Volume 62 Number 1
6 May 2008
ISSN 0024-0966

Journal of the Lepidopterists' Society

Published quarterly by 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: *Miracavira brillians* (Barnes) (Noctuidae) larvae showing their striking coloration and resting posture.
Photo Credit: David Wagner, University of Connecticut, email: david.wagner@uconn.edu.

JOURNAL OF THE LEPIDOPTERISTS' SOCIETY

Volume 62 | 2008 | Number 1

Journal of the Lepidopterists' Society
62(1), 2008, 1–17

A CHARACTERIZATION OF NON-BIOTIC ENVIRONMENTAL FEATURES OF PRAIRIES HOSTING THE DAKOTA SKIPPER (*HESPERIA DACOTAE*, HESPERIIDAE) ACROSS ITS REMAINING U.S. RANGE

RONALD A. ROYER

Division of Science, Minot State University, 500 University Avenue West, Minot, ND 58707, USA; email: ron.royer@minotstateu.edu

ROSE A. MCKENNEY

Department of Geosciences and Environmental Studies Program, Pacific Lutheran University, Tacoma WA 98447, USA

AND

WESLEY E. NEWTON

U.S. Geological Survey, Biological Resources Division, Northern Prairie Wildlife Research Center, 8711 37th Street SE, Jamestown, ND 58401, USA

ABSTRACT. Within the United States, the Dakota Skipper now occurs only in Minnesota, North Dakota, and South Dakota. In these states it has been associated with margins of glacial lakes and calcareous mesic prairies that host warm-season native grasses. Preliminary geographic information system (GIS) analysis in North Dakota has indicated a close congruency between historic distribution of the Dakota Skipper and that of specific near-shore glacial lake features and related soil associations. This study analyzed humidity-related non-biotic microhabitat characteristics within three remaining occupied Dakota Skipper sites in each state during the larval growth period in 2000. Measured parameters included topographic relief, soil compaction, soil pH, moisture, and temperature at various depths, soil bulk density, soil texture, and temperature and humidity within the larval nest zone. Results of these efforts reveal two distinctive habitat substrates, one of relatively low surface relief with dense but relatively less compact soils, and another of relatively high relief with less dense but more compact soils. In the low-relief habitat, grazing appears to compact soils unfavorably in otherwise similar prairies in the more xeric western portion of the range, potentially by affecting groundwater buffering of larval nest zone humidity.

Additional key words: Dakota Skipper, habitat, climate, soils, management.

Numerous survey efforts have clearly defined present limits of distribution for the Dakota Skipper (*Hesperia dacotae* Skinner, 1911) (McCabe 1979, 1981; Dana 1991; Royer 1988a, 1988b, 2003; Royer & Marrone 1992; Orwig 1995, 1996; Schlicht 1997; Royer & Royer 1997, 1998; Skadsen 1997, 1999, 2000). Some recent work also has characterized this species' habitat floristically at selected sites (Dana 1997, ND Parks and Recreation Department 1999). However, there has been no systematic attempt to define physiographic or other non-biotic features of habitat across the species' entire U. S. range. A primary intention of this project was to identify and characterize non-biotic features that might help habitat managers better understand and more easily recognize favorable sites in areas where the species remains, has recently suffered decline, or is believed historically to have occurred but is now absent.

The original range of the Dakota Skipper is believed to have extended from Illinois northwestward as far as southeastern Saskatchewan (Royer 2003) and Manitoba (Klassen *et al.* 1989). It is known to occur within the U.S. now only in the states of Minnesota, North Dakota, and South Dakota, and a few populations still exist in Canada. The U. S. range originally included Iowa and Illinois, in both of which the species is now believed to have been extirpated (Scott 1986, T. Orwig, Morningside College, pers. comm.). In parts of this range the Dakota Skipper has been specifically associated with the margins of glacial lakes (McCabe & Post 1977, McCabe 1981). Many workers have also associated it with calcareous mesic prairies (McCabe 1981), such indicator plants as smooth camas (*Zygadenus elegans* Pursh., Liliaceae) (Royer & Marrone 1992), and warm-season native grasses (ND Parks and Recreation Department 1999).

Recently a very close relation has been noted in McHenry County, North Dakota, between recorded distribution of the Dakota Skipper, glacially related

surface geology, and soil associations defined by the United States Department of Agriculture (USDA) (Royer & Royer 1998, Lord 1988, see Fig. 1). Subsequent preliminary GIS analysis has suggested a statewide congruency of known distribution of the Dakota Skipper with these soil associations (Tom Sklebar, retired USGS NPWRC, pers. comm.). McCabe (1981) proposed that precipitation/evaporation ratios may be an important defining feature of this species' habitat requirements. Presence of "hydrofuge glands" on larval segments 7 and 8 (McCabe 1981) suggests a historic or present need of the species for protection from inundation. This led to our hypothesis that factors limiting Dakota Skipper populations may have more to do with such non-biotic habitat elements as temperature and local humidity during sensitive larval and pupal stages than with such biotic factors as host plant or nectar source availability or predation during the adult flight period, when this species has been most extensively studied.

Specifically, we hypothesized that such edaphic features as soil moisture, soil compaction, and soil bulk density, as well as related non-biotic factors such as temperature and relative humidity at and near (within 2.0 cm of) the soil surface, where several authors have noted that early stages abide in a silken nest during most of the summer (cf. McCabe 1981, Dana 1991), may be significant factors in larval survival potential. Microtopography substantially affects soil evaporation rates in the north-central United States (Cooper 1960). Soil compaction and vegetation removal (whether by herbivory, hay mowing, or fire) substantially alter soil water movement and evaporation, thereby altering near-surface humidity (Frede 1985, Miller & Gardiner 1998, Hausenbuiller 1985). Livestock grazing has been shown to increase bulk density (Zhao *et al.* 2007) and soil compaction (Greenwood *et al.* 1997), which are correlated with decreased soil water content and hydraulic conductivity (Zhao *et al.* 2007). In summer months these changes are likely to restrict the movement of shallow groundwater to the soil surface, thus preventing groundwater buffering of surface humidity conditions. Water loss from moist soils in contact with dry air occurs rapidly, usually exceeding the rate of upward movement of water through the soil (Hausenbuiller 1985). As a result a dry soil layer forms, inhibiting further evaporation. Formation of a dry soil layer would decrease surface humidity at precisely those times later in the summer when young larvae of the Dakota Skipper are most vulnerable to desiccation.

The principal objectives in this study therefore were (1) to characterize non-biotic features related to hydrology and microclimate (microtopography, soil compaction, soil pH, soil moisture, soil temperature, soil bulk density, soil texture, near-surface humidity) and the variability of those features within and across occupied sites in the context of average summer climate conditions generally, and also (2) to compare those features between grazed and hay-mowed sites within the more xeric portion of the range in North Dakota.

STUDY AREA AND METHODS

Western Minnesota, eastern North Dakota and eastern South Dakota were shaped by Laurentide ice sheets. This shaping profoundly affected the landforms and materials found at the surface in these areas. The Des Moines lobe cut across Minnesota and the eastern margin of South Dakota (South Dakota Geological Survey 1965). Slightly to the west, the James lobe cut through North Dakota and eastern South Dakota. These lobes deposited extensive moraines that contained unsorted clay to boulder sized material (Agnew *et al.* 1962, Hobbs and Goebel 1982). During the last glacial retreat, many areas were submerged under melt water lakes (South Dakota Geological Survey 1965, Hobbs and Goebel 1982, Lord 1988). Thus our study area contains relatively level areas with sorted sediment typical of lake bottom and near shore deposits, as well as rolling hills composed of poorly sorted sediment typical of glacial moraine deposits. Original Dakota Skipper habitat across the region ranged from tall-grass to mixed-grass native prairie. Much of the remaining habitat is now privately owned and managed either as hay meadow or pasture. Within this context, we specifically sought sites that were under public ownership or at which conservation is a management goal.

Climatically, the study area crosses a transition zone from humid, middle latitude with severe winter type in western Minnesota to mid-latitude steppe in central North and South Dakota (Ackerman 1941). This transition can be seen in summer average monthly temperatures and precipitation for the period of record (1895–2003) and the data collection year (2000, Table 1). South Dakota has average monthly temperatures that exceed Minnesota and North Dakota average monthly temperatures by 1–2°C. Minnesota's average monthly precipitation exceeds North and South Dakota average monthly precipitation by 20–50mm. Despite these differences in statewide values, temperature patterns are similar at climate stations near the study sites. Precipitation, however, is far more variable throughout the summer season and the region. State averages show that monthly precipitation declines from June through September, and that Minnesota has the largest average precipitation for each month of the

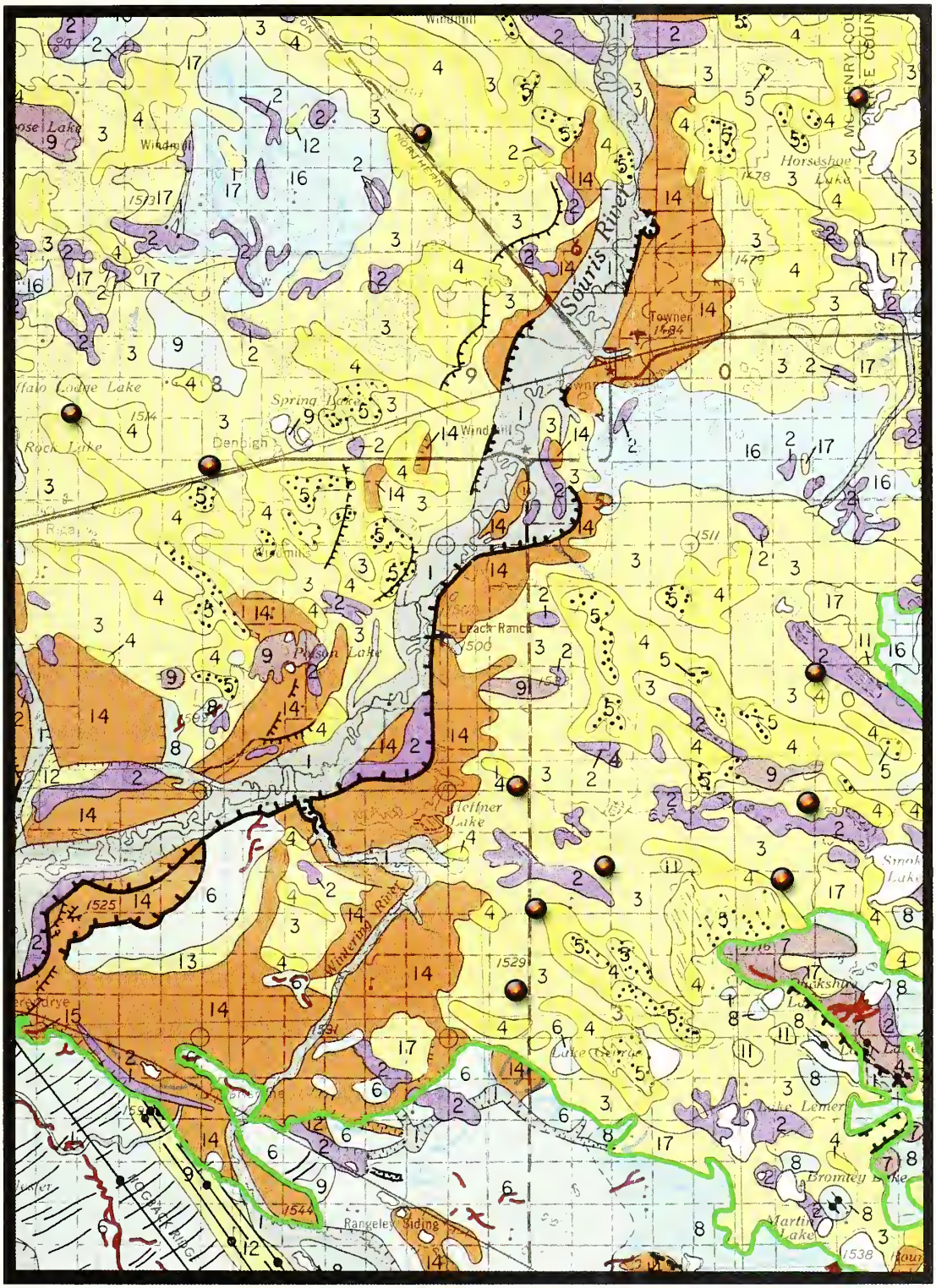


FIG. 1. Superimposition on a surface geology map (Lord 1988) of recently confirmed occurrence sites for *Hesperia dacotae* in McHenry County, North Dakota (dots) indicating close congruency with distribution of windblown soil units (#3 and #4) in the near-shore environment of glacial Lake Souris. Unit #3 was described by Lord as "silt and sand, fine to medium grained, moderately to well sorted…, gradational to unit 4." Unit #4 was described as "Sand, fine to medium grained, well sorted… (with dunes) as high as 5 metres." Both of these were characterized as having been reworked from unit 17, "nearshore lake sediment … up to 30 metres thick." The green line represents putative glacial lake margin, and the background map grid indicates square miles. (After Royer and Royer 1998.)

TABLE 1. Monthly mean temperatures (°C) and precipitation (mm) during summer months for Minnesota, North Dakota, and South Dakota (data from National Climatic Data Center, 2004).

	Average Temperature (°C)		Average Rainfall (mm)	
	1895–2003	2000	1895–2003	2000
Minnesota				
June	17.8	16.6	163.4	192.5
July	20.6	20.4	142.5	150
August	19.4	19.8	136.2	135.8
September	14.1	13.7	113	65.7
North Dakota				
June	17.1	15.7	136.2	129.9
July	20.4	20.3	103.1	74.4
August	19.2	20.1	82.7	102.8
September	13.4	13.7	64.2	55.9
South Dakota				
June	18.8	18.9	130.3	107.9
July	22.6	22.8	94.5	99.2
August	21.5	22.8	82.7	58.3
September	16.7	15.8	63.8	25.2

summer (Table 1). Climate stations near the study sites show that in addition to having greater average summer rainfall, the Minnesota site experiences its peak precipitation later in the summer than the North Dakota site and the South Dakota site. In 2000, however, average precipitation patterns were not experienced. North Dakota experienced higher precipitation during August than July in 2000 and South Dakota had much less than average precipitation during both August and September. Because of this variability in precipitation, onsite recording of humidity was deemed necessary.

Field sites. Field sites selected for this study all had an extensive history of involvement in earlier work on the Dakota Skipper (McCabe 1979, 1981; Royer 1988a, 1988b; Royer & Marrone 1992; Royer & Royer 1997, 1998; Dana 1991, 1997; Skadsen 1997, 1999). Involving three states, these sites spanned the known remaining U. S. range of the Dakota Skipper (Table 2, Fig. 2).

Sampling methods. We first developed a three-state map depicting all known U. S. populations of the Dakota skipper as points (Fig. 2). We then both sampled and monitored habitats at three specific sites in each state that were known to be hosting viable Dakota Skipper populations. (We here use the term "sample" to denote data from a point in time and the term "monitor" to denote continuous data collection with HOBO® loggers.) Sampling was conducted to determine spatial variability within Dakota Skipper habitat; monitoring was conducted to determine temporal variability throughout the most vulnerable period of the larval growth season (eclosure to onset of winter diapause).

At all study sites, sampling was conducted in four randomly oriented 50m by 40m gridded plots (Fig. 3), each centered on a monitoring point determined in the field by either (i) directly observing oviposition or (ii) using locations of documented skipper activity within the past three years (Royer & Royer 1997; Schlicht 1997; Skadsen 1997, 1999). Treating each plot as a rectilinear set of five parallel 50m transects, we took

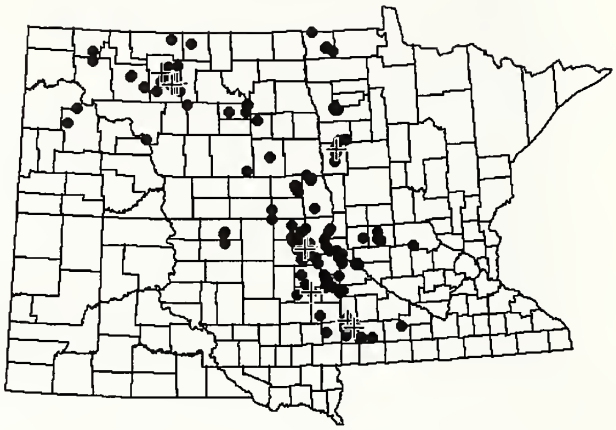


FIG. 2. Distribution of all known Dakota Skipper (*Hesperia dacotae*) records from the three states in which the species is known to persist. Site locations for this project are designated as crosses.

TABLE 2. Dakota Skipper (*Hesperia dacotae*) study sites by state, county, ownership, approximate extent (ha), and general soil texture classification (TNC=The Nature Conservancy, DNR=Department of Natural Resources, WMA=Wildlife Management Area, USFWS=U.S. Fish and Wildlife Service).

State/Site	County	Ownership	ha	Texture[a]
Minnesota				
Felton Prairie (FP)	Clay	County/TNC	200	L/SL
Hole-in-the Mountain (HM)	Lincoln	DNR/TNC/Private	65	SL
Prairie Coteau (PC)	Pipestone	TNC	25	SL
North Dakota				
Mount Carmel Camp (MCC)	McHenry	ND State School	65	SL/LS
Smokey Lake School Sect. (SLS)	McHenry	ND State School	65	SL
Swearson School Sect. (SSS)	McHenry	ND State School	65	SL
South Dakota				
Scarlet Fawn Prairie (SFP)	Roberts	Sioux Tribal	30	SL
Knapp Pasture (KNP)	Roberts	Private	65	SL
Cox Lake WMA (CXL)	Hamlin	USFWS	30	SL/LS

[a] L=loam, SL=sandy loam, LS=loamy sand.

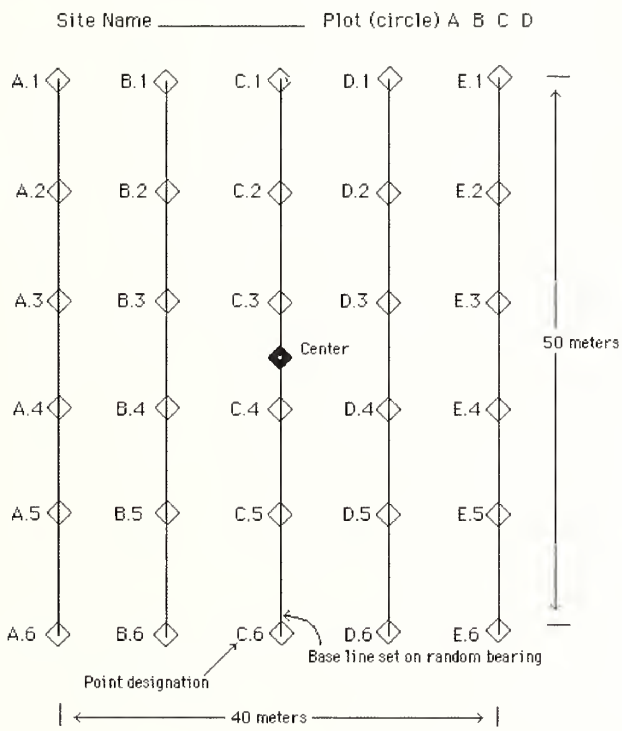


FIG. 3. Grid design for sampling within each plot. Center was determined by (a) observed oviposition or (b) reference to most recent confirmed adult skipper activity. Samples were taken for compaction and pH at all grid points and for other parameters generally at points A1, A3, A5, B2, B4, B6, C1, C2, C5, D2, D4, D6, E1, E3, and E5. Compass bearing for the grid axis (center transect line) was randomized for each sampling period.

probe readings at alternate 10 meter intervals within all four grids in each site. At four points in each grid, soil samples were also taken during one sample period for determining soil texture and bulk density within that grid (a total of 16 samples per site). For possible future GIS reference, precise center-point UTM coordinates (NAD 27) were confirmed during each sampling period. At each of these gridded plots we recorded local surface relief (in meters), soil texture, soil bulk density, and pH; with moisture, temperature, and compaction each measured at three depths (20, 40, 60cm). We also quantified both temperature and humidity within the primary larval nest zone (estimated to be 0–2cm above the soil surface).

Data loggers were used to monitor surface humidity and larval nest zone temperature continuously, in half-hour intervals, at all study sites from time of oviposition (approximately 5 July) through estimated initiation of larval diapause (23 September). A HOBO® Temp/RH data recorder was placed at the center point of at least two plots at each study site. In North Dakota, data recorders were placed at all plot center points except in grazed habitat. At Minnesota and South Dakota sites, data loggers were placed at two of four plots for each site except Scarlet Fawn Prairie (South Dakota), where there was only one plot and hence only one data logger was needed. One data logger failed at the Prairie Coteau site in Minnesota, and loss of another necessitated reducing the total number of useful Minnesota data sets to four. The resulting array of monitoring devices provided a continuous record of

both spatial and temporal variability in larval nest zone temperature and humidity across the range of the Dakota Skipper in all three states.

