Volume 63 Number 3
October 22, 2009
ISSN 0024-0966

Journal of the Lepidopterists' Society

Published quarterly by The Lepidopterists' Society

THE LEPIDOPTERISTS' SOCIETY

The object of The Lepidopterists' Society, which was formed in May 1947 and formally constituted in December 1950, is "to promote the science of lepidopterology in all its branches, . . . to issue a periodical and other publications on Lepidoptera, to facilitate the exchange of specimens and ideas by both the professional worker and the amateur in the field; to secure cooperation in all measures" directed towards these aims.

Membership in the Society is open to all persons interested in the study of Lepidoptera. All members receive the *Journal* and the *News of The Lepidopterists' Society*. Prospective members should send to the Assistant Treasurer full dues for the current year, together with their full name, address, and special lepidopterological interests. In alternate years a list of members of the Society is issued, with addresses and special interests.

Active members—annual dues $45.00 within the U.S., $50.00 outside the U.S.
Affiliated members—annual dues $10.00 within the U.S., $15.00 outside the U.S.
Student members—annual dues $20.00 within the U.S., $25.00 outside the U.S.
Sustaining members—annual dues $60.00 within the U.S., $65.00 outside the U.S.
Life members—single sum $1,800.00
Institutional subscriptions—annual $60.00, $65.00 outside the U.S.
Airmail postage for the *News* $15.00, $30.00 outside North America (U.S., Canada, Mexico)

Send remittances, payable to *The Lepidopterists' Society*, to: Kelly M. Richers, Treasurer, 9417 Carvalho Court, Bakersfield, CA 93311; and address changes to: Julian P. Donahue, Natural History Museum, 900 Exposition Blvd., Los Angeles, CA 90007-4057. For information about the Society, contact: Ernest H. Williams, Department of Biology, Hamilton College, Clinton, NY 13323. To order back issues of the *Memoirs*, write for availability and prices to Kenneth R. Bliss, 28 DuPont Avenue, Piscataway, NJ 08854.

The additional cost for members outside the U.S. is to cover mailing costs.

Journal of The Lepidopterists' Society (ISSN 0024-0966) is published quarterly by The Lepidopterists' Society, % Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, CA 90007-4057. Periodicals postage paid at Los Angeles, CA and at additional mailing offices. POSTMASTER: Send address changes to The Lepidopterists' Society, % Natural History Museum, 900 Exposition Blvd., Los Angeles, CA 90007-4057.

Cover Illustration: Face to face with a sixth instar larva of *Hesperia colorado idaho*. This instar aestivates for 6 weeks in early summer prior to pupation and eclosion during July–August in the Pacific Northwest. Photo by David James. See journal article on page 129.

JOURNAL OF
THE LEPIDOPTERISTS' SOCIETY

Volume 63 2009 Number 3

Journal of the Lepidopterists' Society
63(3), 2009, 129–136

COMPARATIVE STUDIES ON THE IMMATURE STAGES AND BIOLOGY OF *HESPERIA COLORADO IDAHO* AND *HESPERIA JUBA* (HESPERIIDAE)

DAVID G. JAMES

Department of Entomology, Washington State University, Irrigated Agriculture Research and Extension Center, 24105 North Bunn Road, Prosser, Washington 99350; email: david_james@wsu.edu

ABSTRACT. Comparative illustrations and notes on morphology and biology are provided on the immature stages of *Hesperia juba* and *Hesperia colorado idaho* (Hesperiidae) in the Pacific Northwest. Overwintering is demonstrated to occur as either eggs or first/second instar larvae in *H. juba*, and the presence of final instar dormancy/aestivation in summer larvae of both species is reported for the first time in *Hesperia*. High quality images of all stages including larval instars are provided and differences between the species highlighted. As larvae matured, *H. juba* was generally darker colored than *H. colorado idaho* and retained a black head capsule throughout development. The head capsule of mature *H. colorado idaho* larvae was characterized by broad pale areas. *Hesperia juba* overwintered as first or second instars when eggs were laid in September or as fully formed embryonic larvae in unhatched eggs laid in October. Post-winter larval development was rapid, developing from second instar to adult in 7 weeks at 15–22°C. Development of the spring larval generation was rapid until early-mid July when fifth instars entered a non-feeding aestival dormancy, delaying pupation until late August. *Hesperia c. idaho* mostly overwintered as eggs containing fully formed embryonic larvae; however, a small number of eggs from one cohort hatched during August–September into dormant, yellow-orange, non-feeding first instars that overwintered. The majority (~95%) of overwintered eggs exposed to 25 ± 0.5° C and continuous illumination did not hatch but remained viable. Eggs that did hatch produced larvae that developed rapidly at 25 ± 0.5° C reaching fifth instar after 36–39 days. Fifth (or sixth) instar larvae entered a non-feeding dormancy extending this instar to 27–46 days. Final instar larvae of both species produced a flocculent secretion from two pairs of ventral glands between segments 7 and 9, which was incorporated into the pupal shelter and is presumed to function as a moisture repellent.

Additional key words: overwintering, aestivation, development, instar, duration, flocculent

Hesperia juba (Scudder) and *Hesperia colorado idaho* (Judder) (Hesperiidae) occupy similar ranges in the Pacific Northwest and are often found flying in the same habitats (Pyle 2002, Warren 2005). Similarly marked and sized, the two species can be confused, particularly when individuals have aged. Whilst the taxonomy of *H. juba* is straightforward with no described geographic variation across its large North American range, this is not the case with *H. colorado idaho* (Warren 2005). *Hesperia c. idaho* is part of the *Hesperia comma* (L.) complex, with many described species and subspecies occurring across boreal North America and Eurasia (Forister *et al.* 2004). In areas east of the Cascade Mountains in Washington State and Oregon, *H. c. idaho* is the widespread phenotype (Pyle 2002, Warren 2005). The immature stages and biology of both species are not well known, and since the landmark publication on *Hesperia* spp. by MacNeill (1964) have only received sporadic attention. No detailed images of immature stages have been published except for a color photograph of a late instar larva of *H. juba* in Allen *et al.* (2005). A late instar larva of *H. comma* is also illustrated in the same publication. The overwintering biology of *H. juba* has been a subject of conjecture since Shapiro (1980) suggested that it overwinters as an adult in high montane areas of California. Circumstantial evidence for adult overwintering was provided by Berkhousen & Shapiro (1994), who found pollen grains of autumn-flowering rabbitbrush (*Chrysothamnus*) on spring-collected butterflies. Scott (1992) and Warren (2005) did not accept this idea and suggested eggs or larvae as the overwintering stage, but again only presented circumstantial evidence. Other biological and ecological studies on the two species are few (Warren 2005).

The current study was conducted as part of a larger study describing the immature stages and biology of Pacific Northwest butterflies (James & Nunnallee in prep.). During 2005–2006, *H. juba* and *H. c. idaho* were reared in the laboratory, and all immature stages (including each larval instar) were photographed. Notes on coloration, patterning and sizes of larval instars and pupae were also made. Information was also obtained on aspects of biology such as overwintering, diapause and developmental duration.

MATERIALS AND METHODS

Gravid females of *H. juba* were obtained in late May 2005 (1 female), mid-October 2005 (2) and mid-September 2006 (8) from near the Tucannon River, 25km southeast of Dayton, WA, Snake River Junction, 15 km northeast of Pasco, WA and Waterworks Canyon, 35km northwest of Yakima, WA, respectively. Gravid females of *H. c. idaho* were obtained in late June 2005 (2) and late August 2005 (1) from Bear Canyon, 48km west of Yakima, WA and along the Grande Ronde River road, approximately 20km east of Troy, OR, respectively. Females were placed in plastic boxes (30 × 23 × 8cm) with muslin-covered lids and held under natural lighting/daylengths and temperatures between 20 and 30 °C. Butterflies were provided with potted or cut grass (*Setaria glauca* L.) and paper toweling as oviposition substrates. Tissue pads soaked in sugar/water solution were provided for nourishment. Butterflies oviposited freely under these conditions. Eggs were measured, photographed and transferred to plastic Petri dishes (13cm diameter). First-third instar larvae were reared in the same-sized Petri dishes, provided with cut grass and examined daily or on alternate days except when overwintering. Later instars and pupae were reared in plastic boxes with muslin lids (30 × 23 × 8cm). The spring–summer generation (May–August) of *H. juba* was reared under temperatures of 20–30°C and natural daylengths.

Overwintering. Eggs of *H. c. idaho* were held from oviposition in July or August until October 1 at temperatures between 20–30 °C under naturally declining daylengths. From October 1, they were stored in outdoor ambient conditions until transferred during January–February to 25 ± 0.5 °C and constant fluorescent illumination. Eggs of *H. juba* laid in October 2005 were overwintered in outdoor ambient conditions of temperature and photoperiod. Larvae that hatched in February–March were reared at 15–22 °C and 13h daylength. Eggs and larvae of *H. juba* obtained from oviposition in September 2006 were held in outdoor ambient conditions until November 23 when they were transferred to conditions of 15–22 °C and 13h daylength.

All larval instars and pupae were measured and photographed. Observations on larval morphology, coloration, behavior, development, predation and mortality were made throughout rearing. Photographs were taken using a Canon EOS 1DS Mark II, digital SLR camera mounted on a tripod. A Canon MP-E 65mm 1X – 5X macro lens was used together with a Macro Twin Lite MT – 24 EX flash lighting system.

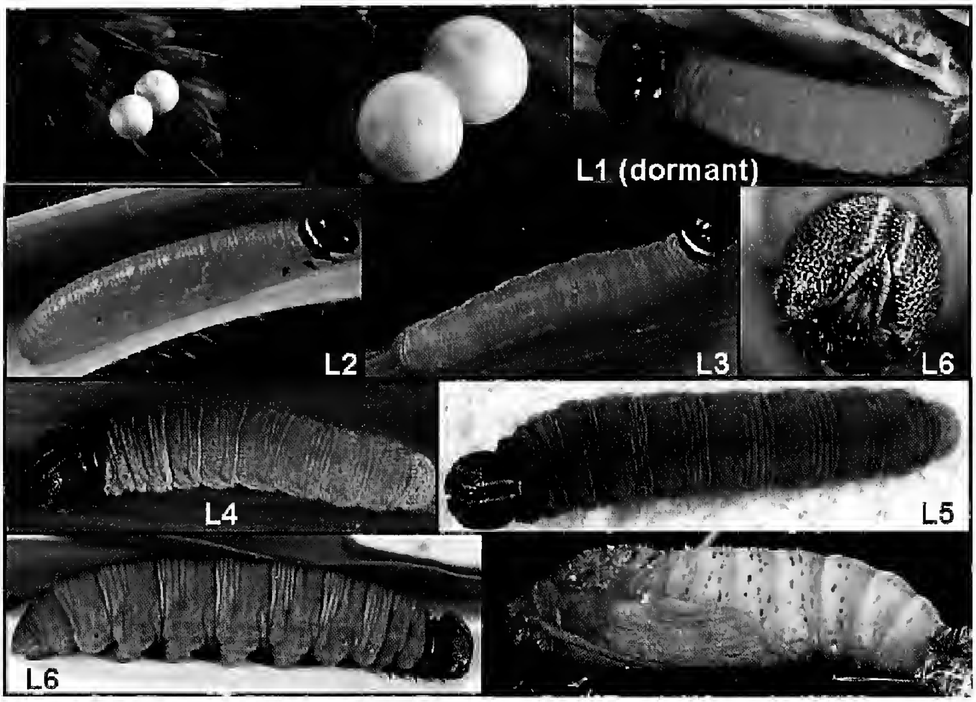
RESULTS

Morphology of immature stages. Eggs, larval instars and pupae of *H. juba* and *H. c. idaho* are shown in Fig. 1 and their dimensions presented in Table 1. The descriptions presented here are brief, focusing on differences between the species. A detailed description of the immature stages of *H. juba* is provided by McNeill (1964).

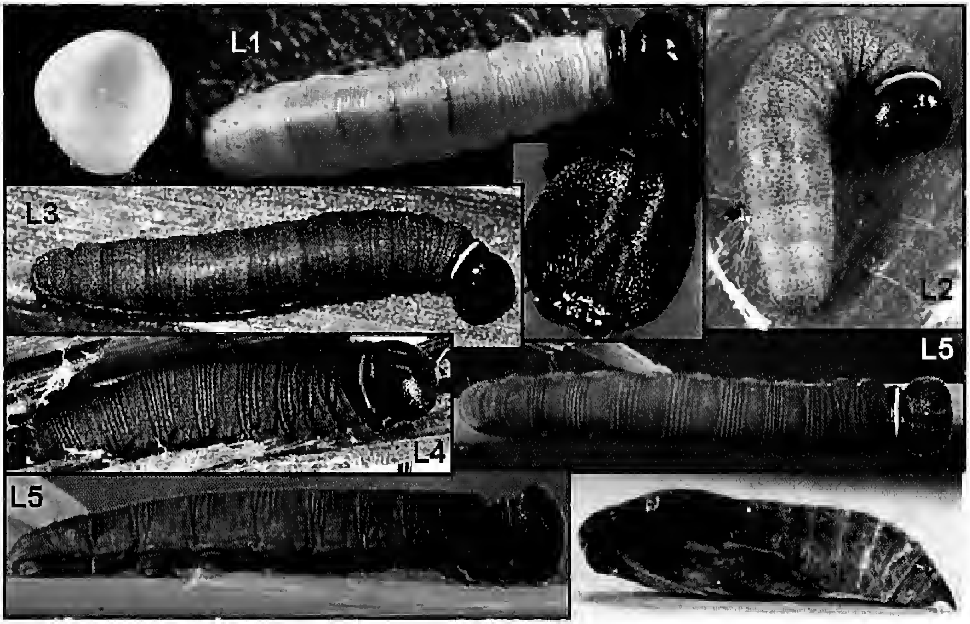
Eggs of both species were creamy white with a pinkish tint developing after 5–7 days. Prior to emergence, the micropyle darkened and, if eggs were examined from underneath, the embryonic larva was visible. The surface of *H. c. idaho* eggs was more prominently reticulated than *H. juba* eggs. Larvae emerged after biting away the micropylar area, sometimes taking 2–3 days from appearance of the larval head until exit. First instar *H. c. idaho* were pale yellow/green (non-dormant) or yellow-orange in non-feeding, overwintering individuals (Fig. 1). Dormant and non-dormant first instar *H. juba* were creamy-white with a greenish tinge developing after feeding. Head capsules of both species were black. Second instar *H. juba* were creamy white with a fine peppering of dark spots. Second instar *H. c. idaho* were yellowish with a peppering of dark spots. Head capsules of both species were black and the cervical shield was conspicuously white-margined anteriorly, a characteristic that persisted during the remainder of larval development. Third instar *H. juba* were dark brown and *H. c. idaho* yellowish-green. Fourth instar *H. juba* were dark brown with an indistinct dorsal black stripe and distinct peppering of minute black spots. Fourth instar *H. c.*

TABLE 1. Sizes (mm) of immature stages of *Hesperia juba* and *Hesperia colorado idaho*. Egg dimensions are height × width. Larval dimensions are lengths measured at commencement and end of each instar. Egg and larval data obtained from examination of 2–4 individuals. Variation was generally less than 0.1mm. Pupae measured from cremaster to tip of head (Mean ± SE). Number of pupae examined in parentheses.

	H. juba	*H. c. idaho*
Egg	1.0 x 1.3	0.9 x 1.3
First instar	2.5 - 5.0	2.5 – 5.0
Second instar	5.0 – 10.0	5.0 – 8.0
Third instar	10.0 – 16.0	8.0 – 11.0
Fourth instar	16.0 – 21.0	11.0 – 17.0
Fifth instar	21.0 – 30.0	17.0 – 25.0
Sixth instar	-	25.0 – 30.0
Pupa	20.5 ± 0.5 (4)	21.5 ± 0.5 (5)



Hesperia colorado idaho



Hesperia juba

FIG. 1. Life stages of *Hesperia juba* and *Hesperia colorado idaho*

idaho were pale tan with no dorsal black stripe. Minute black spots were less distinct than in *H. juba*. Head capsules had distinct pale, vertical parallel stripes with a pale inverted 'V' at their base, more pronounced in *H. c. idaho*. Head capsules were black in *H. juba*, dark brown in *H. c. idaho*. Fifth instar *H. juba* were dark orangish-brown with six transverse ridges on the posterior half of each abdominal segment. Fifth instar *H. c. idaho* were olive-brown to gray with five transverse ridges on each segment. The indistinct dorsal black stripe of fourth instar *H. juba* was virtually absent in the fifth instar, but present in fifth (and sixth) instar *H. c. idaho* (Fig. 1). The vertical parallel head capsule stripes and lower inverted 'V' were more pronounced in the fifth instar of both species. Additional broad pale areas in the occipital regions occurred in *H. c. idaho* while head capsule ground color remained uniformly black in *H. juba* (Fig. 1). Light brown-orange pigmentation replaced the olive cast in sixth instar *H. c. idaho* and the head capsule was light brown due to expansion of the pale occipital area markings (Fig. 1). Final instars of both species developed two pairs of patches of a white flocculent secretion on the ventral surface between abdominal segments 7 and 8, and 8 and 9 (Fig. 2). The pupae of *H. juba* were dark brown-black, particularly the head and thorax with intersegmental light brown-orange banding on the abdomen. The pupae of *H. c. idaho* were lighter, greenish-yellow to tan with few darker markings. The dorsal surface of the thorax was characterized by two wavy, transverse black lines, one of which approximated a 'W' shape. Brown-black dashes were present on the abdominal segments (Fig. 1). Mature larvae of *H. juba* measured 30mm in length prior to pupation. Larvae of *H. c. idaho* that completed six instars also measured 30mm, while those that pupated after the fifth instar measured 25mm. Pupae of both species measured 20–22mm (Table 1).

Biology of immature stages. Oviposition by females of both species generally occurred within 24–48h of caging. Durations of immature stages of both species are shown in Table 2. Both species were reared on *Setaria glauca* (L.) and *Elytrigia repens* (L.) (Poaceae). Both species suffered from predation in culture by the minute pirate bug, *Orius tristicolor* (White) (Hemiptera: Anthocoridae). Both nymphs and adults of *O. tristicolor* preyed on early instar (1–3) larvae. Grass blades silked together to form shelters did not appear to provide good protection against these small (0.5–2.0mm) predators. Appearance of these predators in the larval cultures was thought to have occurred by inadvertent collection of anthocorid eggs oviposited within stems of field-collected grass.

H. juba. Eggs laid in May 2005 and September 2006 took 10–11 days to hatch at temperatures between 20–30°C. In contrast, virtually all eggs laid in mid October 2005 entered dormancy and did not hatch until the following February or March (Table 2). One egg in this cohort (N = 25) hatched in 14 days and overwintered as a first instar larva (see below). Overwintering eggs contained fully developed embryonic first instar larvae, indicated by conspicuous darkening of the micropyle and verified by dissection. Hatching of overwintered *H. juba* eggs was staggered, occurring over a six week period. Development of early instar larvae in the spring (May 2005) cohort was initially rapid with fifth instar reached within four weeks (Table 2). All instars silked grass blades together to form shelters, with construction more complex in each successive instar. Ecdysis invariably occurred within these shelters. First instars simply wove a few silken strands into a vague 'nest', while pre-pupal final instars constructed tightly webbed shelter tubes. Nest-building characteristics may differ under natural conditions (MacNeill 1964). Fifth instar larvae entered an apparent

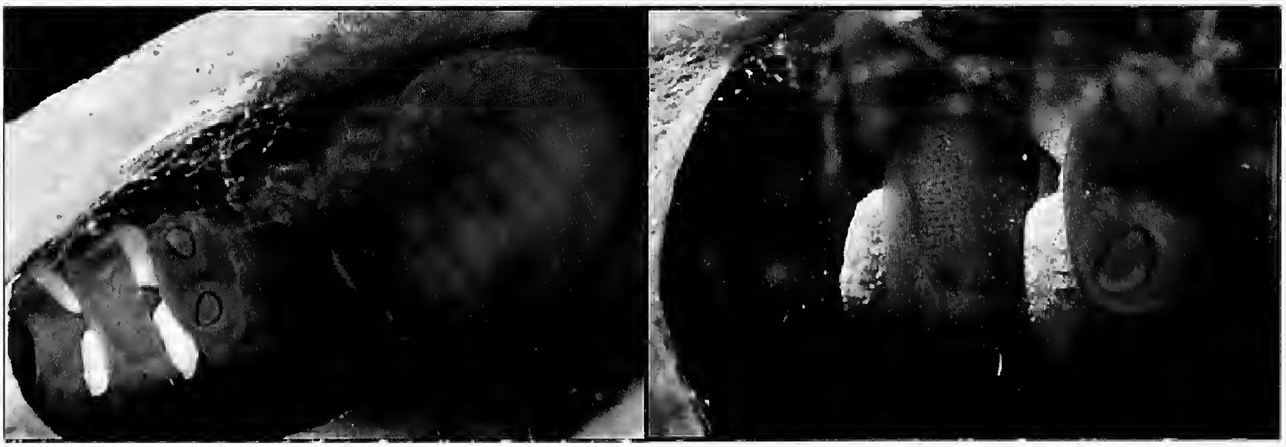


FIG 2. Ventral glands and white flocculent secretion in *H. colorado idaho*

Table 2. Developmental durations (days) for eggs, larvae and pupae of three cohorts of *Hesperia juba* and two cohorts of *Hesperia colorado idaho*. Instar duration data obtained from first appearance of each instar among species cohorts. Rearing conditions: *H. juba* (May): 20–30 °C and natural daylength. (September): outdoor ambient (for eggs-second instar until Nov 23. L2-adult, 15–22 °C/13h daylength. (October): Outdoor ambient for eggs. L1-adult, 15–22 °C/13h daylength. *H. c. idaho*: eggs - July–Sept 20–30 °C/natural daylength, Oct–Feb outdoor ambient. L1-adult - 25 ± 0.5 °C/24h light.

	H. juba **May cohort**	***H. juba*** **September cohort**	***H. juba*** **October cohort**	***H. c. idaho*** **Bear Cyn cohort**	***H. c. idaho*** **Troy, OR cohort**
Egg	10	10	150-170[a]	45-225[a]	200-210[a]
First instar	7	7	7	14-160[a]	10
Second instar	10	74°[a]	10	7	8
Third instar	10	10	10	9	9
Fourth instar	10	11	10	9	9
Fifth instar	31[a]	12	12	12	27[a]
Sixth instar	—	—	—	46[a]	—
Pupa	15	16	15	18	13
Egg- Adult	93	140°	214-234	320-330	276-286

°Second instars prematurely exposed to warm temperatures/long daylengths in late November. Under natural conditions dormancy continues for another 60–80 days.

[a] Dormant stages (hibernal diapause or aestivation)

dormancy in early-mid July, becoming very dark colored, sheltering within grass shelters and not feeding. Dormancy lasted approximately a month with pupae formed from August 10–15. Pupation occurred within a silken cocoon liberally decorated with the flocculent material produced by the ventral abdominal glands. Adult eclosion occurred from August 25–31. The single autumn-hatched larva in 2005 (October 28) fed briefly becoming light green, but was dormant and non-feeding after one week. The larva died in February. The autumn-hatched larvae in 2006 (September 26–28) developed rapidly at first becoming second instars by October 2. Thereafter, feeding decreased and development slowed. By the end of October, most larvae were dormant, non-feeding, mature second instars, resting in silked larval shelters or exposed on grass blades. Inspection of the cohort on November 23 showed substantial mortality with only 2 of ~100 larvae still alive. Temperatures in early November fell to -10°C for a brief period. The two surviving larvae began feeding immediately after exposure to temperatures of 15–22°C developing to pupation (with no final instar dormancy) after 37 days and adults after 51 days.

H. c. idaho. The majority of eggs laid in either July or August 2005 remained dormant until January–March held under ambient outdoor conditions. However, a small number of the Bear Canyon cohort of eggs hatched after 45–65 days during late August and September, into dormant, yellow-orange non-feeding first instars (Fig. 1). None of the Grande Ronde egg cohort hatched before overwintering. Dormant larvae produced slight webbing to cover themselves. Dormant larvae provided with fresh host grass during October refused to feed but rasped the grass surface to obtain water droplets which they imbibed. Overwintering eggs contained fully developed embryonic larvae as indicated by dark micropyles and verified by dissection. A few larvae from both egg cohorts hatched under outdoor ambient conditions during January and February. Most (~95%) eggs transferred to warm, summer-like conditions (25 ± 1°C and continuous illumination) during January–February did not hatch but remained viable. Dissection of unhatched eggs after more than a month in warm temperatures revealed live but apparently dormant larvae. Eighteen larvae were reared, eight of which overwintered as eggs and ten as dormant first instars. Development of larvae from both cohorts occurred rapidly at 25 ± 0.5°C, reaching fifth instar after 36–39 days (Table 2). Larvae in the Grande Ronde River cohort remained as fifth instars for 27 days before pupating. Larvae in the Bear Canyon cohort spent only 12 days as fifth instars but entered a sixth instar. This instar persisted for 46 days before pupation. Thus, both species appeared to exhibit dormancy in the final instar. *H. c. idaho* larvae were similar to *H. juba* in silken shelter construction. On one occasion, a *H. c. idaho* larva removed paper toweling used as water jar plug and constructed a shelter from it. Pre-pupal 'wandering' was observed in some *H. c. idaho* larvae.

DISCUSSION

This is the first published study that comprehensively and pictorially compares all the immature stages of *H. juba* and *H. c. idaho*. It also improves our knowledge of aspects of the biology of the immature stages of these two common Pacific Northwest skipper butterflies. The larvae and pupae show differences in coloration sufficient to provide a reasonable guide to identification. In general *H. juba* larvae were darker colored than *H. c. idaho* and retained a black head capsule throughout development. In contrast, *H. c. idaho* larvae were lighter colored with a progressive increase in pale coloration of the head capsule as larvae matured. No doubt variations in coloration occur within and between regional populations of this subspecies. A late instar larva of the closely related *H. comma* (from Quebec, Canada) shown in Allen *et al.* (2005) appears very similar to *H. c. idaho*. Recent rearing of *H. comma manitoba* (Scudder) showed all larval stages to be colored and marked similarly to *H. c. idaho*, although pupae were darker (James & Nunnallee in prep.). Two well-separated populations of *H. juba* and *H. c. idaho* (eastern slopes of the Cascades and foothills of the Blue Mountains) were studied in this paper and little difference in larval coloration was detected amongst and between the cohorts. There is strong agreement between the images provided here and the meticulous description of immature *H. juba* provided by MacNeill (1964). However, the image of a late instar *H. juba* larva from central California in Allen *et al.* (2005) appears more orange/light brown than the larvae reared in this study. Emmel & Emmel (1973) describe fifth instars of southern California *H. juba* as 'cream colored', suggesting a trend to lighter colored larvae may occur in southern populations of this species.

Both species appear to have the ability to overwinter as eggs or early instar larvae under Pacific Northwest conditions. The identity of the overwintering stage of *H. juba* has been debated since 1980 when Shapiro (1980) suggested it overwintered as an adult in montane areas of California. Berkhousen & Shapiro (1994) found pollen grains from autumn-flowering *Chrysothamnus* on worn spring adults of *H. juba* and suggested this was evidence for adult overwintering. Scott (1992) disputed this idea as did Warren (2005), both indicating it was more likely that overwintering occurred in the egg or larval stage. However, both authors had only circumstantial evidence for this. Scott (1992) showed *H. juba* larvae developed rapidly and concluded there was plenty of time for autumn-oviposited eggs to mature into adults by early-mid spring. Warren (2005) observed freshly-eclosed *H. juba* adults in April at low elevations in Oregon followed by the appearance of worn individuals some weeks later at higher elevations. He concluded that spring *H. juba* are short or even long distance migrants seeking higher elevations, thus accounting for Shapiro's (1980) observations of worn individuals in spring in Californian mountains. This study has shown that *H. juba* in Washington may overwinter either as a fully developed egg or a first instar if oviposited in mid-October, or as a second instar if eggs are laid in mid-September. Eggs laid in early September may hatch and the larvae overwinter as third instars. The rapid development shown by overwintering second instars when transferred to warm temperatures confirms Scott's (1992) assumption that sufficient time is available for complete immature development before April–May. Overwintering larvae likely have the competency to re-commence feeding whenever conditions allow during January–February. Overwintering eggs of *H. juba*, like first instars, appear ready to exploit favorable conditions in January–February, with staggered hatching occurring during this period. The impact of winter temperatures on survival of *H. juba* eggs and larvae is unknown. The cold temperatures (-10 °C) experienced by the 2006 cohort of overwintering larvae, which presumably resulted in the observed high mortality, was unusually early (Nov 1–2) and the larvae may not have fully entered dormancy at this point. These data along with the data and observations of Scott (1992) and Warren (2005) indicate that it is most likely that *H. juba* in the Pacific Northwest overwinters as an egg or early-mid instar larva. Confirming the observations of Warren (2005), studies on spring populations of *H. juba* in the Columbia Basin of eastern Washington during 2003–06 showed individuals captured in April were always in a freshly-eclosed condition (James unpubl. obs.).

Overwintering of species in the *H. comma* complex, including *H. c. idaho*, is reported to occur in the egg stage (Hardy 1954, Scott 1986, Allen *et al.* 2005) over most of its temperate range, although older larvae or pupae also overwinter in the Arctic where the species is biennial (Scott 1986). In this study, *H. c. idaho* mostly overwintered as fully developed eggs, but a significant number of larvae in one cohort (from the eastern Cascades) also overwintered as first instars. Overwintering first instars were distinctively colored (yellow-orange) compared to first instars emerging from overwintered eggs (pale yellow-green). The conditions used in this study (25 °C and continuous illumination) to break dormancy in overwintering stages appeared to be sub-optimal for *H. c. idaho* eggs. Very few hatched under these conditions, most remaining dormant but apparently viable. Possibly the 'long day' lighting regime was inhibitory to hatching, signaling perhaps (under holarctic conditions) too short a period to complete immature development. Under natural conditions, long photoperiods may be involved in preventing summer egg hatch in the majority of individuals. Exposing overwintered eggs of the closely related *H. comma manitoba* to 25 °C and 12 hours of light resulted in >90% hatch (James & Nunnallee in prep.). The overwintering strategies of both *H. juba* and *H. c. idaho* appear to be flexible with diapause not fixed or confined to a single stage. This flexibility clearly confers advantages in terms of optimizing development under marginal temperature conditions.

A second period of dormancy or summer diapause (aestivation) during development was observed in both species and reported for the first time for the genus *Hesperia*. Final instar larvae of *H. juba* in the spring generation became quiescent in July–August and remained in their shelters for about a month before they became pre-pupal and pupated. During this apparent aestivation, no feeding occurred. Final instar dormancy did not occur in the overwintered larval generation. Similarly, last instar larvae (fifth or sixth) of *H. c. idaho* also entered a period of non-feeding dormancy, which lasted for about a month in the fifth instar and almost seven weeks in the sixth instar. Sixth instar larvae of *H. comma manitoba* also enter a six week dormancy (James & Nunnallee in prep.). Duration of the final instar in both species was 3–5 times greater than the other individual instars. Although final instar dormancy/aestivation does not appear to have been reported for North American *Hesperia*, Scott (1986) reported that mature larvae of *Ochlodes sylvanoides* (Bosiduval) aestivate about a month prior to pupation. MacNeill (1964) indicated that one to two weeks in each instar was normal for *Hesperia* spp. and larvae that spent a greater period of time in one stage invariably died. The function of delayed development in the final instar of *H. juba* and *H. c. idaho* is unclear but is likely to be related to synchronization of adult eclosion with optimal conditions for survival and reproduction. Thus, the normal phenology of *H. juba* in the Pacific Northwest with two distinct adult generations (spring and autumn), suggests that environmental conditions are optimal at these times. If summer was also optimal for *H. juba*, there would likely be a series of overlapping generations from spring to autumn as occurs in the related hesperiid *Atalopedes campestris* in eastern Washington (Crozier 2004). The observations of Warren (2005) concerning a possible late spring migration of *H. juba* from lowland to highland areas in Oregon support the hypothesis that cooler or milder environments are preferred. Delayed development of final instar *H. juba* prevents adult eclosion occurring in late July/early August, a time characterized by hot, dry conditions in eastern basin areas of Washington and Oregon. Instead, adults emerge in late August/early September when temperatures have moderated. It is likely that the dormancy is controlled by a combination of temperatures and photoperiods experienced by mid-late instars. The final instar dormancy in *H. c. idaho*, presumably serves a similar function, although in this case (in the Pacific Northwest), there is only a single generation. Peak flight period in the Pacific Northwest occurs during July–August into September. Delayed development of *H. c. idaho* presumably allows much of the population to survive into late summer and autumn, minimizing exposure of eggs to hot, dry conditions. Without final instar aestivation it is likely that many individuals would eclose during April–May. Other factors such as host plant quality, pressures from natural enemies, etc. may also have played a role in shaping this strategy. It would be interesting to determine whether other species in the *H. comma* complex which occur in cooler environments also undergo final instar aestivation.

