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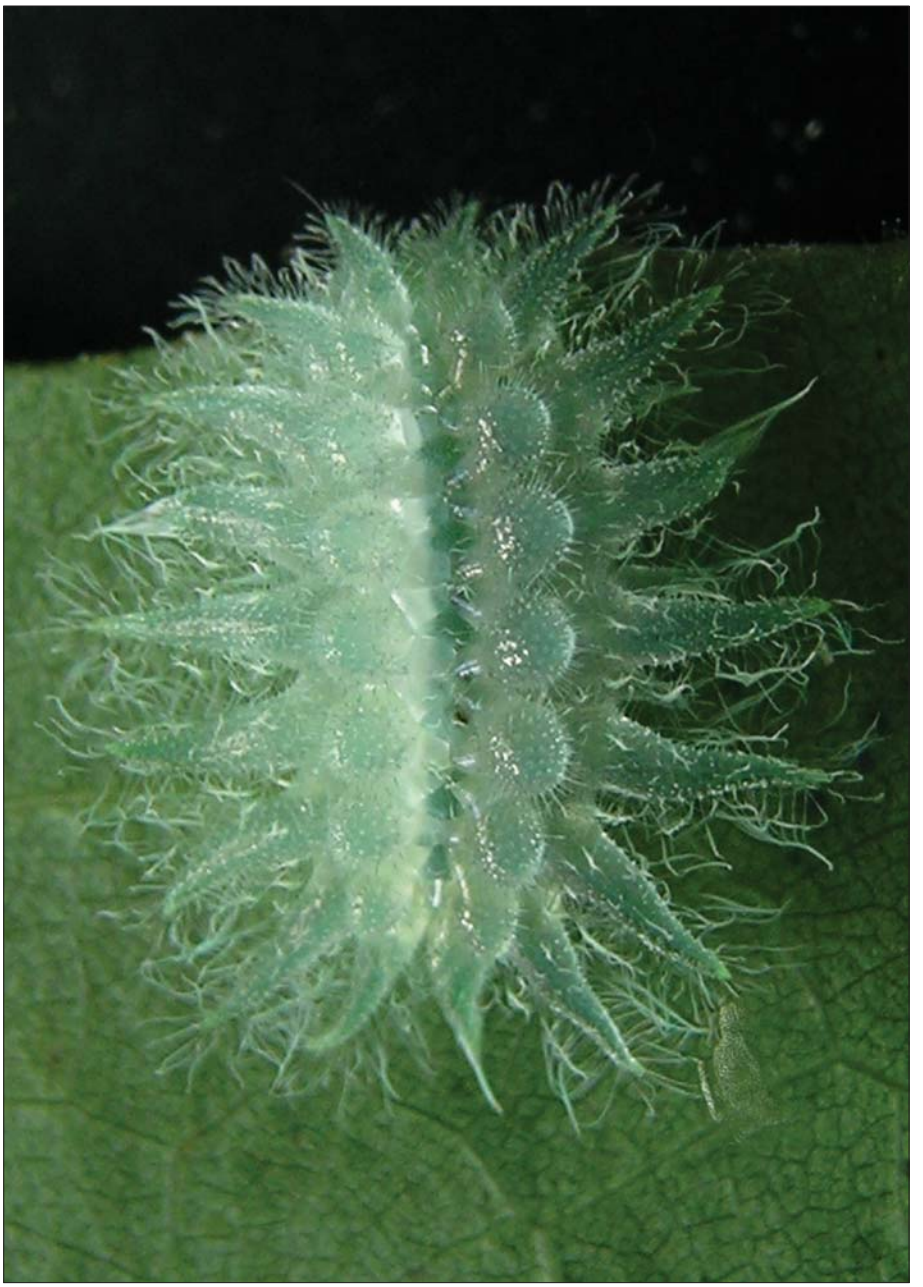

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Cover Illustration: Mid-instar larva of *Isochaetes beutenmuelleri* (Hy. Edwards) collected on 26 July 2004. Larva was found feeding on northern red oak (*Quercus rubra* L.) on Plummers Island (Montgomery County, MD, USA). Photo by J. Lill. See article on next page.

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NATURAL HISTORY OF LIMACODID MOTHS (ZYGAENOIDEA) IN THE ENVIRONS OF WASHINGTON, D.C.

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ABSTRACT. The moth family Limacodidae is notable for its fascinating larval stages, but with the exception of a few important pest species, the natural history of these moths is still poorly known. The goal of this project was to investigate the natural history of moths in the family Limacodidae, as well as a species in the related family Megalopygidae, from the metropolitan Washington, D.C. area. The specific objectives of this study were to (ordered by life cycle from adult to larva): 1) summarize data on the flight times of the adult moths; 2) investigate the oviposition behavior of female moths, specifically their tendency to lay eggs in clusters; 3) document the phenology and host associations of locally-collected larvae; 4) develop an accurate means for assessing larval developmental stage; and 5) determine whether larval growth and cocoon weight predict lifetime fitness for females. In an adult flight dataset that spans ~130 years, we found significant interspecific variation in flight periods collectively encompassing a season running from April through November. Several pairs of sympatric congeners differed significantly in median flight times suggesting temporal niche separation. We found that for two of the species we studied, *Acharia stimulea* and *Euclea delphinii*, females laid eggs in clusters, but females of the other species mostly laid eggs singly. We generally found limacodid larvae from early June through October and most limacodid species were found as larvae on at least eight different host plant species, which supports the presumption that most species are generalists. For *A. stimulea* and *E. delphinii* larvae, we developed a set of equations so that we may estimate larval mass given larval body length, which allows us to estimate a larva's developmental stage in the field. Lastly, we found that for both *A. stimulea* and *E. delphinii*, there was a positive relationship between a female's cocoon mass and the number of offspring she produced the following year; thus, for these two limacodid species, cocoon mass is a predictor of lifetime fitness for females. Here we present all of the natural history observations and data that we have collected and analyzed from a variety of sources.

Additional key words: Limacodidae, Megalopygidae, oviposition behavior, flight times, larval survival, larval growth rate

Lepidoptera in the families Limacodidae and Megalopygidae have charismatic caterpillars (Figure 1). The common name for limacodids, slug caterpillar moths or simply slug moths, is derived from their unusual locomotory habit as larvae that is characterized by a high degree of ventral contact with the substrate by use of abdominal "sucker" appendages in movement and the laying down of semifluid silk ribbons; this is different from other caterpillars that typically use hooks, referred to as crochets, that cling to silk fibers (Epstein 1995). As peculiar as their locomotion is, limacodid larvae are perhaps best known for their unusual dorsal visages, which vary considerably; some species appear to be highly cryptic (e.g., Fig. 1C, G) while others possess intricate and vivid color patterning and various types of protuberances on their dorsal surfaces, some of which are thought to be aposematic (e.g., Fig. 1A, B, Wagner 2005). Megalopygid larvae also have a high degree of ventral contact, but retain rudimentary prolegs with functional crochets that are used to grasp silk strands they lay down on smooth surfaces (Epstein 1995). They are best known for

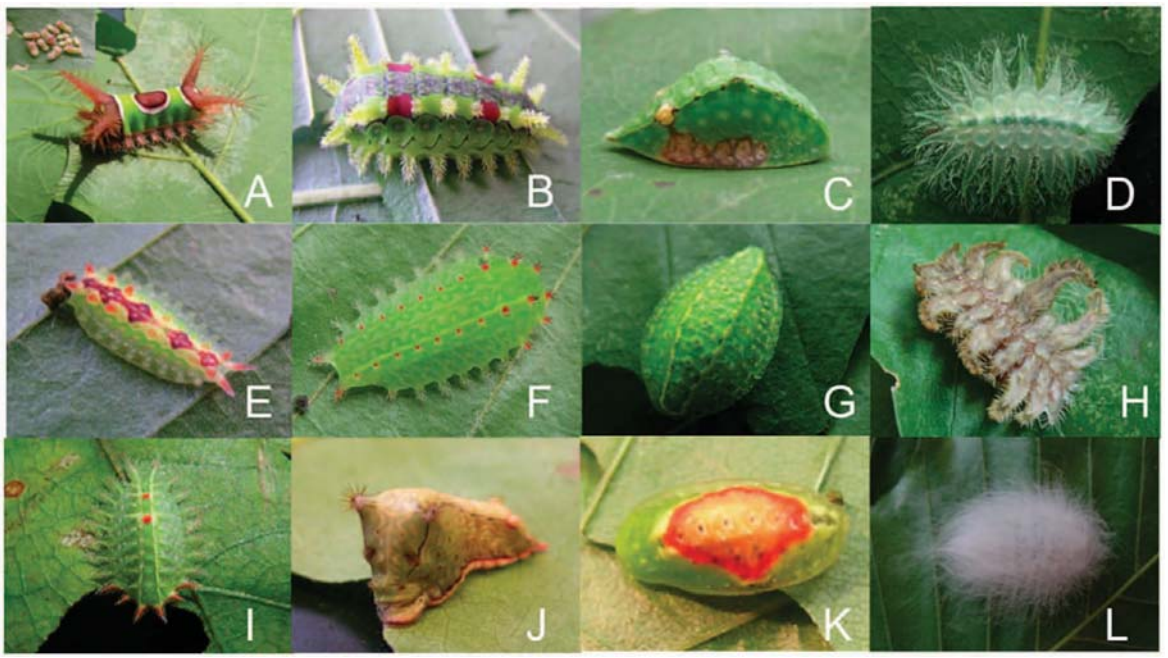

FIG. 1. Representative late-instar larvae of 11 species of Limacodidae: **A**) *Acharia stimulea*, **B**) *Euclea delphinii*, **C**) *Prolimacodes badia*, **D**) *Isochaetes beutenmuelleri*, **E**) *Adoneta spinuloides*, **F**) *Natada nasoni*, **G**) *Lithacodes fasciola*, **H**) *Phobetron pithecium*, **I**) *Isa textula*, **J**) *Parasa chloris* and **K**) *Tortricidia* sp. Representative late-instar larva of one common species of Megalopygidae: **L**) *Megalopyge crispata.*

having a woolly appearance with spines hidden beneath the silken hairs (Fig. 1L), though some have sparse hairs. Many species of both families are also remarkable for an intriguing defensive strategy: stinging setae, commonly referred to as spines. Species such as *Acharia* (=*Sibine*) *stimulea* (Clemens), *Euclea delphinii* (Boisduval) and *Megalopyge* (=*Lagoa*) *crispata* Packard (Fig. 1) possess spines for all or a portion of their larval development (Dyar 1899b) and these stinging spines are an effective defense against a variety of predators (Murphy et al. 2010). Although visually striking caterpillars from both of these families often grace the covers of field guides and other texts (e.g. Tilmon 2008), much of their basic biology remains poorly understood.

Limacodidae (~1700 species, worldwide distribution) and Megalopygidae (242 species, New World distribution) are mostly tropical groups with relatively few species currently occupying temperate climates (M. Epstein unpublished data; Epstein et al. 1998). There have been few natural history observations of North American Limacodidae since a series of detailed articles written in the late 19th and early 20th centuries by Harrison Dyar. Over a period of about five years (1895–1899), Dyar (and, at the onset, his colleague Emily Morton) described the larval stages of 18 limacodid species that live in and near New York in a series of manuscripts in the Journal of New York Entomological Society (Dyar & Morton 1895, 1896; Dyar 1896a, b, 1897a, b, c, 1898a, b, c, e, 1899b, c). During the same era, Dyar compiled a few life histories of other limacodids, including four eastern species (*Adoneta bicaudata* Dyar, *Monoleuca semifascia* (Walker), *Isochaetes beutenmuelleri* (Hy. Edwards), and *Lithacodes fiskeanus* (Dyar)), one from Florida and the Gulf Coast (*Alarodia slossoniae* (Packard)), the Florida form of *Euclea delphinii* and one introduced species from Asia (*Monema flavescens* Walker) (Dyar 1896b, 1905, 1907, 1909, 1914). Most of this work involved detailed descriptions of the caterpillars, including the morphology and number of instars, larval host plants and preferred feeding sites (above or under leaves, etc.), as well as some limited information on adult flight period, mating behavior, and oviposition behavior. Research on megalopygids from eastern North America has focused more on their role in causing allergic skin reactions in humans that get stung (Delgado Quiroz 1978; El-Mallakh et al. 1986) than on other aspects of their natural history (but see Packard 1894; Dyar 1899a). Although all of the 21 described species of limacodids from the Washington D.C. area were studied by Dyar, nearly all of his information was from localities outside of the region; thus, there is very little natural history information on limacodids from Washington, D.C. and its environs.

The overall goal of our research was to investigate the natural history of moths in the families Limacodidae and Megalopygidae from the Washington, DC area. The specific objectives of this study were as follows (ordered by life cycle from adult to larva): 1) summarize data on the flight times of adult limacodid and megalopygid moths; 2) investigate the oviposition behavior of female moths, specifically their tendency to lay eggs in clusters; 3) document the phenology and host associations of locally-collected larvae; 4) develop an accurate means for assessing larval developmental stage; and 5) determine whether larval growth and cocoon weight predict lifetime fitness for females.

MATERIALS AND METHODS

Objective 1 – Adult flight times

We compiled data for the flight times of adult limacodid and megalopygid moths from three sources: 1) our own records of moths collected at lights, 2) the Lepidoptera collections at the Smithsonian Institution's National Museum of Natural History (most of which were also light-collected) and 3) collections of D.C.-area limacodids vouchered in California at the Essig Museum (University of California, Berkeley) and the Los Angeles Co. Museum of Natural History. Together, these data sets include 987 moths collected over a span of ~130 years (1883–2010) and we know the exact collection date for 981 of the moths (several records had day and month but were missing the year or had the year, but not the day or month of collection). Over this period, moths were collected in Washington DC, 38 sites in Maryland near Washington DC or Baltimore MD (Anne Arundel County, Ashton, Baltimore County, Beltsville Agricultural Research Center, Bethesda, C&O Canal National Historic Park, Cabin John, Camp Springs, Carderock, Cheverly, Colesville, College Park, Croom, Finksburg, Forest Glen, Fort Washington Park, Frederick, Glen Echo, Greenbelt, Hickory Point, Hughes Hollow, Indian Mills, Island Creek Road, Laurel, Libertytown, Little Bennet Regional Park, Millersville, Montgomery County, Oxon Hill, Patuxent National Wildlife Research Center, Pleasant Hill, Plummers Island, Prince Georges County, Rockville, Soldiers Delight Natural Environmental Area, Southhaven, Sycamore landing, and Temple hills), 8 sites on Maryland's eastern shore (Bishopville, Elkton, Pickering Creek Audubon Center, Pocomoke City, Sharptown, Snow Hill, Wicomico State Forest, Wittman) and 18 sites in northern Virginia (Alexandria, Annandale, Arlington, Cape Henry Seashore State Park, Chesterfield County, Dismal Swamp, Fairfax County, Falls Church, Falmouth, Fort AP Hill, Franconia, Giles County, Great Falls Park, Heathsville, Konnarock, Mount Vernon, Skyland and Turkey Run Park). Moths from these collections comprise 21 species of Limacodidae including *Acharia stimulea* (Clemens), *Adoneta bicaudata* (Dyar), *Adoneta spinuloides* (H.-S.), *Apoda biguttata* (Packard), *Apoda y-inversum* (Packard), *Euclea delphinii* (Boisduval), *Heterogenea shurtleffi* Packard, *Isa textula* (H.-S.), *Isochaetes beutenmuelleri* (Hy. Edwards), *Lithacodes fasciola* (H.-S), *Monoleuca semifascia* (Walker), *Natada nasoni* (Grote), *Packardia elegans* (Packard), *Packardia geminata* (Packard), *Parasa chloris* (H.-S.), *Parasa indetermina* (Boisduval), *Phobetron pithecium* (J.E. Smith), *Prolimacodes badia* (Huebner), *Tortricidia flexuosa* (Grote), *Tortricidia pallida* (H.-S.), and *Tortricidia testacea* (Packard). In this paper two species of *Tortricidia*, *T. flexuosa* and *T. pallida*, are treated together because the species boundaries, both from a biological and a taxonomic point of view are unclear. Moths in this collection also include one species of Megalopygidae, *Megalopyge crispata* (Packard). Two other species of Megalopygidae (*Norape cretata* and *M. opercularis*) also occur in the area, but flight data for these species were sparse and the larval data were virtually nonexistent, so they are excluded forthwith. For almost all of the collection records, we know the specific date the moth was caught whereas only about half of the moths (N = 440) have been sexed.

Objective 2 – Adult female oviposition behavior

Limacodid and megalopygid females often lay more than one egg during an oviposition bout and these 'egg clusters' vary in the total number of eggs that they contain. To investigate whether females of different species vary in the number of eggs laid per cluster, we counted the number of eggs per cluster for females of six limacodid species (*Acharia stimulea*, *Adoneta spinuloides*, *Euclea delphinii*, *Isa textula*, *Natada nasoni* and *Phobetron pithecium*) and one megalopygid species (*Megalopyge crispata*). All of the moths were from our laboratory colonies and egg counts were made over two summers (2008–2009). For two species, *A. stimulea* and *E. delphinii*, we additionally recorded the time elapsed since mating for females to begin to lay eggs, how many days they laid eggs and their adult life expectancy.

Individuals in our colonies diapaused within cocoons as late-instar larvae; we housed them in individual 0.5L deli containers (Fabri-Kal, Kalamazoo, Michigan) until they pupated and emerged in early summer. As adults emerged, we placed males and females in clear, plastic mating-chambers (60 cm^3 BugDorm-2, BioQuip,

Rancho Dominguez, CA, USA) and allowed them to mate. When possible, we isolated mating pairs while *in copula* and gently placed them in clear, plastic 1L deli containers (Fabri-Kal, Kalamazoo, Michigan) to capture the entirety of a particular female's oviposition events. After mating was completed, we removed the male and left the female to lay eggs on the sides of the container, which females normally do willingly. Limacodids prefer to lay their eggs on smooth host plants (Epstein 1988; Lill et al. 2006) and the clear plastic of both mating chambers and deli containers appeared to serve as an adequate substrate. Not all mating pairs were caught *in copula* and these females laid their eggs on the interior walls of the mating chambers. Each morning during the mating season, we identified new egg clusters, circled them and individually numbered the clusters with a Vis-à-Vis pen (Sanford, Bellview, IL), which enabled us to later count the number of eggs in each cluster. For two species, *A. stimulea* and *E. delphinii*, we were able to isolate large numbers of mating pairs from the mating chambers. Thus, we were able to investigate whether the number of eggs laid by individual females differed between these two species. We counted the number of egg clusters each female laid, the number of eggs per cluster as well as the total number of eggs laid by each female during her lifetime.

We established our lab colonies in 2004 with individuals that were collected as larvae or adults from three field sites in the Washington, DC metropolitan area: Little Bennett Regional Park (Clarksburg, MD), Patuxent National Wildlife Refuge (Beltsville, MD) and Rock Creek Park (Washington, DC). New individuals are added yearly to maintain the genetic diversity within colonies. Adults were collected by light trapping and larvae are found by manually searching the foliage of a variety of tree species, but we focused our efforts on six focal tree species that we are studying as part of an ongoing experiment: American beech (*Fagus grandifolia* Ehrh.), white oak (*Quercus alba* L.), northern red oak (*Quercus rubra* L.), black cherry (*Prunus serotina* Ehrh.), black gum (*Nyssa sylvatica* Marsh) and pignut hickory (*Carya glabra* Mill.).

Objective 3 – Larval occurrence on host plants in the wild

Each summer and autumn (2004–2008), with the help of numerous field assistants, we manually searched for limacodid and megalopygid larvae on the foliage of native trees and shrubs. All five of our field sites are in the Washington, DC metropolitan area: Little Bennett Regional Park (Clarksburg, MD), Patuxent National Wildlife Refuge (Beltsville, MD), Plummers Island (Montgomery County, MD), Rock Creek Park (Washington, DC) and the United States National Arboretum (Washington, DC). Whenever we found a limacodid or megalopygid larva, we noted the species, the date of collection and the host plant on which it was found; each larva was reared in the lab to confirm identity. The seasonal pattern of larval abundance of each species was examined graphically by plotting each species' log-abundance over time, dividing the season into two-week increments.

Objective 4 – Larval growth rates in the laboratory

In 2008 we reared *A. stimulea* and *E. delphinii* larvae on six different host plants in the laboratory in order to develop standard curves relating larval length to larval mass. It is difficult to determine which instar a limacodid or megalopygid larva is in for several reasons. First, their head capsules are hidden from view, tucked under their prothorax, which makes it impossible to measure them and monitor an increase in head capsule width as larvae grow. Secondly, larvae tend to eat their molts, so in order to determine that a larva has molted, you must either observe it as it occurs or before the larva finishes eating the molt. Finally, the number of larval instars for Limacodidae is extremely high, ranging to as many as 11, with some species known to have variable numbers of instars from 8–11 (Nagamine & Epstein 2007) that could represent differences in food quality or sexual dimorphism. Thus, establishing a simple predictor of development stage (larval mass) that can be easily measured in the field is critical.

The offspring in this experiment were from two *E. delphinii* females and hatched on June 9–10, 2008. The neonate larvae were left where they hatched for ~24 hours because if neonate larvae are handled before they successfully molt from the first to second instar, they suffer high levels of mortality; all spiny larvae molt to the second instar on their second day of life and do not begin to feed until this time (Nagamine & Epstein 2007). Once the larvae molted to the second instar, they were placed on redbud (*Cercis canadensis*), which is a plant that newly-hatched larvae are often able to feed upon easily. On June 13, 60 *E. delphinii* larvae were individually placed in 0.5L deli containers (Fabri-Kal, Kalamazoo, Michigan). Each larva was assigned to one of 6 host plants, for a total of 10 larvae per host. The host plants were American beech (*Fagus grandifolia*), white oak (*Quercus alba*), northern red oak (*Quercus rubra*), black cherry (*Prunus serotina*), black gum (*Nyssa sylvatica*), and pignut hickory (*Carya glabra*). Correspondingly, the offspring of two *A.*

stimulea females hatched on June 25 and the neonate larvae were similarly placed on *C. canadensis* after they successfully molted to the second instar. On July 2, 60 *A. stimulea* larvae were moved to individual 0.5L deli containers and randomly assigned one of the same 6 host plants, for a total of 10 larvae per host. These 120 larval containers were provisioned with a moistened filter paper disc (7.5 cm diameter; VWR, West Chester, Pennsylvania) and excised foliage from the focal tree species, which was replaced as needed, at least every 2–3 days. The length and mass of each larva was measured every 7 days until the larva spun a cocoon. Length measurements were made using calipers (to the nearest 0.1 mm) and included the marginal spines present in both species. Mass measurements were made using a microbalance (to the nearest 0.01 mg; Mettler-Toledo XS-105, Columbus, Ohio).

Objective 5 – Cocoon weight as a predictor of lifetime fitness

In 2009 we were able to calculate realized lifetime fitness for individual *A. stimulea* and *E. delphinii* females. These individuals were reared during the summer of 2008 on various host plants and before we put the cocoons into growth chambers for the winter (see Objective 2 for details), we weighed each cocoon using a microbalance (to the nearest 0.01 mg; Mettler-Toledo XS-105, Columbus, Ohio). The following summer (2009) we recorded the number of eggs that each successfully-mated female laid and the number of those offspring that subsequently survived (see Objective 2 for details on how females were isolated). For *E. delphinii*, we only included females that had more than 30 larvae hatch in the analyses, but for *A. stimulea* we had fewer females and thus included any female that had more than 15 larvae hatch; we left-censored the data in this way so that only females that were motivated to oviposit were included in the analyses. This approach allowed us to estimate the realized fitness for each female and determine whether cocoon mass is related to lifetime fitness as has been demonstrated for other Lepidoptera (Slansky & Scriber 1985; Murphy 2007).

Statistical Analyses

For Objective 1, we computed species-specific descriptive statistics (median, 10th, 25th, 75th, and 90th percentiles) on the collection date (using Julian dates) from all Washington, DC and evirons adult moth collection records. In addition, Mann-Whitney U Tests (Zar 1999) were used to compare the median flight dates for four pairs of congeneric species (*Adoneta spinuloides* vs. *A. bicaudata*, *Apoda biguttata* vs. *A. y-inversum*, *Parasa chloris* vs. *P. indetermina*, and *Tortricidia flexuosa/pallida* vs. *T. testacea*) to test for evidence of temporal niche separation. For Objective 2, we log-transformed egg count data and then tested for differences in the number of eggs per cluster among species with one-way ANOVA. All pairwise comparisons between means were tested with Tukey's HSD (JMP v. 6.0.3, SAS Institute Inc., Cary, NC). To test for differences between the number of eggs and clusters laid by *A. stimulea* and *E. delphinii* females, we used two-way ANOVA with species and female as the fixed effects (JMP v. 6.0.3, SAS Institute Inc., Cary, NC). For Objectives 3, 4 and 5, we performed the correlation and regression analyses as well as ANOVA with JMP v.6.0.3. For the correlation and regression analyses we fit both linear and quadratic equations and present the best fit in the results.

RESULTS

Objective 1 – Adult flight times

The data we collected and compiled demonstrate that limacodid adults in the greater DC metropolitan area may be found flying in the field from April through early November (Fig. 2, Table 1). Table 1 lists the earliest and latest recorded flight times for each species including the year in which those specimens were collected. The median collection date for most species occurs in late summer (Fig. 2) and adult flight periods span 48–74 Julian days (the number of days between the earliest recorded date and the latest recorded date for each species). Although the adult flight periods of most of our local limacodids clearly span more than a month, the community separates roughly into three cohorts of species that tend to fly together: the 'early' cohort includes *P. geminata, T. testacea*, *A. y-inversum*, and *A. biguttata*; the 'middle' cohort includes *H. shurtleffi*, *L. fasciola, E. delphinii, P. indetermina*, *A. spinuloides*, *A. stimulea*, and *N. nasoni*; and the 'late' cohort includes *P. pithecium, P. chloris, I. beutenmuelleri, P. badia*, *I. textula*, *T. flexuosa/pallida*, and *A. bicaudata*. The single megalopygid studied, *M. crispata*, would be grouped with the middle cohort. Two species, *Monoleuca semifascia* and *Packardia elegans*, are represented by only a single individual in our dataset and so little can be assessed for the flight times of the adult stage for these species other than that they do occur in the environs of Washington DC. We note that both males and females of all species with at least 10 collection records have been collected at lights; capture of females by this method allows for obtaining larvae ex ovo.

In our locally-occurring community of Limacodidae, five congeneric species pairs occur sympatrically, many of which share the same sets of host plants. For the four

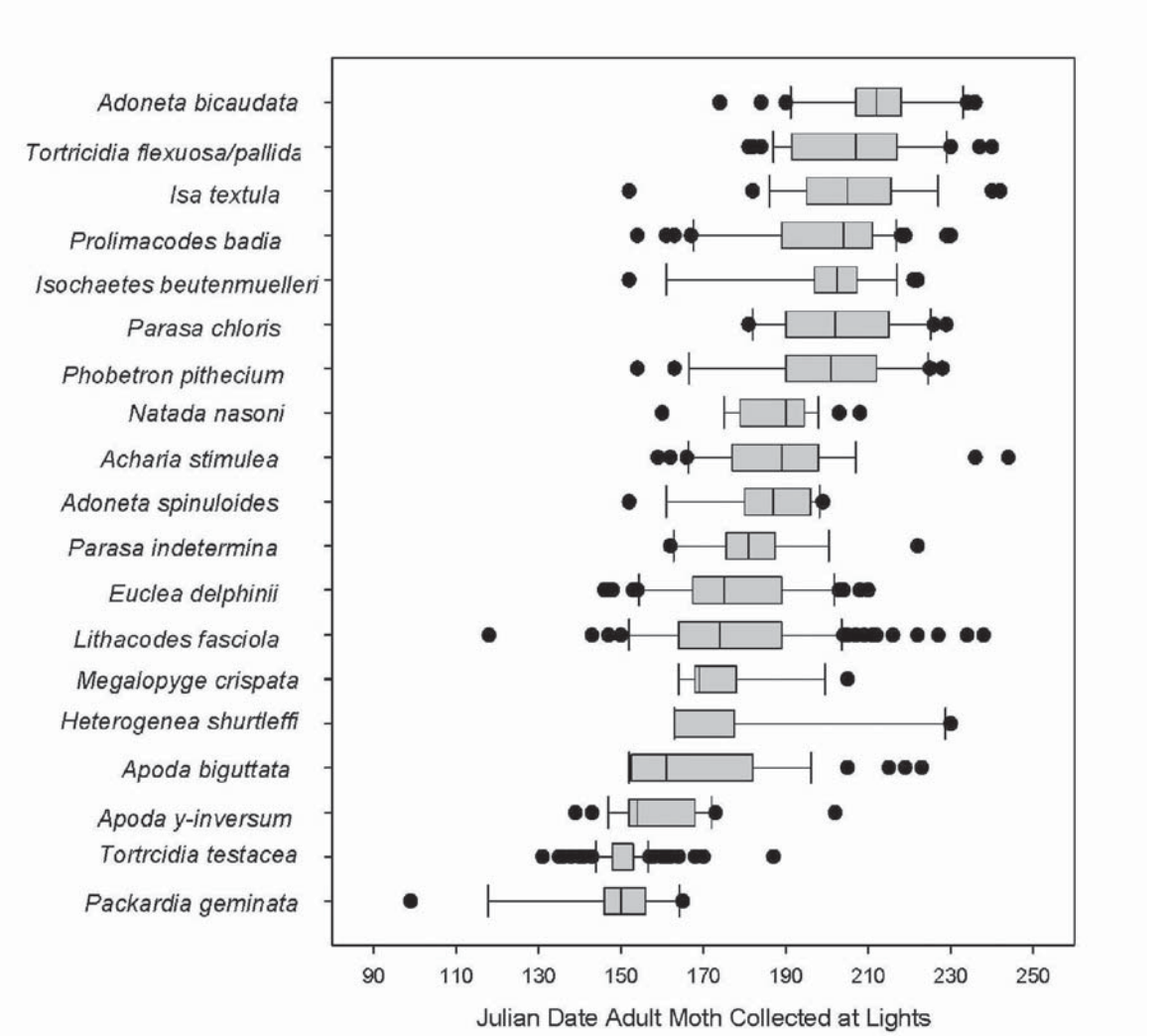

FIG 2. Seasonal occurrence of limacodid and megalopygid adults at sites in the metropolitan Washington DC area and the eastern shore of Maryland during 7 field seasons from 2004–2010 and museum collections from 1883 through 2009. From bottom to top, species are ordered by their median flight date (Julian day). Vertical lines inside of the boxes indicate the median collection date for each species, the box margins are the 25th and 75th percentiles, and error bars (whiskers) indicate the 10th and 90th percentiles. Solid circles indicate outliers. Sample sizes for each species are given in Table 1. There is one outlier data point that is not included in the figure: the latest flight date for *Adoneta bicaudata* is November 13 (Julian day 317), but it is not shown so that the other data points are more easily viewed and interpreted. There were two species that only had a single individual represented in the dataset and are thus not included in the figure: *Monoleuca semifascia* (collected on Julian day 215; 3 August 1940) and *Packardia elegans* (collected on Julian day 186, 5 July 1997).

pairs with sufficient collection data to analyze statistically, adult flight times differed significantly between each pair of congeneric taxa (*Adoneta bicaudata* vs. *A. spinuloides*, U = 756, N_1 = 30, N_2 = 27, two-tailed P < 0.0001; *Apoda biguttata* vs. *A. y-inversum*, U = 2209, N_1 = 59, N_2 = 57, P =0.003; *Parasa chloris* vs. *P. indetermina*, U = 455.5, N1 = 31, N_2 = 17, P < 0.0001; *Tortricidia flexuosa/pallida* vs. *T. testacea*, U = 13,454, N_1 = 132, N_2 = 102, P < 0.0001; compare medians of sister taxa depicted in Figure 2). Notably, most of these species pairs have very similar genitalia (both males and females; MEE, personal observation), suggesting relatively recent divergence times.

Objective 2 – Adult female oviposition behavior

For two species, *A. stimulea* and *E. delphinii*, we recorded the time elapsed since mating for females to begin to lay eggs, how many days they laid eggs and female moth life expectancy. We found that *A. stimulea* females live an average of 9.3 days (± 0.35, n=65, range=3–21 days; all variance measures are ± 1 SEM). Generally, females mate on the 2nd day after emergence (± 0.16, n=83, range=1–7 days), lay their

first egg 2.9 days after mating (± 0.32, n=72, range=0–11 days) and then lay eggs for a total of 2.9 days (± 0.26, n=72, range=1–11 days). *Euclea delphinii* females live an average of 7.6 days (± 0.36, n=37, range=4–16 days). Generally, females mate on the 2nd day after emergence (± 0.14, n=44, range=0–5 days), lay their first egg 1.6 days after mating (± 0.18, n=45, range=0–5 days) and then lay eggs for a total of 2.9 days (± 0.31, n=44, range=1–10 days).