Sampling was conducted at approximately two-week intervals, from the beginning of the mating flight (ca. 1 July 2000) until the estimated beginning of larval diapause in the fall (the first significant frost in North Dakota sites was on 23 September 2000). Each site was subjected to at least four rounds of sample data collection. For the first sampling period at each site, all 30 grid points were sampled for all parameters. For subsequent temperature and moisture readings, half the points were sampled by alternating sample points as follows: A1,3,5; B2,4,6; C1,3,5; D2,4,6; E1,3,5. Soil samples for determining composition, texture, and bulk density were taken similarly at compass-randomized points B2, B4, D2 and D4 within each plot. For relief, we determined the minimum elevation for each plot within each site and then subtracted this minimum from each elevation within the plot to define the response variable "relief," scaled to the minimum elevation value within each plot.

Instrumentation. Equipment included (a) for relief a total station with data logger, (b) for soil compaction a DICKEY-john® Soil Compaction Tester (indicating compaction pressure in lbs/in^2), (c) for soil pH a Kelway® soil pH and moisture meter, (d) for soil moisture content both a Kelway® soil pH and moisture meter (surface moisture) and an Aquaterr® soil moisture, temperature, and salinity probe (moisture at various depths), (e) for soil temperature at various depths an Aquaterr® soil moisture, temperature, and salinity probe, and (f) for temperature, relative humidity, and absolute humidity within the larval nest zone a HOBO® RH data logger programmed to read continuously in 30-minute intervals. To determine soil bulk density samples of known volume were dried to a constant weight. To determine soil texture these same samples were subjected to settling and mechanical analysis in order to define percent sand, silt, and clay. Data were compiled by study site and stored in tabular form in Microsoft Excel®. All were archived electronically at the USGS Northern Prairie Wildlife Research Center in Jamestown, North Dakota.

Data Analysis. To gain an understanding of how variation in the various non-biotic response variables might be partitioned and to take advantage of the completely nested design structure of the study (i.e., 40×50m plots nested within study sites, grid sampling points nested within plots, with repeat sampling considered nested within grid sampling points), we first conducted a variance components analysis using the variance components procedure (PROC VARCOMP) of SAS (1999). This allowed us to compute site-to-site, plot-to-plot, point-to-point, and sampling time-to-sampling time variance components (where applicable) and assess their relative contribution to the total variation for each non-biotic response variable. Variance components are useful descriptive summaries and have their greatest value in planning future studies (e.g., if there is more plot-to-plot variation relative to variation among points within plots for a particular response variable then sampling effort should focus on establishing more plots within sites with less effort focused on the number of grid sampling points within plots to fully characterize Dakota Skipper sites).

We were also interested in isolating specific differences in the various non-biotic response variables among the nine study sites, and if applicable, how those differences might vary with soil depth (20, 40, and 60cm for soil compaction, temperature, and moisture only). To do so, we used analysis of variance (ANOVA) techniques using the mixed linear models procedure (PROC MIXED) of SAS (1999). For the ANOVAs, and as with the variance components analysis described above, we considered the 40×50m plots to be a random factor nested within study sites, with grid sampling points also as a random factor nested within plots. Repeat sampling effort, where applicable, was also considered as a random factor and nested within grid points. We compared not only mean responses among the nine study sites but also mean variances, where variances were calculated across the sampling grid points within each plot, and mean variances then computed by averaging across plots within sites. We examined these mean variances because variation in abiotic response variables may be as important as or more important than mean responses for characterizing Dakota Skipper habitat. For the responses soil compaction, soil temperature, and soil moisture measured at three depths the ANOVA design structure was considered to be a split-plot with depth being the sub-unit (Littell *et al.* 1996). All other ANOVAs were considered to be one-ways, and where applicable, with sub-sampling (Steel and Torrie 1980). For those response variables measured in the "larval nest zone" as described earlier, we did not conduct an ANOVA because of the small sample sizes for most of the sites, but we do report the mean responses for each plot and site, where the means are seasonal means. In North Dakota we also compared these characteristics at three known Dakota Skipper sites (two hay meadows and one grazed site with a similar plant community and topography) in order to assess possible differing effects of hay mowing and grazing on these features. All means reported, unless stated otherwise, are least squares

TABLE 3. Summary statistics for selected physical response variables (RV) measured at occupied Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota (see Table 2 for study site descriptions and abbreviations).

		Minnesota			North Dakota			South Dakota		
RV[a]	Metric[b]	FP	HM	PC	MCC	SLS	SSS	SFP	KNP	CXL
Relief	Mean	0.38	3.99	4.36	0.38	0.37	0.45	2.02	3.16	3
	SD	0.21	2.2	2.37	0.34	0.25	0.31	1.48	2.27	1.86
	Min.	0	0	0	0	0	0	0	0	0
	Max.	0.76	8.68	9.01	1.26	0.98	1.29	4.28	8.67	8.19
	n	3	3	4	4	4	4	1	4	4
BD	Mean	0.86	0.86	0.91	1.04	1.14	1.28	0.78	0.96	0.92
	SD	0.13	0.09	0.1	0.16	0.18	0.23	0.05	0.21	0.13
	Min.	0.65	0.68	0.76	0.73	0.7	0.77	0.73	0.53	0.74
	Max.	1.12	1	1.14	1.21	1.35	1.55	0.84	1.41	1.23
	n	4	4	4	4	4	4	1	4	4
pH	Mean	6.26	6.28	6.61	6.4	6.73	6.39	6.45	6.66	6.4
	SD	0.25	0.22	0.3	0.55	0.58	0.46	0.22	0.27	0.28
	Min.	5.4	5.8	6	4.9	5.6	5.5	6	5.9	5.8
	Max.	7	7	7.4	7.8	8	7.6	6.80	7	7
	n	4	4	4	4	4	4	1	4	4
Clay	Mean	8.3	9.2	7.7	6.9	9	11.7	5.8	4.8	3.7
	SD	4.6	6.3	4.3	5.2	5.9	4	3.2	4.2	3.2
	Min.	3.3	0	3.3	0	0	3.3	3.3	0	0
	Max.	16.7	23.3	16.7	20	23.3	20	10	16.7	10
	n	4	4	4	4	4	4	1	4	4
Sand	Mean	53.3	61.7	60.8	65.6	61	74.4	56.7	56.2	61.5
	SD	8	8.3	11.1	12.7	8.6	5.9	8.6	9.8	8.8
	Min.	40	46.7	40	33.3	46.7	60	46.7	40	50
	Max.	66.7	80	76.7	86.7	73.3	80	66.7	80	86.7
	n	4	4	4	4	4	4	1	4	4
Silt	Mean	38.3	29.2	31.5	27.5	30	14	37.5	38.9	34.8
	SD	5.2	6.1	9.2	11.8	6.7	5.1	6.9	8.3	7.8
	Min.	30	16.7	20	6.7	16.7	6.7	30	20	10
	Max.	46.7	40	46.7	60	40	26.7	46.7	53.3	43.3
	n	4	4	4	4	4	4	1	4	4

[a]RV=response variable; relief in meters above lowest elevation, BD=bulk density (g/cm^3), texture (clay, sand, silt) as percent composition.
[b]Mean=arithmetic mean of all data (as distinguished from least squares means reported in later tables), SD=standard deviation, n=number of 40×50 meter plots within each site

means (LSMEANS) with separations among LSMEANS done using Fisher's protected least significant value (LSD) as recommended by Milliken and Johnson (1984) and only for significant site effects at α=0.05. All statistical tests were considered significant at the 0.05 level.

Because of the correlated nature of many of the response variables, we also conducted a principal components analysis (PCA) (McCune and Grace 2002) to help visualize separations among the study sites along the principal component gradient variables. For the PCA, we did not include any of the responses measured in the "larval nest zone" because of small sample sizes and because no data were collected on the Swearson School Section study site. Although no soil compaction data were collected at the Prairie Coteau (PC) site, and

TABLE 4. Variance components for site-to-site, plot-to-plot within sites, point-to-point within plots, and sampling time-to-sampling time across the season at occupied Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota (see Table 2 for study site descriptions and abbreviations); values in parentheses are within row percents of total variation attributed to that variance component.

Response Variable	Site (%)	Plot (%)	Point (%)[a]	Sampling (%)[a]
Total relief (m)	10.39 (91)	1.06 (9)	nm	nm
Mean relief (m)	2.91 (55)	0.03 (1)	2.32 (44)	nm
Bulk density (g/cm3)	0.021 (43)	0.000 (<1)	0.028 (57)	nm
pH	0.023 (13)	0.027 (15)	0.126 (72)	nm
Clay (%)	5.24 (18)	0.00 (<1)	24.11 (81)	nm
Sand (%)	29.71 (25)	20.01 (17)	70.13 (58)	nm
Silt (%)	55.81 (47)	12.07 (10)	50.42 (43)	nm
Compaction 20 cm (kg/cm^2)	18.39 (47)	5.74 (15)	7.23 (19)	7.43 (19)
Compaction 40 cm (kg/cm^2)	26.02 (51)	8.96 (17)	8.79 (17)	7.64 (15)
Compaction 60 cm (kg/cm^2)	30.03 (52)	9.62 (17)	10.28 (18)	8.02 (14)
Temperature 20 cm (°C)	2.51 (14)	0.21 (1)	0.00 (<1)	15.40 (84)
Temperature 40 cm (°C)	2.00 (17)	0.14 (1)	0.00 (<1)	9.83 (82)
Temperature 60 cm (°C)	1.12 (13)	0.19 (2)	0.00 (<1)	7.03 (84)
Moisture surface (% sat.)	23.07 (9)	47.21 (18)	196.44 (73)	nm
Moisture 20 cm (% sat.)	28.59 (7)	13.27 (3)	0.00 (<1)	357.57 (90)
Moisture 40 cm (% sat.)	47.70 (14)	11.74 (3)	0.00 (<1)	276.13 (82)
Moisture 60 cm (% sat.)	79.94 (26)	14.59 (5)	0.00 (<1)	213.00 (68)
Larval zone temperature (°C)	0.75 (1)	0.00 (<1)	nm	52.02 (98)
Larval zone dew point (°C)	0.29 (1)	0.24 (1)	nm	29.20 (98)
Larval zone abs. hum. (g/m3)	0.21 (1)	0.19 (1)	nm	18.49 (98)
Larval zone rel. hum. (%)	3.08 (1)	5.50 (1)	nm	314.14 (98)

[a]nm= not measured at that level.

TABLE 5. Analysis of variance results for total relief (i.e., maximum elevation - minimum elevation within plots), relief (all elevations - minimum elevation within plots), and variance in relief within plots at occupied Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota; all units are in meters.

	Total relief		Relief		Variance in relief	
SV[a]	df	F[b]	df	F[b]	df	F[b]
S	8	27.41°°	8	35.48°°	8	10.89°°
P(S)	22	--	22	--	22	--
T(P S)	--	--	505	--	--	--
Total	30		535		30	

[a]SV=sources of variation; S=site, P(S)=plot nested within site, T(P S)=sampling point within plot.
[b]P(S) served as the appropriate error term for testing significance of S based on expected mean squares; °=significant at α=0.05, °°=significant at α=0.01, ns=not significant.

TABLE 6. Least squares means (LSMEAN ± SE) for total relief (i.e., maximum elevation-minimum elevation within each plot), relief (all elevations-minimum elevation within plots), and variance in relief within plots at occupied Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota; all units are in meters. LSMEANs within columns followed by the same letter are not significantly different using Fisher's protected LSD value at α=0.05 (see table 2 for study site descriptions and abbreviations).

		Total relief		Relief		Variance in relief	
Site	na	LSMEAN	SE	LSMEAN	SE	LSMEAN	SE
FP	3	0.66 a	0.66	0.38 a	0.31	0.03 a	0.78
HM	3	7.64 c	0.66	3.99 de	0.31	4.68 c	0.78
PC	4	7.89 c	0.57	4.38 e	0.28	5.37 c	0.68
MCC	4	0.96 a	0.57	0.38 a	0.27	0.10 a	0.68
SLS	4	0.79 a	0.57	0.37 a	0.27	0.06 a	0.68
SSS	4	1.02 a	0.57	0.45 a	0.27	0.10 a	0.68
SFP	1	4.28 b	1.14	2.02 b	0.54	2.20 b	1.35
KNP	4	6.35 bc	0.57	3.17 cd	0.27	4.78 c	0.68
CXL	4	6.06 bc	0.57	3.00 c	0.27	3.51 bc	0.68

[a]n=number of 40×50 m plots within each site.

TABLE 7. Analysis of variance results for bulk density (g/m^3), variance of bulk density, pH, variance of pH, surface moisture (% saturation), and variance of surface moisture at occupied Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota (no surface moisture data were available for study site=HM).

		Bulk density		pH		Surface moisture	
Response	SV[a]	df	F[b]	df	F[b]	df	F[b]
Mean	S	8	13.30**	8	3.26*	7	4.76**
	P(S)	24	--	24	--	18	--
	T(P S)	99	--	956	--	749	--
	Total	131		988		774	
Variance	S	8	1.76 ns	8	4.58**	7	0.86 ns
	P(S)	24	--	24	--	18	--
	T(P S)	--	--	--	--	--	--
	Total	32		32		25	

[a]SV=sources of variation; S=site, P(S)=plot nested within site, T(P S)=sampling point within plot.
[b]P(S) served as the appropriate error term for testing significance of S based on expected mean squares; *=significant at α=0.05, **=significant at α=0.01, ns=not significant.

because all other responses were collected there, we chose to include the PC study site in the PCA. We therefore substituted the mean soil compaction values from all of the other study sites for soil compaction at PC. We realize this is not ideal, but for descriptive visualization we believe it suffices. We also conducted a separate PCA for the eight sites using only the "larval nest zone" variables. We used the principal components procedure (PROC PRINCOMP) of SAS (1999) to conduct the PCAs.

RESULTS

General. Table 3 presents the arithmetic means, standard deviations (SD), and ranges (minimum and maximum) for selected physical non-biotic attributes (non-climatic) measured at each of the nine study sites. Table 4 presents the results of the variance component analyses with each of the non-biotic response variable results described below. In general and as would be expected, most of the variation in climatic variables (temperature and moisture) relates to sampling time across the season, with mixed results for the more physical attributes.

Relief. Nearly all of the variation in total relief (maximum elevation minus minimum elevation within each plot) is attributable to site-to-site (91%) differences (Table 4), implying consistency of plot-to-plot total relief within sites (i.e., plots, once established, all had nearly identical total relief within sites but substantial differences among sites). However, relief (all elevations within a plot minus minimum elevation within each plot) from site-to-site accounted for 55%, with less than 1% of the variation in relief being plot-to-plot, and 44% from point-to-point within plots. These results imply that the relief, or "roughness" in microtopography within plots, was consistent from plot-to-plot within sites, while still maintaining substantial variation in relief from site-to-site. Table 5 presents the ANOVA table results for comparing specific differences among the nine sites with respect to total relief, relief, and variance of relief (all *F*-tests for the main effect [site] are highly significant, implying that differences exist among sites). Table 6 presents the LSMEANS and mean separations using Fisher's protected LSD test. In

TABLE 8. Least squares means (LSMEAN ± SE) bulk density (g/m³), variance of bulk density (g/m³), pH, and variance of pH at occupied Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota. LSMEANs within columns followed by the same letter are not significantly different using Fisher's protected LSD value at α=0.05 (see Table 2 for study site descriptions and abbreviations).

	Bulk density		Variance in bulk density		pH		Variance in pH	
Site[a]	LS MEAN	SE	LS MEAN	SE	LS MEAN	SE	LS MEAN	SE
FP	0.86 ab	0.04	0.02 a	0.01	6.26 a	0.09	0.04 a	0.05
HM	0.86 ab	0.04	0.01 a	0.01	6.28 a	0.09	0.05 a	0.05
PC	0.91 ab	0.04	0.01 a	0.01	6.61 bc	0.09	0.06 a	0.05
MCC	1.04 c	0.04	0.03 a	0.01	6.39 ab	0.09	0.27 b	0.05
SLS	1.14 c	0.04	0.04 a	0.01	6.73 c	0.09	0.27 b	0.05
SSS	1.28 d	0.04	0.06 a	0.01	6.39 ab	0.09	0.21 b	0.05
SFP	0.78 a	0.08	0.00 a	0.03	6.45 ab	0.18	0.05 a	0.09
KNP	0.96 bc	0.04	0.04 a	0.01	6.66 bc	0.09	0.06 a	0.05
CXL	0.92 ab	0.04	0.02 a	0.01	6.40 ab	0.09	0.07 a	0.05

[a]n=4 40×50 m plots within each site, n=1 for SFP

general, ND sites had less relief and variation in relief than those in either MN or SD.

Soil Bulk density, pH, and surface moisture. Nearly 60% of the total variation in bulk density, and an even greater percentage of the variation in pH (72%) and surface moisture (73%) is attributable to point-to-point samples within plots, with consistency in this variation from plot-to-plot among all sites (i.e., all plot-to-plot variation < 18%), with some even less so site-to-site (Table 4). This implies high micro-scale variation in these attributes within the plots (e.g., bulk density varies substantially from point-to-point within a plot, and this variation is fairly constant from plot-to-plot, and to a lesser extent, site-to-site). Table 7 presents the ANOVA table results, showing that significant differences occur among site mean responses and for variance in pH (all *F*-tests for the main effect "Site" are significant; no surface moisture data were collected at the Hole-in-the Mountain study site). Specific differences in LSMEANS among the sites using Fisher's protected LSD test are presented in Table 8 for bulk density, variance in bulk density, pH, and variance in pH (mean surface moisture comparisons are presented with other moisture responses below). In general, MN and SD sites had the lowest mean bulk density with ND sites having the highest (no differences were observed among sites with respect to variance in bulk density). While there was no consistent difference in LSMEANS for pH among sites with respect to states, ND sites showed consistently higher variance in pH than the other study sites.

Soil texture (% clay, sand, and silt). Samples across all plots and study sites generally were classified as sandy loams, occasionally as loamy sand, with occasional plot points yielding soils that would be classified strictly as loams. Variance component results (Table 4) show great variation in clay from point-to-point within plots (81%), little to no plot-to-plot variation (<1%), with the remainder variation in clay site-to-site (18%). Sand and silt also show approximately half of the variation attributable to point-to-point comparison (58% and 43% respectively), but with more plot-to-plot variation (17% and 10% respectively) than clay, while much more variation is attributable to site-to-site comparison (25% and 47% respectively). These results imply that while there is substantial variation within each plot with respect to soil texture, there is also substantial variation within sites from plot to plot (sand and silt), and even more from site to site. ANOVA results indicated that mean % clay, % sand, and % silt varied significantly among sites with no significant differences in mean variances (Table 9). Further comparisons among LSMEANS indicated a tendency for SD sites to have lower % clay, whereas ND sites tended to have more sand and less silt (Table 10).

Soil compaction, temperature, and moisture. Variance components analyses were conducted separately for each of these response variables and separately for each depth (20, 40, and 60cm), with results presented in Table 4. As mentioned above, almost all of the variation in the two climatic variables, temperature and moisture, is attributable to sampling time across the season, with the remaining variation mostly attributable to site-to-site differences. However, with increasing soil depth, more and more variation is attributable to site-to-site differences, particularly for moisture, than to sampling time, the latter nevertheless still accounting for 68% of the variation. Nearly half of the variation in soil compaction can be attributable to site-to-site differences, with the other 50% distributed nearly equally among the other variance components,

TABLE 9. Analysis of variance results for texture composition (clay, sand, silt) and variance in texture composition at occupied Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota.

		Clay (%)		Sand (%)		Silt (%)	
Response	SV[a]	df	F[b]	df	F[b]	df	F[b]
Mean	S	8	3.97°°	8	3.64°°	8	8.68°°
	P(S)	24	--	24	--	24	--
	T(P S)	99	--	99	--	99	--
	Total	131		131		131	
Variance	S	8	1.08 ns	8	0.93 ns	8	0.88 ns
	P(S)	24	--	24	--	24	--
	T(P S)	--	--	--	--	--	--
	Total	32		32		32	

[a]SV=sources of variation; S=site, P(S)=plot nested within site, T(P S)=sampling point within plot.
[b]P(S) served as the appropriate error term for testing significance of S based on expected mean squares; °=significant at α=0.05, °°=significant at α=0.01, ns=not significant.

regardless of the depth. ANOVA results for comparison among sites and how those differences might vary with soil depth are presented in Table 11, with the interaction of depth and site being significant in all cases (no soil compaction data were available for the Prairie Coteau site where equipment failure precluded collection of data). Because of these significant interactions and the numerous possible pair-wise comparisons, we plotted the LSMEANS (± 1 SE) for soil compaction (Fig. 4), soil temperature (Fig. 5), and soil moisture (Fig. 6), noting in the legend the approximate Fisher's LSD values that can be used for specific pair-wise comparisons.