Variation in instar number in *Hesperia* spp. was reported by MacNeill (1964). In his rearings, six appeared to be the normal instar number, but he acknowledged variation between subspecies and even within cohorts from a single female. Larvae of *H. juba* in a single cohort were recorded going through five or six instars in a ratio of approximately 50:50. All individuals of *H. juba* reared in the current study pupated at the end of the fifth instar. One cohort of *H. c. idaho* (Bear Canyon) passed through six instars while individuals in the other cohort (Grande Ronde River) passed through five. *Hesperia comma manitoba* larvae from adults obtained in southern British Columbia developed through six instars (James & Nunnallee in prep.). Instar number variation in some instances may be an artifact of laboratory rearing or associated with diseased individuals that may go through as many as eight instars, but become progressively smaller after the sixth instar (MacNeill 1964).

The two grass species (*S. glauca, E. repens*) used for rearing *H. juba* and *H. c. idaho* larvae in this study do not appear to have been previously reported as hosts (Scott 1986, Pyle 2002). In common with many other grass skippers, these species appear to have a wide host range in the Poaceae. Larval hosts for *H. c. idaho* have not been reported in the Pacific Northwest but in Colorado include species of *Bromus*, *Bouteloua*, *Andropogon*, and *Lolium* (Scott 1992). Species of *Bromus*, *Poa*, *Deschampsia* and *Stipa* have been recorded as hosts for *H. juba* (Scott 1986). The white flocculent secretion produced by ventral glands in the final instar of both species has been reported for a number of hesperiids (Dethier 1942, MacNeill 1964) but has rarely been illustrated (Fig. 2), (but see pages 133 and 137 in Allen *et al.* (2005)). The secretion appears to serve as a moisture repellent. Dethier (1942) showed that the secretion is insoluble in water and repels water. The secretion was readily incorporated into the pupal shelters or loose cocoons formed by final instar *H. juba* and *H. c. idaho*, where it presumably helps protect the pupae from excessive moisture.

ACKNOWLEDGEMENTS

I thank Dave Nunnallee, Jon Pelham and Andrew Warren for their advice and suggestions during the course of these studies.

LITERATURE CITED

ALLEN, T. J., J. P. BROCK, & J. GLASSBERG. 2005. Caterpillars in the field and garden. Oxford University Press, New York. 232 pp.

BERKHOUSEN, A. E. & A. M. SHAPIRO. 1994. Persistent pollen as a tracer for hibernating butterflies: The case of *Hesperia juba* (Lepidoptera: Hesperiidae). Great Basin Naturalist. 34 (1): 71–78.

CROZIER, L. 2004. Field transplants reveal summer constraints on a butterfly range expansion. Oecologia 141: 148–157.

DETHIER, V. G. 1942. Abdominal glands of Hesperiinae. J. New York Ent. Soc. 50 (2): 203–206.

EMMEL, T. C. & J. F. EMMEL. 1973. The butterflies of Southern California. Nat. Hist. Mus. of Los Angeles Co. Science Series 26: 1–148.

FORISTER, M. L., A. FORDYCE, & A. M. SHAPIRO. 2004. Geological barriers and restricted gene flow in the holarctic skipper *Hesperia comma* (Hesperiidae). Mol. Ecol. 13: 3489–3499.

HARDY, G. A. 1954. Notes on the life history of *Hesperia comma* L. *manitoba* Scud (Lepidoptera: Rhopalocera) on Vancouver Island. Ent. Soc. Brit. Col. Proc. 51: 21–22.

JAMES, D. G. & D. NUNNALLEE. In prep. Life histories of Cascadia butterflies. Oregon State University Press.

MACNEILL, C. D. 1964. The skippers of the genus *Hesperia* in western North America with special reference to California. University of California Publications in Entomology, University of California Press, Berkeley and Los Angeles. 35: 1–221.

PYLE, R. M. 2002. The butterflies of Cascadia. Seattle Audubon Society. 420 pp.

SCOTT, J. A. 1986. The butterflies of North America. Stanford University Press, Stanford. 583 pp.

_____. 1992. Host plant records for butterflies and skippers (mostly from Colorado) 1959–1992, with new life histories and notes, oviposition, immatures and ecology. Papilio (New Series) 1–182.

SHAPIRO, A. M. 1980. Does *Hesperia juba* (Hesperiidae) hibernate as an adult? J. Lep. Soc. 33(4): 258–260.

WARREN, A. D. 2005. Butterflies of Oregon, their taxonomy, distribution and biology. Lepidoptera of North America 6. Contributions of the C. P. Gillette Museum of Arthropod Diversity. Colorado State University, Fort Collins. 408 pp.

Received for publication 6 October 2008; revised and accepted 3 February 2009.

Journal of the Lepidopterists' Society
63(3), 2009,137–140

PRODOXUS PRAEDICTUS, **N. SP.**, A NEW BOGUS YUCCA MOTH FROM SOUTHERN CALIFORNIA

OLLE PELLMYR,
Department of Biology, University of Idaho, Moscow, ID 83844-3051, USA; email: pellmyr@uidaho.edu

JEREMY B. YODER,
Department of Biology, University of Idaho, Moscow, ID 83844-3051, USA

AND

WILLIAM K. GODSOE
Department of Biology, University of Idaho, Moscow, ID 83844-3051, USA

ABSTRACT. Fruits of most fleshy-fruited yuccas host non-pollinating bogus yucca moths. A peculiar exception has been the widespread and abundant *Yucca schidigera* Roezl ex Ortgies (mojave yucca), where extensive search has failed to document a resident species. Here we report on the discovery of this predicted taxon, *Prodoxus praedictus* **n. sp.**, from a small geographic area in southern California, provide a formal description and results of a phylogenetic analysis, and information on species biology.

Additional key words: Prodoxidae, Agavaceae, mutualism

The pollinating yucca moths (*Tegeticula* Zeller and *Parategeticula* Davis; Prodoxidae) are perhaps the most widely recognized monotrysian moths, based on their obligate pollination mutualism with yuccas (Riley 1872, 1892, Powell & Mackie 1966, Davis 1967, Powell 1984, 1992, Pellmyr 2003). Containing at least 27 species (Davis 1967, Pellmyr *et al.* 2008), they constitute a mature system for ecological and evolutionary studies of diversification on several time scales. Meanwhile, the sister group of the pollinators, *Prodoxus* Riley, referred to as 'bogus yucca moths' (Riley 1880a, b) which coexist as non-pollinators with the pollinators on yuccas, have received less attention. They differ ecologically from the seed-feeding pollinators by feeding on plant parts not used by the pollinators, such as peduncles, non-seed parts of the fruit, and leaf tissue (Riley 1892, Powell and Mackie 1966, Davis 1967, Powell 1984, Wagner and Powell 1988). A recent revision recognized 22 species (Pellmyr *et al.* 2006). This diversity of life habits among the yucca moth community in its broadest sense will permit analyses of prodoxid community assembly; individual yucca species are known to host as many as six prodoxid species, thus offering sufficient diversity and near-complete information that is unique among recognized models of obligate mutualisms involving seed-parasitic pollinators (e.g., senita moths, gracillariids, fig wasps; Holland and Fleming 1999, 2002, Kato *et al.* 2003, Kawakita and Kato 2006, Machado *et al.* 2005).

Before a comprehensive diversification analysis can be done for the bogus yucca moths, it will be important to identify all moth species. The number has accrued with several studies (e.g., Davis 1967, Powell 1984, Pellmyr *et al.* 2006), such that virtually all known feeding sites of prodoxids on all yucca species have been checked in the field. A puzzling observation has been the failure to find a fruit-feeding *Prodoxus* on *Yucca schidigera*, a common, wide-ranging fleshy-fruited yucca of the Mojave Desert and parts of adjacent deserts. Adult *Prodoxus* rest in the flowers during the day, and despite many lepidopterists checking yucca flowers over several decades, no one has reported a fruit-feeding species on the mojave yucca. Examination of prodoxid holdings in UCB revealed a series of six individuals of an undescribed species collected on *Y. schidigera* in the current Joshua Tree National Park in 1970 by J.A. Powell and R. Dietz. Subsequent fieldwork in 2006 and 2007 by the present authors recovered adult moths in the flowers and characteristic fruit fragments infested by *Prodoxus* larvae. Here we provide a description of the species. Descriptions of traits other than genitalia are based on three specimens per sex; for genitalia, one male and two females were used.

Prodoxus praedictus Pellmyr **new species**

Fig. 1

Diagnosis. The species is superficially similar to the two *Prodoxus* species of *Yucca brevifolia* Engelmann, *P. sordidus* Riley and *P. weethumpi* Pellmyr (illustrated in Pellmyr *et al.*, 2006). It differs in habitus by having nearly white, more slender and more pointed forewings, and darker brown hindwings than the two *Y. brevifolia* feeders. In the female, signum diameter is only 25–31% of that in *P. weethumpi*, and the apophyses posteriores are 47–57% as long as those of *P. sordidus*. Specimens of *P. coloradensis* Riley, a stalk-borer of *Y. schidigera* and other species, can occasionally be very pale in the Mojave Desert, but they invariably have at least a few dark brown scales scattered across the forewing.

Description. *Wingspan*: male 10.0–10.9 mm, female 11.4–12.8 mm; integument grayish brown. *Head*: with chalk white scales; antennae with basal half or more covered by pale tan scales, then bare. *Thorax*: with chalk white scales; legs very light tan. *Wings*: FW length in male 4.3–5.2 mm, female 5.3–5.9 mm; dorsal surface pale tan, with slightly darker tan toward apex in some individuals; underside solid tan; HW with light brownish (male) to darker brownish gray increasing distally (female); underside brownish grey, without pattern; fringes concolorous with adjacent wing regions. *Abdomen*: male with dorsal scaling brownish tan, mixed with white toward abdominal tip and grayish tan, ventrally white; abdominal brush of linear scales in male light tan with whiter scales mixed toward apex; in female solid brown with little or no brown scales. *Male genitalia* (Fig. 2): vinculum-saccus 0.68 mm in length; valvae with slightly tapering cucullus, with 5–7 stout spines scattered along outer ventral margin to a point near apex; phallus 0.30 mm long, 0.035 mm in diameter. *Female genitalia* (Fig. 3–5): apophyses posteriores 1.68–1.99 mm long; ovipositor 0.20 mm high, with a 0.16 mm long, 0.18–0.20 mm high serrated dorsal ridge with 23 asymmetric teeth starting immediately behind tip; ductus bursae with minutely rugose section of internal spinulae; corpus bursae 0.49–0.87 mm in length, 0.23–0.24 mm wide, with two 0.10 mm wide stellate signa with 8–12 spines each.

Type material. *Holotype*: male, USA: California. Riverside Co., Joshua Tree N.M. [currently National Park], 1 mi [1.6 km] W Cottonwood Spring, elev. 900 m, in *Yucca schidigera* flower. N 33.7363°, W 115.8266°, 31 Mar. 1970, leg. J. Powell. (UCB). *Paratypes*: 2 males, 3 females, same data, except 2 males leg. R.J. Dietz. (UCB).

Other specimens. Specimens for DNA study were gathered 15 Mar. 2006 (larva in old fruit fragment) in Joshua Tree National Park at Pinto Wye, N 34.0209°, W 116.0106°, and as 11 adults 25 Mar.–4 Apr. 2007 in *Y. schidigera* flowers, between Pinto Basin N 33.8185°, W 115.8106° and S of Cottonwood Spring, N 33.7335° W 115.48.639°. All of these specimens are cryopreserved as whole specimens or DNA in the laboratory of the senior author. As a result of transport while frozen, the specimens were too fragmented to include in morphometric data collection.


FIG. 1. Adult female *P. praedictus*, holotype. Forewing length 5.9 mm.

Etymology. The host species alone among the fleshy-fruited yuccas of the section Sarcocarpa did not have a known fruit-feeding *Prodoxus* species, despite the yucca being widespread and subject to extensive observation because of its pollination association with yucca moths. The species epithet reflects that a fruit-feeding bogus yucca moth had been predicted, but never identified, to exist on *Y. schidigera* despite decades of attention by entomologists.

Known hosts, oviposition site, and immature biology. The larva feeds in a gallery inside the fruit wall of developing *Y. schidigera* fruits. Infested fruits often fall into the leaf rosette or onto the ground near the plant, where they can persist for several years. Dried fruits inhabited by diapausing larvae often display diagnostic bumps on the surface, as well as round emergence holes from eclosed individuals (Fig. 6).

Flight period. Late March–early April, coincident with flowering period of the only known host.

Distribution. The species is so far only known from the southernmost Mojave Desert and adjacent Colorado Desert, in the central portion of Joshua Tree National Park in Riverside Co, California. Elevational range, 900–1000 m. The restricted range is puzzling as the host species is a widespread and common component of the Mojave Desert and Colorado Desert, occurring from S Nevada, SW Utah, NE Arizona, in California north to near Los Angeles along the coast and to areas south of Death Valley in the eastern part of the state, as well as in the northern portion of Baja California of Mexico. In fact, the few known sites straddle the rather sharp Colorado-Mojave Desert transition within Joshua Tree National Park, suggesting that perhaps abiotic factors are unlikely to play a significant role in limiting the range. Flowers of *Y. schidigera* have been extensively examined for lepidopteran visitors across much of the host range by many investigators, yet the fruit-feeding *Prodoxus* has only been recovered in the area described in the present paper. Additional surveys will be required to determine its actual range, but it appears likely to be quite small.

Phylogenetic position. Phylogenetic relationships of 21 *Prodoxus* species were analyzed based on molecular data in a recent paper (Pellmyr *et al.*, 2006). Here we used the same data set—a 2105-bp region of the mitochondrial COI-COII regions—with addition of *P. praedictus* (GenBank accession numbers GQ981319 and GQ9881320). Bootstrap analyses with 100 replicates using maximum parsimony (MP) and maximum likelihood (ML) criteria, respectively, both

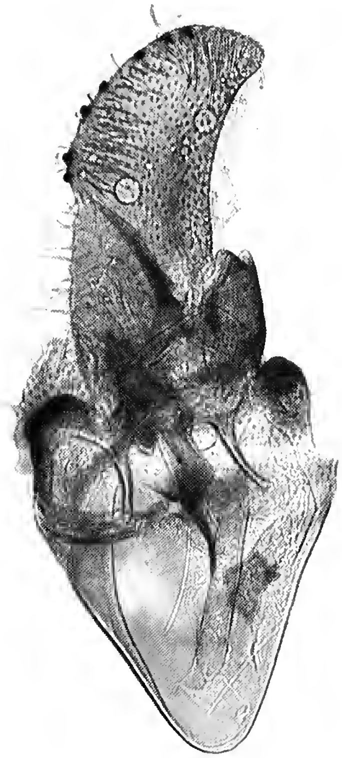


FIG. 2. Male genitalia. Vinculum-saccus, valva , and phallus. One valva removed, phallus not detached.

FIG. 3. Female genitalia, containing entire ovipositor and apophyses, and bursa with signa. For dimensions, see species description.

FIG. 4. Ovipositor tip, left lateral view. Dorsal serrated ridge of ovipositor protruding in part outside membranous portions of the abdomen.

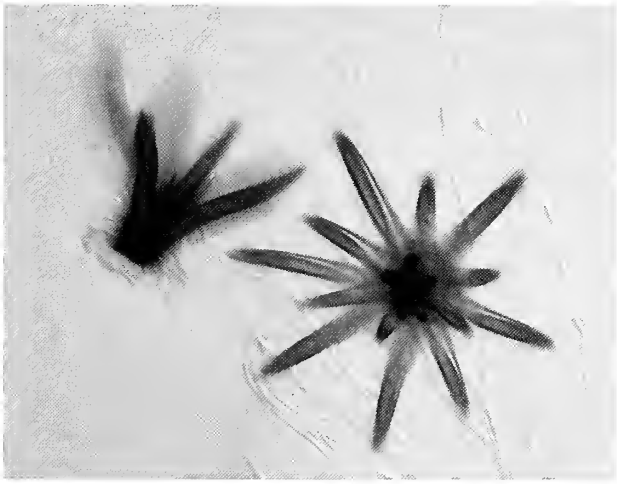


FIG. 5. Signa in lateral view and from below, respectively. Diameter 0.10 mm.

recovered *P. praedictus* as sister species of *P. y-inversus* Riley, a species with similar larval feeding biology on *Y. baccata* Torrey, a yucca with partly overlapping geographic range. Bootstrap values were 83% (MP) and 69% (ML), respectively, and in both analyses they were part of a clade with 100% support containing two other fruit feeders, *P. atascosanellus* Pellmyr and *P. carnerosanellus* Pellmyr.

DISCUSSION

With the discovery of *P. praedictus*, there is reason to believe that we have documented all extant yucca-feeding *Prodoxus* species in the northern part of its range. Surveys among the fleshy-fruited yuccas in the southern, mostly Mexican, part of the range have yielded both stem- and fruit-feeders in all taxa that have been reasonably well surveyed. They remain to be sought after in the epiphytic *Y. lacandonica* Pompa & Valdés, and in the recently discovered *Y. queretaroensis* Piña Lujan, neither of whose flowers have been available for examination. Meanwhile, the extent of *P. praedictus*' range remains exceptionally limited in the face of extended search by numerous investigators. Its

FIG. 6. Section of dried *Yucca schidigera* fruit fragment with several emergence holes created by individual *P. praedictus*. Exit hole diameter ~1 mm.

apparent absence in many areas begs an explanation.

In terms of life history diversification, the present analyses are consistent with previous analyses (Pellmyr *et al.* 2006), as it identifies stem feeding as the basal condition, with three separate origins of fruit feeding. The state of knowledge among the yucca moths in its broadest sense now is sufficiently complete as to permit analyses of diversification in this ecologically important group.

ACKNOWLEDGEMENTS

We thank Jerry Powell for generous access to UCB's prodoxid collections, and much additional biological information that facilitated successful fieldwork. Work was funded by NSF grant DEB-051684, a grant for fieldwork from the Joshua Tree National Park through the Cooperative Ecosystem Studies Units National Network (CESU), and a grant from the Joshua Tree Park Foundation Graduate Student Research Grant Program to JBY. WKG was supported by a pre-doctoral fellowship from the Canadian National Science and Engineering Research Council, with a supplement from the Foundation for Orchid Research and Conservation. Death Valley National Park, Desert National Wildlife Refuge, Mojave National Preserve, and Nevada Test Site (United States Department of Energy) provided permission to check plants for presence of *P. praedictus* within their respective jurisdictions.

LITERATURE CITED

Davis, D. R. 1967. A revision of the moths of the subfamily Prodoxinae (Lepidoptera: Incurvariidae). U.S. Natl. Hist. Mus. Bull. 255:1–170.

Holland, J. N. & T. H. Fleming. 1999. Mutualistic interactions between *Upiga virescens* (Pyralidae), a pollinating seed-consumer, and *Lophocereus schottii* (Cactaceae). Ecology 80:2074–2084.

______. 2002. Co-pollinators and specialization in the pollinating seed-consumer mutualism between senita cacti and senita moths. Oecologia 133:534–540.

Kato, M., A. Takimura, & A. Kawakita. 2003. An obligate pollination mutualism and reciprocal diversification in the tree genus *Glochidion* (Euphorbiaceae). Proc. Natl. Acad. Sci. USA 100:5264–5267.

Kawakita, A. & M. Kato. 2006. Assessment of the diversity and species specificity of the mutualistic association between *Epicephala* moths and *Glochidion* trees. Molec. Ecol. 11:1573–1578.

Machado, C. A., N. Robbins, M. T. P. Gilbert, & E. A. Herre. 2005. Critical review of host specificity and its coevolutionary implications in the fig/fig-wasp mutualism. Proc. Natl. Acad. Sci. USA 102:6558–6565.

PELLMYR, O. 2003. Yuccas, yucca moths and coevolution: a review. Ann. Missouri Bot. Gard. 90:35–55.

PELLMYR, O., M. BALCÁZAR-LARA, K. A. SEGRAVES, D. M. ALTHOFF. & J. LEEBENS-MACK. 2006. Phylogeny and life history evolution of *Prodoxus* yucca moths (Lepidoptera: Prodoxidae). Syst. Entomol. 31:1–20.

PELLMYR, O, K. A. SEGRAVES, D. M. ALTHOFF & M. BALCAZAR-LARA. 2008. Phylogeny of the pollinating yucca moths, with revision of Mexican species (*Tegeticula* and *Parategeticula*; Lepidoptera, Prodoxidae). Zool. J. Linn. Soc. 152:297–314.

POWELL, J. A. 1984. Biological interrelationships of moths and *Yucca schottii*. Univ. Calif. Publ. Entomol. 100:1–93.

______. 1992. Interrelationships of yuccas and yucca moths. Trends Ecol. Evol. 7:10–15.

POWELL, J. A. & R. A. MACKIE. 1966. Biological interrelationships of moths and *Yucca whipplei*. Univ. Calif. Publ. Entom. 42:1–49.

RILEY, C. V. 1872. The fertilization of the yucca plant by *Pronuba yuccasella*. Canad. Entomol. 4:182.

______. 1880a. The true and the bogus yucca moth; with remarks on the pollination of *Yucca*. Amer. Entomol. 3:141–145.

______. 1880b. On a new tineid genus allied to *Pronuba*, Riley. Amer. Entomol. 3:155–156.

RILEY, C. V. 1892. The yucca moths and *Yucca* pollination. Ann. Rep. Missouri Bot. Gard. 3:99–158.

WAGNER, D. L. & J. A. POWELL. 1988. A new *Prodoxus* from *Yucca baccata*: first report of a leaf-mining prodoxine (Lepidoptera: Prodoxidae). Ann. Entomol. Soc. Amer. 81:547–553.

Received for publication 6 August 2008; revised and accepted 3 February 2009.

Journal of the Lepidopterists' Society
63(3), 2009, 141–153

GENITALIA, DNA BARCODES, AND LIFE HISTORIES SYNONYMIZE *TELLES* WITH *THRACIDES*—A GENUS IN WHICH *TELLES ARCALAUS* LOOKS OUT OF PLACE (HESPERIIDAE: HESPERIINAE)

JOHN M. BURNS

Department of Entomology, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, MRC 127, room E-515, Washington, DC 20013-7012, USA; email: burnsj@si.edu

DANIEL H. JANZEN

Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, USA; email: djanzen@sas.upenn.edu

WINNIE HALLWACHS

Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, USA; email: whallwac@sas.upenn.edu,

MEHRDAD HAJIBABAEI

Department of Integrative Biology, University of Guelph, Guelph, ON, Canada N1G 2W1; email: mhajibab@uoguelph.ca

AND

PAUL D. N. HEBERT

Department of Integrative Biology, University of Guelph, Guelph, ON, Canada N1G 2W1; email: phebert@uoguelph.ca

ABSTRACT. Independent characters—genitalia (male and female), DNA barcodes, and larval foodplants—show that *Telles arcalaus* (Stoll), despite its exceedingly distinctive facies and small size, belongs in the genus *Thracides*, where it relates closely to *Thracides phidon* (Cramer). Because *phidon* and *arcalaus* are the type species of their respective genera and *Thracides* is the older name, *Telles* is a **synonym** of *Thracides*. Because the only other species in *Telles*, *T. pyrex* Evans, is not a species of *Thracides*, it is ***incertae sedis***. Either in Trinidad or in Pará, Brazil, as in Area de Conservación Guanacaste (ACG), Costa Rica, caterpillars of *Thracides phidon* and *Thracides arcalaus*, **new combination**, eat plants in the genera *Heliconia* and *Musa* (Zingiberales), whereas members of the *Thracides nanea* species complex eat *Cyclanthus* and *Asplundia* (Cyclanthaceae). Taxa of the mostly South American *nanea* species complex include *Thracides nida* Evans, **new status** and, in ACG, *T. chiricana* Röber, **new status**. For now, owing to the numbers of cryptic species recently discovered within supposedly well-known species of neotropic hesperiids, the taxa treated here are viewed as morphospecies. DNA barcodes, which have proved so useful in distinguishing among cryptic species, are noteworthy in this study for supporting the union in a single genus of ostensibly unrelated species.

Additional key words: morphospecies, secondary sex character, panneotropic, Zingiberales, Cyclanthaceae, *"Telles" pyrex* Evans *incertae sedis*.

Ever since Scudder & Burgess (1870), genitalia have been used effectively in distinguishing and describing species of skipper butterflies. But what follows is an example of their utility (still underexploited) in pulling a misclassified species into the proper genus (Burns 1994, 1996).

Because the facies of *Telles arcalaus* (Stoll) is both complex and strange (Figs. 1–4), it was startling when the male genitalia, upon KOH-dissection, looked familiar. Might déjà vu reflect genitalic convergence? No. Direct comparison of the new genitalia dissection (Figs. 16–18) with prior ones (Figs. 19–24) revealed morphologic similarity too pervasive for anything other than close phylogenetic relationship. It was clear that *Telles arcalaus*, a species in the K Group of neotropic hesperiids (Evans 1955), really belongs in *Thracides*, a genus in Evans's O Group.

Genitalic characters for this move are supported by characters derived from life histories and DNA barcodes: a neighbor-joining tree links *Thracides arcalaus*, **new combination**, with *Thracides phidon* (Cramer); and caterpillars of both species eat *Heliconia latispatha* and *H. irrasa* (Heliconiaceae) in Area de Conservación Guanacaste (ACG) in northwestern Costa Rica.

The disparate characters noted above are illustrated and discussed, along with some others, in a broader context below. But first, consider the rationale for applying certain names to several of the taxa involved.

NAMES

Because the type species of *Thracides* 1819 is *phidon* and that of *Telles* 1900 is *arcalaus*, because these two species are congeneric, and because *Thracides* is the older generic name, *Telles* is a **synonym** of *Thracides*. Over the course of the long, erratic taxonomic history that preceded its segregation in the monotypic genus *Telles*, *arcalaus* was variously placed in five other genera: *Papilio*, *Augiades*, *Hesperia*, *Goniloba*, and *Proteides* (Mielke 2005).

Telles pyrex Evans (1955), the only species added to *Telles*, was described from a single Colombian female, caught in 1932. Owing to her sex, Evans did not examine and figure genitalia. Study of the facies and genitalia of another female, taken in eastern Peru in 1992, shows that *pyrex* is not a species of *Telles* (see *pyrex* Postscript). So *pyrex* cannot follow *arcalaus* to *Thracides* and is left, for now, without a generic name, in nomenclatural limbo (***incertae sedis***).

Recent literature (Mielke 2004, 2005) ascribes seven species, exclusive of *arcalaus*, to *Thracides*. However, in light of the 14 cryptic, relatively specialized, neotropic skipper species recently shown to be masquerading as two, common, widespread, and ecologically generalized species, each described in 1775—i.e., *Astraptes fulgerator* (Walch) and *Perichares philetes* (Gmelin) (Hebert *et al.* 2004, Burns *et al.* 2008)—some species of *Thracides* may comprise species complexes. Until more data are available, the taxa noted in this paper should be viewed as morphospecies.

If an ACG morphospecies turns out to be a member of a superspecies or a species complex, its specific name may change. Take the simplest case: both *Thracides arcalaus* and *T. phidon* were originally described from Surinam, which is historically, geographically, and ecologically so far removed from ACG that the populations in ACG may well be specifically distinct from their counterparts in Surinam (and adjacent areas) and need different names. Nevertheless, provided that the original specific name has not been too broadly and uncritically applied, it can be a convenient and helpful (though hopefully temporary) peg on which to hang new biologic data for analysis and discussion.

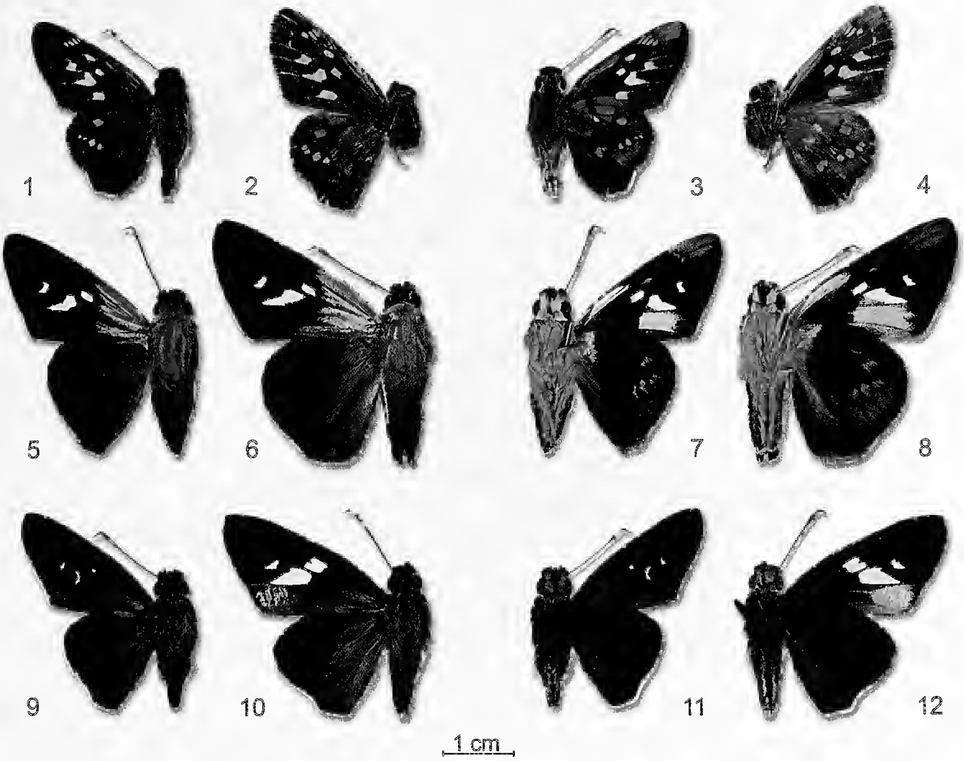
Not so simple is the third species of *Thracides* reared in ACG, which belongs to a "*nanea* species complex." Even a provisional name for what is in ACG is debatable. *Thracides nanea* (Hewitson) itself is a skipper of the Amazon drainage (eastern Peru to Pará, Brazil) and Maranhão, Brazil (from which it was described). Two subspecies have been described from extremely limited material: *T. nanea chiricana* Röber (1926) from one male from Chiriqui and *T. nanea nida* Evans (1955) from one male and one female from interior Colombia. Both original descriptions are brief; and, in an important respect, Röber's is incorrect (he states that the male has no stigma when, in fact, it has a good one). *Thracides nanea nida* differs from *T. nanea nanea* primarily in having a white hyaline spot in forewing space 3. Although Röber did not say so, *T. nanea chiricana*, like *T. nanea nanea*, lacks this spot; and Mielke (1989), having examined holotypes, synonymized the former with the latter, without discussion. The seven ACG specimens in the *nanea* complex have this spot (but its expression is so variable that in one male it is reduced to a tiny point, and so it may occasionally vanish). Inasmuch as ACG specimens share this spot with the male holotype of *T. nanea nida*, that name might apply to them.