We found that females of different species vary significantly in the number of eggs laid per cluster ($F=281.3$, df=6, $P<0.0001$; Table 2). With a mean of over 7 eggs/cluster (and as many as 85 eggs observed in a single batch), *A. stimulea* females lay significantly larger batches than any other species ($P<0.05$) and *E. delphinii* females (which average slightly more than 4 eggs/batch) lay larger batches than all of the remaining species (Table 2; $P<0.05$). The number of eggs per cluster did not differ significantly between *A. spinuloides*, *I. textula*, *N. nasoni, P. pithecium* or *M. crispata* ($P>0.05$).

There was significant variation in the number of eggs laid per cluster by individual females, even within a single species (*A. stimulea*: $F=6.7$, df=23, $P<0.0001$; *E. delphinii*: $F=33.9$, df=9, $F<0.0001$). Yet, after we controlled for this individual variation, we found that *A. stimulea* females generally laid more eggs per cluster than did *E. delphinii* females ($F=12.9$, df=1, $P=0.0003$; Table 2), similar to the results we found above when egg data were pooled across females. Although the mean number of eggs per cluster differed among females for both *A. stimulea* and *E. delphinii*, we found that neither the number of clusters ($F=1.05$, df=1, $P=0.3$) nor the total number of eggs ($F=0.06$, df=1, $P=0.8$) that were laid by individual females differed between these two species.

Finally, the incubation period (period from oviposition to larval hatching) of limacodids is approximately 7–8 days (mean = 8.74 ± 0.22 and 7.8 ± 0.37 days for *E. delphinii* and *A. stimulea*, respectively) although more detailed measures for a wider number of species under constant temperature are needed before making more general conclusions.

Objective 3 – Larval occurrence on host plants in the wild

We found limacodid and megalopygid larvae on the foliage of 19 different native plant species (Table 3). A majority of the larval species were found feeding on at least 8 different host plants; *A. stimulea*, *A. spinuloides* and *L. fasciola* larvae were each found on 10 plant species, *E. delphinii* and *N. nasoni* larvae were found on 9 plant species and *I. textula*, *M. crispata* and *P. badia* larvae were found on 8 plant species. The remaining larval species (*A. y-inversum*, *I. beutenmuelleri*, *P. chloris, P. geminata, P. pithecium* and *Tortricidia sp.*) were found on 5 or fewer plant species. We tested the possibility that host range estimates are a function of sampling effort by regressing the number of host plant species recorded per caterpillar species on the number of larval collections. We found that there was a significant, positive relationship between a caterpillar species' diet breadth and sampling effort (number of larval collections/species) ($F=10.5$, df=1, $P=0.008$).

We found limacodid and megalopygid larvae in the field from early June through early October (Fig. 3). In Figure 3, we have ranked species by abundance, which is a proxy for our confidence in the completeness of each species' records; for species with a greater number of records, the likelihood of having accurately identified their peak abundance is increased. The species for which we found larvae earliest in the year was *E. delphinii*, which was found on 13 June 2008 on *Nyssa sylvatica.* The species for which we found larvae latest in the year was *P. pithecium*, which was found on 5 October 2004 on *Quercus alba*. Larval abundances for most species peak sometime between late June and late August (Fig. 3). For the four species for which we had adequate records for both adults and larvae, we found that the larval abundances lagged behind adult abundances, typically by a few weeks (Fig. 4), as expected based on the adult life span and incubation estimates given above.

Objective 4 – Larval growth rates in the laboratory

For both *A. stimulea* and *E. delphinii* we found that larval length is a good predictor of larval mass. We found a significant correlation between the log of larval length and the log of larval mass for *A. stimulea* ($R^2=0.99$, df=1, $P<0.0001$), but significant variation could be attributed to both the host plant upon which the larva was reared ($F=7.73$, df=5, $P<0.0001$) and the interaction between host plant and log length ($F=5.97$, df=5, $P<0.001$). Despite this variation among host plants, the correlation between the log of larval length and mass remains significant and explains a large portion of the variation even when the data are pooled across host plants. From these pooled data, the following equation may be used to estimate the mass of an *A. stimulea* larva given its length:

$$(\text{Log mass in mg}) = -3.55 + 3.23(\text{Log length in mm}) \quad \text{(Eq. 1)}$$

We also found a significant correlation between the log of larval length and the log of larval mass for *E. delphinii* ($R^2=0.99$, df=1, $P<0.0001$) and neither host

TABLE 1. For each species, the earliest and latest seasonal recordings of adult flight; the year for each record is given in parentheses and the sex (M or F) is given if known; the total number of adult flight records is also given (N). These data are from sites in the metropolitan Washington DC area and the eastern shore of Maryland during 7 field seasons from 2004–2010 and museum collections from 1883 through 2009. There were two species that only had a single individual represented in the dataset and are thus not included in the table: *Monoleuca semifascia* (collected on August 3, 1940) and *Packardia elegans* (collected on July 5, 1997). Detailed statistics on flight data are given in Figure 2.

	Earliest flight date	**Latest Flight Date**	**N**
Limacodidae			
Acharia stimulea	June 8 (1900, M)	September 1 (1912)	43
Adoneta bicaudata	June 23 (1911, F)	November 13 (1987, M)	31
Adoneta spinuloides	June 1 (1975)	July 17 (2007, F)	27
Apoda biguttata	June 1 (1975)	August 11 (1993, F)	58
Apoda y-inversum	May 19 (1990, M)	July 21 (2002)	59
Euclea delphinii	May 26 (1914)	July 29 (1997 and 2005, M)	93
Heterogenea shurtleffi	June 12 (1996, F)	August 18 (2001, F)	10
Isa textula	June 1 (1930, M)	August 30 (1976)	49
Isochaetes beutenmuelleri	June 1 (2005)	August 10 (1912)	39
Lithacodes fasciola	April 28 (2002, F)	August 26 (2001)	144
Natada nasoni	June 9 (2001, F)	July 27 (2005, F)	37
Packardia geminata	April 9 (1988, F)	June 14 (1974, F)	13
Parasa chloris	June 30 (1995, M)	August 17 (1971)	31
Parasa indetermina	June 11 (1908, M)	August 10 (2003)	17
Phobetron pithecium	June 3 (1902, F)	August 16 (1912)	23
Prolimacodes badia	June 3 (1976)	August 18 (1997)	59
Tortricidia flexuosa/pallida	June 30 (1995)	August 25 (1988, F)	102
Tortricidia testacea	May 11 (2002)	July 6 (2005)	132
Megalopygidae			
Megalopyge crispata	June 13 (2009, M)	July 24 (2005, F)	12

TABLE 2. For each species, the number of eggs laid per egg cluster, the number of egg clusters laid per female and the total number of eggs laid per female are given. Data for each of these measures are presented as the mean ± SE with the range (min-max) given in parentheses. Data on eggs/cluster combine the oviposition events of a large number of lab-mated females. For a much smaller subset of two species (*A. stimulea* and *E. delphinii*), we kept track of the total oviposition events for individual females to quantify levels of intraspecific variation in both the number of cluster laid over their lifetime and total egg numbers.

Species	N Clusters (Eggs)	# Eggs/ Cluster	N Females (Clusters, Eggs)	# Clusters/ Female	# Eggs/ Female
Limacodidae					
Acharia stimulea	1423 (10,369)	7.28 ± 0.20 (1-85)	24 (946, 6,467)	39.4 ± 4.8 (1-116)	269.5 ± 27.9 (1-499)
Adoneta spinuloides	608 (1,444)	2.38 ± 0.11 (1-30)			
Euclea delphinii	1438 (5,850)	4.07 ± 0.14 (1-76)	10 (661, 3,055)	52.5 ± 9.5 (4-98)	305.5 ± 74.4 (4-618)
Isa textula	13 (13)	1.00 ± 0.00 (1-1)			
Natada nasoni	21 (21)	1.00 ± 0.00 (1-1)			
Phobetron pithecium	365 (435)	1.91 ± 0.03 (1-4)			
Megalopygidae					
Megalopyge crispata	144 (214)	1.49 ± 0.09 (1-7)			

TABLE 3. Percentage of larvae found on the foliage of various plant species at several field sites in the Washington, DC metropolitan area: Little Bennett Regional Park (Clarksburg, MD), Patuxent National Wildlife Refuge (Beltsville, MD), Plummers Island (Montgomery County, MD), Rock Creek Park (Washington, DC) and the United States National Arboretum (Washington, DC). Larvae were collected from 2004–2008. *=the six host plant species that were most intensively and consistently searched.

	Larval Species						
Host Plant Species	*Acharia stimulea* (N=56)	*Adoneta spinuloides* (N=89)	*Apoda y-inversum* (N=2)	*Euclea delphinii* (N=51)	*Isa textula* (N=403)	*Isochaetes beutenmuelleri* (N=50)	*Lithacodes fasciola* (N=160)
Acer negundo	4						1
Acer saccharinum	7						
Acer sacharum					1		1
Amelanchier sp.		2		4			
Asimina triloba	5	1					
Carpinus caroliniana							
*Carya glabra**	7	6	100	10	4		11
Cercis canadensis				2			1
Diospyros virginiana		1		2			
*Fagus grandifolia**	13	30		14	32	50	57
Lindera benzoin	4						
*Nyssa sylvatica**		5		8	1		3
*Prunus serotina**	4	1		23	3		8
*Quercus alba**	30	7		8	28	6	4
Quercus montana		1			10		
*Quercus rubra**	21	46		29	21	44	13
Quercus velutina							1
Robinia pseudoacacia	5						
Vaccinium sp.							

	Larval Species						
Host Plant Species	*Megalopyge crispata* (N=31)	*Natada nasoni* (N=164)	*Packardia geminata* (N=26)	*Parasa chloris* (N=39)	*Phobetron pithecium* (N=9)	*Prolimacodes badia* (N=114)	*Tortricidia sp.* (N=25)
Acer negundo							
Acer saccharinum							
Acer sacharum							
Amelanchier sp.							
Asimina triloba							
Carpinus caroliniana		2	4				
*Carya glabra**	10	8		18		7	
Cercis canadensis	16						
Diospyros virginiana	3	1				2	
*Fagus grandifolia**	10	49	77	23	78	46	24
Lindera benzoin				3			
*Nyssa sylvatica**		10	4			7	
*Prunus serotina**	7	5			11	5	4
*Quercus alba**	48	4	4		11	8	36
Quercus montana		1				2	
*Quercus rubra**	3	20	11	56		23	36
Quercus velutina							
Robinia pseudoacacia							
Vaccinium sp.	3						

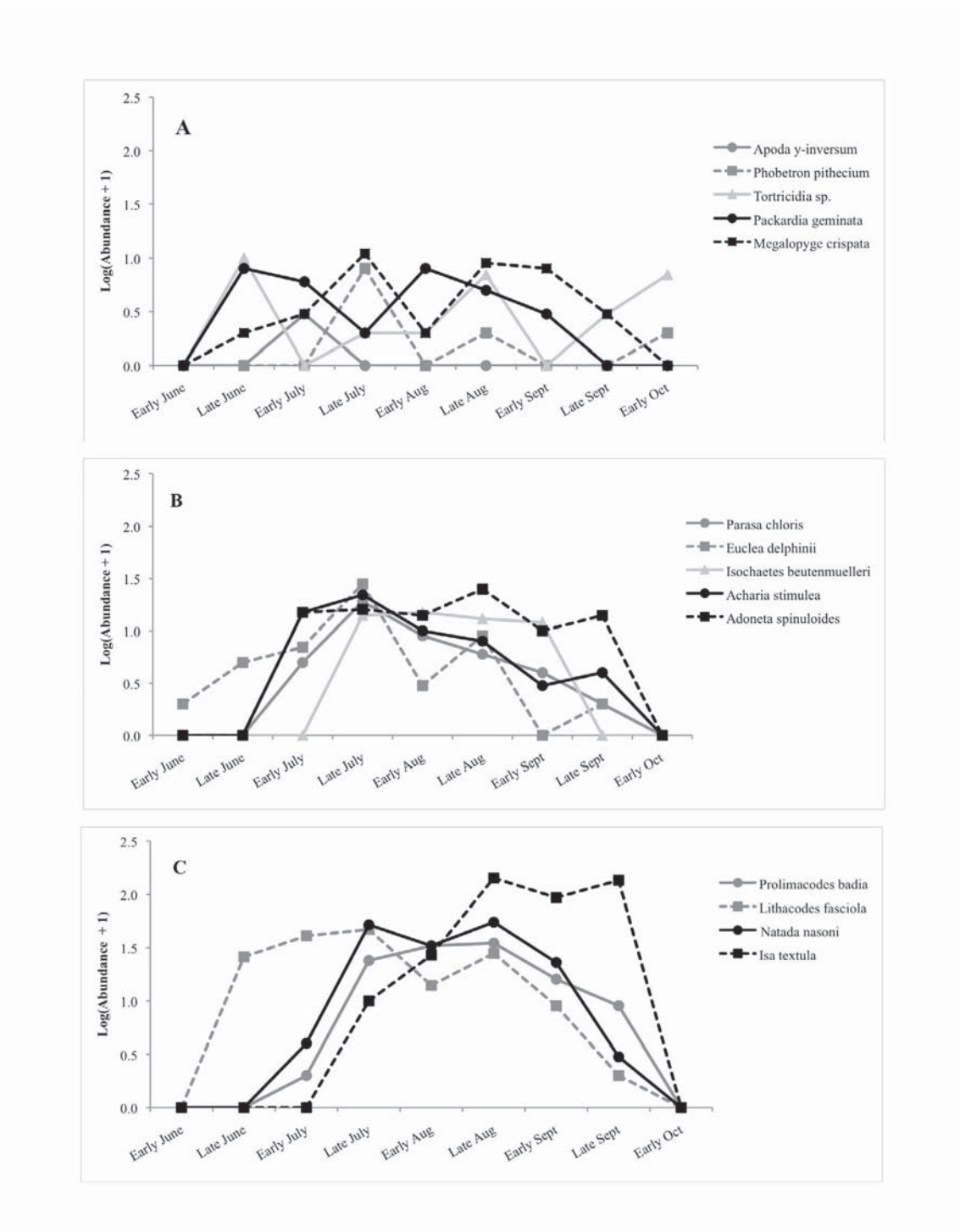

FIG. 3. Seasonal occurrence of limacodid and megalopygid larvae at sites in the metropolitan Washington DC area during 5 field seasons, from 2004–2008. Species are listed in order of abundance, which is a proxy for our confidence in the completeness of each species' records; for species with a greater number of records, we feel more confident that we have more accurately identified their peak abundance. **A**) Relatively uncommon species (*Apoda y-inversum*, N=2; *Phobetron pithecium*, N=9; Tortricidia spp., N=25; *Packardia geminata*, N=26; *Megalopyge crispata*, N=31). **B**) Moderately common species (*Parasa chloris*, N=39; *Euclea delphinii*, N=49; *Isochaetes beutenmuelleri*, N=50; *Acharia stimulea*, N=56; *Adoneta spinuloides*, N=88). **C**) Relatively common species (*Prolimacodes badia*, N=113; *Lithacodes fasciola*, N=160; *Natada nasoni*, N=164; *Isa textula*, N=402).

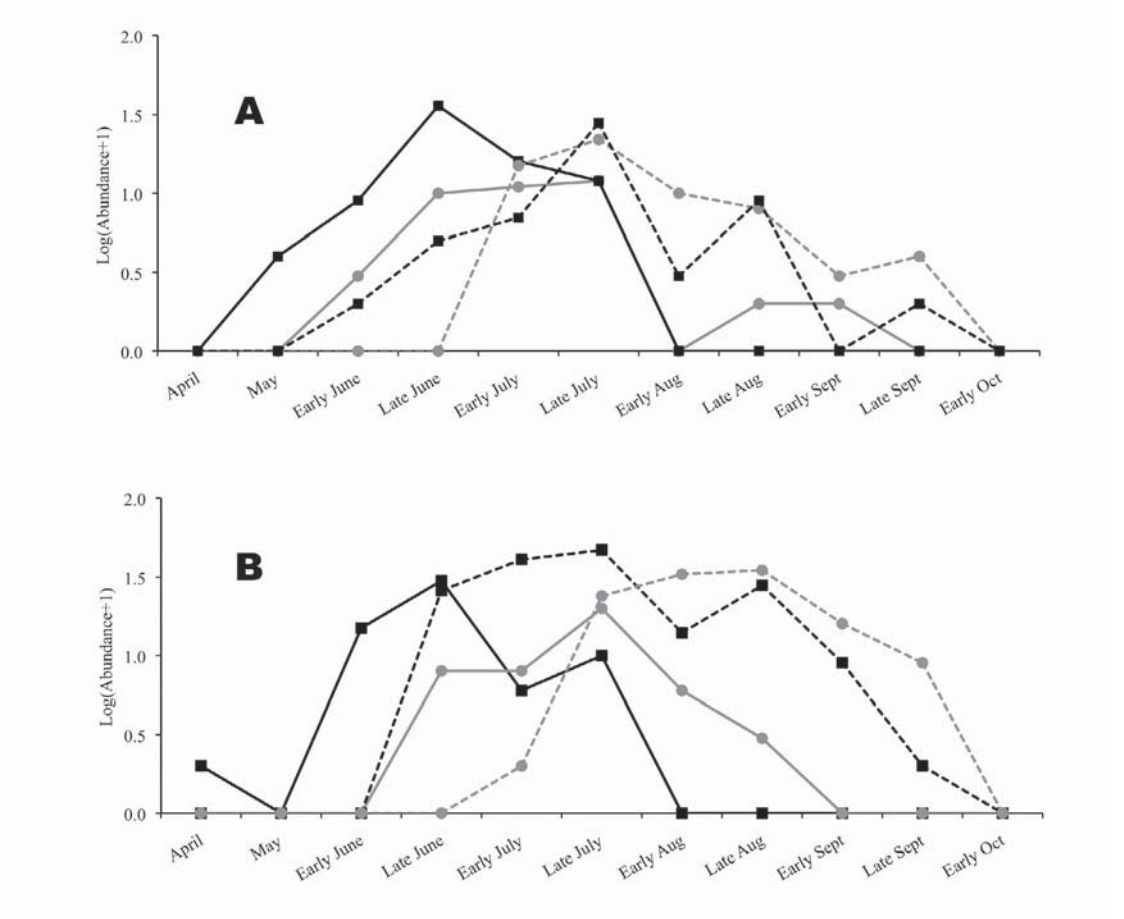

FIG. 4. Adult flight times compared to seasonal occurrence of larvae for four limacodid species. These are the same data as presented in Figures 2 and 3, but focus on the four species for which we have abundant adult and larval collection records. For all graphs, adults are solid lines and larvae are dashed lines. A) *Euclea delphinii* (black squares) and *Acharia stimulea* (gray circles). B) *Lithacodes fasciola* (black squares) and *Prolimacodes badia* (gray circles).

plant (F=0.99, df=5, P=0.42) nor the interaction between host plant and log length (F=1.28, df=5, P=0.27) were significant sources of variation in the model. Thus, given the length of an *E. delphinii* larva, we can estimate its mass with the following equation:

(Log mass in mg) = -3.01 + 2.85(Log length in mm) (Eq. 2)

Objective 5 – Cocoon weight as a predictor of lifetime fitness

We found that for both *A. stimulea* and *E. delphinii*, there was a positive relationship between a female's cocoon mass and the number of offspring she produced the following year. In other words, females that weigh more as final-instar larvae tend to have greater lifetime fitness than females that weigh less. For *A. stimulea* the relationship is nearly significant and explains 33% of the observed variation (Fig. 5; N=11 females, R^2=0.33, F=4.38, P=0.06). For *E. delphinii* the relationship between female cocoon mass and the number of viable offspring is less strong, but still positive (Fig. 5; N=23 females, R^2=0.1, F=2.27, P=0.15).

DISCUSSION

Here, for the first time in over 100 years, we compile additional information on the natural history of limacodid and megalopygid species found in eastern North America. Notably, this is the first natural history review for species found near metropolitan Washington D.C. Our findings support much of what has been commonly assumed about the biology and life histories of these species, but we have also discovered some new patterns that were not previously recognized in the literature.

Adult Life Stage

Most limacodid and megalopygid species are thought to be univoltine in temperate regions and, indeed, most of our data support this assertion. It's difficult to

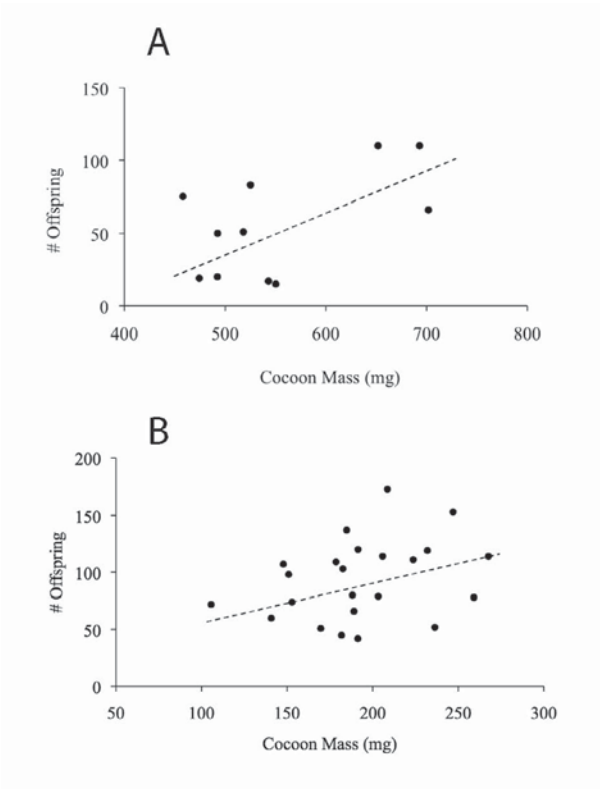

FIG. 5. Correlations between cocoon mass and the number of offspring for each female. A) *Acharia stimulea* (N=11 females, R2=0.33, F=4.38, P=0.06). B) *Euclea delphinii* (N=23 females, R2=0.1, F=2.27, P=0.15).

conclude too much from this dataset, however, because much depends on when the sampling was conducted; our records span ~130 years, but the sampling was not conducted systematically and indeed there are several decade-long gaps in the dataset (e.g., there are no records from 1918–1930 or 1945–1967) as well as spotty collecting efforts within particular years. Since 2000, collections in the DC area have been conducted more frequently and in the future it would be very helpful to devise a more systematic sampling scheme so that flight patterns could be elucidated more easily. For instance, we have anecdotal evidence that *E. delphinii* may be facultatively bivoltine, with a partial second flight in September (G. Shlichta, personal communication), but we did not include these observations in our dataset because exact dates remain unknown. As populations south of Washington, DC are reported to be multivoltine (MEE, personal observation) the partial second generation observed for *E. delphinii* may also occur in other species (e.g., *A. bicaudata*, which has a very late flight record; Table 1) and requires further investigation.

Because this community of moths is largely sympatric and the larvae occupy the same habitats (and even share many of the same host plants), there exists the potential for hybridization among closely related species (i.e., congeners or sister taxa). To our knowledge, hybridization in North American Limacodidae has not been explored, but we found it rather striking that each of the four congeneric pairs of moths in our adult dataset occupies a distinct (statistically significant) temporal window from its closest relative. Moreover, for the fifth congeneric pair, which was not compared statistically (*Packardia geminata* vs. *P. elegans*) due to a sample size of one adult collected for *P. elegans*, the median collection dates differ by more than a month (36 days), which supports the highly significant pattern of temporal niche separation in the other four congeneric pairs. Phenological separation among related taxa in sympatry has been viewed as a potentially important prezygotic reproductive isolating mechanism that either promotes or maintains species boundaries (MacArthur & Levins 1967). Most of these sister taxa also have almost indistinguishable genitalia, suggesting the observed temporal separation may serve to limit hybridization. Examination of more sympatric pairs of congeners (i.e., in the tropics where there is greater phylogenetic diversity within Limacodidae) and laboratory mating trials between congeners are necessary to test the generality of these findings.

We have found that in the lab, *A. stimulea* and *E. delphinii* females live about a week (9.3 days and 7.6 days respectively), but *A. stimulea* females in particular can live much longer as evidenced by several females who survived ~3 weeks in the lab; these data are likely upper bounds of adult lifespan in the wild, which is expected to be shorter due to predation and other stochastic events. Limacodid and megalopygid males and females mate most often at night, and the nuptial coupling normally lasts ~8–48 hours (JTL and SMM, personal observations). A notable exception is *Phobetron pithecium*, which we have found mating during daylight hours (JTL personal observation). Diurnal flight in this species is also suggested by a collection record of a male *P. pithecium* in a malaise trap (LACM: Colesville, MD, coll. Scott Miller, Aug. 1979) and an even sex ratio at light traps (both for *P. pithecium* in our study (data not shown) and for *Phobetron hipparchia* (Cramer) in Costa Rica (MEE, unpublished data)). This is the only temperate limacodid in the New World that exhibits sexual dimorphism in adult color patterning; males have clear patches in their wings and are thought to mimic wasps, which suggests daytime activity.

During mating, limacodid females prefer to hang from the substrate (leaves, twigs, branches or the mating chamber wall) by their front tarsi where they

apparently 'call' for males. Once males locate the females, the male 'climbs' down the hanging female and copulates with her while hanging from his engaged abdomen. We've found that *A. stimulea* and *E. delphinii* females typically mate on the second day after they emerge and usually begin to lay eggs a day or two later and continue to lay eggs for about 3 days. Anecdotal evidence from lab-mated *L. fasciola, P. pithecium* and *M. crispata* suggest a similar pattern and this pattern was also noted for *H. shurtleffi* in Dyar (1898d).

Female limacodids appear to be very fecund and are able to lay a considerable number of eggs over the course of their lifetime; *A. stimulea* and *E. delphinii* females averaged 270–300 eggs per female, but some females laid >500 eggs! Limacodid species vary in whether females lay eggs in batches or as singletons, as noted by Dyar & Morton (1895) in their general comments about that family. We found that some species, such as *I. textula*, *N. nasoni,* and *P. pithecium*, usually laid eggs singly, which corresponds with previous studies except that *N. nasoni* has been reported to lay eggs either singly or in small groups (Dyar 1899c). We found that *A. spinuloides* did not differ in the mean number of eggs laid per batch from these singleton species, but its variation was much greater and females sometimes laid several dozen eggs in one batch, which the other singleton species never did; Dyar (1897a) also noted that *A. spinuloides* females sometimes laid batches of 2–10 eggs. Non-quantitative, observational evidence from ovipositing females in the lab suggest that *Tortricidia* spp., *P. geminata, and P. badia* lay eggs singly, which supports earlier observations by Dyar (1896a, 1898a, b, c). Two field collections of egg clusters of *P. chloris* suggested that this species lays eggs in small clusters of 2–3 eggs, which is again consistent with Dyar (1897b) who reported that this species laid eggs singly or in small group of a few eggs. In contrast, two of the limacodid species that we studied, *A. stimulea* and *E. delphinii*, usually laid eggs in batches. In the case of *A. stimulea*, this corresponds well with field observations of the larvae (and indeed other *Acharia* species from the Neotropics), which commonly form feeding aggregations (JTL and MEE personal observation). Our observation of batch-laid eggs of *E. delphinii*, not correlated with feeding aggregations as in *A. stimulea*, does contradict the findings of Dyar (1897b), who reported eggs laid "singly, or but few together, not in … large patches of *Sibine* (=*Acharia*)." Even larger feeding aggregations of spiny, aposematic limacodid larvae have been reported in several Australian species, including *Doratifera casta* (Reader & Hochuli 2003).

These results suggest a possible causal link between clutch size and 'spiny-ness' as the species with the brightest, aposematic coloration (and often the worst stings) tend to be batch-layers while the more cryptic species tend to lay solitary eggs. Group-feeding often accompanies aposematism and is hypothesized to enhance the warning signal (Gamberale & Tullberg 1998). One locally-occurring species, *Parasa indetermina* (known as the 'stinging rose caterpillar', Wagner 2005) has highly aposematic larvae compared with its congener, *P. chloris*, whose larvae are quite cryptic. Based on this line of reasoning, we might predict that *P. indetermina* lays its eggs in batches, which is supported partially by Dyar's (1897a) report that this species lays eggs "singly or in small batches." Alternatively, it has previously been suggested that clutch size and 'spiny-ness' may also be related to whether or not larvae feed during the first instar; spiny caterpillars do not feed during the first instar while limacodids that become smooth (= gelatines) after the first instars or retain first–instar tubercles (e.g., *Phobetron*) do feed during the first instar (Nagamine & Epstein 2007). Although the adaptive significance of this is currently unclear, it is possible that the batch-laying, spiny caterpillars may avoid feeding in the first instar to prevent them from consuming the eggs containing adjacent siblings. Furthermore, these first instars can be thought of in the same way as other stadia, which cease feeding prior to molting: the only difference is that it occurs soon after eclosion. The delayed development of the plentiful sharp spines into the second instar may additionally serve to prevent the eggs, which have among the thinnest chorions in Lepidoptera (Epstein 1996; Nagamine & Epstein 2007), from rupturing. Comparative study of the oviposition behaviors of a wider sample of species within a phylogenetic framework is clearly necessary to test these hypothesized links.

Larval Life Stage

Limacodid and megalopygid larvae utilize at least 19 native plant species in the environs of Washington DC. Most species in our study fed on at least 8 different host plants. Our statistical analyses indicate that the actual host range is likely to be much greater as we found a positive linear relationship between the number of larvae found and the number of host plants utilized. Thus, our records for the number of species utilized by these generalist herbivores are likely conservative and would increase with continued sampling. Further, we have only been studying and rigorously searching native plant species for limacodid and megalopygid caterpillars, but we know from haphazard sampling that they are also found on introduced exotic species. For instance, we have found *A. stimulea* caterpillars on Mongolian oak (*Quercus mongolica*) and an ornamental

baobab houseplant that one of our colleagues placed on her porch one summer; *A. stimulea* is perhaps the most polyphagous of all of the eastern limacodids given the large number of unusual host records, including woody plants, vines (English ivy) and even corn (Forbes 1905; Wagner 2005). These anecdotal collection records on exotic species emphasize that our approximation of the number of host plant species utilized by limacodids is likely an underestimate as many species may also be using introduced plants as hosts as well.

We note, however, that one species, *Apoda y-inversum*, has only been recorded feeding on the genus *Carya* (hickories; Junglandaceae), both in our larval sampling and in Dyar's records from a century ago. While our larval sampling for this species is embarrassingly poor (N = 2 larvae collected in 6 years of sampling), finding a specialist species in this group of broadly polyphagous caterpillars would indeed be notable and worthy of further study.

Limacodid and megalopygid larvae can be found in the field near Washington D.C. from early June through early October, with peak abundances from late July through August. As such, these larvae are characterized as 'late-season' caterpillars that feed almost exclusively on the rather tough, low quality foliage characteristic of this time of year (Lill et al. 2006). *Isa textula*, in particular, is one of the most abundant larvae collected in the late fall and caterpillars are frequently found feeding on leaves in the midst of turning color in late October right up until leaf drop (JTL and MEE, personal observations). For the four species for which we have adequate sampling of both adults and larvae (*A. stimulea*, *E. delphinii*, *L. fasciola* and *P. badia*) the peak larval abundance is within a month of the peak adult abundance, but usually lags by a few weeks. The large temporal spread for larval collections likely results from environmental variation in both adult emergence time and larval development time, the latter of which is strongly related to host plant quality, which is highly variable among plant species (e.g., development time for *A. stimulea* larvae reared on red oak can be up to a month longer than larvae reared on black cherry; JTL and SMM, unpublished data). While our collection efforts for limacodid larvae are systematic and quantitative, this is not true for the adult flight data and more systematic sampling for adults in flight should be pursued in the future.

As determination of larval instar is difficult for both limacodids and megalopygids (for the specific reasons, refer to Objective 4 in the methods section), we often record body length and mass as estimates of developmental stage in laboratory experiments, instead of the more traditional measure of head capsule width. However, for field experiments, larval mass is not feasible to measure and so we wished to learn whether we could use larval length to approximate larval mass. Indeed, we found that we could estimate larval mass quite accurately given a measure of the larva's body length for both *A. stimulea* and *E. delphinii* (Equations 1 and 2, respectively). These equations facilitate the measurement of relative growth rate in field situations where obtaining accurate measurements of mass can be a challenge.