Pair-wise comparisons of LSMEANS indicated that soil compaction increases with depth at all sites, and that this rate of increase varies depending on site. With

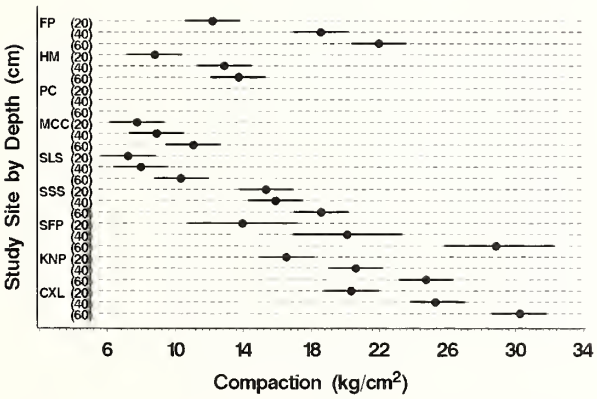


FIG. 4. Least squares means (LSMEAN ± SE) for soil compaction (kg/cm^2) at depths of 20, 40, and 60cm at Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota, USA (Fisher's LSD≈4.5 for n=n=4 and LSD≈7.1 for n=4, n=1; see Table 2 for study site descriptions and abbreviations, no compaction data were collected at PC, n=1 for SFP, n=4 for all other sites).

the exception of the Swearson School Section study site, ND sites tended to have the lowest soil compaction values, with SD having among the highest at all depths. Although not significant, soil temperatures tended to increase with depth at the MN sites whereas temperatures declined significantly with depth at the ND and SD sites. Minnesota sites tended to have substantially higher soil temperatures on average. In general, soil moisture tended to stay the same at various depths or in some cases to decline with depth, depending on the site. Soil temperature tended to be consistent within depth for all sites, with MN sites tending to have higher soil temperatures for all depths than either ND or SD. We did not compute and compare mean variances using ANOVA among sites for soil compaction, soil temperature, or soil moisture because of the added complexity of incorporating soil depths, and because we did not think it would add substantially to understanding these response variables.

Principal component analysis (PCA). Table 12 presents the results of the PCA using the listed 15 response variables. The first two principal components accounted for 66% of the variation, with the first three principal components accounting for 80%. Examination of the principal component variable coefficients, or "loadings," reveals that the first component variable (PC-1) can be considered a physical-moisture gradient, the second component variable (PC-2) a temperature-relief gradient, and the third component variable (PC-3) a textural gradient. Figure 7 is a plot of the mean principal component values illustrating separation among sites along PC-1 and PC-2. All sites separate out well along the PC-1 axis, with ND sites to the far right and SD sites to the far left, and the MN sites centered (note: the Prairie Coteau study site lies at zero, most

TABLE 10. Least squares means (LSMEAN ± SE) for texture composition (clay, sand, silt) and variance in texture at occupied Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota. LSMEANs within columns followed by the same letter are not significantly different using Fisher's protected LSD value at α=0.05 (see Table 2 for study site descriptions and abbreviations).

		Clay (%)		Sand (%)		Silt (%)	
RV[a]	Site[b]	LS MEAN	SE	LS MEAN	SE	LS MEAN	SE
Mean	FP	8.3 cd	1.2	53.3 a	3.1	38.3 c	2.5
	HM	9.2 cd	1.2	61.7 ab	3.1	29.2 b	2.5
	PC	7.7 bc	1.2	60.8 ab	3.1	31.5 bc	2.5
	MCC	6.9 abc	1.2	65.6 bc	3.1	27.5 b	2.5
	SLS	9.0 cd	1.2	61.0 ab	3.1	30.0 b	2.5
	SSS	11.7 d	1.2	74.4 c	3.1	14.0 a	2.5
	SFP	5.8 abc	2.4	56.7 ab	6.2	37.5 c	5.1
	KNP	4.8 ab	1.2	56.2 a	3.1	38.9 c	2.5
	CXL	3.7 a	1.2	61.5 ab	3.1	34.8 bc	2.5
Var.	HM	47.5 a	12.3	66.2 a	39.1	34.7 a	42.1
	FP	16.2 a	12.3	53.4 a	39.1	28.3 a	42.1
	PC	18.8 a	12.3	48.7 a	39.1	22.9 a	42.1
	MCC	26.7 a	12.3	163.3 a	39.1	149.0 a	42.1
	SLS	42.2 a	12.3	63.4 a	39.1	40.1 a	42.1
	SSS	18.5 a	12.3	34.1 a	39.1	23.9 a	42.1
	SFP	10.3 a	24.5	74.1 a	78.3	47.4 a	84.1
	KNP	14.7 a	12.3	48.4 a	39.1	38.3 a	42.1
	CXL	11.6 a	12.3	82.3 a	39.1	67.0 a	42.1

[a]RV=response variable, Var.=variance in texture (clay, sand, and silt).
[b]n=4 40×50 m plots within each site, n=1 for SFP.

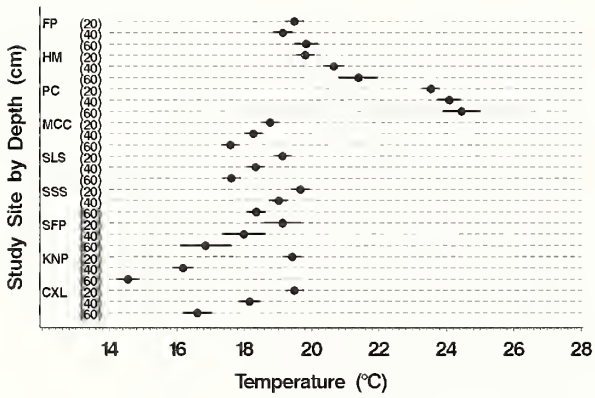


FIG. 5. Least squares means (LSMEAN ± SE) for soil temperature (°C) at depths of 20, 40, and 60cm at Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota, USA (Fisher's LSD ≈ 1.1 for n=n=4 and LSD ≈ 1.7 for n=4, n=1; see Table 2 for study site descriptions and abbreviations, n=1 for SFP, n=4 for all other sites).

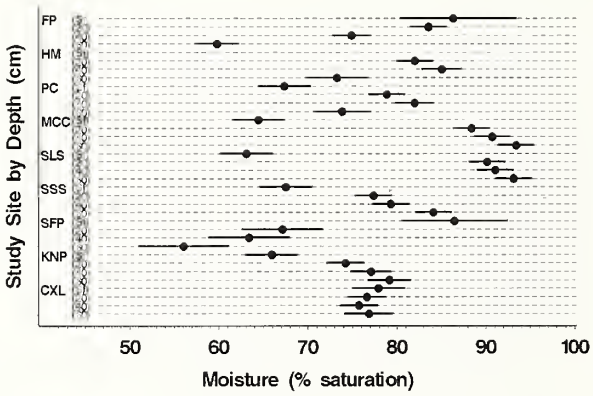


FIG. 6. Least squares means (LSMEAN ± SE) for soil moisture (% saturation) at depths of 20, 40, and 60cm at Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota, USA (Fisher's LSD ≈ 1.6 for n=n=4 and LSD ≈ 2.5 for n=4, n=1; surface moisture, denoted as Sf, is only presented for comparative purposes but was not included in analysis of variance, separate ANOVA yielded an LSD ≈ 9.9; see Table 2 for study site descriptions and abbreviations, n=1 for SFP, n=4 for all other sites).

TABLE 11. Analysis of variance results for soil compaction (kg/cm²), temperature (°C), and moisture (% saturation) at depths of 20-, 40-, and 60 cm at Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota, USA (no compaction data were collected at PC, see Table 2 for site descriptions and abbreviations).

	Compaction		Temperature		Moisture	
SV[a]	df	F[b]	df	F[b]	df	F[b]
S	7	13.73°°	8	50.80°°	8	12.32°°
P(S)	21	--	24	--	24	--
T(P S)	808	--	924	--	925	--
D	2	250.17°°	2	46.44°°	2	9.61°°
D°S	14	10.37°°	16	16.82°°	16	17.01°°
D°P(S)	42	--	48	--	48	--
D°T(P S)	1365	--	1383	--	1388	--
R(D T P S)	4071	--	3539	--	3539	--
Total	6330		5944		5950	

[a]SV=sources of variation; S=site, P(S)=plot nested within site, T(P S)=sampling point within plot, D=depth at each point within plot, R=up to five readings at each point across the season (here considered as sub-sampling in time, not repeated measures).

[b]P(S) served as the appropriate error term for testing significance of S, D°P(S) served as the appropriate error term for testing significance of D and D°S interaction based on expected mean squares; °=significant at α=0.05, °°=significant at α=0.01, ns=not significant.

TABLE 12. Summary of principal component analysis and associated principal component variables; the first two principal components accounted for 66% and the first three principal components accounted for 80% of the variation (PC-1 could be considered as a physical structural component-moisture gradient, PC-2 could be considered as a temperature-relief gradient, with PC-3 as a textural gradient).

	Principal component variable coefficients		
Response Variable	PC-1	PC-2	PC-3
Relief (m)	-0.18	0.33	0.01
Bulk density (g/cm3)	0.29	-0.20	0.32
pH	0.05	-0.05	-0.14
Clay (%)	0.28	0.12	0.22
Sand (%)	0.24	-0.06	0.49
Silt (%)	-0.28	0.01	-0.46
Compaction 20 cm (kg/cm²)	-0.28	-0.09	0.38
Compaction 40 cm (kg/cm²)	-0.35	-0.03	0.23
Compaction 60 cm (kg/cm²)	-0.37	-0.05	0.19
Moisture 20 cm (% sat.)	0.32	0.01	-0.29
Moisture 40 cm (% sat.)	0.34	0.04	-0.18
Moisture 60 cm (% sat.)	0.30	-0.18	0.02
Temperature 20 cm (°C)	-0.02	0.48	0.13
Temperature 40 cm (°C)	0.08	0.53	0.08
Temperature 60 cm (°C)	0.10	0.52	0.03

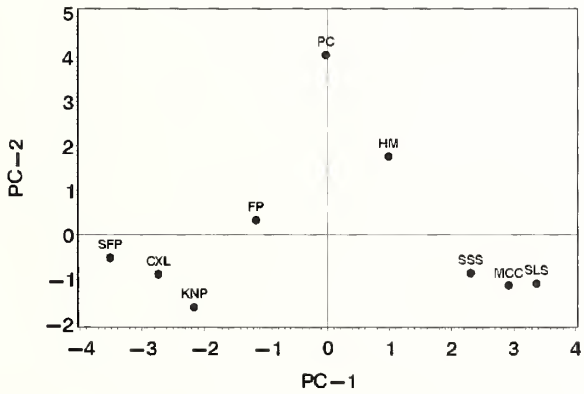


FIG. 7. Plot of the means of the first two principal components illustrating separation among study sites for all response variables except those quantified in the larval zone; PC-1 can be considered a physical structural-moisture gradient with PC-2 considered a temperature gradient (see Table 2 for study site descriptions and abbreviations).

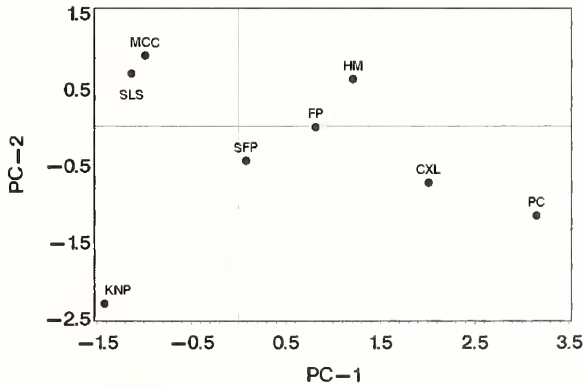


FIG. 8. Plot of the means of the first two principal components illustrating separation among study sites for response variables quantified in the "larval zone" (see table 13, no data were collected at study site=SSS); PC-1 can be considered a dew point-absolute humidity gradient with PC-2 considered a temperature-relative humidity gradient (see Table 2 for study site descriptions and abbreviations).

TABLE 13. Seasonal mean temperature (°C), dew point (°C), absolute humidity (g/m^3), and relative humidity (%) in the "larval zone" (between the soil surface and 2.0 cm) at the center of monitored plots at occupied Dakota Skipper (*Hesperia dacotae*) study sites in Minnesota, North Dakota, and South Dakota (see Table 2 for study site descriptions and abbreviations; values were taken in 30-minute intervals continuously between the beginning of oviposition and at the approximate time of onset of larval diapause in September).

Site	Plot	Temp. (°C)	Dew pt. (°C)	Abs. hum. (g/m^3)	Rel. hum. (%)
FP	1	19.14	16.24	13.85	83.81
	3	19.13	15.36	13.11	80.20
HM	1	18.73	15.84	13.75	83.50
	3	18.96	15.93	13.83	83.45
PC	3	20.53	16.77	14.47	81.16
MCC	1	17.76	14.65	12.52	81.74
	2	18.05	14.46	12.40	80.66
	3	17.95	15.25	13.16	84.07
	4	17.94	15.34	13.22	85.11
SLS	1	17.96	14.73	12.67	82.23
	2	17.83	15.08	13.04	84.20
	3	18.41	14.71	12.68	80.28
	4	17.96	14.85	12.82	82.45
SFP	1	19.03	15.44	13.14	80.79
KNP	1	19.45	13.90	12.05	72.51
	3	19.68	15.27	13.04	78.41
CXL	3	19.95	16.41	14.10	82.53
	4	19.90	16.16	13.78	80.90

likely due to using the mean compaction values from the other sites). The axis for PC-2 separates the MN sites from ND and SD sites along this temperature gradient.

Larval nest zone temperature, dew point, and humidity. Table 13 presents the seasonal means for temperature, dew point, absolute humidity, and relative humidity in the zone between the soil surface and 2.0 cm above (the "larval nest zone") at the center of monitored plots at each site. Note that since Swearson School Section site was under intermittent grazing during the study, loggers were not placed and that site is therefore not represented in the table. As expected, nearly all of the variation in temperature, dew point, absolute humidity, and relative humidity can be attributed to sampling time across the season (Table 4). Although not compared statistically, ND tended to have lower mean responses for each of these variables than either MN or SD sites. Table 14 presents the results of the PCA using only the four response variables from Table 13. The first principal component accounted for 64% and the first two principal components accounted for 99% of the variation. Examination of the principal component variable coefficients, or "loadings," reveals that the first component variable (PC-1) can be considered a dew point – absolute humidity gradient while the second component variable (PC-2) can be considered a temperature – relative humidity gradient. Figure 8 is a plot of the mean principal component values illustrating separation among study sites along PC-1 and PC-2. Using these somewhat limited data, no clear pattern emerged when comparing sites from a state perspective.

DISCUSSION

Objective 1: Characterization of non-biotic habitat parameters. A review of the above information leads us to two observations. First, there appear to be two relatively distinctive types of habitat substrate for the Dakota Skipper. These were earlier proposed by Royer and Marrone (1992) as "Type A" and "Type B" habitats. The sites in this study that would be designated Type A are topographically of low relief (<1m), with more nearly saturated soils at greater depths (40–60cm), and with soil bulk density exceeding 1.0g/cm^3. At least to a depth of 60cm, soils may be sandy but are relatively free of gravel. This is the habitat that McCabe (1979, 1981) associated with the margins of glacial lakes and that Royer and Royer (1998) restricted in ND to glacial lake near-shore Oahe Formation geology (Fig. 1). The ND study sites designated Mount Carmel Camp and Smokey Lake School Section are typical of this habitat,

and most historical sites in the Devils Lake and other glacial lakes areas within North Dakota appear to be as well. Soils in these situations are classified as sandy loams, occasionally as loamy sands. These environments have a high water table and are subject to intermittent flooding in the spring, but they offer sufficient relief to provide segments of non-inundated habitat during the spring larval growth period within any single season. Their position in the western part of the historical range of the Dakota Skipper may relate to a larval need of humidity in an otherwise more xeric climate, as earlier noted by McCabe (1981).

The second habitat type (Type B) is associated with more gravelly glacial landscapes of relatively higher relief, more variable soil moisture, and somewhat higher soil temperatures. Mean bulk density was in all Type B study sites below 1.0g/cm^3, but soils in these environments were found to be considerably more compact at all depths (Fig. 4). (It should be noted that higher soil compaction findings may relate to the presence of gravel and its effect on accuracy of the instrument, particularly at depths below 20cm.) Again, these soils were classified predominantly as sandy loams, occasionally as loamy sands.

Given that all study sites were known to harbor viable populations of the Dakota Skipper, analysis of logger readings from within the "larval nest zone" across all plots and sites helps to define acceptable levels for the studied microclimatological variables temperature, dew point, and humidity. For example, the mean season-long larval nest zone temperature for all sites ranged between a low of 17.8°C at Mount Carmel Camp and Smokey Lake School Section plots in North Dakota and a high of 20.5°C at the Prairie Coteau site in Minnesota. The range-wide season-long mean was 18.79°C. The season-long mean larval nest zone dew point ranged across sites from 13.9°C at Knapp Ranch in South Dakota to 16.8°C at Prairie Coteau in Minnesota.

TABLE 14. Summary of principal component analysis and associated principal component variables for response variables quantified in the "larval zone;" the first principal component accounted for 64% and the first two principal components accounted for 99% of the variation (PC-1 can be considered a dew point-absolute humidity gradient with PC-2 considered a temperature-relative humidity gradient).

	Principal component variable coefficients	
Response Variable	PC-1	PC-2
Temp. (°C)	0.41	-0.63
Dew pt. (°C)	0.62	0.05
Abs. hum. (g/m^3)	0.62	0.07
Rel. hum. (%)	0.24	0.77

Within this context, relative humidity in the larval nest zone remained basically consistent across all sites, with the lowest recorded season-long means being 72.5 percent and 78.4 percent at the Knapp Ranch site in South Dakota and the highest being 84.2 percent at Smokey Lake School Section and 85.1 percent at Mount Carmel Camp in North Dakota. The season-long mean for South Dakota sites was 78.8 percent, for Minnesota sites was 82.2 percent, and for North Dakota sites was 82.6 percent relative humidity.

Objective 2: Grazing vs. hay-mowing in North Dakota. Review of bulk density values revealed that, in support of the above-noted two-habitats distinction, LSMEANS for two ND study sites (Smokey Lake School Section and Swearson's School Section) were statistically different from those for all study sites in SD and MN except Knapp Ranch (see Table 8). Mean bulk density measurements for all study sites indicate both that all North Dakota sites exceed 1.0g/cm^3, and that Swearson's School Section, the only site that was under active grazing during the study, had the highest mean bulk density of all sites. (Knapp Ranch had been grazed, but was not under grazing during the study.) It should also be noted, however, that within ND the LSMEANS for Mount Carmel Camp and Swearson's School Section are themselves also statistically different. Swearson's School Section produced a bulk density LSMEAN that was significantly higher than those from any of the eight other study sites. This site has a history of leased grazing, and Dakota Skippers are rare in the grazed portion of the site, although often quite common in adjacent (contiguous) private, ungrazed hayland habitat.

This difference is even more apparent when soil compaction data for the North Dakota ("Type A") sites are considered alone. Figure 4 illustrates that Swearson's School Section soils were significantly different from those from either Mount Carmel Camp or Smokey Lake School Section. All three of these sites are part of the Towner-Karlsruhe Habitat Complex, which has been proposed (Royer & Royer 1997) as the only potentially secure Dakota Skipper habitat area remaining in ND.

Swearson's School Section also contained lower percent moisture at all depths than the other two ND sites (Fig. 6). These findings are consistent with decreased soil water content found in grazed areas (e.g., Pietola *et al.* 2005, Donkor *et al.* 2005, Zhao *et al.* 2007). Higher bulk density values likely result from the loss of porosity, which decreases water movement through the soil (Warren *et al.* 1986, Greenwood *et al.* 1997). Decreased water movement through the soil would readily explain both the slightly higher surface moisture

values and lower subsurface moisture values at SSS compared to those in other North Dakota sites. However, the texture of the soil also affects water movement through the soil; sandy soils tend to allow water to pass through them readily, whereas clayey soils impede water movement. The grazed site (SSS) contains a greater percentage of sand than the two hayed sites (MCC and SLS), although for MCC the difference is not significant at the 95% level. Regardless of the cause, the lower moisture at all depths at the SSS site suggests that a dry layer may be formed at this site during years when normal summer precipitation patterns occur.

CONCLUSIONS

Two habitat types were distinguished by the study. One ("Type A") is found in near-shore glacial lake deposits, the other ("Type B") in glacial moraine deposits. The most obvious difference between these habitat types is topographic relief, Type A habitat being relatively flat and featureless, Type B being rolling or hilly. Soil textures in both habitat types are generally classified as sandy loams, but those in moraine deposits are gravelly, whereas the deposits associated with glacial lakes are not.