However, in Evans's dry-dissection of the *nida* holotype's genitalia (glued to a bit of card on the specimen's pin), the valvae are pointed at their distal end. See the valval caricature for *nida* in Evans (1955: pl. 87), which is actually less pointed than are the valvae themselves. Evans also indicates that the valvae of *nanea* are still more pointed than are those of *nida*. The valvae of *T. nanea* and *T. nida*, **new status**, differ significantly from each other and differ sharply from the rounded valvae of ACG males (Fig. 26). Indeed, valvae are rounded in all three of the *Thracides* species in ACG (Figs. 17, 20, 23, 26). Because genitalic form is usually stable within skipper species (but see Burns 2000 for a striking exception), it is safe to assume that neither *T. nanea* nor *T. nida* is conspecific with the ACG population.

Although the latter may represent a fourth taxon in the *nanea* complex, a conservative (but tentative) action extends the name *T. chiricana*, **new status**, to the ACG population, owing to the proximity of Chiriqui (western Panama) to ACG and to the similarity of the skipper fauna and the ecosystems in these two areas. Future studies may show that the shape, in males, of the forewing spot in space 2 (which looks like a parenthesis in the four ACG males but like an Erlenmeyer flask in the male *chiricana* holotype) is more important in discriminating between species than is presence vs. absence of the variably expressed spot in space 3; but that remains to be seen. In the *nanea* complex (and, no doubt, in myriad others), arriving at names that are both apt and stable will require ample samples from many and various localities and further analysis.

FACIES (FIGS. 1–15)

Wings (Figs. 1–12). Dark wings (ventrally reddish brown) with a structural blue to greenish blue sheen, a few hyaline white forewing spots, and ventrally orange palpi are elements of the prevailing color pattern in *Thracides*. *Thracides chiricana* exemplifies this pattern (Figs. 9–12). Two South American species, *T. panimeron* H. H. Druce and *T. thrasea* (Hewitson), always lack white spots.

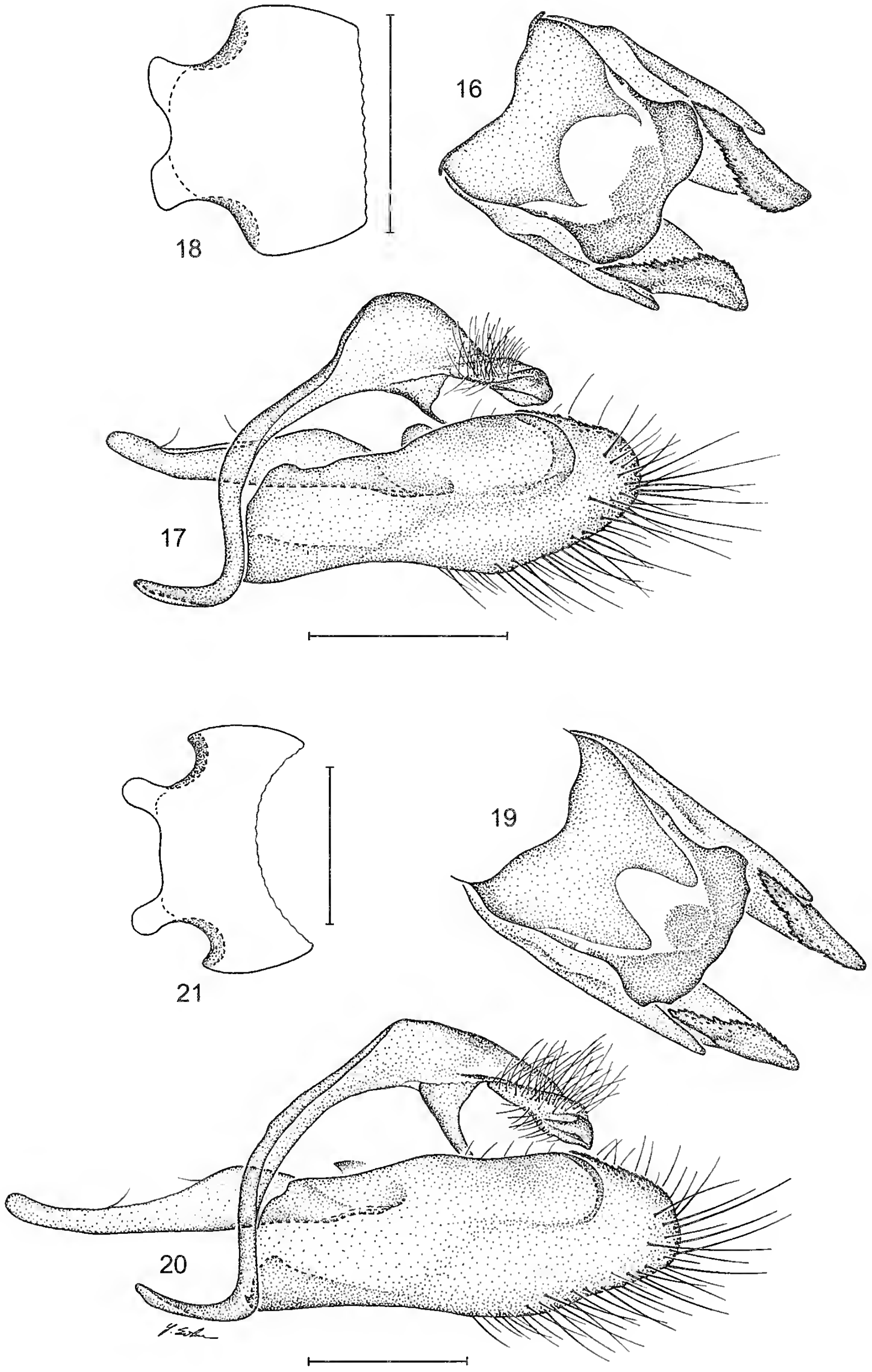


FIGS. 1–12. Adults of three species of *Thracides* in dorsal and ventral view: *T. arcalaus* (top row), *T. phidon* (middle row), *T. chiricana* (bottom row); males (columns 1 and 3), females (columns 2 and 4); dorsal (columns 1 and 2), ventral (columns 3 and 4). Voucher codes denote reared specimens from Area de Conservación Guanacaste, Costa Rica. Specimens in USNM. **1, 3,** 07-SRNP-42031. **2, 4,** Cana, 400 m, Darien, Panama, 10 September 1982, leg. G. B. Small (Burns genitalia dissection X-5795). **5, 7,** 03-SRNP-34311. **6, 8,** 04-SRNP-48834. **9, 11,** 05-SRNP-5086. **10, 12,** 03-SRNP-20435.

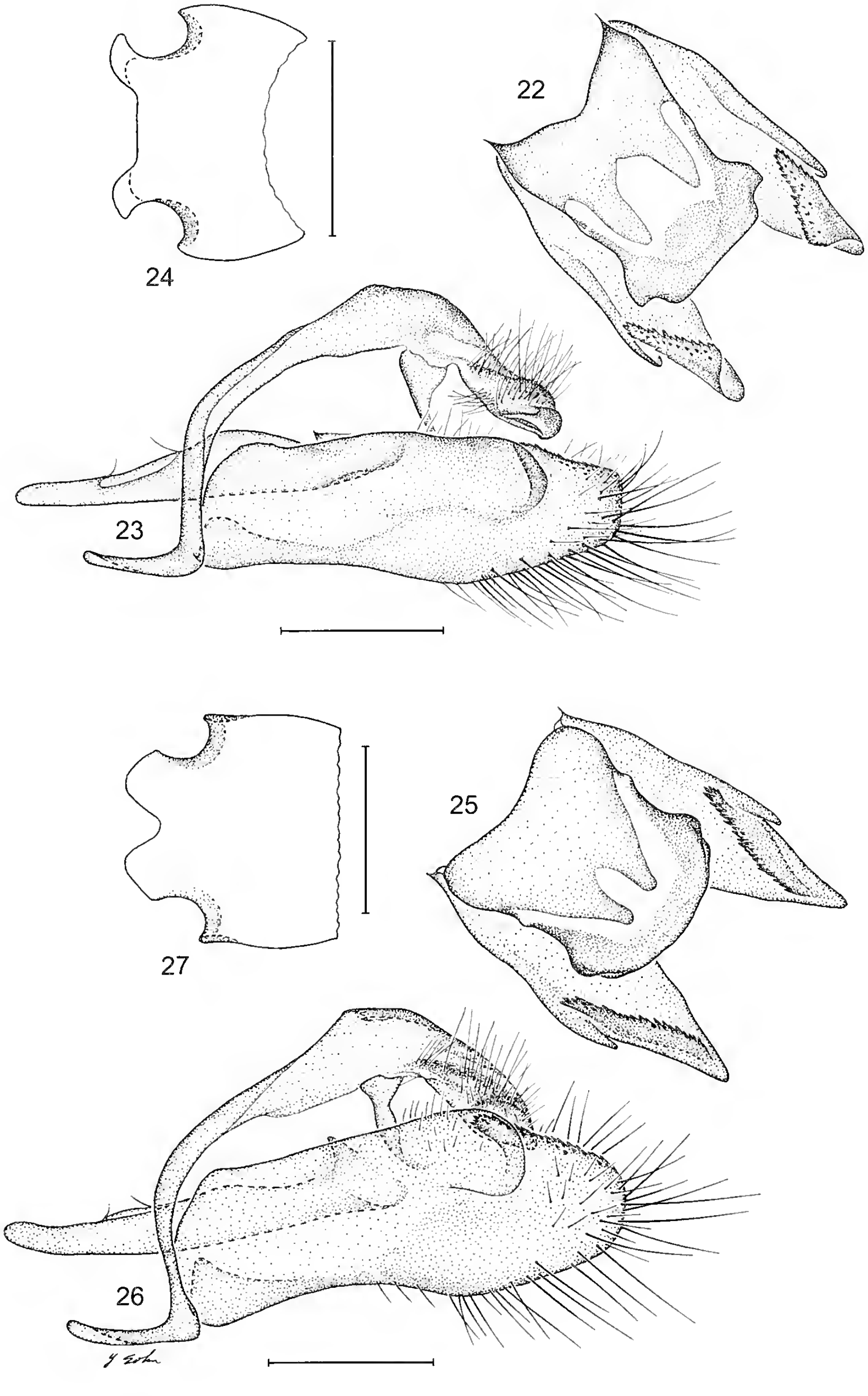
White spots usually include two in the cell; and, in most of the spotted species, one spot is directly above the other. These spots are so much larger in females than in males that they unite (Figs. 10, 12). In sharp contrast, the upper cell spot of *T. arcalaus* and *T. phidon* is not above the lower one but distal to it. The proximal, lower spot in both of these species is medium-sized and expressed to the same degree both dorsally and ventrally (Figs. 1–8). The distal, upper spot is similar in size to the proximal one and is equally expressed on both wing surfaces in *T. arcalaus* (Figs. 1–4). But in *T. phidon*, the distal spot is far smaller than the proximal one and is usually expressed ventrally (Figs. 7, 8); and when it appears dorsally (in ~60% of 88 individuals examined), it is only a point.

Though bizarre, much of the appearance of *T. arcalaus* (Figs. 1–4) relates to other species of *Thracides* (primarily to *T. phidon* [Figs. 5–8], which, itself, departs appreciably from its congeners). In *T. arcalaus*, the ventral ground color of both pairs of wings, although paler than in other species, is still reddish brown. The pale yellowish hyaline spots of the forewing are white spots in other species. On the ventral forewing, the bright yellow strip along the proximal half of the costa

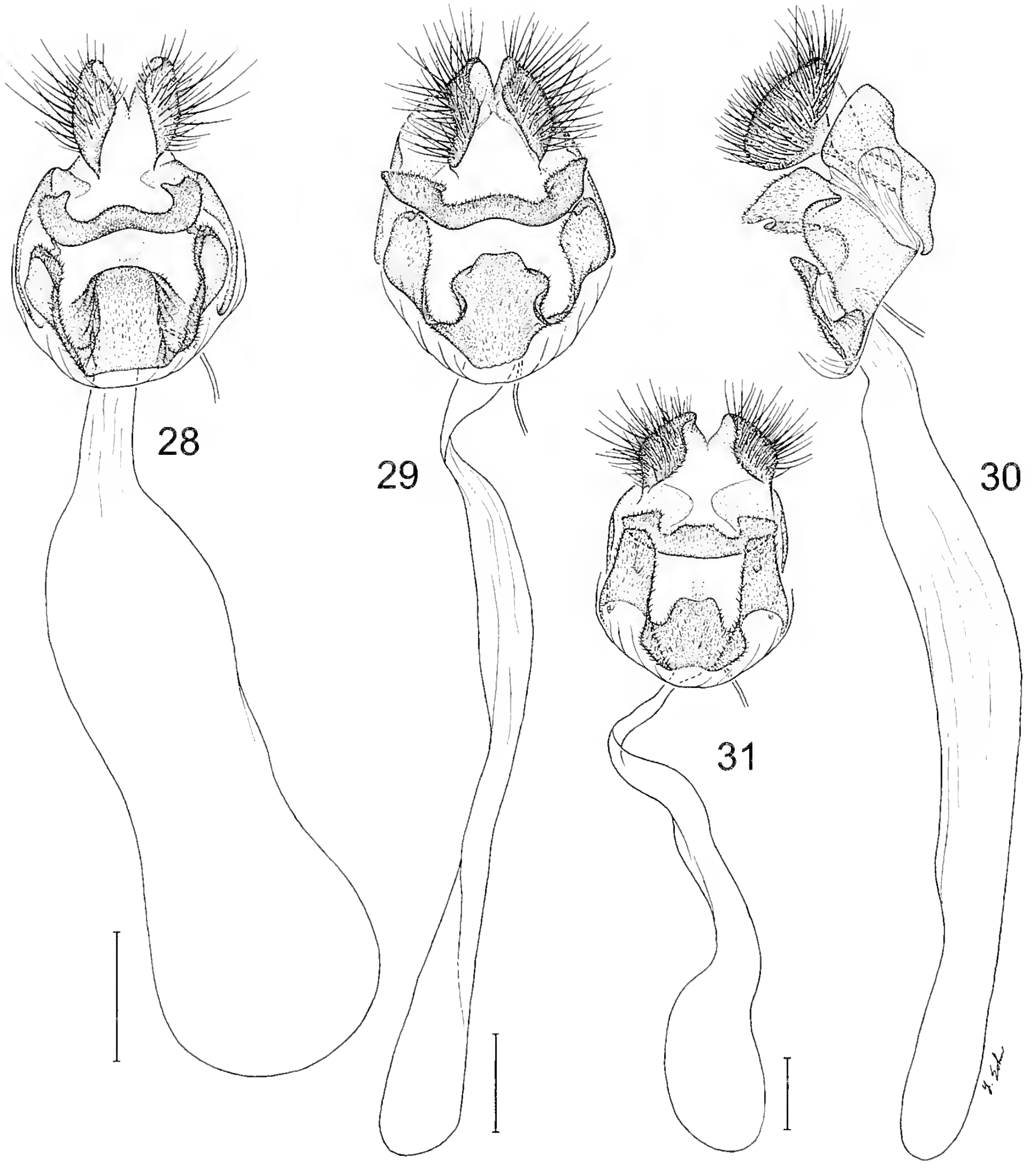
FIGS. 13–15. Stigma, centrally located on the dorsal forewing of the *Thracides* males in Figs. 1, 5, and 9. **13,** *T. arcalaus*, absent. **14,** *T. phidon*, vestigial. **15,** *T. chiricana*, well-developed.



FIGS. 16–21. Male genitalia of *Thracides arcalaus* (above), dissection X-5764, voucher 03-SRNP-8957, and *T. phidon* (below), dissection X-5541, voucher 00-SRNP-2027, from ACG, Costa Rica (specimens in USNM). **16, 19,** Tegumen, uncus, and valvae in dorsal view; scale = 1 mm. **17, 20,** Genitalia in left lateral view; scale = 1 mm. **18, 21,** Juxta in dorsal view; scale = 0.5 mm.



FIGS. 22–27. Male genitalia of *Thracides phidon* (above), dissection X-5546, voucher 00-SRNP-2549, and *T. chiricana* (below), dissection X-6669, voucher 05-SRNP-5087, from ACG, Costa Rica (specimens in USNM). **22, 25,** Tegumen, uncus, and valvae in dorsal view; scale = 1 mm. **23, 26,** Genitalia in left lateral view; scale = 1 mm. **24, 27,** Juxta in dorsal view; scale = 0.5 mm.



FIGS. 28–31. Female genitalia of *Thracides* (specimens in USNM); scale = 1 mm. **28,** *T. arcalaus*, ventral view; Colon (Sta. Rita), 1500 ft [457 m], Panama, 15 February 1991, leg. S. S. Nicolay; dissection X-5794. **29, 30,** *T. phidon*, ventral and right lateral views; ACG, Costa Rica; dissection X-5544, voucher 00-SRNP-11721. **31,** *T. chiricana*, ventral view; ACG, Costa Rica; dissection X-6670, voucher 03-SRNP-20434.

corresponds to a white strip in *T. phidon*; and the wider, duller yellow patch at the distal end of the costa corresponds to a largely pale lilac patch in *T. phidon.* At the proximal end of this ventral forewing patch, small, yellow subapical spots in spaces 6, 7, 8, and 9 correspond to tiny bluish lilac spots usually visible in more or less unworn specimens of *T. phidon.* Dorsally, in *T. arcalaus*, these yellow subapical spots are conspicuous in spaces 6, 7, and 8 and may even become hyaline. Similarly, on both surfaces of the hindwing of *T. arcalaus*, yellow submarginal spots in spaces 2, 3, 4, 5, 6, and 7 correspond to pale greenish to bluish spots on the ventral hindwing of *T. phidon*, and to those of *T. cilissa* (Hewitson), as well. (In *T. arcalaus*, the spots in spaces 4 and 5 are tiny and not always present.) On the ventral hindwing of *T. arcalaus*, distal to these spots, light yellow overscaling (which is most evident in the upper part of space 1c and in spaces 2 and 3) corresponds to sparser overscaling in the same places in *T. phidon*.

Basically, many spots, much yellow, and the suppression of structural blue, plus a few unique features of the proximal ventral hindwing, are what superficially set *T. arcalaus* far apart from its congeners—that, and its obviously smaller size (Figs. 1–12).

Stigma (Figs. 13–15). In *Thracides*, this male secondary sex character of the dorsal forewing varies from all to nothing. When well-developed, as it is in *T. chiricana* (Figs. 9, 15), it is wide and tripartite, extending from near the middle of vein 1 to the origin of vein 3, with parts one and two together spanning space 1b and part three spanning the proximal part of space 2; there, part three runs mostly along the lower edge of the cubital vein; the bottom of part three is medially displaced, and therefore conspicuously offset from part two. The stigma is greatly and variably reduced in *T. phidon* (Figs. 5, 14), in which it is narrow and relatively straight instead of conspicuously staggered; the parts vary not only in length but also in presence (i.e., part two, and especially part three, may be missing; and part three, when present, is always so short that it never even approaches the cubitus). *Thracides arcalaus* (Figs. 1, 13) lacks a stigma.

GENITALIA (FIGS. 16–31)

Dissected genitalia that are free instead of mounted can be viewed from every angle, and they can be placed side by side and oriented in parallel. Their liberation is critical for comparing species, especially those with similar to virtually identical genitalia. So is an appreciation of individual variation. The genitalia of two males of *T. phidon* are illustrated (Figs. 19–24) in order to give some sense of intraspecific variation, which must be taken into account in detecting real interspecific differences in morphology.

Male genitalia (Figs. 16–27). The general genitalic theme in *Thracides* involves (1) an uncus that is wide and, at its distal end, undivided; (2) a valva with (in lateral view) a long, low, roughly rectangular body whose dorsal half distally splits to form a distinctive, dorsally dentate division, situated in a slightly more mesial plane; (3) a juxta with a pair of short, rounded, anteriorly to anterolaterally directed lobes; and (4) a penis with a dorsodistal pair of more or less mammate titillators.

In dorsal view (Figs. 16, 19, 22, 25): (1) Where the tegumen joins the uncus is a mid-dorsal, membranous area with a strongly curved anterior margin; and flanking this area are sclerotized, posteriorly directed projections of the tegumen. In *T. arcalaus*, the membranous area is wider, leaving narrow tegumen projections that taper to a sharp point. This area is narrower, leaving wide, bluntly rounded projections in both *T. phidon* and *T. chiricana*; but it is narrower in *T. chiricana* than it is in *T. phidon*. (2) The distal end of the uncus is concave in *T. arcalaus*, more or less straight in *T. phidon*, and straight to convex in *T. chiricana*. (3) The distolateral lobes of the uncus are more protuberant in *T. arcalaus* and *T. phidon* than they are in *T. chiricana*, but are more evenly rounded in *T. arcalaus* and *T. chiricana* than they are in *T. phidon*. (4) The paired anterior lobes of the juxta (Figs. 18, 21, 24, 27) are relatively narrow and far apart in *T. phidon*, wider and closer together in *T. arcalaus*, and widest and closest in *T. chiricana*.

Female genitalia (Figs. 28–31). The lamellae antevaginalis and postvaginalis are the two major sclerotized elements. Those of ACG *Thracides* have the following aspect in ventral view: (1) A lamella antevaginalis that is peripherally U-shaped but, at the bottom of the U, expanded into a wide, robust, midventral piece (with a flared base) extending posteriorly, ventral to both the ostium bursae and a membranous area (resembling an inverted U) that joins the anterior edge of (2) a lamella postvaginalis that is about as wide as the lamella antevaginalis, but smaller, and shaped like a very low W, with a pair of small, short, medially pointing lobes at the top of the W.

In the middle of the membranous area that separates the two lamellae, some sclerotization runs from the ostium bursae to (or at least partway to) the lamella postvaginalis. The ductus bursae and corpus bursae are membranous. The connection of the ductus seminalis to the ductus bursae is as far posterior as possible, i.e., at about the level of the ostium bursae.

Obvious interspecific differences are in the shape of the midventral sclerotized piece that extends posteriorly, beneath the ostium bursae, from the bottom of the U of the lamella antevaginalis. This piece is large and rectangular, with splayed sclerotized sides, in *T. arcalaus* (Fig. 28); large, with a pair of (variably expressed) lateral lobes in *T. phidon* (Fig. 29); and smaller, laterally tapered, and distally a bit concave (altogether suggesting a symmetric volcanic cone) in *T. chiricana* (Fig. 31). The paired, short, medially directed lobes at the top of the lamella postvaginalis W are well-developed in both *T. arcalaus* and *T. phidon* and are moderately developed in *T. chiricana*. (Note that the size and shape of these lobes—and of the W itself—vary with the angle of observation and with the degree to which the lamella postvaginalis is tilted. The lobes appear smaller in Figs. 29 and 31 than they really are.)

FOODPLANTS (TABLE 1)

In ACG, *T. phidon* caterpillars have been found feeding primarily on *Heliconia* (Heliconiaceae) and secondarily on an introduced species of *Musa* (Musaceae). (A single record of *T. phidon* on *Pleiostachya leiostachya* [Marantaceae] is suspect because the plant may be misdetermined.) Two of the five reared specimens of *T. arcalaus* ate *Heliconia latispatha*, which seems to be by far the most favored foodplant of *T. phidon*; and the other three specimens ate *H. irrasa*, which *T. phidon* also uses. The above plant families are closely related and are grouped in the order Zingiberales. On the other hand, caterpillars of *T. chiricana* have been found mostly on two species of *Asplundia* but also on *Cyclanthus* (both in the unrelated family Cyclanthaceae).

TABLE 1. Larval foodplants of three species of *Thracides* in Area de Conservación Guanacaste, northwestern Costa Rica, and number of rearing records for each species of plant.

Thracides arcalaus			
	Heliconiaceae		
		Heliconia irrasa	3
		Heliconia latispatha	2
Thracides phidon			
	Heliconiaceae		
		Heliconia irrasa	33
		Heliconia latispatha	644
		Heliconia longa	5
		Heliconia longiflora	3
		Heliconia mathiasiae	22
		Heliconia metallica	16
		Heliconia pogonantha	53
		Heliconia tortuosa	2
		Heliconia umbrophila	10
		Heliconia vaginalis	52
		Heliconia wagneriana	1
	Musaceae		
		Musa acuminata (introduced)	102
Thracides chiricana			
	Cyclanthaceae		
		Asplundia microphylla	16
		Asplundia utilis	20
		Cyclanthus bipartitus	5

Foodplant selection is geographically conservative. In Pará, Brazil, Moss (1949) found caterpillars of *T. phidon* feeding "on Banana [*Musa*], *Heliconia*, and similar plants," and of *T. nanea* (in a species complex that includes *T. chiricana*) on *Cyclanthus bipartitus*. In Trinidad, M. J. W. Cock "twice reared [*T. arcalaus*] from larvae collected on *Heliconia hirsuta*," and F. J. Simmonds reared it once from *H. psittacorum* (Cock 2005).

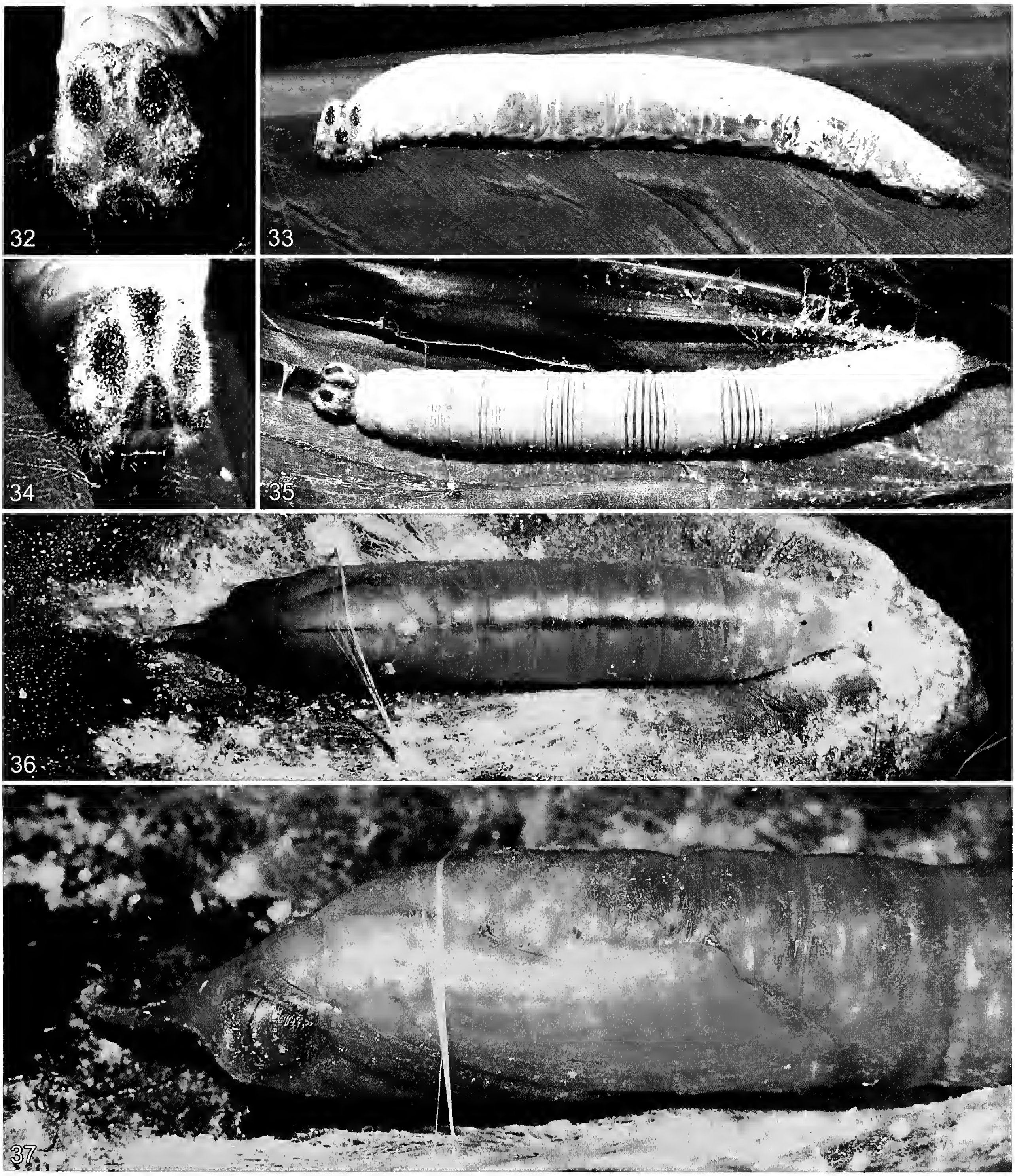
This particular pattern of foodplant selection involving genera in both the Zingiberales and Cyclanthales is unique among the many lepidopteran species that have been reared to date in ACG (Janzen & Hallwachs 2008).

IMMATURES (FIGS. 32–37)

Caterpillars (Figs. 32–35). In frontal view, the light brown head of the last instar caterpillar of *T. phidon* presents five big, bold, black spots whose arrangement resembles that of the dots denoting five on dice. The central spot is on the frontoclypeus, and the peripheral spots are at roughly 2, 4, 8, and 10 o'clock. There may be an additional spot, generally less obvious than the others, at 12 o'clock. In frontal view, the head of the last instar caterpillar of *T. chiricana* is similar, but with an obvious sixth black spot at 12 o'clock and a tendency for the peripheral spots to connect to the central spot. Powdery white wax produced by *Thracides* caterpillars can mask the pattern on the head (but not the appearance of the body, which is already pale and almost patternless).

The caterpillar of *T. arcalaus*, which has rarely been found in ACG, must resemble that of *T. phidon* because the parataxonomists who have encountered it have called it *T. phidon* and therefore have seen no reason to take its picture and swell an ample photographic record of a common species.

The spot patterns in Moss's (1949: plate V, figs. 19, 20) frontal views of the heads of caterpillars of *T. phidon* and *T. nanea* from Pará, Brazil, recall those described and illustrated here (Figs. 32, 34). On the other hand, Cock's (2005: fig. 38) dorsolateral view and verbal description of a mature *T. arcalaus* caterpillar indicate a



FIGS. 32–37. Head (frontal view) and entire last-instar caterpillar, plus pupa (dorsal and left lateral views), of *Thracides* from ACG, Costa Rica. **32, 33,** *T. phidon*, vouchers 01-SRNP-4824, 06-SRNP-21519. **34, 35,** *T. chiricana*, 03-SRNP-20435. **36, 37,** *T. phidon*, 01-SRNP-2400.

much reduced spot pattern (but, since the text also notes that the head is "entirely covered with white waxy powder," some elements may possibly be obscured).

The arresting head patterns of *T. phidon* and, especially, *T. chiricana* approach the crisper, black on orange patterns of *Neoxeniades luda* (Hewitson) and *N. pluviasilva* Burns (Janzen & Hallwachs 2008) in what is probably the sister genus to *Thracides*.

Pupa (Figs. 36, 37). The most striking feature of the light green pupa of *T. phidon* is a single, conical, slender, elongate, pointed "horn" that projects straight forward from the anterior end of the head. In lateral view (Fig. 37), the downward slope of the dorsal edge of the thorax and head continues into the horn at the same angle. The body of the pupa is long, narrow, and cylindrical, with a uniform diameter. Cock (2005) describes the "frontal spike" of *T. arcalaus* as "strongly curved upwards for distal half."

