during the 1890s in the vicinity of Manchester, Kennebec County, Maine, vary from near-*alope* to mostly *nephele*-like, with a wide range of intermediates. Fifty-four specimens at MCGL, collected in 1985 from a single locality in western Oxford County, Maine, vary from distinctly *alope*-like to distinctly *nephele*-like, with many intermediates. A single female collected near the northern limits of this region in Fulton County, Ohio, produced an assortment of phenotypes, from *alope*-like

to *nephele*-like (Sourakov 1995, 2008). Museum specimens from this region strongly suggest that *nephele*-like and intermediate phenotypes are more frequent than fully patched, *alope*-like butterflies, even southward. Nonetheless, some populations mostly produce *alope*-like butterflies. This is well documented in parts of Illinois (Irwin & Downey 1973, Sedman & Hess 1985) and I have personally observed this in northeastern Indiana. Such "islands" of opposite phenotypes were noted by Klots (1951). Patched or patchless phenotypes can also be limited to certain habitats. In central Ohio, *nephele*-like butterflies are found in wetlands with more northern affinities (e.g. bogs and fens), while *alope*-like butterflies occur in adjacent upland habitats (Iftner et al. 1992).

The transitional region between patched and patchless phenotypes of *C. pegala* is remarkably wide and exhibits characteristics of a mosaic hybrid zone, at least in part. A fairly recent concept proposed by Harrison (1986), a mosaic hybrid zone was defined by Howard (1993) as having "a patch quality" in which one taxon occurs in one patch and the other taxon occurs in another patch, while some patches contain a mix of the two taxa. Mosaic hybrid zones may be frequent where subspecies make contact along interdigitating environmental gradients (Jones & Collins 1992). This certainly describes the contact zone of *C. pegala*, which incorporates numerous biotic communities and elevations, from sea level coastal marshes to montane forest clearings. Larson et al. (2013) observed that hybrid zones across heterogeneous landscapes may exhibit a combination of different dynamics. *Cercyonis pegala* also seems to exhibit a high degree of genetic plasticity at the local level. Shifts at the same locality from one primary phenotype to the other during different years have been observed in western Illinois (Sedman & Hess 1985) and in parts of New York (M. B. Prondzinski pers. comm.). While the complex hybrid zone between patched and patchless *C. pegala* is very poorly understood, it is most likely of secondary origin, resulting from recolonization following the Wisconsin Glacial Episode (roughly 85,000–11,000 YBP). Another extensive hybrid zone in northeastern North America, likely also of secondary origin, involves the distinctive butterfly subspecies *Limenitis a. arthemis* (Drury) and *L. a. astyanax* (F.) (Mullen et al. 2008). A scenario of genetic differentiation, isolation, and reintegration of taxa along a portion of this shared contact zone was proposed by Remington (1968).

The southern boundary of the hybrid zone between patched and patchless *C. pegala* undulates with the occurrence of *nephele*-like and intermediate phenotypes at higher elevations, especially from Pennsylvania north through Massachusetts. Localized populations of these phenotypes also occur in the mountains of western Maryland and northern West Virginia (Simmons & Anderson 1971, Allen 1997). Although *nephele*-like phenotypes within the hybrid zone may closely resemble typical *C. p. nephele*, they are best regarded as transitional (i.e. "form *nephele*"). Brightly patched *alope*-like adults, mostly females, occasionally occur within hybrid zone populations as far northeast as New Brunswick and Nova Scotia, Canada. The northern limit of the hybrid zone between Lake Ontario and New Brunswick is difficult to determine, as relatively few specimens of *C. pegala* are known from that area. It should be noted that intermediate-like phenotypes with reduced forewing patches can occur anywhere within the eastern range of *C. pegala*, even in the extreme south (where they are rare). Such individuals are more frequently encountered at higher elevations in the Appalachians and Piedmont, where they appear to represent extreme variants or aberrations.

Edwards (1880) described *Satyrus nephele* var. *olympus* as a "slightly changed form of *Nephele*" found "somewhere between New York and Illinois . . . to and on the eastern slopes of the Rocky Mountains." Edwards (1882) subsequently restricted this to "Indiana and westward to the Rocky Mountains." Brown (1964) later proposed "Chicago, Illinois" as the type locality of *olympus* based on eggs that W. H. Edwards received in 1878 from Charles E. Worthington, who lived in that city. A male specimen that resulted from one of those eggs was designated by Brown (1964, fig. 19) as the lectotype of *S. nephele* var *olympus*. According to the specimen's label, as well as Edwards' journal "H" (WVSA), the butterfly emerged during the first week of June 1879. The proposed type locality of *olympus* ("Chicago, Illinois") lies 580 km (360 mi) almost due south of the type locality of *Hipparchia nephele* (=*C. p. nephele*), yet the ranges of these taxa are typically segregated in the literature from east (*nephele*) to west (*olympus*). Although Brown ([1966b]) suggested a vague type locality for *nephele* of "extreme western end of North Channel, Lake Huron [Ontario, Canada]," he simultaneously defined it as "vicinity of St. Josephs Island, Ontario, Canada" (Brown [1966a]). Ultimately, Miller and Brown (1981) suggested "possibly Little Manitou I., Ontario," referring to what is now known as Cockburn Island in northeastern Lake Huron, within the Manitoulin District of Ontario. Today, *olympus* is often treated as a synonym of *C. p. nephele* (Layberry et al. 1998, Scott 2006, 2008).

There are two significant problems with W. H. Edwards' description and subsequent recognition of *olympus*. Firstly, Edwards (1880) based his concept of

olympus on butterflies from within the hybrid zone between patched and patchless phenotypes of *C. pegala* (Fig. 36, right map). This explains the presence of faint to fairly evident forewing patches in some adults from so-called *olympus* populations, a condition also mentioned by Edwards (1882). As expected, patched *alope*-like adults have been recorded (albeit rarely) around the type locality of Chicago (Irwin & Downey 1973), which is located at the extreme northern fringe of the hybrid zone. Secondly, Edwards (1882) claimed that the larva and chrysalis of *olympus* are "readily differentiated" from those of *nephele* and *alope*, which he reported were analogous to one another. However, his early stages of "*nephele*" were all reared from ova obtained at Hunter, New York, which is located in the Catskill Mountains within the extreme southern portion of the hybrid zone. Edwards (1882) reported that one reared adult from the Catskills was "a typical female *alope*" and another was a female "intergrade." The former was figured by Edwards (1882, Pl. *Satyrus* II, figs. 3, 4). Edwards himself considered the Catskills to be located within the "belt of dimorphism," where both patched and patchless adults occur. He remarked, "In the Catskills, I have taken *Alope* as conspicuously banded as any in Virginia, but such examples are rare, forming, perhaps, two or three per cent of the flight" (Edwards 1882). Shapiro (1974) recorded "intermediate" populations from the Catskills and specimens at MGCL from that area are quite variable. In addition, some of the "*alope*" that Edwards reared for his comparison were received from Albany, New York. Like Hunter, Albany is also located at the southern edge of the hybrid zone. Edwards (1882) reported that one of the ova from Albany resulted in an "intermediate" adult without a forewing patch. Edwards therefore unwittingly compared early stages from three hybrid zone populations, thereby nullifying this key piece of evidence for differentiating *olympus*.

Although the early stages of *C. pegala* are extremely variable (Sourakov 1995), the differences that Edwards perceived can possibly be explained by the origin of the material. The "*olympus*" ova were from the far northern edge of the hybrid zone, where introgression from true *nephele* undoubtedly is greater. Conversely, populations in Hunter and Albany presumably experience a greater degree of introgression from *alope*. The similarity that Edwards observed between the early stages of "*alope*" and "*nephele*" can at least partially be attributed to his inclusion of "*alope*" ova from a locality less than 80.5 km (50 mi) from that of his purported "*nephele*" ova. Because his ova of "*nephele*" originated so far south of populations of "true" *nephele*, Edwards' (1877) description of the early stages of "*Satryus nephele*" is not applicable to the subspecies *C. p. nephele* as recognized today.

Patchless specimens that were described as *C. pegala* race *borealis* F. Chermock (TL Trumbull County, Ohio) are also from the hybrid zone. The holotype of *borealis*, a female with a red label signed "F. H. Chermock," is preserved at MGCL and is herein figured for the first time (Fig. 33). Although this taxon was described as "*Cercyonis* (*Satyrus*) *pegala* race *borealis*," its label identifies it as "*Satyrus pegalia* [sic]. race. *borealis*" (Fig. 35e).

West of Indiana and Kentucky, distinctive patched phenotypes identified as the subspecies *C. p. texana* (W. H. Edwards) blend with those of *C. p. pegala* and *C. p. alope* (Fig. 36, left map). Northward, *texana/alope* phenotypes hybridize with *C. p. nephele*. In western Illinois, especially southward, some individuals express traits associated with *C. p. texana*, such as paler ventral ground color with more distinct dark striations. These characters are evident on the large male lectotype of *S. alope* var. *texana* from Bastrop, Texas (Figs. 34, 35f). Northward, adults of *C. p. texana* are somewhat smaller and darker than those found farther south. A fairly narrow blend zone between *C. p. texana* and *C. p. pegala* occurs along the Gulf Coast, mostly within Louisiana.

The curious patched phenotype known at the "Salem Uplift form" of the Salem Plateau of the Missouri Ozarks (see Heitzman & Heitzman 1987) occurs where principal phenotypes intersect at higher elevations. These butterflies, whose males often have a greatly reduced or absent lower forewing eyespot, resemble those from the Appalachians. This is not surprising given that they occur under similar elevated conditions at the northern edge of a blend zone involving *C. p. pegala*. A series of Ozark *C. pegala* at MGCL, from the collection of the Missouri lepidopterist John "Richard" Heitzman (1931-2013), are accompanied by a typescript cabinet label that identifies them as "*Cercyonis pegala meinersii* Bouseman & Hess," implying a planned descriptive publication by the Illinois geologist David F. Hess and the late entomologist John K. Bouseman (1936-2006) of the Illinois Natural History Survey. According to D. F. Hess (pers. comm.), the description of *meinersii* was actually to be published by Hess and Heitzman during the 1980s to define a "color morph" of *C. pegala* that occurs in the Salem Plateau of southern Missouri and north-central Arkansas. The name honors Edwin P. Meiners (1893-1960), who collected the proposed holotype in Carter County, Missouri, in 1926 (deposited at the Univ. of Missouri, Columbia). Meiners was a physician and amateur entomologist from St. Louis, Missouri (Remington 1962). Hess and

Heitzman were ultimately dissuaded from publishing the description of *meinersii* to mitigate the proliferation of names ascribed to *C. pegala* (D. F. Hess pers. comm.).

Butterflies with forewing patches become less prevalent westward until they disappear just east of the Rocky Mountains in central Colorado. There, populations often attributed to the subspecies *C. p. olympus* occur within the western extension of the hybrid zone between patched and patchless phenotypes; in this case *C. p. texana* and C. p. *nephele* (Fig. 36, right map). Some authors identify at least some of the darker phenotypes in eastern Colorado as the subspecies *C. p. boopis* (Behr) (TL Contra Costa Co., California), but the application of this name to those populations is questionable (Fisher 2005). Northward, butterflies have been attributed to the subspecies *C. p. ino* G. Hall (TL Calgary, Alberta, Canada), but this is also controversial and some authors (e.g. Layberry et al. 1998, Scott 2008b) treated *ino* as a synonym of *nephele*. The characters used to separate *ino* (e.g. lack of ventral eyespots in the female) are not uncommon farther east. Westward in the hybrid zone, patched *texana*-like butterflies become less common and spottier in occurrence, possibly due to more pronounced differences in elevation. Many patchless butterflies from the hybrid zone west of Illinois possess more contrasting ventral patterns and larger ventral hindwing eyespots reminiscent of *C. p. texana*. This further supports the notion that *olympus* is comprised of an assemblage of hybrid populations within the contact zone between patched and patchless phenotypes, involving multiple parent taxa, extending from eastern Canada to the Rocky Mountains (Fig. 36, right map). Because of their apparent hybrid status, populations attributed to *olympus* should not be recognized as a discrete subspecies.

The selective forces acting upon patched and patchless phenotypes of *C. pegala* are unknown. Unlike the divergence between the subspecies *L. a. arthemis* and *L. a. astyanax*, hostplant specificity and mimetic factors are not known to play a role in *C. pegala*. It is possible that smaller, darker phenotypes have an advantage in colder climates by promoting heat absorption (Sourakov 1995). Butterflies without colorful patches may also rely on cryptic coloration to avoid predation, while brightly colored forewing patches may help to draw the attention of predators to the eyespots as part of a startle and/or deflection mechanism. Bowers and Wiernasz (1979) established the palatability of *C. pegala* to avian predators, but there is disagreement about the effectiveness of marginal eyespots as anti-predation devices (Lyytinen et al. 2003). More recent studies suggest that invertebrate predators are attracted to such patterns (Prudic et al. 2014).

The distribution of *C. pegala* phenotypes in eastern North America was compared against various ecological and climatological maps to reveal any potential correlation. A remarkably strong parallel was found with average annual minimum temperature (Fig. 36, right map). The boundaries of some of these temperature zones correspond to changes in elevation. Within the southeastern coastal plain, *C. p. pegala* is found within temperature Zones 8 and 9 (-12° to -1°C) (this subspecies is replaced westward by *C. p. texana*). The blend zone between *C. p. pegala* and *C. p. alope*, primarily within the Appalachians and Piedmont, corresponds to Zone 7 (-18° to -12°C). The range of *C. p. alope* is analogous to Zone 6 in the east (-23° to -18°C) (this subspecies is replaced westward by a somewhat smaller, darker phenotype of *C. p. texana*). The southern boundary of the hybrid zone between *C. p. alope* and *C. p. nephele* roughly follows the southern limits of Zone 5 (-29° to -23°C). Populations of *C. p.nephele* are mostly found within Zones 3 and 4 (-40° to -29°C).

The actual influence of temperature on phenotypic expression in *C. pegala* is uncertain. The temperature map in Figure 36 is based on data recorded 1974–1986 (USDA 1990) and more recent data are less acutely correlated. Nonetheless, significant long-term trends minimize the importance of such deviations. It is conceivable that the apparent ability of some hybrid populations to shift primary phenotypes from year to year is also temperature-related. The young larvae of *C. pegala* diapause during the winter, thus it is possible that a greater percentage of *nephele*-like adults are produced in response to colder temperatures, or more prolonged cool temperatures, during their development. This may help to explain the patchy, habitat-specific and elevational distribution patterns of phenotypes within some areas of the hybrid zone. Occasional southeastern butterflies with reduced patches may result from similar influences. How these and other potential factors combine to maintain the polymorphisms in *C. pegala* deserves investigation.

Proposed taxonomic arrangement. Despite over two centuries of study, a great deal more research is needed to understand the relationships between the various phenotypes of *C. pegala*. The extensive blend and hybrid zones that exist across eastern North America encourage a conservative arrangement as proposed by Sourakov (1995), in which all populations are considered to represent one polymorphic subspecies, *C. p. pegala*. The treatment of patched populations as *pegala* and all patchless populations as

nephele (as forms or subspecies), has long been employed in popular literature (e.g. Opler & Krizek 1984, Scott 1986, Layberry et al. 1998, Cech & Tudor 2005). However, this usage overlooks the obvious differences between regional phenotypes.

Pelham (2008, 2014) presented an arrangement of five eastern subspecies. Pending a more thorough revision of the group, I advocate a slightly more modest approach that recognizes four subspecies in eastern North America. The most obvious difference is that *C. p. olympus*, which consists of an assemblage of hybrid populations, is not recognized as a subspecies. The recently described *C. p. agawamensis* is regarded as a synonym of *C. p. alope*, not of *C. p. pegala* as indicated by Pelham (2014). Due to its closer resemblance to the nominotypical subspecies, *C. a. carolina* is listed as a synonym of *C. p. pegala*, rather than of *C. p. alope* as suggested by previous authors. For the purposes of this arrangement, the dark hybrid phenotypes denoted by the names *olympus* and *borealis* are aligned with *C. p. nephele*, though the primary types of these taxa do not represent "true" *C. p. nephele*.

Due to the previous misapplication of the name *P. alope*, Scott (2008b) considered *C. p. maritima* to be the valid name for all northeastern populations that had historically been associated with the subspecies *C. p. alope*. Because the names *S. a.* var. *maritima* and *S. a.* var. *texana* were proposed in the same publication (i.e. Edwards 1880), Scott (2008a) invoked the Principal of the First Reviser (ICZN 1999, Art. 24.2) to "make *maritima* the correct name [i.e. senior subjective synonym] for those who think they are synonymous," adding that the butterflies associated with these names "look similar." Not only are these taxa markedly dissimilar (Figs. 19, 34), such an action only applies when it is accepted that the entities involved are synonymous. Virtually all those who recognize multiple subspecies of *C. pegala* (e.g. Emmel 1969, Ferris 1981, Miller & Brown 1981, Neck 1996, Tveten & Tveten 1996, Fisher 2005, Pelham 2008, 2014) consider the name *texana* to apply to patched populations west of the Mississippi River. My own research endorses this view.

The following synonymy is proposed for *C. pegala* in eastern North America. Admittedly subjective, this arrangement acknowledges the undeniable trends that exist in wing pattern morphology. Current nomenclature is given for each subspecies, followed by its name as originally published (only original name combinations are given for subjective synonyms). Type localities (TL) and locations of primary types are also indicated.

Cercyonis pegala (Fabricius, 1775).

a. *Cercyonis pegala pegala* (Fabricius, 1775). P[apilio]. N[ymphalis]. G[emmata] *Pegala*. TL: vic. Charleston, Charleston Co., South Carolina. Lectotype ♂ at HMUG.

   =*Cercyonis alope carolina* New Race F. Chermock & R. Chermock, 1942. TL: Connestee Falls, Transylvania Co., North Carolina. Holotype ♂ at UANH.

   =*Cercyonis pegala abbottii* F. Brown, 1969. TL: Chipley, Washington Co., Florida. Holotype ♂ at CMNH.

b. *Cercyonis pegala alope* (Fabricius, 1793). P[apilio]. S[atyri]. *Alope*. TL: vic. New York, New York. Described from an illustration by William Jones at OUMNH. The specimen that served as the model for Jones' figures, probably lost, is herein selected as the lectotype.

   =[*Satyrus alope*] var. *Maritima* W. H. Edwards, 1880. TL: Oak Bluffs, Martha's Vineyard, Dukes Co., Massachusetts. Lectotype ♂ at CMNH.

   =*Cercyonis alope ochracea* New Form F. Chermock & R. Chermock, 1942. TL: Washington Park, Providence, Providence Co., Rhode Island. Holotype ♂ at UANH.

   =*Cercyonis pegala agawamensis* Arey & Grkovich, 2014. TL: Boston Road, Newbury, Essex Co., Massachusetts. Holotype ♂ to be deposited at MGCL.

c. *Cercyonis pegala texana* (W. H. Edwards, 1880). [*Satyrus alope*] var. *Texana*. TL: Bastrop, Bastrop Co., Texas. Lectotype ♂ at CMNH.

d. *Cercyonis pegala nephele* (W. Kirby, 1837). *Hipparchia Nephele*. TL: possibly Little Manitou Island, Manitoulin District, Ontario, Canada. Loc. of type(s) (probably a holotype ♀) unknown; possibly lost.