Soil compaction, presumably a result of long-term cattle grazing, appears to be affecting vertical water distribution in soils within Type A habitat in North Dakota, although minor differences in soil texture may also be a contributing factor. Altered vertical distribution of water may render Dakota Skipper larvae vulnerable to desiccation during the drier late summer months, thus stressing a population.

ACKNOWLEDGEMENTS

This project was funded by USGS cooperative agreement 00HQAG00331, under that agency's 2000 Species at Risk (SAR) program, and by the Division of Science at Minot State University. Northern Prairie Wildlife Research Center (NPWRC), of the U.S. Geological Survey (USGS), contributed both GIS and statistical support. The formal contact there was Thomas Sklebar. Guy A. Hanley conducted the bulk of Minnesota fieldwork. Karew Schumaker and Heidi Richter, undergraduate students in the MSU Division of Science, assisted in both fieldwork and analysis of soil samples. Jeremy Horrell contributed significantly to mapping. A substantial portion of remaining Dakota Skipper habitat in North Dakota is on state-owned public school trust land for use of which formal permission was granted by the state land department and lessees Vernon Kongslie, Daniel Kuntz, and Terry Bailey. In Minnesota, permission was granted by both the Department of Natural Resources (DNR) and The Nature Conservancy (TNC). In South Dakota permission was granted by TNC, the U. S. Fish and Wildlife Service, and a private landowner, Roger Knapp. These permissions are all gratefully acknowledged. We thank R.A. Gleason, G.A. Sargeant, P. Scherr, and two anonymous reviewers for comments on earlier drafts.

LITERATURE CITED

ACKERMAN, E.A. 1941, The Koppen classification of climates in North America, Geographical Review, 31 (1): 105–111.

AGNEW, A.F., M.J. TIPTON, & F.V. STEECE. 1962. South Dakota's groundwater needs and supplies, Miscellaneous Investigations #4.

COOPER, A.W. 1960. An example of the role of microclimate in soil genesis. Soil Science 90: 109–120.

DANA, R. 1991. Conservation management of the prairie skippers *Hesperia dacotae* and *Hesperia ottoe*: basic biology and threat of mortality during prescribed burning in spring. University of Minnesota Ag. Exp. Sta. Bull. 594–91 (AD-SB-5511-S).

——. 1997. Characterization of three Dakota Skipper sites in Minnesota. Unpublished report to the US Fish and Wildlife Service.

DONKOR, N.T., R.J. HUDSON, E.W. BORK, D.S. CHANASYK, & M.A. NAETH. 2006. Quanitification and simulation of grazing impacts on soil water in boreal grasslands. J. Agronomy & Crop Science 192: 192–200.

FREDE, H.G. 1985. The importance of pore volume and pore geometry to soil aeration. *In* Monnier G., & M.J. Gross, eds., Soil compaction and regeneration: proceedings of the workshop on soil compaction. Commission of European Communities, Boston. 167pp.

GREENWOOD, K.L., D.A. MACLEOD, & K.J. HUTCHINSON. 1997. Long-term stocking rate effects on soil physical properties. Aust. J. Exp. Agric. 37(4): 413–419.

HAUSENBUILLER, R.L. 1985. Soil science: principles and practices. Wm. C. Brown, Publishers: Dubuque, Iowa. 610pp.

HOBBS, H.C., & J.E. GOEBEL. 1982. Geologic map of Minnesota, Quaternary geology: MGS State Map Series S-1, 1:500,000.

KLASSEN, P.A., R. WESTWOOD, W.B. PRESTON, & W.B. MCKILLOP. 1989. The butterflies of Manitoba. Manitoba Museum of Man and Nature, Winnipeg.

LITTELL, R.C., G.A. MILLIKEN, W.W. STROUP, & R.D. WOFINGER. 1996. SAS system for mixed models. Cary, NC: SAS Institute, Inc. 633pp.

LORD, M.L. 1988. Surface geology of the Souris River map area, North Dakota. *In* North Dakota Geological Survey Atlas Series Map 4.

MCCABE, T.L. 1979. Report on the status of the Dakota Skipper (*Hesperia dacotae* (Skinner) Lepidoptera: Hesperiidae) within the Garrison Diversion Unit. Unpubl. ms. 46pp.

——. 1981. The Dakota Skipper, *Hesperia dacotae* (Skinner): range and biology, with special reference to North Dakota. J. Lepid. Soc. 35(3): 179-193.

—— & R.L. POST. 1977. Skippers (Hesperioidea) of North Dakota. ND Insects Pub. No. 11, Schafer-Post Series. NDSU Ag. Exp. Sta., Fargo.

MCCUNE, B. & J.B. GRACE. 2002. Analysis of ecological communities. Gleneden Beach, OR: MjM Software Design. 300pp.

MILLER, R.W. & D.T. GARDINER. 1998. Soils in Our Environment. Prentice Hall: Upper Saddle River, New Jersey. 736pp.

MILLIKEN, G.A. & D.E. JOHNSON. 1984. Analysis of messy data, volume I: designed experiments. New York, NY: Van Nostrand Reinhold Company. 473pp.

NORTH DAKOTA PARKS AND RECREATION DEPARTMENT. 1999. Characterization of Dakota Skipper habitat in the Towner-Karlsruhe prairie complex, McHenry County, North Dakota. Unpublished report to the US Fish and Wildlife Service.

ORWIG, T. 1995. Butterfly surveys in North Dakota: 1995. Unpublished report to The Nature Conservancy and U. S. Fish and Wildlife Service, Bismarck, ND.

——. 1996. Butterfly surveys in southeastern North Dakota: 1996. Unpublished report to Tewaukon National Wildlife Refuge, Cayuga, ND.

PIETOLA, L., R. HORN, & M. YLI-HALLA. 2005. Effects of trampling by cattle on the hydraulic and mechanical properties of soil. Soil & Tillage Research 82: 99–108.

ROYER, R.A. 1988a. Butterflies of North Dakota: an atlas and guide. Minot State University Science Monograph Number One. 192pp.

——. 1988b. *Hesperia dacotae* (Skinner) [Hesperiidae, Lepidoptera]: A North Dakota population update, with information on three new population complexes, including first records from southwest of the Missouri River. Proc. ND Ac. Sci. 42.

——. 2003. Butterflies of North Dakota: an atlas and guide, 2nd edition. Minot State University Science Monograph Number Two. 192pp.

—— & G. M. MARRONE. 1992. Conservation Status of the Dakota Skipper (HESPERIA DACOTAE) in North and South Dakota. U. S. Fish and Wildlife Service Endangered Species Office. Denver. 44pp.

—— & M.R. ROYER. 1997. A final report on conservation status of the Dakota Skipper [HESPERIA DACOTAE (Skinner 1911)] at selected sites in North Dakota during the 1996 and 1997 flights, including observations on its potential for recovery in the state. Report to the ND Department of Parks and Recreation. 26pp. plus maps and appendices.

—— & M.R. ROYER. 1998. Report on an inventory of habitat and occurrence of the Dakota Skipper [*Hesperia dacotae* (Skinner 1911)] in the Towner-Karlsruhe habitat complex (McHenry County, North Dakota) during 1998. Unpublished report to USFWS. 25pp. plus photographs, maps, and appendices.

SAS INSTITUE, Inc. 1999. SAS/STAT user's guide, version 8. Cary, NC: SAS Institute, Inc. 3884pp.

SCHLICHT, D. 1997. Surveys for the Dakota Skipper in Minnesota. Unpublished report to the Minnesota Department of Natural Resources.

SCOTT, J.A. 1986. The butterflies of North America: a natural history and field guide. Stanford University Press, Stanford, CA. 583pp.

SKADSEN, D.R. 1997. A report on the results of a survey for Dakota Skipper [*Hesperia dacotae* (Skinner, 1911)] in northeast South Dakota during the 1996 and 1997 flights. Unpublished report to SD Department of Game, Fish and Parks.

——. 1999. Addendum to a report on the results of a survey for Dakota Skipper in northeast South Dakota, 1998 flight period. Unpublished report to SD Department of Game, Fish and Parks.

——. 2000. Progress report for continued Dakota skipper surveys and monitoring on USFWS lands in Minnesota. Unpublished report, Minnesota Department of Natural Resources, Natural Heritage and Nongame Research Program, St. Paul, MN. July 26, 2000. 2pp.

SOUTH DAKOTA GEOLOGICAL SURVEY 1965. Reprint of the South Dakota part of INQUA guidebook and supplemental data for field conference C, upper Mississippi valley. South Dakota Guidebook Series 1. 33pp.

STEEL, R.G.D. & J.H. TORRIE. 1980. Principles and procedures of statistics: a biometrical approach, 2nd edition. New York, NY: McGraw-Hill Book Co. 633pp.

WARREN, S.D., T.L. THUROW, W.H. BLACKBURN, & N.E. GARZA. 1986. The influence of livestock trampling under intensive rotation grazing on soil hydrologic characteristics. Journal of Range Management 39(6): 491–495.

ZHAO, Y., S. PETH, J. KRUMMELBEIN, R. HORN, Z. WANG, M. STEFFESN, C. HOFFMAN, & X. PENG. 2007. Spatial variability of soil properties affected by grazing intensity in Inner Mongolia grassland. Ecological Modelling 205(1/2): 241–254.

Received for publication 2 December 2005; revised and accepted 17 December 2007.

Journal of the Lepidopterists' Society
62(1), 2008, 18–30

RESPONSES OF NORTH AMERICAN *PAPILIO TROILUS* AND *P. GLAUCUS* TO POTENTIAL HOSTS FROM AUSTRALIA

J. MARK SCRIBER

Dept. Entomology, Michigan State University, East Lansing, MI 48824, USA; School of Integrative Biology, University of Queensland, Brisbane, Australia 4072; email: scriber@msu.edu

MICHELLE L. LARSEN

School of Integrative Biology, University of Queensland, Brisbane, Australia 4072

AND

MYRON P. ZALUCKI

School of Integrative Biology, University of Queensland, Brisbane, Australia 4072

ABSTRACT. We tested the abilities of neonate larvae of the Lauraceae-specialist, *P. troilus*, and the generalist Eastern tiger swallowtail, *Papilio glaucus* (both from Levy County, Florida) to eat, survive, and grow on leaves of 22 plant species from 7 families of ancient angiosperms in Australia, Rutaceae, Magnoliaceae, Lauraceae, Monimiaceae, Sapotaceae, Winteraceae, and Annonaceae. Clearly, some common *Papilio* feeding stimulants exist in Australian plant species of certain, but not all, Lauraceae. Three Lauraceae species (two introduced *Cinnamomum* species and the native *Litsea leefeana*) were as suitable for the generalist *P. glaucus* as was observed for *P. troilus*. While no ability to feed and grow was detected for the Lauraceae-specialized *P. troilus* on any of the other six ancient Angiosperm families, the generalist *P. glaucus* did feed successfully on Magnoliaceae and Winteraceae as well as Lauraceae. In addition, some larvae of one *P. glaucus* family attempted feeding on *Citrus* (Rutaceae) and a small amount of feeding was observed on southern sassafras (*Antherosperma moschatum*; Monimiaceae), but all *P. glaucus* (from 4 families) died on Annonaceae and Sapotaceae. Surprisingly, the North American Lauraceae-specialist (*P. troilus*) died on all Lauraceae species by day #12, but some generalist *P. glaucus* larvae survived. Most of the generalist (*P. glaucus*) offspring survived and grew very well on all 3 species of Magnoliaceae assayed (*Magnolia virginiana*, *Michelia champaca*, & *Michelia doltsopa*) and on *Tasmannia insipida* (Winteraceae). The ability of these larvae to feed and grow on *T. insipida* but not *T. lanceolata* suggests significant phytochemical differences may exist within the Winteraceae. Two Monimiaceae "sassafras" plant species were unsuitable to both North American *Papilio* species despite their very close phylogenetic relationship with the Lauraceae.

Additional key words: Annonaceae, detoxification, Lauraceae, Magnoliaceae, Monimiaceae, neonate survival, Papilionidae, Rutaceae, Winteraceae, *P. glaucus*, *P. troilus*

Rutaceae-feeding is the primary pattern in 75–80 % of the genus *Papilio* (Scriber 1984a). In section IV of the Papilionidae (Munroe 1961), *Papilio* (*Heraclides*) *cresphontes* Cramer is constrained to Rutaceae, unable to survive on plants of the Magnoliaceae, Lauraceae, Rosaceae, or Salicaceae (Scriber *et al.* 1991a,&b). However, in Section III of the Papilionidae, ancestors of the polyphagous North American *P.*(*Pterourus*) *glaucus* L. group and their *P. troilus* L. sister group are believed to have been Rutaceae feeders (Hancock 1983; Scriber *et al.* 1991a), with subsequent specialization on the Lauraceae and Magnoliaceae, as Rutaceae became scarce after the Cretaceous (Hancock 1983; Scriber 1995). With the Troidini tribe believed to have origins in remnant Gondwana 65–90 mya (Braby *et al.* 2005), the phylogenetic distances and geological timing (late Jurassic and early Cretaceous; Soltis *et al.* 2005) of the evolutionary divergence of these plant groups has been recently suggested to be 30–50 million years ago (Gaunt and Miles 2002; Zakharov *et al.* 2004). Such diversification of the roots of Papilionidae lineages in the Leptocircini (=Graphiini) and Papilionini tribes also corresponds to plate tectonics and subsequent diversification of early Angiosperm families (e.g. Annonaceae).

There are shared groups of key phytochemicals among the Rutaceae, Lauraceae, Magnoliaceae, Annonaceae, Apiaceae, and Aristolochiaceae (Berenbaum 1995; Brown *et al.* 1995; Nishida 1995) and these can affect oviposition (Dethier 1941,1954; Feeny 1995) as well as larval survival and growth (Munroe 1961; Nitao *et al.* 1992; Johnson *et al.* 1996). Our goal here was to examine neonate larval survival on reported host plants of other Australian Papilionidae and representative species from these chemically-related plant families, including the Australian Winteraceae and Monimiaceae which are ancient angiosperms very closely related to the Lauraceae, Magnoliaceae, and Annonaceae (Bremer *et al.* 2003) with presumed similarity in phytochemicals. The ancient *Doryphora sassafras* Endl.(Monimiaceae) and *Tasmannia* (=*Drimys*) *insipida* R.Br. ex DC. (Winteraceae) are reported in Australia as host plants for *Graphium sarpedon* (L.) and *G. macleayanum* (Leach) butterflies along with the Lauraceae and Rutaceae (Braby 2000).

Papilio troilus L. (spicebush swallowtail) is a Lauraceae-feeding specialist found across the eastern

half of the USA which naturally feeds on sassafras, *Sassafras albidum* (Nutt.) Ness, and spicebush, *Lindera benzoin* (L.) Blume, across most of its range, and red bay, *Persea borbonia* (L.) Spreng., in Florida and the southeast coastal areas (Scriber 2005). Preliminary bioassays with *P. troilus* in North America confirm that this species is a host plant family specialist and will not initiate feeding on plants other than members of the Lauraceae, including all other families used by *Papilio glaucus* L. (eastern tiger swallowtail; Scriber *et al.* 1991b), which also occurs across the eastern USA. *P. glaucus* is the most polyphagous of all 563 species of swallowtail butterflies in the world (Scriber 1984a, 1995). It feeds occasionally on spicebush and sassafras (Lauraceae; Scriber *et al.* 1975), but also includes several dozen other host plant species from 9 different families (including the Magnoliaceae, Rutaceae, Oleaceae, Rosaceae, Tiliaceae, Betulaceae, Platanaceae, and others; Scriber 1986, 1988).

Plant species for neonate larval survival and growth bioassays were selected from lists of recorded host plant species for *Papilio aegeus* Donovan and *Graphium* species in Australia (Braby 2000; Edwards *et al.* 2001, Scriber *et al.* 2006, 2007).

Lauraceae feeding and oviposition in *P. troilus* are apparently determined by phytochemical feeding/oviposition stimulants (Lederhouse *et al.* 1992, Carter & Feeny 1999, Carter *et al.* 1999, Frankfater & Scriber 1999, 2003). Sassafras and spicebush are the preferred hosts throughout most of the butterfly's range. In Florida, where these plants are scarce, red bay (*Persea* spp.), is used by *P. troilus* populations. Preliminary studies indicated that extracts of *Persea* painted on leaves of *Lindera* depress neonate growth rates of northern populations of *P. troilus* (Nitao *et al.* 1991). It is clear that among various geographical populations of this Lauraceae specialized butterfly species, there is variation in the suitability of different plant species for oviposition, larval acceptance and larval growth (Nitao *et al.* 1991; Scriber *et al.* 1991b; Scriber & Margraf 2005).

We wanted to evaluate the abilities of the ancestral Papilionidae, North American section III, Munroe (1961) species *P. troilus* and *P. glaucus* larvae to consume, process and grow on these ancient Australian angiosperm species including unique genera of the Lauraceae that differentiated independently of the North American Lauraceae. In Australia, there exist at least two species of plants called sassafras, *Doryphora sassafras* Endl. and *Antherosperma moschatum* Poir. (southern sassafras). These plants are both in the Monimiaceae, which is an ancient angiosperm family very closely related to the Lauraceae (Bremer *et al.* 2003). *Tasmannia insipida* and *T. lanceolata* (Poir.) A.C. Smith are ancient angiosperms in the Winteraceae, which is also closely related to the Lauraceae and Monimiaceae. Both of these ancient plant families have aromatic species used by Australian swallowtail butterflies, such as *Graphium macleayanum*. Australia seemed to be the best place to evaluate suitability of ancient Angiosperm species (Bremer *et al.* 2003; see also Grimaldi & Engel 2005) since this may have been the "cradle" of flowering plant evolution, including basal families such as the Winteraceae and Monimiaceae (both used by Australian swallowtail butterfly species) as well as the more widespread Lauraceae, Magnoliaceae, Rutaceae, Annonaceae, and Aristolochiaceae (Bremer *et al.* 2003). The phylogenetically basal angiosperm families have their origins, when geological plate drifting had not fully separated the continents (Grimaldi & Engel 2005), and the Papilionidae are believed to have roots concurrent with these early flowering plants (Gaunt & Miles 2002; Braby *et al.* 2005; cf. Miller 1987).

The modern phylogeny and systematics of the ancient Angiosperm families, examined here for their relative suitability as larval host plants, have recently been revised based on many independent molecular analyses (Bremer *et al.* 2003). The phylogenetically basal angiosperms, including the 4 orders, Laurales, Magnoliales, Canellales, and Piperales are all supported as monophyletic, and molecular analyses put them together in a group called the magnoliids, despite the lack of support using morphological traits alone (Bremer *et al.* 2003). Within this single basal group (magnoliids), the Laurales includes the Hernandiaceae, Lauraceae and the closely-related Monimiaceae. The Magnoliales includes the Magnoliaceae and Annonaceae. The Piperales includes the Aristolochiaceae and Piperaceae. The Canellales includes the primitive Winteraceae with *Tasmannia* (=*Drimys*) species reported as hosts for other species of swallowtails (Scriber 1984a; Braby 2000). All of these families have some swallowtail butterfly species (Papilionidae) reported as feeding on them, but 75% of all swallowtail butterfly species feed on the Rutaceae (Scriber 1984a; Berenbaum 1995). The Rutaceae (including *Flindersia*, *Geijera*, *Citrus*, & *Zieria*) are believed to have survived the extensive worldwide Cretaceous-Tertiary extinctions in the eastern part of Gondwana (the Australian landmass) of the southern hemisphere, along with other ancient angiosperms, such as the Winteraceae, some Lauraceae, and Monimiaceae (Raven & Axelrod 1974).

This study of the North American *P. troilus* and *P. glaucus* was conducted to validate host use abilities (or

inabilities) of the neonate larvae in their first bites (Zalucki *et al.* 2002) on species of 7 families of ancient angiosperms. In order to determine the relative suitability of each host for larval consumption, growth, and survival, we conducted controlled environment bioassays using neonates from eggs of different wild females. Results provided clues to the historical (phylogenetic) or potential (future) abilities of geographically-widespread specialist and generalist species of North American *Papilio* to use different Australian plant families.

MATERIALS AND METHODS

Adult capture and female oviposition. Females of *P. troilus* and *P. glaucus* were captured in Levy County, Florida in March and April of 2006. Using methods as described by Scriber (1993), individual females were placed in clear plastic boxes containing red bay leaves for *P. troilus* and several species of potential host plants for *P. glaucus* (including sweet bay, *Magnolia virginiana* L. (Magnoliaceae), black cherry, *Prunus serotina* Ehrh. (Rosaceae) and white ash, *Fraxinus americana* L. (Oleaceae). Eggs were collected daily, counted, and placed in a controlled environment chamber for 1–5 days at 4–6 ° C, until express mailed to our Australian quarantine lab in the School of Life Sciences Goddard Building (Australian DEH and AQIS permits had been obtained previously; also with clearance from Biosecurity Australia). Constraints of the AQIS permit and Biosecurity Australia prevented us from sending adults to Australia for oviposition preference assays on native plants there.