In its general form, the pupa is similar to those of the closely related species *N. luda* and *N. pluviasilva* (whose green pupae are patterned, however, with a heavy dorsal and dorsolateral speckling of small brown spots) and to

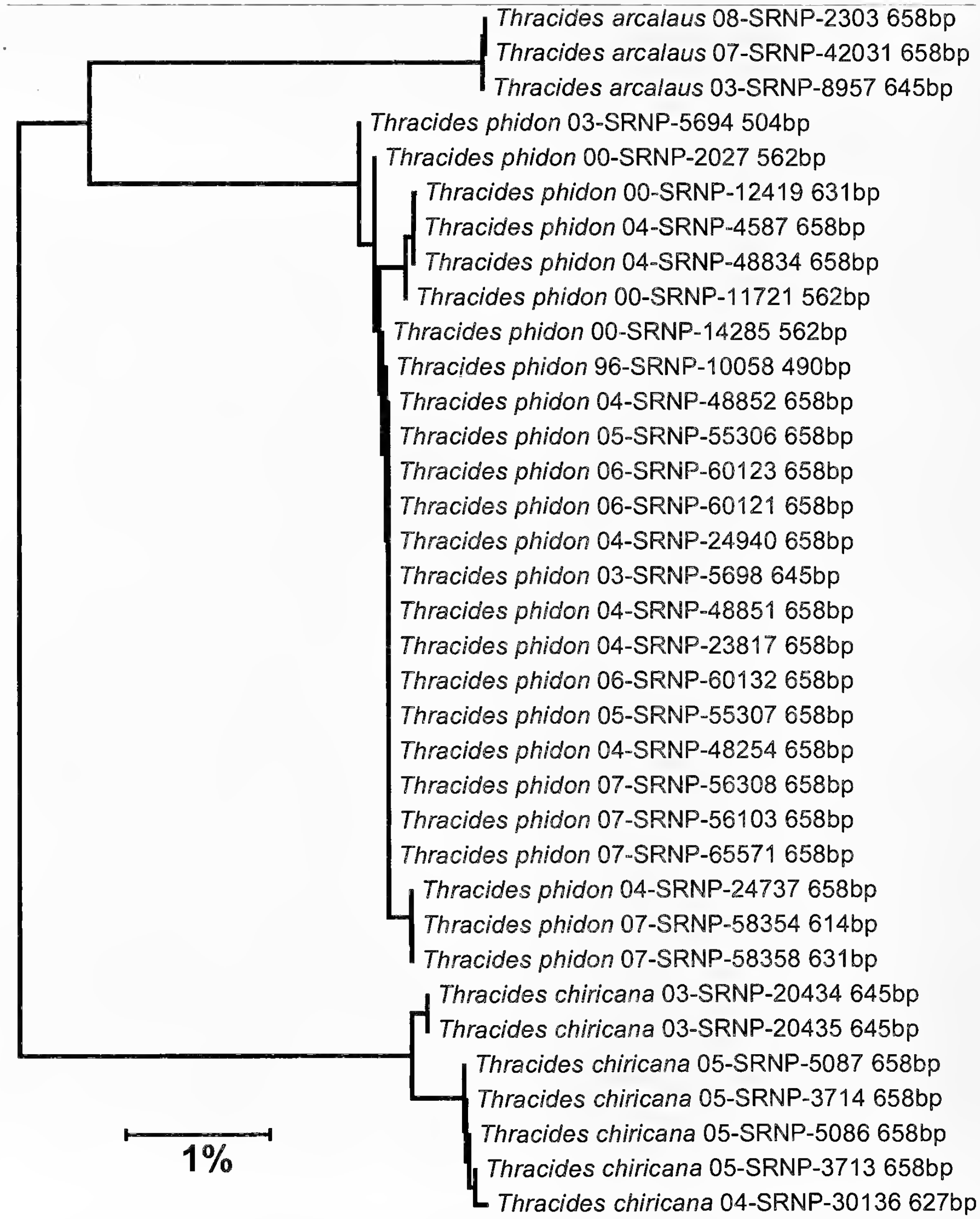


FIG. 38. Neighbor-joining tree based on Kimura two-parameter distances for COI DNA barcodes of three species of *Thracides* reared in ACG, Costa Rica. Species name, voucher code, and sequence length (i.e., number of base pairs, or bp) given for each individual.

those of species in more distantly related genera such as *Saliana*, *Calpodes*, *Panoquina* (whose thorax is dorsally humped), and *Aroma* (whose horn, although conical, is basally broad, sharply upturned, and bright white; and whose thorax and anterior abdomen are each dorsally humped) (Janzen & Hallwachs 2008).

DNA Barcodes (Fig. 38)

Together, morphologic evidence and foodplant choice indicate that *T. arcalaus* is genetically closer to *T. phidon* than it is to *T. chiricana*; and a genomic fragment as limited as a barcode says the same thing (Fig. 38). The agreement of data as different and independent as these makes a convincing case for the relationship. This is not to say that additional information from DNA sequences of certain nuclear genes is irrelevant, but only that, for some taxonomic purposes, the cheap, fast, short barcode may be all the molecular data required.

GenBank numbers for all barcoded specimens appear in Table 2.

Table 2. GenBank numbers for the individuals in Fig. 38. Numbers beginning with DQ were published in Hajibabaei *et al.* 2006; numbers beginning with FJ are new.

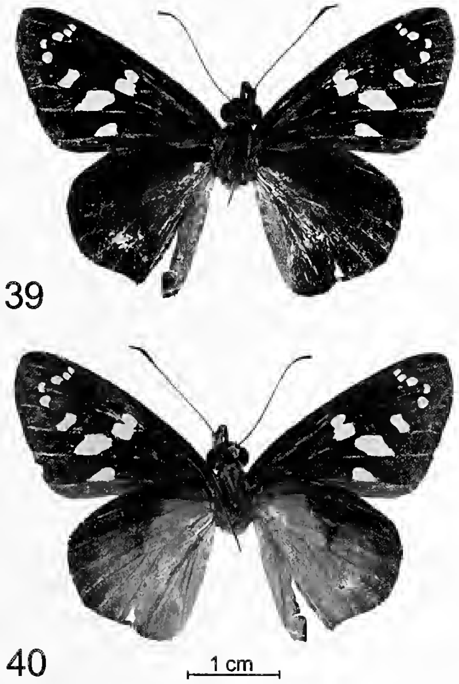
03-SNRP-8957	DQ293590
03-SNRP-20435	DQ293593
03-SNRP-20434	DQ293594
04-SNRP-30136	DQ293595
03-SNRP-5694	DQ293596
03-SNRP-5698	DQ293597
00-SNRP-11721	DQ293598
00-SNRP-12419	DQ293599
00-SNRP-14285	DQ293600
00-SNRP-2027	DQ293601
96-SNRP-10058	DQ293602
05-SNRP-3713	FJ769051
05-SNRP-5086	FJ769052
05-SNRP-3714	FJ769053
05-SNRP-5087	FJ769054
06-SNRP-60132	FJ769055
06-SNRP-60121	FJ769056
06-SNRP-60123	FJ769057
05-SNRP-55307	FJ769058
05-SNRP-55306	FJ769059
04-SNRP-24737	FJ769060
04-SNRP-48254	FJ769061
04-SNRP-23817	FJ769062
04-SNRP-48851	FJ769063
04-SNRP-24940	FJ769064
04-SNRP-48852	FJ769065
04-SNRP-48834	FJ769066
04-SNRP-4587	FJ769067
07-SNRP-58358	FJ769068
07-SNRP-58354	FJ769069
07-SNRP-65571	FJ769070
07-SNRP-56103	FJ769071
07-SNRP-56308	FJ769072
08-SNRP-2303	FJ788099
07-SNRP-42031	FJ788100

Geographic Distribution

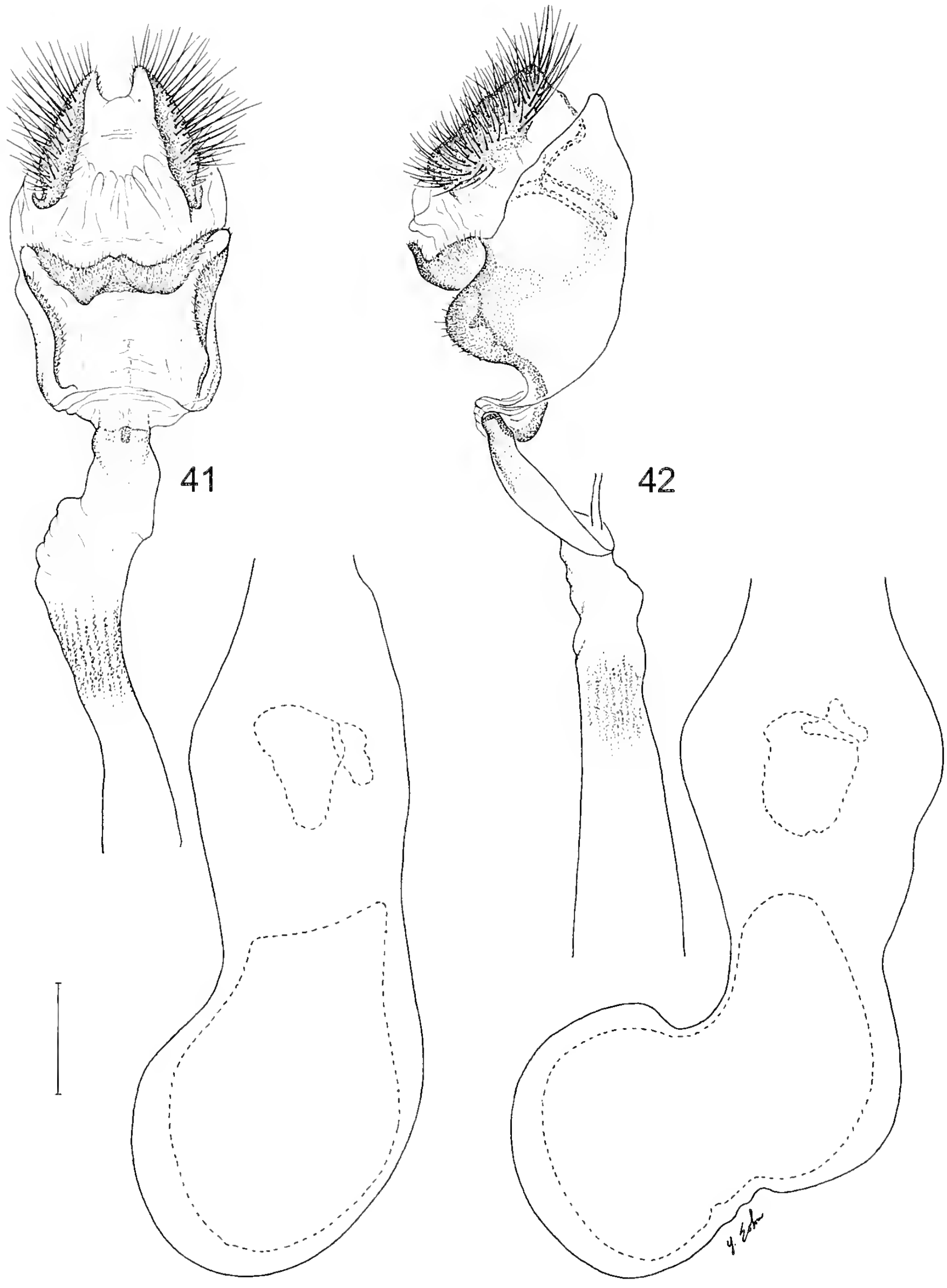
Thracides is a panneotropic genus ranging from Mexico to Bolivia, Paraguay, northeastern Argentina, and southern Brazil. Both *T. phidon* and *T. arcalaus* are widespread, spanning all but the southmost extent of the generic range. Each of these taxa probably consists of more than one biologic species. *Thracides chiricana* is rare in collections and of limited and uncertain distribution (known from Costa Rica and Panama). It is the northern taxon in the *nanea* species complex, which is mainly South American (known from Colombia, eastern Peru, and Brazil) (see Names).

pyrex Postscript (Figs. 39–42)

The following illustrations and observations are provided both to warrant the exclusion of *pyrex* from *Thracides* and to aid future efforts in placing this



Figs. 39, 40. Adult female of *pyrex*, "IX-XI-1992 100 km L [= east of] / PUERTO MALDONADO / PERU. Tello leg.," Mielke collection (Burns genitalia dissection X-6392). **39,** Dorsal view. **40,** Ventral view.



FIGS. 41, 42. Female genitalia (dissection X-6392) of mated *pyrex* in Figs. 39, 40. Long bursa copulatrix shown in two parts; persistent spermatophore(s) indicated; scale = 1 mm. **41,** Ventral view. **42,** Right lateral view.

skipper to genus. The wings of *pyrex* (Figs. 39, 40) are rounder than are those of *Thracides*, and the forewing does not extend as far beyond the hindwing as it does in *Thracides*. In *Thracides* the club of the antenna swells gradually, but conspicuously, and then decreases slightly in thickness before turning sharply backward into a long, delicate apiculus. The nudum segments are somewhat evenly divided between the club and the apiculus (e.g., 7/10 in *T. arcalaus*, 8/10 to 8/11 in *T. phidon*, 8/10 to 9/13 in *T. chiricana*, and 8/10 to 9/12 in the remaining species of *Thracides*). In the lone specimen of *pyrex*, the less damaged antennal club (which lacks one or more terminal segments) is slender throughout, the apiculus is not sharply reflexed, and the nudum (comprising 12+ segments) is entirely on the apiculus.

Genitalia can be just as useful in removing misfits from a polyphyletic genus as they are in bringing truly congeneric species together. Compare the mostly membranous female genitalia of *pyrex* (Figs. 41, 42) with the much more sclerotized female genitalia of *Thracides* (Figs. 28–31). In *pyrex*, the lamella antevaginalis is anteroventrally membranous and laterally sclerotized in a pair of small plates. As in *Thracides*, the sclerotized lamella postvaginalis is narrow and transverse, spanning the width of the genitalia; but its posterior edge, in *pyrex*, is shaped like a bracket whose posteriorly directed, midventral point is slightly notched. The beginning of the ductus bursae is lightly sclerotized ventrally and ventrolaterally. The connection of the ductus seminalis to the ductus bursae is conspicuously anterior to the ostium bursae. The outer edge of an ovipositor lobe, in lateral view, is straight instead of curved; and the entire structure looks more rectangular than elliptical.

Differences in the shape of the corpus bursae are irrelevant. The corpus bursae is collapsed in reared females (Figs. 29–31) because they are virgin. In wild-caught females (Figs. 28, 41, 42), the corpus bursae is distended because those females have mated and received one or more spermatophores—parts of which persist in the figured *pyrex* female (Figs. 41, 42), despite KOH-dissection.

ACKNOWLEDGEMENTS

We thank Sarah Burns for divers assistance, Donald Harvey for dissecting genitalia, Young Sohn for figuring genitalia, Karie Darrow for photographing adults and assembling plates, Olaf Mielke for photos of holotypes and the loan of critical specimens, Tanya Dapkey for plucking and shipping legs for DNA barcoding, parataxonomists for finding and rearing caterpillars and adults, ACG for conserving the ecosystems in which they live, Sujeevan Ratnasingham for facilitating analysis of the DNA sequence data, and Stephanie Kirk for aid with lab work. Support for this study came from the National Museum of Natural History Small Grants Program (J.M.B.); from National Science Foundation grants BSR 9024770 and DEB 9306296, 9400829, 9705072, 0072730, and 0515699 (D.H.J.); and from grants from the Gordon and Betty Moore Foundation and Genome Canada through the Ontario Genomics Institute (P.D.N.H.).

LITERATURE CITED

BURNS, J. M. 1994. Genitalia at the generic level: *Atrytone* restricted, *Anatrytone* resurrected, new genus *Quasimellana*—and yes! we have no *Mellanas* (Hesperiidae). J. Lepid. Soc. 48: 273–337.

_____. 1996. Genitalia and the proper genus: *Codatractus* gets *mysie* and *uvydixa*—in a compact *cyda* group—as well as a *hyster*ectomy, while *Cephise* gets part of *Polythrix* (Hesperiidae: Pyrginae). J. Lepid. Soc. 50: 173–216.

_____. 2000. *Pyrgus communis* and *Pyrgus albescens* (Hesperiidae: Pyrginae) are separate transcontinental species with variable but diagnostic valves. J. Lepid. Soc. 54: 52–71.

BURNS, J. M., D. H. JANZEN, M. HAJIBABAEI, W. HALLWACHS, & P. D. N. HEBERT. 2008. DNA barcodes and cryptic species of skipper butterflies in the genus *Perichares* in Area de Conservación Guanacaste, Costa Rica. Proc. Natl. Acad. Sci. USA 105: 6350–6355.

COCK, M. J. W. 2005. The skipper butterflies (Hesperiidae) of Trinidad. Part 13, Hesperiinae, genera group K. Living World, J. Trinidad and Tobago Field Nat. Club 2005: 23–47.

EVANS, W. H. 1955. A catalogue of the American Hesperiidae indicating the classification and nomenclature adopted in the British Museum (Natural History). Part IV (Groups H to P). Hesperiinae and Megathyminae. British Museum, London. 499 pp., pls. 54–88.

HAJIBABAEI, M., D. H. JANZEN, J. M. BURNS, W. HALLWACHS, & P. D. N. HEBERT. 2006. DNA barcodes distinguish species of tropical Lepidoptera. Proc. Natl. Acad. Sci. USA 103: 968–971.

HEBERT, P. D. N., E. H. PENTON, J. M. BURNS, D. H. JANZEN, & W. HALLWACHS. 2004. Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator*. Proc. Natl. Acad. Sci. USA 101: 14812–14817.

JANZEN, D. H. & W. HALLWACHS. 2008. Event-based database of caterpillars, their host plants, and their parasitoids in Area de Conservación Guanacaste, northwestern Costa Rica. (http://janzen.sas.upenn.edu).

MIELKE, O. H. H. 1989. Sobre os tipos de Hesperiidae descritos por Roeber (Lepidoptera). Rev. Brasileira Zool. 6: 131–146.

_____. 2004. Hesperioidea. Pp. 3–11, 25–86. *In* Lamas, G. (ed.), Checklist: Part 4A, Hesperioidea-Papilionoidea. *In* Heppner, J. B. (ed.), Atlas Neotrop. Lepid. vol. 5A. Assoc. Trop. Lepid., Scientific Publishers, Gainesville, Florida.

_____. 2005. Catalogue of the American Hesperioidea: Hesperiidae (Lepidoptera), vol. 5, Hesperiinae 2, pp. 1059–1383. Soc. Brasileira Zool., Curitiba, Brazil.

MOSS, A. M. 1949. Biological notes on some "Hesperiidae" of Para and the Amazon (Lep. Rhop.). Acta Zool. Lilloana 7: 27–79, pls. I–V.

RÖBER, J. 1926. Neue tropische Falter. Ent. Rundschau 43: 26–27.

SCUDDER, S. H. & E. BURGESS. 1870. On asymmetry in the appendages of hexapod insects, especially as illustrated in the lepidopterous genus *Nisoniades*. Proc. Boston Soc. Nat. Hist. 13: 282–306.

Received for publication 3 December 2008; revised and accepted 30 April 2009.

Journal of the Lepidopterists' Society
63(3), 2009, 154–163

THE COMPLEX HISTORY OF "INSECTS INJURIOUS TO VEGETATION" BY THADDEUS W. HARRIS, WITH A DATE CORRECTION AND LECTOTYPE DESIGNATION FOR *VANESSA COMMA* HARRIS (NYMPHALIDAE)

JOHN V. CALHOUN
977 Wicks Dr., Palm Harbor, FL 34684,
Research Associate: McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, Gainesville, FL;
Florida State Collection of Arthropods, DPI, FDACS, Gainesville, FL.

ABSTRACT. In 1841, Thaddeus W. Harris (1795-1856) published *A Report on the Insects of Massachusetts, Injurious to Vegetation.* Three more editions of the book were issued, one posthumously. Many taxa of Lepidoptera were described in the book, including twelve butterflies. The book's complex history is reviewed and publication dates of each edition are proposed. The publication date of *Vanessa comma* Harris is corrected and a lectotype of this taxon is designated. It is also revealed that Samuel Henshaw (1852-1941) and Charles W. Johnson (1863–1932) prepared determination and type labels contained in the insect collection of T. W. Harris

Additional key words: Charles W. Johnson, Lepidoptera, Samuel Henshaw, Thomas Say, type locality.

In 1841, Thaddeus William Harris (1795-1856) authored a groundbreaking publication on injurious insects, which was commended for its scholarly detail and "familiar language" (Harris 1841). The work was so popular that it was revised twice and reprinted for many years. Harris' son, Edward Doubleday Harris, described the book as a "ready helper to every student of entomology in the land" (Harris 1882). Among others, it inspired the entomological pursuits of John H. Comstock and Leland O. Howard (Howard 1930, Herrick & Smith 1953). Comstock (1897) credited the book with having "done more to stimulate an interest in the study of insects than any other American work." In addition to providing practical details on the biology of insects, it contained the descriptions of many new taxa, including Lepidoptera.

Harris' book is considered among the classics of early American zoological literature, yet its production remains poorly documented. Brown (1975) revealed that the final edition consisted of several issues. Elliott (2008) discussed some aspects of the book and its impact on the entomological community. My own analysis of this influential work exposed a complicated history that extended over 50 years. Due to confusion about the various editions of Harris' book, the description of the butterfly *Vanessa comma* Harris (=*Polygonia comma*) was repeatedly attributed to the wrong year. As an adjunct to this study, I also examined Harris' insect collection and associated manuscripts to better understand his concept of *V. comma*.

METHODS

Information about the book by T. W. Harris was obtained from copies in bookstores and libraries (including my own), as well as descriptions and photographs of numerous copies for sale on the Internet. Additional facts were retrieved from historical literature sources. Relevant manuscripts were reviewed in the Ernst Mayr Library of the Museum of Comparative Zoology (MCZ), Harvard University. Copies of additional manuscripts were received from the Mayr Library and the Cambridge Historical Society. Also examined were butterfly specimens and labels in the Harris insect collection, MCZ. Label calligraphy was analyzed using handwritten letters in the Mayr Library and images from the MCZ Type Database (MCZ 2006).

RESULTS

The *Report*. In February 1837, the Boston Society of Natural History (BSNH) recommended to the Massachusetts Legislature that the state's animals and plants be more thoroughly surveyed (Bouvé 1880). In April of that year, after conferring with a committee from the BSNH, the Legislature authorized a geological, mineralogical, botanical, and zoological survey of the state (Emerson 1839). Following his earlier successes in compiling lists of all the known insects of Massachusetts (Harris 1833, 1835), Thaddeus W. Harris was appointed to serve as the Commissioner for the entomological segment of the new survey. Harris submitted a portion of his report to the Massachusetts Legislature in April 1838 (Everett 1838). Comprising only the Coleoptera, it was later published with several other preliminary survey reports (Harris 1838). Harris requested additional time to complete the remainder of his report (Emerson 1838).

Harris had previously expressed his disappointment in the lack of publications on American insects, stating, "There is no work on Entomology fully applicable to the wants of the rising generation in this country" ([Calvert] 1940). With this in mind, he continued to develop his survey report, basing it on a manuscript initially entitled "Habits of some of the Insects injurious to vegetation in the vicinity of Boston, Massachusetts" (Mayr Library). On 20 January 1840 Harris wrote that he was "very busily employed" in finishing his report, which he hoped to present to the Massachusetts Legislature before the end of February (fair copy letter to E. C. Herrick, Mayr Library). Far exceeding this deadline, Harris disclosed on 12 April 1841 that his final report was "already in the press" with 240 pages printed, but "150 pages or more are still to be written." He also noted, "it must be finished before July" (draft letter to E. Doubleday, Mayr Library).

Printing was nearly completed by 24 November 1841, when Harris mentioned that he had sent a "specimen" (probably unbound printed pages) to his friend Edward C. Herrick, stating, "I regret that the Report had not been more abridged before passing through the press" (fair copy letter to Herrick, Mayr Library). An incomplete advanced copy was also sent to the North American Review, prompting that publication to request a sample of the title page (undated note from T. D. Treadwell, Cambridge Historical Society). The front matter (prefatory pages) was printed after Harris supplied the printer with a handwritten example of the title page, which included instructions for the insertion of the table of contents and an introductory letter to George B. Emerson, dated 1 December 1841 (Cambridge Historical Society). Emerson served as the Chairman of the Commissioners on the Zoological and Botanical Survey of Massachusetts.

The Massachusetts Legislature authorized that 1,500 copies of each survey report be printed and distributed almost entirely within the State of Massachusetts (Massachusetts 1839). Harris was given ten copies of his own report, which was published under the title, *A Report on the Insects of Massachusetts, Injurious to Vegetation* (Harris 1841). The date of Harris' introductory letter suggests that there was insufficient time to complete the printing and binding of the *Report* before the end of December 1841. Nonetheless, Harris maintained that it was printed and submitted to the Massachusetts Legislature in 1841 (Harris 1842, 1852). This claim is supported by the State of Massachusetts (1851a). The swift publication of the *Report* was probably made possible by its inexpensive binding. Like previous survey reports by Emerson (1839), Dewey (1840), Emmons (1840), and Gould (1841), Harris' *Report* was bound in tan paper wrappers. Nearly all surviving copies of the Report possess later bindings of board covers, thus few modern workers have seen the book in its original form (Fig. 1). For the purposes of the Code (ICZN 1999, Art. 21.3), a publication date of 31 December 1841 is tentatively adopted for the *Report*.

Most copies of the *Report* were probably distributed after December 1841. The Boston Society of Natural History received a copy from the Massachusetts Legislature in March 1842 ([Dillaway] 1842]). A copy in the Library of Congress is inscribed "Presented by the Commonwealth of Massachusetts May 9th 1842." Another in the Entomology Library of the National Museum of Natural History (Smithsonian Institution) includes the notation, "Received June 12th 1843." This copy was possibly received by the U.S. District Court of Massachusetts as a record of publication (R. Greene, pers. comm.).

The *Report* was written for the benefit of agriculture, and was the first government publication on insects to be issued in the United States. Harris understood that a more comprehensive study would be scientifically valuable, but not "expected to prove either interesting or particularly useful to the great body of the people" (Harris 1841). Many new insects were described in the *Report*, including two butterflies: *Thecla humuli* Harris (=*Strymon melinus humuli*) and *Vanessa comma*. Because of their economic importance, Harris was very interested in Lepidoptera. He wrote, "There are perhaps no insects which are so commonly and so universally destructive as caterpillars" (Harris 1841). Harris devoted 162 pages of the *Report* to Lepidoptera, much more than for any other order of insects.

Harris was very critical of his *Report*, citing its "imperfections" and hoping that there was "enough of readable & practically useful matter in it to compensate for its numerous faults" (fair copy letter to E. C.

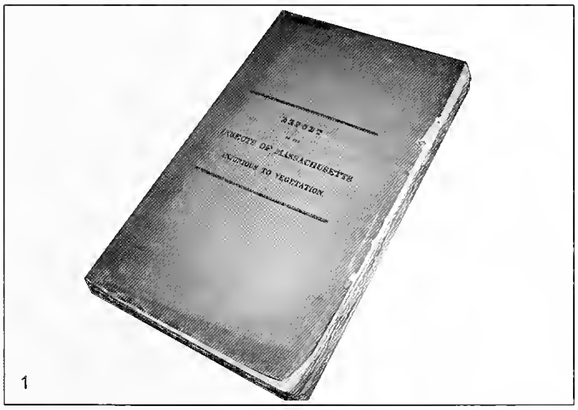


FIG. 1. *A Report on the Insects of Massachusetts, Injurious to Vegetation* by Thaddeus W. Harris, as originally issued in 1841 in printed paper wrappers (J. V. Calhoun).

Herrick, 24 Nov. 1841, Mayr Library; Harris 1841). Nonetheless, other opinions were very favorable, forging Harris' reputation as a competent entomologist. The British lepidopterist Edward Doubleday informed Harris, "We are all delighted with your *Report*." Doubleday also requested that a few more copies be sent "as presents for your English correspondents" (letter dated 30 April 1842, Mayr Library). Another British entomologist, John Curtis, considered it to be the best book of its kind ever published (letter from E. Doubleday, 16 April 1846, Mayr Library). Published reviews praised the *Report*, asserting that it would "induce many more to assist in reaping the large harvest which lies before American entomologists" (Anon. 1842). Despite this positive reception, some readers bemoaned the book's lack of illustrations. Morris (1846) believed that figures would have been helpful to those who "do not easily recognize an insect from a bare description, however accurate." Reviewers also complained about the restricted availability of the *Report*, which induced one critic to complain that it was "only furnished to a number which must be small in comparison with the number of those who would wish to read it" ([Peabody] 1842).

The first *Treatise*. Before the *Report* was completed, Harris realized its significance and decided to reissue the book at his own expense. The *Report* was intended primarily for the Massachusetts Legislature, thus Harris desired to provide a version "for more general circulation, and to meet the wishes of some of his friends" (Harris 1842). Because many of the insects in the *Report* occurred throughout New England, Harris decided to give the book "a more comprehensive title" (Harris 1852). He no longer considered it to be a mere report, but rather *A Treatise on some of the Insects of New England which are Injurious to Vegetation* (Harris 1842).

On 1 January 1841, Harris stated that publication of the *Treatise* had been delayed "in order that the '*Report*' may be first issued by the Secretary of State" (letter to E. C. Herrick, Mayr Library). However, the delay continued into the following year, well beyond the issuance of the *Report*. Harris hinted at political pressures, remarking, "it is enough to say, perhaps, that there were strong reasons inclining me to submit to a delay, not of my own seeking." He also admitted that he did not want to "interfere with the distribution of the State document by an untimely or overhasty publication of my own edition" (fair copy letter to E. C. Herrick, 3 Nov. 1842, Mayr Library). Harris did not expect to sell more than fifty copies of the *Treatise* at first, after which he would keep the remainder "till they are called for, & if no demand is made for them I can give them away you know, or sell them to the trunk makers" (fair copy letter to E. C. Herrick, 1 Jan. 1841, Mayr Library).

Harris chose John Owen to be the publisher of the *Treatise*, possibly because Owen was a fellow Harvard graduate who had an interest in insects (Harris 1841, 1842). Owen is best known for publishing the early works of another Harvard graduate, Henry Wadsworth Longfellow (Wilson & Fiske 1900). Only 250 copies of the *Treatise* were printed (Elliott 2008) and Harris paid extra to bind them in cloth boards. They were available for distribution on 20 October 1842, which is hereby adopted as the date of publication. Two weeks later, Harris granted permission to his friend, E. C. Herrick, to help sell copies for two dollars apiece (fair copy letter to Herrick, 3 Nov. 1842, Mayr Library). A reviewer of the *Treatise* proclaimed, "Much knowledge may be gained on this topic from the pages of the work before us, and many valuable hints suggested" (Anon. 1843).

Harris presented copies of his *Treatise* to various societies and libraries. The Boston Society of Natural History received a copy from Harris in January 1843 ([Dillaway] 1843). Probably around this same time, Harris provided a copy to the Massachusetts Horticultural Society (M. Horn pers. comm.). Harris also distributed copies outside of Massachusetts, as demonstrated by his inscription in my own copy that reads, "Bowdoin College Library from the Author." Bowdoin College is located in Brunswick, Maine. This copy may have influenced the entomologist Alpheus S. Packard, Jr., who grew up in Brunswick and attended Bowdoin College. Harris probably also sent copies of the *Treatise* to his foreign correspondents, as this title was included in the library of his good friend, Edward Doubleday (Stevens 1850). Despite his modest expectations, Harris had little trouble dispensing copies of the *Treatise*.

The second *Treatise*. In November 1842, Harris wrote, "Should the [*Treatise*] sell readily, and a call is made for another edition, I may think it best to issue one" (fair copy letter to E. C. Herrick, 3 Nov. 1842, Mayr Library). Harris explained, "In the course of eight years, all the copies of the *Report*, and of the other impression were entirely disposed of. Meanwhile, some materials for a new edition were collected" (Harris 1852). In 1850, the Massachusetts Legislature ordered that 2,000 copies of a second edition of the *Treatise* be published, and that Harris "be authorized to secure the copyright of all future editions for the benefit of himself and his heirs" (Massachusetts 1851a, 1851b). As compensation for updating the text and supervising its printing, Harris received $150 (Massachusetts 1851a) (usually misquoted as $175). Although this sum seems trivial, it is equivalent to over $4,000 today.

Harris completed the changes for this edition by 23 February 1852, when he wrote, "notified the Secretary that I was ready for the printer" (Harris notes, Mayr Library). Although he received the third proof from the printer on 7 April 1852, the date of the preface indicates that the book was not available until after 15 October 1852 (Harris 1852). Harris filed for the copyright before the title pages were printed. A publication date of 31 October 1852 is tentatively adopted for the second edition of the *Treatise*.

Copies of this edition were bound in tan paper wrappers with brown cloth spines. As with the *Report*, few surviving volumes possess their fragile original wrappers, which bore the incorrect title "Report on Insects Injurious to Vegetation." Copies were primarily distributed to agricultural and horticultural societies in Massachusetts. Harris received 200 copies (Massachusetts 1851a, 1851b). Few of the remaining books were available for purchase (Anon. 1853).