   =[*Satyrus Nephele*] var. *Olympus* W. H. Edwards, 1880. TL: Chicago, Cook Co., Illinois. Lectotype ♂ at CMNH.

   =*Cercyonis* (*Satyrus*) *pegala* race *borealis* F. Chermock, 1929. TL: Trumbull Co., Ohio. Holotype ♀ at MGCL.

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BUTTERFLY BIODIVERSITY IN A THREATENED COASTAL DESERT ECOSYSTEM OF NORTHWESTERN MEXICO, WITH A FOCUS ON THE LIFE HISTORY AND ECOLOGY OF POTENTIALLY ENDANGERED SPECIES

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ABSTRACT. Butterfly biodiversity in a threatened coastal ecosystem of northwestern Mexico, near Guaymas, Sonora, is documented based on presence data obtained weekly or biweekly from November 2013 to July 2015 combined with periodic observations and collection records dating back to 1978. The survey region and adjacent coastal areas on the Gulf of California are currently undergoing major environmental degradation owing to rapid urbanization, tourism development and construction of aquaculture facilities. A total of 105 species was recorded in the study region, representing about 30% of the total number of butterfly species currently recorded for the state of Sonora. Based on specific larval host plant requirements and known geographic distributions, several species dependent upon vegetation growing in a narrow coastal strip of sand dunes, mangrove estuaries and coastal plains are suggested to be the most threatened. The ecology, systematics and conservation biology of these potentially threatened species, in addition to several other species of special interest, are discussed.

Additional key words: butterfly conservation, Sonoran Desert, thornscrub biome, threatened species, presence data

Coastal regions of the Gulf of California (also known as the Sea of Cortez) in northwestern Mexico are currently undergoing rapid and extensive ecological modifications owing to urban development, dredging of coastal lagoons for new marinas, tourism projects, and construction of aquaculture facilities (DeWalt et al. 2002, Glenn et al. 2006, Luers et al. 2006). Additional factors contributing to environmental degradation of the coastal ecosystem include invasion of exotic plants, especially buffelgrass *Pennisetum ciliare* (L.) Link (Franklin et al. 2006), the increased and currently uncontrolled use of all-terrain vehicles, cattle grazing, and runoff of agricultural pesticides and other terrestrial pollutants into coastal lagoons (McCullough & Matson 2011). Much of this ecological disturbance is centered in Sonora, but these changes are also underway on the Baja California Peninsula, including the outer Pacific coast, as well as in the mainland states of Sinaloa and Nayarit. Sensitive habitats especially threatened include subtropical sand dunes, coastal plains, mangrove estuaries and saltgrass marshes.

Most of Sonora and the two peninsular states (Baja California and Baja California Sur [BCS]) are located in the Sonoran Desert Region (Fig. 1). Sonora in particular is rich in both plant and animal biodiversity, as well as endemic species, owing to its location in a transition zone between Nearctic and Neotropical regions of North America (Molina-Freaner & Van Devender 2010, Jones et al. 2013, Holmgren et al. 2014). A variety of other biomes are also present in Sonora, including grasslands, thornscrub, tropical deciduous forest, pine–oak woodland, pine forest, and mixed conifer forest of the Sierra Madre Occidental (Dimmitt 2000, Martínez-Yrízar et al. 2010).

Although knowledge of the overall diversity of insects in Sonora is rudimentary, the biodiversity of butterflies is relatively well known, mainly owing to field work conducted over the last 30 years (reviewed by Bailowitz & Palting 2010). During this period, two species new to science, *Polites norae* (Hesperiidae) (MacNeill 1993) and *Euchloe guaymasensis* (Pieridae) (Opler 1987) were discovered at, or near Guaymas in southern Sonora.
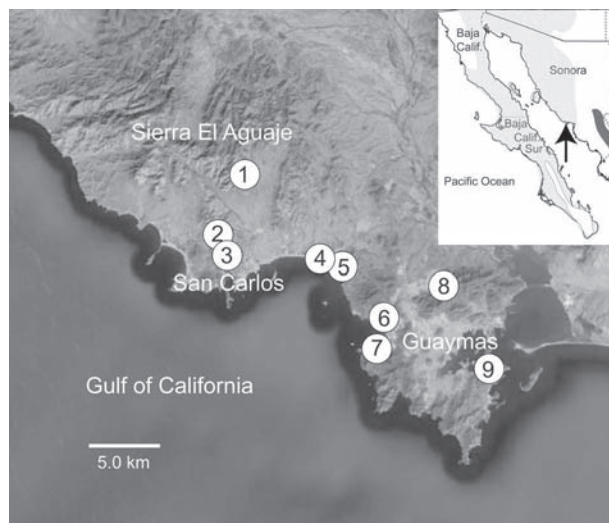
FIG. 1. Map of northwestern Mexico (inset) showing the location of the study area in the Guaymas region of coastal southern Sonora (arrow). Approximate boundaries of the Sonoran Desert (light gray shading) and the northwestern limit of the tropical deciduous forest biome in North America (dark gray shading) are shown on the inset. The Google™ Earth satellite photograph shows the location of the principal study sites. **1**, Cañón de Nacapule; **2**, Sierra El Aguaje foothills; **3**, El Esterito; **4**, Coastal sand dunes; **5**, Estero del Soldado; **6**, Estero de Bacochibampo; **7**, Bahía de Bacochibampo; **8**, Cerro Microondas El Vigía; **9**, Bahía de Guaymas.

Bailowitz and Palting (2010) list a total 338 species for the state of Sonora and predicted that this number will increase with additional field work. Brock (2009) lists 353 species in an online database, and most recently, Llorente-Bousquets et al. (2014) report a total of 257 species, excluding the Hesperiidae. The biodiversity and ecology of species inhabiting or restricted to the coastal environment in Sonora, however, have received little attention, and published information on life histories and ecology of Sonora butterflies in general is scarce. Thus, it is difficult to assess the degree to which the ongoing loss, fragmentation and pollution of the coastal landscape in northwestern Mexico are affecting populations of these insects.

Currently only two butterfly species are officially listed as threatened or protected in Mexico, the well-known migratory monarch, *Danaus plexippus* and *Papilio esperanza* (Beutelspacher 1975) from Oaxaca (Diario Oficial de la Federación 2010, Hernández-Baz et al. 2013). The creation of the Monarch Butterfly Biosphere Reserve by the Mexican government in the year 2000 has been instrumental in reducing illegal logging and protecting the overwintering sites of the monarch in the states of Michoacán and México (Vidal et al. 2014). But as will be shown here, other, less charismatic and often inconspicuous species are also

potentially threatened by habitat loss and fragmentation.

To gain an understanding of butterflies that might be particularly threatened by anthropogenic changes in the coastal ecosystem of northwestern Mexico, an inventory of species present in the Guaymas region is presented based mainly on systematic presence data obtained over a 21-month period (November 2013 to July 2015), but also including general observations and collection records dating back to 1978. A discussion then follows of the life history, ecology and population biology of several species that may be the most vulnerable to habitat modification. The rationale used is that threats will be highest for species with poor dispersal capability that are dependent on a single larval host plant growing only, or mainly, in the threatened habitat. Larval host plants for several coastal butterfly species from both Sonora and the Baja California Peninsula are already known from previous studies (Bailowitz 1988, Brown et al. 1992, MacNeill 1993, Pfeiler 2011). Loss of a specific host plant would be predicted to extirpate local populations dependent on that resource, unless affected butterfly species were able to adapt to new, alternative hosts. Although the survey area is relatively small, the species identified as potentially threatened are found throughout coastal Sonora, and most of these are also present in Baja California Sur, thus the butterfly conservation issues raised here should also apply over a broader geographic area of northwestern Mexico.

MATERIALS AND METHODS

Study region. The study region is located in the vicinity of Guaymas, Sonora, Mexico (27°55'30''N, 110°54'20'' W), a major commercial port city on the Gulf of California near the southern periphery of the mainland portion of the Sonoran Desert (Fig. 1). Butterfly biodiversity was determined by sampling and monitoring at nine sites within an area of about 50 km² (Fig. 1). The sites were located in a variety of habitats (see Fig. 2), including coastal desert mountains (Cañón de Nacapule in the Sierra El Aguaje [site 1], foothills of the Sierra El Aguaje near San Carlos [site 2] and Cerro Microondas El Vigía located immediately behind Guaymas [site 8]), mangrove "esteros" (negative estuaries or hypersaline lagoons with little or no permanent freshwater inflow; El Esterito [site 3], Estero del Soldado [site 5] and Estero de Bacochibampo, also known as Estero Miramar [site 6]), coastal sand dunes and adjacent coastal plains (site 4), and coastal areas with rocky shores (sites 7 and 9).

To the south and east of Guaymas desert thornscrub replaces Sonoran Desert vegetation. In the Guaymas region, the coastal plain immediately behind the sand
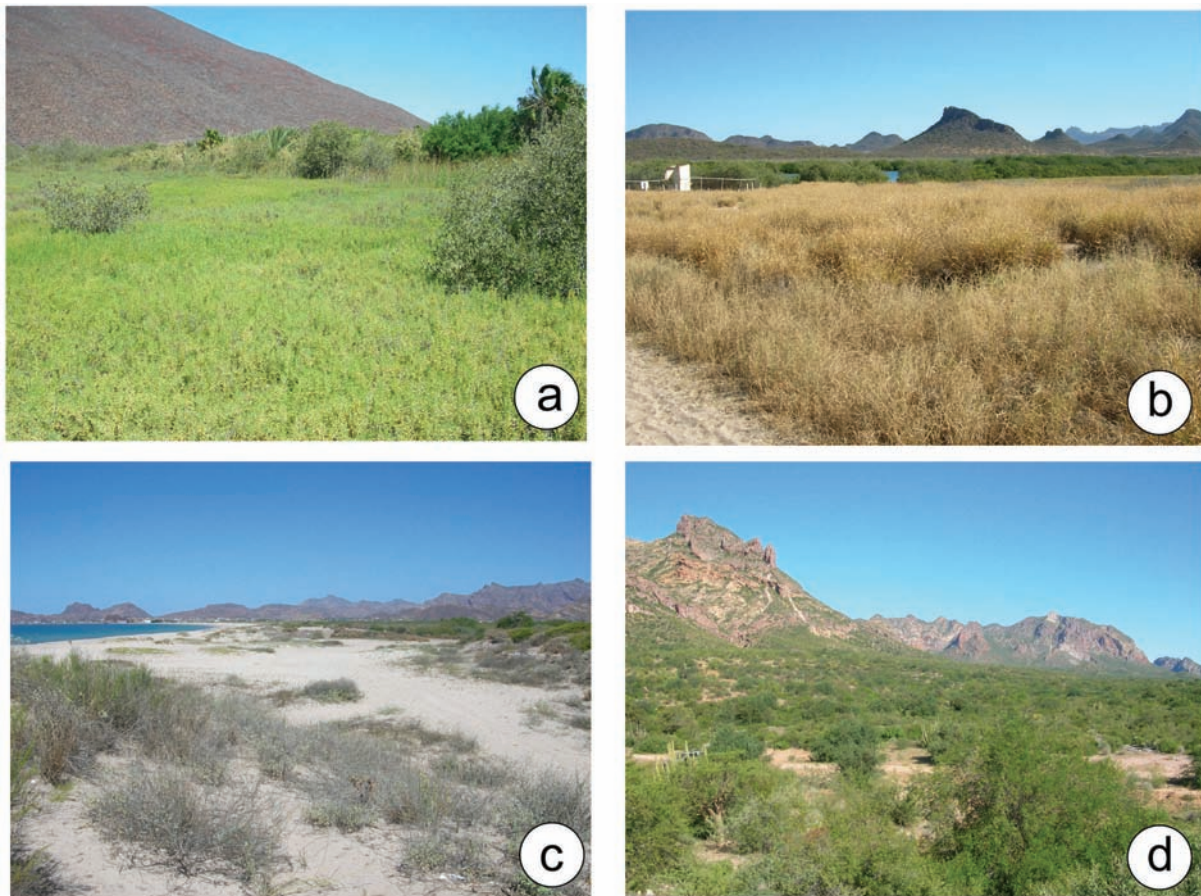
Fig. 2. (**a**) North part of Estero de Bacochibampo (site 6) showing large field of saltwort *Batis maritima*, with southern cattail *Typha domingensis* Pers. (Typhaceae) in the background, and two small black mangrove trees *Avicennia germinans* in the foreground. *Ascia m. monuste* is especially abundant here, flying with smaller numbers of *Junonia genoveva*; (**b**) Buffelgrass (*Pennisetum ciliare*) invasion of coastal sand dunes (foreground) adjacent to mangrove trees at Estero del Soldado (site 5, seen in background); (**c**) Coastal sand dunes (site 4) west of Estero del Soldado. Desert palafox *Palafoxia arida* is an important nectar source on the dunes, attracting large numbers of different species, especially *Danaus gilippus thersippus* in the fall; (**d**) Sierra El Aguaje, north of San Carlos. Cañón de Nacapule (site 1) is in the distant center at the base of mountains.

dunes and extending to the base of the Sierra El Aguaje is comprised primarily of vegetation characteristic of a desertscrub–thornscrub ecotone. Currently, urban sprawl in the Guaymas region is rapidly degrading and fragmenting this habitat, as well as the immediate coastal areas, although much of the vegetation of the rugged desert mountains of the Sierra El Aguaje remains largely unaltered (Felger 1999). The northernmost extent of the tropical deciduous forest biome in western North America occurs approximately 140 km east of Guaymas (Martínez-Yrízar et al. 2010; also see Fig. 1), and tropical elements from this biome enter the protected canyons in the study area, especially at Cañón de Nacapule (Felger 1999). The spring-fed oases of the most accessible lower tropical canyons of the Sierra El Aguaje, especially at Nacapule, are becoming popular local tourist destinations and

increased and largely unregulated human use is also threatening the biodiversity of the flora and fauna in these isolated freshwater microhabitats (Bogan et al. 2014).

The climate in the Guaymas region is characterized by generally frost-free winters and high summer temperatures that can exceed 40°C (see Brito-Castillo et al. 2010). Relative humidity during the summer is also high, averaging about 70%, with daily values often exceeding 85%. Rainfall, which is highly variable, averages about 220 mm per year, most of which occurs during the summer and early fall (Durrenberger & Murrieta 1978). The remainder occurs during the winter and spring associated with North Pacific frontal systems, but in many years these winter storms are absent. In the 8-month period from November 2013 through June 2014, only 6 mm of rain was recorded at
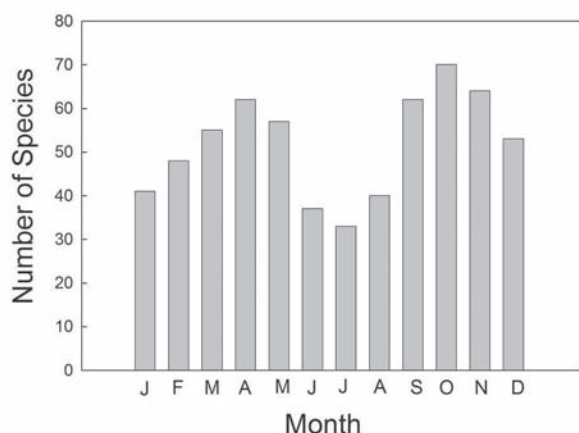
FIG. 3. Total number of butterfly species recorded during each month in the Guaymas region (data from all sites combined) summarized from Table 1.

San Carlos, and only about twice that amount occurred during the same period of 2012/2013 (EP, personal observation). The extreme heat and seasonal drought severely limits most plant life (Felger 1999), which in turn can have profound effects on butterfly abundance by influencing range expansions and contractions (Bailowitz & Palting 2010). Larvae of several species in the Guaymas region, however, feed solely, or mainly on halophytes (see Discussion), and thus their populations appear to be largely independent of the variable annual rainfall.

Butterfly monitoring. Presence data were obtained by systematically monitoring coastal areas deemed to be under the greatest threat of habitat degradation based on current and projected development (sites 3 to 6) from November 2013 to July 2015. Walking surveys lasting about one hour and following approximately the same route on each survey were conducted weekly or biweekly by EP. We also included additional periodic observations and collection records from all sites in the data set, mainly obtained from 2003 to 2012, although some records were from earlier years (1978, 1983–85, 1996 and 1998). A previous study (Pfeiler et al. 2012a) reported on the relative seasonal abundance of the mangrove buckeye *Junonia genoveva* at site 5. Because of the large number of species surveyed here it was not feasible for a single observer to determine seasonal abundance for each one. However, general observations on relative seasonal changes in overall butterfly abundance are mentioned. A recent study (Casner et al. 2014) has shown the usefulness of multi–species presence data, as reported here, in inferring population trends over time. Species records for the Guaymas region also were obtained from the literature and from

two excellent websites, the Butterflies of America (Warren et al. 2013) and the Butterflies and Moths of North America (Lotts & Naberhaus 2014).

With minor exception, nomenclature follows Pelham (2008) for species that are also recorded in the USA, and Warren et al. (2013) for those with tropical affinities. In Pelham (2008), the spelling of the original specific epithet is retained and not changed to conform to the gender of the genus name. Common butterfly names follow those given on the Butterflies of America website. Identification of species utilizing this website as a guide was straightforward in most cases. However, two species of the Hesperiidae listed by Brock (2009) for Sonora, *Urbanus procne* (Plötz) and *Achalarus toxeus* (Plötz), are often difficult to distinguish from their congeners in Mexico. To provide support for taxonomic assignments, DNA barcodes were obtained for several specimens tentatively assigned to these species. Methods for extracting DNA from butterfly legs, and for amplifying and sequencing a 658 bp segment of the mitochondrial cytochrome c oxidase subunit I gene (COI) are described elsewhere (Pfeiler et al. 2012b). Comparison of the new COI sequences (accession numbers given below) with reference sequences available in the Barcode of Life Data Systems (BOLD) (Ratnasingham & Hebert, 2007) confirmed our identifications of *U. procne* (GenBank KT290034–KT290036) and *A. toxeus* (KT290038). Names for plants generally follow the Southwest Environmental Information Network (SEINet 2014) or Turner et al. (1995).

RESULTS

Butterfly presence data from the four coastal sites obtained during the intensive survey (2013 to 2015), together with data obtained from all sites in all years, were combined and presented as species observed over monthly intervals (Table 1). A total of 105 butterfly species was recorded over the 38-year period in the Guaymas region, representing about 30% of the 353 butterfly species currently recorded for the state of Sonora by Brock (2009). Of the total, only five species were not recorded along the immediate coast. These include *Agathymus fieldi* (Hesperiidae), a species not personally observed by us but which has been reported for Cañón de Nacapule (site 1) by J. P. Brock (Warren et al. 2013), *Anartia jatrophae luteipicta*, *Microtia elva* and *Texola perse* (Nymphalidae) from site 2, and *Euchloe guaymasensis* (Pieridae) from site 8.