Larval bioassays and rearing. Eggs from each *Papilio* female were kept in sterile clear plastic Petri dishes (20 mm deep; 100 or 150 mm diameter) in the same controlled environment chamber until they eclosed as neonate larvae. Newly emerged neonates were distributed in a split-brood design across an array of potential host plant species, with 2–3 larvae per dish (each dish containing a new leaf and a mature or fully-expanded leaf of one plant species supported with their petioles immersed in a water-soaked florist "oasis" foam wrapped tightly with aluminum foil to retain moisture) for each 96-hour period. Neonate larvae were introduced to each species with a fine camel hair brush by gently placing them on the aluminum foil at the base of both petioles (the new leaf and the mature leaf) in order for the larvae to choose which leaf they crawled onto. Daily survival and growth were monitored and recorded. The total number of fecal pellets, the estimated leaf area consumed (mm^2), the instar stage (or molt), and the larval weights (for all survivors) were recorded at 96 hours. Fresh, new and mature leaves were introduced at 96 hours for continued larval feeding and growth for another 96 hours, when they were weighed again. These assay methods were used successfully in our previous studies of host use by the Australian *P. aegeus* (see Fig. 1; Scriber *et al.* 2007).

Numbers were assigned for each instar (e.g. 1, 2, 3, 4) and molts were assigned the midpoint (e.g. 1.5 = molting from first to second instar). Survivors of *P. glaucus* and *P. troilus* at 12 days were destroyed because of constraints imposed by the AQIS import permit (#200520165).

Plant species used for bioassays. Plant species for neonate larval survival and growth bioassays were selected from lists of recorded host plant species for *P. aegeus* and *Graphium* species in Australia (Braby 2000; Edwards *et al.* 2001; Scriber *et al.* 2006, 2007). These native Australian plants were obtained as seedlings from Fairhill Native Plants (Yandina, QL), Barung Landcare Nursery (Maleny, QL). Anthony Hiller at Mount Glorious Biological Centre (Mt. Glorious, QL), Turner's Garden Center at Rochdale, near South Brisbane, and Greening Australia Nursery (near The Gap, QL), and from the University of Tasmania at Hobart. Seedlings were brought to the University of Queensland Glasshouse during mid-October, where they were transplanted into 4-liter pots with standard sterilized potting soil (half sand). Each tree seedling was then fertilized with Flowfeed EX7 fertilizer (Grow Force Australia Ltd; N-P-K, 20.8%, 3.3% and 17.4% respectively). New leaves (not fully-expanded) had developed on all plants by the time the larval feeding bioassays started in mid-March 2006.

Some plant species' leaves (3 species of Magnoliaceae, 2 species of Rutaceae) used in these studies were field-collected at the Brisbane Botanical Gardens (with the assistance of Director Phil Cameron). Camphor tree leaves were collected from the UQ Campus nearby the lab. The full list of plants tested is given below.

Rutaceae (native unless noted):

Citrus sinensis Osbeck (sweet orange; "Joppa" introduced.);
Geijera salicifolia Schott (brush wilga);
Flindersia australis R.Br (Australian Teak),

Magnoliaceae (all introduced):

Magnolia virginiana L. (sweet bay; North America);
Michelia champaca L. (yellow magnolia; Asia);
Michelia doltsopa Buch.–Hum. ex D.C. (silver cloud) an Asian species endemic to the Himalayan region of China and Tibet,

Lauraceae (native unless noted):

Beilschmedia obtusifolia (F. Muell. ex Meis.)

(Blush walnut);
Cinnamomum camphora (L.) J. Presl (camphor laurel) an introduced tree, abundant in Queensland and NSW;
Cinnamomum oliveri (F.M. Bailey) (Oliver's sassafras);
Cinnamomum virens R.T. Baker;
Cryptocarya glaucescens R.Br. (jackwood);
Cryptocarya microneura Meisn. (Murrogun);
Endiandra discolor Benth. (rose walnut);
Litsea leefeana (F. Muell.) (bollywood);
Neolitsea dealbata (R.Br.) Merr. (bolly gum),

Monimiaceae (native):
Doryphora sassafras Endl. (sassafras);
Antherosperma moschatum Poir. (southern sassafras) found in Tasmania and Victoria (the only host for Tasmanian swallowtail butterfly subspecies, *G. m. moggana* Couchman),

Annonaceae (introduced):
Annona muricata L. (soursop);
Annona reticulata L. (custard apple),

Winteraceae (native):
Tasmannia insipida R.Br. ex DC. (purple cherry);
Tasmannia lanceolata (=*Drimys aromatica*) (Poir.) A. C. Smith (mountain pepper, winterberry) found in Tasmania and Victoria and NSW,

Sapotaceae (native):
Pouteria (= *Planchonella*) *australis* (R.Br) Baehni (black apple).

RESULTS

Neonate larvae of the Lauraceae specialist, *P. troilus* died on all species in all families except Lauraceae. While some of the species within this favored family

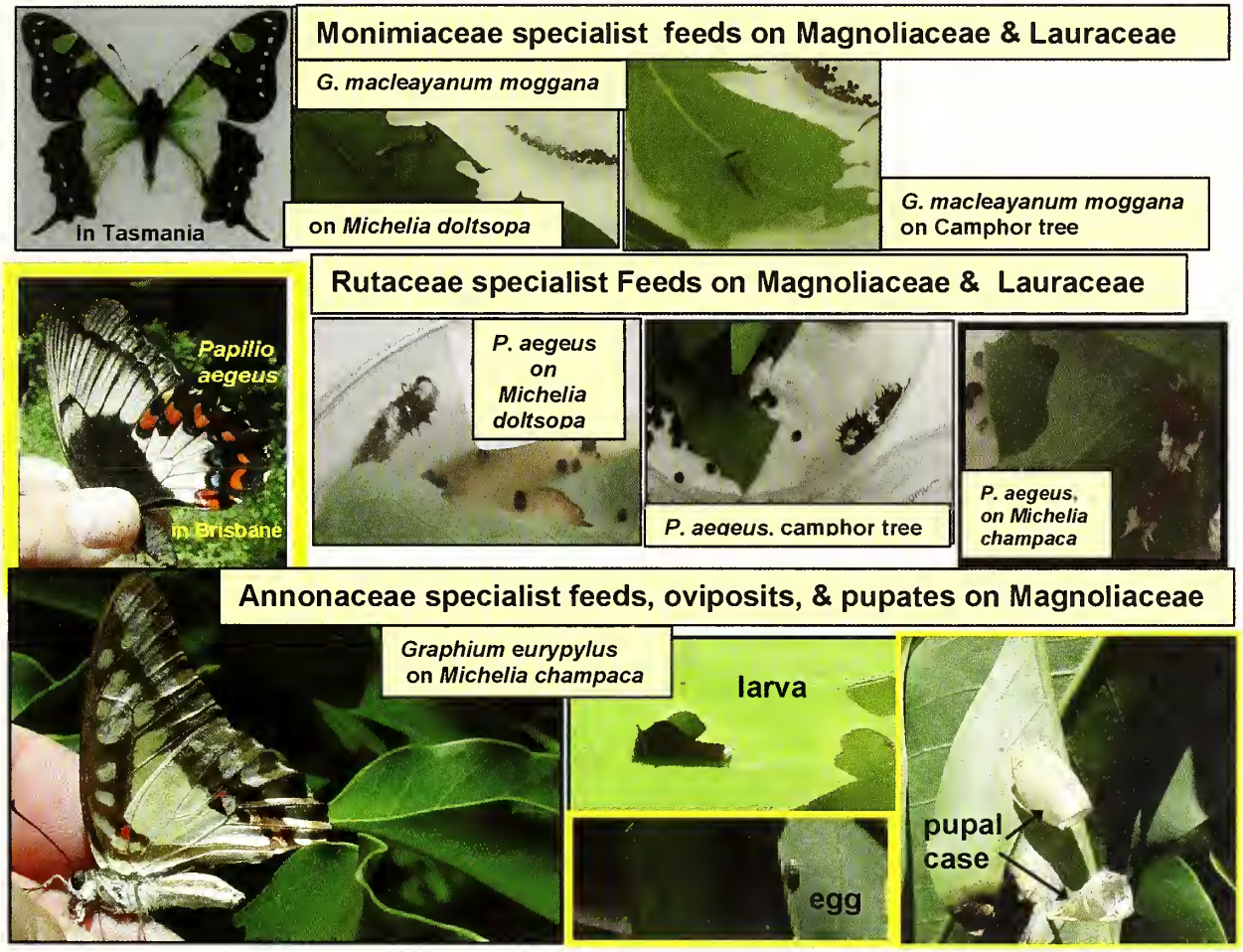


FIG. 1. Feeding assays with family-specialized Australian Lepidoptera that also survived on Magnoliaceae: **1a**) Macleay's swallowtail (Tasmanian subspecies, *G. m. moggana*) is a specialist on the Monimiaceae, but feeds and pupates on Magnoliaceae and Lauraceae (Scriber et al. 2006), **1b**) *Papilio aegeus* is a Rutaceae specialist, but feeds on 3 species of Magnoliaceae and camphor tree in the Lauraceae (Scriber et al. 2007), **1c**) *Graphium eurypylus* is an Annonaceae specialist that oviposits, feeds, and pupates on Magnoliaceae near Brisbane, Australia (Larsen et al. 2008).

TABLE 1. Mean survival and growth indices of neonate larvae of *P. glaucus* families (G1-G4) and *P. troilus* (T1 & T2) reared on various ancient Angiosperm plant species at 4 days, 8 days, and 12 days.

		4 Days			8 Days			12 Days		
Larval Family	(n)	% surv.	mean wt.	instar	% surv.	mean wt.	instar	% surv.	mean wt.	instar
RUTACEAE										
Citrus sinensis "joppa"										
G1	0	na								
G2	3	33.3	3.7	1	0	died				
G3	0	na								
G4	0	na								
T1	0	na								
T2	3	0	died							
Flindersia australis										
G1	0	na								
G2	3	0	died							
G3	0	na								
G4	0	na								
T1	3	0	died							
T2	0	na								
Geijera salicifolia°										
G1	2	0	died							
G2	3	0	died							
G3	2	0	died							
G4	2	0	died							
T1	2	0	died							
T2	2	0	died							
MAGNOLIACEAE										
Magnolia virginiana										
G1	2	100	9.9	1.5	100	39.6	2.5	100	147.1	4
G2	3	66.7	8.4	1.5	66.7	31.8	2.8	66.7	125.1	3.5
G3	2	50	8.4	1.5	50	27	2.5	50	106.7	3
G4	2	50	7.6	2	50	44.7	3	50	214.3	4
T1	2	0	died							
T2	3	0	died							
Michelia champaca										
G1	2	100	10.3	1.5	50	72.8	3	50	427.1	4
G2	3	66.7	17.7	2	33.3	111.9	3	33.3	450	4
G3	2	100	10.7	1.8	100	41.4	2.8	100	205.6	4
G4	2	0	died							
T1	2	0	died							
T2	3	0	died							
Michelia doltsopa										
G1	2	100	4.9	1	100	9.5	1.8	100	17.1	2
G2	3	66.7	4.6	1	100	7.4	1.3	100	6.7	1.3

TABLE 1. (continued)

		4 Days			8 Days			12 Days		
Larval Family	(n)	% surv.	mean wt.	instar	% surv.	mean wt.	instar	% surv.	mean wt.	instar
Michelia doltsopa (cont.)										
G3	2	100	7	1.8	100	27.2	2.8	100	136.9	3.3
G4	2	0	died							
T1	2	0	died							
T2	3	0	died							
LAURACEAE										
Beilschmiedia obtusifolia°										
G1	2	0	died							
G2	3	0	died							
G3	2	0	died							
G4	2	0	died							
T1	2	0	died							
T2	2	0	died							
Cinnamomum camphora										
G1	2	0	died							
G2	3	100	8.7	1	100	15.1	2	100	41.3	2.8
G3	0	na								
G4	2	0	died							
T1	2	0	died							
T2	3	66.7	3.8	1.3	66.7	4	1.5	0	died	
Cinnamomum oliveri										
G1	0	na								
G2	3	66.7	4	1	0	died				
G3	0	na								
G4	0	na								
T1	0	na								
T2	3	66.7	3.7	1.3	66.7	4	1.5	0	died	
Cinnamomum virens										
G1	0	na								
G2	3	33.3	2.7	1	0	died				
G3	0	na								
G4	0	na								
T1	0	na								
T2	0	na								
Cryptocarya glaucescens°										
G1	2	0	died							
G2	3	0	died							
G3	2	0	died							
G4	2	0	died							
T1	2	0	died							
T2	2	0	died							
Cryptocarya microneura										
G1	0	na								
G2	3	0	died							
G3	0	na								
G4	3	0	died							
T1	0	na								
T2	0	na								

TABLE 1. (continued)

		4 Days			8 Days			12 Days		
Larval Family	(n)	% surv.	mean wt.	instar	% surv.	mean wt.	instar	% surv.	mean wt.	instar
Endiandra discolor°										
G1	2	0	died							
G2	3	0	died							
G3	2	0	died							
G4	2	0	died							
T1	2	0	died							
T2	2	0	died							
Litsea leefeana										
G1	2	0	died							
G2	3	33.3	2.3	1	33.3	2.9	1	0	died	
G3	2	0	died							
G4	2	0	died							
T1	2	50	3.8	1	50	2.4	2	0	died	
T2	2	0	died							
Neolitsea dealbata°										
G1	2	0	died							
G2	3	0	died							
G3	2	0	died							
G4	2	0	died							
T1	2	0	died							
T2	2	0	died							
MONIMIACEAE										
Antherosperma moschatum										
G1	2	0	died							
G2	3	0	died							
G3	2	50	1.1	1	0	died				
G4	2	0	died							
T1	2	0	died							
T2	3	0	died							
Doryphora sassafras°										
G1	2	0	died							
G2	3	0	died							
G3	2	0	died							
G4	2	0	died							
T1	2	0	died							
T2	3	0	died							
WINTERACEAE										
Tasmannia insipida										
G1	2	100	4.7	1	100	10	1.8	100	17.1	2
G2	3	66.7	4.6	1	66.7	7.4	1.3	66.7	6.7	1.5
G3	2	100	2.3	1	50	7.4	1	50	6.5	2
G4	3	50	3.7	1	50	7.9	1.5	50	18.1	2
T1	2	0	died							
T2	2	0	died							

TABLE 1. (concluded)

		4 Days			8 Days			12 Days		
Larval Family	(n)	% surv.	mean wt.	instar	% surv.	mean wt.	instar	% surv.	mean wt.	instar
WINTERACEAE (cont.)										
Tasmannia lanceolata°										
G1	2	0	died							
G2	3	0	died							
G3	2	0	died							
G4	2	0	died							
T1	2	0	died							
T2	2	0	died							
ANNONACEAE										
Annona muricata°										
G1	2	0	died							
G2	3	0	died							
G3	2	0	died							
G4	2	0	died							
T1	2	0	died							
T2	3	0	died							
Annona reticulata°										
G1	2	0	died							
G2	3	0	died							
G3	2	0	died							
G4	2	0	died							
T1	2	0	died							
T2	3	0	died							
SAPOTACEAE										
Pouteria australis°										
G1	2	0	died							
G2	3	0	died							
G3	2	0	died							
G4	2	0	died							
T1	2	0	died							
T2	2	0	died							

° There was no nibbling or feces in any of the dishes of *Geijera salicifolia* (Rutaceae); *Beilschmiedia obtusifolia*, *Cryptocarya glaucescens*, *Endiandra discolor*, or *Neolitsea dealbata* (Lauraceae); *Doryphora sassafras* (Monimiaceae); *Annona muricata* or *A. reticulata* (Annonaceae); *Tasmnannia lanceolata* (Winteraceae); or *Pouteria australis* (Sapotaceae).

were unsuitable for survival and growth (e.g. *Beilschmiedia abtusifolia*, *Cryptocarya glaucescens*, *Endiandra discolor* and *Neolitsea dealbata*), *Cinnamomum camphora*, *C. virens* and *Litsea leefeana* supported feeding (producing 327, 398, and 192 fecal pellets, respectively) and some growth of larvae (Table 1). However, even with some feeding stimulants in these 3 hosts, all *P. troilus* larvae died before the third instar and day 12 (Table 1).

One family of the generalist *P. glaucus* also fed (producing 335, 220, and 187 fecal pellets, respectively) and grew on the same 3 Lauraceae species as *P. troilus*. Only *C. camphora* supported growth to the third instar and up to day 12 (when killed in accordance with the AQIS permit). In addition, neonates from all 4 families of *P. glaucus* could feed and survive on *Tasmannia insipida* (Winteraceae). However, the congeneric *T. lanceolata* was unsuitable for any of the *P. glaucus* larvae and there were no feces. Some attempts to feed on the Monimiaceae and Rutaceae were observed for certain *P. glaucus* families, but this was not successful since all larvae died before day 8. Excellent survival and growth were observed on the Magnoliaceae (Table 1). *Magnolia virginiana* (sweet bay) is a favorite of *P. glaucus* in Florida (Scriber 1986, Scriber *et al.* 2001) and larvae grew well on the leaves of this large tree species from the Brisbane Botanical Gardens. All 4 families of *P. glaucus* also grew very well on leaves of *Michelia*

champaca and *M. doltsopa*, despite their geographically distant Asian origins. Phytochemical common denominators among *Magnolia* species might largely explain this high suitability of such allopatric plant species for *P. glaucus*.

The phylogenetic closeness of Winteraceae and Magnoliaceae may reflect some phytochemical similarities, as is suggested by the high survival and successful growth of *P. glaucus* on *Tasmannia insipida* as well as the *Michelia* and *Magnolia* species. However, no survival (or feeding) on *T. lanceolata* (= *Drimys aromatica*) was observed, suggesting different suitabilities (or toxicities) within this plant genus.

DISCUSSION

The evolutionary constraints that have restricted *P. troilus* to only Lauraceae, and the ecological opportunities that were taken by *P. glaucus* on 9 families of plants in North America (see Fig.2; Scriber 1988; Scriber *et al.* 1991b) were confirmed with our neonate larval assays here using 22 species of Australian plants. With a very narrow host range, the Spicebush Swallowtail, *P. troilus*, grows with 2–4 times the efficiency and rate of the generalist *P. glaucus* on the same plant, (Scriber & Feeny 1979; Scriber 1984b). In fact there have been no other species of insects ever reported with significantly higher growth rates and efficiencies in various instars than *P. troilus* on spicebush (Scriber 2005). Potential loss of abilities to accept and detoxify closely related families (or Rutaceae; Scriber *et al.* 2008a) is suggested by the unwillingness and/or inability of neonate *P. troilus* to feed and grow on any plants in the 6 plant families other than Lauraceae in these bioassays. Despite the close phylogenetic relationships of the ancient Australian Monimiaceae and Winteraceae with the Lauraceae, their leaves are unsuitable (repellent or toxic) for the Lauraceae specialist, *P. troilus*. It was evident that some of the Lauraceae assayed here (*Beilschmiedia*, *Cryptocarya*, *Endiandra*, and *Neolitsea* species) were unsuitable for neonate growth and survival, although they did feed on one *Litsea* and two *Cinnamomum* species (Table 1). Differential utilization abilities of plant species within the Lauraceae has been documented for *P. troilus* (Lederhouse *et al.* 1992) and among its geographical populations in the USA (Nitao *et al.* 1991). The introduced southeast Asian *Cinnamomum camphora* has elicited oviposition and larval feeding by *P. troilus* on an ornamental planting of this tree in the USA (Morris 1989). It is known that the furanocoumarin-metabolizing cytochrome P450 enzymes found in many Rutaceae feeders (including *P. glaucus* and *P. canadensis*; Li *et al.* 2001) are lacking in *P. troilus* (Cohen *et al.* 1992). Behavioral cues (stimulants) to *P. troilus* adults and larvae also seem to be missing in plants other than Lauraceae (Carter & Feeny 1999; Carter *et al.* 1999; Frankfater and Scriber 1999; Scriber *et al.* 2001).

While *P. glaucus* can and does use spicebush and sassafras naturally, they are not favored hosts. Survival of 2042 individuals from 44 different populations from 17 different States (and Canada and Mexico) was only 14% overall, compared to 68% for *P. troilus* (6 States, 28 families, 621 larvae: Scriber 2005). While the generalist *P. glaucus* does naturally feed on sassafras and spicebush (Scriber *et al.*1975), red bay (*Persea borbonia*, also of the Lauraceae) is toxic to all neonates tested, killing 228 larvae of the Florida population and 432 larvae of the northern *P. glaucus* populations (Scriber *et al.* 1995, Scriber 2005, Table 2). Although unknown regarding specific toxins for *Papilio*, insect toxins have been identified from *Persea* (Ma *et al.* 1988; Gonzalez-Coloma *et al.* 1990).

TABLE 2. Neonate larval survival of *P. troilus* and *P. glaucus* on plants of North American Lauraceae, and Australian Monimiaceae, and Winteraceae. Data are presented as % survival, and (n= total larvae).