Harris was again critical of his work, describing the *Treatise* as "very homely" and worrying that it was "beneath the dignity of a naturalist" (draft letter to J. O. Westwood, 1854, Mayr Library). Despite this modesty, reviewers commended the book as "neither exclusively scientific, nor exclusively practical" (Anon. 1853). This edition was depleted and the book remained in high demand.

The third *Treatise*. In 1858, two years after Harris' death, a committee was formed by the Boston Society of Natural History to explore the possibility of reissuing the *Treatise*, "if possible with illustrations" (Anon. 1859). The committee recommended that the society lobby the Massachusetts Legislature and "take the steps necessary to procure a new edition" (Parsons 1859). In April 1859, the Massachusetts Legislature ordered the production of no more than 2,500 copies of a third edition at a cost not exceeding $8,000 (Massachusetts, 1859a, 1859b, 1861a, 1861b). Published in 1862, it was edited by Charles L. Flint, Secretary of the Massachusetts Board of Agriculture. Flint was authorized to "procure such assistance as may be necessary" (Massachusetts 1859a). He solicited the help of several entomologists, including the lepidopterist John G. Morris, who reviewed sections and contributed footnote comments. Flint targeted an even greater audience by removing "New England" from the title and adding over 270 wood cut engravings and eight hand-colored steel plate engravings, all created exclusively for the book under the supervision of the celebrated zoologist Louis Agassiz.

The Massachusetts Legislature resolved that the new edition would also incorporate "suitable additions" (Massachusetts 1859b). At the urging of the entomologist Samuel H. Scudder, Flint inserted additional text on butterflies (Scudder 1889). This text, which included the descriptions of ten new taxa, was resurrected from Harris' draft manuscript. This manuscript was acquired after Harris' death by the Boston Society of Natural History, whose museum evolved into the Boston Museum of Science. The manuscript was gifted in 1992 to the Ernst Mayr Library along with numerous other Harris documents (Calhoun 2007). It is apparent that Harris wrote his entire segment on butterflies prior to 1841, but crossed out extensive passages before publishing his *Report*. Harris admitted that he left out more than 30 pages from his *Report* to achieve a "less voluminous size" (letter to E. C. Herrick, 24 Nov. 1841, Mayr Library). Flint restored the section on butterflies as originally written by Harris, adding nearly 33 printed pages to the *Treatise* (all or portions of pgs. 266–269, 272–278, 280–295, 298, and 302–306). The third edition incorporated 46 more butterfly taxa than previously.

This edition of the *Treatise*, with its attractive illustrations, was described as "magnificent" (Cady 1862, Hoyt 1862). Hinks (1862) declared, "No one need desire a more pleasing book for his library than Dr. Harris's work in its present form." One reviewer admired the color plates, claiming to perceive "the down on a butterfly's wing" (Anon. 1862a). The plates evoked admiration from a popular magazine; "All creeping and flying things seem harmlessly swarming in vivid beauty of color over its pages. Such gorgeous moths we never saw before out of the flower-beds, and there are some butterflies and caterpillars reposing here and there between the leaves that must have slipped in and gone to sleep on a fine warm day in July" (Anon. 1862b). Not everyone, however, was happy with the illustrations. The Ohio lepidopterist Eugene Pilate described the wood cut engravings as "very poor, coarse, indistinct, confused, and Black indeed" (letter to H. Strecker, 23 Dec. 1874, Field Mus. Nat. His.). Such criticism notwithstanding, an entire section of the whimsical book *Catoninetales* (Linton 1891) was based on this edition of the *Treatise*; "It is that insect Harris book, Ma said, the nasty insect book put maggots in your head…The more curious may look in this book for private circulation 'Of the Insects injurious to vegetation'." Harris' work had finally reached beyond farmers and entomologists, earning recognition within trendy society.

The publication of the third edition of the *Treatise* was complicated. Brown (1975) recognized multiple issues, but this notion was rejected by Gatrelle (2002). Although some details remain obscure, additional evidence exposes a complex production history that embraces at least five issues and numerous reprintings.

Progress on the third edition of the *Treatise* was considered "satisfactory" by 5 January 1861 (Andrew 1861). It was in press and expected to be issued during the ensuing summer. It was delayed, however, until early January 1862 when copies were "nearly ready for delivery" (Flint 1861, Andrew 1862). Harris' widow, Catherine H. Harris, filed the copyright before the title pages were printed in 1862. This edition was available by 22 January 1862 (Flint 1862), which is tentatively adopted as the publication date.

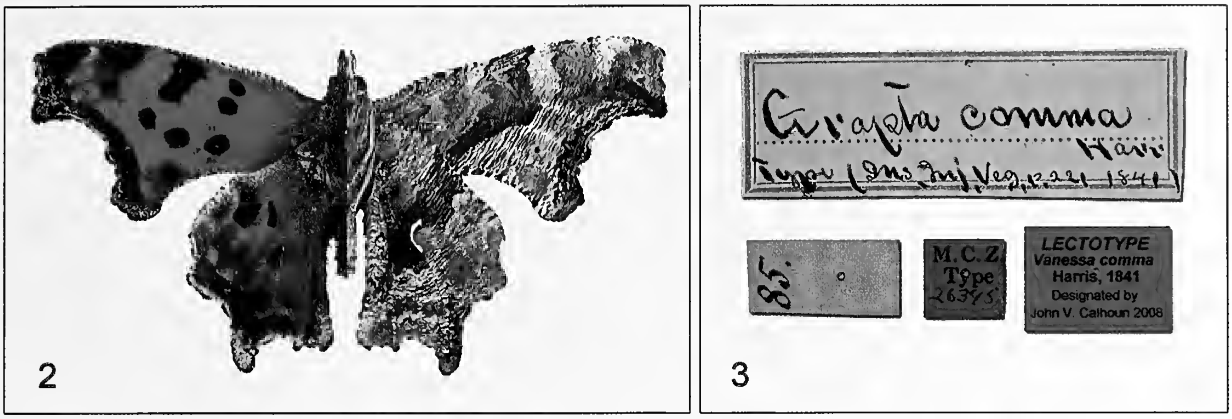
Initial copies of the third edition were, by law, gratuitously distributed to every town in Massachusetts, as well as all agricultural and horticultural societies in the state. This was intended to bring the book "within the reach of most farmers who desire to possess it" (Flint 1862). Flint referred to this first issue as the "edition for the Commonwealth," but it was also known as the State Edition (Harris 1862a, French 1862, Brown 1975). These copies were elaborately bound in dark brown embossed cloth with the state seal of Massachusetts on the spine. In February 1862 the Massachusetts Legislature determined how the copies would be distributed (Massachusetts 1862). Among the many recipients was the Boston Society of Natural History, who received 15 copies a few days later (Scudder 1862). Twenty-five copies were given to the legal representatives of T. W. Harris (Massachusetts 1861c). I possess a neatly rebound presentation copy that was inscribed in 1864 by "C. Harris" (probably Catherine Harris or her son, Charles Harris) to William Minot, a prominent Boston attorney.

Pending the success of the first issue, the Massachusetts Legislature made provisions in April 1861 to authorize the printing of additional issues "for the benefit of the heirs of the late Dr. Harris, but without any further expense to the Commonwealth" (Massachusetts 1861c). The anticipated popularity of the State Edition prompted C. L. Flint to amend the original preface in January 1862 to announce the publication of "one or more editions designed for a wider circulation than that for the State can be expected to have" (Harris 1862a). In this case, Flint used the term "editions" to denote slightly different versions, or issues, of the same book.

Issues of the third edition that were designed for wider circulation were collectively recognized as the Flint Edition (see Banks 1900). Flint altered the title to include references to the added text and illustrations. A limited issue was initially made available to Flint expressly for private circulation (Harris 1862b). Issues for general release (Harris 1862c) included early copies that were printed on premium paper that sold for $6.00 each (Hoyt 1862). A more affordable issue was available by May 1862, offered with uncolored or colored plates for $2.50 and $3.50, respectively (Cady 1862, French 1862, Hoyt 1862). This issue was hugely popular. Although the Governor of Massachusetts had stated that the book would "not be reproduced for another twenty years" (Andrew 1862), the later issue of the Flint Edition was reprinted by four different publishers in Boston, New York, and Philadelphia. New impressions appeared in 1862, 1863, 1869, 1880, 1883, 1884, and 1890. The publishers were commended for reprinting the book without alteration ([Walsh & Riley] 1869). Copies were bound in tooled boards of green, brown, burgundy, or blue cloth, with an image of the moth *Eumorpha achemon* (Drury) on the cover, based on the engraving for Plate V, fig. 3 in the book. This issue is the most common incarnation of the *Treatise*.

Confusion. Because of their complex publication histories, various aspects of the *Report* and *Treatise* were misconstrued. Some authors (e.g. [Dillaway] 1842, Hagen 1862, Drake 1872, Dyar 1902) provided incorrect dates of publication. Others treated the *Report* and *Treatise* as a single series, confusing the editions and even alluding to a "4th edition" (Osten-Sacken 1878, Strecker 1878, Holland 1898, Gatrelle 2002). The State of Massachusetts (e.g. 1851a, 1862b) casually referred to the *Treatise* as the "Report," which may explain why the cover of the second edition of the *Treatise* bore an improper title. More recently, the University of Michigan Library and Hard Press began offering print-on-demand copies of the third edition of the *Treatise* under the title of the second edition.

Mistakes also found their way into original description citations. Kirby (1871) and Beccaloni *et al*. (2003) wrongly attributed the descriptions of T. humuli and *V. comma* to the 1852 edition of the *Treatise*. Probably following Kirby (1871), Scudder (1875) stated that *V. comma* "was not named until 1852." Perhaps the result of a typesetting error, Morris (1862) attributed the description of *V. comma* to 1842, rather than 1841. This error proved pervasive. The description of *V. comma* was attributed to 1842 in subsequent checklists and catalogs by Strecker (1878), Skinner (1898), Dyar (1902), dos Passos (1964), Miller & Brown (1981, 1983), Ferris (1989), Opler & Warren (2002, and later editions), and Pelham (2008). Most authors correctly attributed the description of *T. humuli* to 1841. In his bibliography of original descriptions, Bridges (1984) expressly recorded "Harris 1841" for *T. humuli* and "Harris 1842" for *V. comma*. Countless other publications have unwittingly reiterated this error. The correct citations for these taxa should read as follows: *Thecla humuli* Harris, 1841, Rpt. Ins. Mass. Inj. Veg.:215–216; *Vanessa comma* Harris, 1841, Rpt. Ins.



FIGS. 2–3. Lectotype of *Vanessa comma*. **2**, dorsal (left) and ventral aspects. **3**, associated labels, including the "type" label by C. W. Johnson. Images courtesy MCZ

Mass. Inj. Veg.:221.

Vanessa comma. Harris (1841) did not suggest a type locality for *V. comma*. Miller & Brown (1981) proposed "New England," but the description of *V. comma* in the *Report* makes Massachusetts a more suitable choice. Pelham (2008) suggested "Massachusetts" for this reason. Moreover, all the new descriptions of butterflies that appeared in the *Report* and *Treatise* were derived from a manuscript on the insects of Massachusetts (Calhoun 2007). Unless another (or more specific) type locality was suggested by Harris, all such taxa should tentatively be attributed to Massachusetts.

Referring to *V. comma*, Harris (1841) wrote, "The butterflies appear first in the beginning of May; I have obtained them from the chrysalids in the middle of July, and on the first of September." These records presumably correspond to three male specimens and one pupal exuvia of *Polygonia comma* in the T. W. Harris insect collection, MCZ. One of these specimens is a ventral mount and another currently has a detached right forewing. Although all three specimens lack data, Harris documented them in his "Index Lepidopterum," a manuscript catalog that is also preserved in MCZ. Harris numbered his specimens in accordance with the entries in his "Index." His entry for *V. comma* (no. 85) lists records for "Sept. 1, 1827," "May 1, 1828," "from pupa July 15, [18]29," and "Sept. 10, 1841." Given that Harris supposedly possessed three specimens prior to 1841, I did not assign the latter record to any of the surviving specimens. Although Harris (1841) implied that his specimen from 1 September was obtained ex-pupa, he made no mention of this in his "Index," and there is only one pupal exuvia in his collection. The specimen with a detached right forewing probably served as the model for the illustration of *P. comma* on Plate IV of the third edition of the *Treatise*.

Unlike Boisduval & Le Conte (1829–[1837]), who believed that specimens of the then undescribed *P. comma* were applicable to the Old World butterfly *Polygonia c-album* (L.), Harris wrestled with the identity of his *Polygonia* specimens for many years. As early as 1826, he and the naturalist Nicholas M. Hentz discussed the likelihood that the "American butterfly is a distinct species" from *P. c-album* (letter from Hentz, 1 January 1826, Mayr Library; Scudder 1869). In his "Index," Harris originally identified his specimens of *P. comma* as "Progne?" (i.e. *Polygonia progne* (Cramer)). Harris also identified them as *Vanessa progne* among a series of small papers that he used in 1837 to record the species of North American butterflies in his collection (Mayr Library). He observed that these specimens were "certainly much like *c-album*," but he made no allusions to another species of *Polygonia* except *P. interrogationis* (F.). Dates in his "Index" suggest that Harris became convinced that he possessed another species after August 1839 when he actually collected adults of *P. progne*. He then created a new entry in his "Index" for *progne*, noting that he "formerly confounded" this species with another, which he subsequently named *Vanessa comma*. Harris' collection contains four adult specimens and two pupal exuviae of *P. progne*. Harris gave no localities in his "Index" for *P. comma* or *P. progne*, but he did not always record this information for specimens that he presumably collected in the vicinity of Boston, Massachusetts. When Harris obtained his specimens of *P. comma* during the 1820s, his field explorations were almost entirely confined to the vicinity of Milton, Massachusetts where he resided (Elliott 2008).

Harris' Latin name, *comma*, reflects his proposed English name of "Comma Butterfly," derived from the silvery comma-shaped markings on the ventral hindwings of the adult insect (Harris 1841). This name has its roots in England, where *P. c-album* has been known as the "Comma" since the early 18th century (Salmon 2000). The English naturalist Philip H. Gosse was the first to apply this name to the North American species, referring to the then undescribed *P. comma* as the "Orange Comma" (Gosse 1840). This name may have influenced Harris, who received a copy of Gosse's book from Edward Doubleday in 1840 (letter from Doubleday, 27 May 1840, Mayr Library). Coincidentally, Millard (1821) created the name *Papilio comma alba* for *P. c-album*, and Rennie (1832) proposed the genus *Comma* for the same species. Harris, who had limited access to European publications, probably was unaware of these earlier names.

Pinned next to the best dorsal specimen of *P. comma* in the Harris collection is a large handwritten ink label that reads, "*Grapta comma* / Harr / Type (Ins. Inj. Veg. p. 221 1841)" (Figs. 2, 3). Fifty-five similar red-bordered labels are found in the Harris butterfly collection. Most are determination labels, but some also denote "type" specimens of taxa that were described by Harris. Careful inspection revealed that none were written by Harris, nor were they prepared during his lifetime. For example, one label refers to the genus *Mitoura* Scudder, which was proposed sixteen years after Harris' death. I was able to identify the authors of these labels using other labels in the MCZ insect collection, as well as several handwritten letters and documents. It is very important to understand the provenance of labels to avoid misconceptions about the status of historical specimens.

The T. W. Harris insect collection arrived at MZC in 1941 (Darlington 1941). It was previously in the possession of the BSNH after being purchased in 1858 from Harris' widow, Catherine Harris ([Binney] 1859, Creed 1930). Samuel H. Scudder (1837–1911) served as Curator of the BSNH entomological collections from 1859 to 1870 (Bouvé 1880). Although Scudder "revised and arranged" the Harris butterfly collection in 1870 (Scudder 1871), none of the existing labels are in his hand, nor is the nomenclature consistent with his published writings. During the period 1876–1892, Samuel Henshaw (1852–1941) served as a general assistant in the BSNH museum (Hyatt 1900, Wade & Hyslop 1941). Henshaw worked up to "seven hours daily" with the Harris collection and other insects in the BSNH, chores that included "naming and labeling" (Hyatt 1877, Bouvé 1880, Henshaw 1895). Writing about Harris' specimens of Hemiptera in 1878, Henshaw indicated that he was attempting to "finish the arrangement of the collection" (fair copy letter to P. R. Uhler, 16 April 1878, Mayr Library). Based on the handwriting in two of Henshaw's letters from 1878, he created 41 of the large determination labels for butterflies in the Harris collection. The nomenclature is consistent with Edwards (1877), thus these labels were probably prepared around 1880.

The remaining 14 determination and type labels, including that of *Grapta comma* (Fig. 3), were prepared by Charles W. Johnson (1863–1932), who was Curator of Insects and Mollusks at the BSNH from 1903 until his death. Johnson's label calligraphy is very distinctive, something that Melander (1932) described as "neatly written." In addition, the labels that Johnson employed for many of his own specimens of Diptera in the MCZ, with red dotted lines across their centers, match those in the Harris collection. Johnson possessed a "keen sense of curatorial duties," resulting in a "methodical arrangement of specimens" (Brooks 1932). The Latin names that Johnson used suggest that he created at least some of the labels for Harris' butterflies around 1925 when he published a catalog of the Diptera in the Harris collection (Johnson 1925). Labels by Henshaw and Johnson are also associated with other Harris specimens, as well as insects in the MCZ that were collected by the pioneer entomologist Thomas Say (1787–1834). Mawdsley (1993) wrongly credited Harris for some of these type labels.

Affixed to the "type" specimen of *V. comma* is a small red label that reads, "M.C.Z. / Type / 26345" (Fig. 3). Despite this label, all three of Harris' specimens (syntypes) shared equal status as components of the name-bearing type (ICZN 1999, Art. 73.2). The "type" specimen (Fig. 2) is in good condition and represents the overwintering form, which is consistent with the original description in Harris (1841). To establish this specimen as the sole name-bearing type of *Vanessa comma* Harris, 1841, it is designated as the lectotype and labeled accordingly (Fig. 3). The type locality is suggested to be the vicinity of Milton, Massachusetts. Additional research is necessary to evaluate the status of other such "type" specimens of taxa described by Thaddeus W. Harris.

ACKNOWLEDGEMENTS

Thanks are extended to Philip D. Perkins (MCZ) for granting access to the T. W. Harris insect collection. Robert Young (Ernst Mayr Library, MCZ) allowed me to examine the Harris manuscripts and bestowed other valuable assistance. Ted Hansen supplied copies of documents from the Cambridge Historical Society (Cambridge, Massachusetts). Beverly Pope (Div. Plant Industry Library, Gainesville, Florida) helped to locate publications. Naomi Allen (State Library of Massachusetts), Richard Greene (National Museum of Natural History Library, Smithsonian Institution), Maureen Horn (Massachusetts Horticultural Society), Tracy Potter (Massachusetts Historical Society), and librarians of the Library of Congress assisted in searching for books and documents. David M. Wright alerted me to the existence of the "Index Lepidopterum." Finally, I thank David Wright and an anonymous reviewer for commenting on than manuscript.

Literature Cited

Andrew, J. A. 1861. Inaugural address of his Excellency John A. Andrew, pp. 565–591. *In* Anonymous, Acts and resolves passed by the general court of Massachusetts, in the year 1861. Together with the messages of the Governor, list of the civil government, changes of names of persons, etc, etc., etc. William White, Boston.

______. 1862. Inaugural address of his Excellency John A. Andrew, pp. 246–288. *In* Anonymous, Acts and resolves passed by the general court of Massachusetts, in the year 1862: together with the messages of the Governor, list of the civil government, changes of names of persons, etc, etc., etc. William White, Boston.

Anonymous. 1842. 9. [Review of] A report on the insects of Massachusetts, injurious to vegetation. By Thaddeus William Harris, M.D. Published agreeably to an order of the Legislature, (of Massachusetts,) by the Commissioners on the zoological and botanical survey of the State. Cambridge, 1841. pp. 459. Amer. J. Sci. & Arts 43:386–388.

______. 1843. Art. 1. [Review of] A treatise on some of the insects of New England, which are injurious to vegetation. By Thaddeus William Harris, M. D. 1 vol. 8vo. 459 pages. Cambridge, 1842. Mag. Hort., Bot. 9:216–231.

______. 1853. 3—[Review of] A treatise on some of the insects of New England, which are injurious to vegetation. By Thaddeus William Harris, M.D. Second edition. Boston. Printed by White & Potter. 1852. 8vo. Pp. 513. No. Amer. Rev. 76:255–256.

______. 1859. [Reprinting of Dr. Harris's work on insects]. Proc. Boston Soc. Nat. His. 6:416.

______. 1862a. [Harris's 'treatise on some of the insects injurious to vegetation']. Christ. Exam. 231:454–456.

______. 1862b. [Review of] A treatise on some of the insects injurious to vegetation. By Thaddeus William Harris, M. D. A new edition, enlarged and improved, with additions from the author's manuscripts and original notes. Illustrated by engravings drawn from nature under the supervision of Professor Agassiz. Edited by Charles L. Flint, Secretary of the Massachusetts State Board of Agriculture. 8vo. Atlantic Monthly 9:652.

Banks, N. 1900. A list of works on North American entomology compiled under the direction of the entomologist, for the use of students and other workers, as well as for those about to begin the collecting and study of insects. Bull. U.S. Dept. Agr., Dept. Entomol. 24:1–95.

Beccaloni, G. W., M. J. Scoble, G. S. Robinson & B. Pitkin. 2003. The global Lepidoptera names index (LepIndex). http://www.nhm.ac.uk/entomology/lepindex. Accessed 15 May 2008.

[Binney, A.] 1859. [T. W. Harris collection delivered to Boston Society of Natural History]. Proc. Boston Soc. Nat. His. 6:416.

Boisduval, J. B. A. D. de & J. E. Le Conte. 1829–[1837]. Histoire générale et iconographie des Lépidoptères et des chenilles de l'Amérique septentrionale. Librairie Encyclopédique de Roret, Paris. 228 pp., 78 pl.

Bouvé, T. T. 1880. Historical sketch of the Boston Society of Natural History; with a notice of the Linnaean Society, which preceded it. Boston Soc. Nat. His., Boston, Massachusetts. 250 pp.

Bridges, C. A. 1984. Notes on species-group names mentioned in the Miller & Brown catalogue/checklist of the Nearctic Rhopalocera (Lepidoptera). Printed by the author, Urbana, Illinois. [176] pp.

Brooks, W. S. 1932. Charles Willison Johnson. Bull. Boston Soc. Nat. His. 65:305.

Brown, F. M. 1975. The third edition of Thaddeus William Harris's "treatise on some of the insects injurious to vegetation.", 1862. Entomol. News 86:65–68.

Cady, I. F. 1862. "Insects Injurious to Vegetation." R. J. Schoolmaster 8:152.

Calhoun, J. V. 2007. The manuscripts of Thaddeus William Harris (1795–1856). News Lepid. Soc. 49:118–119.

[Calvert, P. P.] 1940. An unpublished letter of Dr. Thaddeus William Harris. Entomol. News 51:65–66.

Comstock, J. H. 1897. Insect Life: an introduction to nature-study and a guide for teachers, students, and others interested in out-of-door life. D. Appleton & Co., New York, New York. 349 pp.

Creed, P. R. (ed.). 1930. Milestones: the Boston Society of Natural History 1830–1930. Merrymount Pr., Boston, Massachusetts. 117 pp.

Darlington, P. J., Jr. 1941. The insect collection of Thaddeus W. Harris (1795–1856). Entomol. News 52:273.

Dewey, C. 1840. Report on the herbaceous flowering plants of Massachusetts, arranged according to the natural orders of Lindley and illustrated chiefly by popular descriptions of their character, properties, and uses. Published agreeably to an order of the legislature, by the Commissioners on the Zoological and Botanical Survey of the State. Folsom, Wells, & Thurston, Cambridge, Massachusetts. viii+277 pp.

[Dillaway, C. K.] 1842. Additions to the library. Proc. Boston Soc. Nat. His. 1:62–63.

______. 1843. Additions to the library. Proc. Boston Soc. Nat. His. 1:97–98.

dos Passos, C. F. 1964. A synonymic list of the Nearctic Rhopalocera. Lepid. Soc. Memoir No. 1. 145 pp.

Drake, F. S. 1872. Dictionary of American biography, including men of the time; containing nearly ten thousand notices of persons of both sexes, of native and foreign birth, who have been remarkable, or prominently connected with the arts, sciences, literature, politics, or history of the American continent. Giving also the pronunciation of many of the foreign and peculiar American names, a key to the assumed names of writers, and a supplement. James R. Osgood & Co., Boston, Massachusetts. 1019 pp.

Dyar, H. G. 1902. A list of North American Lepidoptera and key to the literature of this order of insets. Bull. United States Nat. Mus. No. 52. xix+723 pp.

Edwards, W. H. 1877. Catalogue of the diurnal Lepidoptera of America North of Mexico. Trans. Amer. Entomol. Soc. 6:1–68.

Elliott, C. A. 2008. Thaddeus William Harris (1795–1856): nature, science, and society in the life of an American naturalist. Lehigh Univ. Pr., Bethlehem, Pennsylvania. 294 pp.

Emerson, G. B. 1838. Mr. Emerson's report, pp. 53–55. *In* Emerson, G. B. (ed.), Reports of the Commissioners on the zoological survey of the State. Mass. House Doc. 72. Dutton & Wentworth, Boston, Massachusetts.

______ (ed.). 1839. Reports on the fishes, reptiles and birds of Massachusetts. Published agreeably to an order of the legislature, by the Commissioners on the Zoological and Botanical Survey of the State. Dutton & Wentworth, Boston, Massachusetts. xii+425 pp., 4 pl.

Emmons, E. 1840. Report on the quadrupeds of Massachusetts. Published agreeably to an order of the legislature, by the Commissioners on the Zoological and Botanical Survey of the State. Folsom, Wells, & Thurston, Cambridge, Massachusetts. 86 pp.

Everett, E. 1838. Special Messages. No. XI, pg. 772. *In* Massachusetts [State of], resolves of the general court of the commonwealth of Massachusetts, passed at the several sessions, commencing January, 1835, and ending April 1838. Dutton & Wentworth, Boston, Massachusetts.

FERRIS, C. D. (ed.). 1989. Supplement to: a catalogue/checklist of the butterflies of America north of Mexico. Lepid. Soc. Mem. No. 3. 103 pp.

FLINT, C. L. 1861. [notice regarding the "Treatise on insects injurious to vegetation"]. Ann. Rpt. Sec. Mass. Brd. Agric. 8:271.

_____. 1862. Harris on insects. Ann. Rpt. Sec. Mass. Brd. Agric. 9:195–196.

FRENCH, J. 1862. Insects injurious to vegetation. New Eng. Farmer 14:357–358.

GATRELLE, R. R. 2002. A review of *Poanes hobomok* (Hesperiidae: Hesperiinae) with the description of a new subspecies from the southern Appalachians. Taxon. Rpt. 3:1–8.

GOSSE, P. H. 1840. The Canadian naturalist. A series of conversations on the natural history of lower Canada. John Van Voorst, London. 372 pp.

GOULD, A. A. 1841. Report on the invertebrates of Massachusetts, comprising the mollusca, crustacean, annelida, and radiata. Published agreeably to an order of the legislature, by the Commissioners on the Zoological and Botanical Survey of the State. Dutton & Wentworth, Boston, Massachusetts. Folsom, Wells, & Thurston, Cambridge, Massachusetts. xiii+373 pp. 15 pl.

HAGEN, H. A. 1862. Bibliotheca entomologica: die literatur über das ganze gebiet der entomologie bis zum jahre 1862. Wilhelm Engelmann, Leipzig, Germany. 512 pp.

HARRIS, E. D. 1882. Memoir of Thaddeus William Harris, M. D. Proc. Massachusetts His. Soc. 19:313–322.

HARRIS, T. W. 1833. Insects, pp. 566–595. *In* Hitchcock, E. (ed.), Report on the geology, mineralogy, botany, and zoology of Massachusetts. J. S. & C. Adams, Amherst, Massachusetts.

_____. 1835. Insects, pp. 553–602. *In* Hitchcock, E. (ed.), Report on the geology, mineralogy, botany, and zoology of Massachusetts. Second edition, corrected and enlarged. J. S. & C. Adams, Amherst, Massachusetts.

_____. 1838. Dr. Harris's report, pp. 57–104. *In* Emerson, G. B. (ed.), Reports of the Commissioners on the zoological survey of the State. Mass. House Doc. 72. Dutton & Wentworth, Boston, Massachusetts.

_____. 1841. A report on the insects of Massachusetts, injurious to vegetation. Published agreeably to an order of the Legislature, by the Commissioners on the zoological and botanical survey of the State. Folsom, Wells, & Thurston, Cambridge, Massachusetts. viii+459 pp.

_____. 1842. A treatise on some of the insects of New England, which are injurious to vegetation. John Owen, Cambridge, Massachusetts. 459 pp.

_____. 1852. A treatise on some of the insects of New England which are injurious to vegetation. Second edition. White & Potter, Boston, Massachusetts. viii+513 pp.

_____. 1862a. A treatise on some of the insects injurious to vegetation. Third edition. William White, Boston. xi+640 pp., 8 pl.

_____. 1862b. A treatise on some of the insects injurious to vegetation. A new edition, enlarged and improved, with additions from the author's manuscripts, and original notes, illustrated by engravings drawn from nature under the supervision of Prof. Louis Agassiz. Edited by Charles L. Flint, Secretary of the Massachusetts State Board of Agriculture. Printed for Private Circulation, Boston. xi+640 pp., 8 pl.

_____. 1862c. A treatise on some of the insects injurious to vegetation. A new edition, enlarged and improved, with additions from the author's manuscripts and original notes. Illustrated by engravings drawn from nature under the supervision of Professor Agassiz. Edited by Charles L. Flint, Secretary of the Massachusetts State Board of Agriculture. Crosby & Nichols, Boston, Massachusetts. xi+640 pp., 8 pl.

HENSHAW, S. 1895. Insecta. Proc. Boston Soc. Nat. His. 26:132.

HERRICK, G. W. & R. G. SMITH (eds.). 1953. The Comstocks of Cornell: John Henry Comstock and Anna Botsford Comstock. An autobiography by Anna Botsford Comstock. Comstock Publ. Assoc., New York, New York. 286 pp.

HINKS, W. 1862. [Review of] A treatise on some of the insects injurious to vegetation. By Thaddeus William Harris, M.D. A new edition, enlarged and improved, with additions from the author's MSS. and original notes. Illustrated by engravings drawn from nature, under the supervision of Professor Agassiz. Edited by Charles L. Flint, Secretary of the Massachusetts State Board of Agriculture. Boston: Crosby & Nichols; New York: Oliver S. Felt. 1862. Can. Jour. (new series) 7:521–522.

HOLLAND, W. J. 1898. The butterfly book. A popular guide to a knowledge of the butterflies of North America. Doubleday, Page & Co. 382 pp., 48 pl.

HOWARD, L. O. 1930. A history of applied entomology (somewhat anecdotal). Smith. Misc. Coll. 84:i–viii, 1–564.

HOYT, J. W. 1862. "Insects injurious to vegetation"—a new and magnificent edition of a most valuable book. Wisconsin Farmer 14:146–147.

HYATT, A. 1877. [Biological collection has been partially rearranged]. Proc. Boston Soc. Nat. His. 19:191.

_____. 1900. Report of the Curator, Alpheus Hyatt. Proc. Boston Soc. Nat. His. 29:¬223–233.

ICZN (International Commission of Zoological Nomenclature). 1999. International code of zoological nomenclature. Fourth edition. Int. Trust Zool. Nomen., London, England. 306 pp.

JOHNSON, C. W. 1925. Diptera of the Harris collection. Proc. Boston Soc. Nat. His. 38:57–99.

KIRBY, W. F. 1871. A synonymic catalogue of diurnal Lepidoptera. John Van Voorst, London, England. 690 pp.

LINTON, W. J. 1891. Catoninetales. A domestic epic by Hattie Brown, a young lady of colour who lately deceased at the age of 14. Lawrence & Bullen, London. 100 pp.

MASSACHUSETTS [STATE OF]. 1839. Resolves passed by the Legislature of Massachusetts: 1839. Chapter 84. Resolve to provide for printing the reports of the scientific surveys, pp. 110–111. *In* Massachusetts [State of], Acts and resolves passed by the Legislature of Massachusetts in the year 1839. Dutton & Wentworth, Boston, Massachusetts.