Based on our long-term observations, most species recorded are permanent residents in the study area. In addition, these observations reveal no obvious trends in population increases or decreases in the resident species

over four decades. Several species, however, were only seen once and are considered strays from nearby thornscrub or tropical deciduous forest habitats. These include *Astraptes fulgerator azul* (see footnote to Table 1), *Panoquina ocola ocola, Battus polydamas polydamas, Phoebis neocypris virgo, Chlorostrymon simaethis sarita, Smyrna blomfildia, Anartia jatrophae luteipicta, Microtia elva, Anthanassa tulcis* and *Texola perse*. It is possible, however, that *T. perse*, which is quite similar to the abundant *Dymasia dymas chara*, may actually occur more regularly in the region but was overlooked. One tropical species, *Heliconius charithonia vazquezae*, is known to stray widely (Bailowitz & Brock 1991; Cardoso 2010). Single sightings of *H. charithonia vazquezae* occurred in San Carlos in November and December, 1983, March, 1984, and April and November, 1985, but this species has not been seen by us in the survey area since 1985. The migratory monarch *Danaus plexippus plexippus* is occasionally observed (20 confirmed sightings since 2012) from November through February (Table 1).

As mentioned above, it was not feasible for a single observer to obtain systematic abundance data for the large number of species recorded here during the intensive survey. Relative butterfly abundance, however, was highest after the summer rains, usually peaking in October and November, with dramatic decreased abundance evident beginning in early January and lasting throughout the spring and summer to about mid August. Presence data during January to August for many of the species shown in Table 1 were based on sightings of only one or a few individuals, whereas large numbers of many of these same species were seen in the fall. The total number of species observed was highest in October and lowest during July (Fig. 3).

During this study we documented several important nectar sources for butterflies along the coast of Sonora, especially during seasonal drought, including Berlandier's wolfberry *Lycium berlandieri* Dunal (Solanaceae), honey mesquite *Prosopis glandulosa* Torr., coastal sand verbena *Abronia maritima* Nutt. ex S. Watson (Nyctaginaceae), and desert palafox *Palafoxia arida* B.L. Turner & Morris (Asteraceae).

DISCUSSION

Potentially threatened species. Four of the 105 species recorded in the Guaymas region, *Polites norae* (Hesperiidae), *Panoquina errans* (Hesperiidae), *Hypostrymon critola* (Lycaenidae), and *Junonia genoveva* (Nymphalidae) are dependent on specific larval host plants growing in the intertidal zone, or adjacent sand dunes and coastal plains, and thus are considered under the greatest threat owing to coastal

habitat degradation. Only Estero del Soldado (site 5), designated as a "Natural Protected Area" administered by the State of Sonora, presently receives partial protection. In addition, three species of mangroves found in the coastal lagoons near Guaymas, black mangrove *Avicennia germinans* (L.) L. (Acanthaceae), red mangrove *Rhizophora mangle* L. (Rhizophoraceae), and white mangrove *Laguncularia racemosa* (L.) Gaertn. f. (Combretaceae) are officially recognized in Mexico as species at risk requiring protection and conservation, and are currently listed as a threatened species (Diario Oficial de la Federación 2003, 2010). Sweet mangrove *Tricerma phyllanthoides* (Benth.) Lundell [= *Maytenus phyllanthoides* Benth.] (Celastraceae), which grows in close association with the other mangroves and on the nearby coastal plains, is abundant and not protected. The principal native grasses (Poaceae) growing in coastal areas are saltgrass *Distichlis spicata* (L.) Greene and shoregrass *Monanthochloe littoralis* Engleman which was recently transferred to the genus *Distichlis* based on molecular studies (Bell & Columbus 2008). To the list of native grasses can now be added the invasive exotic Old World buffelgrass *Pennisetum ciliare* (Fig. 2b). A brief description of the ecology, larval host plant requirements, geographic distribution and taxonomic history of the four potentially threatened butterfly species is given below. Several additional species, either on the periphery of their geographic distribution or of special taxonomic or ecological interest, are also discussed. Photographs of all species listed in Table 1 can be found in Warren et al. (2013).

Polites norae. The Guaymas skipper, *P. norae*, is an inconspicuous species which was recently described from material collected primarily during April 1988 at Bahía de Bacochibampo, Guaymas (MacNeill 1993). The habitat description mentioned the presence of cattails (Typhaceae), which indicates the types were collected at the northern end of Estero de Bacochibampo (site 6; see Figs. 1 and 2a). The larval host plant was presumed to be saltgrass, *Distichlis spicata* (MacNeill 1993), but is now known to be shoregrass *Distichlis littoralis* (J.P. Brock, personal communication; also see Warren et al. 2013). *Polites norae* was never common during the intensive survey, but was seen during most months (Table 1), suggesting at least two broods per year. Adults were found only along the immediate coast at sites 4 and 5 (about 5 km from the type locality) where both *D. littoralis* and *D. spicata* are present. Interestingly, no records for *P. norae* were obtained at the type locality (site 6) or at El Esterito (site 3), sites where *D. littoralis* was absent or at least not easily located.

Table 1. Monthly presence records (+) for the 105 butterfly species observed in the Guaymas region.

	J	F	M	A	M	J	J	A	S	O	N	D
HESPERIIDAE												
Eudaminae												
Polygonus leo arizonensis (Skinner)							+					
Chioides albofasciatus (Hewitson)		+	+	+	+	+			+	+	+	+
Chioides zilpa (Butler)		+	+	+	+	+			+	+	+	+
Urbanus proteus proteus (Linnaeus)										+	+	+
Urbanus dorantes dorantes (Stoll)	+							+	+	+	+	+
Urbanus procne (Plötz)					+	+	+			+	+	+
Astraptes fulgerator azul (Reakirt)[a]			+									
Achalarus toxeus (Plötz)	+	+	+	+	+					+	+	+
Cogia hippalus hippalus (W.H. Edwards)				+	+	+	+	+	+	+		
Pyrginae												
Bolla clytius (Godman & Salvin)	+	+	+							+		
Staphylus ceos (W.H. Edwards)			+	+						+		
Pholisora catullus (Fabricius)			+				+	+	+	+		
Timochares ruptifasciata (Plötz)		+	+	+					+	+		
Chiomara georgina georgina (Reakirt)		+		+	+			+	+	+	+	+
Erynnis funeralis (Scudder & Burgess)	+	+	+	+	+	+		+	+	+	+	+
Systasea zampa (W.H. Edwards)	+	+	+	+	+	+			+	+		+
Celotes nessus (W. H. Edwards)							+	+	+			
Pyrgus albescens Plötz		+	+	+	+				+	+	+	+
Heliopyrgus domicella (Erichson)		+		+	+		+		+	+		+
Heliopetes laviana laviana (Hewitson)		+	+	+	+	+		+	+	+	+	
Hesperiinae												
Agathymus fieldi H. Freeman										+		
Ancyloxypha arene (W.H. Edwards)									+	+	+	
Copaeodes aurantiaca (Hewitson)	+	+	+	+	+	+	+		+	+		
Copaeodes minima (W. H. Edwards)					+				+	+		
Panoquina errans (Skinner)	+	+	+	+	+	+	+	+	+	+	+	+
Panoquina ocola ocola (W.H. Edwards)				+								
Amblyscirtes tolteca prenda Evans					+	+	+	+	+			
Lerodea eufala eufala (W.H. Edwards)	+	+	+	+	+	+	+	+	+	+	+	+
Lerodea arabus (W.H. Edwards)	+	+	+		+					+	+	+
Lerema accius (J. E. Smith)		+	+								+	
Hylephila phyleus phyleus (Drury)	+	+	+	+	+	+	+	+	+	+	+	+
Polites norae C. MacNeill	+	+	+	+	+	+		+			+	+

Table 1. Continued

| | Month | | | | | | | | | | | |
	J	F	M	A	M	J	J	A	S	O	N	D
PAPILIONIDAE												
Papilioninae												
Battus philenor philenor (Linnaeus)	+	+		+	+	+	+	+	+	+	+	+
Battus polydamas polydamas (Linnaeus)										+		
Papilio polyxenes asterius (Stoll)		+		+	+	+	+					
Heraclides rumiko Shiraiwa & Grishin			+	+	+	+	+	+	+	+		
PIERIDAE												
Coliadinae												
Kricogonia lyside (Godart)	+	+	+	+	+	+	+	+	+	+	+	+
Nathalis iole Boisduval	+	+	+	+	+				+	+	+	+
Eurema daira sidonia (R. Felder)										+	+	
Eurema boisduvaliana (C. Felder & R. Felder)	+	+	+	+	+	+			+	+	+	+
Eurema mexicana mexicana (Boisduval)			+	+	+				+	+	+	+
Pyrisitia proterpia (Fabricius)	+								+	+	+	+
Pyrisitia lisa (Boisduval & Le Conte)		+	+	+	+				+	+	+	
Pyrisitia nise nelphe (R. Felder)	+		+	+	+	+		+	+	+	+	+
Abaeis nicippe (Cramer)	+	+	+	+	+	+	+	+	+	+	+	+
Colias eurytheme Boisduval				+	+		+	+	+		+	
Zerene cesonia cesonia (Stoll)	+	+	+	+	+	+	+	+	+	+	+	+
Anteos clorinde (Godart)									+			
Anteos maerula (Fabricius)							+	+	+		+	
Phoebis sennae marcellina (Cramer)	+	+	+	+	+	+	+	+	+	+	+	+
Phoebis agarithe agarithe (Boisduval)			+	+	+	+	+	+	+	+	+	+
Phoebis philea philea (Linnaeus)									+		+	
Phoebis neocypris virgo (Butler)						No Date						
Pierinae												
Euchloe guaymasensis Opler		+										
Pontia protodice (Boisduval & Le Conte)	+		+	+			+	+	+	+	+	
Ascia monuste monuste (Linnaeus)	+	+	+	+	+	+	+	+	+	+	+	+
Ganyra howarthi (Dixey)	+	+	+	+	+	+	+	+	+	+	+	+

TABLE 1. Continued

	J	F	M	A	M	J	J	A	S	O	N	D
LYCAENIDAE												
Theclinae												
Atlides halesus corcorani Clench			+									
Arawacus jada (Hewitson)				+								
Chlorostrymon simaethis sarita (Skinner)					+							
Strymon melinus franki W.D. Field	+	+	+	+	+	+			+	+	+	
Strymon bebrycia (Hewitson)				+	+					+		+
Strymon bazochii bazochii (Godart)					+							
Strymon istapa istapa (Reakirt)			+	+	+				+	+	+	+
Ministrymon leda (W.H. Edwards)	+			+	+	+			+	+	+	+
Hypostrymon critola (Hewitson)	+	+	+	+	+	+			+	+	+	+
Polyommatinae												
Leptotes marina (Reakirt)		+	+	+	+	+				+	+	
Brephidium exilis exilis (Boisduval)	+	+	+	+	+	+	+	+	+	+	+	+
Hemiargus ceraunus gyas (W.H. Edwards)	+		+	+	+	+	+	+	+	+	+	+
Echinargus isola (Reakirt)			+								+	
RIODINIDAE												
Riodininae												
Calephelis nemesis nemesis (W.H. Edwards)	+	+	+	+	+	+			+	+	+	+
Calephelis arizonensis McAlpine						+	+	+				
Apodemia mejicanus mejicanus (Behr)				+	+		+	+	+	+		
Apodemia palmerii arizona Austin		+	+	+	+			+	+	+	+	
Apodemia multiplaga Schaus			+					+				
Baeotis zonata zonata Felder		+		+								
NYMPHALIDAE												
Libytheinae												
Libytheana carinenta streckeri Austin & J. Emmel	+	+	+	+	+			+	+	+	+	+
Danainae												
Danaus plexippus plexippus (Linnaeus)	+	+									+	+
Danaus gilippus thersippus (H. Bates)	+	+	+	+	+	+	+	+	+	+	+	+
Danaus eresimus montezuma Talbot											+	+
Heliconiinae												
Agraulis vanillae incarnata (N. Riley)	+	+	+	+	+	+	+	+	+	+	+	+
Heliconius charithonia vazquezae W. Comstock & F. Brown			+	+							+	+
Euptoieta claudia (Cramer)							+					
Euptoieta hegesia meridiania Stichel	+			+	+	+		+	+	+	+	+

TABLE 1. Continued

	J	F	M	A	M	J	J	A	S	O	N	D
						MONTH						
NYMPHALIDAE (continued)												
Apaturinae												
Asterocampa idyja argus (H. Bates)										+		
Biblidinae												
Mestra amymone (Ménétriés)	+								+	+		
Myscelia cyananthe skinneri Mengel	+	+	+	+		+	+	+	+	+	+	
Hamadryas februa (Hübner)[b]									+			
Hamadryas glauconome grisea Jenkins[b]		+							+	+		+
Nymphalinae												
Smyrna blomfildia (Fabricius)							+					
Vanessa virginiensis (Drury)											+	+
Vanessa cardui (Linnaeus)	+	+	+	+				+	+	+	+	+
Vanessa annabella (W.D. Field)				+	+						+	+
Vanessa atalanta rubria (Fruhstorfer)		+										
Anartia jatrophae luteipicta Fruhstorfer						No Date						
Junonia nigrosuffusa W. Barnes & McDunnough			+							+	+	+
Junonia genoveva (Cramer)	+	+	+	+	+	+	+	+	+	+	+	+
Chlosyne eumeda (Godman & Salvin)	+		+	+	+				+	+	+	+
Chlosyne lacinia crocale (W.H. Edwards)				+					+			
Microtia elva H. Bates						No Date						
Dymasia dymas chara (W.H. Edwards)			+	+			+	+	+	+	+	
Texola perse (W.H. Edwards)					+							
Anthanassa tulcis (H. Bates)												+
Anthanassa texana texana (W.H. Edwards)	+	+	+	+	+	+			+	+	+	
Charaxinae												
Anaea aidea (Guérin-Méneville)	+	+		+				+	+	+	+	+

[a] The correct name for this taxon is uncertain as *Astraptes fulgerator* is now considered a complex of species–level taxa (Hebert et al. 2004; Brower, 2010).

[b] *Hamadryas* spp. were observed in April, July, October, November and December, but specimens were not collected and thus could not be confidently identified to species (see Bailowitz & Brock 1991).

MacNeill (1993) had foreseen the potential for habitat degradation at the type locality, and shortly after the types were collected construction of a marina and dredging of Estero de Bacochibampo began. Although most of the lagoon was drastically altered, legal and environmental issues have halted construction for more than 20 years. The mangroves and cattails at the type locality were spared, but enough habitat disruption and loss of larval host plant may have occurred to extirpate the local population of *P. norae*. An extensive area of saltwort *Batis maritima* L. (Bataceae) is now present at this site (Fig. 2a).

Polites norae has been recorded from Puerto Peñasco, Sonora, at the extreme northern end of the Gulf of California (J.P. Brock, personal communication), to Mazatlán, Sinaloa (MacNeill 1993). It was not reported in checklists of butterflies farther south in the states of Jalisco (Vargas et al. 1996) or Colima (Warren et al. 1998), nor is it present on the Baja California Peninsula (Brown et al. 1992, MacNeill 1993). Thus, the distribution of *P. norae* appears to be limited to the narrow coastal strand of northwestern mainland Mexico. Along the coast, near Bachoco in extreme southern Sonora, large stands of *D. littoralis* are found and adults and larvae of *P. norae* were reported to be abundant as recently as the mid-2000s (J.P. Brock, personal communication). But given its restricted distribution and ongoing habitat destruction and loss of host resources, *P. norae* is considered potentially threatened and populations should be monitored.

Panoquina errans. The wandering skipper, *P. errans*, has a wide geographic distribution, found from southern California, USA, the Baja California Peninsula, and mainland Mexico to at least the state of Oaxaca (Warren et al. 2013). But as with the previous species, *P. errans* is restricted to coastal habitats where its host plant *D. spicata* is found (Brown et al. 1992; Pfeiler & Jump 2010). *Panoquina errans* is currently ranked on the IUCN Red List (IUCN 2013) as Lower Risk/near threatened. NatureServe (http:www.natureserve.org) lists *P. errans* as G4G5 (apparently secure or secure globally), but in southern California, at the northern limit of its range, it is listed as S1 (critically imperiled at the state level) owing to the loss of most of its coastal wetland habitat (Speth 1971). Brown et al. (1992) also commented that the continued degradation of coastal salt marshes on the Baja California Peninsula posed a serious threat to this species. In the Guaymas region, *P. errans* was found at coastal sites throughout the year (Table 1) suggesting that the population is healthy. But given its dependence on the threatened coastal habitat the species should be considered potentially at risk.

The fact that *P. errans* is not listed as imperiled at the global level is based on the assumption that the species is panmictic. The possibility of genetic differentiation among geographic populations of *P. errans* throughout its range, however, has not been examined. MacNeill (1962) reported a clinal change in specimens from Santa Barbara, California, USA to the peninsular Cape Region, with southern peninsular specimens from Cabo San Lucas, BCS being slightly larger and darker than those from California. There is also a possibility that disjunct populations from the peninsula and mainland Mexico separated by the Gulf of California may show genetic differentiation similar to that seen in several other species of insects and arachnids (Pfeiler & Markow 2011, Pfeiler et al. 2013). Phenotypic differences between peninsular populations of other butterfly species that also occur on the mainland have resulted in the recognition of several unique peninsular subspecies (MacNeill 1962, Brown et al. 1992). The possibility of genetic differentiation among populations of *P. errans* would have important implications relating to its conservation and management (e.g. McHugh et al. 2013).

Hypostrymon critola. The Sonoran hairstreak, *H. critola*, is found throughout most of the year in the Guaymas region (Table 1), and was especially abundant at site 4 during March, April and December. This species utilizes sweet mangrove (*Tricerma phyllanthoides*) as a larval host in northwestern Mexico (Clench 1975; Brown et al. 1992; Warren et al. 2013), a plant that grows well on wet, saline soils typical of coastal flats of Sonora and Baja California Sur (Turner et al. 1995). Adults are usually found in close association with the host plant. In the Sonoran Desert, however, *H. critola* is also found inland and in southern Mexico (see below), where sweet mangrove is not found, suggesting that other larval hosts may be utilized (Clench 1975, Bailowitz & Brock 1991).

Hypostrymon critola was described by W.C. Hewitson in 1874 (as *Thecla critola*) who listed the type locality only as "Mexico". Historical evidence was later presented indicating that the type locality should be restricted to Guaymas (Clench 1967). In 1891, a very similar species, *H. festata* (Weeks) was described from the Cape Region of the Baja California Peninsula. In subsequent works, Clench (1967, 1975) considered *H. festata* a subspecies of *H. critola*, and in his 1975 paper described two new species from Mexico, *H. margaretae* from Sinaloa and *H. aderces* from Colima and Guerrero. Pelham (2008) considered the names *festata*, *margaretae* and *aderces* junior synonyms of *H. critola*, although possible genetic differentiation among populations has not been studied. Clench (1975) noted that genitalia of all his proposed species in Mexico were

similar. Here we follow Pelham (2008) and recognize a single species, *H. critola*, but it is clear that understanding the phylogeography and systematics of this species also would benefit from molecular genetic studies. It is provisionally listed as potentially threatened in the study area until more information is available on possible alternative host plants.