Limacodid larvae are known for their interesting morphologies and behavior. Species that possess stinging spines are well defended against a variety of predators (Murphy et al. 2010), but the effectiveness of the spines against predators appears to be increased by larval behavior. For example, when *A. stimulea* larvae are attacked by predatory paper wasps, they tend to rock back and forth in order to 'aim' their spines directly towards the offending predator and prevent access to the more vulnerable central portion of their dorsum (JTL and SMM, personal observations), but this behavior has not yet been fully studied. The biochemistry of the caterpillar's venom is not well understood, but the toxin is thought to be a protein (Foot 1922). Even some of the 'cryptic' species, which do not possess stinging spines, appear to still be chemically defended. Larvae of *Prolimacodes badia* are rather cryptic, but when disturbed they secrete droplets of fluid from pores on the dorsum (Patton 1891; Epstein 1996); however, both the effectiveness and the chemistry of this putative defense remains to be tested. Other species that are purported to have stinging spines (e.g., *Phobetron pithecium* and *Isochaetes beutenmuelleri*) have failed to yield a response in limited lab trials (JTL personal observation; Dyar 1896a; Wagner 2005). Incidentally, both of these species possess spines on deciduous tubercles that can be removed without noticeably harming the caterpillars and are regenerated when lost in early instars; in *P. pithecium* these tubercles are incorporated into their cocoons (Epstein 1996).

At the end of the larval stage, limacodid and megalopygid larvae spin cocoons in which they diapause as prepupae (Epstein 1996). They generally pupate within their cocoon the following spring and then emerge as adults shortly thereafter. Assessing the evolutionary fitness of larvae reared in the lab or in the field is a time consuming prospect because one must wait until the following year when the moths emerge, allow the adults to mate, allow females to lay eggs and then care for the eggs until they hatch and the surviving larvae may be counted. Often, however, pupal or cocoon mass is used as a predictor of lifetime fitness (the

number of surviving offspring from a single individual female) for other species of Lepidoptera (Slansky & Scriber 1985), but this relationship has not been studied in limacodids. We found that for both *A. stimulea* and *E. delphinii*, there is a positive relationship between a female's cocoon mass and the number of offspring she produces the following year. In other words, it appears that a female's realized fitness is a function of her cocoon mass. Although this relationship was only marginally significant for *A. stimulea*, it explained a large portion of the variance. One likely explanation for the lack of significance so far is our limited sample size; collecting these types of data is difficult and time consuming and we plan to continue with these efforts this year to see if the patterns hold.

Here we have documented the current state of the natural histories of North American Limacodidae and Megalopygidae for the first time since Dyar's series of papers in the 1890s. While we have a fairly detailed understanding of the phenologies of adults and larvae for multiple species, the oviposition behaviors of a few species, and the larval growth rates for an even smaller set, there is still quite a bit that we do not currently know about these charismatic species. For instance, a modern, species-level phylogeny is lacking for the group, which makes it difficult to perform research that requires a phylogenetic context. Such a phylogeny could be used to examine the evolution of the variety of defensive traits employed by different limacodid species that range from crypsis to aposematism. Because it appears that limacodid species that are physically defended with stinging spines are also the species in which females tend to lay eggs in clusters (Nagamine & Epstein 2007), it would be very interesting to study the relationship between larval defense mechanism and oviposition behavior of adult females. We are also interested in mapping key ecological associations (e.g., host-plant and host-parasitoid associations) onto such a phylogeny to investigate whether these ecological factors may have played a role in patterns of herbivore diversification. Finally, studying the chemical basis of the sting bestowed by stinging spines is yet another area of research about which almost nothing is known for these species. In sum, while we have added significantly to our understanding of limacodid and megalopygid natural history, there is still much more to be learned.

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A REVIEW OF WEST HIMALAYAN NEPTINI (NYMPHALIDAE)

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ABSTRACT. Neptini reliably recorded from the Western Himalaya are listed. A new subspecies, *Neptis clinia praedicta* ssp. n. and two new combinations, *Neptis nata yerburii* Butler comb. n. and *Neptis capnodes pandoces* Eliot comb. n., are proposed, *Neptis capnodes* Fruhstorfer is raised to species rank and the distribution of several subspecies is extended.

Additional key words: *Neptis*, palatability, *Neptis clinia praedicta* ssp. n., *Neptis nata yerburii* Butler comb. n., *Neptis capnodes capnodes* Fruhstorfer **stat. n**.; *Neptis capnodes pandoces* Eliot **comb. n.**

Progressing from east to west, the Himalayan range west of Nepal is divided into the Kumaon Himalaya with Nainital as the principal town; the Garhwal Himalaya, with Mussoorie and Dehra Dun as the principal towns; Himachal Pradesh with Shimla and Kulu as the principal towns; Kashmir, with Jammu the principal town in the outer ranges, and the Pakistan Himalaya, with the hill station of Murree. This area is known as the Western Himalaya (fig. 3).

On a north to south axis, the Himalayan range can be divided into three parallel ranges, the foothills or Siwaliks rising in parts to nearly 3000 m elevation; the middle ranges, rising to a maximum of a little over 3000 m elevation in parts of Garhwal, and the main range, comprising forested hills and snow covered mountains rising to over 7000 m elevation.

Eliot (1969) reviewed the Asian Neptini, based mainly on material in the collection of the Natural History Museum, London. However, there was apparently little material from the Himalaya west of Nepal available to him at the time. Consequently, the distribution and taxonomy of some taxa were not satisfactorily established.

All the Neptini known from the western Himalaya are found in the foothills and some also occur in the main range. None have so far been recorded from the trans-Himalayan areas of Ladakh, Lahoul and Spiti.

Eastern and western Himalayan populations of several butterfly species have been divided into subspecies based on the shade of pigments and the extent of pale area on the wings. In the Neptini, where the wings have a pattern of pale and dark bands, the western Himalayan populations often have broader pale bands than their eastern Himalayan counterparts (Eliot 1969).

The present paper is the result of fieldwork in various parts of the Himalaya during the past quarter century as well as observations of earlier workers.

Two species, *Neptis manasa* Moore and *Neptis jumbah* Moore have been excluded, although they have been reported from the Kumaon Himalaya by Atkinson (1882). There are no extant specimens of either species from this area. However, some typically Eastern Himalayan butterfly species that had been reported by earlier workers but were not recorded for most of the 20th century have re-appeared during the last two decades. *Talicada nyseus* Guérin-Menéville (Lycaenidae) was originally reported by Atkinson (1882) and has recently been recorded by Singh (2005a) from Dehra Dun and has been quite common in Kumaon for the past seven years. *Delias acalis* Godart, which was originally reported from the western Himalaya by Evans (1932), was recently confirmed from the Kumaon Himalaya by Smetacek (2001). A few species appear to have extended their ranges westward recently, such as the lycaenids *Rapala pheretima* Hewitson (Smetacek 1995) and *Zesius chrysomallus* Hübner (Singh 2005b). Therefore, it is possible that the two Neptini mentioned above will appear in the eastern part of the study area in the years to come.

All the Neptini recorded occur in broadleaf evergreen forests. Above 1200 m elevation, such forests comprise mostly Himalayan Oak (*Quercus leucotrichophora; Q. glauca; Q. floribunda*) forests while below 600 m, the forests containing Neptini are dominated by Sal (*Shorea robusta*) trees. In between there is a belt of miscellaneous deciduous forest, which does not support many Neptini.

Within the forests of oak, there are altitudinal divisions, so that species such as *Neptis narayana* Moore and *Neptis mahendra* Moore do not occur below 1700 m, although most of the plant species do so.

Almost all *Neptis* species are frequent visitors to damp mud on hot days and some, such as *Neptis zaida* Westwood, have been most often recorded there. Only *N. mahendra* has not been reported puddling. Flowers

are not frequently visited, although *Buddleia* and Lantana flowers as well as Asteraceae, such as marigolds, are visited. *N. narayana, N. ananta* Moore and *N. sankara* Kollar occasionally visit horse chestnut (*Aesculus indica*) blossoms. Honey dew on citrus is a potent attractant, with tens of *N. soma* Moore, *N. nata* Moore and *N. clinia* Moore fluttering about an affected tree.

Within the forest, different species have a preferred height at which they are most often found: *N. sankara* and *N. ananta*, if not descending to puddle, frequent the tree tops; *N. zaida* is usually found near the ground in glades, while *N. narayana* also frequents the tree tops, provided the trees are not very high. *Neptis sappho* Pallas, *N. hylas* Linnaeus and *N. soma* are found lower, usually up to 5 m above the ground. *N. clinia* descends readily to water, but in the forest frequents tree tops, as does *N. nata*. Similar vertical stratification of flight has been reported in some neotropical ithomiines (Medina et al. 1996; Papageogorgis 1975).

Males of *N. sankara*, *N. narayana*, *N. ananta*, *N. sappho*, *N. nata*, *N. clinia* and *N. soma* are occasionally territorial, especially at the edge of glades, where they will occupy a prominent perch and make sallies to investigate passing butterflies.

MATERIALS AND METHODS

Most parts of the Kumaon Himalaya were visited during the past 25 years. Consultation with the late Lt. Col. J.N. Eliot established the taxonomic revisions proposed in the systematic section, while Mr. Philip Ackery at the Natural History Museum, London (BMNH) kindly compared some of the present material with type material in the collection there. In addition, I examined the Neptini in the main and subsidiary collections of the University Museum, Oxford, U.K. as well as in the Forest Research Institute, Dehra Dun, India.

Genitalia of male specimens of *N. nata*; *N. soma* and *N. clinia* were examined by soaking the tip of the abdomen in 10% KOH overnight, separating the soft tissue and examining the valvae under a low power microscope. Subsequently, the genitalia were mounted on card papers under a drop of Canada Balsam and allowed to dry for a few months. Then these cards were pinned under their specimens. Alternatively, the genitalia of fresh specimens were extruded by pressing the penultimate abdominal segments with a pincer and the valvae examined using a 10x lens.

Palatability. Wynter-Blyth (1957) asserted that there was a Batesian mimicry relationship between *Athyma opalina* Kollar, the model and *Apatura* (*Mimathyma*) *chevana* (Moore), the mimic. In order to test this, over a period of three years at my address above, 10 specimens of *Neptis sappho astola* Moore, 20 specimens of *N. soma butleri* Eliot; 6 *N. hylas kamarupa* Moore; 6 *Pantoporia sandaka* (Butler); 10 each of *Athyma opalina, A. perius* (Linnaeus) and *A. cama* (Moore) were offered to wild, free ranging insectivorous birds (mainly family parties of White Crested and White Throated Laughing Thrushes). All except *N. hylas* were eagerly devoured. In the case of *hylas*, the tests were inconclusive and require further work. It is abundantly clear, however, that if either *A. opalina* or *N. soma* or both are deriving some advantage out of occurring together and looking and behaving similarly, the relationship is neither Batesian nor Müllerian. The same may be said for the relationship between *A. opalina* and *Apatura* (*Mimathyma*) *chevana*, since one may presume that the latter is palatable to predators. It might be a case of Self Detractive Mimicry (Smetacek 1987).

SYSTEMATIC SECTION

In the following account, the species appear in the same order as in Eliot (1969). Butterfly collections containing West Himalayan Neptini have been abbreviated as follows:

Coll. A.P. Singh: Dr. Arun Pratap Singh, Forest Research Institute, Dehra Dun, Uttarakhand, India.
Coll. BMNH: The Natural History Museum, London, U.K.
Coll. OUM: University Museum, Parks Road, Oxford, U.K.
Coll. FRI: Forest Research Institute, Dehra Dun, Uttarakhand, India.
Coll. Smetacek: Peter Smetacek, The Retreat, Jones Estate, Bhimtal, Nainital, Uttarakhand, India.

Pantoporia hordonia hordonia (Stoll)

Papilio hordonia Stoll, 1790:149, pl 33, figs. 4, 4D.
Pantoporia hordonia (Stoll); Eliot, 1969: 33.

Distribution: Dehra Dun eastwards along the foothills and on the adjoining plains, to Burma, Malaya and Vietnam. Peninsular Indian specimens appear to be intermediate between this and the Sri Lankan ssp. *sinuata* (Moore).

Remarks: Reported by Atkinson (1882) and all subsequent authors (Mackinnon & de Niceville (1899); Hannyngton (1910); Evans (1932); Peile (1937); Wynter Blyth (1957.)) from the Kumaon and Garhwal Himalaya but not by Eliot (1969).

This and the next species, *Pantoporia sandaka*, occur sympatrically in India. *P. hordonia* is not as common as *sandaka* in Kumaon. Both species are common in

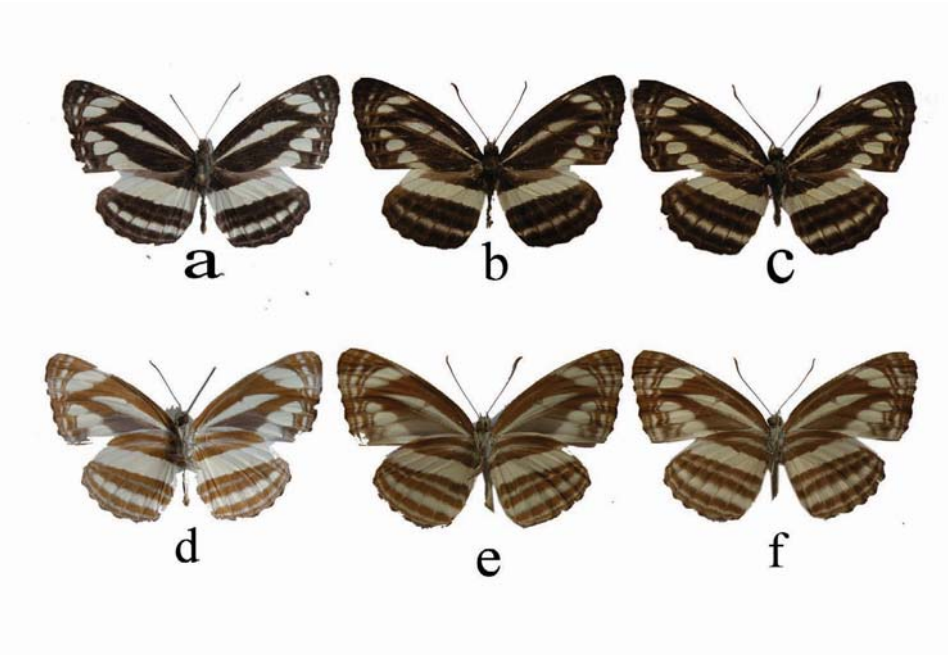

FIG. 1. **a**) *Neptis clinia praedicta* holotype Dry Season Form recto. **b**) *Neptis clinia praedicta* Wet Season Form recto. **c**) *Neptis nata yerburii* recto. **d**) *Neptis clinia praedicta* holotype Dry Season Form verso. **e**) *Neptis clinia praedicta* Wet Season Form verso. **f**) *Neptis nata yerburii* verso.

evergreen forest at the foot of the hills and on the adjoining plains. Both are less common at 1500 m, a few stragglers ascending to 2200 m in the outermost range.

There are specimens in the Coll. FRI from Dehra Dun (Roonwal et al. 1963).

Both species are on the wing from March to June and again from September to November.

FIG. 2. A female *Neptis mahendra* ovipositing on *Pyracantha crenulata.*

*Pantoporia sandaka davidson*i Eliot
Pantoporia sandaka davidsoni Eliot 1969: 35.

Distribution India, Burma, Siam and Hainan.

Remarks: More common than *P. hordonia* at low elevation in Kumaon. There are specimens from Dehra Dun in Coll. A.P. Singh. See under *P. hordonia*.

Neptis clinia praedicta ssp. n.
(Fig. 1a, b, d. e)

Material examined: Holotype: Male: Jones Estate, Bhimtal, Nainital, Kumaon, India. 1500 m; 8.iv.2007; Leg. P. Smetacek. Deposited in the Indian National Forest Insect Collection, Forest Research Institute, Dehra Dun, India. Accession number: NFIC-FRI 21811. Paratypes: 126 specimens taken from March to June and October and November 1986 to 2008 in Bhujiaghat, Nainital district, Kumaon, India 600 m and Jones Estate, Bhimtal, Nainital, Kumaon, India 1500 m, all Leg. P. Smetacek; all in Coll. Smetacek.

Diagnosis: (the following terminology follows Eliot 1969, Text fig. 1, p. 16): In both seasonal forms, the white bands, particularly the discal band on the hindwing, are 15% to 20% wider than in the corresponding seasonal forms of *N. clinia susruta* Moore. While the narrow banded Wet Season Form of *praedicta* has white bands that would fall within the range of variation of Dry Season Form *susruta*, the Dry Season Form of ssp. *praedicta* has perhaps the widest white bands of any known population of *N. clinia*.

Description: Forewing length: 18–29 mm. Expanse: 48 mm. Dry Season Form: Head, thorax and abdomen unmarked fuscous, iridescent under artificial light; antennae with tip of nudum brown. *Recto* surface of wings with ground colour black. Forewing cell streak clear white, discocellular bar faint, streak beyond cell wider than cell streak at discocellular bar; upper postdiscal band consists of 4 spots, the 2 costal spots reduced to small streaks; lower postdiscal band complete; postdiscal fascia obscure; submarginal series on an

even arc; submarginal fascia obscure; cilia chequered black and white. Hindwing with broad discal band of even width; discal fascia obscure, postdiscal band with spot in space 6 obscure; submarginal fascia faintly marked. Outer margin crenulate, the cilia darker along the convexities. *Verso* ground colour ochreous. Forewing: spots on upper postdiscal band coalesced; lower postdiscal band with spots not clearly separated; postdiscal fascia clearly marked; submarginal series and submarginal fascia complete. Hindwing with basal streak prominent; subbasal streak reaching discal band at vein 7; discal band broad, extending as a tooth along wing margin at vein 7, where it meets discal fascia, postdiscal band and submarginal fascia; marginal fascia clearly marked.

Extreme Wet Season Form: differs from Dry Season Form on the forewing *recto* in the narrower cell streak, which is sometimes suffused with dark scales; discocellular bar dark and prominent; upper postdiscal band with spots smaller, spot in space 8 reduced to a speck; postdiscal fascia and submarginal series not reaching above vein 7; submarginal fascia obscure; marginal fascia obsolete. Hindwing *recto* discal band narrower, not extending along margin to vein 7; discal fascia and submarginal fascia obscure; postdiscal band reduced to a series of lunules; marginal fascia obsolete. *Verso* ground colour darker than Dry Season Form. Cell streak not suffused with dark scales; postdiscal band with spots separated; markings on distal half of wing obscure above vein 7. Hindwing subbasal streak disintegrates before reaching discal band, which is narrower than in DSF; markings on distal half of wing do not meet discal band at margin above vein 7; discal fascia, postdiscal band, submarginal fascia clearly marked; marginal fascia obscure.

Distribution Western Himalaya (Dehra Dun to Kumaon); also recorded in Delhi (Larsen 2002).

Remarks: In the above description, two extreme forms have been described and referred to as Dry Season Form and Wet Season Form. It should be noted that both forms as well as intermediates occur together during the dry season and the terms used are merely in keeping with common usage with reference to some other species in the genus, whose narrow and wide banded forms are usually referred to as seasonal forms.

Recorded by Atkinson (1882) as *Neptis nandina* (Moore) from the Kumaon Terai and outer ranges. Moore (1896–1899), who described *Neptis clinia susruta* in 1872, gave a range from Kumaon to Malaya for *susruta*. Mackinnon & de Nicéville (1899) recorded a single specimen from Mussoorie. Eliot (1969) noted a single specimen from Dehra Dun in the BMNH collection, adding that it probably represented a distinct subspecies. When he examined further material from Kumaon, he confirmed to me (in litt.) that it was indeed a new subspecies. Larsen (2002) recorded a specimen from Delhi.

It is quite common at low elevation in Kumaon, ascending to 1500 m. It is on the wing from March to June and again in October and November. The earlier brood has the narrow banded "wet season form" and the wider banded "dry season form" on the wing together, especially during May and June.

Both sexes come to water and are quite common in damp, forested ravines. Honey dew secreted by scale insects on citrus trees is a powerful attractant.

It occurs with *Neptis nata* and, since the facies of the two are often quite similar, it is best to examine the valvae in the field to separate the two species, which saves dissecting them later.

Etymology: The name *praedicta* refers to the fact that Eliot (1969) noted that the single specimen from Dehra Dun examined by him probably represented a different subspecies, an observation that was subsequently borne out when further material was examined.

Neptis sappho astola Moore

Neptis astola Moore, 1872: 560.
Neptis sappho astola Moore; Eliot, 1969: 60.

Distribution Pakistan, throughout the Himalaya and N.E. India, to Thailand, Vietnam and South China.

Remarks: A ubiquitous insect that is found from 2500 m in the main Himalayan range down to the plains adjoining the foothills, where it is common up to 40 km south of the nearest hills.

It is on the wing throughout the year at 1500 m elevation. The Wet Season Form is on the wing during July to September.

Neptis hylas kamarupa Moore

Neptis kamarupa Moore, 1874: 570.
Neptis hylas kamarupa Moore, Eliot, 1969: 61.

Distribution: Along the Himalaya from Mussoorie in Garhwal to N.E. India, Thailand, Vietnam and S. China.

Remarks: Not as common as *N. sappho astola*. Stragglers ascend to 2400 m. The subspecies is apparently restricted to the outermost range and the adjoining plains where it is common up to 40 km south of the foothills.

It is on the wing from March to June, and again from September to November. The Wet Season Form has been recorded in September.

Neptis soma butleri Eliot

Neptis soma butleri Eliot 1969: 70.

Distribution: Pakistan (Chitral) to Western Nepal.

Remarks: A common insect in the belt between 1000 m and 2800 m wherever its larval hostplants, species of *Celtis*, grow. There is considerable individual variation, in addition to seasonal variation. Although I have recorded both seasonal forms together after a spell of wet weather in Bhimtal in April, the WSF is usually on the wing in September and October. This butterfly is on the wing from March to June and from September to November.

Neptis nata yerburii Butler **comb. nov.**
(Fig. 1c, f)
Neptis yerburii Butler 1886: 360.
Neptis nata peilei Eliot 1969: 74, **syn. nov.**

Material examined: 30 specimens taken from March to June and October and November 1991 to 2009 in Bhujiaghat, Nainital district, Kumaon, India 600 m and Jones Estate, Bhimtal, Nainital, Kumaon, India 1500 m, all Leg. P. Smetacek; all in Coll. Smetacek.
Forewing Length: 25–30 mm.

Distribution: Pakistan (Murree) to the Kumaon Himalaya.

Remarks: *Neptis yerburii* was described on the basis of a "male" (*recte* female *vide* Eliot 1969) from Murree in Pakistan in the collection BMNH. The unique type is in poor condition, with the cilia almost entirely worn away and the antennae broken. Eliot (1969), who examined and figured the type, had expressed doubt about the true affinities of Butler's type specimen in the following words, "There is nothing else like it in BMNH, and until its male is found some doubt must remain as to its true affinities. It resembles [*N.*] *capnodes* and [*N.*] *pandoces* better than any other forms, differing from them, as would be expected in a *Neptis* from the N.W. Himalayas, in having wider white markings and a paler under surface ground colour. It is definitely not the species which all subsequent authors, including Butler himself (1888), have treated as *N. yerburii* (usually emended to *yerburyi*) and which must henceforth be known as *N. soma* Moore…..".

Eliot (1969) described *N. nata peilei* on the basis of 2 males and 5 females, consisting of a male from Kumaon and the remainder from Mussoorie in Garhwal. I have 3 female *N. nata* specimens from April and May that are similar to Butler's holotype of *N. yerburii* (Eliot 1969, plate 2, fig. 13) and 2 males identical to Eliot's type of *N. nata peilei* (Eliot 1969, Plate 1, fig. 2), as well as several intermediate examples. After examining several specimens of both sexes of *Neptis nata* from Kumaon, Eliot was of the opinion (in litt.) that the type specimen of *yerburii* is, in fact, an extreme Dry Season Form of *nata*. Since the name *N. nata* Moore 1857 antedates *yerburii*, *yerburii* becomes a subspecies of *nata* and *Neptis nata peilei* Eliot 1969 from the western Himalaya must be synonymised with the new combination of *Neptis nata yerburii*, which is the older available name.

The right clasper of the male genitalia of *N. nata yerburii* is identical to the right clasper of *N. nata hampsoni* Moore figured by Eliot (1969, fig. 36). Since *N. yerburii pandoces* Fruhstorfer 1913 and *N. yerburii capnodes* Eliot 1969 are distinct from *N. nata*, for they are separable on features of the male genitalia (Eliot 1969, figs.30 (*N. yerburii capnodes*) and 36 (*N. nata hampsoni*)), *N. yerburii capnodes* Fruhstorfer and *N. yerburii pandoces* Eliot must now be known as *Neptis capnodes capnodes* Fruhstorfer **stat. nov.** and *Neptis capnodes pandoces* Eliot **comb. nov.**, respectively.

Neptis nata yerburii is on the wing from March to June, August and October in Kumaon. It has been recorded from low elevation to 1600 m and is nowhere common. There is a specimen from Bhowali (1700 m) in Nainital district, Kumaon, in the Coll. OUM. This was probably a straggler. Adults are attracted to flowers of *Toona ciliata* as well as honey dew ejected by scale insects on citrus trees.

Neptis mahendra mahendra Moore
Neptis mahendra Moore, 1872: 560, pl. 32, fig. 3.

Distribution: Pakistan (Chitral) to western Nepal.

Remarks: This species occurs between 1700 m and 2700 m in the main as well as outer ranges. It is found sporadically along sunny paths and in glades, where the flight is slow and leisurely, generally less than 3 m above the ground.

On May 18, I photographed a female which settled briefly on a solitary bush of *Pyracantha crenulata* (Rosaceae) (fig.2). Upon examining the photographs, it turned out that she was ovipositing, although from the time she settled and her agitated activity, it did not appear so. Of the four ova she laid, one each on the tip of a new leaf, one ovum was located but the larva that emerged did not feed upon the fresh shoots offered and died.

It is on the wing from April to October. Peile (1937) noted that it does not come to water. He also noted that there was a remarkable difference between the seasonal forms. I have not had the good fortune to obtain examples of the narrow banded wet season form of this species.

Neptis pseudovikasi (Moore)
Bimbisara pseudovikasi Moore, 1899: 7, pl. 291, figs. 1–10.
Neptis pseudovikasi Moore; Eliot, 1969: 86.

Distribution: Kumaon to northern Myanmar, Tonkin.

Remarks: Atkinson (1882) recorded this species from the outer ranges as "*vikasi* Moore". Hannyngton (1910) recorded it in August and September from wooded ravines between 914m and 1219 m. Apparently, there were several records from different localities, both in the main as well as the outer range.

I have neither taken it nor seen a specimen from Kumaon.

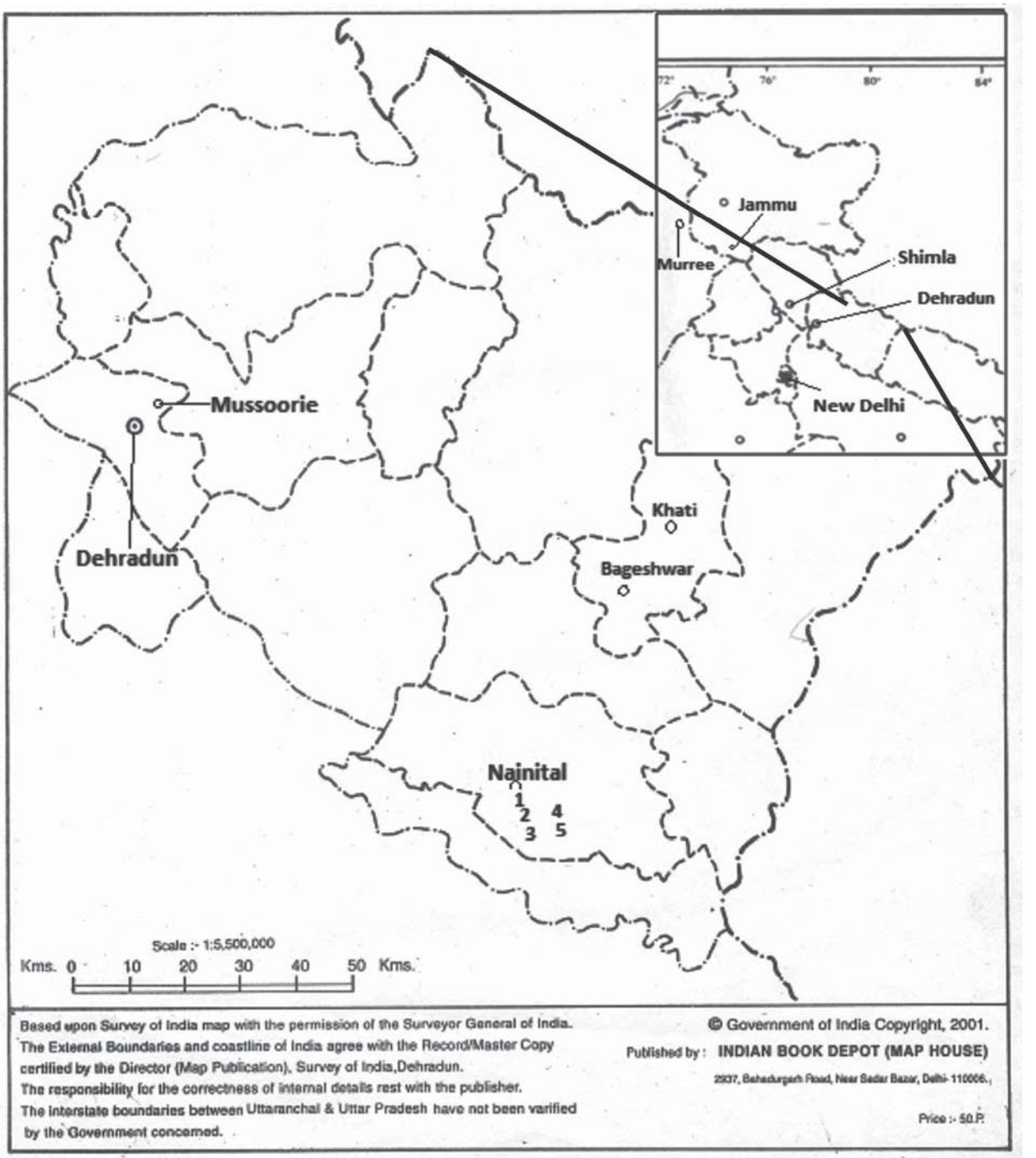

FIG. 3. Uttarakhand State, India. 1: Nalena; 2: Bhujiaghat; 3: Haldwani; 4: Bhowali; 5: Bhimtal. Inset: The west Himalayan states of India.

Neptis miah varshneyi Smetacek
Neptis miah varshneyi Smetacek, 2004: 269–270.

Distribution: Kumaon Himalaya.

Remarks: This appears to have been confused with *Lasippa viraja* (Moore) by earlier authors, eg. Hannyngton (1910), Evans (1932), etc.. *L. viraja* does not seem to occur west of Nepal (Smetacek 2004).

There is no seasonal variation in the two recorded broods, from March to June and from October to mid-November. It is not rare from 600 m to 1500 m in the outermost range. Prefers damp, sunlit ravines in dense broadleaf forest, where it occurs in the company of the

two *Pantoporia* species. Comes readily to water. It has not been noted visiting flowers.

Neptis sankara sankara (Kollar)
Limenitis sankara Kollar, 1844: 428.
Neptis sankara sankara (Kollar); Stichel, 1909: 177.

Distribution Kashmir to Kumaon.

Remarks: A hill insect, common in dense forest of Himalayan Oak between 1200 m and 2500 m in the main as well as outer ranges. Both the wide banded "Dry Season Form" *amboides* Moore 1882 and the narrow banded "Wet Season Form" *sankara* are found in Kumaon. I have only found *sankara* in company with *amboides* during the dry season, i.e. from April to June. There is a single male of the species taken in August in Jones Estate, at the height of the wet season. It is of the wide banded *amboides* form.

Peilie (1937) suggested that this species might be mimicked by *Apatura* (*Mimathyma*) *ambica* Kollar in Garhwal.

Recorded from April through August and October.