_____. 1851a. Resolves of 1850. Chapter 55. Resolves for reprinting a report on the insects of Massachusetts, which are injurious to vegetation, pg. 507. *In* Massachusetts [State of], Acts and resolves passed by the general court of Massachusetts for the years 1849, 1850, 1851, together with the messages. Dutton & Wentworth, Boston, Massachusetts.

_____. 1851b. Resolves of 1851. Chapter 53. Resolves for reprinting a report on the insects of Massachusetts, which are injurious to vegetation, pg. 507. *In* Massachusetts [State of], Acts and resolves passed by the general court of Massachusetts for the years 1849, 1850, 1851, together with the messages. Dutton & Wentworth, Boston, Massachusetts.

_____. 1859a. General laws. Chapter 273. An act supplemental to an act making appropriations to meet certain expenditures authorized the present year, and for other purposes, pg. 82. *In* Massachusetts [State of], General laws and resolves passed by the Legislature of Massachusetts during the session of 1859. William White, Boston, Massachusetts.

_____. 1859b. General resolves. Chapter 93. Resolves for printing a report on the insects of New England, which are injurious to vegetation, pg. 96. *In* Massachusetts [State of], General laws and resolves passed by the Legislature of Massachusetts during the session of 1859. William White, Boston, Massachusetts.

_____. 1861a. Acts, general and special. Chapter 93. An act making appropriations for the maintenance of the government during the current year, pp. 401–410. *In* Massachusetts [State of], Acts and resolves passed by the general court of Massachusetts, in the year 1861. Together with the messages of the Governor, list of the civil government, changes of names of persons, etc, ete., etc. William White, Boston, Massachusetts.

_____. 1861b. Acts, general and special. Chapter 208. An act in addition to an act making appropriations to meet certain expenditures authorized the present year, and for other purposes, pp. 532–534. *In* Massachusetts [State of], Acts and resolves passed by the general court of Massachusetts, in the year 1861. Together with the messages of the Governor, list of the civil government, changes of names of persons, etc, etc., etc. William White, Boston, Massachusetts.

_____. 1861c. Resolves, general and special. Chapter 80. Resolves for further distribution of a report on insects injurious to vegetation, pp. 555–556. *In* Massachusetts [State of], Acts and resolves passed by the general court of Massachusetts, in the year 1861. Together with the messages of the Governor, list of the civil government, changes of names of persons, etc, etc., etc. William White, Boston, Massachusetts.

_____. 1862. Resolves, general and special. Chapter 5. Resolve for the further distribution of a report on insects injurious to vegetation, pp. 212–213. *In* Massachusetts [State of], Acts and resolves passed by the general court of Massachusetts, in the year 1862: together with the messages of the Governor, list of the civil government, changes of names of persons, etc, etc., etc. William White, Boston.

MAWDSLEY, J. R. 1993. The entomological collections of Thomas Say. Psyche 100:163–171.

MCZ (MUSEUM OF COMPARATIVE ZOOLOGY). 2006. MCZ type database@ Harvard Entomology. http://mcz–28168.oeb.harvard.edu/mcztypedb.htm. Accessed 15 May 2008.

MELANDER, A. L. 1932. The entomological publications of C. W. Johnson. Psyche 39:87–99.

MILLARD, S. W. 1821. Outlines of British Entomology, in prose and verse. With plates. Publ. by the author. Bristol, England. xxiii+231 pp., 3 pl.

MILLER, L. D. & F. M. BROWN. 1981. A catalogue/checklist of the butterflies of America north of Mexico. Lepid. Soc. Mem. No. 2. 280 pp.

_____. 1983. Papilionoidea. Pp. 49–65. *In* Hodges, R. W. (ed.), Check list of the Lepidoptera of America north of Mexico including Greenland. E. W. Classey, Ltd., London.

MORRIS, J. G. 1846. Contributions toward a history of entomology in the United States. Amer. J. Sci. Arts (second ser.) 1:17–27.

_____. 1862. Synopsis of the described Lepidoptera of North America. Part 1.—diurnal and crepuscular Lepidoptera. Smith. Misc. Coll., Washington D.C. xxvii+358 pp.

OPLER, P. A. & A. D. WARREN. 2002. Butterflies of North America. 2. Scientific names list for butterfly species of North America, north of Mexico. Contrib. C. P. Cillette Mus. of Arth. Biodiv., Colorado State Univ., Ft. Collins, Colorado. 79 pp.

OSTEN-SACKEN, C. R. 1878. Catalogue of the described Diptera of North America. Smiths. Misc. Coll. 270:1–xlvi, 1–276.

PARSONS, T. 1859. [Reprinting of Dr. Harris's work]. Proc. Boston Soe. Nat. His. 6:417.

[PEABODY, W. B. O.]. 1842. Art. III.—[Review of] A report on the insects of Massachusetts injurious to vegetation. By Thaddeus William Harris, M.D. Published agreeably to an order of the Legislature, by the Commissioners on the zoölogical and botanical survey of the State. Cambridge: Folsom, Wells, & Thurston. 1841. 8vo. No. Am. Rev. 54:73–101.

PELHAM, J. P. 2008. A catalogue of the butterflies of the United States and Canada, with a complete bibliography of the descriptive and systematic literature. J. Res. Lepid. 40:i–xiv, 1–652.

RENNIE, J. 1832. Conspectus of British butterflies and moths. Vol. 1. Orr, London. 37 pp.

SALMON, M. A. 2000. The Aurelian legacy: British butterflies and their collectors. Univ. California Pr., Berkeley, California. 432 pp., 41 pl.

SCUDDER. S. H. 1862. [Donation of fifteen copies of the illustrated edition of Harris's "insects injurious to vegetation" from the State of Massachusetts]. Proc. Boston Soc. Nat. His. 9:46.

_____. 1869. Entomological correspondence of Thaddeus William Harris, M.D. Oec. Pap. Boston Soc. Nat. His. 1:i–xlvii, 1–375.

_____. 1871. [Entomological collections]. Proc. Boston Soc. Nat. His. 13:321–322.

_____. 1875. Historical sketch of the generic names proposed for butterflies: a contribution to systematic nomenclature. Proe. Amer. Acad. Arts Sci. 10:91–293.

_____. 1889. Excursus XX.—The three pioneer students of butterflies in this country, pp. 651–658. *In* Scudder, S. H., The butterflies of the eastern United States and Canada with special reference to New England. Vol. 1. Introduction, Nymphalidae. Publ. by the author, Cambridge, Massachusetts.

SKINNER, H. 1898. A synonymic catalogue of the North American Rhopalocera. Amer. Entomol. Soc., Philadelphia. xv+99+xiv pp.

STEVENS, J. C. 1850. A catalogue of the library of books on natural history, science, the classics and general literature, the property of the late Edward Doubleday, Esq., F.L.S., &c. &c; also his valuable microscopes, by Ross; a small collection of British insects, many of them of very rare occurrence; and a mahogany entomological cabinet of 24 drawers; which will be sold at auction, by Mr. J. C. Stevens, at his great room, 38, King Street, Covent Garden, on Friday, the 7th day of June, 1850, at twelve for one o'clock precisely. Stevens, London. 12 pp.

STRECKER, F. H. H. 1878. Butterflies and moths of North America, with full instructions for collecting, breeding, preparing, classifying, packing for shipment, etc., a complete synonymical catalogue of macrolepidoptera, with a full bibliography, to which is added a glossary of terms and an alphabetical and descriptive list of localities. B. F. Owen, Reading, Pennsylvania. 283 pp.

WADE, J. S. & J. A. HYSLOP. 1941. Obituary notice of Samuel Henshaw. Proc. Entomol. Soc. Wash. 43:108–110.

[WALSH, B. D. & C. V. RILEY]. 1869. On our table: Harris's insects injurious to vegetation. Amer. Entomol. 1:165.

WILSON, J. G. & J. FISKE. 1900. Appleton's cyclopaedia of American biography. Vol. IV: Lodge—Pickins. Revised edition. D. Appleton & Col, New York, New York. 769 pp.

Received for publication 5 June 2008; revised and accepted 3 February 2009.

Journal of the Lepidopterists' Society
63(3), 2009, 164–165

SYNAXIS TRIANGULATA (BARNES & MCDUNNOUGH) MOVED TO *CARIPETA* WALKER (GEOMETRIDAE: ENNOMINAE)

CLIFFORD D. FERRIS[1]
5405 Bill Nye Ave., R.R. 3, Laramie, WY 82070, USA, cdferris@uwyo.edu

ABSTRACT. Based upon genitalic characters, the ennomine geometrid *Synaxis triangulata* is removed from genus *Synaxis* and placed in *Caripeta*. The genitalia of the type species of *Synaxis, Caripeta*, and adults and genitalia of *Caripeta triangulata* are illustrated.

Additional key words: Arizona, *Caripeta divisata, Caripeta triangulata*, New Mexico, *Sabulodes*, taxonomy, Texas.

Examination of genitalia within the genus *Synaxis* Hulst (1896, *senso stricto*) has revealed the male and female genitalia of the taxon *triangulata* Barnes & McDunnough correspond to those of *Caripeta* Walker and not to *Synaxis*. The male genitalia of *Synaxis* manifest a single robust tubular furca originating from the midline of the juxta plate, as shown in Fig. 1 for the type species, *Tetracis pallulata* Hulst, 1887. The gnathos has a quadrate dorso-caudal margin with one or more pairs of slender tapered spinose projections (in some individual specimens there are multiple asymmetric projections). The aedeagus (Fig. 2) has a ring of spines or setae at the base of the vesica, which when everted and inflated is dome-like, usually partially covered with setae or small chitinized nodules. The female genitalia of *S. pallulata* are shown in Figs. 9–10. Pitkin (2002, p. 245) characterized the male genitalia of *Caripeta* as having a curved sender rod-like uncus, gnathos with a bilobed median spinulose area in the form of a W, valva without processes, anellus with spinulose right-directed furca, and juxta with a right-deflected tiny elongate median depression or sac. The aedeagus has a tapered posterior extension and the vesica may or may not have a patch of denticles. The corpus bursa of the female genitalia has a large ovate dentate signum. The male and female genitalia of the type species, *Caripeta divisata* Walker, are illustrated in Figs. 3–5 and 11–12 respectively.

Caripeta triangulata (Barnes & McDunnough) **new combination**

Sabulodes triangulata Barnes & McDunnough, 1916, Contr. nat. Hist. N. Am. 3(1), p. 33, pl. I, fig. 15; TL Paradise, Cochise Co., Arizona; female HT in USNM.

Synaxis triangulata; McDunnough, 1938

Material examined. (8 males, 1 female; 2 males, 1 female, dissected): ARIZONA, Cochise Co., Chiricahua Mts.: Cave Creek Canyon area, 1585m, 5–16.viii.1979–80 (4 males); Pinery Canyon, 2130m, 23.vi.05 (1 male); Onion Saddle area, 2325m, 22.vii.07 (2 males); Stewart C.G., 9.viii.1999 (1 female). NEW MEXICO, Hidalgo Co., east end of Skeleton Canyon, 1465m, 9.ix.2002, (1 male). Males collected by author; female by R. M. Brown.

Discussion. Barnes & McDunnough provided a detailed description of the habitus of this species and no additional elaboration is required here. Adults are illustrated in Figs. 15–16. By comparing the male genitalia of *Caripeta divisata* (Figs. 3–5) with those of "*Synaxis*" *triangulata* (Figs. 6–8) one can see that they are nearly identical and quite different from those of *Synaxis* (Figs. 1–2). On this basis, I transfer *triangulata* from *Synaxis* to *Caripeta*. The male genitalia of *Sabulodes*, in which *triangulata* was originally described, are very different from those of either *Synaxis* or *Caripeta* (see Rindge 1978). McGuffin (1987) illustrated the adults, male and female genitalia of *Caripeta divisata* and *C. piniata* (Packard).

The biology of *C. triangulata* is unknown. Based upon available records, adults fly from mid-June into early October. Geographic distribution includes Cochise Co., Arizona, Hidalgo Co., New Mexico, and Texas (Brewster, Burnet, Comal, Jeff Davis, Presidio, Terrell, Uvalde, and Val Verdi counties). The moth appears to be uncommon in the western portion of its range, but common in Texas in September and October.

ACKNOWLEDGEMENTS

I thank Richard M. Brown, Stockton, CA for providing a female specimen of *Caripeta triangulata* for photography and dissection, and Edward C. Knudson, Houston, TX for Texas records. Two anonymous reviewers made helpful suggestions.

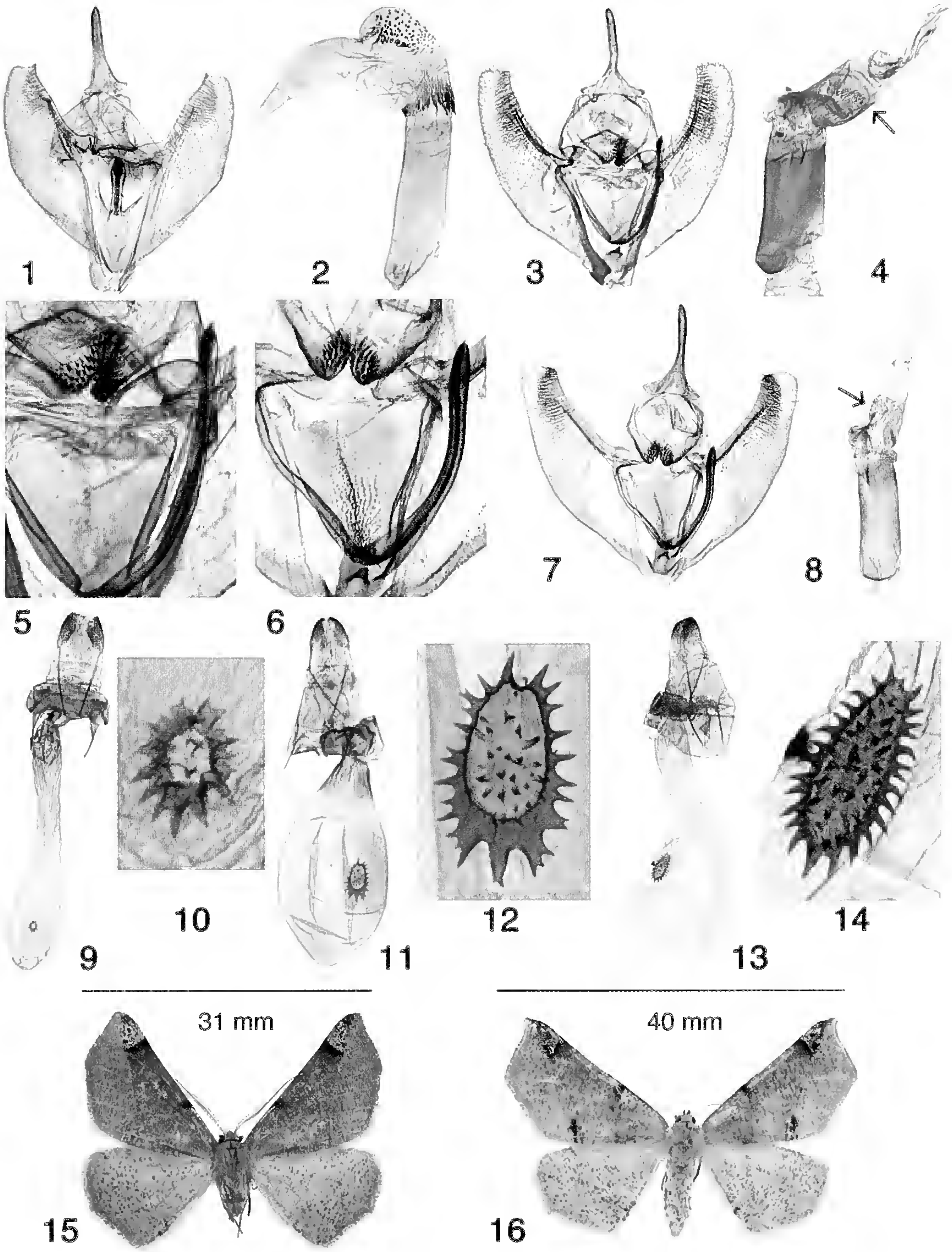
LITERATURE CITED

Barnes, W. H. & J. McDunnough, 1916. Contributions to the natural history of the Lepidoptera of North America, 3(1): 1–51.

McDunnough, J. 1938. Check list of the Lepidoptera of Canada and the United States of America. Part I. Macrolepidoptera.

---

[1] Research Associate: McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL; C. P. Gillette Museum of Arthropod Diversity, Colorado State University, Ft. Collins, CO; Florida State Collection of Arthropods, Gainesville, FL.



FIGS. 1–14. Figs. 1–2. *Synaxis pallulata*: **1**, male genitalia (aedeagus removed); **2**, aedeagus with vesica everted and inflated. Figs. 3–5. *Caripeta divisata*: **3**, male genitalia (aedeagus removed); **4**, aedeagus with vesica everted and inflated (arrow points to denticles); **5**, enlarged view showing bilobed median spinulose area of gnathos. Figs. 6–8. *Caripeta triangulata*: **6**, male genitalia (aedeagus removed); **7**, aedeagus with vesica everted and inflated (arrow points to denticles); **8**, enlarged view showing bilobed median spinulose area of gnathos. Figs. 9–10. *Synaxis pallulata*: **9**, female genitalia; **10**, enlarged view of signum. Figs. 11–12. *Caripeta divisata*: **11**, female genitalia; **12**, enlarged view of signum. Figs. 13–16. *Caripeta triangulata*: **13**, female genitalia; **14**, enlarged view of signum; **15**, adult male; **16**, adult female.

Mem. So. California Acad. Sci., I: 1–272.

McGuffin, W. C. 1987. Guide to the Geometridae of Canada (Lepidoptera) II. Subfamily Ennominae. 4. Mem. Entomol. Soc. Canada 138:1-182.

Pitkin, L. M. 2002. Neotropical ennomine moths: a review of the genera (Lepidoptera: Geometridae). Zool. J. Linn. Soc. 135: 121–401.

Rindge, F. H. 1978. A revision of the genus Sabulodes (Lepidoptera, Geometridae). Bull. Am. Mus. Nat. Hist., 160(4): 193–292, figs. 1–154.

Scoble, M. J. (ed). 1999. Geometrid moths of the World: a catalogue. CSIRO, Collingwood, Australia. 2 vol. 1,016 pp. + 129 pp. index in each vol.

Received for publication 26 May; revised and accepted 3 February 2009.

Journal of the Lepidopterists' Society
63(3), 2009, 166-168

METANEMA BRUNNEILINEARIA GROSSBECK MISPLACED IN *SYNAXIS* HULST (GEOMETRIDAE: ENNOMINAE)

CLIFFORD D. FERRIS[1]
5405 Bill Nye Ave., R.R. 3, Laramie, WY 82070, USA, cdferris@uwyo.edu

ABSTRACT. . Based upon genitalic characters, the ennomine geometrid species *brunneilinearia* is removed from genus *Synaxis* and returned to *Metanema*. The male genitalia of typical species of *Synaxis* and *Metanema* are illustrated. The female holotype, a typical male and female adult, and the male and female genitalia of *Metanema brunneilinearia* are illustrated.

Additional key words: California, *Metanema determinata*, *Metanema inatomaria*, Nevada, taxonomy.

In conjunction with an ongoing revision of the genus *Synaxis* Hulst (*senso stricto*), I have been examining type material and making genitalic dissections of typical specimens. The male genitalia of the taxon *brunneilinearia* Grossbeck are very different from those found in *Synaxis*, and on this basis I am returning this species to *Metanema* Guenée, in which it was originally described. As shown in the accompanying figures, the male genitalia of *Synaxis* manifest a single robust tubular furca originating from the midline of the juxta plate, the apex of which may be blunt (Fig. 1) or taper to a point (Fig. 2), depending upon species. The gnathos has a quadrate dorso-caudal margin with one or more pairs of slender tapered spinose projections (in some individual specimens there are multiple asymmetric projections). McGuffin (1987) discussed the generic characters of *Metanema* and illustrated the adults and male and female genitalia of *M. determinata* Walker and *inatomaria* Guenée. The furca in *Metanema* is double consisting of two slender projections that arise from either side of the juxta plate as shown in Figs. 3 (*inatomaria*) and 8–9 (*brunneilineara*). The gnathos tapers to a point. There are two prominent coremata, which are absent in *Synaxis*. McGuffin characterized the female genitalia of *Metanema* as having a narrow ductus bursae, elongate corpus bursae with one signum, and a posterior-to-anterior apophyses length ratio of approximately 2:1.

Ptikin (2002, p. 324) provided only a brief mention of *Metanema*, citing all of the species to be Nearctic and outside of the geographic scope of her study. Scoble (1999) implied that additional species study is required and placed entries under *Metanema* and "*Metanema*".

Metanema brunneilinearia **Grossbeck**
new combination

Metanema brunneilinearia Grossbeck, 1907; TL Verdi [Washoe Co.], Nevada; female HT in AMNH (Figs. 4–5). The holotype label (Fig. 5) shows the species name "brunneilineata," but the name as published in the original description is *brunneilinearia*.
Synaxis brunneilinearia; McDunnough, 1938
Synaxis brunneilinearia; Scoble, 1999

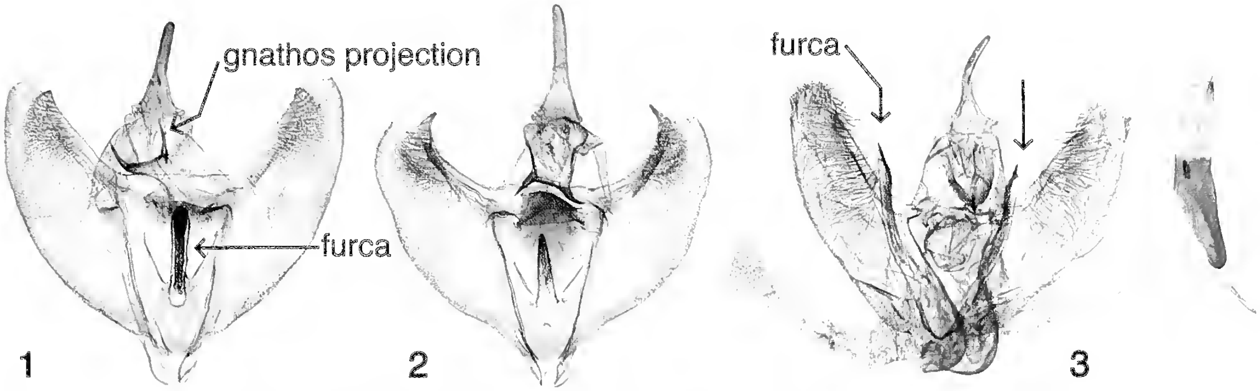
Material examined (5 males, 5 females; 1 male, 1 female, dissected): CALIFORNIA. Alpine Co., 1 mi. E. of Monitor Pass, 1.viii.1992 (1 female), R. M. & S. A. Brown; El Dorado Co., 2 mi. E. Silver Lake, 9.vii.88 (1 male), J. A. Smith; Mono Co., hwy. 395 W. Mono Lake, 19-30.vi.1986 (3 males, 1 female) A. H. Porter; Plumas Co., Johnsville, 16.vii.1968 (1 female), 18.vii.1969 (1 female), H. Pini; no locality, 25.vii.1936, (1 male), M. Walton. NEVADA. [Washoe Co.], female HT by photograph.

Discussion. Grossbeck (1907) provided a detailed description of the color and maculation of this species, and adults are adequately shown in Figs. 4, 6–7. The sexes are similar in size and the male antennae are bipectinate, as in the two other North American species, *M. determinata* and *inatomaria*. The forewing shape of *brunneilinearia* is consistent with those species. The outer margin is prominently produced at vein M_3 in the forewing, and crenulate in the hindwing. The wing ground color is pale yellowish-white, but appears pale gray because of peppering by black scales. Both wings have prominent dark discal spots. The distal quarter of the forewing displays irregular patches of black scales divided by a subterminal pale band that parallels the contour of the outer margin. There are faint orange-brown am and pm lines on the dorsal forewing, and a postdiscal line on the dorsal hindwing. Figs. 8–11 illustrate the male and female genitalia, both of which are nearly identical to those of *M. inatomaria*.

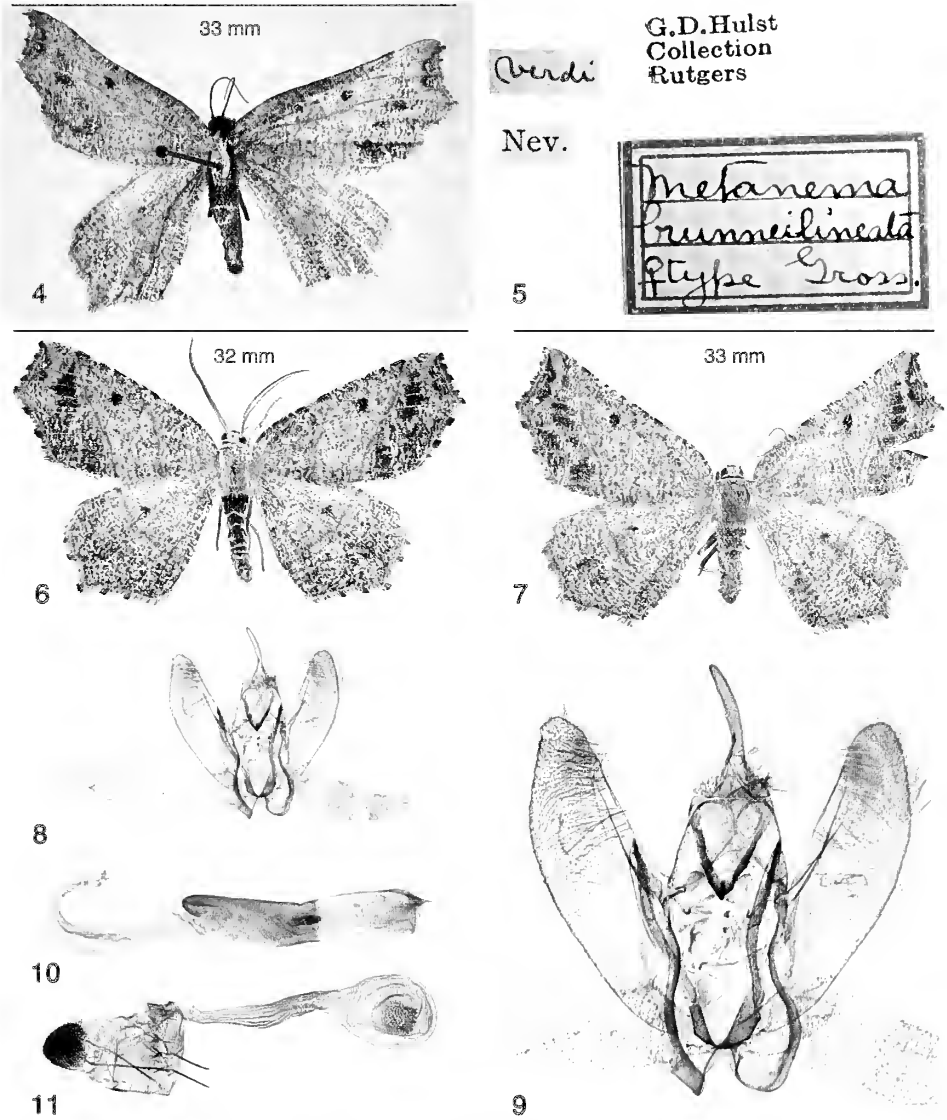
It has been suggested that *M. brunneilinearia* and *M. inatomaria* might be conspecific, with *brunneilinearia* simply a western form of the latter. While the male

---

[1] Research Associate: McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL; C. P. Gillette Museum of Arthropod Diversity, Colorado State University, Ft. Collins, CO; Florida State Collection of Arthropods, Gainesville, FL.



FIGS. 1–3. Figs. 1–2. Male genitalia (aedeagus removed) of *Synaxis* species: **1**, *jubararia* (Hulst); **2**, *barnesii* (Hulst). Fig. **3**. Male genitalia of *Metanema inatomaria* with aedeagus removed and shown at right.



FIGS. 4–11. Figs. 4–5. Female holotype of *Metanema brunneilinearia*: **4**, holotype; **5**, pin labels (AMNH photos). Figs. 6–7. *Metanema brunneilinearia* adults: **6**, male, CA, Mono Co.; **7**, female, CA, Alpine Co. Figs. 8–10. *Metanema brunneilinearia* male genitalia: **8**, genitalia showing full extent of coremata with aedeagus removed; **9**, genitalia, aedeagus removed; **10**, aedeagus. Fig. **11**. *Metanema brunneilinearia* female genitalia.

genitalia of the two entities are very similar, the color and maculation of the adults are quite different. On this basis, I don't feel it appropriate to make the synonomy. DNA analysis (barcoding) could resolve this issue, but that is beyond the intent and scope of this article, which is simply to return *brunneilinearia* to the genus where it belongs.

The biology of *M. brunneilinearia* is unknown. Based upon available records, adults fly from mid-June into early August. The geographic distribution includes Washoe Co., NV and several counties in California north and south of Lake Tahoe along the border with Nevada.

ACKNOWLEDGEMENTS

I thank Richard M. Brown, Stockton, CA and Dr. Steven A. Heydon, Bohart Museum, University of California, Davis, CA for providing specimens for examination. Suzanne Rab Green, American Museum of Natural History, New York, NY kindly provided digital photographs of the holotype. Two anonymous reviewers made helpful suggestions.

LITERATURE CITED

GROSSBECK, J. A. 1907. Some new species of western Geometridae. Canad. Entomol. 39(10): 345–348.

MCDUNNOUGH, J. 1938. Check list of the Lepidoptera of Canada and the United States of America. Part I. Macrolepidoptera. Mem. So. California Acad. Sci., I: 1–272.

MCGUFFIN, W. C. 1987. Guide to the Geometridae of Canada (Lepidoptera) II. Subfamily Ennominae. 4. Mem. Entomol. Soc. Canada 138:1–182.

PITKIN, L. M. 2002. Neotropical ennomine moths: a review of the genera (Lepidoptera: Geometridae). Zool. J. Linn. Soc. 135: 121–401.

SCOBLE, M. J. (ed). 1999. Geometrid moths of the World: a catalogue. CSIRO, Collingwood, Australia. 2 vol. 1,016 pp. + 129 pp. index in each vol.

Received for publication 7 May 2008; revised and accepted 4 February 2009.

Journal of the Lepidopterists' Society
63(3), 2009, 169–172

EARLY STAGES AND NATURAL HISTORY OF *CITHAERIAS P. PIRETA* (SATYRINAE) FROM COSTA RICA

LUIS RICARDO MURILLO-HILLER

Museo de Insectos, Escuela de Agronomía, Universidad de Costa Rica; email: murillo.luis@lycos.com

ABSTRACT. The early stages of *Cithaerias pireta* are described from a Costa Rican lowland rain forest on the Caribbean slope. The host plant is *Philodendron herbaceum* (Areaceae), which grows in the dark understory areas in very humid habitats. Implications for palatability and mimicry are discussed with respect to the bright colors of the adults of this and related genera. The caterpillars had five instars and the total cycle from egg to butterfly eclosion lasted 66 days. Photographs and descriptions are provided of the larvae and pupa, and observations on behavior, habitat and host plants are discussed.

Additional key words: *Cithaerias menander, Pierella helvetia, Dulcedo polita, Haetera macleannania, Philodendron herbaceum*, Batesian mimicry, Mullerian mimicry.