Junonia genoveva. The mangrove buckeye, *J. genoveva*, is a common inhabitant of mangrove estuaries and adjacent coastal areas of northwestern Mexico, including Baja California Sur (Brown et al. 1992, Pfeiler et al. 2012a). The larval host plant is black mangrove (Pfeiler 2011), thus larvae of *J. genoveva* have a reliable food source that is independent of the highly variable seasonal rainfall in this region. Although previously assigned to *J. evarete* (Cramer) (Brown et al. 1992), or referred to as a hybrid between *J. evarete zonalis* C. Felder & R. Felder and *J. coenia* Hübner (Hafernik 1982), molecular studies suggest that this species should be reassigned, at least provisionally, to *J. genoveva* (Pfeiler et al. 2012b). Although its taxonomy is unstabilized, the ecology and phenology of *J. genoveva* is relatively well known (Pfeiler 2011, 2012a). Adults are on the wing throughout the year (Table 1), but are most abundant during the summer and fall months (Brown et al. 1992, Pfeiler et al. 2012a).

In the Gulf of California, most of the mangrove estuaries have been modified for aquaculture, although these farms are mainly located in sections of the estuaries not occupied by the mangroves (DeWalt et al. 2002, Glenn et al. 2006). However, the long–term ecological effects of secondary impacts of aquaculture on the mangrove ecosystem, such as discharge of nutrients and organic matter (Páez-Osuna et al. 1997, 1998) and the removal of associated coastal flora during construction of the facilities, are unknown. Worldwide, the mangrove forest ecosystem is also highly threatened, primarily owing to aquaculture and tourism developments (Aburto-Oropeza et al. 2008). Because available life history information suggests that populations of *J. genoveva* in northwestern Mexico are restricted to a single threatened larval host plant (Pfeiler 2011), the butterfly also should be considered as potentially threatened.

Additional species of interest. The great southern white, *Ascia monuste monuste* (Pieridae), is a common resident throughout the year in coastal regions of Sonora (Table 1), being especially abundant in the intertidal zone of mangrove estuaries and sand dunes where saltwort *Batis maritima* occurs, its principal larval host plant in northwestern Mexico (Brown et al. 1992). The subspecies, *A. m. raza* Klots is found in coastal areas of the southern half of the Baja California Peninsula and offshore gulf islands (Brown et al. 1992). Although larvae of *A. m. monuste* are polyphagous (DeVries 1987, Janzen & Hallwachs 2009), and the butterfly is widely distributed (southwestern USA to northern South America) and secure globally (ranked G5), we include it here as a species of interest because the principal saltwort host occurs in the region most threatened by development.

Howarth's white, *Ganyra howarthi* (Pieridae), is also a common inhabitant of the survey area often found closely associated with its larval foodplant, desert caper *Atamisquea emarginata* Miers (Capparaceae) (Bailowitz 1988). The foodplant is found throughout much of the Sonoran Desert, including the states of Sonora, Baja California Sur, and southern Baja California, showing a preference for gravelly or sandy plains in maritime climates, but can also be found inland (Turner et al. 1995, SEINet 2014). Distribution records for *G. howarthi* generally reflect the maritime distribution of the larval foodplant (Bailowitz 1988, Brown et al. 1992, Turner et al. 1995), although the butterfly also occurs inland and is known to stray to southeastern Arizona (Bailowitz & Brock 1991). The southernmost verified record is Los Mochis in northern Sinaloa (Bailowitz 1988). As on the Baja California Peninsula (Brown et al. 1992), *G. howarthi* is multiple brooded in the survey region and adults can usually be found throughout the year (Table 1).

The spelling and location of the type locality of *G. howarthi* deserve special mention. The species was originally described as *Pieris howarthi* by Dixey (1915) from specimens collected by Osbert H. Howarth at Tembabichi Bay in Lower California [Baja California Sur, Mexico]. This locality is now listed as "Timbabichi" (INEGI 2014)], but other spellings (e.g. "Tambobiche" and "Tambibiche") are found on maps and navigation charts. Although the latitude of the type locality was originally listed as 26°05′ N (Dixey 1915), this latitude is probably an error as the geographic coordinates of Timbabichi on the Gulf coast of the peninsula are 25°16′ N, 110°57′ W) (INEGI 2014; Google™ Earth [labeled "Tambobiche"]). Desert caper occurs on several of the Midriff Islands in the upper Gulf of California (Turner et al. 1995; SEINet 2014) and given that *G. howarthi* is a relatively strong flier, it is generally assumed that the peninsular and mainland populations are panmictic. But genetic confirmation for the lack of population structure and genetic diversification is lacking. A name is available for the mainland population (Bailowitz 1988) if it is ultimately shown to be genetically distinct from the peninsular population.

Although presently not considered at risk, the Sonoran marble, *Euchloe guaymasensis* (Pieridae), is

also a species of interest because of its relatively recent discovery near Guaymas (Opler 1987). The species is widespread in Sonora (Holland 1995), and given its distribution that includes mountain regions with limited access, the species would appear to be secure. As mentioned earlier, *E. guaymasensis* was found only at site 8 at an altitude of about 215 m where its reported larval host plants, western tansymustard *Descurainia pinnata* (Walt.) Britt. (Brassicaceae) (Holland 1995) and rockmustard *Dryopetalum runcinatum* A. Gray (Brassicaceae) (Back et al. 2011) are found. Both host plants are recorded from the Sierra El Aguaje (SEINet 2014) and additional field work during the main flight period (January to March) may reveal the occurrence of the butterfly there as well. Of concern, however, is that buffelgrass appears to be crowding out the native larval foodplants of *E. guaymasensis* in some areas (J.P. Brock, personal communication).

Species occurring at or near the geographic limits of their range can potentially offer important insight into the relative importance of ecological, environmental, and anthropogenic factors that impact population range expansions and declines (Pfeiler 2013). The narrow-winged metalmark, *Apodemia multiplaga* (Riodinidae), was recorded on the coastal sand dunes, but apparently is near the northwestern limit of its distribution and is quite sporadic in its occurrence. In late March 1998, *A. multiplaga* was relatively abundant on the dunes near San Carlos (J.P. Brock, personal communication), but there have been no subsequent reports until 2014 (present study) when four adults (mid- to late March), and one adult (mid-September), were found feeding on flowers of desert palafox at site 4. The species is widely distributed throughout central and southern Mexico in both coastal and inland regions (Warren et al. 1998, UNIBIO 2014), and is found as far south as northwestern Costa Rica in tropical deciduous forest (DeVries 1997). It has not been reported from the Baja California Peninsula (Brown et al. 1992). Although *A. multiplaga* was described more than a century ago (Schaus 1902), the early stages and larval host plant(s) have not been reported (DeVries 1997). Thus, it is unknown whether the species breeds in the study region, but because it is only rarely seen here it is included as a species of interest that may be threatened by coastal development. It is also possible, however, that the scarcity of sightings is a result of seasonal fluctuations in abundance of a species on the periphery of its distribution (Bossart & Carlton 2002).

The mottled sootywing, *Bolla clytius* (Hesperiidae), is another widespread species, occurring from northern Mexico to Honduras, with rare strays recorded for southeastern Arizona and southern Texas (Bailowitz &

Brock 1991; Warren et al. 2013). It has not been reported from the Baja California Peninsula (Brown et al. 1992). Although apparently common in tropical deciduous forest and thornscrub habitat in Sonora (Bailowitz & Brock 1991; Glassberg 2001), it is also a species which is near the northwestern limits of its distribution and apparently is not common in the study region. Only five adults were recorded, one in October 2010 at San Carlos, and four at site 4 from January to March, 2014 feeding on flowers of Berlandier's wolfberry. As with *A. multiplaga*, the larval host plant of *B. clytius* has not been reported, and the butterfly is also listed as a species of interest.

Conservation prospects. A thorough understanding of regional biodiversity is essential before conservation measures can be considered on taxa of interest in the face of landscape conversion and fragmentation. The present study provides the first comprehensive baseline data on species richness of the butterfly fauna in coastal southern Sonora, a region currently undergoing rapid and extensive landscape transformation. We focused on the butterflies because they are relatively easy to identify and monitor. The conservation issues raised here, however, obviously apply to invertebrates in general, terrestrial and aquatic, dependent on the coastal habitat in northwestern Mexico.

In addition to an inventory documenting species richness, knowledge of the ecology of potentially threatened species is crucial to predicting what the overall impact of landscape transformation might have on survival of the species in question. Previous studies cited above have documented the specific host plant requirements of *Polites norae*, *Panoquina errans*, *Hypostrymon critola* and *Junonia genoveva*. Knowing that each species requires a specific larval host plant largely restricted to coastal habitats allowed us to predict that these four species are potentially the most vulnerable to habitat degradation. The continued fragmentation and loss of the natural vegetation in this region is highly probable given that the land is privately owned and designated for development. Although there is little prospect of setting aside and preserving the sand dunes and coastal plains near Guaymas, the Mexican government has specified a large tract of coastal habitat in extreme southern Sonora as a "priority area" for protection (Arriaga et al. 2000). It is unknown whether the "priority area" will ultimately receive official protected status, but the four species of butterflies we identified as potentially threatened, and their larval host plants, are present there.

Note added in proof. A single individual of *Ministrymon clytie* (W.H. Edwards), a species not previously observed by us in the study region, was

photographed by EP at site 4 on 24 October 2015, thus bringing the total number of species to 106. Also, a single individual of *Anartia jatrophae luteipicta* Fruhstorfer (Table 1) was seen at site 1 on 29 October 2015, providing an additional record and confirmed date for this species. Site 1 has recently been added to the list of "Natural Protected Areas" by the State of Sonora.

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DISMORPHIA MELIA (GODART, [1824]) (PIERIDAE: DISMORPHIINAE): EXTERNAL MORPHOLOGY OF THE LAST INSTAR AND PUPA, WITH NOTES ON ITS TAXONOMY, VARIATION AND DISTRIBUTION

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ABSTRACT. The external morphology of the last instar and pupa of *Dismorphia melia* (Godart, [1824]) are described from specimens collected at São Bento do Sul, Santa Catarina, Brazil. Morphological descriptions and illustrations are provided on the basis of observations through stereoscopic microscope attached to camera lucida; results are compared and discussed with immature stages of other species of Dismorphiinae, Coliadinae and some tribes of Pierinae with the "type I" pupae. Moreover, the taxonomy of the species is discussed, on the basis of informations and illustrations of the intraspecific variability of the imagoes, the morphology of the genitalia of both sexes, and the geographic distribution.

Additional key words: *Inga*, Fabaceae, pupa, *Actinote*, mimicry

Dismorphiinae is a well-defined and mostly Neotropical subfamily of Pieridae, with about sixty species (Lamas 2004a, Braby et al. 2006). Species of this subfamily are characterized by the long, trisulcate antennae, particularly developed in the distal antennomers; flavones as pigments in the wings; tegumen much shorter than uncus or absent, uncus bilobed; valvae fused; and corpus bursae single, and several species are involved in mimicry with species of Nymphalidae (DeVries 1987, Ackery et al. 1998, Lamas 2004b). In a recent molecular phylogenetic analysis, Dismorphiinae was recognized as sister to the remaining subfamilies of Pieridae (Wahlberg et al. 2014), despite its presumed long association with the Pseudopontiinae. Of the seven recognized genera of Dismorphiinae, six are exclusively Neotropical (Braby et al. 2006); among these, *Dismorphia* Hübner, 1816 encompasses 30 recognized species. The Dismorphiinae genera can be distinguished chiefly by wing venation and characters of the male genitalia (Lamas 1979, Lamas 2004b), and *Dismorphia* was comprehensively diagnosed by Llorente (1984).

Dismorphia melia (Godart, [1824]) (Figs 1–8) is a species regarded as "rare" and indicative of well preserved forests (Brown 1992; Brown & Freitas 2000). This species is distributed in the Atlantic forests of Southeastern and Southern Brazil, from Rio de Janeiro to Rio Grande do Sul (e.g. Teston & Corseuil 2000, Iserhard et al. 2010, Monteiro et al. 2010). The male (Figs 1–2, 5–6) is mostly bright yellow or orange and dark brown, and the dimorphic female (Figs 3–4, 7–8) mimics species of *Actinote* Hübner, [1819], a fact that yielded a number of synonyms (Lamas 2004a).

Despite most species of Pieridae being common and abundant, their immature stages are surprisingly poorly known in the Neotropics, with the exception of a handful of species of agricultural interest. The immature stages of Pieridae could be generally described as follows: eggs are spindle-shaped and ribbed; larva usually with six annulets in the abdominal segments and protuberances of any type (i.e. scoli) absent, except for chalazae (Toliver 1987); pupa slender and tapered at the ends, usually keeled, with a single cephalic projection, and the metathoracic wing cases not visible ventrally (Mosher 1916); the pupa is attached to the substrate by a silk girdle and the cremaster attached to a silk pad. Some recent efforts shed some light on the biology and morphology of Neotropical species of the family (Braby & Nishida 2007, Freitas 2008, Braby & Nishida 2010, Kaminski et al. 2012), nevertheless, focusing in subfamilies other than Dismorphiinae. To illustrate the lack of knowledge of immature stages of Dismorphiinae, the host plant is known to less than one third of the species of *Dismorphia* (Beccaloni et al. 2008) — the largest and most known genus of the subfamily — and even less species were properly described. D'Almeida (1944) and DeVries (1986, 1987) offer brief accounts on the biology and morphology of some species of *Dismorphia*, but only three species were described in more detail. Most species of *Dismorphia* use *Inga* (Fabaceae: Mimosoideae) as host plants, but there are records for some other species of legumes (Beccaloni et al. 2008). This paper aims to describe the external morphology of the last instar and pupa of this species, since information provided by immature stages are referred as important

to the taxonomy of Pieridae (Braby et al. 2006) and Dismorphiinae (Lamas 1979, Llorente 1984); additionally, notes on the taxonomy of the species based on the intraspecific variability of the imagoes, the genitalia morphology and geographic distribution are provided.

MATERIAL AND METHODS

Immature stages. Eggs of *D. melia* were observed in São Bento do Sul, Santa Catarina, Brazil, immediately after they were laid in an unidentified species of *Inga* by the female and reared on the host plant until the last instar. Last instars were collected and brought to the "Laboratório de Estudos em Lepidoptera Neotropical", Universidade Federal do Paraná (LELN-UFPR) and kept in laboratory under ambient conditions in a branch of the host plant inside a plastic bag. Immature stages were measured and observed in detail with the aid of a stereoscopic microscope equipped with micrometric lenses and camera lucida. Nomenclature follows Mosher (1916), Peterson (1962), and Stehr (1987) for larval and pupal morphology. Eggs, head capsules and pupal skins were dehydrated and preserved; voucher specimens were retained at the Coleção Entomológica Pe. Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Coleção de Imaturos de Lepidoptera (DZUP-IL).

Taxonomy, distribution and variation. Adult specimens were photographed and are illustrated in actual size; scale bars provided for other structures. Dissected specimens had their abdomens detached and placed in a test tube with potassium hydroxide 10% solution (KOH 10%). The test tube was heated in a bain-marie inside a beaker filled with water for 2–5 minutes; the genitalia were removed, dissected, and analyzed under stereoscopic microscope. Illustrations were prepared with the aid of a camera lucida. Full lines represent sclerotized structures, thin lines represent membranous structures, and dotted lines represent structures visible through transparent body parts. Distribution maps were prepared using DIVA-GIS 7.3.0 (Hijmans et al. 2011) software; distributional data are from specimens deposited at the DZUP and data available in the literature (Zikán & Zikán 1968, Brown 1992, Brown & Freitas 2000, Iserhard & Romanowski 2004, Zacca 2009, Iserhard et al. 2010, Monteiro 2010, Dolibaina 2011, Francini et al. 2011, Beltrami et al. 2014, Marchiori et al. 2014, Piovesan 2014); in the examined material section, this data are presented in increasing order of precision, such that the most precise piece of information is presented last. Species level and higher taxonomy follows Lamas (2004a) and Wahlberg et al. (2014), respectively.

RESULTS AND DISCUSSION

Immature stages. Last instar. (Figs 9–13, 17–18) Head capsule mostly green, slightly lighter than the body, rounded, with tapered translucent light brown setae over light brown chalazae; on the dorsal and lateral areas of the epicrania, the chalazae are larger and connected by light brown lines in a reticulated pattern (Fig. 11); epicanial suture yellowish green; frontoclypeus green, narrow, about three thirds the height of the head capsule (Fig. 17), clypeal area bulged; adfrontal areas narrow, but wider and nearer to the epicranial notch; labrum transluscent yellowish green, somewhat rectangular, with a deep ventral triangular indentation (Fig. 17); mandibles strong, heavily sclerotized along the smooth cutting edge, without cuspids; stemmata 1–4 lateral and anteriorly directed, equidistant and arranged in a semicircle, stemmata 2–4 elevated, 5 slightly elevated; stemma 5 ventral and ventrally directed; stemma 6 lateral and laterally directed, posterior to and somewhat in the same line of the stemmata 3–4 (Figs 17–18). Body (Figs 9–10, 12–13) nearly cylindrical, tapering posteriad after A6 and conspicuously at A9+10 (Figs 12–13); dorsal, subdorsal and supraspiracular areas green, spiracular area with a lighter yellowish green stripe that runs from T1 to A8, somewhat faded on T1 and A9+10; subspiracular area green, subventral and ventral areas light green; digestive tube visible through transparency, as a darker green shade along the dorsal area; spiracles bordered in light brown, with yellowish green peritrema; dorsal, subdorsal and supraspiracular areas covered by rows of translucent yellowish green truncated, knobby setae, which give the larva a velvety appearance; setae long and tapered on the subventral and ventral areas, longer over the thoracic legs and abdominal prolegs; thorax with four annulets per segment; thoracic legs translucent yellowish green, with brownish tarsal claws; T1 shield indistinct; prothoracic gland ventral, between the head capsule and T1; T1 spiracle ellipsoidal, on the subspiracular area (i.e. slightly ventral to the spiracular stripe) of the second annulet, larger than others; abdomen with six annulets per segment from A1–A6, A7 with five annulets, A8 with three annulets; no annulets are clearly discernible on A9+10; the first annulet of each segment is somewhat larger than the others; spiracles on A1–A6 more rounded and smaller, spiracle on A7 ellipsoidal and larger, but not as large as T1 and A8 spiracles, A8 similar in size to T1 spiracle; spiracles on the second annulet (A1, A7–A8) or between the second and third annulet (A2–A6); A9+10 posteriorly projected dorsally (Fig. 12); anal shield slightly lighter green than the body,

FIGS. 1–8. *Dismorphia melia* (Godart, [1824]). **1–4.** Specimens from Santa Catarina, Brazil. **1–2.** Male, dorsal and ventral. **3–4.** Female, dorsal and ventral. **5–8.** Specimens from Rio de Janeiro state, Brazil. **5–6.** Male, dorsal and ventral. **7–8.** Female, dorsal and ventral. Scale bar = 1cm.

with tapered translucent light brown setae over light brown chalazae, somewhat trapezoidal in dorsal view; posterior edges of the anal shield with a pair of long, tapered terminal setae in each side of the projection and brown hook-shaped setae along the posterior edge (Fig. 13) ("anal comb"); crochets on the abdominal prolegs on A3–A6 as uniserial, triordinal, homoideous mesoseries, A9+10 crochets as a uniserial, triordinal, homoideous mesal pennelipse. Head capsule width: 4.1–4.3mm (n=2); length one day before prepupae: 4.15–4.25cm (n=2).