Neptis cartica cartica Moore
Neptis cartica Moore 1872: 562.

Distribution: Garhwal Himalaya to northern Myanmar, Tonkin.

Remarks: Subsequent to my report of the species from Kumaon (Smetacek 1993), I discovered that Atkinson (1882) had reported it from the outer ranges and that there is a specimen from Mussoorie in the collection of the Forest Research Institute in Dehra Dun. Hannyngton (1910) did not record it.

There seems to be a single brood in May, which occurs in the company of *N. sankara* and *N. zaida*. Recorded between 1200 m and 1800 m elevation.

Neptis ananta ananta Moore
Neptis ananta Moore, 1857: 166.

Distribution: Garhwal (Chamba) to Kumaon Himalaya.

Remarks: Mr. Philip Ackery kindly compared material from Kumaon with the series in the BMNH collection and concluded that it belonged to the nominate subspecies. Eliot (1969) recorded this subspecies from Chamba to Mussoorie in Garhwal. The present records extend the known distribution of this taxon eastwards to the Bhimtal valley and Maheshkhan Reserve Forest, both in Nainital district.

The subspecies *ochracea* Evans occurs in Nepal (T. Katayama in litt.).

A rather rare insect, I have found it in the belt between 1200 m and 2600 m, although Hannyngton (1910) reported it from 900 m elevation in Kumaon. The flight is powerful. There are two broods, the first during May and June and the second from August to October. No seasonal variation has been noticed.

Neptis zaida zaida Westwood
Neptis zaida Westwood 1850: 272, pl. 35, fig. 3.

Distribution: Garhwal (Mussoorie area) to the Kumaon Himalaya.

Remarks: Occurs in the main as well as outer ranges between 1000 m and 2500 m elevation from May to June in the outer range and in July in the main range.

Mr. Ackery kindly compared photos of specimens from Kumaon with specimens in the BMNH. According to Eliot (1969), the nominate subspecies occurs only in the Mussoorie area of the N.W. Himalaya. The present report extends the known distribution of this subspecies eastwards to the Sattal valley in Nainital district and Khati village in Bageshwar district in Kumaon.

Neptis radha radha Moore
Neptis radha Moore, 1857: 165, pl. 4a, fig. 2.

Distribution: Kumaon Himalaya to N.E. Myanmar.

Remarks: Recorded by Hannyngton (1910) in May from Nalena (1370 m)(Nainital district) in the outer range and Bageshwar (975 m)(Bageshwar district) in the middle range in October. I have visited Nalena in May and June but not found the butterfly. There does not seem to be any suitable habitat for this species around Bageshwar at present, although there might have been some a century ago when Hannyngton surveyed the area.

I have neither taken this species nor seen a specimen from Kumaon.

Neptis narayana narayana Moore
Neptis narayana Moore 1858: 6, pl. 49, fig. 3.

Distribution: N.W. Himalaya (Kulu to Kumaon).

Remarks: Recorded in the main range in July and in the outer ranges in May and June. Peile (1937) excerpted Hannyngton's (1910) list and added September: whether this is a mistake is uncertain, since the next butterfly on Hannyngton's (1910) list, *N. vikasi pseudovikasi*, is reported in August and September in the original list but only in August in Peile (1937). I have not seen a specimen recorded in September.

Around the tops of trees, the flight is strong like *Neptis ananta* and *N. sankara*, but near the ground it

affects a very weak flight, as reported by Wynter-Blyth (1957). In suitable localities, it is quite common and swarms during the second half of May in some years, when it is by far the commonest Neptini, if not the commonest nymphalid.

Phaedyma columella ophiana (Moore)
Neptis ophiana Moore, 1872: 561.
Phaedyma columella ophiana (Moore); Eliot, 1969: 120.

Distribution: Dehra Dun, Garhwal to northern Myanmar.

Remarks: Eliot (1969) gave a range from N.E. India to north Burma. There are 7 specimens from Dehra Dun in the Coll. FRI (Roonwal et al.1963). It is also common in Kumaon, especially near water in April and May in the plains adjoining the foothills. Stragglers ascend to 1500 m.

Recorded from April to July (*mihi*) and again during December and January in Kumaon (Hannyngton 1910).

DISCUSSION

In terms of species, the West Himalayan Neptini form a significant part of the total nymphalid representation in the area. Most of the species are quite common, so they form a large part of most butterfly assemblages in the foothills. Along with similarly patterned genera like *Athyma* and *Symbrenthia*, they often dominate the nymphalid component of Himalayan Oak forest butterfly assemblages above 2000 m elevation and Sal forest assemblages below 600 m during May and June. In general, the West Himalayan Neptini appear to have broader pale bands as compared to the East Himalayan populations. In several species, the Wet Season Form is distinguished by narrower pale bands and darker groundcolour, especially on the *verso* surface.

In the West Himalaya, during the dry summer months from mid-March to mid-June, relative humidity is generally less than 40% and often less than 10%. From mid-June to mid-September, during the South West Monsoon, humidity is often near 100%. However, broad banded and narrow banded "seasonal forms" of *Neptis clinia* and *N. sankara* occur together during the dry season, suggesting that humidity is not the only factor determining the width of the pale bands.

A comparison with species recorded a century ago (Hannyngton 1910) suggests that two species, *N. pseudovikasi* and *N. radha* have been "lost". Both of these are forest insects and while the forest cover in one of the places where they were recorded, i.e. Nalena, a village on the road between Haldwani and Nainital, leaves nothing to be desired even today, the same cannot be said of other places where they were recorded, i.e., Kapkot (Bageshwar district) and Bageshwar. Therefore, while forest degradation might be a reason for their absence in the latter two localities, the same cannot be said for their absence at present from Nalena.

Concerning *N. narayana*, it is certainly not "Very rare" anymore. Whether the species has actually established larger populations during the last century or Hannyngton just did not visit the right places at the right times will never be known.

On the whole, the community of Neptini in Kumaon seems to be quite stable and given that there are many Reserve Forests and other protected areas with healthy populations, the future outlook for this group of butterflies in the area is certainly not cause for worry.

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This paper would not have been possible without the generous help of the late Lt. Col. J.N. Eliot, who came to the conclusion about the proper status of *Neptis yerburii* a fortnight before he passed to his eternal reward. He therefore entrusted me with the task of "sorting out the mess", as he put it and I hope, with the current paper, to have accomplished this. Mr. Philip Ackery kindly compared material in the Natural History Museum, London, U.K. for which I am very grateful. I am grateful to Basil Wirth for literature, photographs and stimulating discussions on this group, to Toshihiko Katayama, who generously shared his experience and expertise with me and to Dr. Michael Toliver, whose valuable comments on an earlier version of this paper did much to improve it. The paper was further improved by useful suggestions and references from the anonymous referees, for which I am, again, very grateful. A part of the fieldwork was carried out under a Times Fellowship 1991 and three Rufford Small Grants in 2006 and 2008 and 2009, for which I am very grateful to the Times of India Group, India and the Rufford Small Grant Foundation, U.K.

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ERESIA CARLOTA REAKIRT (NYMPHALIDAE): THE DESIGNATION OF A LECTOTYPE AND THE RETURN OF THE TYPE LOCALITY TO COLORADO

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ABSTRACT. The description of *Eresia carlota* Reakirt, 1866 (currently recognized as *Chlosyne gorgone carlota*) was based on specimens collected in 1864 in the foothills of the Front Range, west of Denver, Colorado. A subsequent neotype designation established the type locality as Cedar Hill, Missouri. The neotype, however, is inconsistent with the phenotype of this taxon as understood by Reakirt. More important, the neotype designation was based on an erroneous interpretation of the Code and is nomenclaturally invalid. A lectotype of *Eresia carlota* is designated, which restores this nominal taxon to its original concept and returns the type locality to Colorado.

Additional key words: *Chlosyne gorgone, Chlosyne nycteis,* Herman Strecker, James Ridings, lectotype, Tryon Reakirt

Around the year 1865, the Philadelphia lepidopterist Tryon Reakirt (1844–ca.1873) received specimens of a supposed new species of butterfly from James Ridings (1803–1880), an English entomologist who also lived in Philadelphia. The specimens were collected by Ridings in Colorado during June of 1864. Reakirt (1866) named this taxon *Eresia carlota* and attributed it to "Rocky Mountains, Colorado Territory." A century later, Brown (1974) decided that a neotype was necessary to properly define the name *E. carlota*. He selected a male specimen from Missouri and also figured a female from the same population, both of which were collected on 18 May 1947 by Pardon S. Remington.

Although Brown (1974) indicated that the neotype of *carlota* and its associated female were deposited in the Allyn Museum of Entomology (Sarasota, Florida), they were not found subsequent to the 2004 transfer of specimens from the Allyn Museum to the McGuire Center for Lepidoptera and Biodiversity (MGCL, Florida Museum of Natural History, Gainesville). In June of 2010, Lawrence F. Gall unexpectedly located these specimens in the collection of the Peabody Museum of Natural History (PMNH, Yale University, New Haven, Connecticut) (catalog no. YPM ENT 413267; the male lacks the neotype label mentioned by Brown). This discrepancy is explained in a letter from F. Martin Brown to Charles L. Remington of PMNH, dated 28 March 1975; "There is one specimen among the butterflies that technically belongs to the Allyn Museum of Entomology. That is the neotype for Reakirt's carlota. It makes no difference to me where it is preserved but it is stated in the designation that it is at Allyn. I thought that I had retained it but found that I had returned the specimens some years back" (archives, PMNH Div. Entomol.). The collection of P. S. Remington, father of C. L. Remington, is deposited at PMNH. In keeping with Brown's (1974) statement of disposition, these specimens will be transferred from PMNH to MGCL (L. F. Gall pers comm.).

The rediscovery of the neotype prompted me to re-examine its status. I concluded that Brown's (1974) designation does not satisfy the Code (ICZN 1999) and is nomenclaturally invalid. This is fortunate, as the neotype from Missouri is inconsistent with Reakirt's concept of this taxon, which was based on higher elevation specimens from Colorado.

METHODS

The original description of *Eresia carlota* by Reakirt (1866) and the subsequent neotype designation by Brown (1974) were reviewed. The relevant provisions of the Code (ICZN 1964, 1999) were consulted to determine the validity of the neotype. Images were obtained of the neotype and its associated female. Also obtained were images of the Colorado specimens for which the name *E. carlota* was originally proposed. Microfilm printouts of the manuscripts of William H. Edwards (1822–1909) (MGCL archives) were examined for references to relevant taxa.

RESULTS

Reakirt (1866) included no written description or figure of *Eresia carlota*, but cited an earlier description by Edwards (1861), who had misidentified specimens of this species from Illinois and Missouri as *Melitaea nycteis* Doubleday (now recognized as *Chlosyne nycteis*). Reakirt (1866) criticized William H. Edwards for his earlier mistake; "I cannot imagine how Mr. Edwards could have regarded this very distinct species as identical with Mr. Doubleday's figure [of *nycteis*]; it no more resembles it, than does *Tharos* [*Phyciodes tharos* (Drury)]". No written description accompanied the original figure of *M. nycteis* in Doubleday ([1847]), and only the dorsal surface of this species was portrayed.

Consequently, the identity of *Melitaea nycteis* was very poorly understood throughout much of the 19th century and very few specimens were known. Scudder (1862) was aware of several specimens, which he described as a new species, *Melitaea oenone*. Only after examining types of *M. nycteis*, "received directly from Doubleday," did Scudder realize his mistake (Scudder 1868).

Edwards' own confusion about these butterflies was more persistent. In 1864, *C. nycteis* was common near Edwards' home in West Virginia, but he identified the species as *Melitaea ismeria* Harris (nec Boisduval & Le Conte) (Edwards' journal "A"), which is synonymous with *Melitaea harrisii*, a butterfly described that same year by S. H. Scudder. Edwards (1870) later attempted to correct this mistake by identifying specimens of *C. nycteis* as *M. harrisii*. Probably in response to Reakirt's (1866) admonition, and supported by the capture (by a "Mr. Eaton") of a single specimen of "*carlota*" near his home in July of 1867 (Edwards' journal "B"; Edwards 1894), Edwards (1871) concluded that his earlier interpretation of *M. nycteis* was synonymous with *E. carlota*. By the mid–1870s, Edwards acknowledged that he had previously misapplied the name *M. harrisii* (Edwards 1875), and he accurately remarked that *carlota* "abounds in Colorado" (letter to H. Edwards, 23 Dec. 1874). The latter statement was partially based on his receipt of specimens from his future son-in-law, Theodore L. Mead, who had collected them in Colorado in June of 1871 (see Mead 1875) (at least two such specimens from Mead are preserved in the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, where the collections of Mead and Edwards are deposited). Having finally sorted out the names, Edwards (1877) listed *carlota*, *harrisii,* and *nycteis* as separate species within the genus *Phyciodes*.

Around that same time, Scudder (1875) determined that *E. carlota* was synonymous with the nominal taxon *Dryas gorgone* Hübner. After decades of confusion surrounding the application of these two names, *carlota* is now recognized as the subspecies *Chlosyne gorgone carlota*. The name *Melitaea ismeria* Boisduval & Le Conte also was applied to *C. gorgone*, but irrevocable confusion about its identity warranted its suppression (Calhoun 2003; Calhoun et al. 2005; ITZN 2006).

Despite its broad distribution in North America, only two subspecies of *C. gorgone* are currently recognized. The nominotypical subspecies is purported to occur within a restricted area of the upper coastal plain of Georgia and adjacent South Carolina (Gatrelle 1998), while all other populations are tentatively regarded as *C. g. carlota*. If we must define the original concept of the nominal taxon *Dryas gorgone*, then perceived differences in western montane populations (see below) emphasize the need to properly recognize the original concept of *Eresia carlota* Reakirt.

Reakirt's collection was acquired in 1868 by the lepidopterist F. H. Herman Strecker (1836–1901) of Reading, Pennsylvania (Brown 1964). In a catalog of supposed types in his collection, Strecker (1900) listed a pair (male and female) of *carlota* that he received from Reakirt. Eight years later, Strecker's collection of over 50,000 specimens was purchased for $20,000 by the Field Museum of Natural History (FMNH, Chicago, Illinois) (Anonymous 1908; Skiff 1909). Strecker's collection at FMNH still contains the two specimens of *carlota* that he listed in 1900 (Figs. 1, 2). Labels, most likely prepared by Strecker (or under his supervision), identify them as *Eresia carlota* and attribute them to Reakirt (Fig. 3).

The two specimens of *C. gorgone* in the Strecker collection were long considered to represent syntypes of *E. carlota* and labels identify them as "types" (Fig. 3). However, Higgins (1960) argued that because Reakirt did not provide a written description or figure of *Eresia carlota*, but merely cited the earlier description by Edwards (1861), *Eresia carlota* therefore represents a replacement name (*nomen novum*) for *Melitaea nycteis* Edwards (nec Doubleday). As such, these names would be objective homonyms and the nominal taxa they denote would share a name-bearing type. Consequently, only those specimens from Illinois and Missouri on which Edwards based his description of "*nycteis*" would represent syntypes of *E. carlota*. Brown (1974) agreed with this analysis and took it one step further. Following an unsuccessful search for Edwards' specimens, Brown designated a neotype of *E. carlota* using a male *C. gorgone* that was collected in Cedar Hill, Missouri (Fig. 4). He also figured a female from the same population (Fig. 5). The type locality of *E. carlota* was thereby relocated over 1200 km (746 mi) east of its original location in Colorado. This treatment is still recognized (Pelham 2008).

Although *C. gorgone* is highly variable throughout its range, Reakirt's (1866) concept of *carlota* is not analogous to that of Edwards (1861), nor the neotype of Brown (1974). Reakirt (1866) noted that J. Ridings obtained his specimens of *carlota* "among the mountains" of Colorado. While in Colorado, Ridings explored westward to Empire City (now Empire) in Clear Creek County, and northward to Burlington (now Longmont) in Boulder County (Brown 1966). Comments by Reakirt (1866) suggest that in June of 1864 Ridings most likely was traveling through Jefferson County, Colorado on his way to Empire City. Jefferson County is one of the 17 original Colorado counties that were established in 1861. Ridings probably followed one

FIGS. 1-6. Specimens related to *Eresia carlota*; dorsal (left) and ventral aspects. **1**, male *C. gorgone* (Strecker coll., FMNH), herein designated as the lectotype of *E. carlota*. **2**, female *C. gorgone* (Strecker coll., FMNH), herein considered a paralectotype of *C. carlota*. **3**, Strecker's large cabinet label (top) and five smaller labels from the lectotype specimen. **4**, invalid male neotype of *E. carlota*. **5**, female *C. gorgone* from the same population as the invalid neotype. **6**, labels from the invalid neotype (top) and associated female.

of the existing wagon trails that connected Denver to destinations in the mountains (Scott 1999).

Although Kons (2000) did not perceive any geographic variation in *C. gorgone*, many adults from higher elevations in Colorado possess expanded dark maculation (especially pronounced in females) and the white ground color of the ventral hindwing tends to be more silvered. The dorsal orange coloration also tends to be paler and more uneven in tone. This is the prevailing phenotype of the first brood, when adults fly in May and June. Fisher (2006) discussed such differences between populations in eastern Colorado. Observations of *C. gorgone* in Colorado by Andrew D. Warren (pers. comm.) suggest that these distinctions are likely the result of both geographic and generational variation. Higgins (1960), who considered typical *carlota* to be represented by populations of *C. gorgone* from Illinois and Missouri, was still unsure about the widespread application of the name; "I cannot say whether it will be correct to accept *carlota* for the high level form of Colorado, or whether, in fact, the name should be used for a different subspecies." Populations of *C. gorgone* along the western slope of the Colorado Rockies also reportedly exhibit subtle differences from those found east of the continental divide (Ferris 1981). The two specimens of *C. gorgone* from Reakirt's collection are very dark and consistent with the first brood phenotype found in the foothills west of Denver, where this species remains locally common (Figs. 1, 2). Although the neotype designated by Brown (1974) is also from the first brood, it originated from a region where the species is not known to normally produce the phenotype found in the higher elevations to the west.

Brown's (1974) action dissociated the type of *carlota* from the higher elevation populations of *C. gorgone* in Colorado, which represent Reakirt's true concept of this nominal taxon. There is no evidence that Reakirt previously examined specimens of this species from any other locality. Fortunately, I discovered a nomenclatural error by Brown (1974) that permits the reinstatement of the original type specimens and type locality of *carlota*. Similar errors may affect other taxa that are currently recognized using alleged replacement names.

The current International Code of Zoological Nomenclature (ICZN 1999) invalidates the neotype of *Eresia carlota*. Although Brown (1974) was governed by the second edition of the Code (ICZN 1964), it too included provisions that invalided his action. The neotype of *E. carlota* is untenable for the following reasons. Applicable definitions and articles from the

second edition of the Code (ICZN 1964) are given in brackets.

1) The Code defines a replacement name (*nomen novum*) as "a name established expressly to replace an already established name" [a new name adopted "to replace an earlier name, and valid only if the latter is preoccupied"]. Such names are typically proposed for junior objective homonyms. Reakirt (1866) did not expressly indicate that *carlota* was a replacement name and criticized Edwards (1861) for misidentifying the species. Reakirt proposed *carlota* as a "nov. sp." (new species). Conversely, Edwards (1861) did not identify his "*Melitaea nycteis*" as a new species and credited this name to Doubleday. Edwards (1862) published similar written descriptions of taxa that were figured, but not described, by Doubleday & Westwood (1846–1852). Considering his general confusion about these butterflies, it is obvious that Edwards (1861) merely attempted to define *M. nycteis* as figured by Doubleday (in Doubleday & Westwood 1846–1852; Pl. 23 fig. 3), but did so using specimens of the wrong species.
2) Article 49 of the Code states, "A previously established specific or subspecific name wrongly applied to denote a species-group taxon because of misidentification cannot be used as an available name for that taxon" ["A specific name used in an erroneous species identification cannot be retained for the species to which the name was wrongly applied"]. As argued in no. 1 (above), the name *Melitaea nycteis* as used by Edwards (1861) constitutes a misidentification, thus it cannot be accepted as an established name for the taxon subsequently described as *Eresia carlota*, and therefore is unavailable for replacement.
3) Reakirt (1866) did not provide his own description, yet his reference to Edwards (1861) represents an acceptable indication as permitted for new names proposed before 1931 per Art. 12.2.1 [Art. 12] of the Code.
4) Two specimens that Reakirt (1866) evidently consulted for his description of *E. carlota* are extant and represent syntypes. Because Reakirt partially based *carlota* on Edward's misidentification, the specimens from Illinois and Missouri that were examined by Edwards constitute part of the type series per Art. 72.4.2 of the Code. The latter specimens are apparently lost or unrecognizable (Brown 1974), thus the only available syntypes known to exist are the Colorado specimens in the Strecker collection (ex Reakirt, ex Ridings) now deposited in FMNH.

In accordance with Art. 74.1 of the Code (ICZN 1999), the male syntype in the Strecker collection at FMNH (Fig. 1) is hereby designated as the **lectotype** of *Eresia carlota* Reakirt, 1866. This action invalidates the neotype of Brown (1974) per Art. 75.8 of the Code. The lectotype bears four labels (Fig. 3): a red-bordered label, probably prepared by Strecker [*E. carlota* / Reak. / Colorado. / Orig. Type / Coll. Reak.]; a small handwritten label with a male symbol; and two printed FMNH labels [*Eresia carlota* Reak. / Colorado. / Reak." / "Orig. Types" / Strecker Colln. 14673 / Field Museum Nat. Hist.] [Lepidoptera Type / Photograph No. 108 / Field Museum]. There also is a large, red-bordered label associated with these specimens, probably used by Strecker as a cabinet label, which was placed at the head or foot of these specimens [*Eresia carlota* / Reak. / Colorado / orig. Types, Coll. Reak.] (across the top is the penciled name, "*Phyciodes gorgone* Hub," probably written during the 20th century). A red lectotype label has been affixed to this specimen [LECTOTYPE / *Eresia carlota* / Reakirt 1866 / Designated by / John V. Calhoun 2010] (Fig. 3). The accompanying female in the Strecker collection (no. 14674) is a paralectotype and is labeled accordingly. The type locality is suggested to be the Front Range foothills of Jefferson County, Colorado, west of Denver.

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LIFE HISTORY AND MORPHOLOGY OF THE BLACK CUPID BUTTERFLY, *TONGEIA KALA* (DE NICÉVILLE)(LYCAENIDAE), FROM MYANMAR

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ABSTRACT. A rare lycaenid butterfly, *Tongeia kala*, is distributed from NE India to eastern Myanmar. In appearance there are no closely related species in the genus, and therefore it is of much interest to study this species from an evolutionary point of view. In order to extract phylogenetic information of *T. kala*, the immature stages and biology were studied in a high mountain area of Chin State, Myanmar. We describe egg, larval, pupal stages, adult wing pattern and male genitalia of the species, and compare with its related species. We also record *Sedum multicaule*, as its hostplant.

Additional key words: Chin State, Everes section, Polyommatini, *Sedum multicaule, Sedum emarginatum*.

The Black Cupid butterfly, *Tongeia kala* (de Nicéville, 1890), is known as a rare lycaenid species, occurring only from Naga Hills of NE India to southern Shan State of eastern Myanmar (Bingham 1907; Evans 1932; Wynter-Blyth 1957). About 15 *Tongeia* species are distributed in the East and SE Asia (D'Abrera 1986, 1993; Bridges 1988; Huang & Chen 2006), but the genetic status of *T. kala*, *T. potanini* (Alphéraky, 1889) and *T. arcana* (Leech, 1890) seems to be doubtful because of their unique wing markings (Kawazoé & Wakabayashi 1976). Therefore, it is of much interest to study the speciation process of *T. kala* and the monophyly of *Tongeia*. However, there are few available data to shed light on phylogenetic aspects of this species. Only short morphological and biological notes have been published (de Nicéville 1890; Bingham 1907; Seitz 1927; Evans 1932; Wynter-Blyth 1957; Cantlie 1964; Huang & Chen 2006).

In November 2009, we conducted a butterfly research project in the northern part of Chin State, Myanmar, in cooperation with the Department of Hotel and Tourism of Myanmar and the Myanmar Japan Relations Center. During the survey, the third author discovered adults, eggs and larvae of *T. kala* at Mt. Kennedy of the Letha Mountains. Although during his 23 research trips over the past 12 years in Myanmar he had found two congeners, *T. potanini* and *T. ion* (Leech, 1891), *T. kala* had never been recorded anywhere. For the purpose of clarifying the immature stages of this species, we reared some larvae of the species at Mandalay, Mandalay Division.

Here we describe the morphological and biological characteristics of *T. kala* based on the morphology of immature and adult stages. Moreover, we discuss the similarities to and differences from other *Tongeia* species, and provide some preliminary data to elucidate the evolutionary processes relating to this species.

MATERIALS AND METHODS

The adults and larvae of *T. kala* were found at a high altitude (2,000 m) of Mt. Kennedy, in the Letha Mountains (Figs 1–2) on 3–12 November 2009. Mt. Kennedy (2,704 m) is located 30 miles west of Kalaymyo and 16 miles southeast of Tiddim in Chin State, Myanmar. Although the climatic condition of this area is characterized by a tropical monsoon with comparatively distinct rainy (May–October) and dry (November–April) seasons, rather high altitudes of the mountains are characterized by a consistently cool mountainous climate with chilly nighttime temperatures.

The third author collected some eggs, two second instar and one third instar larvae of *T. kala* in the field. We reared them individually in plastic cases (90 mm diameter, 30 mm height), placed in a room (22±1°C; 14L–10D) at Mandalay, which is the second largest city in Myanmar and the last royal capital of Burma. Until they reached the pupal stage, the larvae were fed on two hostplants, and the details are discussed in the results of this paper. Although the eggs did not hatch, the growth of the larvae and pupae was monitored every day until they reached the adult stage. The individuals were recorded using a digital camera Nikon D70 with a micro lens (Nikon AF Micro Nikkos 60 mm) and a combined electronic flash (Nikon Wireless Speedlight Commander SU-800 and Nikon Wireless Remote Speedlight SB-R200), and with a Kenko Extension Tube 12/20/36 mm as necessary. The body lengths of all the larval instars were measured just before diapause.

For the purpose of male genitalia examination, apical parts of the abdomen were placed in 10 % KOH solution at about 100°C for 10 minutes. After this treatment, they were washed with distilled water and placed in 80 % ethanol for dissection and examination. The genitalia were examined and illustrated using a Leica L2 and stereoscopic microscope with magnifications of up to 40X. Terminology of the male genitalia followed Shirôzu (1960), except for the substitution of 'falx' for 'brachium'.

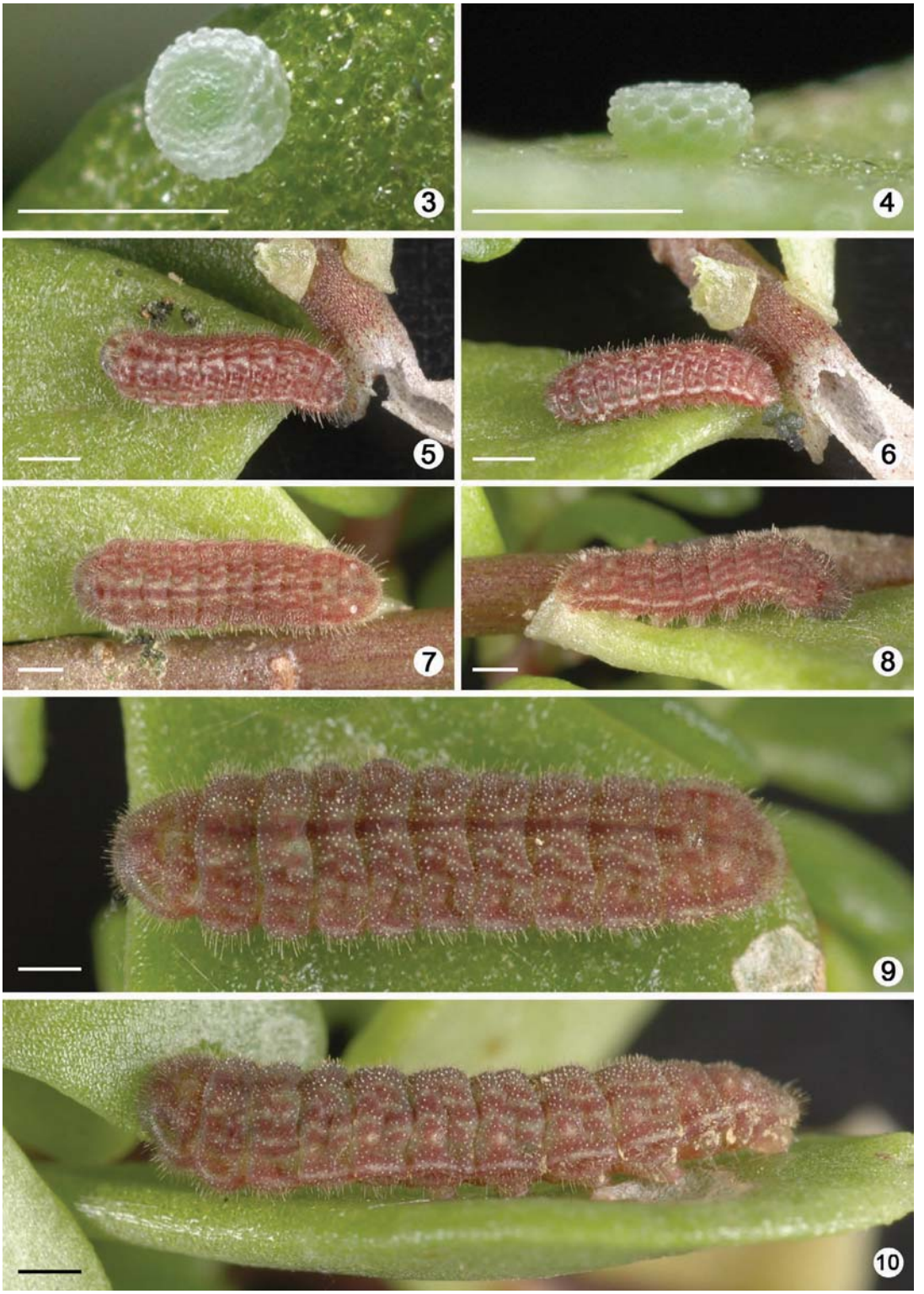
RESULTS

Description. *Egg* (Figs 3–4). Approximately 0.7 mm (n = 5) in diameter, and 0.3 mm (n = 5) in height. Exochorion whitish, disc-liked, rounded in dorsal view, turban-shaped laterally, with upper surface almost flattened but forming gentle slope from its shoulder toward micropylar area, bottom surface flattened. Micropylar area greenish, smooth, rather small, enclosed by weak elevation but slightly depressed in central axis. Remaining surface composed of concave chorionic cells and thick prominent ridges without spines. Chorionic cells depressed, circular and usually surrounded by four intersected nodular processes and four-sided chorionic ridges. Cells largest at lateral side, becoming smaller (about one-tenth) toward micropylar region. In dorsal view chorionic cells radiate in spiral shape from central axis, but in lateral view forming checker-pattern with their ridges.