The genus *Cithaerias* Hübner (1819) is a neotropical group of Satyrinae which is recognized by their largely transparent wings (DeVries 1987). According to Lamas *et al.* (2004) there are five species, and only one occurs in Central America. This genus is found from Mexico through the Amazon basin where it is more diverse. In Costa Rica, *Cithaerias pireta pireta* (Stoll 1780) occurs in all rain forest habitats from sea level to 1000m on the Caribbean and the Pacific side (DeVries 1987 as *C. menander*). They usually fly around small light gaps in the forest understory associated with trails, river sides and hills. Both sexes fly around areas where their food plants are growing, from early morning until afternoon if there is sunshine. However, in a study done in Corcovado, Costa Rica (Whittaker 1983), most of the individuals showing this behavior were females, and individual butterflies did not stay more than one day in the same area. This behavior is opposite to that described by Young (1972) where the same individuals returned to the same place day after day. All the host plants reported by DeVries (1987) for the Satyrinae are in the families Poaceae, Marantaceae, Arecaceae and Cyperaceae, all of which are monocots, and Selaginellaceae and Neckeraceae (clubmosses and mosses). The host plants of this subfamily are generally thought to have relatively few secondary compounds and the generally cryptic color patterns of adult Satyrinae may result from an inability to sequester toxic compounds (Whittaker 1983). Larval food preference among monocot feeders does not appear to have evolved in line with plant defenses as it has in other groups (Ehrlich & Raven 1964). However, *Cithaerias*, feeding on Araceae, generally found to be highly toxic monocots, provides an interesting exception on which I elaborate.

MATERIALS AND METHODS

An extensive search for butterfly larvae was carried out on 18 November 2006, at the Rain Forest Aerial Tram property (450m), on the border of Braulio Carrillo National Park, Limón, Costa Rica, 10° 10' 47.76" N, 83° 55' 07.66" W. The climate of the locality is defined as Tropical Wet Forest, Premontane Belt Transition (Tosi 1969). According to the butterfly species composition of the area it is defined as swamp forest (DeVries 1987). In this habitat I followed dozens of females of *C. pireta*. At 1300 h. in a dark hilly area one butterfly finally laid an egg on the host plant. The egg was collected by removing the leaf of the host plant and placing it in a plastic jar, which was then transported and reared in the Museo de Insectos at the Universidad de Costa Rica, with an average room temperature of 23–24°C. The caterpillar was put into a plastic bag and fed with leaves of the host plant which were brought every week from the place where the egg was found. The host plant identification was done by the botanist Carlos O. Morales. The adult obtained from this study and the empty pupae are deposited in the author's collection. The photographs were taken with a Cannon camera model Rebel G.

RESULTS

Host Plant: *Philodendrom herbaceum* Croat & Grayum (Araceae). This plant is a vine that grows in dark areas in the understory, climbing rocks, trees and vines to a height of one or two meters. The plant is very abundant in the study area.

Egg (Fig. 1a): 0.8 mm diameter, spherical, creamy white, chorion smooth. Laid singly on the underside of the leaf at 15cm height in a dark forest area. The female flew slowly around the plant and selected a place close to the central vein of the leaf. The egg hatched eight days later.

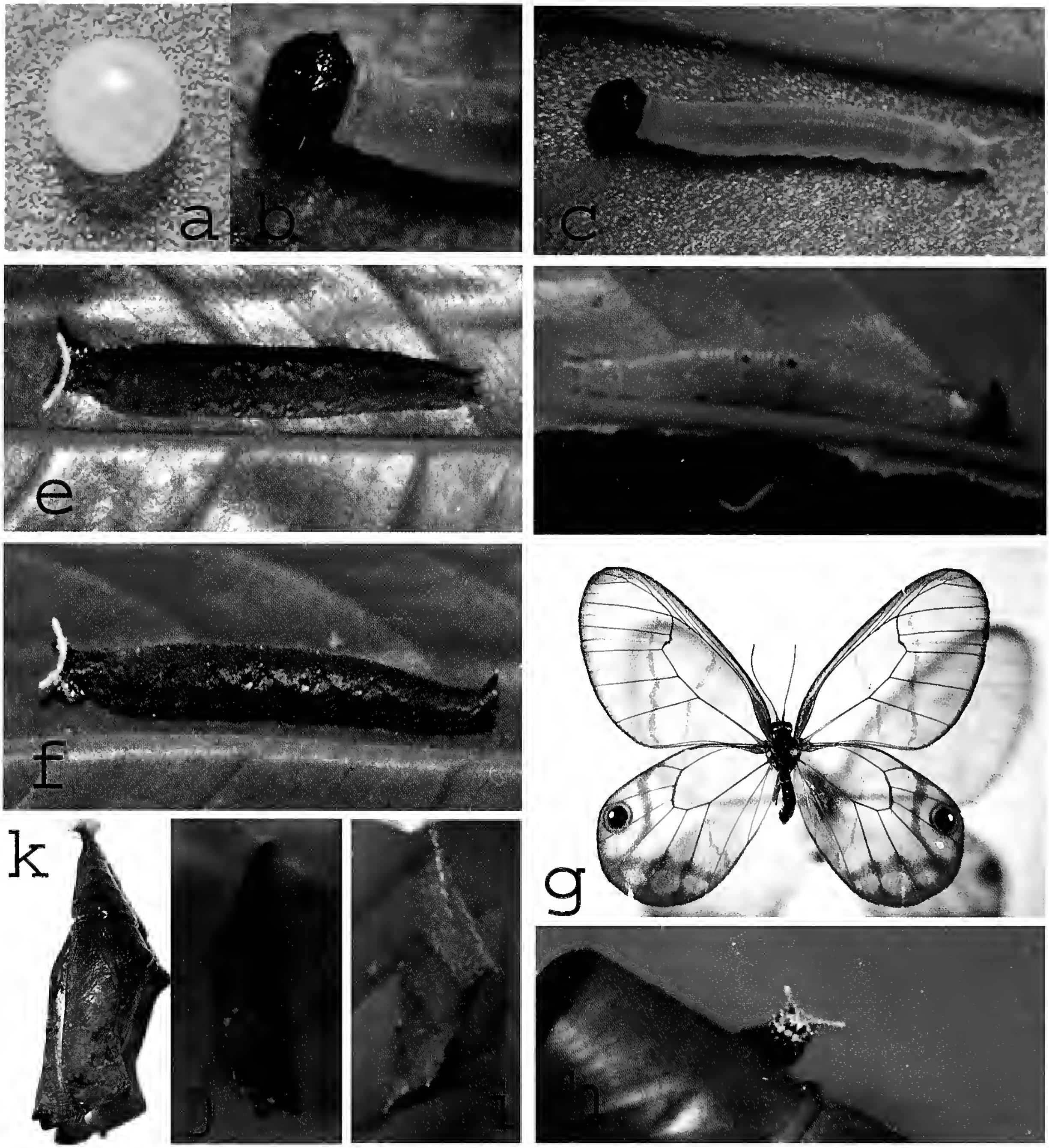


FIG. 1. **a**: egg, **b & c**: first instar, **d**: fourth instar, **e, f & h**: fifth instar, **g**: adult of *C. p. pireta*. **i, j & k**: pupa

First instar (Fig. 1b, c): 0.75–2mm. Head capsule black, stemmata black. Two small dorso-laterally projecting horns on each side of the epicranium and a few long black setae on each side. Body light green, spiracles same color, no setae covering the body. The larva has a bifurcate suranal plate half as long as A9 segment, the same color as the body. Time: 8 days to molt.

Second instar: 2–4.5mm. Head capsule same as previous instar but with longer head horns. Body light green, with a black dot on the dorsal part of T1 segment. A3 has a dorso-lateral black dot on each side of the body, and the same is repeated on A4. A smaller black dot is situated in A5 but closer to the spiracles. Another black dot, the same size as the previous one on A8 in lateral position. Bifurcate suranal plate conically elongated backward. Similar to fourth instar but smaller. Time: 12 days to molt.

Third instar: 4.5–12.5mm. Head capsule same as previous instar but with longer head horns. Bifurcate suranal plate conically elongated backward. Body similar to fourth instar but smaller. Time: 10 days to molt.

Fourth instar (Fig. 1d): 12.5–21mm. Head capsule same as previous instar but the dorso-lateral horns are as long as half the head diameter. Body light green, same as second and third instars. Time: 7 days to molt.

Fifth instar (Fig. 1e, f, h): 21–32mm. Head capsule same shape as previous instars but frons with upper half black and lower half white, clypeus black, stemmatal area black and mandibles white. Dorso-lateral horns same as previous instar but white. Four creamy yellow conical protuberances on lateral area of the epicranium. Body dark brown with two dorso-lateral bands of triangular light brownish-orange spots highly accentuated from A3 to A6 segments, and with very small white spots in dorso-lateral position, one per segment from A2 to A7. Bifurcate suranal plate same as previous instars but light brownish-orange and with white tip. Time: 6 days to molt.

Pupa (Fig. 1i, j, k): 17mm. Dark brown. Abdomen with conical shape, and two dorsally projected conical horns on segment A3. The thorax has a dorsal conical projection. The angle between the ventral cremaster and the abdomen is almost 180°. Duration of pupal stage: 14 days.

DISCUSSION

In Costa Rica, *C. p. pireta* (Fig. 1g) is abundant in places that lack a marked dry season (DeVries 1987). Its habitat is the shade of the wet understory where plants are adapted to little light, and the host plant of *C. p. pireta* is one of these plants.

The external morphology of the larvae of *C. p. pireta* follows the typical form of Satyrinae, which have a pair of cephalic horns and a bifid tail (Scoble 1992). The head capsule is similar to the illustration of *Cissia confusa* in DeVries (1987) and as displayed at Janzen *et al.* (2005). The first four instars are light green and last instar is dark brown, which coincides with the larval behavior of always resting on the undersides of leaves in the first 4 instars and on tree trunks in the last instar (Janzen pers. comm.). The pupae have a brown cryptic pattern, and the two dorsal projections are rare in this subfamily, although other species of Satyrinae that resemble *Cithaerias* pupae in basic shape include *Cissia usitata* and *Cissia alcinoe.* In Satyrinae, there are two basic pupal shapes, one with a ventral 110° angle between cremaster and abdomen, as in *Manataria* (Murillo & Nishida 2003), and the other with a 180° angle (Fig. 1i, j, k).

Young (1972) reported small, close demes with the same individuals of *Cithaerias* returning to the same place day after day. This territorial behavior may be coupled with structures that help males protect the place from other males.

Cithaerias possesses a swelling of the sub-costal vein. The function of this structure in this species is still unknown, but it may be used to produce sounds to attract mates or to fight with others individuals, as has been described in species of Satyrinae from South America (Murillo-Hiller 2006), and it is probably the source of the acoustic signals found by Kane (1982) in another south American satyrine species.

All known host plants for other neotropical Satyrinae are thought to lack dramatically toxic secondary compounds and, as a consequence, the species are always palatable to predators and the group does not show mimicry rings (DeVries 1987). Viloria (2004) argued that there is no direct evidence that species of Pronophilina (and other groups in Satyrinae) are unpalatable and therefore classical Batesian or Mullerian mimicry does not offer an appropriate explanation for the resemblance between these satyrine species.

In the case of this recently recorded family of satyrine host plants, many secondary compounds are known (Laurito *et al.* 2005). It is possible that there is Mullerian or Batesian mimicry among species of *Cithaerias* and *Haetera*, especially now that it has been found that the host plant of the latter genus also is a toxic Araceae plant (Constantino 1993). *Dulcedo polita* is a related species similar to *C. pireta*, but even when sympatric it does not show any red or rose colors on its wings. This makes sense since the host plants of *Dulcedo* are *Geonoma* and *Welfia* (Arecaceae) (DeVries 1987), which probably do not have secondary compounds that can be used as defense by the butterfly. Another species related to and sympatric with *Cithaerias* is *Pierella helvetia*, which also has bright red coloration on the hind wings, and whose host plants are species of Heliconiaceae and many other monocots (Janzen *et al.* 2005). More research should be done to find out if they are aposematic or if, on the other hand, these markings are for directing bird attacks to that area, as proposed by Hill & Vaca (2004).

ACKNOWLEDGEMENTS

I would like to thank Paul Hanson for providing helpful comments on the manuscript and Carlos Morales for the host plant identification. I also thank the Rain Forest Aerial Tram of the Caribbean for allowing me to develop this research on their property.

LITERATURE CITED

CONSTANTINO, L. M. 1993. Notes on Haetera from Colombia, with description of the immature stages of *Haetera piera* (Lepidoptera: Nymphalidae: Satyrinae). Tropical Lepidoptera 4(1): 13–15 + 5 figs.

DEVRIES, P. J. 1987. The butterflies of Costa Rica and their natural history: Papilionidae, Pieridae, Nymphalidae. Vol. 1. Princeton University Press, New Jersey. 327 pp.

EHRLICH, P. R. & P. H. RAVEN. 1964. Butterflies and plants: a study in coevolution. Evolution 18: 586–608.

FEENY, P. 1975. Biochemical coevolution between plants and their insect hervivores. Pp. 5–19. *In* L. E. Gilbert and P. H. Raven, eds., Coevolution of animals and plants. Univ. of Texas Press, Austin.

HILL, R. & J. VACA. 2004. Differential wing strength in *Pierella* butterflies (Nymphalidae, Satyrinae) supports the deflection hypothesis. Biotropica 36(3): 362–370.

JANZEN, D. H. & W. HALLWACHS. 2005. Dynamic database for an inventory of the macrocaterpillar fauna, and its food plants and parasitoids, of Area de Conservacion Guanacaste (ACG), northwestern Costa Rica (nn-SRNP-nnnnn voucher codes) <http://janzen.sas.upenn.edu>.

KANE, S. 1982. Notes on the acoustic signals of a neotropical satyrine butterfly. J. Lep. Soc. 36: 200–206.

LAURITO, V., P. SÁNCHEZ-VINDAS, & R. ABARCA. 2005. Hierbas y arbustos comunes en cafetales y otros cultivos. Herbario Juvenal Valerio Rodríguez. San José, Costa Rica. 246 pp.

MURILLO-HILLER, L. R. 2006. A new noise producing butterfly, Iphthimoides castrensis (Nymphalidae, Satyrinae) from south Brazil. J. Lep. Soc. 60(1): 61–63.

MURILLO, R. & K. NISHIDA. 2003. Life history of *Manataria maculata* (Lepidoptera: Satyrinae) from Costa Rica. Rev. Biol. Trop. 51(2): 463–470.

SCOBLE, M. 1992. The Lepidoptera: form, function and diversity. New York, Oxford University Press. 404 pp.

TOSI, J. A. 1969. Mapa ecológico, República de Costa Rica: según la clasificación de zonas de vida del mundo de L. R. Holdridge. San José. Centro Científico Tropical.

VILORIA, A. 2004. The Pronophilina: synopsis of their biology and systematics (Lepidoptera: Nymphalidae: Satyrinae). Tropical Lepidoptera 15(1–2): 1–17.

WHITTAKER, P. L. 1983. Notes on the satyrid butterfly populations of Corcovado National Park, Costa Rica. J. Lep. Soc. 37(2): 106–114.

YOUNG, A. M. 1972. Community ecology of some tropical rain forest butterflies. American Mid. Nat. 87:146–157.

Received for publication 30 September; revised and accepted 3 February .

Journal of the Lepidopterists' Society
63(3), 2009, 173–176

A NEW SPECIES OF *PLAGIOMIMICUS* GROTE (NOCTUIDAE: STIRIINAE) FROM NORTHERN ARIZONA AND SOUTHEASTERN UTAH

JAMES K. ADAMS
Department of Biology, Dalton State College, Dalton, GA 30720; email: jadams@daltonstate.edu

AND

J. DONALD LAFONTAINE
Canadian National Collection of Insects, Arachnids, and Nematodes, Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada K1A 0C6; email: LafontaineD@agr.gc.ca

ABSTRACT. *Plagiomimicus kathyae* Adams (Noctuidae: Stiriinae) is described from 11 specimens collected at Cameron, Coconino Co., Arizona and Moab, Grand Co., Utah in September of 1995 and August/September of 1996. Adults and genitalia of *P. kathyae* and the similar *P. hilli* (Barnes & Benjamin) are illustrated, and the differences between the species are discussed.

Additional key words: fall flight time

During a trip through parts of the western United States in early September of 1995, James K. Adams (JKA) collected a specimen of a pale olive-yellow stiriine noctuid in Moab, Grand Co., Utah. A few days later, more specimens of the same species were collected in Cameron, Coconino Co., Arizona. A similar trip in late August/early September 1996 produced one more individual in Moab, UT and a few more in Cameron, AZ. A specimen was later sent to Eric Quinter, at the time on staff at the American Museum of Natural History (AMNH) in New York City, in an attempt to identify the species. Eric Quinter returned the specimen to JKA with the indication that, although clearly stiriine, the species was unknown to him and there were no comparable specimens in the AMNH.

In March of 2000, JKA took several specimens to the Smithsonian Institution in Washington, D.C., in a further attempt at identification. Although similar in appearance to *Plagiomimicus hilli* (Barnes & Benjamin), the specimens are generally smaller than *P. hilli*, and the wing patterns on the two species are a bit different. As with the AMNH, there were no specimens of the species in question in the Smithsonian collection. Pictures of the species sent electronically to many noctuid enthusiasts also failed to uncover any other individuals of this moth, and the species is unknown from southeastern Arizona (Bruce Walsh pers. comm.). In 2005, JKA passed specimens to Don Lafontaine at the Canadian National Collection (CNC), who confirmed that the species in question was undescribed. In this paper, the new species is described, and differences with the apparently closely related *P. hilli* are discussed.

Plagiomimicus kathyae Adams **sp. nov.**

Diagnosis. *Plagiomimicus kathyae*, although similar to *P. hilli*, is quite distinct from *P. hilli* in size, maculation, and genitalic features. The smaller *Plagiomimicus kathyae* has a forewing (FW) length ranging from 11.3mm (smallest male) to 12.4mm (largest female) [mean = 11.77mm; n=11], whereas *P. hilli* has a FW length from 12.6 to 13.2mm [mean = 12.95mm; n=15]; the mean length reported for *P. hilli* in Poole (1995) is 13.04mm [n=10]. The forewing maculation, although obscure in both species, is abundantly different between *hilli* and *kathyae*. The white subterminal (ST) line is always visible, complete, and even in *P. kathyae*; the ST line is at best partial and indistinct to absent in *P. hilli*, and when it is evident it is irregular and ragged. The white antemedial (AM) and postmedial (PM) lines, which have suffused edges in both species, are distinctly thinner in *P. kathyae*, with the AM line completely absent in some specimens of *P. kathyae* (but always present in *P. hilli*). The PM line in *P. kathyae* follows a course that is more angled outward toward the apex than in *P. hilli* (compare Fig. 1 and Fig. 3). When the AM line is present in *P. kathyae*, the angled PM line and AM line together appear like a "V"; in *P. hilli*, the two lines run nearly parallel. The male abdomen of *P. hilli* has an unusual and reportedly unique for the genus (Poole, 1995) sclerotization of the sixth, seventh and eighth terga, with the posterior apex of the seventh sternum in particular heavily sclerotized. Male *P. kathyae* have a similar strongly sclerotized ridge on the posterior edge of the seventh tergum (somewhat visible in Fig. 3), and a small sclerotized U-shaped ridge on the anterior edge of the eighth. There is no sclerotization on the sixth tergum in males of *P. kathyae*.

The male genitalia of *P. kathyae* (Figs. 7, 8) differ from those of *P. hilli* (Figs. 5, 6) in several respects. The valves in both species are broad, but the ampulla in *P. kathyae* is 4/3 proportionally longer in relation to valve (16% of valve length) than for *P. hilli* (12% of valve length). The triangular saccus appears pinched at the point of attachment to the vinculum in *P. kathyae*, but the saccular margins blend smoothly into the vinculum in *P. hilli*. The aedeagus is proportionally longer and thinner (4.4× as long as wide) in *P. kathyae* (3.5× as long as wide in *P. hilli*), a difference clearly visible in Figures 6 & 8. The vesica of *P. kathyae* lacks a subbasal pouch (present in *P. hilli*). In the female genitalia of *P. kathyae* (Fig. 10), the corpus bursae is proportionally broader and significantly less sclerotized than in *P. hilli* (Fig. 9); the corpus bursae is also mesially constricted in *P. kathyae*. The anal papillae are also slightly longer proportionally and more pointed in *P. kathyae*. Indeed, the long, thin, heavily sclerotized anal papillae are easily visible in female specimens of *P. kathyae*, without any brushing of scales from the genitalia.

Description. Most features typical for genus (Poole 1995: 86) except where noted. Males and females of *P. kathyae* very similar in overall appearance; female slightly larger and slightly darker than male and with slightly more dusting of olive-gray scales on the hind wing (HW).

Vestiture: cream in male, olive buff in female; vestiture of head, thorax, legs, and abdomen largely concolorous. Scales of meso- and metanotum, and posterior end of tegulae two-toned, with light brown bases and cream colored tips. Scales on dorsum of abdomen slightly darker than on rest of body.

Head: Antennae simple in both sexes, scaled with cream colored scales along dorsum, finely ciliate ventrally. Eyes naked. Frontal protuberance on head nearly round and very large (takes up almost all of frons); protuberance with a strongly sclerotized, raised rim, with a small projection ventrally, and a similar, smaller projection dorsally; center of frontal protuberance with raised "cone," notched ventrally. Labial palps as for genus (Poole 1995: 87), with heavily scaled basal and second segments; short, stout third segment barely protrudes beyond coiled proboscis.

Thorax: Apex of tibia of prothoracic leg with heavily sclerotized sharply pointed spine-like seta approximately one-half length of first tarsal segment; other legs as for genus. *Forewing:* Similar in shape to *P. hilli*, though narrower (Figs. 1–4), without sharply pointed apex typical of many other species in the genus; ground color pale olive yellow; scales, two-toned with yellow tips and basally olive brown, with basal color taking up proportionally more of the scales in subterminal region; dusting of white scales throughout. Fringes yellow at wing edge, apically white. Maculation on FW as described above, with ST and PM lines always present (though PM can be quite faint); PM line angled toward apex of wing; AM line (when present) makes a "V" with PM line. In seven of eleven specimens, faint line joins PM line under reniform, continues along medial aspect of reniform up to costa, with this line and PM line forming a "y" (somewhat visible in Fig. 3). *Hindwing:* Ground color largely white basally, lightly dusted with olive-gray scales toward wing edge. Scales very fine and tightly pressed to wing; fringe scales long and white. Overall impression is HW lightly scaled, with venation quite visible, especially from underside.

Abdomen: Male *P. kathyae* with strongly sclerotized ridge on posterior edge of seventh tergum (somewhat visible in Fig. 3), and a small sclerotized U-shaped ridge on anterior edge of eighth tergum; otherwise as for genus.

Male genitalia (Figs. 7–8): very similar to *P. hilli* (Figs. 5–6) and other members of *Plagiomimicus*; valves symmetrical, broad, and rectangular, with visible ampulla (16% of length of valve); uncus as in *P. hilli*, thin, cylindrical; distal end pointed and reflected ventrally; tegumen arms broad, forming an inverted "V"; saccus narrowed near base where it joins vinculum; aedeagus long, thin (4.4× longer than width at apex); vesica without pronounced subbasal pouch, with large field of apical cornuti, and a row of very small cornuti basally (near apex of aedeagus), these two cornutal patches typical for genus (Poole 1995).

Female genitalia (Fig. 10): corpus bursae large and membranous, with a mesial constriction, posterior part sclerotized with short longitudinal ridges visible for a short distance anteriorly along corpus; ductus bursae lightly sclerotized; anterior apophyses long, extending to corpus; posterior apophyses 1 1/4 × longer; positioned farther back; papillae anales long and heavily sclerotized, tapering to a narrow, blunt tip.

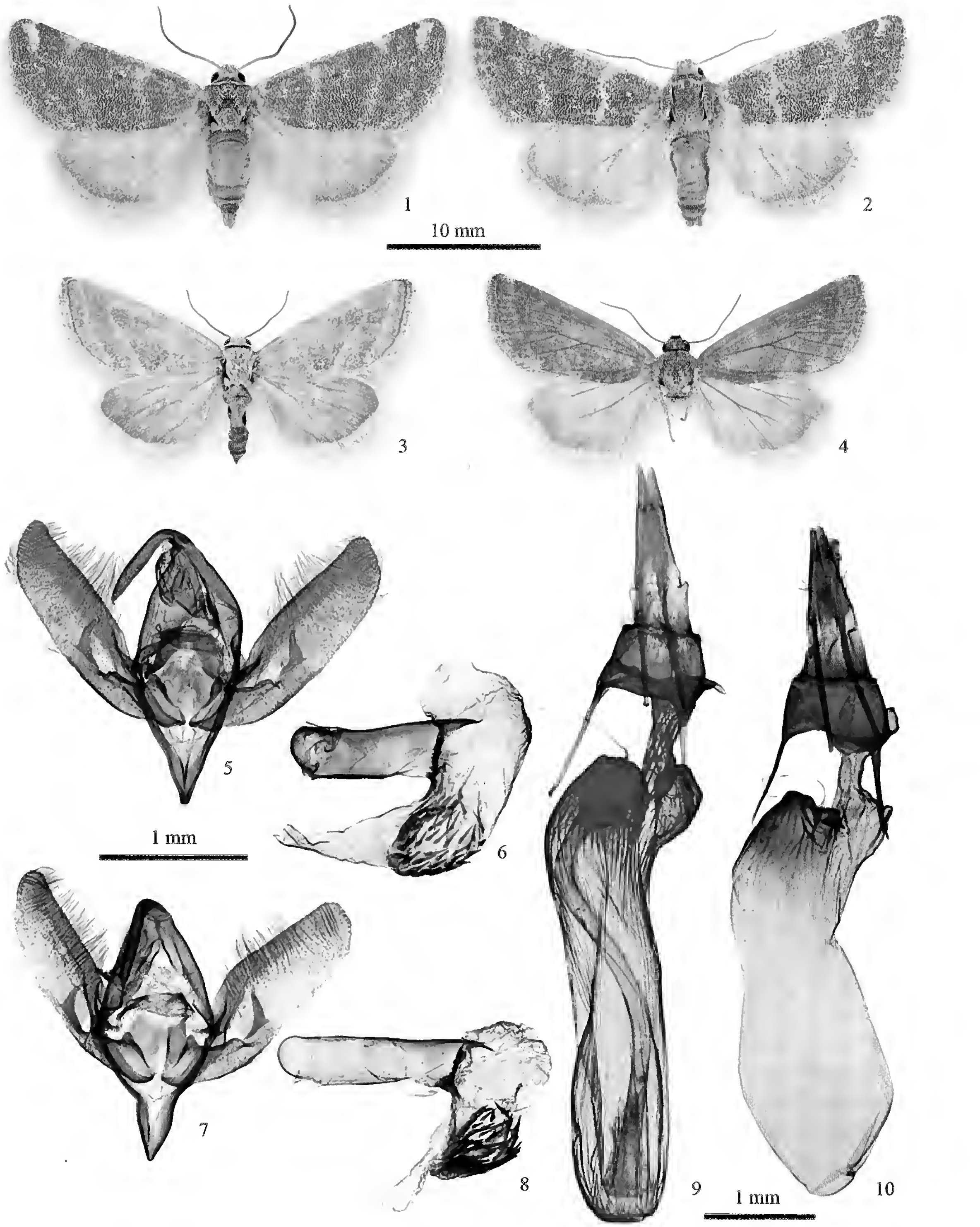
Type material: Holotype male (Fig. 4): **Arizona:** Coconino Co., Cameron (nr. Little Colorado River), at lights, 7 Sep. 1995, J. Adams (deposited in CNC). Paratypes (4 males, 6 females): **Arizona:** Same locality as holotype, 7 Sep. 1995 (2 males, 3 females) and 1 Sep. 1996 (1 male, 2 females); **Utah:** Grand Co., Moab, at lights, 5 Sep. 1995 (1 female) and 28 Aug. 1996 (1 male), J. Adams. The precise location for collection of the Arizona specimens is the Cameron Trading Post, Cameron, AZ, at 35° 52' 30" N, 111° 24' 47" W, just south of the Little Colorado River and just W of Hwy. 89. Paratypes deposited in CNC, personal collection of JKA, and USNM.

Etymology. The species is named in honor of the wife of JKA, Katherine Parker-Adams. This name is particularly appropriate as James and Kathy were on their honeymoon at the time of discovery of the first specimens in 1995.

DISCUSSION

The genus *Plagiomimicus* Grote (Poole 1995) is a large genus of stiriine noctuids, most of which are found in xeric habitats in western United States and northern Mexico. The pattern in adults of *Plagiomimicus* is typically subdued, with a light gray ground color in some, olive yellow, yellow gray or dark brown in others. One constant pattern element in virtually all species is a visible postmedian line on the forewings; other pattern elements (spots, bars, other lines) may be accentuated in some, completely absent in others. Another virtual constant is the late summer/early fall flight time. The genitalia (both male and female) are quite similar among species in the genus (including *P. kathyae*).

The known distribution for *Plagiomimicus kathyae* is currently defined by the two collection localities: Cameron, Coconino Co., Arizona, along the Little Colorado River east of the Grand Canyon, and Moab, Grand Co., Utah. It seems reasonable to assume that the species should be found in any appropriate habitat between the two locations, and possibly over a broader area in the southern Great Basin. The species appears to be a denizen of very dry scrub habitat, similar to *P. hilli*, which is found in the Mojave Desert region south and west of the range of *P. kathyae* (south-central Arizona to southern California; Poole 1995). The larva, as for many



FIGS. 1–10. **1,** *P. hilli*, male, Palm Springs, California, 22 Oct 1927, C. A Hill. **2,** *P. hilli*, female, Indio, California, 21 Oct 1921. **3,** *P. kathyae*, male holotype, Cameron, Coconino Co., Arizona, 7 Sept., 1995, James K. Adams. **4,** *P. kathyae*, female paratype, Cameron, Coconino Co., Arizona, 7 Sept., 1995, James K. Adams. **5,** *P. hilli*, male genital capsule, 19 mi W Blythe, Riverside Co., California, 10 Oct 1958, W. E. Ferguson. **6,** *P. hilli*, aedeagus and vesica. Same data as 5. **7,** *P. kathyae*, male genital capsule, Moab, Grand Co., Utah, 28 Aug. 1996, J. K. Adams. **8,** *P. kathyae*, aedeagus and vesiea. Same data as 7. **9,** *P. hilli*, female genitalia, Hopkins Well, Riverside Co., California, 11 Oct 1958, W. E. Ferguson. **10,** *P. kathyae*, female genitalia, Cameron, Coconino Co., Arizona, 7 Sept., 1995, James K. Adams.

species in the genus, is unknown, but it would seem likely that the immatures of *P. kathyae* should feed on some plant species in the Asteraceae, because the known larvae of other species of *Plagiomimicus* (*P. spumosum* (Grote), *P. tepperi* (Morrison), *P. pityochromus* Grote, and *P. expallidus* Grote) all feed on species of plants in the Asteraceae (Poole 1995).

The flight time for the species is currently defined by the eleven collected specimens—August 28 – September 7. This flight time falls within the typical late summer flight time for many stiriine noctuids. Additional trips through the Moab and Cameron areas in early August have not resulted in collection of any more specimens, so it clearly begins its flight sometime in mid–late August. It is not known how late into September the species could be encountered.

The closest relative to *P. kathyae*, as already indicated, appears to be the similarly colored *P. hilli*. The genitalia (Figs. 5–10), of both male and female, are quite similar between the two species, and are rather typical for the genus *Plagiomimicus* (Poole 1995). As *P. hilli* is the apparent sister species for *P. kathyae*, and there are two records of *P. hilli* (in the CNC) from April, suggesting a spring brood, it could prove fruitful to search for *P. kathyae* in the spring months as well.

ACKNOWLEDGEMENTS

Our thanks to Jocelyn Gill for preparing the plate. Our thanks also to Jan Metlevski and one anonymous reviewer for helpful comments on the manuscript.

LITERATURE CITED

POOLE, R. W. 1995. Noctuioidea, Noctuidae (part), Cuculliinae, Stiriinae, Psaphidinae (part). *In* Dominick, R. B., *et al.*, The moths of America north of Mexico, fascicle 26.1: 1–249

Received for publication 12 November; revised and accepted 20 April 2009.