Pupa. (Figs 14–16, 19–21) mostly green, duller green dorsally, with a continuous yellowish green longitudinal stripe from the basilar tubercle, along the longitudinal ridge of the mesothorax and the abdomen, from A4 to the cremaster, fading posteriad; three pairs of small and irregular dark brown dorsal markings on the prothorax, A2 and A3 (Figs 14, 16); pupae slender and tapered at the ends, strongly keeled ventrally; silk girdle attached to the second abdominal segment. Head with a conical vertical projection about one fifth the length of the pupa; scape and pedicel dorsal, the former larger than
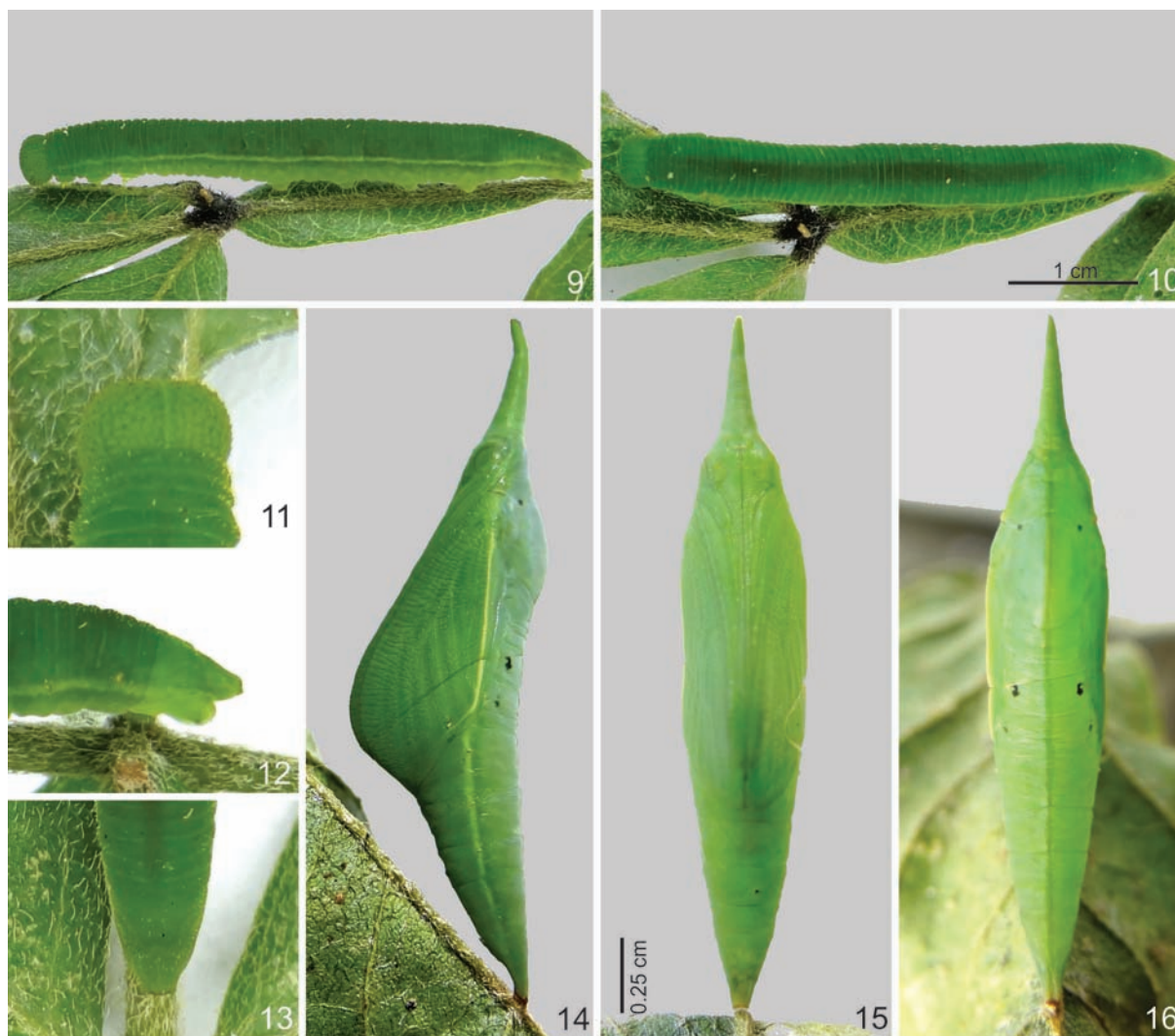
Figs . 9–16. Last instar and pupa of *Dismorphia melia* (Godart, [1824]). **9–10.** Last instar, lateral and dorsal. **11.** Head capsule, dorsal. **12–10**. A9+10, lateral and dorsal. **14–16.** Pupae, lateral, ventral and dorsal. Scale bar: figs 9–10 = 1cm; figs 14–16 = 0.25mm.

the latter; antennae flagellum dorsal at first, extending ventrally and posteriorly between the mesothoracic wing cases; eye cases lateral; frons and clypeus indistinguishable from the genae; anterior tentorial fovea faint; mandibles pentagonal; labium narrow and long, somewhat lozenge-shaped, ventral to the mandibles and dorsal to the galeae; galeae extending between the mesothoracic legs not reaching the posterior end of the mesothoracic wing cases, but slightly longer then the antennae. Prothorax wide; mesothoracic spiracle slit-shaped, in a bulge between the prothorax and the mesothorax; mesothorax dorsally slightly bulged at the mesonotum; basilar tubercle and longitudinal ridge lateral, extending posteriorly in a more or less straight line and then bending ventrally to

the posterior end of the mesothoracic wing cases; longitudinal ridge indented at the silk girdle; mesothoracic wing cases greatly enlarged ventrally, forming a keel, forewing shape and venation visible; prothoracic and mesothoracic legs between the galeae and the antennae, the former wider and slightly shorter than the latter; metathoracic legs not externally visible; metathorax, narrow, not bulged, 'M' shaped; metathoracic wing cases mostly covered by the mesothorax, not visible ventrally. First three abdominal segments subretangular, the remaining segments as conical sections, tapering posteriad; A1–A3 totally and A4 partially covered by the thorax ventrally; abdominal spiracles yellowish-brown and slit-shaped; A1 spiracle not visible; spiracles A2 and A3 dorsal, partially covered

by the metathorax, spiracles A4–A8 lateral, on the anterior area of the segment; A8 spiracle reduced and apparently not functional; cremaster (i.e. A9+10) with a pair of anterior and ventral pointed projections, posteriorly dorsally and ventrally excavated, posterior end curved ventrally and flattened, with several tiny reddish brown hooks. Length: 2.02–2.25cm; greatest width in dorsal view: 0.45–0.47; greatest width in lateral view: 0.51–0.53cm; duration: 8 days (n=2).

Discussion

All obtainable sources report species of Fabaceae, Mimosoideae, as host plants of species of *Dismorphia*, with only one exception in Caesalpinoideae (an unidentified species of *Cassia*) by Lamas (1985) (Beccaloni et al. 2008). The vast majority of records belong to species of *Inga*, but there are records of species of *Acacia, Cojoba, Mimosa* and *Zygia* (Becalloni et al. 2008, Janzen & Hallwachs 2015). As noted by Young (1973) and Aiello (1981), the cryptic behavior and the color of the larvae, which matches almost exactly the color of the leaves of the host plant, may confer protection against visually orientated predators; to a similar effect, the shape and color of the pupae resemble leaves and flower buds.

There are very few species of Dismorphiinae with descriptions of the immature stages; most accounts, as those provided for *D. amphione astynome* (Dalman, 1823), by D'Almeida (1944), and *D. zaela oreas* (Salvin, 1871), *D. crisia lubina* Butler, 1872; *D. zathoe pallidula* Butler & Druce, 1874; *D. amphione praxinoe* (Doubleday, 1844), by DeVries (1987) are very brief and scarce in illustrations. *Dismophia zaela oreas* was also described by Young (1973), but focusing in the biology and natural history rather than in morphology, nevertheless, brief descriptions and black and white illustrations were provided. *Dismophia amphione beroe* (Lucas, 1852) and *Dismorphia spio* (Godart, 1819), were decribed by Aiello (1981) and Torres (1991), respectively; those authors, in addition to the biological information, provide descriptions of the external morphology, with black and white illustrations. Later instars and pupae of *D. theucharila fortunata* (Lucas, 1854), *D. amphione praxinoe, D. crisia lubina* and *D. eunoe desine* (Hewitson, 1869) were illustrated in color by Janzen and Hallwachs (2015) (Figs 22–27), and some information on parasitoid biology are provided; last instars and pupae of *D. amphione* (Cramer, 1779) and *D. crisia* (Drury, 1782) were also illustrated by Le Crom et al. (2004).

Based on the information about the number of instars of other species of *Dismorphia*, the larvae of species of the genus usually undergo five stages. The fifth or last
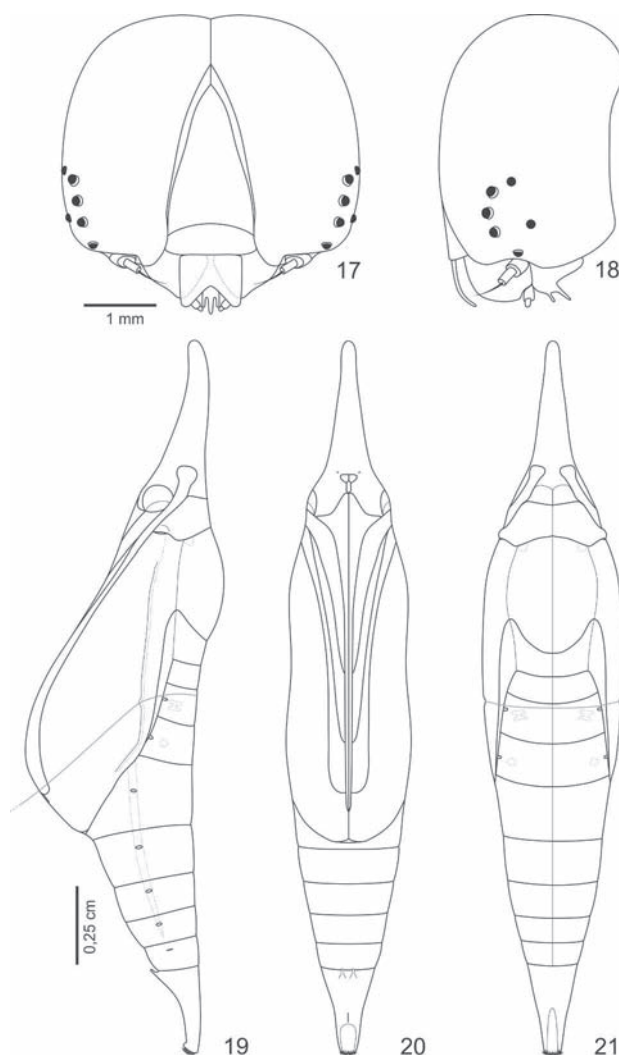
Figs . 17–21. Head capsule of last instar and pupa of *Dismorphia melia* (Godart, [1824]). **17–18.** Head capsule, anterior and lateral. **19–21.** Pupa, lateral ventral and dorsal. Scale bar: figs 17–18 = 1mm; figs 19–21 = 0.25cm.

instars of species of Dismorphiinae are apparently very similar, with limited species specific characters. DeVries (1987) noted that the immature stages of the Dismorphiinae are similar to each other and to generalized pierids, without any exceptional characteristics; the illustrations of *Enantia lina* (Herbst, 1792) and *Lieinix nemesis* (Latreille, [1813]) provided by Le Crom et al. (2004) support that assumption. Nevertheless, detailed examination reveals potential specific or supraspecific informative characters, as the color of the head capsule and chalazae, length, shape and color of the setae, number and development of annulets per segment, presence and development of a spiracular stripe and color and position of the spiracles. The color of the head capsules of *D. zaela oreas* and *D.*
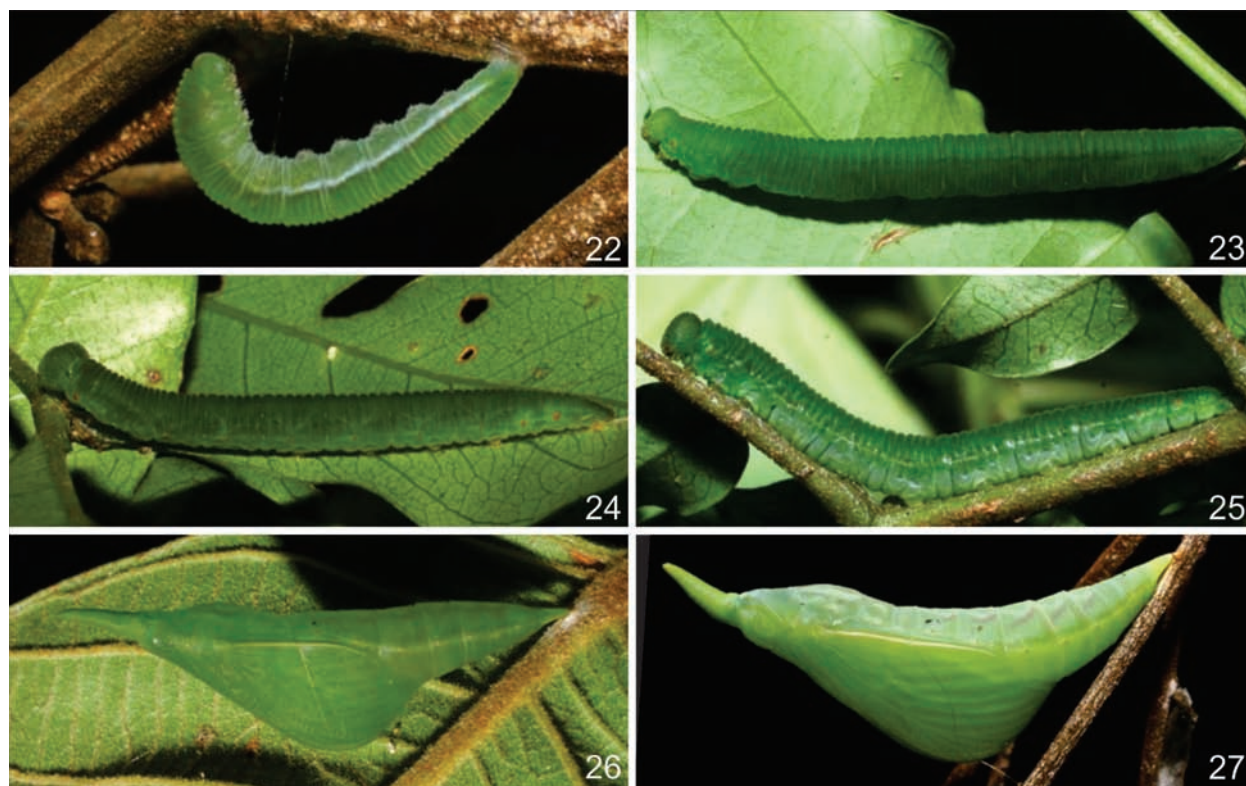
Figs . 22–27. Last instar and pupae of species of *Dismorphia* Hübner, 1816 from Costa Rica illustrated by Janzen & Hallwachs (2015), with respective voucher numbers. **22–25.** Last instar, lateral. **22.** *D. theucharila fortunata* (Lucas, 1854), in prepupa, 05-SRNP-35409. **23.** *D. eunoe desine* (Hewitson, 1869), 09-SRNP-35899. **24.** *D. amphione praxinoe*, 05-SRNP-35409. **25.** *D. crisia lubina* Butler, 1872, 08-SRNP-36448. **26–27.** Pupae, lateral. **25.** *D. amphione praxinoe*, 07-SRNP-5106. **26.** *D. crisia lubina* 07-SRNP-35720.

zathoe pallidula are described as grey-green by Young (1973) and DeVries (1987), while green in other species; but with brown reticulated markings in *D. melia* (this study). The number of annulets per segment and the position of the spiracles on the annulets are identical in *D. melia* and in all species in which these characters could be directly observed from the illustrations, namely, *D. amphione praxinoe*, *D. crisia lubina* and *D. eunoe desine* (Janzen & Hallwachs 2015), but this character is usually neglected in descriptions. The spiracular stripe of *D. melia* are wider and lighter in color than other described species, in which the spiracular stripe is absent, faint or not continuous along the segments; the prepupa of *D. theucharila fortunata* illustrated by Janzen and Hallwachs (2015) (Fig. 22), the spiracular stripe appears to be well developed, but this may be due to its closeness to pupation. In all last instars of Dismorphiinae the spiracles are elliptical, as in species of Coliadinae (Toliver 1987).