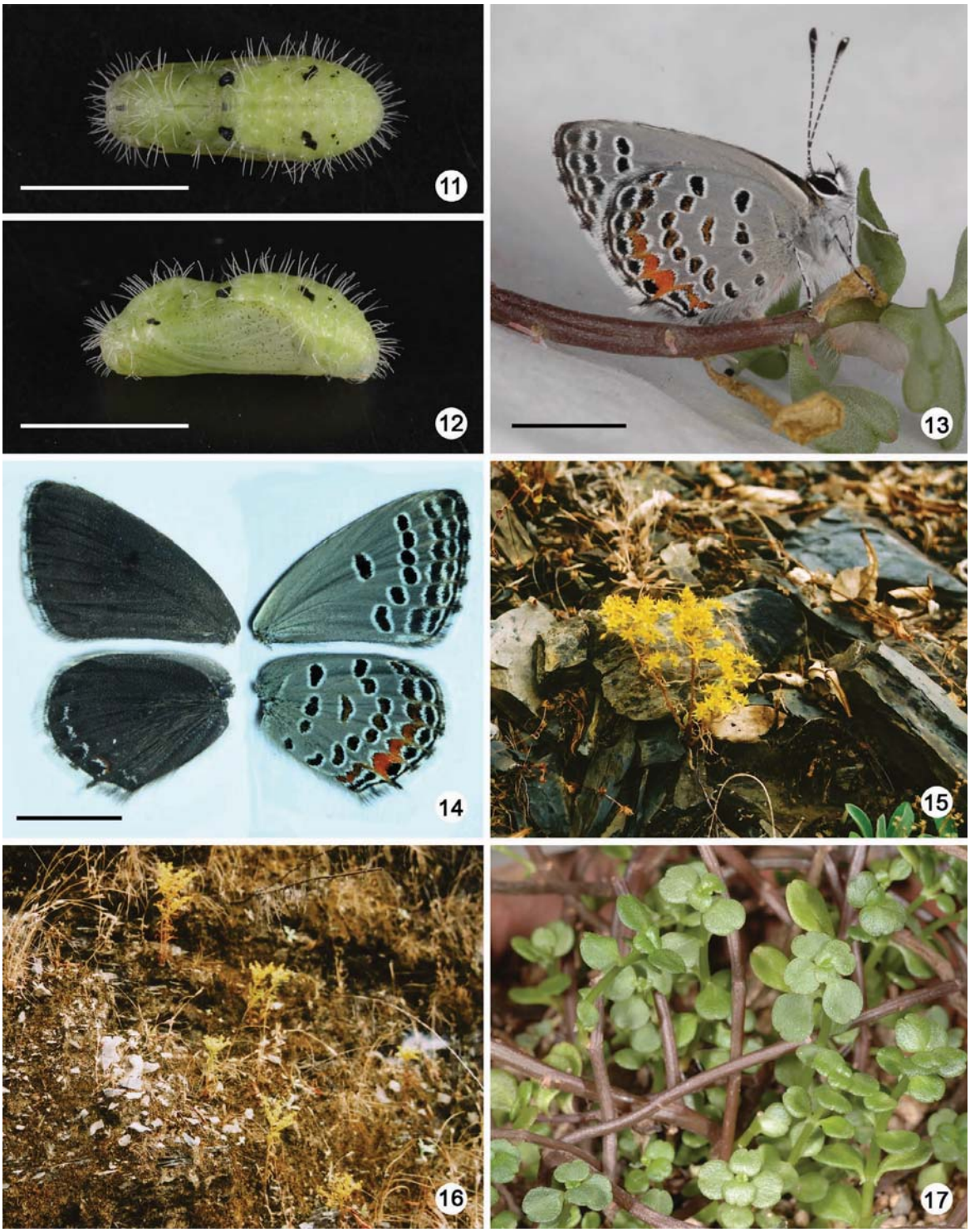
The eggs were laid singly at the base of flowers of the hostplant, on stems near the flowers, and on a bifurcation between stems of the flowers.

Larva (Figs 5–10). All larval instars except the first instar were examined (n = 3). From second to final instar larvae, larval shape unisciform as in other lycaenids, but somewhat slender and flattened. Larval body color reddish in general with pale creamy white in pattern. Prothoracic shield pale creamy white with green tint. In dorsal view, mid dorsal line distinguished by darker color running from mesothorax to last abdominal segment, and bordered by pale creamy white subdorsal line, which is distinct in early instar larvae but

FIGS 1–2. Habitat of *Tongeia kala*. **1**) A view of Mt. Kennedy and its surroundings in Chin State, Myanmar. **2**) A sunny cliff (2,000 m alt.) along a mountain track running sparse shrubs. The butterfly adults fly actively on the cliff, where the hostplant also sparsely grows.



FIGS 3-10. Egg and larvae of *Tongeia kala*. **3**) Egg, dorsal view. **4**) Egg, lateral view. **5**) Second instar larva, dorsal view. **6**) Second instar larva, lateral view. **7**) Third instar larva, dorsal view. **8**) Third instar larva, lateral view. **9**) Final (fourth) instar larva, dorsal view. **10**) Final (fourth) instar larva, lateral view. Scale bar 1 mm.



FIGS 11-17. Pupa, adults and hostplants of *Tongeia kala*. **11**) Pupa, dorsal view. **12**) Pupa, lateral view. **13**) Male adult just after emergence on substitute hostplant, lateral view. **14**) Male wings, upperside (left) and underside (light). **15–16**) Hostplant, *Sedum multicaule* (Crassulaceae). **17**) Substitute hostplant, *Sedum emarginatum* (Crassulaceae). Scale bar 5 mm.

reduced in late instars. On dorsolateral portion, three rows of faint, slanted, pale white lines waved and extending posterolaterally in each segment. In lateral view, spiracles white in color and located parallel to lateral line in each abdominal segment. Lateral line white and running along body edge. All instar larvae with short transparent prominent setae throughout body, especially in lateral side, as in larvae of many lycaenid butterflies. Stellate based setae distinctly visible, represented as small white and brown dots, and dispersed throughout dorsal surface of thorax and abdomen, especially in final instar larvae. Second to final instar larvae with three types of chemical signaling myrmecophilous organs (ant-association organs): dorsal nectary organ (DNO) on dorsum of seventh abdominal segment, paired eversible tentacle organs (TOs) on dorsolateral portion of eighth abdominal segment posterior to spiracle, and pore cupola organs (PCOs) scattered throughout body surface, concentrated near DNO and spiracles. Body length 4.0 mm (n = 2) in second instar, 6.5–7.0 mm (n = 2) in third instar, and 10.5–11 mm (n = 3) in final instar.

The larvae usually eat into thick leaves or stalks of their hostplants and eat from the inside, especially in early instars. They remained four days in the third instar, five days in the final instar, and two days in the prepupal stage.

Pupa (Figs 11–12). Typical lycaenid shaped, slightly long and slender, gourd-like dorsally but rather flattened ventrally, and with abdomen somewhat swollen and rounded, body surface weakly wrinkled and covered with minute long setae except for ventral portion and wings. Ground color light green, more yellowish on abdominal segments, tinged by paired prominent dark brown dots on base of wings and dorsolateral portion of first and fourth abdominal segments, and by small dark brown dots covering body surface, especially on wings. Body length 8.0–8.5 mm (n = 2).

Pupation took place on the stalk near a base of the hostplant in rearing. The pupal stage before emergence is 13 to 15 days.

Adult (Figs 13–14). Wing shape very similar to those of congeners, but in female slightly more rounded than that in male. Hindwing with very small, black, white-tipped tail at vein 2. Wing markings on upper- and underside almost the same in both sexes, but wing shape more rounded in female. On upperside, both wings evenly black in ground color. Forewing with rather prominent oval discocellular deep black spot. Hindwing with discocellular deep black spot and submaginal series of oval indistinct black spots, each of which outwardly defined by fine white or pale blue arched line, but somewhat with orange tint in cell 2. Cilia white edged and with black scales at each vein. On underside, both wings somewhat dark grey in ground color. Forewing margined by fine black line, then following with two series of oval dull black spots circled by white line, inner one larger and more quadrate than outer one. Discal spots comprising of series of six black spots circled by fine white line, similar round discocellular spot present. Hindwing with submarginal markings similar to forewing, but inner one arranged by series of wide submarginal orange lunules from cells 1a to 4 or 5 (but orange lunules occasionally narrowed in cells 3–5), then changed to dull fuscous toward cell 7. Discal cell markings represented by eight irregular black spots with orange stain and somewhat parallel with wing margin. Linear discocellular spot and four subbasal spots present as in forewing, but duller in color. Cilia similar to those on upperside, but black scales at each vein more widely expanded. Forewing length 11.5–12 mm (n = 2) in male and 11–12 mm (n = 3) in female.

Male genitalia (Fig. 18). Tegumen short and inclined posterodorsally. Uncus claw-like, bearing thin hairs. Falx slender, shorter than uncus and gently curved inwardly under uncus. Vinculum in lateral view rather broad but slightly concave below. Valva nearly rectangular, hairy on posterior portion and with bifurcate, flattened but sharply pointed apices, of which the lower one (harpe) in ventral view crosses the upper one (ampulla); valvae close to each other at dorsal margin of sacculi. Juxta slender, V-shaped and connected ventrally with sacculi of valvae. Phallus slender, almost straight, as long as height of ring and bearing small hook on posterioventral portion.

Habitat (Figs 1–2, 15–16). The habitat and its surroundings of *T. kala* are covered mostly with mixed evergreen and deciduous broad-leaved forest (Fig. 1), dominanted by members of the Betulaceae (*Alnus*), Fagaceae (*Quercus*) and Ericaceae [*Rhododendron* (*Hymenanthes*)]. This butterfly species was found on a sunny cliff (2,000 m; Fig. 2) facing west along a mountain track with sparse shrubs and with some deforestation for fuel. During fine weather the male and female adults fly actively, close to the cliff between 12:00 and 16:00. Some females are often found on or near the hostplant, and one individual was observed laying an egg on a bifurcation of peduncles (Figs 15–16). The hostplant grows on the cliff where the adults fly (Fig. 2).

Hostplants (Figs 13, 15–17). At the habitat of *T. kala*, all eggs and larvae that the third author found were discovered on or near flowers of *Sedum multicaule* Wallich ex Lindley (Crassulaceae; Figs 15–16). The hostplant is widely distributed from Nepal, India and Myanmar to China (alt. 1,300–3,500 m), along the Himalayas and its surroundings (Ohba 1975; Fu et al. 2001). Rearing at Mandalay, we fed all three larvae on *Sedum emarginatum* Migo (Crassulaceae; Figs 13, 17) as a substitute hostplant. The *Sedum* plant is native to S, SE and E China (alt. 600–1,800 m) (Fu et al. 2001). According to local people, there has been a continuing influx of Chinese immigrants and imports mainly from SW China in the past 20 years, and the substitute hostplant is also likely to have come from Sichuan, China, for ornamental or medicinal purposes.

DISCUSSION

The descriptions of immature stages of the genus *Tongeia* are still preliminary. Of about 15 described species of the genus, only three have been studied: *T. hainani* (Bethue-Baker, 1914), *T. filicaudis* (Pryer, 1877) from Taiwan (Igarashi & Fukuda 2000) and *T. fischeri* (Eversmann, 1843) from Japan (Fukuda et al. 1984). Here we compare some morphological aspects of *T. kala* to these related species. The eggs of *T. kala* have chorionic cells and chorionic ridges somewhat larger than *T. hainani* and *T. filicaudis* (Igarashi & Fukuda 2000). In appearance, the external morphology of the immature stages in *T. kala* does not differ significantly from those in the three related species. The remarkable difference was found only in coloration. *Tongeia filicaudis* larvae are the most similar to *T. kala*. in that they share several external, morphological characters such as the reddish body color, the series of faint transverse lines and the white lateral line. On the other hand, larvae of *T. hainani* and *T. fischeri* are represented as somewhat plain green in the larval body surface (Igarashi & Fukuda 2000; Fukuda et al. 1984), though they have some body color variations from green to

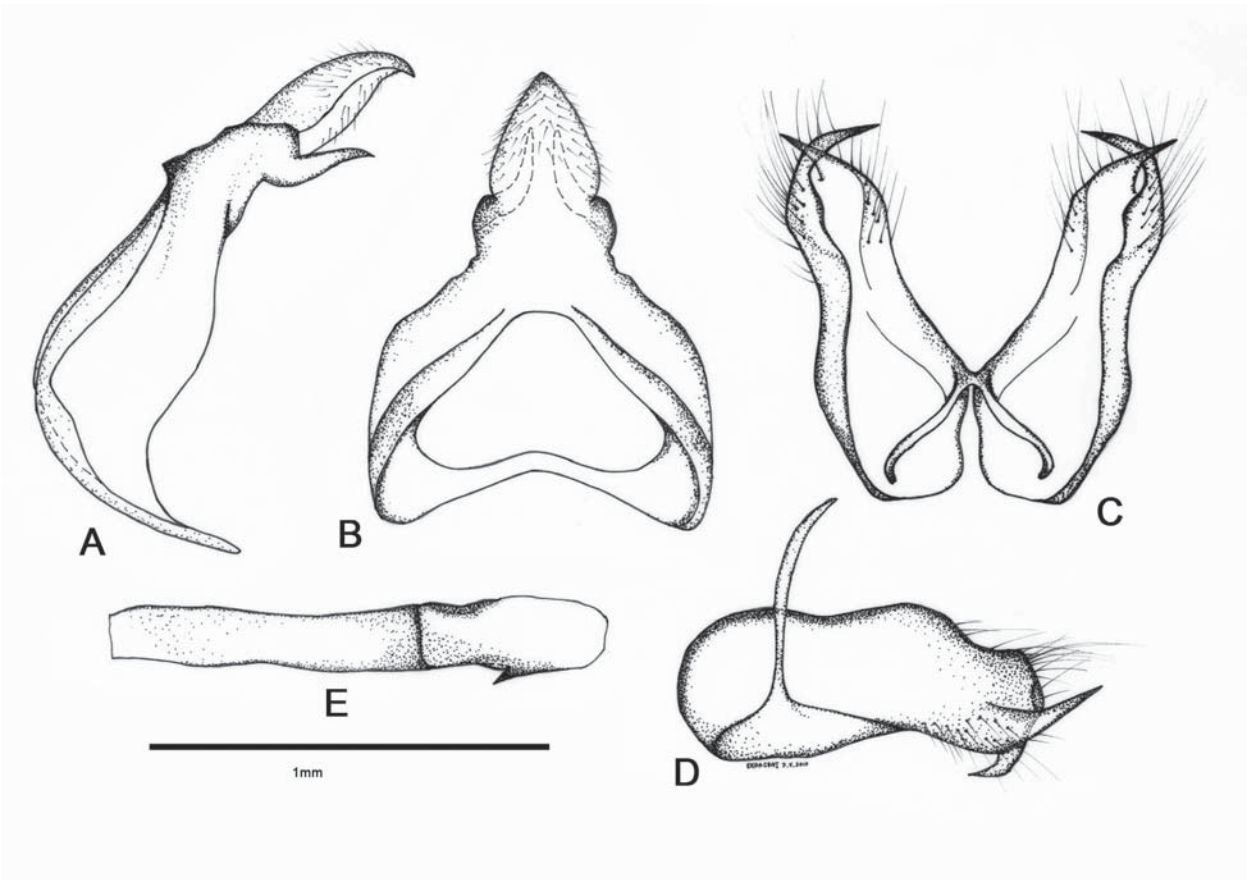


FIG. 18. Male genitalia of *Tongeia kala*. **A**) Ring (vinculum + tegumen), lateral view. **B**) Ditto, dorsal view. **C**) Valvae, dorsal view. **D**) Right valva, lateral view. **E**) Phallus, lateral view. Scale bar 1 mm.

reddish brown, probably due to the chemical compounds and the color of their hostplants. On the larval body surface, stellate-based or crown-like setae are commonly found in polyommatine butterflies (Ballmer & Pratt 1989; Fiedler 1991), and *T. kala* larvae also possess white or brown stellate-based setae represented as small white and brown dots throughout the body surface. These setae are recognized as white in *T. filicaudis*, but as dark brown in *T. fischeri* and *T. hainani*. (Igarashi & Fukuda 2000; E. Jeratthitikul unpublished). For pupal coloration, *T. kala* has the same color pattern as *T. hainani* and *T. filicaudis* (Igarashi & Fukuda 2000), but differs considerably from *T. fischeri* in having no dark brown smudges over the pupal surface (Fukuda et al. 1984; E. Jeratthitikul unpublished).

The majority of lycaenids are known to have associations with ants. This relationship has exerted strong selection on lycaenid larval morphology (Pierce et al. 2002). *Tongeia kala* also exhibits this trend; for example, the larvae have a thick cuticle and a small head that is retractable under a sclerotized prothoracic plate to defend against ant bites. In addition to more general adaptations, lycaenids possess two highly specialized sets of organs either for chemical or acoustic signaling, used to interact with ants (Pierce et al. 2002; Fiedler 1991). Larvae of *T. kala* possess three types of myrmecophilous organs for chemical signaling: dorsal nectar organ (DNO), tentacle organs (TOs) and pore cupola organs (PCOs), which are similar to those usually found in other lycaenids (Pierce et al. 2002; Fiedler 1991; Kitching 1985) and in reported related species, *T. hainani, T. ion* and *T. fischeri* (Fiedler 1991; E. Jeratthitikul unpublished). The DNO and TOs are easily visible under the stereo microscope or even by the unaided eye in late instar larvae (two small white dots in Fig. 7). Although no acoustic signaling was observed in the larval and pupal stages of *T. kala* according to our preliminary study, Fiedler (1992) suggested that the ability to produce calls may be universal in Lycaenidae, based on a biological study of *Hypolycaena othona* (Hewitson, 1865). In fact, several authors also reported that lycaenid larvae and pupae

[e.g. *Jalmenus evagoras* (Donovan, 1805)] produce sounds when disturbed or associated with ants (Travassos & Pierce 2000; see review by Pierce et al. 2002).

Despite possessing the myrmecophilous organs, the evidence of ant-association in *T. kala* was not observed during the field study, and the larvae were able to pupate and become adults successfully in the absence of ants under laboratory condition. In the case of other allied species, *T. hainani* and *T. ion* are assigned as moderately myrmecophilous because ant-associations regularly occur at least with part of the larvae (Fiedler 1991). Moreover, it is reported that almost all older larvae of *T. fischeri* are nearly permanently attended by ants (Fukuda et al. 1984; Fiedler 1991). The relationship with ants in *T. fischeri* was also found clearly nonspecific and facultative, since three ant genera in two subfamilies were recorded (E. Jeratthitikul unpublished). Based on the myrmecophily of the closely related species and the presence of myrmecophilous organs in *T. kala*, they must have at least the larval stage of their life history associated with ants, and the association seems to be a facultative relationship because larvae do not necessarily require attendant ants for survival.

In the wing markings, all *Tongeia* species including *T. kala* share the blackish upperside in both sexes and no androconia in males (Corbet & Pendlebury 1978, 1992). As described by some researchers (e.g. Kawazoé & Wakabayashi 1976), however, there are many distinctive differences between *T. kala* and the other congeneric species. In particular, *T. kala* has the following unique characters on the wing underside: 1) ground color dark grey, 2) all black dots evenly larger and prominent, 3) submarginal orange lunules on hindwing extremely well developed, 4) black scales of cilia widely expanded. These conditions are also never found in species of allied genera (e.g. *Everes* and *Shijimia*), though submarginal orange lunules are somewhat expanded in some species of Everes. Accordingly, the four character states are regarded as apomorphic within the genus.

The male genitalia of *Tongeia* species have been illustrated in the following literature: Shirôzu (1960) for *T. hainani* and *T. filicaudis*, Kawazoé & Wakabayashi (1976) for *T. fischeri*, Corbet & Pendlebury (1978, 1992) for *T. potanini*, Huang (1998) for *T. ion*, *T. zuthus* (Leech, 1893) and *T. menpae* Huang, 1998, Huang (2001) for *T. bella* Huang, 2001, *T. amplifascia* Huang, 2001 and *T. pseudozuthus* Huang, 2001, Huang (2003) for *T. confusa* Huang, 2003, and Huang & Chen (2006) for *T. dongchuanensis* Huang & Chen, 2006. Although those of *T. kala* can be also found in Cantlie (1964), there has been no detailed work on the comparative morphology of the male genitalia. In this study, we re-examined the male genitalia of *T. kala* and other congeners. *Tongeia* species share the following genital characters: 1) uncus produced into claw-like process and tapered to posterior portion, 2) valva almost rectangular, 3) ampulla and harpe rather flattened, 4) ampulla produced ventrally and pointed at apex. Since these conditions are usually not present in species of allied genera such as *Everes* and *Shijimia*, some of them may be synapomorphies of *Tongeia* species. In addition, *T. kala* differs from other congeners in having the following features: 1) phallus straight (curved ventrally in other congeners), 2) ampulla and harpe of valva sharply pointed and crossed each other (harpe lobed with or without projection in other congeners). However, similar conditions are observed in species of *Everes* and *Shijimia* (Kawazoé & Wakabayashi 1976). Thus, the character states seem to be more plesiomorphic than apomorphic within *Tongeia*.

In the present paper, *Sedum multicaule* is recorded not only as a hostplant of *T. kala* but also for lepidopterans for the first time. Plants in the family Crassulaceae are known as a major hostplant for the genus *Tongeia* (Igarashi & Fukuda 2000; Fiedler 1991; Fukuda et al. 1984). Although one hostplant and one substitute hostplant of *T. kala* larvae are reported here, other related species use various hostplant species as follows. *Tongeia hainani* from Taiwan feeds on *Kalanchoe pinnata, K. daigremontiana, K. garmbiensis, K. spathulala, Sedum alfredii, S. formosanum* etc. of Crassulaceae as well as *Gynura formosana* (Compositae) and *Hoya carnosa* (Asclepiadaceae). *Tongeia filicaudis* from Taiwan feeds on *S. nokoense* and *S. sekiteiense* (Igarashi & Fukuda 2000), and *T. fischeri* from Japan on *Orostachys erubescens, O. iwarenge, O. aggreatus, S. sordidum, S. makinoi, S. tricarpum, S. lineare, S. oryzifolium, S. japonicum* and *Hylotelephium sieboldi* (Crassulaceae) (Fukuda et al. 1984). Moreover, *T. potanini* from Thailand was recorded feeding on *K. integra* (Ek-Amnuay 2006). The data mentioned above indicate the wide host range among *Tongeia* species, so that they usually use more than one hostplant species within one genus, several genera or even different families. Although *T. kala* is perhaps a stenoligophagous or oligophagous species as compared with other related species, the use of crassulaceous plants as common hostplants among *Tongeia* butterflies could be a synapomorphy supporting the monophyly of the genus.

Morphological and ecological characters of *Tongeia* species from previous reports and this study show that *T. kala* should be surely assigned to the genus *Tongeia*, and that it seems to share many characteristics inherited from the common ancestor of the genus. Judging from

the adult morphology, however, this species may form a unique subgroup within the genus. Other analyses such as using SEM as well as genetic evidence will allow us to discover other features not reported here or previously, that likely will support our hypothesis.

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A NEW SPECIES OF *EUCOSMA* HÜBNER (TORTRICIDAE) RELATED TO *E. DORSISIGNATANA* (CLEMENS) AND *E. SIMILIANA* (CLEMENS)

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Abstract. *Eucosma oraria*, new species, is described from the mid-Atlantic coast of North America. It is distinguished from its closest congeners, *Eucosma dorsisignatana* (Clemens) and *Eucosma similiana* (Clemens), by size and details of forewing maculation. Reviews are provided of the last two species, including a reevaluation of their relationships with *Eucosma dorsisignatana diffusana* Kearfott, *Eucosma dorsisignatana confluana* Kearfott, and *Eucosma engelana* Kearfott. The new species appears to be associated with marsh habitat.

Additional key words: Olethreutinae, Eucosmini, coastal marsh.

In 1860, Clemens proposed the names *dorsisignatana* and *similiana* for two species of *Eucosma* Hübner, 1823, that have long been a source of confusion for North American taxonomists. Uncertainty with regard to the limits of intraspecific variation, coupled with a lack of diagnostic genitalic characters, resulted in *similiana* being treated as a synonym of *dorsisignatana* for nearly a century, from Fernald (1882) to Miller (1985). In 1905, Kearfott elevated two phenotypes of the then considered *E. dorsisignatana* to subspecies status as *E. d. confluana* and *E. d. diffusana*, and in 1908 he described *E. engelana* based on specimens similar to but allegedly distinct from *E. dorsisignatana*. The history of the nomenclature is complicated by the fact that Fernald (1882) misspelled *similiana* as *similana*, a name that at the time was preoccupied by *Paedisca similana* Hübner, 1793 (now *Epinotia trigonella* Linnaeus, 1758). That error persisted in the literature until Miller (1985) reviewed the situation, treating *E. dorsisignatana* and *E. similiana* as separate species distinguishable by whether the subbasal and median fasciae are disjunct or fused, respectively. His interpretation, with *E. d. confluana* and *E. d. diffusana* as synonyms of *E. similiana*, became the accepted arrangement, though Brown (2005) lists both subspecific names as synonyms of *E. dorsisignatana*. Miller (1985) did not comment on *E. engelana*, which has been treated as a subspecies of *E. dorsisignatana* since Heinrich (1923).

Several years ago I received a *dorsisignatana*-like specimen with unusual forewing markings that had been collected by Steve Johnson in coastal marsh habitat in southern New Jersey. Subsequent investigation revealed that there is no intergradation in maculation between this phenotype and typical *E. dorisignatana*, and I readily assembled a series of similar specimens that had accumulated in the *E. dorsisignatana* material at the United States National Museum of Natural History. The genitalia of these specimens resemble those of *E. dorsisignatana*, but the adults are substantially larger and appear to be restricted to the Atlantic coast (Nova Scotia to North Carolina). I am persuaded that they represent a previously unrecognized species. This paper proposes a name for the new taxon and reviews *E. dorsisignatana* and *E. similiana*, treating *E. engelana* and *E. d. confluana* as synonyms of *E. similiana* and *E. d. diffusana* as a synonym of *E. dorsisignatana*.

MATERIALS AND METHODS

I examined 265 specimens and 29 genitalia preparations from the following collections: American Museum of Natural History, New York (AMNH); University of Connecticut, Storrs (UConn); United States National Museum of Natural History, Washington D.C. (USNM), and Donald J. Wright (DJW). Morphological terminology follows Gilligan et al. (2008), "≈" stands for "approximately equal to," and aspect ratio (AR) refers to the ratio of forewing length (FWL) to medial forewing width. Illustrations were edited in Adobe Photoshop CS.

The type fixation issues associated with *E. dorsisignatana* and *E. similiana* are discussed in Miller (1973). My conclusions regarding *E. d. confluana*, *E. d. diffusana*, and *E. engelana* are based on examination of the lectotypes. In the case of *E. d. confluana*, Klots (1942) reported a lectotype in the AMNH, attributing the designation to Heinrich (1923), but Heinrich's remarks do not single out a unique specimen. For the sake of nomenclatorial stability, a lectotype designation is included below for the specimen interpreted as such by Klots.

SPECIES ACCOUNTS

Eucosma dorsisignatana (Clemens)
(Figs. 1–7, 17–19, 23–25)

Poecilochroma dorsisignatana Clemens 1860:353.
Paedisca dorsisignatana: Fernald 1882:42.
Eucosma dorsisignatana: Fernald [1903]:459; Barnes and McDunnough 1917:171; Heinrich 1923:120; McDunnough 1939:47; Powell 1983:34; Miller 1985:244; Miller 1987:53; Brown 2005:319; Gilligan et al. 2008:111.
Paedisca clavana Zeller 1876:303.
Carpocapsa distigmana Walker 1863:394.
Eucosma dorsisignatana diffusana Kearfott 1905:355; Barnes and McDunnough 1917:171; Heinrich 1923:121; McDunnough 1939:47; Powell 1983:34; Miller 1985:246; Brown 205:319.

Discussion. *Paedisca clavana* and *Carpocapsa distigmana* were first recognized as synonyms of *E. dorsisignatana* by Fernald (1882), a decision that is supported by the forewing maculation of the type specimens (Figs. 5, 6).

Kearfott (1905) described *E. d. diffusana* from 11 syntypes. I examined 5 of those specimens and found that they present two different forewing patterns. It seems from the original description that Kearfott intended the name to apply to the phenotype illustrated in Figs. 10 & 11, and apparently Miller (1985) was operating under that assumption when he placed *diffusana* in the synonymy under *E.* similiana. However, the lectotype (Fig. 7) for *E. d. diffusana*, designated by Heinrich (1923), has the *dorsisignatana* forewing maculation, and therefore *diffusana* belongs in the synonymy under *E. dorsisignatana*. [Heinrich's comments "Type – In American Museum" and "Type Locality – Vernon Parish, Louisiana" constitute a valid designation since the AMNH has only one syntype of *E. d. diffusana* from that location.] As in Miller (1985), individuals with the forewing appearance depicted in Figures 10 and 11 are treated here as *E. similiana*.

The *E. dorsisignatana* forewing pattern (Figs. 1–7) consists of three transverse marks: a fragment of a subbasal fascia, extending from dorsum to cell but not reaching the radius; a median fascia that is almost always incomplete near the dorsum, where usually it is represented by a small disjunct spot; and a postmedian band that terminates at the tornus and frequently is interrupted near the costa. The markings are reddish brown to blackish brown and thinly edged with white, contrasting with pale gray to reddish-brown interfascial areas that are extensively overlaid with brown to reddish-brown reticulations. The separation of the subbasal and median fasciae by a broad interfascial band is the basis for distinguishing *E. dorsisignatana* from *E. similiana* (Miller 1985). Forewing statistics: ♂ FWL 6.6–11.5 mm (mean = 9.3, n = 44), AR = 2.89; ♀ FWL 8.8–11.4 (mean = 9.9, n = 9), AR = 2.70.

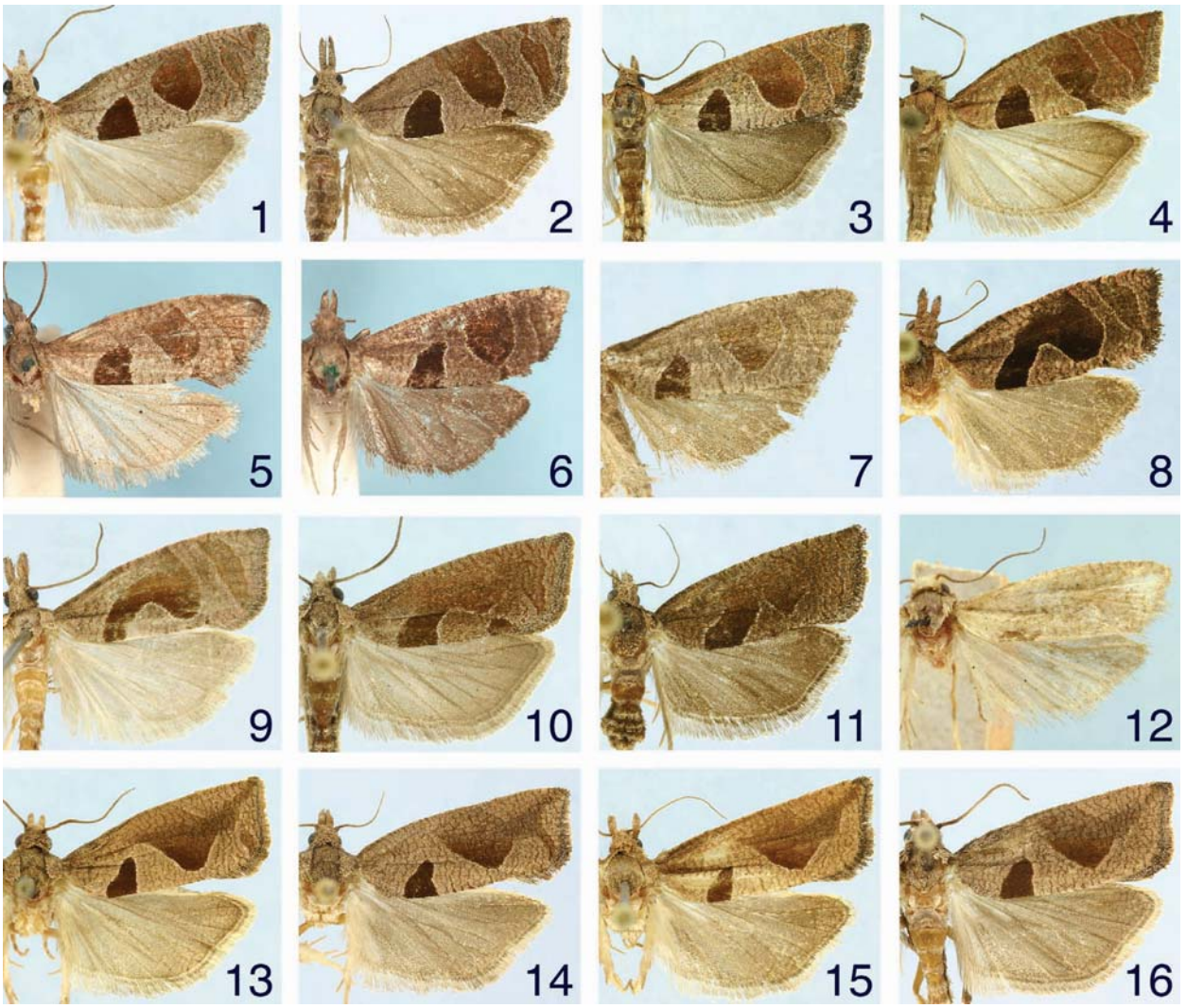
The literature contains several illustrations of the male genitalia: Heinrich (1923, fig. 180), Miller (1985, fig. 21), Miller (1987:53), Gilligan et al. (2008:218). Figures 17–19 give some indication of the variation in valval shape. The female genitalia was illustrated by Miller (1985, figs. 22, 23); the sterigma by Miller (1987:53) and by Gilligan et al. (2008:271). Figures 23 and 24 show what seems to be the extent of the variation in the lamella postvaginalis.