Journal of the Lepidopterists' Society
63(3), 2009, 177–178

BOLORIA FRIGGA SAGA (NYMPHALIDAE), A SIGNIFICANT NEW RECORD FOR MAINE AND NORTHEASTERN NORTH AMERICA

Boloria frigga saga (Staudinger), is locally distributed in Alaska and much of Canada south to the northern Great Lakes region of the U.S. where it is limited to northern Minnesota, Wisconsin, and Michigan's Upper Peninsula (Opler & Malikul 1992, Layberry *et al.* 1998, Nielsen 1999). Other subspecies occur in the Rocky Mountains of the western states. Until recently, the southeastern most documented locality for this butterfly was in central Quebec, near Chicoutimi (Layberry *et al.* 1998). It was thus by accident that a single very worn female of *B. frigga* was collected on 24 June 2002 by the first investigator, in Northeast Carry Twp in Piscataquis Co., Maine, approximately three miles northeast of Moosehead Lake during surveys for new sites of *Boloria eunomia dawsoni* Barnes & McDunnogh. During a subsequent visit on 12 June 2003 to confirm that a colony of Frigga fritillary existed in this peatland, 82 adults (65 males, 17 females) were observed between 1200 and 1700h (Fig. 1). Adults were also common at this site on 11 June 2004 and 12 June 2007. Other likely breeding resident adult butterflies noted during *B. frigga* surveys at this locality included *Papilio canadensis* Rothschild & Jordan, *Callophrys augustinus* (Westwood), and *Oenis jutta ascerta* Masters & Sorensen. The discovery of the Frigga fritillary was important, both for its significant southward extension of the insect's eastern range in North America, and for its addition to the relatively well-studied butterfly fauna of Maine (Brower 1974, Webster & deMaynadier 2005).

The habitat where Frigga fritillary adults were found can be characterized as an acidic, sphagnum-dominated fen with open-grown, stunted tamarack (*Larix laricina*), and scattered black spruce (*Picea mariana*). Adults were most common in lightly wooded sections of the fen with open flat areas of saturated green sphagnum and patches of bog willow (*Salix pedicellaris*). Other dominant flora in the immediate area included sheep laurel (*Kalmia angustifolia*), rhodora (*Rhododendron canadense*), bog rosemary (*Andromeda polifolia*), Labrador tea (*Rhododendron groenlandicum*), pitcher plant (*Sarracenia purpurea*), northern blue flag (*Iris versicolor*), buckbean (*Menyanthes trifoliata*), bog maianthemum (*Maianthemum trifolium*), cotton grass (*Eriophorum* sp), and other sedges. In northern portions of its range, the Frigga fritillary occupies wet shrubby areas of tundra, or willow swamps and bogs in the boreal forest (Layberry *et al.* 1998, Scott 1986). To the south, in the northern Great Lake states, the butterfly is limited to muskeg and wetter portions of sphagnum bogs (Nekola 1998, Kriegel & Nielson 2000).

The probable larval host plant for Frigga fritillary at the Maine site is bog willow, which was common in the shrub layer where adults were most common. In Alberta, females have been observed ovipositing on willows and dwarf birch, *Betula glandulosa*, and the larvae feed on these plants (Bird *et al.* 1995). The larvae have also been reared in captivity on a related dwarf birch (*Betula pumila*) in Michigan (Nielsen 1999). However, dwarf birch was not present at the Maine site, and Frigga fritillary was not present in other northern peatlands in Maine where dwarf birch was common. In Alaska, females have been observed ovipositing on arctic avens, *Dryas integrifolia* (Scott 1986).

Adults were generally freshly emerged (males fresh to slightly worn, females freshly emerged) on 12 June 2003, 11 June 2004 and 12 June 2007, suggesting that peak flight occurred in mid June during these years at this locality. One mating pair (Fig. 1) was observed at 1550h on 12 June 2003. Adult nectaring was observed at the Maine locale on several common flowering bog shrubs, including Labrador tea, black chokeberry (*Photinia melanocarpa*), pale bog laurel (*Kalmia polifolia*), rhodora, bog maianthemum, and bog rosemary.

It was anticipated that Frigga fritillary might be patchily distributed in Maine's northern ecoregions, and thus surveys for the species have been on-going after

FIG. 1. Mating pair of *Boloria frigga saga* in Northeast Carry Twp, Piscataquis Co., Maine, 12 June 2003

the initial discovery (deMaynadier & Webster 2007). Named appropriately after Frigga, the wife of Odin and goddess of the clouds and heavens in Norse mythology (Bird *et al*. 1995), the flight season of Frigga fritillary is both condensed (approximately two weeks or less) and timed for a period in late spring when cloudy, rainy weather is common at northern latitudes. Hence it may require significantly more survey effort before we fully understand the distribution and status of this insect in the Acadian forests of northern New England and the Maritime Provinces. Nonetheless, eleven additional potential sites have been surveyed to date in Maine, several hosting moderate to abundant populations of bog willow, but no new populations of Frigga fritillary have been found. Notably, the microhabitat at Number 5 Bog, near Jackman, ME was almost identical to the fen in Northeast Carry Twp with an abundance of bog willow. However, Frigga fritillary appears to be absent from this site having been undetected during surveys in both 2004 and 2007. With still only one known breeding colony, the Frigga fritillary is currently listed as a species of special concern in Maine, and the possibility should be considered that only a few isolated, glacial relict populations persist in the Acadian ecoregions of northeastern North America.

ACKNOWLEDGEMENTS

We thank Brian Scholtens for preliminary confirmation of the first worn *B. frigga* specimen collected in 2002 and Don Cameron (Maine Natural Areas Program) for help with identification of the likely host plant, *Salix pedicillaris*. We appreciate critical review of the manuscript by Dale Schweitzer and one other anonymous reviewer. Funding for rare invertebrate surveys in Maine is made possible by contributions to the state's Nongame and Endangered Wildlife Fund, supported by proceeds from the Loon License Plate and Chickadee Cheek-off.

LITERATURE CITED

BIRD, C. D., G .J. HILCHIE, N. G. KONDLA, E. M. PIKE, & F. A. H. SPERLING. 1995. Alberta butterflies. The Provincial Museum of Alberta, Edmonton. 349 pp.

BROWER, A. E. 1974. A list of the Lepidoptera of Maine – Part 1. The Macrolepidoptera. Tech. Bull 66. Life Sci. & Agri. Expt. Sta., Univ. Maine, Orono, ME. 136 pp.

DEMAYNADIER, P. & R. WEBSTER. 2007. Frigga fritillary. Pps 55-60. *In* G. J. Matula, T. P. Hodgman, & P. deMaynadier (eds), A survey of rare, threatened, and endangered fauna in Maine: Aroostook Hills and Lowlands Ecoregions (2003-2005). Maine Department of Inland Fisheries and Wildlife, Bangor, Maine. Technical Bulletin 66. University of Maine, Orono, 136 pp.

KRIEGEL, R. D. & M. C. NIELSEN. 2000. A survey of *Boloria freija* and *B. frigga* in northern Michigan sphagnum heath bogs. Technical report submitted to Michigan Dept. of Natural Resources, Lansing, MI.

LAYBERRY, R. A., P. W. HALL, & J. D. LAFONTAINE. 1998. The butterflies of Canada. University of Toronto Press, Toronto. 280 pp.

NEKOLA, J. C. 1998. Butterfly faunas of three peatland habitat types in the Lake Superior drainage basin of Wisconsin. Great Lakes Entomologist 31(1): 27-38.

NIELSEN, M. C. 1999. Michigan butterflies and skippers: a field guide and reference. Michigan State University Extension Press, MI. 248 pp.

OPLER, P. A., & V. MALIKUL. 1992. A field guide to eastern butterflies. Houghton Mifflin Co., New York, NY. 396 pp.

SCOTT, J. A. 1986. The butterflies of North America: a natural history and field guide. Stanford University Press, Stanford, CA. 688 pp.

WEBSTER, R. P. & P. G. DEMAYNADIER. 2005. A baseline atlas and conservation assessment of the butterflies of Maine. Technical report submitted to Maine Dept. of Inland Fisheries and Wildlife, Bangor, ME.

PHILLIP G. DEMAYNADIER *Maine Department of Inland Fisheries and Wildlife, 650 State Street, Bangor, ME 04401; email: phillip.demaynadier@maine.gov* and REGINALD P. WEBSTER *24 Millstream Drive, Charters Settlement, NB, Canada E3C 1X1; email: rwebster@nb.sympatico.ca.*

Received for publication 9 January 2009; revised and accepted 1 April 2009.

Journal of the Lepidopterists' Society
63(3), 2009, 179–181

FOLLOWING THE LEADER: HOW *HELICONIUS ETHILLA* BUTTERFLIES EXCHANGE INFORMATION ON RESOURCE LOCATIONS

Additional key words: communal roosts, cooperation, flight formation, Heliconiinae.

Neotropical forest-dwelling *Heliconius* butterflies exhibit different types of social behavior such as nocturnal communal roosting—aggregations at specific locations to spend the night together (Benson 1971; Turner 1971a, 1975; Young & Thomason 1975; Young & Carolan 1976; Waller & Gilbert 1982; Mallet 1986) and cooperative egg laying, where females of some species are believed to cooperate in jointly laying batches of eggs (Turner 1971b; Mallet & Jackson 1980; Reed 2003; but see Turner 1981). In addition, the ability of *Heliconius* to learn and incorporate resource locations into daily routes and broadly overlapping generations (Ehrlich & Gilbert 1973) has led some authors to propose that younger butterflies may learn resource locations by following more experienced ones (Gilbert 1975; Brown 1981; Turner 1981). However, evidence for the education of younger butterflies remains scarce.

Heliconius ethilla narcaea Godart 1819, one of the largest butterflies in the genus, is common in forest patches across southeastern Brazil. It flies faster and higher than most other *Heliconius* and home range size (3.0 ha) is three times that of sympatric *H. erato phyllis* (1 ha; Pinheiro 1987). In contrast to *H. erato* and other *Heliconius*, which cluster tightly on nocturnal communal roosts (examples in Brown 1981; Mallet 1986), *H. ethilla* rests solitarily or forms loose aggregations of few individuals (pers. obs.; see also Turner 1971a; Brown 1981). During a two year capture-recapture program conducted with *H. ethilla* in southeastern Brazil and occasional observations in other parts of country, I observed this butterfly to engage in what appear to be three kinds of pursuits in which individuals follow one another and could obtain information on resources locations, especially plants visited for pollen (Gilbert 1972; Beltrán *et al.* 2007). In this note I describe these interactions and provide information on sex and age of butterflies (including six categories based on scale loss: VF = very fresh, F = fresh, I = intermediate, IW = between intermediate and worn, W = worn, and VW = very worn butterflies; Ehrlich & Gilbert 1973) that were utilized to test the prediction that "followers" are younger than "leaders" (= first butterfly in a queue), as might be expected if following serves mainly to educate young butterflies. Three types of following behaviors could be distinguished.

(1) "Acrobatic" flights. The most spectacular and certainly the best demonstration that *H. ethilla* butterflies transmit information on food locations is found in the "acrobatic" flights. This behavior occurs in groups of 2 to 5 butterflies in a line formation, approximately 1 m apart, engaging in acrobatic flights in the forest middlestory. From time to time butterflies would dive, passing within a few centimeters of flowers of *Lantana camara* L.—the most utilized pollen plant in the study site that may elicit strong feeding responses in *Heliconius* butterflies (Andersson & Dobson 2003)—before ascending and moving on to a neighboring area or flower patch. Although butterflies did not stop to feed, flowers clearly constituted important reference points in these flights, allowing followers to learn many flower locations shown by the leader. However, on the few occasions I was able to capture part or all butterflies of a given group, often close to *L. camara* flowers, only relatively older males were found (mostly I and IW individuals; see Table 1). In groups 1–3, two or more butterflies were captured together and it was not possible to separate leaders and followers. However, on two additional occasions only a leader (an I male; group 4) and only a follower (another I male, group 5) were captured. "Acrobatic" flights were more common in mid-afternoon, when butterfly feeding is reduced. Most observations were from the end of the wet season, when populations tend to be larger.

(2) "Long distance" flights. Another kind of following behavior exhibited by *H. ethilla* consisted of "long distance" flights. These often involved two butterflies engaging in a relatively fast, straight flight through the forest middlestory, with the leader flying approximately 1m higher and 2m ahead of the follower. In an open forest near Campinas, São Paulo, it was possible to keep butterflies in sight for relatively long periods. Butterflies engaged in "long distance" flights are often difficult to sample because of the distance from the ground. However, on one occasion I succeeded in capturing the follower after the leader had just passed 5 m up overhead (an I male, group 6 in Table 1). The leader flew on for about 40 m, but suddenly returned, seemingly in search of its follower, performing circular flights close to vegetation along the same route previously taken, when I captured it (a W male). After learning to "capture the follower first" I was

TABLE 1. Social flights performed by groups of *H. ethilla* males. The number of individuals captured in each group, the group size (before capture) and the age category of participating butterflies based on wing-wear are also given (F = fresh, I = intermediate, IW = between intermediate and worn, W = worn; note the absence of VF = very fresh and VW = very worn butterflies); social role: L= leader, Fo= follower.

INTERACTION TYPE	GROUP NUMBER	N. INDIVS. CAPTURED / GROUP SIZE	WING-WEAR CATEGORIES (SOCIAL ROLE)
"ACROBATIC"	1.	3/5	[I, IW & IW]
	2.	2/3	[I & I]
	3.	2/2	[IW & IW]
	4.	1/3	[I (L)]
	5.	1/2	[I (Fo)]
"LONG DISTANCE"	6.	2/2	[I (L) & F (Fo)]
	7.	2/2	[W (L) & F (Fo)]
"PURSUING"	8.	4/4	[I (L), I (Fo), F (Fo), IV (Fo)]
	9.	I/3	[I (Fo)]
	10.	I/2	[IW (Fo)]

able to use this technique to sample a second pair of butterflies. As in the previous case, the leader came back and was captured. The butterflies were both males and the age categories of the leader and follower were W and F respectively (group 7 in Table 1). Although "long distance" flights seemed to be relatively common in *H. ethilla*, especially between mid and late afternoon, I was unable to discover the origin and the final destination of these flights and, therefore, their objective. Despite that, it appears that some sort of information is transmitted from leader to follower in these flights. It may be significant that followers were younger than leaders in both groups investigated.

(3) "Pursuing" flights. These involve 2–4 butterflies that chase the leader in a fast, erratic flight. At first glance, pursuing activities appear unrelated to the education of butterflies, as the leader seems to try to escape from its pursuers and not show them resources. This behavior suggests that *H. ethilla* interactions include non-cooperative relationships as well as cooperative. Moreover, one unusual observation suggests another capability of *H. ethilla* yet undemonstrated: that butterflies may follow each other with the aid of chemical cues in addition to vision. This possibility was suggested by an event in which all butterflies in a group were captured in sequence (group 8 in Table 1). I was walking on a forest-edge trail when a *H. ethilla* appeared 2m ahead coming from the inside forest in a very fast flight. The butterfly stopped to hover for a few seconds over the middle of the trail, approximately 1m above the ground, and turned to my direction in the trail (it was an I male). I had the butterfly in my hand when a second *H. ethilla* flew out of the forest at the same place and height, hovered for some seconds and flew towards me just as had the leader (another I male). Some seconds later a third butterfly emerged from the forest at the same spot and repeated the same movements of its two predecessors (a F male). Finally, a fourth butterfly appeared and repeated everything once again (an IV male). Because no follower had visual contact with its predecessors – each had been captured by the time the next butterfly arrived – the butterflies probably followed a chemical track to pursue the leader. My impression was that hovering at locations where predecessors changed flight directions played some role in helping the butterflies to perceive such chemicals and orient themselves. Thus, it seems possible that male butterflies use both visual and chemical signals to follow or pursue one another. On other occasions, usually away from flowers, I was in doubt whether or not butterflies were in following activities, for they were far apart, or just orienting to shared feeding routes that shorten the distance between feeding patches (Ehrlich & Gilbert 1973). It still remains to confirm and identify chemicals utilized by butterflies to follow one another, and document the advantage(s) of engaging in pursuing activities. In two additional cases of pursuing flights, only followers were caught (an I male and an IW male; groups 9 and 10 in Table 1).

These examples suggest that *H. ethilla* has evolved sophisticated forms of following behavior, uncommon in other butterfly taxa, which may be used to transmit information on the location of food resources. However, the fact that both leader and follower butterflies include several age classes (beyond VF only VW individuals were not found) suggest that whatever information may be transmitted is not necessarily addressed to younger butterflies. This larger demographic set may consist of distinct, as in the case of "long distance" flights, or same generation, as in the case of the "acrobatic" and "pursuing" flights, individuals. It seems therefore that information transmission in *Heliconius* butterflies may involve a more extensive network than that originally conceived for the simple education of young butterflies. Cooperative interactions of this kind are expected to be facilitated by relatively high levels of kinship, a possibility that has been suggested in *Heliconius* populations (Benson 1971; Turner 1981; Mallet & Singer 1987).

The fact that only males were observed to engage in following activities suggests they have evolved more developed forms of social behavior than females, which do not seem to cooperate with other females in laying eggs (females usually oviposit only 1 or 2 eggs under young leaves or tendrils of *Passiflora*; Brown 1981) and do not seem to participate in any following activity reported here. Male-restricted social behavior is also reported for *Actinote surima surima* (Shaus) 1902 (Heliconiinae) in which only males join communal roosts (Paluch *et al.* 2005). The possibility that social interactions are also restricted to males in the case of *H. ethilla* is, therefore, a real one, and should be further investigated.

ACKNOWLEDGEMENTS

I thank K. S. Brown Jr. and W. W. Benson for their support and illuminating ideas on *Heliconius* behavior. W. W. Benson also read a previous version of the manuscript and furnished many helpful suggestions

LITERATURE CITED

ANDERSSON, S. & H. E. M. DOBSON. 2003. Behavioral foraging responses by the butterfly *Heliconius melpomene* to *Lantana camara* floral scent. J. Chem. Ecol. 29: 2303-2318.

BELTRÁN, M., C. D. JIGGINS, A. V. Z. BROWER, E. BERMINGHAM, & J. MALLET. 2007. Do pollen feeding, pupal mating and larval gregariousness have a single origin in *Heliconius* butterflies? Inferences from multilocus DNA sequence data. Biol. J. Linn. Soc. 92: 221-239.

BENSON, W. W. 1971. Evidence for the evolution of unpalatability through kin selection in the Heliconiinae (Lepidoptera). Amer. Nat. 105: 213-226.

BROWN JR., K. S. 1981. The biology of *Heliconius* and related genera. Ann. Rev. Entomol. 26: 427-456.

EHRLICH, P. R. & L. E. GILBERT. 1973. Population structure and dynamics of the tropical butterfly *Heliconius ethilla*. Biotropica 5: 69-82.

GILBERT, L. E. 1972. Pollen feeding and reproductive biology of *Heliconius* butterflies. Proc. Nat. Acad. Sci. USA 69: 1403-1407.

_____. 1975. Ecological consequences of a coevolved mutualism between butterflies and plants. *In* L. E. Gilbert & P. R. Raven (eds.), Coevolution of animals and plants. University of Texas Press, Austin.

MALLET, J. L. B. 1986. Gregarious roosting and home range in *Heliconius* butterflies. Natl. Geog. Res. 2: 198-205.

_____. & D. A. Jackson, 1980. The ecology and social behavior of *Heliconius xanthocles* Bates in Colombia. Zool. J. Linn. Soc. 69: 1-13.

_____. & M. C. SINGER. 1987. Individual selection, kin selection, and the shifting balance in the evolution of warning colours: the evidence from butterflies. Biol. J. Linn. Soc. 32: 337-350.

PALUCH, M., M. M. CASAGRANDE, & O. H. H. MIELKE. 2005. Comportamento de agregação noturna dos machos de *Actinote surima surima* (Schaus) (Lepidoptera, Heliconiinae, Acreini). Rev. Bras. Zool. 22: 410-418.

PINHEIRO, C. E. G. 1987. Dinâmica populacional e áreas de vida de *Heliconius erato* e *Heliconius ethilla* (Lepidoptera, Nymphalidae) em Campinas, SP. Master Dissertation. Unicamp, Campinas, São Paulo.

REED, R. D. 2003. Gregarious oviposition and clutch size adjustment by a *Heliconius* butterfly. Biotropica 35: 555-559.

TURNER, J. R. G. 1971A. Experiments on the demography of tropical butterflies: Longevity and home range behaviour in *Heliconius erato*. Biotropica 3: 21-31.

_____. 1971b. Studies of Müllerian mimicry and its evolution in burnet moths and heliconid butterflies. Pp. 224-260, *In* E. R. Creep (ed.), Ecological Genetics and Evolution. Blackwell, Oxford.

_____. 1975. Communal roosting in relation to warning colour in two Heliconiine butterflies (Nymphalidae). J. Lepid. Soc. 29: 221-226.

_____. 1981. Adaptation and evolution in *Heliconius*: a defense of neodarwinism. Ann. Rev. Ecol. Syst. 12: 99-121.

WALLER, O. A. & L. E. GILBERT. 1982. Roost recruitment and resource utilization: observations on a *Heliconius charitonia* L. roost in Mexico. J. Lepid. Soc. 36: 178-184.

YOUNG, A. M. & J. H. THOMASON. 1975. Notes on communal roosting of *Heliconius charitonius* (Nymphalidae) in Costa Rica. J. Lepid. Soc. 29: 243-255.

_____. & M. E. CAROLAN. 1976. Daily instability of communal roosting in the neotropical butterfly *Heliconius charitonius* (Lepidoptera: Nymphalidae). J. Kansas Entomol. Soc. 49: 346-359.

CARLOS E. G. PINHEIRO, *Depto. de Zoologia, Universidade de Brasília - UnB, 70910-900 Brasília, DF, Brazil; email: cegp@unb.br*

Received for publication 12 March 2008; revised and accepted 11 March 2009.

Journal of the Lepidopterists' Society
63(3), 2009, 182–183

FIELD GUIDE TO THE BUTTERFLIES OF THE SAN FRANCISCO BAY AND SACRAMENTO VALLEY REGIONS.By A.M. Shapiro & T.D. Manolis. 351 pages, 31 color plates; Hardcover (US$50) ISBN 978-0-520-24469-6, Softcover (US$18.95) ISBN: 978-0-520-24957-8. University California Press. Publication date: 2007.

Among academic cognoscenti Art Shapiro represents the stuff of legend. But perhaps most familiar are his significant scientific works that have their core in the study of butterflies. In a voice that is uniquely his own, he has often breathed the vital spark of life into marginal or disregarded topics, or the work of little known authors, and in doing so, managed to provide important insights into the ecology and evolution of butterflies. In that same voice he has also, upon occasion, held up shoddy work in the glaring public spotlight. Given his consistent history of eclectic scholarly work one comes to expect important and interesting things from him. In this field guide, however, it seems to me that Shapiro has done something extraordinary. Rather than follow charted bureaucratic procedures, technologies, and list of topics that are *de rigueur* in a great many butterfly books, this one charts new territory by being breathtakingly simple and direct. It is written to inform a lay audience how to see butterflies in nature, look beyond the object, and appreciate complex natural history and habitat associations—butterfly biology, as it should be. And this book does so with such disarming ease that trained biologists can understand its importance, and learn from reading it.

The workhorse of any field guide is the collection of identification plates. This is the first place one goes to start learning. It is where one compares a real butterfly with a photograph or illustration. Logically, identification plates should be good, but they often disappoint. The plates painted by Timothy Manolis are a mixture of traditional flat winged illustrations with more dynamic portraits of butterflies flying, or at rest in the field. They are extremely good, and represent an intelligent mix of art with a naturalist's eye to practicality. In combination with the notes on the facing pages, identifying most butterflies treated in this field guide should be a rewarding experience. To test this idea I recommend using this book ruthlessly, and put the binding through grueling field tests under any and all weather conditions.

Butterfly field guides can be many things. When assessing a new one I am inexorably drawn to the species accounts to see what the author has to say. Consider *Danaus plexippus*; perhaps the best-known butterfly species in the world. What biologist who works on butterflies hasn't been asked about their biology? I'll bet that most of us have given an abbreviated version of…, migration, unpalatability, mimicry, yada-yada-yada. Well, the entry in this book shows how a ponderous amount of scientific information on the monarch butterfly can be condensed succinctly into a few short pages. Even my own mother could read it, understand it, and then prod me with non-trivial questions—for hours. Let's take another well-known species, *Parnassius clodius*. Here its distribution and natural history is considered crisply in succinct words, but the account also includes some wonderful lagniappe on mating behaviors and the sphragis that are meant to entice researchers. Nice to see new life breathed into the well-known species. But what about rare species with identity problems like *Polygonia oreas*? Well, learn all about it on p. 188. But be advised that, "This species is, or isn't conspecific with *P. progne*, depending on this weeks reading of goat entrails". What a dexterous way of pointing out taxonomic squabbles and territories among the experts. But after allusions to goats, Shapiro gets serious by noting that this is "another poorly understood species of cool, moist forest", and provides his own field observations, thereby directly asking for more evidence, not just opinion. Like anyone reading the account, I found myself thinking about working in these mysterious cool, moist Californian forests to get some answers. In sum, it seems that each and every one of the species accounts are logical, informative, easy to use, and very well written.

The topical subjects an author chooses to write about form an important part of any field guide, and Shapiro does not disappoint. It is likely that more words have been expended on taxonomic classification in the butterfly literature than any other topic. Indeed, this is among the first things the incipient student of butterflies learns about and feels is important, and Shapiro suggests (p.69) that according to the book of Genesis, taxonomy is the world's oldest profession. Do I detect a hint of Shapirian double entendre? He then gives account of the historical development of taxonomy and classification, ranging from Linnaeus through cladistics, all the while maintaining his central theme that phylogeny is important to understanding butterfly evolution and ecology. Although it has been said many times before, we are reminded (p. 71) that, "Butterfly taxonomy is a mess". Those five words encapsulate what

I call, '*butterflyology*' (Hey, it's time someone coined the term). *Butterflyology* may be defined as the perennial squabbling jihad fueling the constant flux of scientific and/or common names, often at the expense of what is really interesting or important. Using a low-key, elegant approach Shapiro describes the tempest of the name game, pointing out how stability in the taxonomic system of genera, species, subspecies, forms or just common names seems particularly elusive in butterflies. He also gives examples of how illogical logic fuels the constantly changing sets of names, and why various rules, legislation and mood swings are necessary to put names on the butterflies treated in his field guide. Without a suspicion of goat entrails Shapiro miraculously clarifies this dynamically obfuscated topic, and even employs fuzzy logic (p. 82) to make a thoughtful gumbo of butterfly names. Pass the hot sauce, please.

And what about the frightening, compounded techno phrase, 'molecular phylogeography'? What does it mean? How does it fit into the layman's life, '*butterflyology*', or that of the professional biologist? And why is it important anyway? All is revealed in three paragraphs (pp. 11–12), and it leaves one satisfied that it is important. And those paragraphs makes one ponder the long history of earth and butterflies, and wonder about those mysterious missing mimics of *Battus philenor* in California. Food for thought indeed.

To the potential reader I suggest dipping into all topics, chapters and species accounts in this field guide, and to do so frequently. There is nothing facile here. This is sophisticated work written by someone who is a master of the subject. This book is about the ecological and evolutionary dynamics of butterflies, the effects of civilization, habitat, and climate change on them through the history of California. Art Shapiro inspires everyone to get involved with butterflies, and get to work. Beyond that I think this is a tremendous book, and one that should be on the bookshelf of anyone who can read.

PHIL DEVRIES, *Department of Biological Sciences, University of New Orleans, New Orleans, LA 70148; email: pdevries@uno.edu.*

Received for publication 2 March 2009; revised and accepted 1 May 2009.

NOTICE TO CONTRIBUTORS

Contributions to the *Journal* may deal with any aspect of Lepidoptera study. Categories are Articles, Profiles, General Notes, Technical Comments, Book Reviews, Obituaries, Feature Photographs, and Cover Illustrations. Obituaries must be authorized by the president of the society. Requirements for Feature Photographs and Cover Illustrations are stated in Volume 44(2):111 and on the Society's web site at http://www.lepsoc.org/.

Send *Journal* submissions electronically to: scholtensb@cofc.edu or to the editor at the above address. Contributors should feel free to recommend one or two reviewers upon submission of their manuscript. Send requests to review books for the *Journal* and book review manuscripts to Phil DeVries at the above address (or electronically to: pdevries@uno.edu). Short manuscripts concerning new state records, current events, and notices should be sent to the *News*, Dale Clark, 1732 South Hampton Rd, Glenn Heights, TX 75154-8530. ***Before submitting manuscripts or electronic files,*** consult instructions on the Society's web site at http://www.lepsoc.org/.

Although we prefer electronic submissions, authors may submit hard copy if they are unable to send material electronically. Submit manuscripts in *triplicate*, typewritten, *entirely double-spaced*, with wide margins, on one side only of white letter-sized paper. Prepare manuscript according to the following instructions, and submit them flat, not folded. Submit original illustrations only *after* the manuscript has been revised and accepted. Authors should provide an electronic copy of the *final accepted* manuscript in a standard PC or Macintosh-based word processing format.

Abstract: Include an informative abstract for Articles, Profiles, and Technical Comments.

Additional key words: Up to five key words or terms not in the title should accompany Articles, Profiles, General Notes, and Technical Comments.

Text: Write with precision, clarity and economy, and use the active voice and the first person whenever appropriate. Make title explicit, descriptive, and as short as possible. The first mention of a plant or animal in the text should include the *full scientific name* with *author*, and *family*. Use metric units for measurements, and a 24-h clock (0930 h, not 9:30 AM) to express time. Underline only where *italics* are intended.

Literature cited: References to Articles, Profiles, General Notes, and Technical Comments should be given as Sheppard (1959) or (Sheppard 1959, 1961a,b) and listed alphabetically under the heading Literature Cited, in plain text (do not capitalize author names) and without underlining as follows:

Sheppard, P. M. 1959. Natural selection and heredity. 2nd ed. Hutchinson, London. 209 pp.
—— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. Adv. Genet. 10:165–216.

Illustrations: Again, electronic submissions are preferred. Initial submissions may be low-resolution *.jpg format, but final illustrations should be *.tif format at a resolution of at least 300 pixels per inch (120 pixels per cm) saved to a CD. Illustrate only half of symmetrical objects such as adults with wings spread, unless whole illustration is crucial. Bear in mind that your illustrations will be reduced to fit a *Journal* page (plan to make lettering sufficiently large) and that the figure legend will appear at the bottom of the page (*Journal* page: 16.5 cm width, 22.5 cm height). One-column illustrations should be at least 800 pixels wide; two-column illustrations should be 1700 pixels wide. Illustrations larger than letter-size are not acceptable and should be reduced photographically to that size or smaller. Figures, both line drawings and photographs, should be numbered consecutively in Arabic numerals; do not use "plate." Type figure legends double-spaced, *on a separate sheet* (not attached to the illustrations), headed Explanation of Figures. Use a separate paragraph for each legend. Color illustrations are encouraged; contact editor or consult our web site for submission requirements and cost.

Tables: Number tables consecutively in Arabic numerals. Label them in plain text (e.g., Table 1.) and use a concise and informative heading. Type each table on a separate sheet and place after the Literature Cited section, with the approximate desired position indicated in the text. Avoid vertical lines and vertical writing. Submit tables as Microsoft Excel or Word documents, or as TIF image files at 300 ppi.

Voucher specimens: When appropriate, manuscripts must name a public repository where specimens documenting the identity of organisms can be found. Kinds of reports that require vouchering include descriptions of new taxa, life histories, host associations, immature morphology, and some experimental studies.

Proofs: The edited manuscript and galley proofs will be mailed to the author for correction of printer's errors. Excessive author's changes will be charged to authors at the rate of $3.00 per line. A purchase order for reprints will accompany proofs.

Page charges: For authors affiliated with institutions, page charges are $50 per *Journal* page. For authors without institutional support, page charges are $25 per *Journal* page. For authors who are not members of the Society, page charges are $75 per *Journal* page. Authors unable to pay page charges for any reason should apply to the editor at the time of submission for a reduced rate. Authors of Book Reviews and Obituaries are exempt from page charges.

Correspondence: Address all matters relating to the *Journal* to the editor. Address book reviews directly to the book review editor.

PRINTED BY THE ALLEN PRESS, INC., LAWRENCE, KANSAS 66044 U.S.A.

CONTENTS

General Notes

Book Review