The characters of the pupa of species of *Enantia* Hübner, [1819], *Lieinix* Gray, 1832 and *Dismorphia* (Figs 26–27) are almost identical (Young 1973, Aiello

1981, Torres 1991, Le Crom et al. 2014, Janzen & Hallwachs 2015) and generally similar to those of the Pseudopontiinae, Coliadinae, and the Pierinae tribes Teracolini and Anthocharidini (Braby et al. 2006). Braby et al. (2006) named these type of pupae as "type I" (Fig. 28), and described them as with the vertex tapered apically often forming a prominent point or spine; keeled ventrally at the mesothoracic wing cases; and smooth abdomen, in contrast to the apomorphic form of the Pierini, named "type II", and described as with the vertex with an anterior horn or spine-like process; thorax flat ventrally, but ridged dorsally; and bearing dorsal and/or dorsolateral spines on some segments of the abdomen. Both types of pupae are suspended by a silk girdle, but in "type I" the pupae are usually horizontally loosely suspended by the girdle, ventral side facing upmost, while in "type II" pupae are suspended vertically tight to the substrate, dorsal side facing upmost (Braby et al. 2006). Although similar, the pupae of Dismorphiinae are conspicuously slender than most "type I" pupae, such as species of Elodinini (Fisher 1984), Nepheroniini, species of the
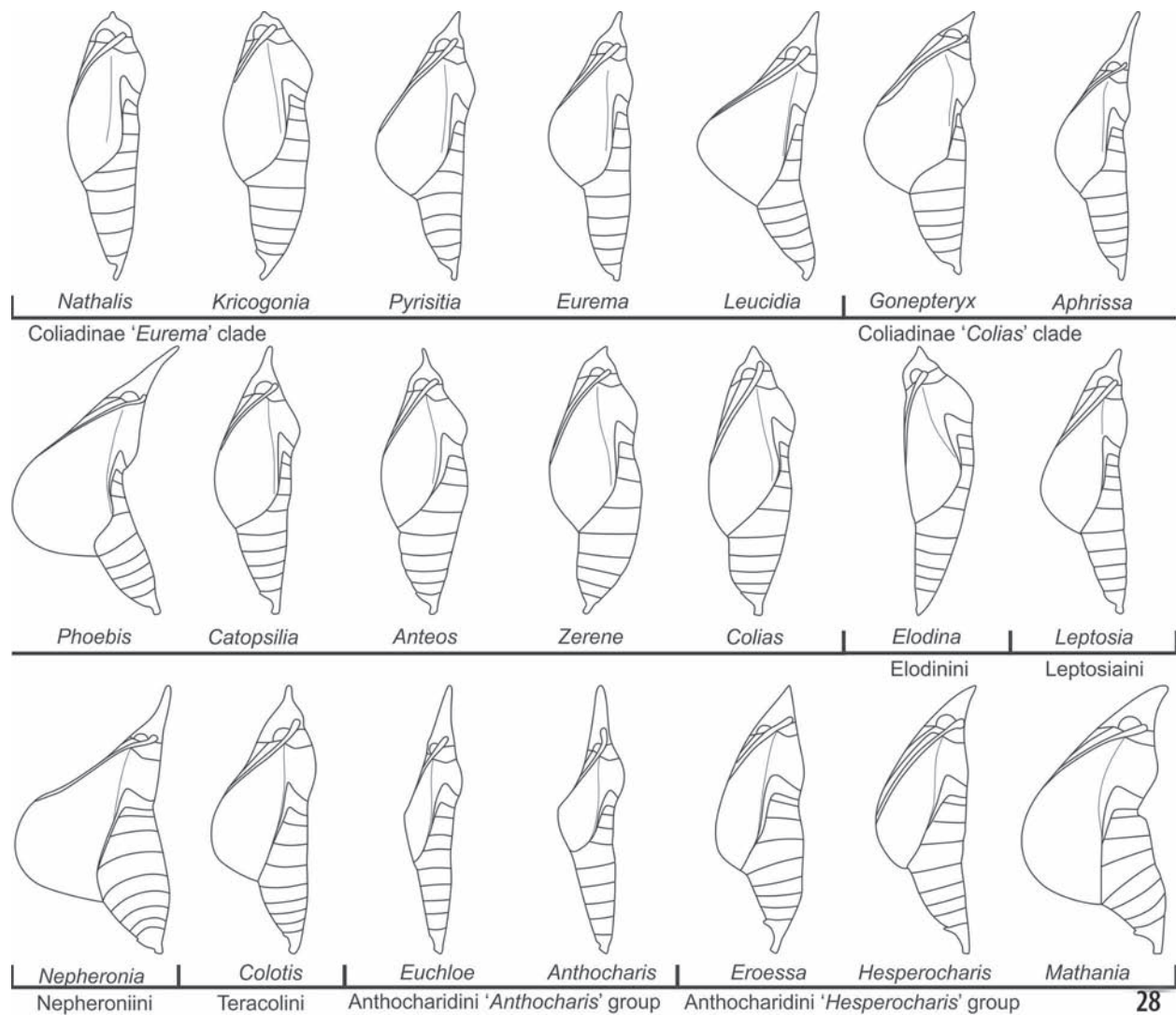
FIG. 28. Schematic representation of pupae of 21 species of Pieridae of the subfamily Coliadinae and the Pierinae tribes Anthocharidini, Elodinini, Leptosiaini, Nepheroniini and Teracolini with "type I" pupae (Braby et al. 2006), lateral. Illustrations not to scale and based on the references cited in the text; species groups by Braby et al. (2006), Braby (2007) and Wahlberg et al. (2014).

"*Hesperocharis*" group of Anthocharidini (Braby et al. 2007), most species of the "*Colias*" clade (Le Crom et al. 2004, van der Poorten & van de Poorten 2013, Wahlberg et al. 2014, Warren et al. 2015) and the divergent *Kricogonia* Reakirt, 1863 and *Nathalis* Boisduval, 1836 of the "*Eurema*" clade. In contrast, species of Teracolini, Leptosiaini (Clarck & Dickson 1967), species belonging to the "*Anthocharis*" group of Anthocharidini (Warren et al. 2015), species of *Aphrissa* Butler, 1873, and most coliadines of the "*Eurema*" clade (Le Crom et al. 2004, Freitas 2008, van der Poorten & van de Poorten 2013, Warren et al. 2015) are morphologically more akin to Dismorphiinae. In comparison, the development of vertical prominence is variable; generally much smaller, but similarly long to the plesiomorphic Dismorphiinae in species of *Aphrissa* and Anthocharidini of the "*Anthocharis*" group. The development of the ventral keel can be considerably variable in coliadines, being characteristically smaller and angled in species of Anthocharidini of the "*Anthocharis*" group. The morphology of the pupa is certainly phylogenetically informative in Pieridae (Le Crom et al. 2004), given its morphological diversity and the association of certain types of pupa to a genus or group of genera (Fig. 28). The morphologic types of pupa recognized here by Braby et al. (2006) and Braby
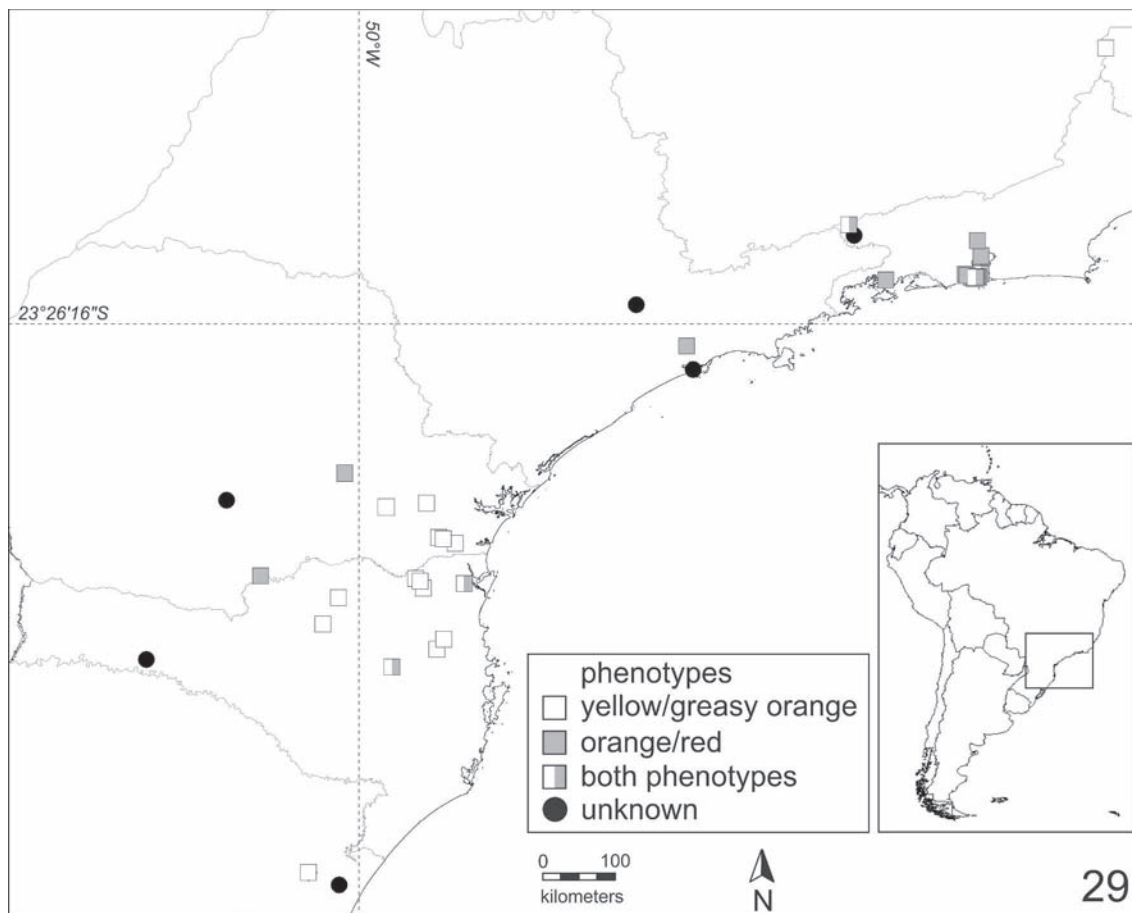
Fig. 29. Distributional map of *Dismorphia melia* (Godart, [1824]). White squares: records of "yellow and dark brown" males or "greasy-orange" females phenotypes; gray squares: records of "orange and dark brown" males or "red" females phenotypes; half gray and white squares: occurrence of both types of phenotypes (see text for detailed description of phenotypes); black circles: data of unknown phenotype from literature.

(2007) match closely the phylogeny of Wahlberg et al. (2014) based on molecular data, indicating that further detailed studies of immature stages may provide morphologic support for the groups recognized by those authors.

Taxonomy, distribution and variation. *Dismorphia melia* occurs in both coastal and interior Atlantic Forest from Minas Gerais to Rio Grande do Sul (Fig. 28), probably occurring in the state of Espirito Santo (Brown & Freitas 2000). Examination of specimens deposited at the DZUP reveals that both sexes are intraspecifically variable in that range, with extremes of variation intercalated by intermediary specimens along a somewhat latitudinal gradient. Male specimens from Southern Brazil are bright yellow and dark brown on the upper side (Figs 1–2), while female specimens are almost perfect mimics of species of *Actinote* of the "greasy-orange" mimicry group (Francini & Penz 2006), with the forewing upper side

dull-colored, and somewhat translucent spots, glossy at the base of the wings, producing a visual effect similar to the greasiness observed in species of the above-mentioned mimicry group (Figs 3–4). In contrast, most male specimens from further North, from Southeastern and Eastern Brazil, are dull to bright orange and dark brown on the upper side (Figs 5–6), while the pattern of the females is variable, with some specimens similar to the described above, but never glossy at the base of the forewing upper side, and some with spots brightly colored, yellow or orange, falling in-between the *Actinote* "red" mimicry groups (Francini & Penz 2006) and the more widespread "tiger" pattern, common to some other species of *Dismorphia*, and species of Heliconiini and Ithomiini (Nymphalidae) (Figs 7–8). These differences in color pattern do not reflect in morphological differences between the genitalia of both sexes (Figs 30–32). It is interesting to note that *D. melia* is the only species of *Dismorphia* that mimics species of

Actinote, an abundant and conspicuous element of the Atlantic Forest, considered impalatable by the presence of cyanogenic glycosides and pyrrholizidine alkaloids and subject to great intraspecific variability (Francini & Penz 2006). In addition to the similarity between the color pattern of those taxa, the mimetic association of *D. melia* as a Batesian mimic of species of *Actinote* is supported by the fact that species of *Dismorphia* are most likely palatable (Young 1973), as species of *Inga* are not known to contain toxic compounds (Ehrlich & Raven 1965), the cryptic color and behavior of the immature stages, and the apparent low abundance of the species. However, Brown (1992) reports that some species of Dismorphiinae are rejected by predators, therefore acting as Müllerian co-models. The intraspecific variation of the female follows closely the high level of intraspecific variation acknowledged in species of *Actinote* (Francini & Penz 2006). This variation, especially because of the dimorphic female, yielded a number of names, all of them currently recognized as synonyms of *D. melia* (Lamas 2004). *Pieris melia* Godart, [1824] was described on the basis of an orange male specimen from "Brazil", which was probably collected in the state of Rio de Janeiro; type specimens of taxonomic names currently recognized as junior subjective synonyms are all females with either the "red" mimicry group wing pattern, (i.e. *Leptalis eumara* Doubleday, 1848, type location unclear "America Meridionali"; *L. acraeoides* Hewitson, 1851, type location Minas Gerais, Brazil; and *D. mimetica* Staudinger, 1884, type location doubtful "French Guiana"); or of the "greasy-orange" mimicry group (i.e. *L. thalia* Müller, 1876, type location Santa Catarina, Brazil and *D. melia f. metallescens* Hoffmann, 1935, type location Santa Catarina, Brazil). Furthermore, two nomina nuda, *D. actinote* Kaye, 1911, **nomen nudum**, and *D. melia moena* Martin, [1923], **nomem nudum**, were supposed to be based on female specimens. Nevertheless, the homogeneity of the genitalia and the presence of both phenotypes sympatrically in some localities prevent the recognition of any of those names as valid taxa.

Examined material. Brazil – no data, 2 ♀, DZ 33.678, 33.679. Minas Gerais: 1 ♂, V-2013, 1200m. Rio de Janeiro: 1 ♂, 8-X-1961, DZ 33.661. Angra dos Reis – Jussaral, 1 ♂, 13-IV-1934, DZ 33.659. Resende – Mauá, 1150m, 1 ♂, IX-1956, H. Ebert leg., DZ 33.656; Serra de Itatiaia, 1500 m, 1 ♂, 14-IV-1951, Ebert leg., DZ 33.660, 800m, 2 ♀, 14-IV-1951, 15-IV-1951, Ebert leg., DZ 33.675, DZ 33.674. Petrópolis – Independência, 900m, 1 ♀, 15-IX-1939, Gagarin leg., DZ 33.676. Rio de Janeiro – 2 ♀, 11-VII-1934, 26-VII-1934, Gagarin leg., DZ 33.666, DZ 33.665, 2 ♀, Ferreira D'Almeida leg., DZ
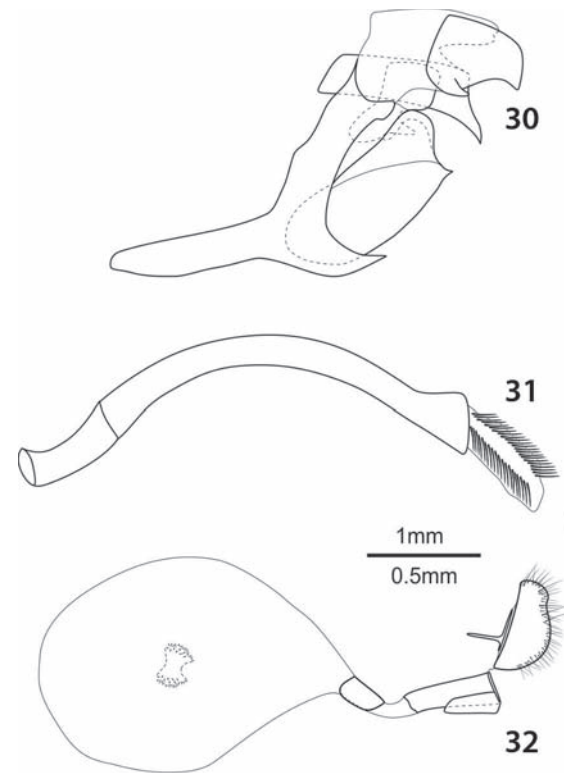
FIGS . 30–32. Genitalia of *Dismorphia melia* (Godart, [1824]). **30–31**. Male genitalia, lateral. **30.** Genital capsule. **31.** Aedeagus. **32.** Female genitalia, lateral. Scale bar: figs 30–31 = 1mm, fig. 32 = 0.5mm.

33.667, DZ 33.668; Floresta da Tijuca, 1 ♂, 7-I-1969, Pe. Moure leg., DZ 33.647, 600m, 1 ♂, 22-III-1953, H. Ebert leg., DZ 33.657; Floresta do Macaco, 1 ♂, XII-1959, Altamiro leg., DZ 33.662; Icatú, 1 ♀, 15-V-1955, Gagarin leg., DZ 33.677; Jacarepaguá, Covanca, 2 ♂, 1-VI-1945, Silva leg., DZ 33.652, 9-IV-1945, DZ 33.651; Jacarepaguá, Três Rios, 2 ♂, 2-VIII-1922, DZ 33.650, 18-IX-1960, [illegible] leg., DZ 33.649; Morro de Santa Marta, 1 ♂, 23-VIII-1938, Gagarin leg., DZ 33.658; Paineiras, 1 ♀, 26-VIII-1982, Gagarin leg., DZ 33.669; Sumaré, 500m, 3 ♂ and 3 ♀, 31-VII-1967, Ebert leg., DZ 33.653, DZ 33.654, DZ 33.655, DZ 33.670, DZ 33.671, DZ 33.672; Sumaré, Serra de Santa Tereza, 1 ♀, 9-IX-1917, Ferreira D'Almeida leg., DZ 33.673. São Paulo: Ribeirão Pires – 800m, 1 ♂, 27-IV-1963, Ebert leg., DZ 33.633. Paraná: Curitiba – 900m, 1 ♀, 14-IV-1977, O. Mielke leg., DZ 33.640. Guaratuba – Pontal do Itararé, 950m, 2 ♂ and 1 ♀, 19-II-2005, O.-C. Mielke leg., DZ 33.619, DZ 33.620, DZ 33.639. Ponta Grossa – 1 ♂, 21-IV-1967, Mielke leg., DZ 33.617; Quintal, 1 ♂, XII-1940, DZ 33.616. Balsa Nova – São Luiz do Purunã, 1 ♂, 30-IV-1-V-2006, Beltrami & Selusniaki, DZ 33.618. Tijucas do Sul – Rincão, 900m, 1 ♀, 25-II-1969, Mielke &

Sakakibara leg., DZ 33.635; Vossoroca, 850m, 1 ♀, 23-I-1977, Mielke leg., DZ 33.634. União da Vitória – 4 ♂ and 3 ♀, III-1950, C. Bruhm leg., DZ 33.612, DZ 33.613, DZ 33.614, DZ 33.615, DZ 33.637, DZ 33.638, DZ 33.663, 1 ♀, III-1950, Justus leg., DZ 33.636. Santa Catarina: 1 ♂, III-1963, DZ 33.621; Alto Rio Itajaí, 400m, 1 ♂, H. Wuff leg., DZ 33.631. Dalbergia, 2 ♀, 11-II-1932, 30-III-1932, d'Almeidaex-coll., DZ 33.664, paralectotype metallescens Hoffman, 1935, DZ 31.900, lectotipo metallescens Hoffman, 1935. Ituporanga, 3 ♂, II-IV-1970, Sommer leg., DZ 33.625, DZ 33.626, DZ 33.648. Joinville – 10-200m, 1 ♂, X-1978, Miers leg., DZ 33.622, 1 ♂ and 1 ♀, 5-IV-1980, 20-IV-1969, Mielke & Miers leg., DZ 33.623, DZ 33.641, 0-200m, 1 ♂, 25-IV-1991, Miers leg., DZ 33.624. Monte Castelo – 800m, 1 ♀, 24-II-1973, Ebert leg., DZ 33.646. São Bento do Sul – 1 ♂, 8-V-1971, Weiss leg., DZ 33.632, 900m, 1 ♀, 12-III-1980, H. Ebert leg., DZ 33.644; Rio Natal, 1 ♀, 2-II-2012, Rank leg., DZ 33.642; Rio Vermelho, 850m, 2 ♂ and 1 ♀, 2-IV-1980, 21-XI-2004, 22-II-1974, Rank leg., DZ 33.630, DZ 33.629, DZ 33.645. Santa Cecília – Campo Alto, 2 ♂, 22-II-1973, O.H. Mielke leg., DZ 33.627, DZ 33.628.

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BENEFITS OF EGG CLUSTERS IN THE EVOLUTION OF LARVAL AGGREGATION
IN THE NEOTROPICAL BUTTERFLY *ASCIA MONUSTE ORSEIS*: REDUCTION
OF EGG FAILURE AND ENHANCED LARVAL HATCHING

Additional key words: decision making, oviposition, hatching, cannibalism

The number of species of phytophagous lepidopterans that aggregate eggs during oviposition indicates that this behavior is rare in nature when compared to those laying single eggs: in North America, only 4.7% of species aggregate eggs (Stamp 1980). Egg clutch size is an important component of these species' life history because it reduces predation risk of newly hatched larvae (Stamp & Bowers 1988, Lawrence 1990) and maintains adequate temperature and relative humidity for proper egg (Clark & Faeth 1998) and larvae development (Stamp 1980, Willmer 1980). In addition, the egg desiccation hypothesis (Stamp 1980, Clark & Faeth 1998) proposes that aggregation of eggs is adaptive per se because it decreases mortality through increasing larvae hatching success.