	Lauraceae					Monimiaceae		Winteraceae	
	RB	SP	SA	CT(US)	CT(A)	Dsas	Amos	Tins	Tlan
P. troilus	55%	86%	77%	50%	75%	0%	0%	0%	0%
	(143)	(156)	(404)	(82)	(4)	(5)	(5)	(4)	(4)
P. glaucus	0%	24%	60%	62%	33%	0%	11%	67%	0%
	(432)	(579)	(306)	(134)	(9)	(9)	(9)	(9)	(9)

RB= red bay; SP= spicebush; SA = *Sassafras albidum*; CT= Camphor tree (in USA & in Australia); Dsas= *Doryphora sassafras*; Amos= southern sassafras, *Antherosperma moschatum*; Tins= *Tasmannia insipida*, and Tlan= *T. lanceolata*.

North American data (4 columns at the left) are from Scriber et al (1991, 1995)

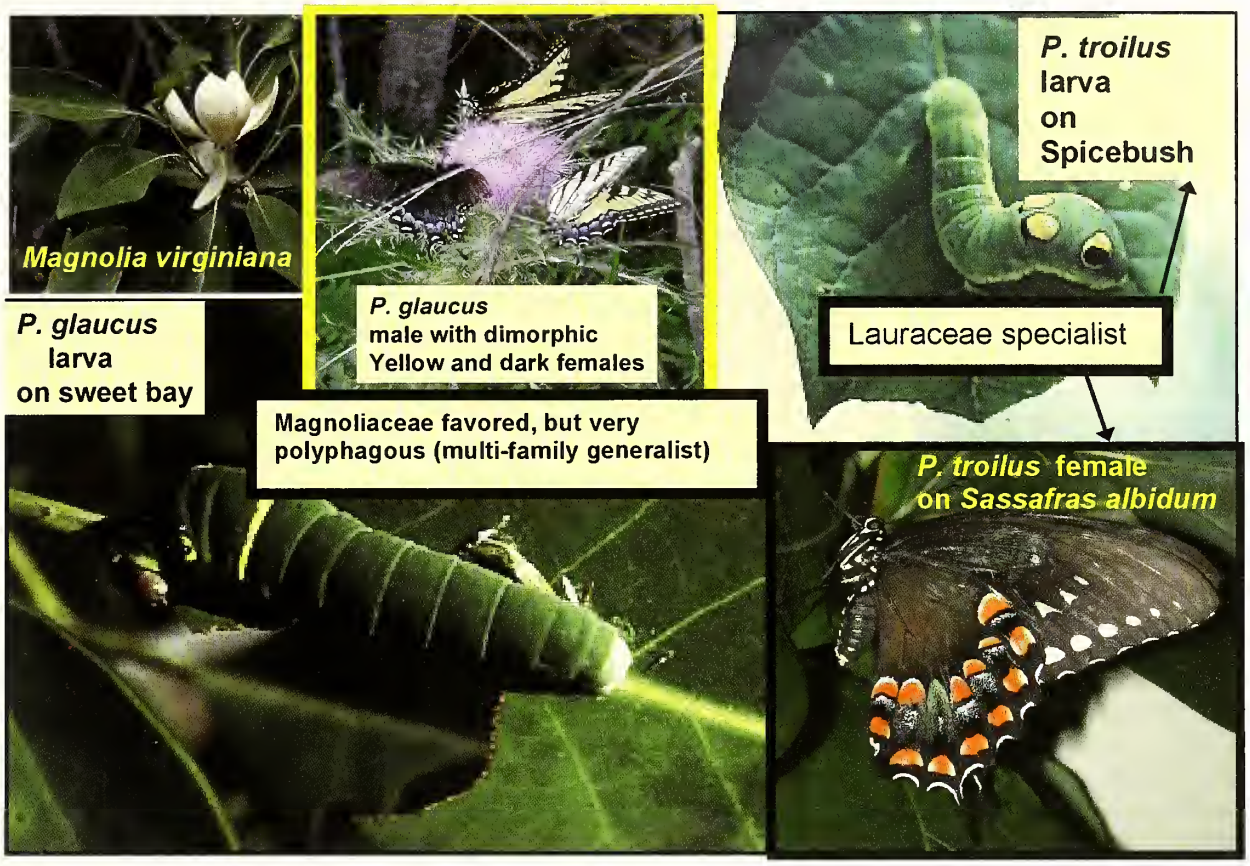


FIG. 2. North American *P. glaucus* and *P. troilus* on their favored hosts.

It is apparent that *P. glaucus* and *P. troilus* attempt to feed on *Litsea leefeana* leaves from Australia as well as 2 species of *Cinnamomum* (*C. cauphora* and *C. oliveri*; Table 1). However, these Lauraceae species are not suitable hosts for either butterfly species. Recent experimental feeding studies with camphor tree (*C. camphora*) have shown this invasive tree species is acceptable for the *Antherosperma moschatum* specialist *Graphium macleayanum moggana* in Tasmania (Scriber *et al.* 2006), as well as for the Rutaceae specialist, *Papilio aegeus* in Queensland (Scriber *et al.* 2007). A fundamental common phytochemical array of nutrients and allelochemicals in camphor tree apparently serves the basic nutritional needs for larvae of phylogenetically divergent Australian and North American taxonomic groups of Papilionidae. However, it remains unknown whether camphor tree has been an ancestral plant for any of the Papilionidae.

Despite the same common names, close phylogenetic origins, and a similar aromatic smell between the Monimiaceae (sassafras= *Doryphora sassafras*; southern sassafras = *Antherosperma moschatum*) and the Lauraceae (sassafras= *Sassafras albidum*), the Australian Monimiaceae were not at all suitable for the North American *P. troilus*. Both of these plant species are hosts of *Graphium macleayanum* Leach (Braby 2000; Scriber *et al.* 2006). However, despite the use of both species of *Tasmannia* (*T. insipida* and *T. lanceolata*) by *Graphium macleayanum* in Australia, these plants were totally unsuitable for *P. troilus*. However, the North American *P. glaucus* grew successfully on *T. insipida* (but died on *T. lanceolata*; Tables 1 & 2). The phytochemical basis and genetically-based differences in feeding behavior and larval detoxification abilities deserve further study. The leaf oil cells of *Tasmannia lanceolata* are known to contain a sesquiterpene chemical called polygodial, which has been shown to have antimicrobial activity (Kubo & Taniguchi 1988) and piscicidal properties (Cimino *et al.* 1982). It has also been shown to have antifeedant properties for some insects (Powell *et al.* 1995).

Species of Magnoliaceae, while toxic to *P. troilus* (Scriber *et al.* 1991), can serve as a host for several Australian Papilionidae even though the plants are not found there naturally. The Rutaceae specialist, *Papilio aegeus* was reared to pupation on Magnoliaceae including *Magnolia virginiana* (sweet bay; from North America), *Michelia champaca* (yellow magnolia; from

Asia), and *Michelia doltsopa* (Asian silver cloud; Scriber *et al.* 2007). Pupae of *P. aegeus* were obtained from all 3 Magnoliaceae species and also for *C. camphora* of the Lauraceae (Fig. 1b). In addition, the Annonaceae specialist, *Graphium eurypylus* L., has recently been shown to naturally oviposit and feed successfully on introduced *Michelia champaca* of the Magnoliaceae (Larsen *et al.* 2008; Fig. 1c), and the Monimiaceae specialist (the Tasmanian subspecies of Macleay's swallowtail) was reared to pupation on *Michelia doltsopa* (Magnoliaceae; Scriber *et al.* 2006; Fig. 1a). The Umbelliferae (=Apiaceae) specialist, *Papilio polyxenes* F., also has the ability to feed and pupate on Magnolia as well as species of Rutaceae in North America (Scriber 1984a).

These examples, and the results with *P. glaucus* in Australia, suggest that some ancient common general phytochemical processing (or detoxification) abilities may be shared in different combinations for the Magnoliaceae, Lauraceae, Monimiaceae, Winteraceae, Annonaceae, Apiaceae and Rutaceae phytochemicals. Such adaptations may involve the very large and diverse furanocoumarin detoxification gene family of CYP6B cytochrome P450 monoxygenases, with differential biochemical inducibilities providing additional plasticity (Berenbaum & Zangerl 1998; Li *et al.* 2001, 2003, 2004).

With the Aristolochiaceae-feeding Troidini tribe of Papilionidae diverging from the Papilionini tribe (with 210 species of *Papilio*) 80–100 million years ago (Zakharov *et al.* 2004; Braby *et al.* 2005), it is not surprising that Aristolochiaceae leaves (e.g. *A. elegans*) are toxic to all neonate larvae of *P. glaucus* and *P. troilus* (Scriber unpubl. data) as well as *Papilio aegeus* Donovan (Scriber *et al.* 2007), which have no recent relatives that have ever fed on this family of plants (see also Brown *et al.* 1995). The earlier diverged Aristolochiaceae-feeding Troidini tribe (including *Battus*) and the Annonaceae-feeding Leptocircini tribe (including *Graphium* = *Eurytides* = *Protesilaus*; Zakharov *et al.* 2004) apparently lack the furanocoumarin detoxification genes needed for Rutaceae use (Berenbaum & Zangerl 1998).

Despite considerable phylogenetic distance from the basal magnoliids (Bremer *et al.* 2003; Scriber *et al.* 2008a), the Rutaceae seem to be the host family used by the ancestors of the North American *Papilio* (*Pterourus*) *glaucus* species group and possibly the paraphyletic *Pyrrhosticta* (=*Papilio*) *scamander* Boisduval, *P. homerus* Fabr. and *P. garamas* Hübner groups in South and Central America (Scriber *et al.* 1991b; Caterino & Sperling 1999), probably due to shared host plant chemistry and shared furanocoumarin detoxification gene families (Li *et al.* 2001, 2004). If the North American *P. troilus* sister group ever possessed such Rutaceae (furanocoumarin) detoxification abilities, they have since lost it (Scriber *et al.* 1991b; Cohen *et al.* 1992; Berenbaum & Zangerl 1998). The abilities of the very polyphagous *P. glaucus* and *P. canadensis* to expand their host range beyond the ancestral Rutaceae and Magnoliaceae appears to be due to a very few mutational changes, allowing novel catalytic activity without loss of the ancestral furanocoumarin activities (Mao *et al.* 2007). In adult *P. glaucus*, oviposition rank order hierarchies are stable over the eastern half of the USA (Mercader and Scriber 2005), but plasticity and genetic variation in "specificities" in preference exist, potentially leading to local host specialization where introgression with *P. canadensis* occurs (on the cooler side of the hybrid zone where tulip tree is not available) in their hybrid species, *P. appalachiensis* (Mercader and Scriber 2007; Scriber *et al.* 2008b).

The variety of secondary chemicals (including very different classes of toxic allelochemicals; Berenbaum 1995; Brown *et al.* 1995; Feeny 1995) in these basal angiosperm plant families is staggering. The ability to consume and grow on plants in several such families, as seen for *P. glaucus* in the USA and *G. macleayanum* and *G. sarpedon* in Australia, seems truly impressive (whether this is a recently derived, or a 50 million year old residual ancestral capability in any current specialist; Nitao 1995). However, while there may be additional detoxification systems for other classes of phytochemicals, the costs of possessing and operating such systems would seem evolutionarily expensive and inefficient (Scriber 2005). As with most insect herbivores both physiological and ecological costs remain basically unknown, and the evolutionary cost of maintaining polyphagous capabilities for millions of years (even with some pleiotrophic fitness value) is hard to imagine and can only be a matter of speculation (Scriber 2002a).

Of course many other ecological factors in addition to plant chemistry (Scriber 2002a) influence local host plant shifts in the Papilionidae and other herbivorous insects, including natural enemies (Murphy 2004) and thermal constraints on voltinism (Scriber & Lederhouse 1992; Scriber 1996, 2002b). Here we only examined the fundamental physiological capabilities to biochemically detoxify and process nutrients from ancient allopatric angiosperms, with which the North American *P. troilus* and *P. glaucus* have never had direct contact. It is unlikely that there would have been any indirect ecological or evolutionary experience in any of their recent ancestors. Nonetheless, the abilities of the generalist, *P. glaucus*, to feed and grow on such

unfamiliar plant species (e.g. *Tasmannia insipida* of the Winteraceae, and camphor tree of the Lauraceae), suggests that the potential to "invade" Australia is feasible, although minimal (except on introduced Magnoliaceae). The Lauraceae specialist, *P. troilus*, would almost certainly fail to establish in Australia, since even the Lauraceae did not support larval survival beyond 8 days.

ACKNOWLEDGEMENTS

This research was supported by the University of Queensland in St Lucia, Brisbane and in part by the Colleges of Natural Science and Agriculture and Natural Resources at Michigan State University (Michigan Agr. Expt. Stat. Project # 01644, JMS). Special thanks are extended to Anthony Hiller for his advice and assistance collecting as well as providing the *Doryphora sassafras* trees. Thanks are also extended to Mary Finlay-Doney for her assistance in collecting larvae, and for providing *Citrus* seedlings. We thank Director Phil Cameron of the Brisbane Botanical Gardens for his assistance. Geoff Allen and Paul Walker provided the *Antherosperma moschatum* and *Tasmannia lanceolata* seedlings from Tasmania. In Florida, Matt Lehnert, Jaret Daniels and Tom Emmel were extremely helpful in providing field assistance and/or lab space for *Papilio* oviposition.

LITERATURE CITED

BERENBAUM, M.R. 1995. Chemistry and oligophagy in the Papilionidae. Pp 27–38 *In*; J.M. Scriber, Y.Tsubaki, & R.C.Lederhouse (eds.), Swallowtail Butterflies; Their Ecology and Evolutionary Biology. Scientific Publ, Gainesville, FL.

——, & A.R. Zangerl. 1998. Population-level adaptation to host-plant chemicals: the role of cytochrome P450 monooxygenases. Pp. 91–112 *In*; S. Mopper & S.Y. Strauss (eds.), Genetic Structure and Local Adaptation in Natural Insect Populations. Chapman and Hall, NY.

BRABY, M.F. 2000. Butterflies of Australia: Their identification, biology and distribution. Vol.1. CSIRO Publishing, Canberra. 976pp.

——, J. Trueman, & R. Eastwood. 2005. When and where did troidine butterflies (Lepidoptera: Papilionidae) evolve? Phylogenetic and biogeographic evidence suggests an origin in remnant Gondwana in the late Cretaceous. Invert. Syst. 19: 113–143.

BREMER, K., B. BREMER, & M. THULIN. 2003. Introduction to phylogeny and systematics of flowering plants. Acta Universitalis Upsaliensis, Symbolae Botanicae Upsalienses. 33(2) Sweden. 102pp.

BROWN, K.S. JR., C. BERLINGERI, C.F. KLITZKE, &. P.E.R. DOS SANTOS. 1995. Neotropical swallowtails: chemistry of food plant relationships, population ecology, and biosystematics. Pp 405–445 *In*; J.M. Scriber, Y. Tsubaki, & R.C. Lederhouse (eds.), Swallowtail Butterflies; Their Ecology and Evolutionary Biology. Scientific Publ, Gainesville, FL,

CARTER, M. & P. FEENY, 1999. Host plant chemistry influences oviposition choice of the spicebush swallowtail butterfly, *Papilio troilus*. J. Chem. Ecol. 25: 1999–2009.

——, P. FEENY, & M. HARIBAL. 1999. An oviposition stimulant for the spicebush swallowtail butterfly, *Papilio troilus* (Lepidoptera: Papilionidae), from leaves of *Sassafras albidum* (Lauraceae) J. Chem. Ecol. 25: 1233–1245.

CATERINO, M.S. & F.A.H. SPERLING, 1999. *Papilio* phylogeny based on mitochondrial cytochrome oxidase I and II genes. Molec. Phylog. & Evol. 11: 127–137.

CIMINO, G., S. DEROSA, S. DESTEFANO, G. SODANOAND, & G.VILLANI, 1982. The chemical defense of four Mediterranean nudibranchs. Comp. Biochem. Physiol 73B: 471–474.

COHEN, M.B., M.A. SCHULER, &. M.R. BERENBAUM. 1992. Host-inducible cytochrome P450 from a host-specific caterpillar: molecular cloning and evolution. Proceedings of the National Academy of Sciences (USA) 89: 10920–10924.

DETHIER, V.G. 1941. Chemical factors determining the choice of foodplants by *Papilio* larvae. Amer. Nat. 75: 61–73

——, 1954. Evolution of feeding preferences in phytophagous insects. Evolution 8: 33–54.

EDWARDS, E.D., J. NEWLAND, & L. REGAN. 2001. Lepidoptera Hesperioidea, Papilionidae. Pp. 427–428 *In*; A.Wells & W.W.K. Houston (eds.), Zoological Catalogue of Australia, 31 (6). CSIRO Publishing, Melbourne.

FEENY, P. 1995. Ecological opportunism and chemical constraints on the host associations of swallowtail butterflies. Pp 9–15 *In*; J.M. Scriber, Y. Tsubaki, & R.C Lederhouse (eds.), Swallowtail Butterflies; Their Ecology and Evolutionary Biology. Scientific Publ, Gainesville, FL.

FRANKFATER, C.R. & J.M. SCRIBER. 1999. Chemical basis for host recognition by two oligophagous swallowtail butterflies, *Papilio troilus* and *Papilio palamedes*. Chemoecology 9: 127–132.

—— & J.M. SCRIBER. 2003. Contact chemoreception guides oviposition of two Lauraceae-specialized swallowtail butterflies (Lepidoptera; Papilionidae). Holarct. Lepid. 7: 33–38.

GAUNT, M.W. & M.A. MILES. 2002. An insect molecular clock dates the origins of insects and accords with palaeontological and biogeographic landmarks. Molec. Biol. & Evol. 19: 748–761.

GONZALEZ-COLOMA, A., M. HERNANDEZ, G.A. PERALES, & B.M. FRAGA. 1990. Chemical ecology of Canarian laurel forest toxic diterpenes from *Persea indica* (Lauraceae). J. Chem. Ecol. 16: 2723–2733.

GRIMALDI, D. & M.S.ENGEL 2005. Evolution of the insects. Cambridge Univ. Press. UK. 796pp.

HANCOCK D.L. 1983. *Princeps aegeus* (Donovan) and its allies (Lepidoptera; Papilionidae): systematics, phylogeny and biogeography. Austral. J. Zool. 31: 771–797.

JOHNSON K.S., J.M. SCRIBER, & M. NAIR. 1996. Phenylpropanoid phenolics in sweetbay magnolia as chemical determinants of host use in saturniid silkmoths (*Callosamia* spp.) J. Chem. Ecol.. 22: 1955–1969.

KUBO, I. & M.TANIGUCHI. 1988. Polygodial an antifungal potentiator. J. Nat. Prod. 15: 22–29.

LARSEN, M.L., J.M. SCRIBER, & M.P. ZALUCKI. 2008. Significance of a new field oviposition record for *Graphium eurypylus* (Lepidoptera: Papilionidae) on *Michelia champaca* (Magnoliaceae). Austral. J. Entomol. 47:58–63.

LI, W., R.A. PETERSON, M.A. SCHULER, & M.R. BERENBAUM. 2001. CYP6B cytochrome P450 monooxygenases from *Papilio canadensis* and *Papilio glaucus*; potential contributions of sequence divergence to host plant associations. Insect Molec. Biol. 11:543–551.

——, R.A. PETERSON, M.A. SCHULER, & M.R. BERENBAUM. 2003. Diversification of furanocoumarin-metabolizing cytochrome P-450 monooxygenases in two papilionids: specificity and substrate encounter rate. Proc. Nat. Acad. Sci. (USA) 100 (supplement 2), 14593-14598.

——, J. BAUDRY, M.R. BERENBAUM, & M.A. SCHULER. 2004. Structural and functional divergence of insect CYP6B proteins: from specialist to generalist cytochrome P450. Proc. Nat. Acad. Sci. (USA) 101: 2939–2944.

MA, W.W., J.E. ANDERSON, C.J. CHANG, D.L. SMITH, & J.L. MCLAUGHLIN. 1989. Majorenolide and majorynolide a new pair of cytotoxic and pesticidal alkene- alkyne δ-lactones from *Persea major*. J. Natur. Prod. 52: 1263–1266.

MAKITA, H.T., K. SHINKAWA, K. KONDO, L. XING, & T. NAZAZAWA. 2003. Phylogeny of the *Graphium* butterflies inferred from nuclear 28S rDNA and mitochondrial ND5 gene sequences. Trans. Lepid. Soc. Japan 54: 91–110.

MAO, W., M.A. SCHULER, & M.R. BERENBAUM. 2007. Cytochrome P450s in *Papilio multicaudatus* and the transition from oligophagy to polyphagy in the Papilionidae. Insect Molecular Biology 16: 481–490.