Types. *Poecilochroma dorsisignatana*. Lectotype designated by Darlington (1947): ♂, no. 7217, Academy of Natural Sciences, Philadelphia. Miller (1973) casts some doubt on whether this specimen is a Clemens syntype. The type locality was reported by Miller (1973) as unknown, by Heinrich (1923) as Pennsylvania ?, and by Brown (2005) as USA (Pennsylvania). *Paedisca clavana*. Lectotype designated by Miller (1985) (Fig. 5): ♂), Cambridge, Boll, genitalia slide 11565, BMNH. *Carpocapsa distigmana*. Holotype (Fig. 6): ♀, North America, genitalia slide 11543, BMNH. Walker (1863) based this name on a single specimen, which he incorrectly reported as a male. *Eucosma dorsisignatana diffusana*. Lectotype designated by Heinrich (1923) (Fig. 7): ♂ Louisiana, Vernon Parish, G. Coverdale, August, genitalia slide DJW 2570, AMNH.

Distribution and biology. Fernald (1882) reported that the larvae feed in the roots of *Solidago canadensis* Linnaeus (Canada goldenrod) (Asteraceae), crediting that information to Kellicott. I examined specimens that document a geographical range extending across southern Canada (Nova Scotia to British Columbia), south to the Gulf of Mexico and southwest to a line running roughly from eastern Oregon to eastern Texas. I am not aware of any records from Nevada, Utah, Arizona, or New Mexico. Powell & Hsu (1998) reported a population of a species "near *dorsisignatana*" from Plumas County, California in the northern Sierra Nevada mountains, but I have not examined those specimens. Adult flight occurs from mid-July to the end of October.

Eucosma similiana (Clemens)
(Figs. 8–12, 20–22, 26, 27)

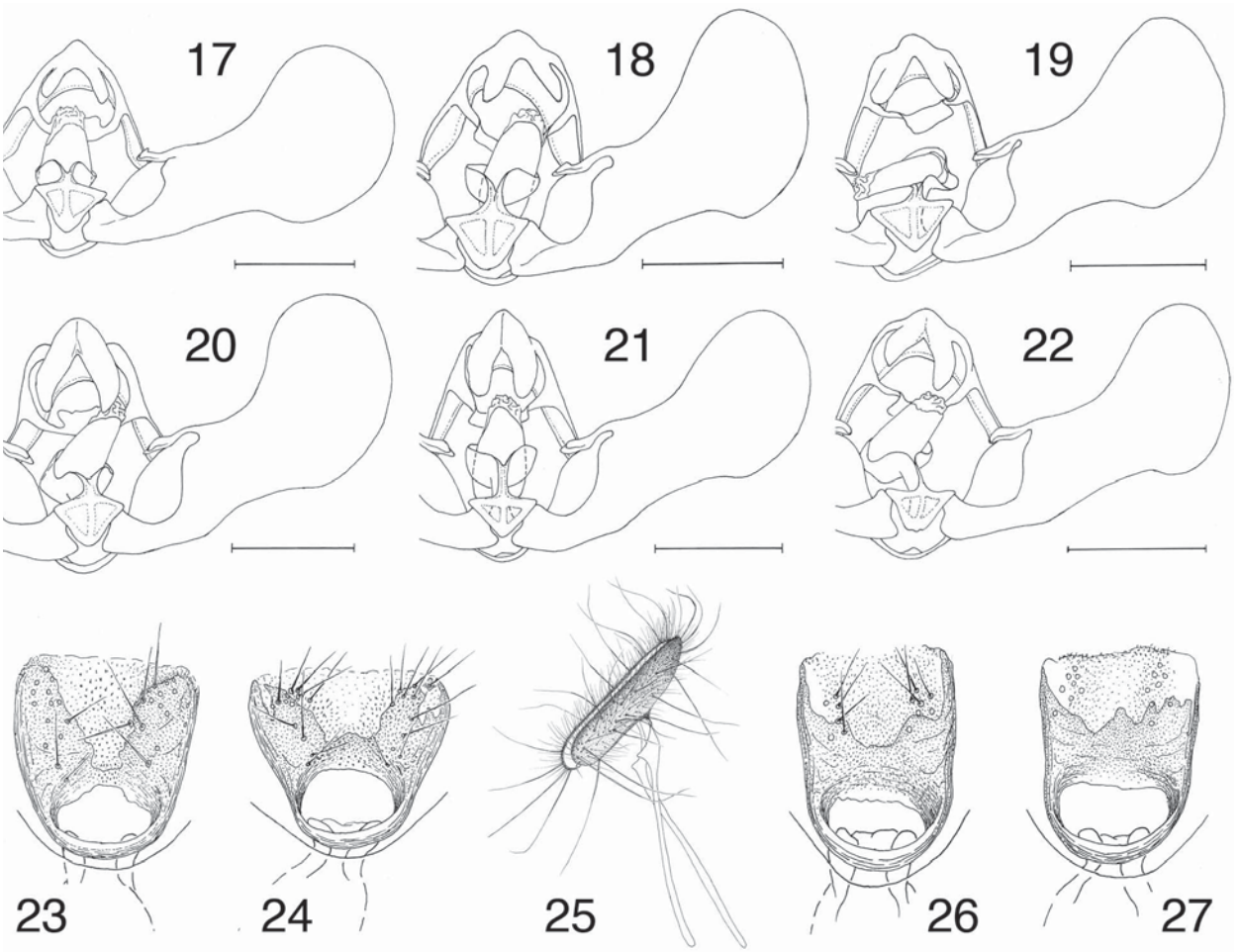
Poecilochroma similiana Clemens 1860:353.
Paedisca similana: Fernald 1882:42 [misspelling].
Eucosma similana: Fernald [1903]:459; Barnes and McDunnough 1917:171. [misspelling].



FIGS. 1–16. **1–7**, *E. dorsisignatana*. **1**, ♂, Adams Co., Ohio. **2**, ♀, Ithaca, New York. **3**, ♂, Larimer Co., Colorado. **4**, ♂, Halifax, Nova Scotia. **5**, *P. clavana* lectotype. **6**, *C. distigmana* holotype. **7**, *E. d. diffusana* lectotype. **8–9**, *E. similiana*, form *confluana*. **8**, ♀, Hamilton Co., Ohio. **9**, ♂, Susquehanna Co., Pennsylvania. **10–11**, *E. similiana*, form *diffusana*, ♂, ♂, Hamilton Co., Ohio. **12**, *E. engelana*, lectotype. **13–16**, *E. oraria*. **13**, Holotype. **14**, ♀, Accomack Co., Virginia. **15**, ♀, Northampton Co., Virginia. **16**, ♂, Worcester Co., Maryland.

Eucosma dorsisignatana similana: Heinrich 1923:121; McDunnough 1939:47; Powell 1983:34 [misspelling].
Eucosma similiana: Miller 1985:246; Miller 1987:53; Brown 2005:327; Gilligan et al. 2008:111.
Eucosma dorsisignatana confluana Kearfott 1905:355; Barnes and McDunnough 1917:171; Heinrich 1923:121; McDunnough 1939:47; Powell 1983:34; Miller 1985:246; Brown 205:319.
Eucosma engelana Kearfott 1908:169; Barnes and McDunnough 1917:170, **new synonymy**.
Eucosma dorsisignatana engelana Heinrich 1923:122; McDunnough 1939:47; Powell 1983:34; Brown 2005:319, **revised synonymy**.

Discussion. In proposing the name *confluana*, Kearfott (1905) intended to recognize the taxon described as *E. similiana* (Clemens) as a subspecies of *E. dorsisignatana*. Because of the prevailing misspelling of *similiana* as *similana*, the Clemens name seemed to be unavailable for this purpose, being preoccupied by *E. similana* Hübner. Miller (1985) interpreted *confluana* as a substitute name for *similiana*, implying that the type for *confluana* is the type for *similiana*. However, by publishing a description, based on 12 syntypes, Kearfott established *confluana* a valid taxon. Klots (1942) reported a lectotype, designated by Heinrich (1923), in the AMNH, but as pointed out above, Heinrich's



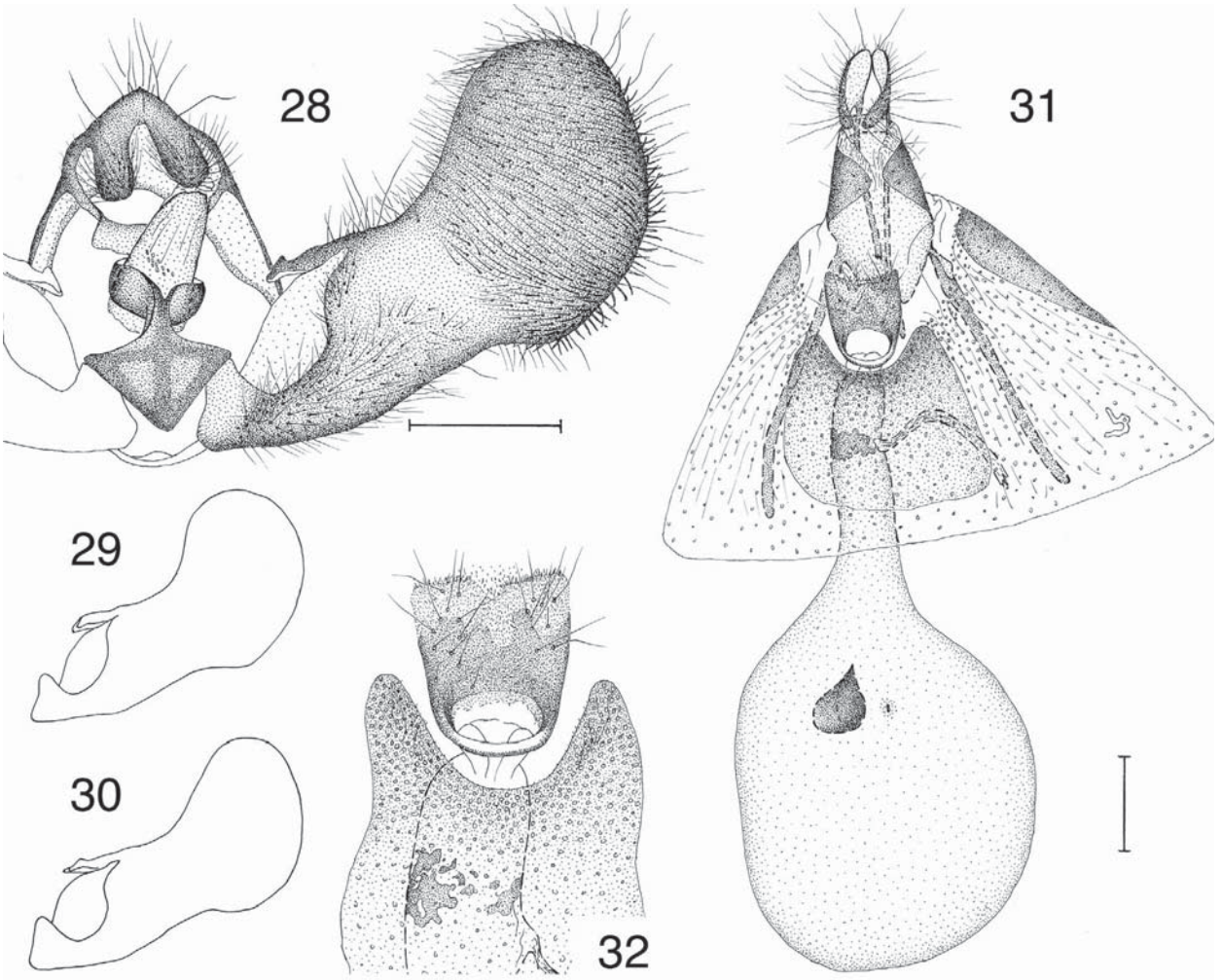
FIGS. 17–27. Genitalia. **17–19**, *E. dorsisignatana* ♂; slides DJW 1307, Adams Co., Ohio; DJW 865, Albany Co., Wyoming; DJW 2449, Baker Co., Oregon. **20–21**, *E. similiana* ♂; slides DJW 1304, Adams Co., Ohio; USNM 70425, Washington, DC. **22**, *E. engelana*, lectotype. **23–24**, *E. dorsisignatana* sterigmata; slides DJW 2446, Adams Co., Ohio; DJW 2447, Grand Co., Colorado. **25**, *E. dorsisignatana* papillae anales, slide DJW 2446, Adams Co., Ohio. **26–27**, *E. similiana* sterigmata; slides DJW 2450, 1305; Adams Co., Ohio. Scale bar = 0.5 mm.

comments do not constitute a valid designation. The lectotype designated below is the specimen mentioned by Klots. It bears a green label, presumably attached by Klots, with the inscription "LECTOTYPE."

With regard to *E. engelana*, Heinrich (1923) noted that the lectotype (Fig. 12) is "so rubbed that no markings are left" but treated the taxon as a subspecies of *E. dorsisignatana*, presumably based on the genitalia (Heinrich 1923, Fig. 170). The reinstatement of *E. similiana* to species status by Miller (1985) raises the question as to which of *E. dorsisignatana* and *E. similiana* is the appropriate senior synonym, particularly since the two taxa are not known to be distinguishable based on male genitalia. My investigations indicate that the uncus and socii are more strongly developed in *E. similiana* than in *E. dorsisignatana* (see below), and in this respect the *E. engelana* lectotype (Fig. 22) more closely resembles *E. similiana*. This is the basis for the new synonymy.

The forewing appearance of *E. similiana* (Figs. 8–12) is like that of *E. dorsisignatana* except that the subbasal and median fasciae merge in the median area forming a single mark, hence Kearfott's subspecific name *confluana*. That mark always contrasts with the interfascial areas along the dorsal margin but often fades into the interfascial color near the costa, the latter condition presumably being the basis for the subspecific name *diffusana*. Forewing statistics: ♂ FWL 8.1–11.0 mm (mean = 9.2, n = 32), AR = 2.88; ♀ FWL 8.2–10.3 (mean = 9.1, n = 21), AR = 2.75.

Illustrations of the male genitalia can be found in Heinrich (1923, figs. 170, 171, 172), Miller (1985, fig.



FIGS. 28–32. *Eucosma oraria* genitalia. **28**, ♂, holotype. **29–30**, male valvae; slides DJW 901, Cumberland Co., New Jersey; DJW 2445, Dukes Co., Massachusetts. **31**, ♀, slide DJW 2443, Accomack Co., Virginia. **32**, sterigma, slide DJW 2454, Dukes Co., Massachusetts. Scale bar = 0.5 mm.

27), and Gilligan et al. (2008:219), of the female genitalia in Miller (1985, figs. 28, 29), and of the sterigma in Miller (1987:53) and Gilligan et al. (2008:271). Figures 20–22 show the variation in valval shape. A comparison of the male genitalia of *E. similiana* (n = 6) and *E. dorsisignatana* (n = 9) revealed that the uncus in *E. similiana* is more strongly developed, with a distinct medial line of division on the ventral surface, and the socii are somewhat larger and more strongly integrated with the uncus (Figs. 20–22 vs. 17–19). Otherwise, I found no consistent differences in male genitalia between the two species. Females exhibit little variation in the shape of the sterigma (Figs. 26, 27).

Types. *Poecilochroma similiana*. Lectotype designated by Darlington (1947): ♀, no. 7316, Academy of Natural Sciences, Philadelphia. An image of the lectotype appears in Miller (1973, fig. 42). The type locality was reported by Miller (1973) as unknown, by Heinrich (1923) as Pennsylvania ?, and by Brown (2005) as USA (Pennsylvania). *Eucosma dorsisignatana confluana*. Lectotype here designated: ♂, New Jersey, [Essex Co.], Montclair, W. D. Kearfott, 24 August 1899, AMNH. *Eucosma engelana*. Lectotype designated by Heinrich (1923) (Figs. 12, 22): ♂, Pennsylvania, [Allegheny Co.], Pittsburgh, Henry Engel, 20 August 1906, genitalia slide CH 16 Dec 1919, AMNH. Genitalia illustrated by Heinrich (1923, fig. 170).

Distribution and biology. *Eucosma similiana* is restricted to eastern North America, the range extending from Nova Scotia to Manitoba and south to Georgia and Mississippi. Adult flight occurs from mid-July to the end of October. The larvae bore in root-stalks of *Solidago* (goldenrod) (Asteraceae). Čapek, (1971)

studied this species as a possible biological control for introduced *Solidago* in Central and Western Europe.

Eucosma oraria, new species

(Figs. 13–16, 28–32)

Diagnosis. *Eucosma oraria* is distinguished from *E. dorsisignatana* and *E. similiana* by size (mean FWL ≈ 10.8 mm vs. 9.4 mm and 9.2 mm, respectively) and by forewing maculation (large semitriangular mark in the median area disjunct from subbasal fascia, separating *E. oraria* from *E. similiana*, but connecting to apex, separating *E. oraria* from *E. dorsisignatana*).

Description. *Head*: Lower frons creamy white; scales of vertex brown with tan apices; labial palpus with lateral surface brown, medial surface whitish, shading to brown along margins; antenna concolorous with head. *Thorax*: Dorsal surface brown; ventral surface whitish; legs with anterior surfaces brown, posterior surfaces whitish; tarsi with inconspicuous tan annular markings at distal extremities of tarsomeres. *Forewing* (Figs. 13–16): ♂ FWL 7.3–12.2 mm (mean = 10.6, n = 30), AR = 2.78; ♀ FWL 10.5–13.2 mm (mean = 11.6, n = 8), AR = 2.78; costa weakly arched, apex nearly 90°, termen weakly concave; dorsal surface with dark brown subbasal and medial markings and pale brown interfascial areas, the latter extensively overlaid with brown reticulations; subbasal fascia represented by sharply defined mark arising on dorsum and narrowing to a rounded apex on cubitus; median fascia fading into ground color near costa but expanding posterior to radius into a large triangular mark with anterior edge running longitudinally through distal portion of cell and extending to apex and with posterior vertex approaching dorsum; subbasal and median fasciae disjunct and thinly edged with white; postmedian band sometimes obsolete (Figs. 15, 16) but usually expressed as a short bar at termen near tornus (Figs. 13, 14), occasionally connecting to medial mark (Fig. 14); ocellus not expressed; costa lacking pale strigulae; fringe scales blackish gray to gray brown, with whitish apices, the darker coloration producing a thin terminal line. *Hindwing*: Gray brown. *Male genitalia* (Figs. 28–30) (n = 3): Uncus semitriangular, with weakly developed central ridge on ventral surface; dorsolateral shoulders of tegumen weakly differentiated; socii finger-like and moderately setose; vesica with 13–15 deciduous cornuti; valva with costal margin concave at neck, apex broadly and sometimes bluntly rounded, distal margin convex, anal angle weakly developed, ventral emargination of neck shallow; cucullus with medial surface densely covered with fine setae. *Female genitalia* (Fig. 31, 32) (n = 3): Papillae anales laterally facing and moderately setose (as in Fig. 25); membrane from papillae anales to tergum 8 microspinulate and folded in collar-like arrangement; lamella antevaginalis ring-like and largely membranous; lamella postvaginalis semirectangular, broadening somewhat posteriorly, length ≈ average width, microspinulate throughout, with medial section weakly depressed at ostium, and with ca. a dozen setae on lateral sections; sclerotization of lamella postvaginalis variable and somewhat blotchy; sternum 7 with posterior margin roundly emarginated to approximately one-half length of sterigma and usually with microspinulae interspersed with scale sockets near posterior margin; ductus bursae with irregularly sclerotized patch at juncture with ductus seminalis; corpus bursae with large signum on dorsal surface and vestigial signum on ventral surface, the latter usually reduced to a tiny speck of sclerotized membrane surrounded by a patch of microspinules.

Holotype (Figs. 13, 28). ♂, Nova Scotia, Kings County, Grand Pré, D. C. Ferguson, 28 August 1952, genitalia slide DJW 2444, USNM.

Paratypes. CONNECTICUT: New Haven Co., Guilford, Leetes Island, D. L Wagner, 18 September 1992 (2 ♂); New Haven Co., Milford Point Audubon Center, M. Volovski, 25 September 2004 (1 ♂). MARYLAND: Worcester Co., Vaughn WMA, J. Glaser, 15 September 1998 (2 ♂); Nassawango Preserve, J. Glaser, 19 September 1995 (2 ♂); Assateaque Island, J. Glaser, 7 October 1993 (1 ♂); Dorchester Co., Taylor's Island WMA, J. Glaser, 5 October 2001 (1 ♂); Somerset Co., Deal Island WMA, J. Glaser, 30 September 1991 (1 ♂). MASSACHUSETTS: [Dukes Co.], Martha's Vineyard, F. M. Jones (3 ♂, genitalia slide DJW 2445; 1 ♀, genitalia slide DJW 2454). NEW JERSEY: Cumberland Co., 2.5 mi. W. Port Norris, S. Johnson, 28 September 2002 (1 ♂, genitalia slide DJW 901). NEW YORK: [Suffolk Co.], Riverhead, Long Island, Roy Latham, 30 May 1953 (1 ♂). NORTH CAROLINA: Carteret Co., Beaufort, J. B. Sullivan, 13 October 1998 (1 ♂), 15 October 1991 (1 ♂); Carteret Co., Fort Macon State Park, maritime shrub, J. B. Sullivan, 6 October 1997 (1 ♀), 14 October 1996 (2 ♂). VIRGINIA: Northampton Co., Kiptopeke, W. E. Steiner, 4–6 October 1986 (2 ♀, genitalia slide DJW 2442); [Accomack Co.], Chincoteaque, D. C. Ferguson, 23 September 1984 (1 ♀, genitalia slide DJW 2443). Depositories: DJW, UConn, USNM.

Etymology. The specific epithet comes from the Latin adjective orarius, meaning coastal, and refers to this insect's apparent preference for coastal habitat.

Distribution and biology. Amongst the 38 examined specimens (30 ♂, 8 ♀) were three males in the USNM labeled "Fernald Collection." Two have no associated data, but one has what I believe to be a Jacob Boll pin label with the inscription "Dallas, Texas." Between 1869 and 1871, while in the employ of Louis Agassiz at the Museum of Comparative Zoology, Boll collected extensively both in New England and in the vicinity of Dallas, Texas (Geiser 1948). There was, therefore, the opportunity for this last specimen to be mislabeled, and I suspect that is what happened. There is no other evidence to indicate the presence of this moth anywhere except along the Atlantic seaboard. Nearly all the types were collected from late August to early October, but one record from Long Island, New York dated 30 May suggests the possibility of a double brooded life cycle.

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THE CONCEPTUAL HISTORY OF *MELITAEA NYCTEIS* DOUBLEDAY, [1847] (NYMPHALIDAE), WITH THE DESIGNATION OF A LECTOTYPE AND A PORTRAIT OF ITS COLLECTOR, DAVID DYSON (1823-1856)

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ABSTRACT. Long thought to be based on a holotype, evidence indicates that the concept of the nominal taxon *Melitaea nycteis* Doubleday was actually based on four female syntypes, which were collected in Ohio in 1843 by the English naturalist David Dyson. A lectotype is designated to stabilize usage and establish a sole name-bearing type of this nominal taxon. The type locality is suggested to be the vicinity of Cincinnati, Hamilton County, Ohio. A previously unknown portrait of David Dyson, depicting him collecting Lepidoptera, was discovered in the possession of his great-grandnephew and is reproduced for the first time.

Additional key words: Jean B. A. D. de Boisduval, Edward Doubleday, syntypes

In 1847, the English entomologist Edward Doubleday (1811–1849) published a figure of a new species of butterfly, which he named *Melitaea nycteis* (currently *Chlosyne nycteis*) (Doubleday [1847]) (Fig. 1). This hand-colored lithographic illustration of a female specimen was based on a drawing by the English artist-naturalist William C. Hewitson (1806–1878). No written description accompanied the figure, but Doubleday (1848) issued separate text that attributed the species to "United States (Middle States)." A copy of Doubleday's figure, and a reference to the occurrence of the species in the United States, subsequently appeared in Lucas ([1851–1852]).

An old female specimen, identified as the "Type" of *M. nycteis*, is currently deposited in The Natural History Museum, London (BMNH) (Figs. 2, 3). This specimen was presumably selected as the type by N. D. Riley and A. G. Gabriel, who attempted to catalog and label all the butterfly type specimens in the British Museum (Natural History) (Riley & Gabriel 1924). A label, most likely created by Gabriel, designates the specimen as "B.M. TYPE / No. Rh8433" (Fig. 4). Gabriel probably also prepared the red-bordered "Type" label, but he incorrectly recorded the specimen as a male in his published list of nymphalid types (Gabriel 1927). This specimen is nearly identical to the figure of *Melitaea nycteis* in Doubleday ([1847]) (Figs. 1, 2), thus it undoubtedly served as the model for the illustration. Most authors (e.g. Higgins 1960; Miller & Brown 1981; Calhoun et al. 2005) considered this specimen to represent the holotype of *M. nycteis*, but evidence indicates that the type series actually consists of four specimens.

In his list of butterfly specimens in the British Museum, Doubleday ([1845]) included four specimens ("a–d") of an unidentified species of *Melitaea* from "Ohio, U. S." Two years later, he named and figured *Melitaea nycteis* from "United States (Middle States)" (Doubleday [1847]). The proximity of these events suggests that the specimens from Ohio represent syntypes of *M. nycteis*. This connection is supported by Doubleday's (1848) reference to "Middle States." In 1848, the United States extended westward to Iowa, Missouri, Arkansas, and Texas. At that time, Ohio was literally located in the middle of the country. A large locality label affixed to the type of *M. nycteis* (Fig. 4), reading "United States. / (Middle States)," evidently was prepared by a later museum worker based on Doubleday (1848).

Type specimen. The type of *M. nycteis* bears a small round label that reads, "U.S." On the verso of this label is written "44 / 1" (Fig. 4), which corresponds to accession number "1844–1" in the museum's register books, denoting the first lot of specimens received by the museum in the year 1844. This lot comprised 81 Lepidoptera specimens from the United States that were purchased from "Mr. Dyson." Also affixed to this specimen is a round label that reads, "2633 / d" (Fig. 4). Such alphanumeric labels on old butterfly specimens in BMNH correspond to entries in an eight-volume manuscript, written by Doubleday, which is thought to be a partial draft for his published list of specimens in the British Museum (Entomology Library, BMNH) (see Harvey 1996). Doubleday assigned a number to each entry in his manuscript and he cited many of these numbers in his published list, especially the second volume (Doubleday 1847a). The corresponding specimen labels were conceivably created by Doubleday himself. In this case, a transcription error is to blame for the reference to 2633, as this corresponds to an entry in Doubleday's manuscript for a single specimen ("a") of an unidentified species of *Thecla*.

FIGS. 1-9. Published figure, specimens, and collector associated with *Melitaea nycteis*. 1, figure from Doubleday ([1847]). **2**, female *C. nycteis* (BMNH), herein designated as the lectotype of *Melitaea nycteis*°. **3**, ventral aspect of lectotype°. **4**, labels affixed to lectotype°; at center is the round locality label, shown recto (left) and verso. **5**, female paralectotype (BMNH)°. **6**, labels affixed to paralectotype (BMNH)°; round locality label shown recto (top) and verso. **7**, female paralectotype (USNM). **8**, female paralectotype (USNM). **9**, detail of portrait of David Dyson by J. A. Wasse (courtesy Norman D. Dyson); inset at top left shows the entire composition; at bottom is Dyson's signature from one of his letters (Univ. of Cambridge). (°Courtesy The Natural History Museum, London).

However, entry 2333 lists four specimens of *Melitaea* from Ohio, "Bt. [bought] of Dyson." The presence of the letter "d" on the label reveals that this female is presumably the fourth specimen of *Melitaea* from Ohio as listed by Doubleday ([1845]).

David Dyson (1823–1856) (Fig. 9) was an English naturalist who spent nearly the entire year of 1843 in the United States, where he reportedly obtained an estimated 18,000 specimens of insects, birds, shells, and plants (Anonymous 1856a; Jackson 1908). Dyson sold his American butterfly specimens to the British Museum during a visit to London in early January 1844. In a letter to the English naturalist Hugh E. Strickland, dated 12 January 1844, Dyson wrote, "I have been to London to dispose of my insects…on my paying a visit to the British Museum I got in company with several gentlemen personally known to you" (H. E. Strickland correspondence, Univ. of Cambridge). One of the gentlemen that Dyson met was Edward Doubleday, who was employed as an Assistant in the Zoology Department of the British Museum. Not long after Dyson's visit to the museum, Doubleday (1844) described him as "an intelligent young man, originally a weaver from Oldham, whose zeal for entomology carried him out last year to the United States." Dyson is better known for his expeditions to "Honduras" (Belize) in 1844–1845 and Venezuela in 1846, both sponsored by the British Museum. Referring to these expeditions, White (1847) declared, "There has not been a more active or intelligent collector in this country than Mr. Dyson." Many of the specimens obtained during Dyson's trips were later described as new species, including *Euterpe dysoni* (now *Leodonta dysoni*), which Doubleday (1847b) named in Dyson's honor. Dyson purportedly served for a time as the curator of the natural history collections of Edward Smith Stanley, 13th Earl of Derby (Anonymous 1856a). Ives (1905) claimed that Dyson could not read or write, but obviously this is erroneous, as some of his letters were published (Anonymous 1912–1914) and others are preserved in various library collections. Dyson is the source of additional butterflies from Ohio in BMNH, including the state's only known specimen of *Chlosyne gorgone* (Hübner), which Doubleday ([1845]) listed as *Melitaea ismeria* Boisduval & Le Conte (Calhoun 2003a). This specimen also was among those sold to BMNH in 1844. Coincidentally, both Dyson and Doubleday died before the age of 40.

Second syntype. Another female specimen of *C. nycteis*, bearing an analogous "44 /1" label, was discovered in the general collection of BMNH (Fig. 5). Unlike the type specimen, this second female bears a handwritten rectangular label that reads "Ohio" (Fig. 6). I have found this style of locality label, with handwritten block letters and two parallel black lines, on other specimens in BMNH (Calhoun 2003a, 2003b). John E. Chainey, Curator of Lepidoptera at BMNH (pers. comm.), believes these labels were originally used as drawer labels, placed with a series of specimens from the same locality. Similar labels are still present in portions of the collection that have received little curatorial attention in recent years. This would explain why only one of the two old specimens of *C. nycteis* possesses such a label. The "Ohio" label was obviously created (possibly during the late 19th century) to reflect the relationship between these specimens and Doubleday's manuscript entry of four *Melitaea* from Ohio.

Remaining syntypes. Only two syntypes of *M. nycteis* were found in BMNH, implying that the other two Ohio specimens listed by Doubleday ([1845]) either were lost or represented a different species. However, Scudder (1868) stated that he had compared specimens with "types of *M. nycteis* in Boisduval's collection, received directly from Doubleday." Doubleday, who was harshly criticized for removing material from collections under his care, often exchanged specimens with the French entomologist Jean B. A. D. de Boisduval (1799–1879). Doubleday died only two years after he figured *M. nycteis*, increasing the likelihood that the specimens he sent to Boisduval did indeed represent the two missing syntypes from Ohio, not just "typical" specimens.

In the National Museum of Natural History (Smithsonian Institution, Washington, D.C.; USNM) are two female specimens of *C. nycteis* that were once owned by Boisduval (Calhoun 2006) (Figs. 7, 8). Boisduval bequeathed his collection in 1876 to the French lepidopterist Charles Oberthür, whose collection was sold in 1924. The American lepidopterist William Barnes obtained numerous North American specimens from this sale, and his own collection was acquired by USNM in 1930. The specimens of *C. nycteis* in USNM are of a similar condition to those in BMNH, supporting the theory that all four were collected together. A series of female syntypes also would explain why Doubleday ([1847]) portrayed a female to represent *M. nycteis*, when males were usually preferred for this purpose. Doubleday evidently retained two specimens for the museum and sent the remaining two to Boisduval in Paris. This most likely occurred between October 1847 (when Doubleday figured *M. nycteis*) and Doubleday's death in December 1849.