Cannibalism is described as an important component of behavior in *A. monuste orseis* larval aggregations in the laboratory (Zago-Braga & Zucoloto 2004, Santana et al. 2011) and in the field (Barros-Bellanda & Zucoloto 2005). Despite the associated costs and benefits related to egg aggregation in this species—like biomass gain (Barros-Bellanda & Zucoloto 2001) and removal of potential competitors (Zago-Braga & Zucoloto 2004)— some implications for this behavior have yet to be identified. It has been shown, for example, that egg cannibalism may reduce reproductive potential (Fordyce 2005) for the parental female. Egg clustering can be a risky behavior for the parental female as well as for the deposited eggs. In fact, *A. monuste orseis* females avoid ovipositing on plants with conspecific larvae (Barros-Bellanda & Zucoloto 2005), because older caterpillars can cannibalize eggs (Zago-Braga & Zucoloto 2004, Barros-Bellanda & Zucoloto 2005). On the other hand, egg mortality in nature also happens due to factors like desiccation when abiotic conditions are variable or suboptimal.

Most hypotheses related to the adaptive significance of egg aggregation focus on the consequences observed in larvae, especially in first instars, when they show higher mortality (Stamp 1980, Kagata & Ohgushi 2002, Zalucki et al. 2002). As every larval aggregation is a result of an egg clutch in phytophagous insects (Stamp 1980), we aimed to evaluate whether there is a variation in the vulnerability of egg clutches of different sizes, based on egg cannibalism and egg failure data. It is hypothesized that eggs in larger clutches are more resistant to environmental effects and would show higher hatching rates than eggs in smaller clutches.

Ascia monuste orseis eggs were collected from kale (*Brassica oleracea* L. var. *acephala* D.C.) leaves in a pesticide-free garden, situated in the Biology Department of Faculdade de Filosofia, Ciencias e Letras de Ribeirao Preto, USP (FFCLRP / USP) (21°05'S, 47°50'W), Brazil. Leaves with eggs were taken to the laboratory and kept in glass jars (12 cm high × 8 cm diameter) to maintain leaf freshness until larval hatching. Newly hatched caterpillars were placed in plastic boxes (10 × 10 × 4 cm) and were fed with fresh kale taken from the host plant. Leaves were offered ad libitum and replaced daily. Boxes were kept in a climate-controlled chamber ELETROLAB® (93,5 × 50 × 51 cm): temperature: 29±1°C, humidity: 75% e photoperiod: 10 light: 14 dark (Barros-Bellanda & Zucoloto 2005, Santana & Zucoloto 2011).

Twenty-four hours after hatching, a butterfly pair, raised in controlled abiotic conditions during the larval period, was placed in an aluminum cage, covered with white tulle, for reproduction. The cage was in an external greenhouse under semi-natural conditions, excluding predators and rain. Kale plants, that were approximately 2 months old, measuring 80cm high and grown in the same substrate, were available for ovipositions and a liquid diet of water and sugar (3:1). The plants were replaced every couple of days. Plants were also checked daily for the presence of eggs; once detected, eggs were separated for observation. Plants with eggs were also kept in the greenhouse under the same conditions.

As females deposited different numbers of eggs, we categorized the clutch sizes as: small (1–9 eggs); intermediate (10–19) and large (more than 20 eggs), according to the frequency of ovipositions distribution (data not shown). Average numbers of hatched larvae from small, intermediate and large clutches were 2.1, 11.5 and 22.6, respectively. Number of deposited eggs, failed eggs and the number of hatched larvae were recorded. Larvae fed from the same plant in which oviposition occurred. There was no manipulation of egg or larvae number to form treatment groups; the natural variation deposited by the female was maintained. The
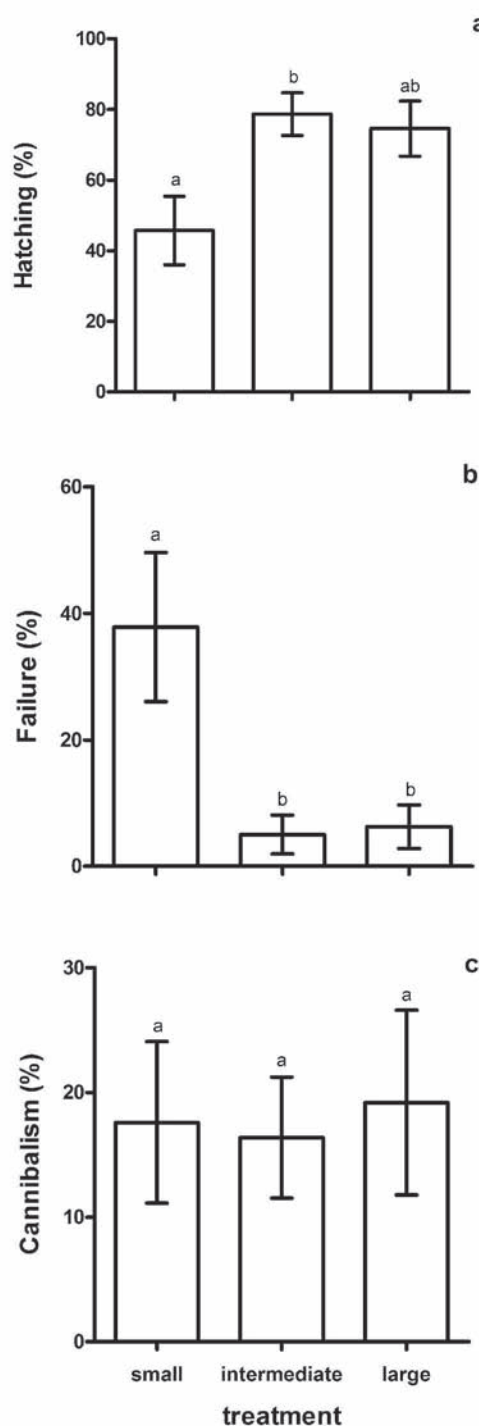
FIG. 1. Larval hatching rate (a), egg failure (b) and eggs/larvae cannibalism (c) (mean ± standard error) of *A. monuste orseis* in different clutch sizes. Small clutch: 1–9 eggs; intermediate: 10–19 eggs and large: more than 20 eggs. N=16 (small), N=14 (intermediate), N=11 (large). In each graph, different letters on the top of bars indicate significance difference among treatments. ANOVA, Tukey Multiple Tests, *P*<0,05.

parameters analyzed were: hatching rate (number of hatching larvae/number of eggs), cannibalism rate ([number of deposited eggs – number of hatching larvae]/number of deposited eggs) and failure rate (number of failed eggs/number of deposited eggs). Larvae mortality by failure and cannibalism were compared among treatments to check the relevance of each in the control of aggregation size.

Hatching, failure and cannibalism rates were compared by Kolmogorov-Smirnov normality tests with consideration given to the homoscedasticity of variances by Bartlett tests. Percentage data were transformed using the arcsin function. After transformation, the data were analyzed using analysis of variance (one factor), followed by Tukey multiple tests, using $\alpha = 0.05$. We used χ^2 tests to analyze failure and cannibalism mortality of eggs and/or larvae for multiple comparison between treatments. To account for the consequences of making multiple comparisons, we used a Bonferroni correction for $\alpha = 0.01$.

Larval hatching rate was directly proportional to the increase of egg clutch size (ANOVA, Tukey Multiple Testes, $P=0.03$) (Fig. 1a), while egg failure decreased with increasing clutch size (ANOVA, Tukey Multiple Tests, $P=0.007$) (Fig. 1b). Although cannibalism rate did not differ among treatments (ANOVA, $P=0.93$) (Fig. 1c), it was a significant cause of mortality (Table 1), especially in intermediate and large clutches. In small clutches, failure was the main mortality cause (Table 1). These results support the idea that the evolution of larval aggregation in *A. monuste orseis* possibly occurred already in the egg phase through decreased egg failure and increased egg hatching in larger clutches.

Egg and newly hatched larvae cannibalism was detected in a similar rate in all clutch sizes tested, supporting the development of this behavior in this species. In previous work from Barros-Bellanda and Zucoloto (2005), the difference between cannibalism rates shown by larvae from different clutch sizes was meaningful only above 60 eggs per clutch. This supports the importance of cannibalism as a strong regulation agent in larger clusters.

Despite small clutches having disadvantages to *A. monuste orseis* survival, due to the higher failure rate in this group, they are found in nature. Female vulnerability to predators during oviposition and conspecific males (in the search for copulation) could explain the presence of smaller clutches. Frequently *A. monuste orseis* males were seen in the field interrupting female oviposition (A.F.K. Santana pers. obs.). These females would not necessarily return to the same place to deposit their remaining eggs, resulting in small clutches.

TABLE 1. Relative rate of *A. monuste orseis* egg mortality in greenhouse by failure and by cannibalism in different treatments. Small clutch: 1–9 eggs; intermediate: 10–19 eggs and large: more than 20 eggs.

Clutch size/mortality	N	by failure (%)	by cannibalism (%)
small	16	59,52 [a]	40,48 [a]
intermediate	14	21,15 [b]	78,85 [b]
large	11	25,00 [b]	75,00 [b]
Statistic		χ^2= 25,35; gl=2; p<0,0001	χ^2= 13,78; gl=2; p=0,001

Different letters in the same columm indicate significant difference between treatments. Mortality by failure: S vs I= 1,85; P<0,0001, S vs L=14,09; P=0,0002 e I vs L=0,32; P=0,57. Mortality by cannibalism: S vs I= 12,32; P=0,0004, S vs L=10,32; P=0,001 e I vs L=0,09; P=0,75. Binomial tests, α = 0,01.

While in some species [e.g. *Chlosyne lacinia* (Geyer)] relative humidity influences directly larval hatching rate (Clark & Faeth 1998)], in others [e.g. *Grammia geneura* Strecker (Arctiidae); *Manduca sexta* Johannson (Sphingidae)], hatching rates are high even when humidity is near zero (Woods & Singer 2001). If nymphalids are taken into consideration, a higher number of North American species aggregate eggs when compared to Neotropical and subtropical species (Stamp, 1980), suggesting that dry and/or cold weather favored the selection of this behavior. Even some Neotropical species, in which water conservation is not apparently a limiting factor for development, benefits for large clutches were also noticed for *A. monuste orseis*. Our data clearly demonstrated that benefits of larval aggregations already happen during the egg phase through the increase of larval hatching and the decrease of egg failure in larger clutches. In some insect species, oviposition in clutches may be a strategy to save time and energy searching for deposition places (Stamp 1980, Courtney 1984). Predation is considered a strong selective pressure not only for eggs (Dimarco & Fordyce, 2013), but also for females in reproductive period (Burger & Gochfeld 2001). Future studies considering the costs of large clutches (predation rates) are extremely important because they influence the decision making process of the female during oviposition period .

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FIRST RECORD OF *PHYCITA IMPERIALELLA* (RAGONOT, 1887) FROM WESTERN EUROPE (PYRALIDAE)

Additional key words: Phycitinae, *Onosma echioides*, Pollino National Park, Italy

Phycita imperialella (Ragonot 1887) is a species of Pyralidae, subfamily Phycitinae, tribe Phycitini. This species was moved several times across different genera. It was described as *Nephopterix imperialella* by Ragonot (1887), reported as *Sciota imperialella* in Fauna Europaea (Karsholt & Van Nieukerken 2015), as *Bradyrrhoa imperialella* in Budashkin & Savchuk (2010), and, finally, as *Phycita imperialella* in Leraut (2014). Perhaps the correct combination is that proposed by Budashkin & Savchuk (2010), and molecular analyses could be useful to assign this species to the correct genus. Few data are given for the distribution of this species. Within the original description, it was generically reported from Caucasus, Armenia and Siberia (Ragonot 1887). Successively, the range was extended to Greece and Macedonia (Klimesch 1968), Ukraine (Krim near Kurortne, Friedmar Graf, www.lepiforum.de; Crimea (Budashkin & Savchuk 2010)), and Turkey (Van province, East Turkey (Koçak & Kemal 2012)). To date, the chorotype of *P. imperialella* can be defined as Caucasian-East Mediterranean. Budashkin & Savchuk (2010) found caterpillars of *P. imperialella* feeding on both stems and flowers of *Onosma polyphylla* Ledeb. (Boraginaceae), from mid-June to mid-July. Adults were found from June to October, but more frequently in August, in xerophilous habitats.

In this paper we report the first record of *P. imperialella* from Italy, significantly expanding the range of this species westward. The collection site is situated in the Pollino National Park on the southern slope of Serra Ambruna Mts., municipality of Saracena, southern Italy (latitude: 39.8234°; longitude: 16.0768°; altitude: 1,035 m). A specimen of *P. imperialella* were found in a clearing surrounded by a *Fagus sylvatica* L. forest with isolated trees and bushes of *Corylus avellana* L., *Fraxinus* spp., *Quercus ilex* L., *Pinus* spp. The shrub-herbaceous layer is characterized by *Spartium junceum* L., *Hieracium* spp., *Dianthus* spp. and some Poaceae species. Geological substratum is calcareous with outcropping rocks. Moths have been sampled by a high brightness UV-LED strips-based light trap (400-315 nm, light angle 120°, 3,000 lumens), positioned at approximately 1.30 meters above the ground, switched on at dusk.

On the 24th of August 2015 we collected one male of *Phycita imperialella* (Fig. 1). The identification was easily carried out comparing the habitus of the specimen with available iconography (Leraut 2014). Wingspan is 29 mm, included within the known measurement range of this species (28–30 mm). The specimen was barcoded (BOLD sequence page: BIBSA855-15; GenBank accession: KU497408) and stored in the collection of the Unità di Ricerca per la Selvicoltura in Ambiente Mediterraneo (CREA-SAM).

The discovery of a new population of this species in the Pollino Massif confirms the biogeographic affinity between south-eastern Europe and southern Italy. In fact, this distribution pattern is shared by several xero-thermophilous Lepidoptera species (Scalercio et al. 2014).

Onosma polyphylla, the food-plant indicated by Budashkin & Savchuk (2010), is absent in southern Italy where two subspecies of *O. echioides* (L.) L. are present (Peruzzi & Passalacqua 2008). The collection area is at the southern boundary range of the nominal subspecies of *O. echioides*, which is probably the food-plant of the Italian population of *P. imperialella*.

FIG. 1. *Phycita imperialella*, male, Serra Ambruna (Italy), 24.VIII.2015, 29 mm, legit Scalercio S. & Infusino M.

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PSEUDOMYRMEX SPP. ANT (HYMENOPTERA: FORMICIDAE) PREDATION ON *ANAEA TROGLODYTA FLORIDALIS* LARVAE (NYMPHALIDAE)

Additional key words: *Croton*, population regulation, conservation, endangered species

The Florida leafwing, *Anaea troglodyta floridalis* F. Johnson and Comstock (Nymphalidae), historically occurred throughout the pine rocklands of southern Florida (Minno & Emmel 1993, Smith et al. 1994), where it is endemic. However, due to extensive habitat loss across much of its former range *A. t. floridalis* is now largely restricted to Everglades National Park (Salvato and Salvato 2010a). Hennessey and Habeck (1991) and Worth et al. (1996) described many aspects of *A. t. floridalis* natural history. Salvato and Hennessey (2003) and Salvato and Salvato (2010a) also discussed *A. t. floridalis* ecology and provided a review of known parasites and predators for the species. More recently we have conducted extensive ecological studies and monitoring within the Long Pine Key region of the Everglades in order to further identify and measure natural mortality factors for immature stages of *A. t. floridalis*.

On 24 February 2009 an early instar *A. t. floridalis* was observed being predated by a single native twig ant, *Pseudomyrmex pallidus* (F. Smith) (Formicidae) (Fig. 1), as the larva was creating a frass chain. A frass chain is created when the larvae attach their fecal pellets to the mid-vein of a partially eaten croton leaf with silk (Freitas and Oliveira 1996, Minno et al. 2005, Greeney et al. 2012). The larvae crawl to the terminus of the strands to avoid predation. However, early instar nymphalid larvae remain vulnerable to ant predation

while constructing new frass chains (Freitas and Oliveira 1996). Subsequently, on 24 December 2011, *P. pallidus* was observed to actively sting, but not immobilize, a late instar *A. t. floridalis* as that larva was attempting to pupate. During this observation, the larva reared up its body and twisted vigorously to repel the attacking *P. pallidus*, a behavior that has been observed during ant interactions with other nymphalid larvae (Freitas and Oliveira 1992, Machado and Freitas 2001,

FIG. 1. An early instar *A. t. floridalis* being predated by a *Pseudomyrmex pallidus* in Long Pine Key on 24 February 2009 (Photo: A. Land).

FIG. 2. An early instar *A. t. floridalis* larva evading predation from *Pseudomyrmex gracilis* in Long Pine Key on 26 February 2011 (Photo: H.L. Salvato).

First documented in southern Florida in the 1960s, *P. gracilis* is now common throughout the state (Whitcomb et al. 1972, Wetterer 2010).

Although little is known regarding ant predation on Florida butterflies, native ant species, such as *P. pallidus*, have likely had a role in the historic ecology of *A. t. floridalis*. One of the earliest natural history accounts of *A. t. floridalis* (Matteson 1930) reported ants as predators of *A. t. floridalis* eggs in Miami. Conversely, recently introduced non-native ant species, such as *P. gracilis*, may pose an unnatural threat to *A. t. floridalis*. On Big Pine Key, Cannon (2006) reported high mortality of swallowtail eggs (*Papilio cresphontes* Cramer and *P. andraemon* Sharpe) from a nonnative species of twig ant (*Pseudomyrmex* spp.), within habitat formerly occupied by *A. t. floridalis*. Deyrup et al. (2000) indicated that the widespread distribution *P. gracilis* in Florida, combined with its large size and use of varied habitats, poses a threat to phytophagous insects—especially Lepidoptera.

Greeney et al. 2012). *Pseudomyrmex pallidus* occurs commonly from the southern United States to Central America and nests opportunistically within the hollow branches of various herbaceous plants (Ward 1985). We have frequently observed *P. pallidus* patrolling on, and visiting the flowers of, pineland croton, *Croton linearis* Jacq. (Euphorbiaceae), the only known hostplant for *A. t. floridalis*.

On 26 February 2011, an early instar *A. t. floridalis* larva was observed evading predation from a single elongate twig ant *Pseudomyrmex gracilis* Fabricius (Formicidae) by descending off the tip of its frass chain using a silk excretion (Fig. 2). This behavior has been noted for several other tropical nymphalid larvae (DeVries 1987, Freitas and Oliveira 1992). The larva was not re-encountered on subsequent visits, nor was there evidence of further feeding suggesting it may have ultimately been predated by the ant. Two additional observations of *P. gracilis* on 10 July 2013 and 14 February 2015 (Fig. 3), demonstrated that this twig ant is a predator of *A. t. floridalis* larvae. The use of frass chains may reduce ant predation for some species of nymphalid larvae, in that ants do not descend the chain (Freitas and Oliveira 1992, 1996). However, in these observations, the ants climbed down the chain to seize the prey, suggesting frass chain use may be ineffective in preventing *P. gracilis* predation on *A. t. floridalis* larvae. *Pseudomyrmex gracilis* native range spans of much of the New World tropics and subtropics (Wetterer 2010).