MERCADER, R. & J.M. SCRIBER. 2005. Phenotypic plasticity in polyphagous *Papilio*: preferences, performances, and potential enhancement by hybridization. Pp. 25–57 *In*; T.N. Ananthakrish-

nan (ed.), Insect Phenotypic Plasticity; Diversity of Responses. Science Publ. Plymouth, UK.

—— & J.M.SCRIBER. 2007. Diversification of host use in two polyphagous butterflies: differences in oviposition specificity or host rank hierarchy? Entomol. Exp. et Appl. 129:89–101.

MILLER, J.S. 1987. Host-plant relationships in the Papilionidae (Lepidoptera): parallel cladogenesis or colonization? Cladistics 3: 105–120.

MUNROE, E. 1961. The classification of the Papilionidae (Lepidoptera). Can. Entom. (Suppl.) 7: 1–51.

MURPHY, S.M. 2004. Enemy-free space maintains swallowtail butterfly host shift. Proc. Nat. Acad. Sci. USA 101: 18048–18052.

MORRIS, M.W. 1989. *Papilio troilus* L. on a new and rare larval foodplant. J. Lepid. Soc. 43: 147.

NISHIDA, R. 1995. Oviposition stimulants of swallowtail butterflies. Pp. 17–26 *In*; J.M. Scriber, Y.Tsubaki, & R.C.Lederhouse (eds.), Swallowtail Butterflies; Their Ecology and Evolutionary Biology. Scientific Publ, Gainesville, FL.

NITAO, J.K. 1995. Evolutionary stability of swallowtail adaptations to plant toxins. Pp 39–52 *In*; J.M. Scriber, Y.Tsubaki, & R.C.Lederhouse (eds.), Swallowtail Butterflies; Their Ecology and Evolutionary Biology. Scientific Publ, Gainesville, FL.

——, M.P. AYRES, R.C. LEDERHOUSE, & J.M. SCRIBER. 1991. Larval adaptation to lauraceous hosts: geographic divergence in the spicebush swallowtail butterfly. Ecology 72: 1428–1435.

——, K.S. JOHNSON, J.M. SCRIBER, &. M.G. NAIR. 1992. *Magnolia virginiana* neolignin compounds as chemical barriers to swallowtail butterfly host use. J. Chem. Ecol. 18: 1661–1671.

POWELL, G., J. HARDIE, & J. PICKETT. 1995. Responses of *Myzus persicae* to the repellent polygodial in choice and no-choice video assays with young and mature leaf tissue. Entomol. Exp. et Appl. 74: 91–94.

RAVEN, P.H. & D.I. AXELROD. 1974. Angiosperm biogeography and past continental movement. Ann. Missouri Bot. Gard. 61: 539–673.

READ, C. & R. MENARY. 2000. Analysis of the contents of oil cells in *Tasmannia lanceolata* (Poir.) A.C. Smith (Winteraceae). Ann. Botany 86: 1193–1197.

SCRIBER, J.M. 1984a. Larval food plant utilization by the world Papilionidae (Lep.): latitudinal gradients reappraised. Tokurana (Acta Rhopalocerologica) 6/7: 1–50.

——. 1984b. Host plant suitability. Pp. 159–202 *In*; W.J. Bell & R.T. Carde (eds.), Chemical Ecology of Insects, Sinauer, Sunderland, MA.

——. 1986. Origins of the regional feeding abilities in the tiger swallowtail butterfly: ecological monophagy and the *Papilio glaucus australis* subspecies in Florida. Oecologia 71: 94–103.

——. 1988. Tale of the tiger: Beringial biogeography, bionomial classification, and breakfast choices in the *Papilio glaucus* complex of butterflies. Pp. 240–301 *In*; K.C. Spencer (ed.), Chemical Mediation of Coevolution, Academic Press. NY.

——. 1993. Absence of behavioral induction in oviposition preference of *Papilio glaucus* (Lepidoptera: Papilionidae). Great Lakes Entomol. 26: 81–95.

——. 1995. Overview of swallowtail butterflies: taxonomic and distributional latitude. Pp. 3–8 *In*; J.M. Scriber, Y. Tsubaki, & R.C. Lederhouse (eds.), Swallowtail Butterflies; Their Ecology and Evolutionary Biology, Scientific Publishers, Gainesville, FL.

——. 1996. A new cold pocket hypothesis to explain local host preference shifts in *Papilio canadensis*. Entomol. exp. & appl. 80: 315–319.

——. 2002a. The evolution of insect-plant relationships; chemical constraints, coadaptation and concordance of insect/plant traits. Entomol. Exp. et Appl. 104: 217–235.

——. 2002b. Latitudinal and local geographic mosaics in host plant preferences as shaped by thermal units and voltinism. European J. Entomol. 99: 225–39.

——. 2005. A mini-review of the "feeding specialization/physiological efficiency" hypothesis: 50 years of difficulties, and strong support from the North American Lauraceae-specialist, *Papilio troilus* (Papilionidae: Lepidoptera). Trends in Entomology 4: 1–42.

—— & P. FEENY. 1979. Growth of herbivorous caterpillars in relation to feeding specialization and to the growth form of their foodplants. Ecology 60: 829–850.

—— & R.C. LEDERHOUSE. 1992. The thermal environment as a resource dictating geographic patterns of feeding specialization of insect herbivores. Pp. 429–466 *In*; M.R. Hunter, T. Ohgushi & P.W. Price (eds.), Effects of Resource Distribution on Animal-plant Interactions, Academic Press, New York, NY.

——, R.C. LEDERHOUSE, & L. CONTARDO. 1975. Spicebush, *Lindera benzoin* (L.), a little known foodplant of *Papilio glaucus* (Papilionidae). J. Lepid. Soc. 29: 10–14.

——, R.C. LEDERHOUSE, & R.DOWELL. 1995. Hybridization studies with North American swallowtails. Pp. 269–282 *In*; J.M. Scriber, Y. Tsubaki, & R.C. Lederhouse, (eds.), The Swallowtail Butterflies: Their Ecology and Evolutionary Biology. Scientific Publishers, Inc., Gainesville, FL.

——, R.C. Lederhouse, & K. Brown. 1991a. Hybridization of Brazilian *Papilio* (*Pyrrhosticta*) (Section V) with North American *Papilio* (*Pterourus*) (Section III). J. Res. Lepid. 29: 21–32.

——, R.C. LEDERHOUSE, & R.H. HAGEN. 1991b. Foodplants and evolution within the *Papilio glaucus* and *Papilio troilus* species groups (Lepidoptera: Papilionidae). Pp 341– 373 *In*; P.W. Price, T.M. Lewinsohn, G.W. Fernandes, & W.W. Benson (eds.), Plant-animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions. Wiley, NY.

——, M.L. LARSEN, & M.P. ZALUCKI. 2007. *Papilio aegeus* Donovan (Lepidoptera; Papilionidae) host plant range evaluated experimentally on ancient Angiosperms. Austral. J. Entomol. 46: 65–74.

—— & N. Margraf. 2005 (2003). Suitability of Florida redbay (*Persea borbonia*) and silk bay (*Persea humilis*) for the *Papilio palamedes* butterfly larvae. Holarct. Lepidopt. 8: 49– 51.

——, N. Margraf, & T. Wells. 2001. Suitability of four families of Florida "bay" species for *Papilio palamedes* and *P. glaucus* (Papilionidae). J. Lepid. Soc. 54, 131–136.

——, M.L. LARSEN, G.R. ALLEN, P.W. WALKER, & M.P. ZALUCKI. 2008a. Interactions between Papilionidae and ancient Australian angiosperms: evolutionary specialization or ecological monophagy? Entomol. Exp. et Appl. (SIP-13 conf. issue).

——, G.J. ORDING, AND R.J. MERCADER. 2008b. Hybrid introgression and parapatric speciation in a hybrid zone. Pp. 69–87 *In*; K.J. Tilmon (ed.), Specialization, Speciation, and Radiation: the Evolutionary Biology of Herbivorous Insects. Univ. California Press.

——, G.R. ALLEN, & P.W. WALKER. 2006. Ecological monophagy in Tasmanian *Graphium macleayanum moggana* and evolutionary reflections of ancient Angiosperm hosts. Insect Science 13: 325–334.

SOLTIS, P.S., P.K. ENDRESS, M.W. CHASE, AND D.E. SOLTIS. 2005. Phylogeny of the Angiosperms. Sinauer Assoc. MA. 370pp.

SPERLING, F.A.H. 2003. Butterfly molecular systematics: from species definitions to higher level phylogenies. Pp. 431–458 *In*; C.L. Boggs, W.B. Watt, & P.R. Ehrlich (eds.), Butterflies: Ecology and Evolution Taking Flight, Univ. Chicago Press, IL.

THOMPSON, J.N. 1995. The origins of host shifts in swallowtail butterflies versus other insects. Pp 195–203 *In*; J.M. Scriber, Y. Tsubaki, & R.C.Lederhouse (eds.), Swallowtail Butterflies; Their Ecology and Evolutionary Biology. Scientific Publ, Gainesville, FL.

ZAKHAROV, E., M.S. CATERINO, & F.A.H. SPERLING. 2004. Molecular phylogeny, historical biogeography, and divergence time estimates for swallowtail butterflies of the genus *Papilio* (Lepidoptera: Papilionidae). Syst. Biol. 53, 193–215.

ZALUCKI, M.P, A.R. CLARKE, & S.B. MALCOLM. 2002. Ecology and behavior of first instar larval Lepidoptera. Ann. Rev. Entomol. 47:361–393.

Received for publication 21 June 2007; revised and accepted 5 December 2007.

Journal of the Lepidopterists' Society
62(1), 2008, 31–35

A NEW SPECIES OF *ZEIRAPHERA* TREITSCHKE (TORTRICIDAE)

CLIFFORD D. FERRIS

5405 Bill Nye Ave., R.R. 3, Laramie, WY 82070, USA, cdferris@uwyo.edu
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.

AND

JAMES J. KRUSE

Interior Alaska Forest Entomologist, USDA Forest Service, State and Private Forestry, Forest Health Protection, Fairbanks Unit, 3700 Airport Way, Fairbanks, Alaska 99709, USA.

ABSTRACT. *Zeiraphera unfortunana* Ferris and Kruse is described from ninety specimens from Canada (type locality: Black Sturgeon Lake, Ontario) and Alaska with illustrations of the adults and genitalia. This species ranges from Nova Scotia to British Columbia, Yukon Territory, and Alaska into northern portions of the United States.

Additional key words: Alaska, Canada, taxonomy, Tortricidae, *Zeiraphera unfortunana*

The purpose of this article is to resolve a long-standing issue of nomenclature. What Mutuura and Freeman (1966) illustrated as *Zeiraphera destitutana* (Walker) in their review of the genus was recognized by Powell (1983; p. 35, entry 3242) as an undescribed species, for which he proposed the name *unfortunana*. Unfortunately this name is a *nomen nudum* because a description, diagnosis, and type designation were not provided (Brown, 2005, note 32, page 741). With Powell's agreement (pers. comm.), we herein correct this situation and provide the documentation required to make this name available in accordance with the International Code of Zoological Nomenclature. We initially proposed a different name, but after checking the numerous Internet citations for *unfortunana*, it became clear that additional confusion would result.

Some initial discussion of forewing maculation is appropriate. Nijhout (1978) formulated a model for wing pattern formation in Lepidoptera, with subsequent elaboration (Nijhout 1991, in Kristensen, 2003). His concepts were applied to the tortricid genera *Epiblema* Hübner by Brown & Powell (1991), and to *Argyoploce* Hübner by Baixeras (2002). *Epiblema* and *Zeiraphera* are assigned to the subfamily Olethreutinae tribe Eucosmini, while Argyroploce is placed in tribe Olethreutini. Several wing pattern definitions applied to and used in discussions of the Tortricidae are: fascia(e), the dark bands or areas in the pattern; strigula(e), the small pale transverse markings distributed along the costa and termen and situated between the veins; stria(e), lines or narrow bands that extend from the costal strigulae toward either the inner or outer wing margin. Strigulae may occur in pairs or fused into a singular strigula; they denote the margins of fasciae. Strigulae may manifest substantial variation (plasticity) within a given species and even relative to the left and right wings of a single specimen. Expanded treatments of these pattern elements appear in Brown & Powell (1991, pp. 108–109) and Baixeras (2002, p. 425).

The habitus of many North American *Zeiraphera* tends to be "muddy" projecting a diffuse mottling of grays and browns with the strigulae poorly defined and obscure (especially in even only slightly worn specimens), and the edges of the fasciae indistinct. For this reason, we have not attempted to show the positions of all of the strigulae in *Zeiraphera*. For purposes of the current discussion, we recognize three principal fasciae in *Zeiraphera*, shown in Fig. 1 as F1 (subbasal fascia), F2 (median fascia), F3 (subapical fascia), with associated borders b1 – b4. F1 and F2 are transverse bands, while F3 is a spot of varying size and shape. The position of b1 is variable across species and within a given species. It may be close to b2, or extend nearly to the base. The feature p is a distal projection from b2 that may be acute (as shown) or blunt. In some instances, p may touch b3. Interfascial areas are paler, reflecting the wing ground color. The lightly shaded area R represents a pale interfascial spot that may or may not be present.

Fig. 2 illustrates the forewing venation in *Zeiraphera*, obtained by photographing (using back lighting) the wing after placing it on a glass side and saturating it with 95% isopropanol to expose the veins. The veins on the resulting print were then traced in black ink, and the tracing scanned to produce the final digital image.

Here we offer some observations relative to the genus

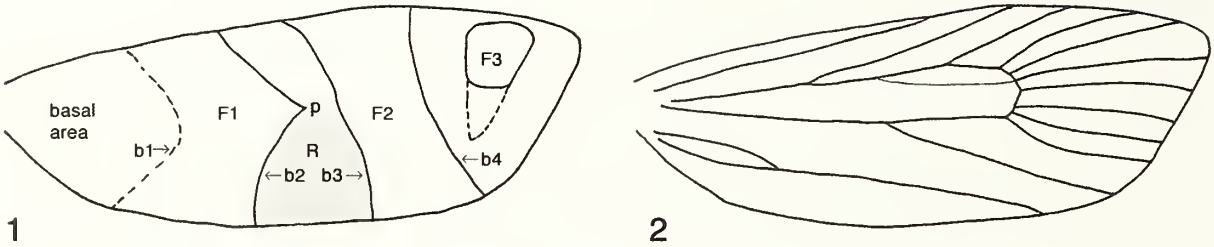


FIG. 1–2. (**1**) Wing plan adopted for this article showing principal fasciae. (**2**) Forewing venation in *Zeiraphera unfortunana*; female specimen from Porcupine Creek, Alaska (ex-pupa on *Picea glauca*).

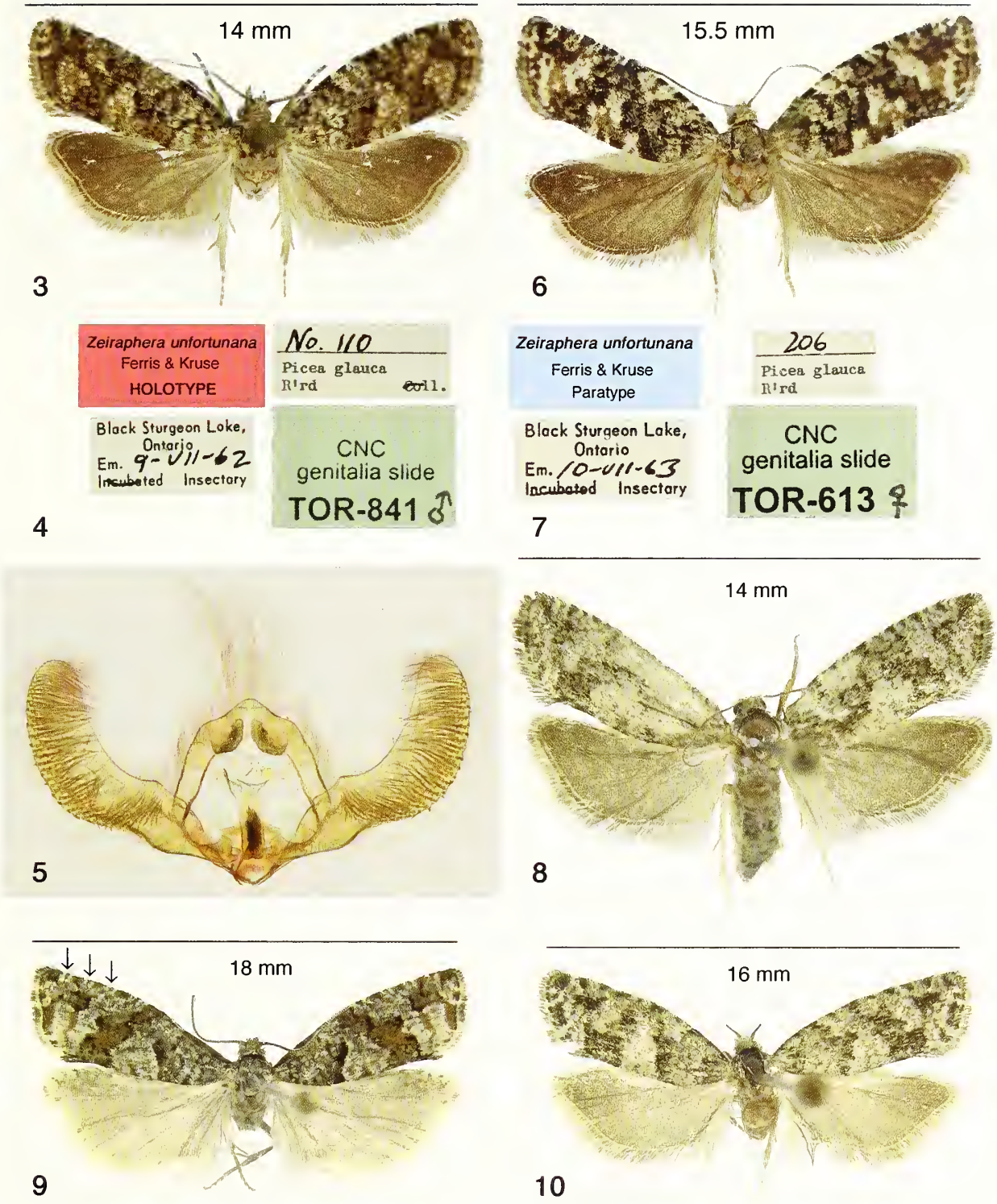
in North America based on our own data, the literature cited, and various Internet sites. There are eight additional currently known species: *canadensis* Mutuura & Freeman; *claypoleana* (Riley); *fortunana* (Kearfott); *griseana* (Hübner) [we have specimens from the Fairbanks area, Alaska]; *hesperiana* Mutuura & Freeman; *improbana* (Walker); *pacifica* Freeman; *vancouverana* McDunnough. Eight species use conifers as larval hosts, while *claypoleana* uses *Aesculus glabra* Willdenow (Horse Chestnut, Ohio Buckeye). Adult maculation separates these species into three groups consisting of *claypoleana*, those that are generally not contrastingly marked or "muddy" in appearance (*griseana, hesperiana, improbana, pacifica, vancouverana*), and those that are normally contrastingly marked (*canadensis, fortunana, unfortunana*). When known, larval hosts can serve to separate some species. *Larix* is the primary larval host of *griseana* (Razowski, 2003) and *improbana*, while *Picea sitchensis* (Bong.) Carr. is preferred by *pacifica* and *vancouverana*, and *Pseudotsuga menziesii* (Mirbel) Franco is used by *hesperiana*. The remaining species use *Picea glauca* (Moench) Voss among other hosts. The wing pattern of Z. *claypoleana* differs from the general plan illustrated in Fig. 1 in that there is usually a broad band extending across the lower third of the forewing from the base nearly to the tornus. This band may be dark, pale, or mottled. When present, the fasciae F1 and F2 are poorly defined. In all species, the females generally exhibit more contrasted maculation than the males.