Type locality. Edward Doubleday explored portions of the United States in 1837 and 1838 and his journey

was documented in a series of accounts, which were published in a popular entomological periodical (Doubleday 1838). Doubleday arrived in New York City and traveled as far west as St. Louis. From Pittsburgh, Pennsylvania, he traveled down the Ohio River, stopping to collect insects along the way, including in the vicinity of Cincinnati, Ohio. Undoubtedly having read about Doubleday's exploits, the 20-year old David Dyson probably chose a portion of the same route for his own exploration of the country. Like Doubleday, Dyson arrived in New York City (Jackson 1908) and his trip was described as "across the Allegheny Mountains, and as far as St. Louis" (Anonymous 1856a). In a letter dated 28 February 1844 (Univ. of Cambridge), Dyson referred to "my friends at Cincinnati," thereby establishing the vicinity of Cincinnati as the most likely origin of Dyson's specimens from Ohio. Founded in 1788, Cincinnati already was a thriving hub of commerce by 1840, with a population of nearly 50,000 and as many as 30 steamboats arriving and departing at any given time (Goss 1912). The four syntypes of *M. nycteis* are consistent with females of this taxon currently found in southern Ohio (J. Calhoun unpubl.).

Lectotype designation. To stabilize the usage of the name *Melitaea nycteis*, [1847], and to establish a sole name-bearing type of this nominal taxon, the syntype long recognized as the "Type" is designated as lectotype and labeled accordingly (Figs. 2–4). This specimen bears six labels: 1) rectangular, "B.M. TYPE / No. Rh8433 / *Melitaea* / *nycteis*, / ♀ D.& H." (printed and handwritten); 2) round, "TYPE" (printed; BMNH), with "*Melitaea* / nycteis / Doubl." (handwritten); 3) rectangular, "United States / (Middle States)" (handwritten); 4) round, "2633 / d" (handwritten); 5) round, "U.S." (recto) and "44 / 1" (verso) (handwritten); and 6) rectangular, "♀ / ♀" (printed). Two additional labels have been added to reflect the status of the specimen: 1) rectangular, "LECTOTYPE / *Melitaea nycteis* / Doubleday [1847] / Designated by / John V. Calhoun, 2010" (printed), and 2) round, "LECTO- / TYPE" (printed; BMNH). The three remaining specimens are considered to be paralectotypes. The type locality is suggested to be the vicinity of Cincinnati, Hamilton County, Ohio. In response to an application to suppress the problematic name *Melitaea ismeria* Boisduval & Le Conte, [1835] (Calhoun et al. 2005), ICZN Opinion 2160 conserved the name *Melitaea nycteis*, Doubleday, [1847] and placed it in the Official List of Specific Names in Zoology (ICZN 2006).

Portrait of David Dyson. I recently discovered a portrait of David Dyson in the possession of his great-grandnephew, Norman David Dyson of Essex, England. Rendered in 1857 by John Angelo Wasse (1817–1885), the watercolor measures 60 x 50 cm (24 x 20 in) in size. It portrays an introspective (and implausibly well-dressed) Dyson relaxing with a cigar during a successful day of collecting Lepidoptera (Fig. 9). Wasse's grandson, Mike Wasse of Cambridgeshire, England, revealed (pers. comm.) that this painting was exhibited in 1857 at Peel Park Museum, Salford, England, as part of an exhibition of local artists. John A. Wasse was a portrait and miniature painter who also became involved in carte de vista photography (Wasse 2010). Previously, the only published likeness of Dyson was a lithographed bust portrait reproduced by Ives (1905) and Jackson (1908). This lithographed portrait also was created by J. A. Wasse in 1857, when he announced, "The friends of the late Mr. David Dyson, of Manchester, have proposed a subscription to procure lithograph copies of his portrait…to preserve a memento of this enthusiastic Naturalist" (Wasse 1857a). Wasse probably executed the lithographed portrait strictly for public consumption, while the larger composition was presented to the Dyson family. Wasse and Dyson obviously were acquainted, as they both resided in Manchester and were members of the Northern Entomological Society (Anonymous 1856b, 1857). Wasse published at least one article on insects (Wasse 1857b) and was the father of the celebrated artist Arthur C. J. Wasse (1854–1930). During the 1850s, J. A. Wasse exhibited artwork at the Royal Manchester Institution, the predecessor of the Manchester Art Gallery (R. Milner pers. comm.).

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CONFIRMATION OF BLACK MANGROVE [*AVICENNIA GERMINANS* (L.) L.] AS A LARVAL HOST FOR *JUNONIA GENOVEVA* (CRAMER) (NYMPHALIDAE: NYMPHALINAE) FROM SONORA, MEXICO

Additional key words: feeding behavior; larval rearing; mangrove buckeye

Mangrove estuaries in northwestern Mexico, including the states of Baja California Sur, Sonora, Sinaloa, Nayarit and Jalisco (Aburto-Oropeza et al. 2008), are inhabited by a species in the genus *Junonia* (Nymphalidae: Nymphalinae) listed as *J. evarete* (Cramer) by Brown et al. (1992) and referred to as an intermediate between *J. evarete zonalis* C. Felder & R. Felder and *J. coenia* Hübner by Hafernik (1982). Recent morphological (Neild 2008; Calhoun 2010) and molecular (Kodandaramaiah & Wahlberg 2007; E. Pfeiler et al., unpublished) studies support the assignment of the mangrove-associated buckeye to the taxon *J. genoveva* (Cramer), an assignment which is followed here. Ongoing research on *Junonia* in the Caribbean region, however, suggests that the taxonomy of the mangrove-associated buckeye is more complex than previously thought, probably consisting of more than one species, and that the name used here may ultimately require revision (C. Brévignon, personal communication).

Plant species typically found in mangrove forests in northwestern Mexico include Black mangrove, *Avicennia germinans* (L.) L. (Acanthaceae), Red mangrove, *Rhizophora mangle* L. (Rhizophoraceae), White mangrove, *Laguncularia racemosa* (L.) Gaertn. f. (Combretaceae) and Sweet mangrove, *Tricerma phyllanthoides* (Benth.) Lundell (Celastraceae). Although *J. genoveva* has long been known to be associated with the coastal mangrove ecosystem in northwestern Mexico (Hafernik 1982), the larval host plant(s) has remained uncertain. Tilden (1971) suggested the genus *Phyla* (= *Lippia*) (Verbenaceae) as a larval host, a genus also used by larvae of the closely related *J. coenia* in California, USA (Shapiro & Biggs 2010). The genus *Stemodia* (Scrophulariaceae) was listed as probable larval host (in addition to *Phyla*) by Brown et al. (1992). Both Hafernik (1982) and Brown et al. (1992) commented on the close association of *J. genoveva* with the mangrove habitat, but mangroves were not mentioned in either reference as a potential larval host. In the Caribbean region, however, the use of *A. germinans* as a larval host plant has been well documented (Turner & Parnell 1985; Elster et al. 1999; Brévignon 2009).

Given the ecological association of *J. genoveva* with mangrove habitat in northwestern Mexico, it was of interest to determine whether *A. germinans* could be used by larvae of *J. genoveva* in this region as well. After much searching, five first and second instar larvae of what appeared to be *Junonia* were found feeding on *A. germinans* at Estero del Soldado (27°57'35''N, 110°59'00'' W), a small hypersaline lagoon (negative estuary) located on the Gulf of California between Guaymas and San Carlos, Sonora Mexico (Fig. 1). Larvae were collected between 11–22 October 2010 and were provided with fresh leaves of *A. germinans* every 2–4 days until pupation. Wild-caught adults were taken mainly between 21 July–5 November 2010 at Estero del Soldado and at San Carlos. A population of *J. genoveva* also was found at a very small mangrove estuary (El Esterito) in San Carlos, 8 km W of Estero del Soldado.

The five larvae fed on *A. germinans* leaves for approximately 21 days and successfully developed to the last instar and pupated (Fig. 2). One of the five pupae died; the remaining four produced adults (2 males and 2 females) 7–10 days after pupation. One adult female and one adult male were taken as vouchers (Fig. 3); the other two individuals were released. Maculation and coloration of both reared (Figs. 2–3) and wild-caught adults from Estero del Soldado were similar to individuals of *J. genoveva* figured from coastal regions of Baja California Sur (Brown et al. 1992) and San Blas, Nayarit (Warren et al. 2010; as *J. evarete* NW Mexican segregate).

The youngest larvae of *J. genoveva* fed by scraping the upper epidermis of leaves, whereas later instars were chewers. Larvae preferred the younger, fresher tree leaves, although they were originally collected in the wild from older leaves ~1 m above the water. This feeding behavior differs from that reported in Colombia where larvae of *Junonia* (listed as *J. evarete*) were never found more than a few centimeters from the water feeding on propagules, young seedlings and pneumatophores of *A. germinans*, but not on the mature tree leaves (Elster et al. 1999). Larvae collected in Jamaica also prefer feeding on the cotyledons of young seedlings of *A. germinans* (Turner & Parnell 1985). The close association between the distribution of *A. germinans* and *J. genoveva* in northwestern Mexico

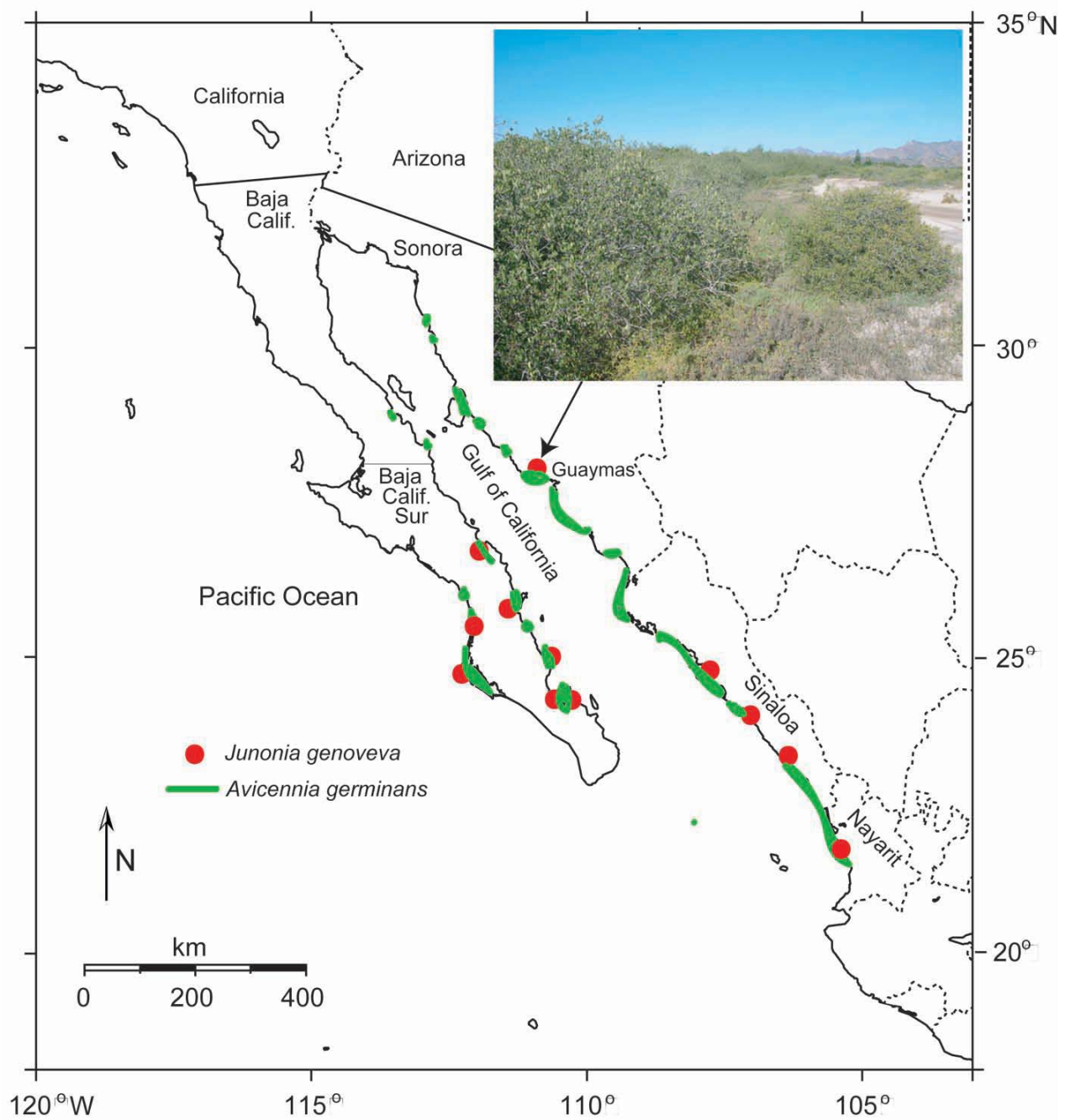

FIG. 1. Map of northwestern Mexico showing location of the study site at Estero del Soldado near Guaymas, Sonora, Mexico, in addition to collection and observation records for *Junonia genoveva* and Black mangrove (*Avicennia germinans*) for this region. Records were compiled from data given in Hafernik (1982), Brown et al. (1992), Turner et al. (1995), Aburto-Oropeza et al. (2008), Warren et al. (2010), and collection data provided by K. Hansen, R. Wells and J. A. Scott (personal communication). Inset shows landward (north) side of Estero del Soldado looking west. Plants in the foreground are *Avicennia germinans* (at left) and *Tricerma phyllanthoides* (at right). Trees in the distance are principally *A. germinans*, together with *Laguncularia racemosa* and a few small *Rhizophora mangle*. All larvae were found in the foreground area on *A. germinans*; adults of *J. genoveva* typically "patrolled" the dirt road and disturbed area seen at far right.

FIG. 3. (opposite page; bottom image) Reared *Junonia genoveva* from Estero del Soldado. Male (top; voucher no. CIAD 10–B37; eclosed 9 Nov. 2010); Female (bottom; CIAD 10–B38; eclosed 20 Nov. 2010). Ventral view is shown in images on the right.

FIG. 2. Developmental stages of *Junonia genoveva* from Estero del Soldado. (**A**) last instar larva feeding on its host plant *Avicennia germinans*; (**B**) head and thoracic region of last instar larva; (**C**) pupa attached to underside of a leaf of *A. germinans* (salt deposits are visible on leaf); (**D**) recently-eclosed female being released.

(Fig. 1) suggests that *A. germinans* is the principal host throughout the region. But because of the low numbers of larvae found it was not possible to test for possible alternative hosts. There is evidence, however, suggesting that larvae of *Avicennia*-feeding *Junonia* in the Caribbean region are host specific (Turner & Parnell 1985; Elster et al. 1999).

Peak flight activity of *J. genoveva* at Estero del Soldado occurred from late August through November in agreement with the findings of Brown et al. (1992) in Baja California Sur. Adults showed a preference for bare ground adjacent to the mangroves (Fig. 1). Adults of a large and dark buckeye, recognized as the subspecies *J. evarete nigrosuffusa* W. Barnes & McDunnough by Pelham (2008), were also found in the Guaymas/San Carlos region, but this subspecies was never observed flying together with *J. genoveva* in the immediate vicinity of the mangroves at Estero del Soldado. Both taxa, however, were observed flying on the beach ~1 km W of Estero del Soldado, and feeding together on Desert broom *Baccharis sarothroides* A. Gray (Asteraceae) at San Carlos and on ornamental *Lantana* (Verbenaceae) at a residential complex adjacent to Estero del Soldado. Most observations of *J. e. nigrosuffusa*, however, were inland from the immediate coast. Thus, the two taxa, although occurring sympatrically, appear to be largely ecologically isolated, similar to the findings in Baja California Sur (Brown et al. 1992).

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LARVAL COLORATION IN *LOPHOCAMPA MACULATA* HARRIS 1841: INSTAR-SPECIFIC PARTIAL DEPIGMENTATION IN CAPTIVE AND WILD POPULATIONS

Additional Key Words: melanin

The Spotted Tussock Moth, *Lophocampa maculata* Harris 1841, (Erebidae, Arctiinae (Lafontaine & Schmidt 2010)), is found across North America on both sides of the US/Canadian border, along the Pacific coast, and in both the Appalachian and Western mountains of the US (Powell & Opler 2009). Eastern and western larvae show differences in coloration, which are most noticeable in the final, 5th instar. The Eastern form, found from Newfoundland to the Southern Appalachians and west to Saskatchewan, as a 5th instar (Fig. 1l), is characterized by black setae at both ends and a yellow central region with black dorsal spots. In addition, there are longer white setae at both ends. The Western form, found from the Rocky Mountains to the Pacific coast, is similar in the 5th instar, except that the central region is orange and there are no dorsal spots (Fig. 1d). California coastal populations show additional color variation, which is under investigation. This note describes a previously unreported instar-specific, partial loss of pigmentation discovered during a larger study of the natural history of this species.

In the course of captive rearing to investigate the larval development of the species, I observed an unusual partial loss of pigmentation in two individuals from two widely separated locations. Eggs were obtained from each of two gravid females having normal coloration, collected at two California locations: the San Bernardino Mountains and the Sierra Nevada Mountains, near Bishop, California. The two locations are approximately 380 km apart and separated by about 100 km of the Mojave Desert, which is unlikely to provide suitable habitat for this species. They are, thus, likely to be genetically isolated. The San Bernardino (SB) and Bishop (B) groups, were reared under identical conditions of temperature, daylight and humidity. They were both fed vine maple, *Acer circinatum* Pursh. The SB group consisted of 62 siblings at the 4th instar stage, when the depigmented individual was found. The B group consisted of 41 siblings at the 3rd instar stage, when the second depigmented individual was found. At the time of discovery, each depigmented individual was removed from the group and reared separately, but under conditions identical to the rest of the population. Except for coloration, these two individuals appeared no different from the rest of their respective siblings. They fed and developed normally. Further observations of these two individuals are presented below.

San Bernardino Individual

All members of the SB group appeared normal until the 3rd to 4th instar molt. Figure 1a-d shows typical 2nd to 5th instar individuals of the Western form. These photos show the "normal" appearance of both the SB and B groups. Figure 1e shows the depigmented individual as a 4th instar. All of the setae are white except for a series of dorsal tufts, of which the most posterior two are black and the remaining six are red-orange. In addition, the head is brown in contrast to the normal black color. The appearance of this individual remained constant through the 4th instar. On molting to the 5th instar, however (Fig. 1f), it reverted to the normal 5th instar appearance (compare Fig. 1d and f). This individual continued to thrive and eventually formed a cocoon.

Bishop Individual

All individuals in the B group developed normally until the 2nd to 3rd instar molt. One individual emerged as a 3rd instar with coloration similar to the 4th instar of the SB individual (Fig. 1g). The setae were all white except for some of the dorsal tufts, which showed the same coloration as the SB individual. In addition, its head was the same brown color as the SB specimen. This individual developed normally and molted to a 4th instar with no change in coloration (Fig. 1h). The 4th instar continued normal development and molted to give a typical 5th instar (Fig. 1i). This individual also eventually formed a cocoon.

Wild Populations

Subsequent to the discovery of these individuals in the two California populations, I conducted a search to see if other photographic documentation of this phenomenon existed. Three cases were discovered: two from Vancouver Island, BC, Canada, which arose within the Western larval phenotype, and another from Bailey's Harbor, WI, which arose in the Eastern phenotype.

The Vancouver Island photos (Fig. 1j,k) show two likely 4th instar individuals. The pattern of coloration, white setae except for the dorsal spots and brown head, match that of the California specimens. The number of dorsal spots and the distribution between two black

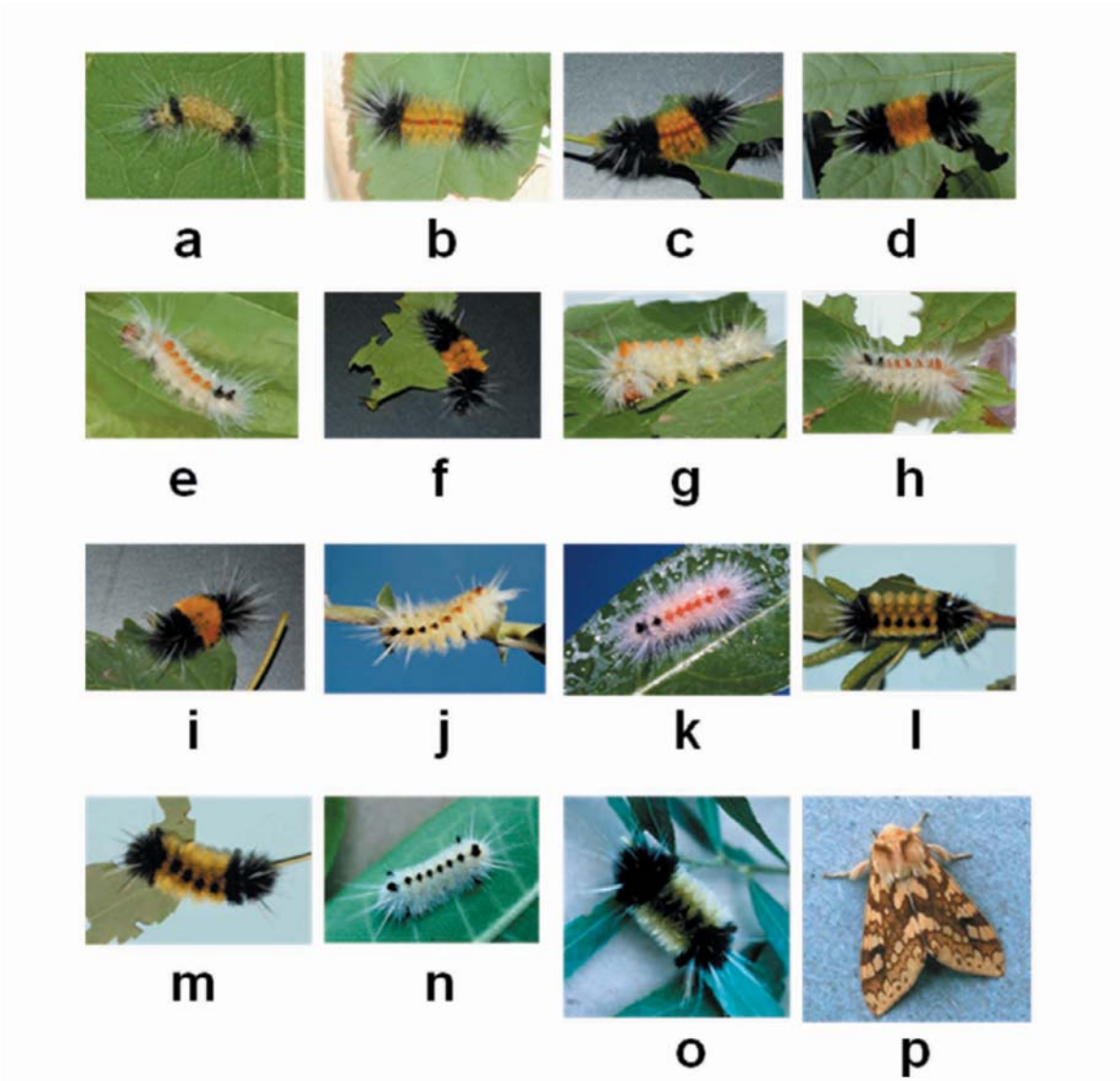

FIG. 1. Normal and instar-specific, partially depigmented individuals of Lophocampa maculata from both captive and wild populations. **a-d**, normal 2nd to 5th instar larvae of the western form of L. maculata (San Bernardino Mtns., CA) raised in captivity; **e**, 4th instar larva from the same female parent as a-d, showing partial depigmentation; **f**, same individual as e, as a 5th instar larva; **g-i**, 3rd, 4th, and 5th instar larva of a single individual from Bishop, CA, raised in captivity, showing depigmentation in the 3rd and 4th instars and reversion to normal phenotype in the 5th instar; **j-k**, two 4th instar individuals found in the wild (Vancouver Island, BC) showing depigmentation similar to that seen in the captive CA populations (j-k courtesy Jeremy B. Tatum); **l-m**, normal pigmentation in typical 4th and 5th instar larvae of the eastern form of *L. maculata* (Prince Edward Island, Canada) raised in captivity; **n-o**, 4th and 5th instar larva of an individual found in the wild (Bailey's Harbor, WI); **p**, adult of the individual shown in o after emergence the following year (n-p courtesy Janice Stiefel).

posterior and four orange anterior spots in Figure 1k match also. In Figure 1j, there appears to be a transition zone between the two black posterior spots and the orange anterior ones where several tufts are a mixture of black and orange setae. Because these individuals were not collected, there is no record of reversion to normal appearance in the 5th instar.

The larval phenotype in Wisconsin is the yellow variety. Figure 1l,m shows the normal 4th and 5th instar Eastern larval appearance, as documented in a captive reared population from Prince Edward Island, Canada. Both 4th and 5th instars have a yellow central area with a series of black dorsal spots, which distinguish them from the Western phenotype. The black regions at both

ends of the body and long white setae are similar to the Western phenotype. Figures 1n–p document the appearance of a single individual from Wisconsin. It was discovered in the wild as a 4th instar (Fig. 1n), showing a depigmentation pattern similar to that of the Western phenotype: white setae over the entire body except for black dorsal spots and, uniquely, a pair of lateral black tufts at both ends of the body. The lateral black tufts do not appear in the Western individuals. This individual was collected and observed to molt into a normal appearing Eastern 5th instar larva (Fig. 1o). The 5th instar larva eventually formed a cocoon and eclosed the following spring. The male adult (Fig. 1p) has the normal coloration of *L. maculata*. This is the only depigmented larval individual for which the adult form has been observed. The reversion to normal coloration in the 5th instar larva leads to a normally pigmented adult.

Comparison of Individuals

Comparison of the depigmented individuals documented here reveals a number of similarities. In both the Western and Eastern depigmented forms, the body is covered with white setae except for the dorsal spots. These spots appear to have the normal pigmentation for the specific instar stage of the individual. The coloration of the dorsal spots appears to follow the normal Western or Eastern phenotype. The lone Eastern individual also has single black tufts laterally at both ends of the body. In all documented cases, the depigmentation was observed in the 3rd or 4th instars with reversion to normal pigmentation in the final, 5th, instar.

Normal individuals of both Western and Eastern phenotypes of *Lophocampa maculata* show an instar-specific pattern of pigmentation. This is shown for the Western phenotype in Figure 1 a-d. The chemical nature of the pigments in this species, and the regulatory mechanisms responsible for the normal patterns of coloration, are unknown, but all of the observed colors could result from various types of melanin (see Wittkopp & Beldade 2009 for a recent review). In the depigmented individuals, the dorsal spots are pigmented in the normal black or red-orange colors, indicating the biochemical pathways necessary for pigment production are intact in these individuals. Regulation of the dorsal spot pigmentation appears to be controlled independently of that of the rest of the body, since they retain normal pigmentation. Thus, some disruption of the regulation of pigment production in particular regions of the body must have occurred. The depigmented areas are normally black and either orange in the western form or yellow in the Eastern form. Therefore, the loss of pigmentation affects more than one pigment production pathway. This suggests a complex situation where different regulatory elements control pigmentation over different regions of the body. The absence of pigment production is likely to result from disruption of a regulatory element that acts as an on/off switch rather than loss of an enzyme in one of the biochemical pathways producing a specific pigment since all affected individuals have some pigmented setae. Thus, each individual transitions from normal pigmentation to the depigmented form for one or two instars and then reverts back to normal pigmentation in the 5th instar. The single case where the resulting adult was documented demonstrates that adult pigmentation is not affected by larval loss of pigmentation.

Larval pigmentation in Lepidoptera is known to be affected by environmental conditions. There are many reports in the literature of changes in larval coloration in response to temperature (Solensky & Larkin 2003; Suzuki & Nijhout 2006), diet (Green 1989; Akino et al. 2004), population density (Fescemyer & Hammond 1986; Lee & Wilson 2006), and color of perceived light (Green 1996) among others. All of these effects were observed throughout the larval period. The present observation differs in two significant ways from these previously reported environmental effects. First, although environmental conditions were identical for each group of siblings from California being raised in captivity, only a single individual in each group exhibited the depigmentation effect. Second, the depigmentation affected only one or, in one case, two of the instar stages, and all individuals reverted to normal pigmentation in the final instar. In addition, the discovery of similar depigmented individuals in wild populations argues against the effect being some consequence of captive rearing. I have been unable to find any mention in the literature of an instar-specific loss of pigmentation.

Some arctiine genera show variations in pigmentation that are believed to be genetic in origin. These include polymorphisms among individuals (Wagner 2009) and, in the case of some species of Acronictinae, within-individual color changes both between instars and within a single instar (Wagner 2005). *Lophocampa maculata* exhibits both inter-instar color changes as well as geographic pigmentation polymorphism.

The depigmentation reported here appears to be genetic in origin. It could result from a particular allele, or combination of alleles of one or more genes. These alleles, although occurring in low frequency, may nevertheless persist in populations over wide geographic areas for long periods of time. This would explain the similarity of the depigmented larvae from

widely separated regions. An alternative explanation is that the depigmented individuals resulted from a spontaneous mutation that affected an instar-specific regulator of pigmentation. However, this would require an unusually mutation-prone site to account for the number of individuals observed.

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This report is dedicated to Janice Stiefel, who first noticed the instar-specific depigmentation phenomenon. I wish to thank Dave Wikle, who kindly provided the gravid females from the Sierra and San Bernardino Mountains, Jeremy Tatum for the photos of the depigmented larvae from Vancouver Island and Janice Stiefel for the photos and observations of the depigmented individual from Wisconsin. Zoe Strothkamp provided valuable assistance in rearing the larvae. I especially thank one reviewer who provided helpful suggestions.

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CARYSTOIDES "MEXICANA" FREEMAN, A SPECIES AND GENUS NEW TO CUBA AND THE CARIBBEAN (HESPERIIDAE)

Few island faunas have been studied as extensively as have the butterflies of the Greater Antilles. Since 1944, there have been six technical book-length treatments of the fauna or major islands (Comstock 1944; Brown & Heineman 1972; Riley 1975; Alayo & Hernández 1987; Smith et.al. 1994; Pérez-Asso et. al. 2009) and the biogeography of the islands has been analyzed extensively (Munroe 1948; Miller & Miller 1989; Davies & Smith 1998). Thus, it surprised us to find a specimen of *Carystoides* (Fig. 1a–b) among miscellaneous Hesperiidae collected by the second author near Santa Clara, Villa Clara Province, on 11 January 2002. *Carystoides* is not previously reported from the Caribbean, and represents a significant new record for the region.

We tentatively identify this specimen as *Carystoides "mexicana"* Freeman, 1969. The genus *Carystoides* is complex with 17 recognized species and two subspecies (Mielke 2005) and species are both very similar and highly variable. Complicating this is the quality of original descriptions for many species. Evans (1955) revised the genus as known at the time, describing six new taxa within the couplets of his taxonomic key to the species, supplemented with freehand drawings of dry-mounted male genitalia that capture the essence of form, but lack detail. More recently, Freeman (1969) described four additional species from Mexico and included black and white photographs of types. Unfortunately, his figures of male genitalia, while superior to those of Evans, are also difficult to interpret

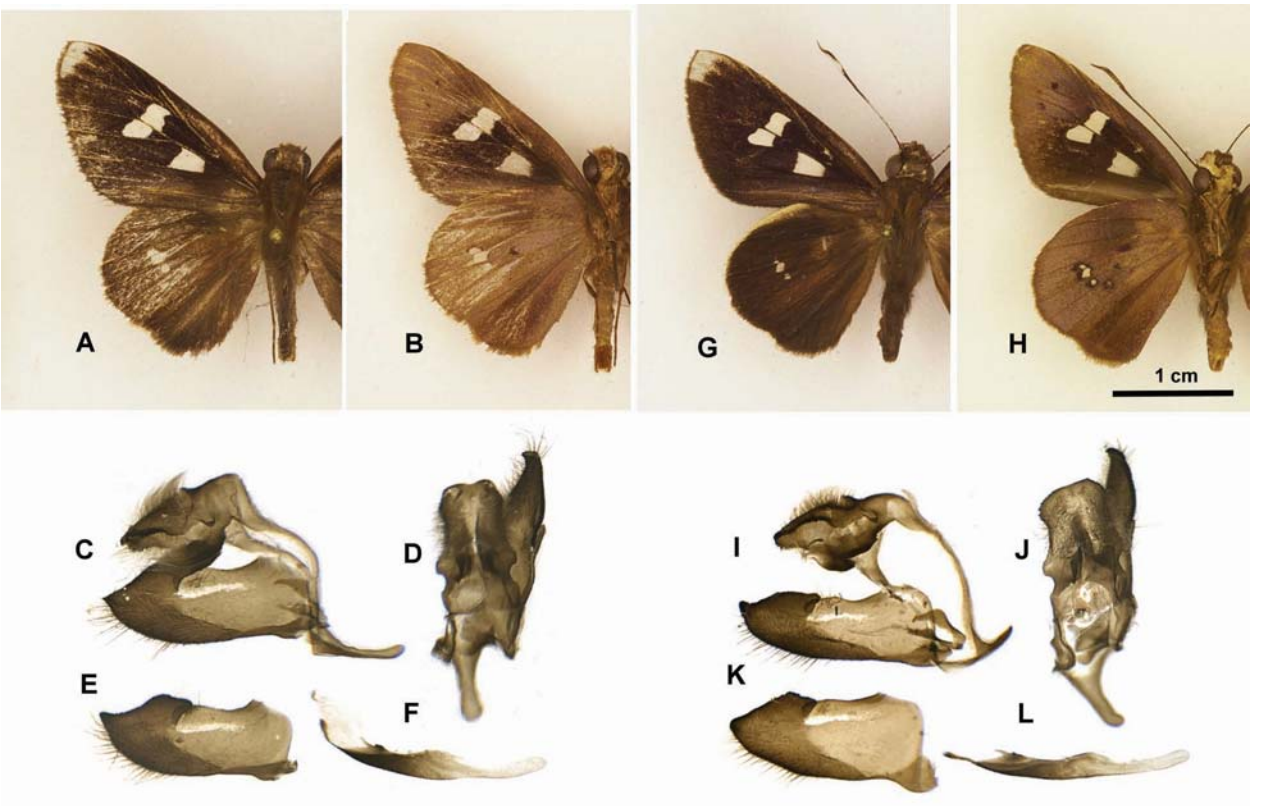

FIG. 1. Male *Carystoides "mexicana"*, wing pattern and genitalia from Cuba and Belize (specimens are in the John Shuey collection). **A–F**, Cuba, Villa Clara Provence, Santa Clara, 11 January 2002, Robert Anderson, Collector: **A)** adult dorsal; **B**) adult ventral; **C)** right valve and uncus, lateral view; **D)** right valve and uncus, dorsal view; **E)** left valve, lateral view; **F)** penis, lateral view. **G–L**, Belize, Orange Walk District, Rio Bravo Conservation Area, Rio Bravo Base Camp, rainforest edge, 12 September 1995, J.A. Shuey, Collector: **G)** adult dorsal; **H)** adult ventral; **I)** right valve and uncus, lateral view; **J)** right valve and uncus, dorsal view; **K)** left valve, lateral view; **L)** penis, lateral view.