FIG. 3. An early instar *A. t. floridalis* being predated by *P. gracilis* in Long Pine Key on 14 February 2015 (Photo: H.L. Salvato).

We have observed numerous *A. t. floridalis* (n = 163) larvae in the field within Long Pine Key during weekly status surveys conducted from January 2006 to February 2015. These studies have previously documented a variety of predators and parasites towards larval *A. t. floridalis* including the fly, *Chetogena scutellaris* (Wulp.) (Tachinidae) (Salvato et al. 2009), crab spiders, *Misumenops bellulus* Banks (Thomisidae) (Salvato and Salvato 2010b), orb spiders, *Neoscona* spp. (Araneidae) (Salvato and Salvato 2011), biting midges *Forcipomyia* (*Microhelea*) *fuliginosa* (Meigen) (Ceratopogonidae) (Salvato et al. 2008) and *F.* (*M.*) *eriophora* (Salvato et al. 2012). However, direct observations of larval predation or parasitism are infrequent and as a result the data available to fully evaluate the influence of select mortality factors, including *Pseudomyrmex* ants, on *A. t. floridalis* natural history, is limited. Additional studies are required to determine the potential influence of ants and other predators, including non-native species, such as *P. gracilis*, towards larvae of the endangered Florida leafwing.

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NOTES ON THE LARVAL HOSTS AND HABITS OF SOME NORTH AMERICAN ERIOCRANIIDAE AND ACANTHOPTEROCTETIDAE

Additional key words: leafmining, *Acanthopteroctetes*, *Eriocraniella*, *Quercus*, *Ribes*

Eriocraniidae and Acanthopteroctetidae are two small families of leaf-mining moths, each assigned to its own superfamily. Eriocraniidae is a Holarctic family with 25 species, of which 13 occur in North America (Heppner 2008). As far as is known, all of the world's species have larval hosts in Fagales, with the exception of the western Nearctic *Eriocrania semipurpurella pacifica* Davis, which feeds on *Holodiscus discolor* (Pursh) Maxim. (Rosaceae) (Davis 1978, Wagner 1985, Ellis 2015). There are 10 known species of Acanthopteroctetidae, with five in the western USA (one of them undescribed), two in South Africa (one undescribed), and one each in Crimea, the Tien Shan region, and Peru (the last two undescribed) (Davis 1978, 1984, Kristensen et al. 2014). *Acanthopteroctetes unifascia* Davis feeds on *Ceanothus* L. (Rhamnaceae) (Davis & Frack 1987, Robinson et al. 2002), and the hosts of the others are unknown.

Five species of Eriocraniidae are known from North America east of the Great Plains. *Dyseriocrania*

griseocapitella (Walsingham) is widespread, mining leaves of both *Castanea* Mill. and *Quercus* L. (Fagaceae). *Eriocrania semipurpurella semipurpurella* (Stephens) occurs from eastern Canada to southern New York; it is known from several species of *Betula* L. (Betulaceae) in the Palaearctic, but has not been reported from any Nearctic birches. *Eriocraniella mediabulla* Davis feeds on oaks in the Gulf Coast states. *Eriocrania breviapex* Davis and *Eriocraniella platyptera* Davis were each described from a few specimens caught in Ithaca, New York (Davis 1978, Davis & Faeth 1986).

From 9 to 12 June 2013, I collected eriocraniid leaf mines (Fig. 1) from scrub oak (*Quercus ilicifolia* Wangenh.) at several locations on Nantucket Island, Massachusetts. Mines of eriocraniids are easily recognized by the stringy frass, and there are few other oak leafminers active in spring. The only other leafminers observed on scrub oak at this time (both of which I successfully reared) were *Japanagromyza*
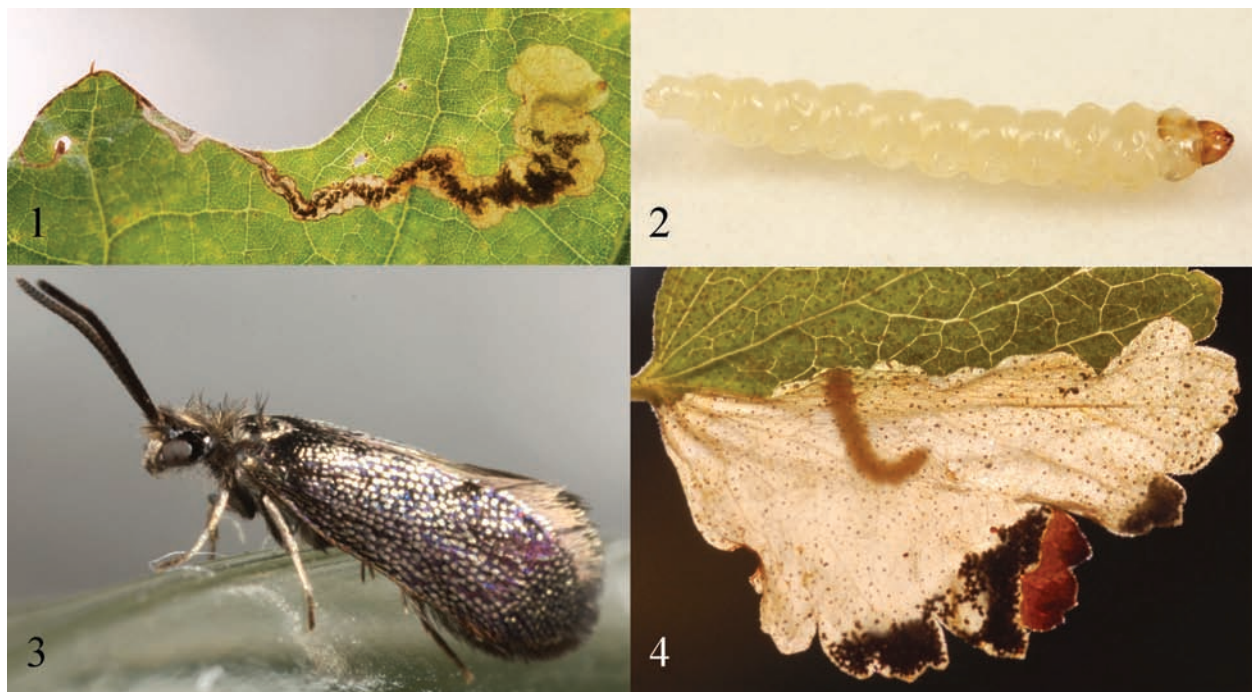
FIGS. 1–3. *Eriocraniella platyptera*. **1**) Larva mining a *Quercus ilicifolia* leaf; **2**) Mature larva; **3**) Reared adult

FIG 4. *Acanthopteroctetes* larva mining a *Ribes* leaf.

viridula (Coquillett) (Diptera, Agromyzidae), which produces frass in irregular lumps and streaks, and *Neurobathra strigifinitella* (Clemens) (Gracillariidae), which mines primarily in the midrib and produces frass in tiny, compact pellets.

The eriocraniid larvae (Fig. 2) began exiting their mines on 11 June. I transferred them to small jars containing a moistened 1:1 mixture of sand and peat, into which they burrowed. Empty leaves were pressed and stored for later study. Between 23 and 30 June, six hymenopteran parasitoids emerged from the eriocraniid mines. C. Hansson determined that they consisted of at least two different species of *Pnigalio* Schrank (Eulophidae), neither of which fit into the existing key to this genus (Yoshimoto 1983). They are deposited in the Museum of Zoology, Lund, Sweden. The jars of soil were stored in a refrigerator at 1–3° C from 6 November to 25 February 2014. Two adult moths (Fig. 3) emerged on 27 and 29 March. I sent one specimen to J.-F. Landry, who identified it as *Eriocraniella platyptera* and deposited it in the Canadian National Collection of Insects, Ottawa, Ontario.

I examined ten complete (not parasitized) *Eriocraniella platyptera* mines, which were always solitary. In each case, the egg was inserted 1–3 mm from the leaf edge (1.5 mm on average), and its location was marked by a small hole in the leaf. The hole ranged from 0.3–4 mm long (average 1.3 mm) and 0.2–1 mm wide (average 0.7 mm). Half of the eggs were in the basal fifth of the leaf, eight were in the basal two-fifths, and all were in the basal three-fifths. The mine was initially linear and always proceeded parallel to or away from the leaf edge (toward the leaf base in all but one instance) for 1–3 mm before curving until it reached the edge. It then followed the leaf margin apically for 15–25 mm (average 20 mm) before beginning to expand into an elongate blotch. Frass was deposited in a broken central line in the linear portion, becoming squiggly and forming a dense, broadening central mass in the blotch. The blotch continued to follow the leaf margin and ultimately occupied 1–2 cm² (average 1.5 cm²). Blotches measured 20–32 mm long (25 mm average), and the total span of the mine was 24–49 mm (average 39 mm). The larva exited through a ragged hole or slit in the lower epidermis at the edge of the blotch. D. L. Wagner (pers. com.) reports that these mines are common in sandy areas of Connecticut, and that he has reared *Eriocraniella* adults from scarlet oak (*Quercus coccinea* Münchh.) there.

The general form of the mine is consistent with that of all other known *Eriocraniella* mines (Davis 1978). However, mines of the other eastern species, *E. mediabulla*, differ from those of *E. platyptera* in that oviposition is usually in the apical half of the leaf and does not cause a hole to form in the leaf (Davis & Faeth 1986). Davis and Faeth (1986) contrasted the mine of *E. mediabulla* with that of *Dyseriocrania griseocapitella*, which they said, in addition to causing a hole to form, "commences near the lower third of the leaf and continues along the leaf edge as a serpentine mine to the distal half." This description suggests a mine identical to that of *E. platyptera*, but is at odds with all other descriptions I have found for the mine of *D. griseocapitella*. Davis (1978) stated that the eggs of *D. griseocapitella* are usually deposited "over the outer half of the leaf" and that the early linear portion of the mine is usually obliterated by the blotch.

T. Harrison provided me with a photograph of 23 *Dyseriocrania griseocapitella* mines on leaves of *Quercus* cf. *velutina* Lam. Although the resolution is insufficient to determine the oviposition sites in all cases, most do appear to have been initiated at or beyond the middle of the leaf. However, one of the mines is confined entirely to the basal half, and 13 others have substantial portions extending into the basal half, if not originating there. Just two mines have what appears to be an oviposition scar outside the blotch. In both cases this is well within 1 cm of the blotch. Since the photograph included a ruler for scale, I was able to measure the area covered by the mines, and these ranged from 2.5–6.25 cm² (average 4.3 cm²). Based on these observations, distinguishing among mines of the three eastern oak-feeding eriocraniids should be straightforward.

As noted above, *Eriocrania semipurpurella semipurpurella* (Stephens) is known to be a birch miner but there are no North American rearing records. The mines are similar to those of *Dyseriocrania griseocapitella* in having a short initial linear portion that is often obliterated by the blotch (Ellis 2015). I found active *Eriocrania* mines on gray birch (*Betula populifolia* Marshall) in Pelham, Massachusetts on 11 May 2012. In one case, two larvae were feeding in a single mine. The larvae began emerging the following day and burrowed into soil that I offered them, but I failed to rear any. I found a few abandoned *Eriocrania* mines on paper birch (*B. papyrifera* Marshall) in Machiasport, Maine on 16 June 2014. Because the host of *E. breviapex* is unknown, it cannot be said with certainty which species was responsible for these mines, although *E. semipurpurella* is most likely based on known distributions. Apart from *E. semipurpurella pacifica*, all confirmed hosts of *Eriocrania* species are in Betulaceae, with *E. alpinella* Burmann on *Alnus viridis* (Chaix) DC. and all others on *Betula* spp. (Davis 1978, Ellis 2015).

On 16 October 2012, along the Metolius River in Oregon, I collected leaf-mining larvae on *Ribes cereum* Douglas (Grossulariaceae) that I assumed to be sawflies (Tenthredinidae: Fenusini). The mines (Fig. 4) were full-depth blotches with the frass in oval pellets, concentrated along one edge of the mine. The larvae fed venter-upwards and had prominent thoracic legs. They died in the mines and became moldy, but two years later DNA barcoding of one of the dried larvae indicated a 97% match for *Acanthopteroctetes bimaculata* Davis. The match is insufficient to confirm that the larvae belonged to this species, which is known only from northeastern Oregon and the southern Sierra Nevada of east-central California (Davis 1978), but it is closer to this than to any of the three other described Nearctic *Acanthopteroctetes* species. D. L. Wagner (pers. com.) recalls having seen these mines commonly in California, but never collected them because he, too, mistook the larvae for sawflies. On 5 and 7 July 2015, I found occupied *Acanthopteroctetes* mines to be common on *R. cereum* in Chaffee and Fremont Counties, Colorado. There were occasionally two larvae per mine. In rearing vials, some larvae were able to establish new mines in fresh leaves, and I kept some alive until early August, but once again all died without pupating. I report these observations in the hope that someone in the western US will be inspired to search for more larvae and rear them to confirm their identity.

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LIVERWORT, *MONOCLEA GOTTSCHEI* LINDB. (MONOCLEACEAE),
NEW HOST PLANT FOR CRYPTIC GEOMETRIDAE CATERPILLAR IN MEXICO

Additional key words: Geometridae, Inchworm, Parque Ecológico Macuiltepetl, plant-insect interactions, Caterpillar, Liver

Research on associations between insects and plants are frequently related to angiosperms (Hendrix 1980). However, interactions between insects and non-vascular bryophyte land plants, liverworts among them, are uncommon and virtually unknown in literature. Reports of some primitive Micropterygidae (Lepidoptera) feeding on liverworts exists (Gerson 1982). However, as far as we know Geometridae has not been previously reported feeding on these non-vascular plants (Janzen & Hallwachs 2013).

Three caterpillars (Lepidoptera) were found among samples of hepatics or liverworts (Marchantiophyta) collected in a mountainous mesophyll forest in Xalapa's Ecological Park Macuilteplt, Veracruz, México, at
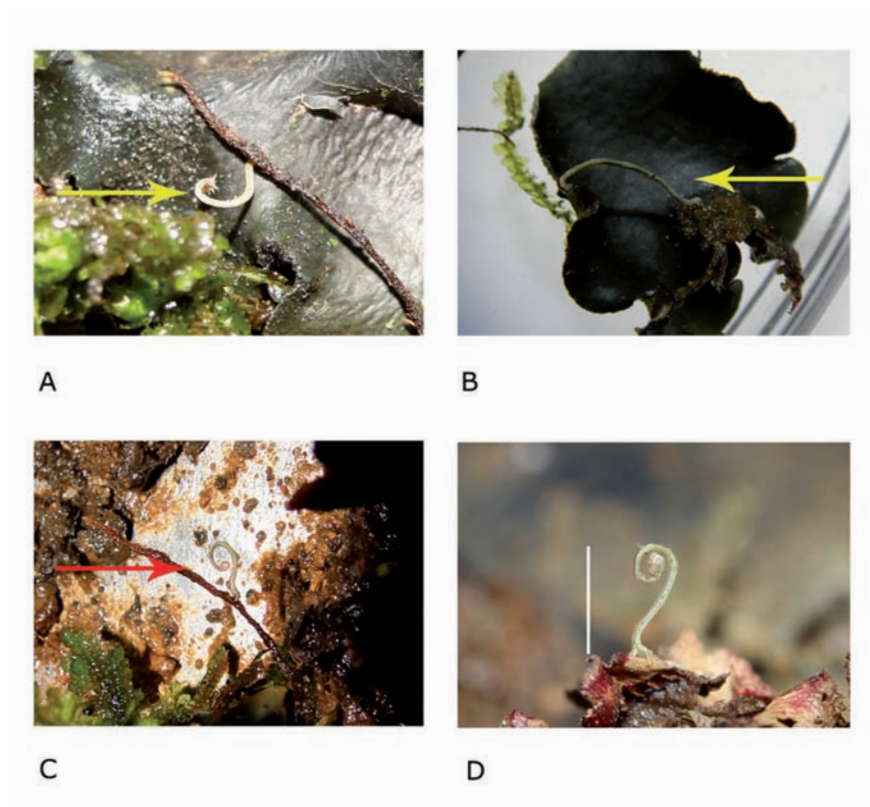
FIG. 1: **A & B**. Geometridae larvae (arrow) on liverwort *Monoclea gottschei* Lindb.; **C.** Cryptic Geometridae larvae in resting position on rhizoid; **D.** Cryptic Geometridae larvae resembling a sort of modified trichome. Scale bar: 5 mm.

1567m (N 19°32' 52.50" W 96° 55'09.22") on June 10, 2014. These larvae are 8 mm long and were found feeding on *Monoclea gottschei* Lindb, 1886, (Monocleales: Monocleaceae) *sensu* Gradnstein et al. (2001). The plant species was corroborated by comparison with specimens deposited at the Facultad de Biología-Xalapa Universidad Veracruzana (XALU) herbarium. The polypod larvae were reared but died before pupating. They were studied in detail and compared with several sources and even though species could not be determined, they are clearly eruciform and belong to the family Geometridae (Lepidoptera) (Chen 1946; IMSS 1930, Stehr 1987; Ide & Costa 2006; Hill et al. 1987; Martins 2006, Stehr et al, 1987).

Geometridae is a lepidopteran family with up to 21,190 species worldwide, and about 2,500 known species are found in Mexico (Heppner 2002). Some 344 species of this family had been recorded from the state of Veracruz (Hernández-Baz & Iglesias 2001). However, the immature stages of this and most moth families are basically unknown, except for those of economic or agricultural relevance (Hernández-Baz 2012).

The three larvae arranged themselves on a straight line along the rim of the plant and moved in a sort of simultaneous "dancing" for 30 seconds at 1 minute intervals during approximately 15 minutes. After this "dancing" ended they placed their body on a straight line, in an angle of 70 ° with regard to the rim of the plant.

The three larvae resembled the trichomes of hepatic plants thus when on the plant, the larvae were completely cryptic. Besides, mimicked the coloration of trichomes showing a very interesting homochromy. They also behaved as if they were trichomes moving slightly, as trichomes do when blown by the wind or breeze.

We observed the larvae feeding from the bottom region of the thallus (Figs. 1A, 1B). In laboratory conditions (~ 25 °C, 70 RH), at night, the larvae moved from the feeding area and hid either at the base of the plant which is brown, or on the cuticle of the plant giving the impression of a thallus gametophyte or even a trichome modified as young foliage of circinate vernation of a fern's new frond (Figs. 1B, 1C)

The larvae of Geometridae are known to feed on the foliage of deciduous trees, shrubs, some ferns, Pinophyta, and in some cases even their seeds (Stehr et al. 1987). Janzen and Hallwachs (2013) register 68

families of host plants for Geometridae, and as far as we know this report constitutes the first record of a liverwort species as a host plant for this lepidopteran family. The larvae mimicking a thrichome or sporophyte is also a clear example of an ecological interaction allowing the development of a favorable adaptation between moth and plant *sensu* Janzen (1980). Additionally, this accidental discovery of such a cryptic situation should motivate investigators to observe in detail the micro-fauna associated to this type of plants. As a result, new interesting interactions should be found.

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