Fig. 2. General view of the habitat in the vicinity of Santa Clara, Cuba. The *Carystoides* was collected along the edge of the forest indicated by the arrows.

relative to species differences. For these reasons, species determinations in the genus are difficult and subject to interpretation.

Over the last decade, the first author has worked through the taxonomy of the *Carystoides* of Belize and adjacent areas and has settled on a tentative taxonomy for the species of Belize. Five species are known from Belize, and by far the most common species has tentatively been determined as *Carystoides "mexicana"*. The Cuban specimen (Fig. 1a–b) is very similar to *C. "mexicana"* from Belize (Fig. 1g–h) and although its wings are worn, its pattern falls within the normal range of specimens tentatively placed under this name from Belize. The genitalia of the Cuban specimen (Fig. 1c–f) indicate a close relationship to Belizean *C. "mexicana"* as well (Fig. 1i–l). However, the distal ends of the valvae are strongly cupped on the Cuban specimen and fall outside the range of genitalia observed in Belize specimens. As more Cuban specimens become known, it is possible that a species or subspecies name could be warranted.

The *Carystoides* was captured within a city park in Santa Clara dedicated to a revolutionary battle won by Che Guevara. The park is a mosaic of highly disturbed habitats with some tropical forest vegetation in the valleys (Figure 2). The specimen was captured adjacent to one of these forest patches.

In Belize, all species of *Carystoides* are found in or along the edges of densely forested habitats. Typically, adults rest on small sapling trunks or lianas in very dense shade, a trait also observed in Mexico by Freeman (1969). During the heat of the day, adults seem sedentary and if disturbed, fly 1–4 meters to a new perch. In the early morning, they can be found visiting nectar sources at the edge of forests but do not typically linger once temperatures begin to rise. Although *C. "mexicana"* is fairly widespread within Belize, Mexico, and Costa Rica, it is closely restricted to forested habitats and has not been seen in open agricultural habitats or savanna. Because of its tight association with densely shaded habitats, it seems an unlikely candidate to disperse across water to Cuba. However, dispersal may take place during dawn and dusk, when adults are most active. We mirror the conclusions of Smith & Hernandez (1992) who described a newly discovered subspecies of forest dwelling *Saliana* from Cuba. Like those authors found for *Saliana*, we believe that *Carystoides* "mexicana" is probably an overlooked

resident species and the subtle morphological differences between the lone Cuban specimen and Central American specimens may indicate long-term evolutionary isolation.

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REPORT OF PARTIAL BILATERAL GYNANDROMORPH OF *DISMORPHIA SPIO* WITH NOTES ON ADULT SEXUAL DIMORPHISM AND ILLUSTRATIONS OF IMMATURE STAGES

Additional Key Words: wing homeosis, polymorphism, sexual mosaics, wing pattern development in butterflies, egg, larva, immature stages, Pieridae, Dismorphiinae

Gynandromorphs have historically attracted the attention of developmental biologists. Their morphology and biology can shed light on evolution, genetic control and the role of sexes in the animal kingdom. For instance, Zhao et al. (2010) recently described the autonomy of the somatic sex identity in chickens based on a few available chicken gynandromorphs. Butterflies have contributed to studies of gynandromorphs more than any other group of animals, thanks to their large and frequently sexually dimorphic wings and their popularity with collectors. Sibatani (1980, 1983) brought attention to the significance of these wing pattern aberrations for understanding developmental biology. An unusual population of *Meleageria daphnis* (Denis & Schiffermüller) blue butterfly, which contained 60% of either mosaics or bilateral gynandromorphs, was discovered in 1988 in southern Russia shortly after the Chernobyl disaster (Dantchenko et al. 1995), raising the question of a possible connection between the events. If the background radiation proves to be the cause of this phenomenon, this unusual butterfly population might prove to be a prelude of an increased rate in human birth defects in the Chernobyl region (Wertelecki 2010). Mark Scriber has used the tiger swallowtail group as a model for many years, and recently illustrated how both laboratory-obtained and wild interspecific hybrids are likely to develop into mosaic and perfect bilateral gynandromorphs (e. g., Scriber et al. 2009). He also showed, in examples of wild-collected sexual mosaics of *Papilio glaucus*, how certain wing-pattern-controlling genes (in this case genes controlling melanism) appear to be sex-specific, and hence account for different degrees and patterns of melanism on male and female parts of the wings. All of the above studies illustrate the importance of reporting new gynandromorphs.

Observations: sexual dimorphism. Although sexual dimorphism in *Dismorphia spio* has been noted previously (e.g. Smith et al. 1994), only the presence/absence of the white androconial patch on the hindwing has been mentioned as a sexually dimorphic characteristic. In addition to the genitalic differences, I have identified four characters of *D. spio* that differ between sexes:

1. Presence (male)/absence (female) of white androconial areas on the dorsal hindwings, as previously noted by various authors.
2. Wing-span/antennal-length ratio is greater in females than in males:
   Measurements of 12 males and 12 females of Dismorphia spio from Jarabacoa, Dominican Republic, chosen at random from the McGuire Center for Lepidoptera and Biodiversity (FLMNH) collection, showed non-overlapping ranges of wing-span/antennal-length ratio between the sexes (Males = 3.91 ± 0.17; Females = 4.32 ± 0.18) (T-test; $P<0.0001$).
3. On the forewing of the female, the postdiscal band tapers marginally. Measurements conducted on 6 males and 6 females chosen at random from the McGuire Center for Lepidoptera and Biodiversity (FLMNH) collection, showed non-overlapping ranges of band length/width in its midpoint ratio (Males = 4.1 ± 0.97; Females = 7.43 ± 1.13) (T-test; $P<0.0003$).
4. The anal margin of the forewing is always more rounded in males. Hence, the anal angle is not defined; instead apical margin gradually transitions into anal margin, which forms a concave line. In females, on the contrary, the anal angle is well defined, with anal margin forming a sinusoid-shaped line.

Observations: gynandromorph. In 1996, I collected an unusual specimen of *Dismorphia spio* Godart (Pieridae: Dismorphiinae) near Jarabacoa, Dominican Republic. Several color morphs were present sympatrically in this locality both in males and females (Fig. 1M-1 to M-3; 1F-1 to F-4). When the same sexually dimorphic characters listed above were examined in this asymmetrical specimen (Fig. 1G), which exhibits orange scales on its right forewing, the conclusions were as follows:

1. The specimen in question possesses extensive white androconial areas on both hindwings, which are characteristic of males regardless of the color morph. It might, therefore, at first glance, be perceived as a male with a mosaic pattern of orange scales on the right forewing.

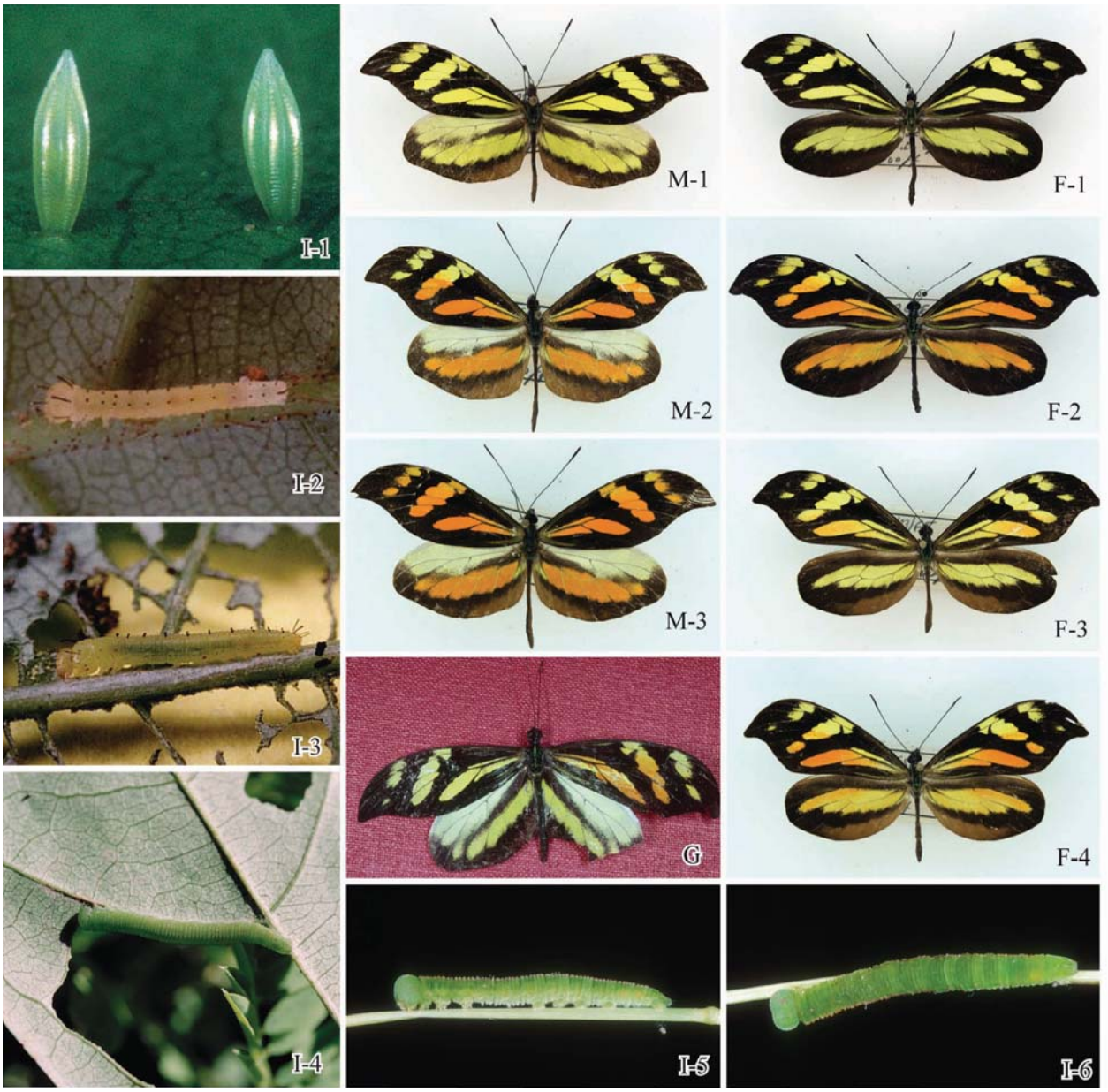

FIG. 1. *Dismorphia spio* (Pieridae) from Cordillera Central, Dominican Republic: (**I**) Immatures on *Inga vera* (Fabaceae): I-1 Eggs; I-2,3 – First instar larva; I-4,5,6 – Last instar larva; (**M**) Males of different color forms; (**F**) Females of different color forms; (**G**) Sexual mosaic gynandromorph - ¾ - male, ¼ female.

2. The right antenna of this specimen is shorter than the left. The relative length of the left antenna in proportion to the wing-span is 4.57, which falls into the range typical for males. The relative length of the right antenna in proportion to the wing-span is 5.7, which falls between the male and female range. The clearly male-like yellow left wing of the specimen is 1% shorter than the mosaic right wing. The shorter right antenna and the longer right wing strongly suggest the presence of female tissue in these two organs.
3. On the right forewing, the postdiscal band tapers marginally, which is typical of females. This band is shorter and maintains uniform width on the left forewing, which is typical of the male specimens. The ratio of band length to its width in its midpoint on the left forewing is 5.1, which falls into the male range, while it is 7.3 on the right forewing, which falls into the female range. This is another indication that the right forewing is of female sex.
4. The shape of the right forewing is more characteristic of the female, with its anal angle better defined than

in the left forewing. The anal margin of the left forewing is concave typically of the males.

Discussion. The color polymorphism in *D. spio* has probably arisen and is maintained as a result of mimicking, in the case of the yellow forms, *Heliconius charithonia* L., and, in the case of the orange form, *Lycorea cleobea* Godart, with both of which *D. spio* occurs sympatrically. Another possible model for the orange form is *Euides melphius* Godart, though it is less likely, since it is relatively rare (Smith et al. 1994). Unlike *P. glaucus*, there is no available evidence linking color to gender in *D. spio*. Therefore, it is possible that the bilateral gynandromorph specimen exhibiting two color forms is simply a result of fertilization of a binucleate egg by two sperms carrying different color genes. The question is: why, if such was the mechanism, the result is not a perfect bilateral gynandromorphy, but rather what can be described as ¾ - male, ¼ female? The sexual mosaics can be formed by the postzygotic loss of one sex chromosome. For instance, if that was the case in one of the blastomeres of a male, following the second division, than a quarter of the resulting adult cells could turn female. In this particular case, if that was the mechanism, the orange coloration was unmasked only after the loss of one sex chromosome, therefore indicating presence of sex-linked color control genes in this species. Further research into molecular and chromosomal mechanisms of color inheritance in *D. spio* would be useful in explaining the observed phenomenon.

Immature stages. Collected on *Inga vera* Wind. (Fabaceae), the eggs (Fig. 1I-1), first instar larva (Fig. 1I-2, 1I-3) and mature larvae (Fig. 1I-4, 1I-5, 1I-6) are photographically illustrated here for the first time. A more detailed description of immature stages including morphological drawings, can be found in Bauza (1991).

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HYBRID ORIGINS: DNA TECHNIQUES CONFIRM THAT *PAPILIO NANDINA* IS A SPECIES HYBRID (PAPILIONIDAE)

Additional key words: engrailed, museum collection, mtDNA, *Papilio dardanus*, Princeps

The idea that a significant number of named species will subsequently be discovered to be species hybrids has long been accepted by botanists, even though establishing particular hybrid origins was rarely straightforward. The application of molecular techniques is rapidly changing this field, and clear-cut demonstrations of hybrid origin are now possible (e.g. Siripun & Schilling 2006). However, in a recent survey of "bad species" among butterflies it was estimated that "around 16% of the 440 European butterfly species are known to hybridize in the wild" (Descimon & Mallet 2009: p219). Although hybridisation can lead to new biological species (Kunte et al. 2011), species hybrids clearly represent a taxonomic problem that needs to be addressed by lepidopterists and, as we endeavour to demonstrate here, molecular methods can and surely will play a particularly valuable role in future investigations of putative hybrid origins.

Papilio nandina was described as a new species by Rothschild and Jordan (1901), based on two male specimens caught in East Africa. Butterflies with the *nandina* phenotype are extremely rare in nature but others have been collected since. Initially, Carcasson (1960) considered *P. nandina* to be an aberration of *Papilio phorcas ruscoei* Krüger, 1928. Then, in the 1970s, Carcasson suggested it was a hybrid between the species *Papilio dardanus* Yeats in Brown, 1776, and *P. phorcas* Cramer, 1775 (see Vane-Wright 1976; Vane-Wright et al. 1999; Clarke 1980), with the absence of females possibly explained by Haldane's rule (but see Vane-Wright & Smith 1992). Clarke & Sheppard (1975) and Clarke (1980) succeeded in crossing *P. dardanus* and *P. phorcas* using the hand pairing method (Clarke & Sheppard 1956) and found that the males produced strongly resembled *P. nandina*. It was therefore proposed that wild-caught individuals of *P. nandina* were hybrids and the existence of such a hybrid was (cautiously) given as evidence supporting the grouping of *P. dardanus* and *P. phorcas* as sister taxa.

The present study examines *Papilio nandina* from a molecular perspective. Using the butterfly collections of the Natural History Museum London, we have now extracted DNA from specimens of *P. dardanus* (Voucher BMNH746801-746802, BMNH746805-746806), *P. phorcas* (including a pinned specimen from the 'Majerus Collection'; BMNH808404, BMNH740210-740213), a wild-caught *P. nandina* (collected in 1984 in City Park, Nairobi; Gill, 1986; Figure 4 and accompanying information in Vane-Wright & Smith 1992; BMNH808400), and a 'laboratory' cross of *P. dardanus* and *P. phorcas* (pinned, from the 'Clarke/ Sheppard/ Gill Collection'; Clarke 1991; BMNH808401).

DNA was extracted from single legs according to the protocols of Thomsen et al. (2009). Amplifiable DNA was extracted from all specimens, demonstrating that usable DNA can be obtained from pinned butterfly specimens collected over 25 years ago. Individuals were sequenced for the mitochondrial gene COI (primers HCO2198 and LCO1490; Folmer et al. 1994) and the nuclear gene engrailed (primers: Pd202: 5'-agccagtacacygcaccac-3' and Pd204: 5'-tcyccgatctgmracaccgtctg-3'; 387 base pair amplicon). Sequences were submitted to GenBank (HQ636437-HQ636452).

If the wild-caught *P. nandina* is a hybrid as proposed, then we would expect the nuclear genome to be inherited 50:50 from both *P. dardanus* and *P. phorcas*, and in this respect to be indistinguishable from that of the 'laboratory' hybrid. This is exactly what is found: sequence traces reveal that the *P. nandina* individual carried a distinct *P. dardanus* and a distinct *P. phorcas* allele. Out of 46 polymorphisms revealed in the engrailed sequence, 24 are fixed in both *P. dardanus* and *P. phorcas* with the *P. nandina* individuals displaying the corresponding ambiguity, 6 show shared polymorphisms between *P. nandina* and one of the other species and 16 are uninformative (polymorphic in only one of *P. dardanus* or *P. phorcas*).

The COI fragment from the wild-caught *P. nandina* exactly matches sequences obtained in this study from *P. phorcas* and differs only at a single position from the *P. phorcas* sequence available on GenBank (AF044001; Caterino & Sperling 1999). Mitochondrial DNA is only inherited from the female parent, therefore the wild *P. nandina* specimen is a hybrid between a male of *P. dardanus* and a female *P. phorcas*.

Our results confirm that *P. nandina*, as first suggested by Carcasson, and subsequently demonstrated by Clarke & Sheppard (1975) and Clarke (1980) by breeding experiments, and by Vane-Wright & Smith (1991) on morphological grounds, is not a 'good' species, but represents a species hybrid (Vane-Wright & Smith 1992).

Given that the male parent of the one wild-caught *nandina* that we have been able to analyze must have

been *P. dardanus*, it is interesting to note that the males of this species are demonstrably promiscuous with respect to female color patterns, consistent with the amusing comment of W. C. Hewitson following the recognition of female-limited polymorphism in *P. dardanus* (then *P. merope*) by Roland Trimen: "it would require a stretch of the imagination, of which I am incapable, to believe that the *P. Merope* [sic] of the mainland, having no specific difference, indulges in a whole harem of females, differing as widely from it as any other species in the genus." (quoted by Trimen 1874: p140; see Cook et al. 1994 for field observations on mate choice by male *P. dardanus*). Whether or not all wild *nandina* hybrids are sired by *P. dardanus* is a matter for speculation at this point, but it should be remembered that many populations of *P. phorcas* also exhibit female-limited polymorphism—although this is not so spectacular as that seen in *P. dardanus* (Vane-Wright & Boppré 1993).

This molecular investigation demonstrates the value of pinned collections as a source of both morphological and molecular data, and the importance of molecular studies for taxonomy. A similar methodological approach has already been used to investigate another demonstrably hybrid "species", *Erebia serotina* Descimon & de Lesse, 1953, as reported by Descimon & Mallet (2009). The value of the technique presented here lies in the fact that it is not dependent on fresh material; we propose the use of both mitochondrial and nuclear markers on museum material as a valuable tool to assess putative hybrids.

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ZYGAENID MOTHS OF AUSTRALIA. A revision of the Australian Zygaenidae (Procridinae: Artonini). Monographs on Australian Lepidoptera. Volume 9. i-vii, 248pp. 2005. Gerhard M. Tarmann . CSIRO Publishing, ISBN:9780643067981 - AU $199.00

The "Zygaenid Moths of Australia. A revision of the Australian Zygaenidae (Procridinae: Artonini)" by Gerhard M. Tarmann is the 9th volume in the *Monographs on Australian Lepidoptera*, a series that has seen several benchmark publications since it was introduced in 1989.

The publication follows a classic format, opening with an abstract, a general introduction to the family and a more specific introduction to the little known Australian fauna, which is considered by the author to comprise only members of the tribe Artonini. This is not surprising considering he limited Australian Zygaenidae to this tribe in the "Checklist of Australian Lepidoptera" (Nielsen et al. 1996). However, since Common (1991) in "Moths of Australia" also included the *Lactura* group in Zygaenidae, this group should at least have been mentioned (it is treated as a separate family in the Checklist and later in the Handbook of Zoology (Kristensen 1998)), more so since "Moths of Australia" is still likely to be the first serious introduction to Australian moths for most students and amateurs. The standard "Materials and Methods" and "Acknowledgements" chapters are followed by a very detailed chapter on zygaenid morphology. This chapter gives an excellent account of the morphology of all zygaenid life stages, useful not only to students of the Australian fauna (for which relevant characters are discussed in particular detail), or even Zygaenidae in general, but for anyone interested in the morphology of lower ditrysian Lepidoptera. The chapter is excellently illustrated and the numerous scanning electron micrographs particularly are highly informative. My only slight criticism here would be that highlights tend to be burned out in some micrographs and could have benefited from contrast adjustment. The genitalia of both sexes are described in great detail, but this section would have been enhanced by generalized illustrations of zygaenid genitalia. The sections on juvenile stages provide another well-illustrated overview of the family.

The next chapter covers various aspects of zygaenid biology and life history, such as larval-host plant relations, pest species, parasitoids, and the family's intriguing defence biology, again with sufficiently broad focus to be of interest to lepidopterists in general. The sections on "Zygaenids as indicator species" and "Conservation" are clearly of more general importance since zygaenids are often very environment-specific and changes in distributions and phenology can thus be excellent indicators of environmental changes, even as they happen. The short chapter on phylogeny (based on a morphological/ecological dataset of 13 species and 31 characters) is unfortunately focused only on the Australian genera, with two other Asian Artonini genera and one genus from Procridini included as outgroups. This is particularly unfortunate as the two Asian genera are shown to be deeply embedded within the Australian genera, so the author wisely does not draw any strong evolutionary conclusions based on these results. In the following chapter on the history and origin of the Australian Zygaenidae, the non-monophyly of the Australian genera is followed by the inescapable conclusion that several Artonini faunal exchanges between the Australian and Asia must have taken place.

The bulk of the work is, as might be expected, dedicated to the taxonomy of Australian species, with keys to genera and species. All known genera and species are redescribed, and a total of four genera, 21 species, and two subspecies described as new. The author also illustrates, but does not formally describe, "taxa recognised as possible distinct species" for which he felt insufficient material precluded formal description. It is debatable whether new species should be described based on single (or very few) specimens, and while there can be good arguments for doing so (e.g. when species are of particular systematic, biological or conservation importance, where a formal name is required for the species to "exist" for scientific or management purposes), the approach followed here is probably commendable in the given situation and may inspire future workers to collect and study these as yet unnamed species. If the need arises (e.g. for conservation purposes), the species can then be quickly named based on the information made available by Tarmann in this work. This chapter is elaborately illustrated with stunning colour paintings (by Dr. F. Gregor) of each species in 6.5–10x life size, and also by photographs of habitats, specimens, eggs and larvae, and genitalia. With respect to the latter, one could argue that ink drawings highlighting important characters would be more user-friendly. But the photographs are consistent and allow for quick comparisons between species. It is perhaps also debatable whether 6–10x paintings of whole animals are more useful for Lepidoptera identification than much lesser

magnifications or life-size illustrations (paintings or photos). However, there is little discussion of the great utility of the large scale paintings here; as pointed out by the author in the abstract, characters that distinguish one zygaenid species from another are often minute differences in wing or body colours that are easily missed (or very hard to illustrate) in smaller illustrations. Plates 36–40 (part of the genus *Hestiochora*) and 51–55 (*Homophylotis* and *Pseudoamuria*) are excellent examples of this. Australian zygaenids are not a group that can be confidently identified through binoculars.

There is little doubt that Gerhard Tarmann has written a valuable contribution to the knowledge of Australian Lepidoptera. But what makes the publication stand out as more than "just" a comprehensive, detailed and beautiful illustrated regional revision of a hitherto poorly known group of insects is the wealth of information on Zygaenidae as a whole and the geographical and biological contexts in which it is presented. The book should be a must for anyone with an interest in the systematics, morphology and evolution of not only Zygaenidae, but lower Lepidoptera in general.

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A GUIDE TO THE LEPIDOPTERA OF JAPAN by F. Komai, Y. Yoshiyasu, Y. Nasu, and T. Saito (editors); xx + 1308 pages, including 248 color plates, 25.5 x 18 cm. Text in Japanese with English figure captions. Tokai University Press, Hadano, Kanagawa, Japan. Publication date: February 2011. ISBN 978-4-486-01856-8. Price: 40,000 Yen (ca. $473.00 US) including postage (payment: Visa or Master Card, contact E. Ina: inaair@tsc.u-tokai.ac.jp).

A picture is worth a thousand words. I trust that this old adage is true because I'm reviewing this book without ever reading a word of it...I've only looked at the pictures! I am assuming that the hundreds of pictures in it are equivalent to hundreds of thousands of words because the text is almost entirely in Japanese, which I cannot read.

With over 1300 pages, this Guide is truly an encyclopedic treatment of the Lepidoptera of Japan, from the most primitive to the most advanced, from morphological structures to the chemical structures of pheromones, from food plants to photographs, and from Adelidae to Zygaenidae, including butterflies and moths and everything in between. The text of this handsome volume is divided into three main sections: Morphology and Biology (56 pages), Phylogeny and Higher Classification (441 pages), and Diversity of Japanese Lepidoptera (445 pages). These sections are followed by 248 beautiful color plates, an impressive list of References, and indices in both English and Japanese.

The first section, Morphology and Biology, is further divided into three chapters: 1. Morphology, 2. Foods and Feeding Habits of the Lepidoptera, and 3. Various Chemical Structures of Lepidopteran Sex Pheromones, each of which is authored or co-authored by well known authorities on these subjects. For example, the chapter on pheromones was written by T. Ando, which based on my very narrow tortricid bibliography (Brown et al. 2010), is the author of countless important laboratory and field studies on pheromones and sex attractants. The text of each chapter is augmented by numerous line drawings. In the morphology chapter, English names of morphological structures are sprinkled throughout the text and labeled on the accompanying figures. There are plates of heads, antennae, thoracic sclerites, legs, wings (including venation and wing coupling mechanisms), female reproductive configurations, male and female genitalia, chaetotaxy of larvae, and structures of the pupae.

The second section, Phylogeny and Higher Classification, starts with a brief historical review of Lepidoptera classification from Linnaeus (1758) through Kristensen et al. (2007); the latter is nearly identical to that presented in the Handbook of Zoology (Kristensen 1998) and is used as the outline/sequence in which superfamilies are presented in the Guide. The most recently proposed classification of the order, currently in press (van Nieukerken et al. 2011), could not be followed because this Guide was already in press by the time the new scheme was proposed. As in the first section, the text is contributed by the leading Japanese experts on each taxon, with each superfamily comprising a standalone treatment accompanied by one or more black-and-white photographs of exemplars and numerous line drawings. The contribution on Gelechioidea, co-authored by T. Saito and T. Ueda, includes two full plates of black-and-white images of spread specimens of gelechioids—44 images total. There is a plate of line drawings of labial palpi, three plates of wing venation, and various drawings of abdominal modifications (e.g., the spines characteristic of Blastobasidae and Coleophoridae), genitalia, and chaetotaxy. There also is a very nice plate illustrating the diversity of submental "pits" of the larval head—and I thought they were found only in blastos and scythridids! Consistent with the instability of gelechioid classification, this contribution includes a table showing the various classifications of the superfamily proposed from 1990 through 1998.

The contribution on Tortricoidea, by F. Komai and Y. Nasu, is among the best (I suspect), given the prominence of these two authors on this taxon. The classification is very up-to-date, with *Arotrophora* treated as a tribe independent from Archipini and Cnephasiini (based on unpublished molecular studies by Sperling, Horak & Zwick). As with other contributions, there are two plates of adults along with line drawings of wing venation, larvae, and pupae. Also illustrated by photographs are interesting features of the antennae, male forewing costal folds, abdominal scent structures, genitalia, and the anal combs of various larvae.

Not surprisingly, the contribution on Noctuoidea requires the greatest number of pages and includes an impressive four-page fold-out summarizing classifications of the superfamily from Hampson (1898–1913) to the contemporary and competing classifications proposed by Lafontaine and Schmidt

(2010), Kononenko (2010), and Zahiri et al. (2010). Each subfamily receives its own brief account.

The third and final section, Diversity of Japanese Lepidoptera, is further divided into four chapters: 1. Lepidopteran Fauna of Japan, 2. Lepidopterous Pests in Japan, 3. Key to the Families and to Some Subfamilies of Japanese Lepidoptera, and 4. Biology of Japanese Lepidoptera. The last represents the lion's share of this section and is comprised primarily of accounts of high profile species of each superfamily/family arranged in a sequence that parallels that of the second section. I actually have no clue what percentage of the fauna is treated, but in Tortricoidea, 122 species accounts (i.e., species numbered 239 through 361, which refer to the plates in the back of the book) are included, which may represent 15–20% of the tortricids known from Japan.

Following the text are 248 pages of color illustrations, with 4 species per page (no translation required!); these are illustrations of the species treated in the accounts of the previous section and are numbered sequentially, consistent with the previous section for easy reference. For many species there is an image of a pinned spread adult, a larva, a pupa, and an adult in typical resting posture, but these vary from family to family and from species to species. For example, for many pyraloids an image of damage to the host plant is substituted for the live adult. For some sexually dimorphic species, both sexes are shown. And for many geometrids, multiple images of larvae are provided instead of the pupa and live adult. The images illustrate a broad range of highly interesting biological features, from mating pairs to gregarious larval feeding, and from egg clusters to everted coremata. All of the images are of high quality.

This "Guide" is an impressive tome; it is a good thing it isn't sold by the pound! Nonetheless, it isn't cheap—no good books are. The four editors have done an exceptional job of enlisting the expertise of 26 authorities on the Japanese Lepidoptera and have brought together the contributions of those experts in a well organized, very attractive, contemporary, and apparently very thorough treatment. Although the text is nearly all in Japanese, the Latin binomials of host plants and animals, the use of English for morphological structures and in figures, and the English index all combine to make this work accessible even to those of us with no ability to decipher Japanese. Anyone who collects books on Lepidoptera will want to add this superlative book to their collection.

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CONTENTS