Zeiraphera unfortunana Ferris and Kruse, **new species**
(Figs. 2–13)

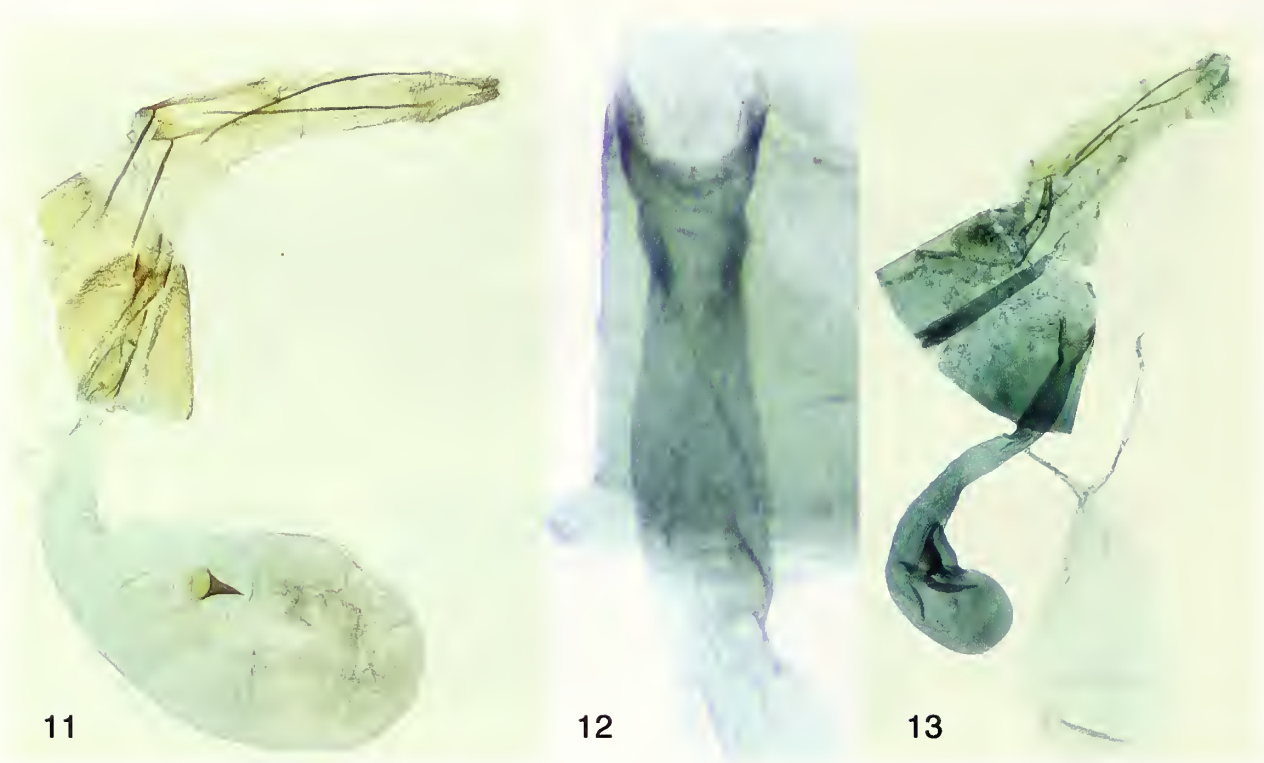
Zeiraphera unfortunana Powell, 1983, *nomen nudum*
Zeiraphera destitutana Mutuura & Freeman, 1966, not Walker
Zeiraphera unfortunana Miller, 1987

Diagnosis. *Zeiraphera unfortunana* is most likely to be confused with Z. *canadensis* and *fortunana*. Z. *unfortunana* has a checkered mosaic pattern (females especially) that is the most color contrasted pattern of the three species. Separation features are (with reference to Fig. 1): ground color of the interfasciac in *unfortunana* is white, ochreous in *canadensis*, pale gray or tan in *fortunana*, except b2–b3 white. F1 – F3 are medium brown (dark brown in some females); brownish-black in *canadensis* and *fortunana*. In F1 of *unfortunana* b1 is irregular, smeared, often extending to the base, and p is blunt; in *canadensis* F1 is generally narrow (especially toward costa) and often more darkly shaded along b2, and p is acute; in *fortunana* F1 may be rather poorly defined with a "blotchy" aspect, and p is blunt. F2 is slightly constricted midway and may be poorly defined above mid-wing; F2 in *canadensis* and *unfortunana* is usually well expressed, sometimes paling in color in *canadensis* toward the costa. F3 in *canadensis* is large and produced toward the tornus; small and restricted to apical region in *fortunana*; large, brown and irregular in *unfortunana* usually with a prominent irregular orange-brown vertical bar extending from the lower edge toward the tornus in the interfascial region. In *fortunana* the margins b2 and b3 are roughly parallel with R rectangular; R is approximately triangular in *canadensis* and *unfortunana*. In *canadensis*, R is pale brownish-tan speckled with brownish scales; in *unfortunana* R is white speckled (heavily in some males) with brown and ochreous scales. The uncus in male *canadensis* is well developed and triangular; in *fortunana* it is reduced and truncated with a slightly notched apex; in *unfortunana* it is poorly developed with an entire (unnotched) apex.

Description. MALE (Fig. 3). *Head*. Frons and vertex with a mixture of grayish-white and brown scales; palpi pale grayish-white inwardly, outwardly mostly brown, slightly longer than eye width; ocellus present. Antenna brown with narrow darker brown band at distal end of each segment. *Thorax*. Brown scales dorsad, whitish ventrad. *Legs*. Prothoracic and mesothoracic legs with mottled appearance produced by dark brown and paler scales, not clearly ringed or checkered; hind legs pale whitish-tan and unmarked. *Abdomen*. Appears brown, but clothed with a mixture of brown and paler gray scales. *Wings*. Expanse 14–17 mm, n = 17 (FW length of holotype 6.5 mm). Forewings very mottled in aspect with brown, pale brown, and pale gray to grayish-white scales; mottled brown basal area extending distad to darker brown subbasal fascia F1, with P blunt;



FIGS. 3–10. *Zeiraphera unfortunana* Ferris and Kruse: **3,** holotype male; **4,** male pin labels; **5,** genitalia of holotype; **6,** paratype female; **7,** female pin labels; **8-10,** female specimens from interior Alaska; arrows in 9 point to strigulae.



FIGS. 11–13. *Zeiraphera unfortunana* female genitalia of Alaskan specimens: **11,** Fairbanks area; **12-13,** Porcupine Creek; **12,** sterigma and ductus bursae; **13,** complete genitalia showing large bursa seminalis.

irregular paler mottled median triangular patch (dorsal patch R) extends from inner margin with blunt apex at mid-wing; median fascia F2 mottled brown band followed by a paler irregular broad interfascial area with included narrower vertical orange-brown band; F3 brown; segmented dark brown terminal line; fringe dark grayish-brown scales, fading at tips. Hindwing uniformly brownish-fuscous with narrow whitish outer-margin line, then brown line at base of fringe; fringe slightly paler than wing. Wings ventrally fuscous; hindwings paler than forewings. *Genitalia* (Fig. 5; 17 dissections, CNC slides nos. TOR-613, 616, 620, 621, 680–682, 821–823, 825–827, 829–832, 841). Uncus poorly developed but entire; tegumen round shouldered; cucullus broad, apically rounded; number of cornuti variable from approximately 24–40 spines. FEMALE (Figs. 6, 8–13). Similar to male in most respects, but dorsal forewing maculation dark and pale areas more contrasted; interfascial area ground color white. *Genitalia.* (Figs. 11–13; 17 dissections, CNC slides nos. TOR-617–619, 622, 676–679, 683–685, 824, 828; 3 Alaska specimens by Ferris). Papillae anales setose elongated ovals; apophyses long and slender (anterior to posterior ratio ca. 0.5); ostium bursae moderately sclerotized, ductus bursae lightly sclerotized from ostium to just above junction with ductus seminalis, incomplete colliculum (sterigma ring) (Fig. 12); corpus bursae elongate with one prominent conical signum (Fig. 11); large bursa seminalis (Figs. 13).

Types. Although ninety specimens were examined, because of the confusion surrounding this moth, we have selected for the type series only reared specimens that have been dissected for genitalic examination as follows: a typical male (*holotype*) and 16 male and 14 female *paratypes* from the type locality from a reared series of *unfortunana* in the Canadian National Collection of Insects, Arachnids and Nematodes (CNC), Ottawa, Ontario, Canada. The type locality is the collection site for specimens illustrated (adults and genitalia) by Mutuura and Freeman (1966, Figs. 16–17, 31, 42) as "destitutana." The holotype male and paratypes are placed in the CNC, Ottawa, Ontario, Canada. *Type locality.* Black Sturgeon Lake, Ontario, Canada.

Variation (n = 90, Alaska and Canada). Dorsal forewing maculation is rather variable in pattern and coloration, and no two individuals were identical in the material examined. Wild caught specimens (Figs. 8–10) have a more subdued aspect from reared material (Figs. 3, 6).

Biology and distribution. Although we know of no print publications that describe the biology, there are numerous Internet sites that provide information with descriptions and photographs of the mature larvae, two of which are Forest Pests (www.forestpests.org) and Natural Resources Canada, Canadian Forest Service (search *Zeiraphera unfortunana*/purple-striped shootworm). The principal larval host is *Picea glauca* (white spruce), but other hosts reported in the literature include *P. englemanni* Parry, *P. stichensis* (Bong.) Carr., *Abies balsamea* (L.) Mill., *A. lasiocarpa* (Hook.) Nutt., and *A. amabilis* (Dougl.) Forbes. There is one generation with last instar larvae from May to July, and adults from July into early August. The over wintering egg is laid near the base of new growth shoots. This species ranges from Nova Scotia to British Columbia, Yukon Territory, and Alaska; also Michigan and Minnesota (Miller, 1987). Internet sites imply occurrence in the northeastern United States, but no specific localities were found. To date, we have seen

only female specimens from Alaska, where collection localities include Chena Ridge above Fairbanks, Sterling (Kenai Peninsula), and Porcupine Butte in south-central Alaska, 61.9317°N, 151.9886°W (NAD83/WGS84) (ex-pupa on *Picea glauca*).

ACKNOWLEDGEMENTS

We thank James T. Troubridge and Jocelyn Gill, Agriculture and Agri-Food Canada (CNC), Ottawa, Ontario, Canada for supplying digital photographs of moths, labels, and genitalia. K. W. Philip, Fairbanks, Alaska, Dominique Collet, Sterling, Alaska, and Ken Zogas, Alaska Reference Collection System, USDAFS Anchorage kindly provided material for examination. John W. Brown, National Museum of Natural History, Washington, DC graciously reviewed a preliminary draft of the manuscript prior to submission. William E. Miller and an anonymous reviewer provided helpful suggestions. This study was supported in part by USDA Chugach National Forest, Anchorage, Alaska (order no. 43-0120-4-0140).

LITERATURE CITED

BAIXERAS, J. 2002. An overview of genus-level taxonomic problems surrounding *Argyroploce* Hübner (Lepidoptera: Tortricidae), with description of a new species. Ann. Entomol. Soc. Am. 95(4):422–431.

BROWN, J.W. 2005. World catalogue of insects, volume 5, Tortricidae (Lepidoptera), Stenstrup, Denmark. 741 pp.

BROWN, R.L. & J.A. POWELL. 1991. Description of a new species of *Epiblema* (Lepidoptera: Tortricidae: Olethreutinae) from coastal redwood forests in California with analysis of the forewing pattern. Pan-Pacif. Entomol. 67(2):107–114.

KRISTENSEN, N.P. (vol. ed). 2003. Handbook of zoology Vol. 4, Part 36. de Gruyter., Berlin. xii + 564 pp.

MILLER, W.E. 1987. Guide to the Olethreutine moths of midland North America (Tortricidae). USDA, Forest Service, Agriculture Handbook 660.

MUTUURA, A. & T.N. FREEMAN. 1966. The North American species of the genus *Zeiraphera*. J. Res. Lepid. 5(3):153–176.

NIJHOUT, H.F. 1978. Wing pattern formation in Lepidoptera: a model. J. Exp. Zool. 206:119–136.

_____. 1991. The development and evolution of butterfly wing patterns. Smithsonian Institution Press, Washington and London. xvi + 297 pp.

POWELL, J.A. 1983 IN HODGES, R. W., et al., (Eds.). Check list of the Lepidoptera of America north of Mexico. E. W. Classey, Ltd. and the Wedge Entomological Research Foundation, London. xxiv + 284 pp.

RAZOWSKI, J. 2003. Tortricidae of Europe, Volume 2, Olethreutinae. Bratislava. 301 pp.

Received for publication 8 June 2007; revised and accepted 28 September 2007.

Journal of the Lepidopterists' Society
62(1), 2008, 36–39

HESPERIIDAE OF RONDÔNIA, BRAZIL: A NEW GENUS AND SPECIES OF PYRGINAE

GEORGE T. AUSTIN

McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History,
University of Florida, P.O. Box 112710, Gainesville, Florida 32611

ABSTRACT. A pyrgine skipper from Rondônia, Brazil, is described from two males. This species, with secondary sex characters including a shiny area on the ventral forewing overlaying a pronounced hump on the hindwing costa, is named *Speculum speculum* **gen. nov.** and **sp. nov.** Its affinities, although not yet certain, may be with the tribe Erynnini.

Additional key words: *Ectomis*, genitalia, *Telemiades*, *Tosta*, tropical rainforest.

Investigations of butterflies in Rondônia, Brazil, have indicated that the region has a megarich fauna of these insects (Brown 1984, 1996; Emmel & Austin 1990; Austin *et al.*, in press). The site, with typical lowland tropical rainforest (Emmel & Austin 1990, Emmel *et al.*, in press), has a distinctly seasonal climate with a pronounced dry season from May through September. Within the fauna of the region, there appear numerous new taxa, especially among the family Hesperiidae (e.g., Austin 1993, 1995, 1996; Austin & Steinhauser 1996; Austin & Mielke 1997, 2000; Austin *et al.* 1997). A new genus and species of hesperiid in subfamily Pyrginae was identified and is here described from the vicinity of Cacaulândia. Forewing length was measured from base to apex. Terminology for structures of the genitalia follows that used by Austin & Mielke (1997).

Speculum Austin, **new genus**
(Figs. 1–3)

Type species: *Speculum speculum* Austin, 2008

Description. MALE. *Forewing* (Figs. 1–2): Narrow costal fold about 1/2 length of costa, interior scales whitish; costa slightly bent caudad at distal end of fold and then slightly convex to pointed apex; termen slightly convex; anal margin nearly straight distad, slightly convex on basal half; discal cell about 2/3 costal length, produced anteriorly; vein CuA_2 originating much nearer CuA_1 than wing base, vein Sc ending on costa far short of distal end of discal cell, vein R_1 ending at costa opposite end of discal cell; ventral forewing with broad, shining gray speculum covering about basal 2/5 from anterior edge of discal cell to anal margin where extended distad about 1/2 distance to tornus; oval brown brand in speculum and about 1/2 its width, situated above to slightly below lower discal cell vein, centered slightly distad of midpoint of wing base and origin of CuA^2; tuft of dark bristle-like scales originating from posterior base of brand.

Hindwing (Figs. 1–2): Costa highly modified basad, produced as hump far cephalad to cover forewing speculum, upper surface of produced portion also shining gray; distal costa slightly convex to sharply produced apex exceeding length of forewing anal margin; termen slightly convex cephalad, slightly concave caudad to inconspicuous, slightly produced, but broad tornal lobe; dorsum of cell 2A–3A with thick and moderately long hair-like scales, this area broadening with cell width distad, nearly reaching tornus; ventral surface of this cell as funnel-like trough.

Palpi: Short, porrect, triangular in dorsal view with parallel third segments protruding about half length of second segments. *Antennae*: Short, slightly less than 1/2 costal length, club arcuate beyond thickest point to apiculus, apiculus relatively long, nudum long and difficult to count but about 33–34 segments. *Legs*: Short, mid-tibia smooth with single outer spur, hind tibia with short, dense hair tuft and two pairs of spurs, outer ones shorter than inner.

Genitalia (Fig. 3): Uncus relatively long, narrow, curved ventrad, narrowly divided; gnathos blunt ended, lightly sclerotized except proximal end, entire; valva blade-like, harpe long with finely dentate dorsal edge and several dentate ridges curving over onto inner surface from outer surface caudad. Aedeagus about length of valva, slightly downcurved in middle, distal end with ventral keel, base of aedeagus short, no cornutus.

FEMALE. Unknown.

Distribution. *Speculum* is known at present only from the vicinity of Cacaulândia in central Rondônia, Brazil.

Fig. 1. *Speculum speculum* holotype (data in text): A. dorsal surface, B. ventral surface.

Etymology. The genus is named after the shining gray areas on the ventral forewing and basal portions of the costa of the dorsal hindwing. *Speculum* is a neuter noun meaning "mirror" in Latin.

Diagnosis and discussion. The affinities of this new and apparently monotypic genus are equivocal. The bend in the costa of the forewing suggests that it is of the tribe Erynnini Brues & Carpenter, 1932 as defined by Warren (2006). Within this tribe, *Tosta* Evans, 1953, includes a species (*Tosta tosta* Evans, 1953) with an expanded costa on the hindwing and a *speculum* on the ventral forewing. *Tosta*, a genus that was suggested as paraphyletic (Warren 2006), differs in several respects from *Speculum*. The seven species now included in *Tosta* (Mielke 2005) have a very short discal cell on the forewing (as nearly universal among Erynnini, Warren 2006), a shorter nudum (21–24 segments), a broad and often divided uncus, and very different valvae. *Tosta tosta* itself (after Evans 1953) has no costal fold, has a brand at the base of the costa of the dorsal hindwing, has no brand within the speculum, and has a hind tibial tuft entering a thoracic pouch. Its genitalia are very different from those of *Speculum* (see figure in Evans 1953). The genitalia of *Speculum*, while possessing elongate valvae as do many Erynnini, are symmetrical unlike most others within the tribe (Warren 2006).

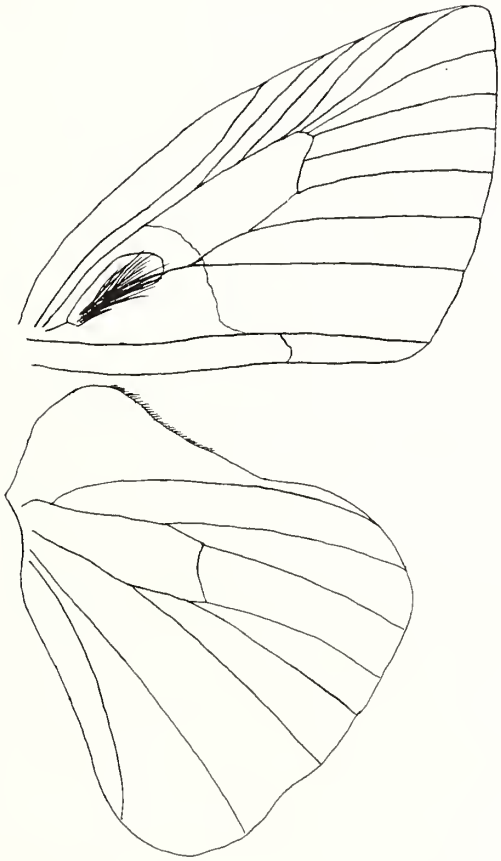


Fig. 2. *Speculum speculum* – wing venation and secondary sexual characters (ventral surface).

Other taxa with prominent specula include *Ectomis* Mabille, 1878 (Eudaminae) represented by a single species *Plesioneura cythna* Hewitson, 1878. On this, the forewing has no costal fold, vein CuA_2 originates at the base of the forewing, vein Sc ends over the end of the discal cell, there is a double hair tuft in front of the *speculum* and no brand, and the antenna has a nudum of 25 segments (Evans 1953). The male genitalia of *Ectomis* have a relatively broad uncus with lateral processes, the end of the gnathos is pointed, and the dorsal ridge of the harpe is not dentate.

Papilio corbulo Stoll 1783, another eudamine and once included in a monotypic genus *Pardalus* Mabille, 1903, has now been subsumed within *Telemiades* Hübner, 1819 (Burns & Janzen 2005). That species has a costal fold similar to *Speculum*, vein CuA_2 arising about 1/2 the distance from the wing base and CuA_1, and a speculum with a brand on the ventral forewing. The speculum on *Telemiades corbulo*, however, is broader, extending 2/3 the distance to the termen, does not extend into the discal cell or above vein CuA_2, and the pale yellowish brand lies above vein 2A. The costa of the hindwing is somewhat produced, but not nearly as grotesquely as on *Speculum*. Additionally, the dorsal hindwing has a large thick hair tuft arising from above the base of the discal cell. The nudum of the antenna has 24–27 segments. The male genitalia are very different from those of *Speculum* with a broad and undivided uncus, two pairs of lateral processes from the tegumen, and a very different harpe. Further, *T. corbulo*, like other *Telemiades*, have cornuti (*e.g.*, Burns & Janzen 2005) that *Speculum* lacks.

Speculum speculum Austin, **new species**
(Figs. 1–3)

Description. MALE. Wings: Forewing length = 21.3 mm (holotype), 20.1 mm (paratype); wing shape and other structural characters given above in description of genus; dorsal surface dark brownish black; basal half of forewing, basal third of hindwing, and vague postmedial bands on both wings darker, nearly black; postmedial of forewing offset distad cephalad of vein M_3, paler areas of wing with slight reddish sheen in side light; fringes of ground color. Venter similar to dorsum; forewing with postmedial band indiscernable; anal margin gray distad of speculum; gray overscaling anterior to this and on hindwing.

Head, thorax and abdomen: Head and body dark brown; head with vague olive-gray scales above palpi; palpi gray-brown on venter; antennae dark brown on dorsum, venter (including nudum) paler gray-brown; legs brown; ventral abdomen whitish-brown with pair of faint brown ventro-lateral lines.

Genitalia: Described above in generic description.

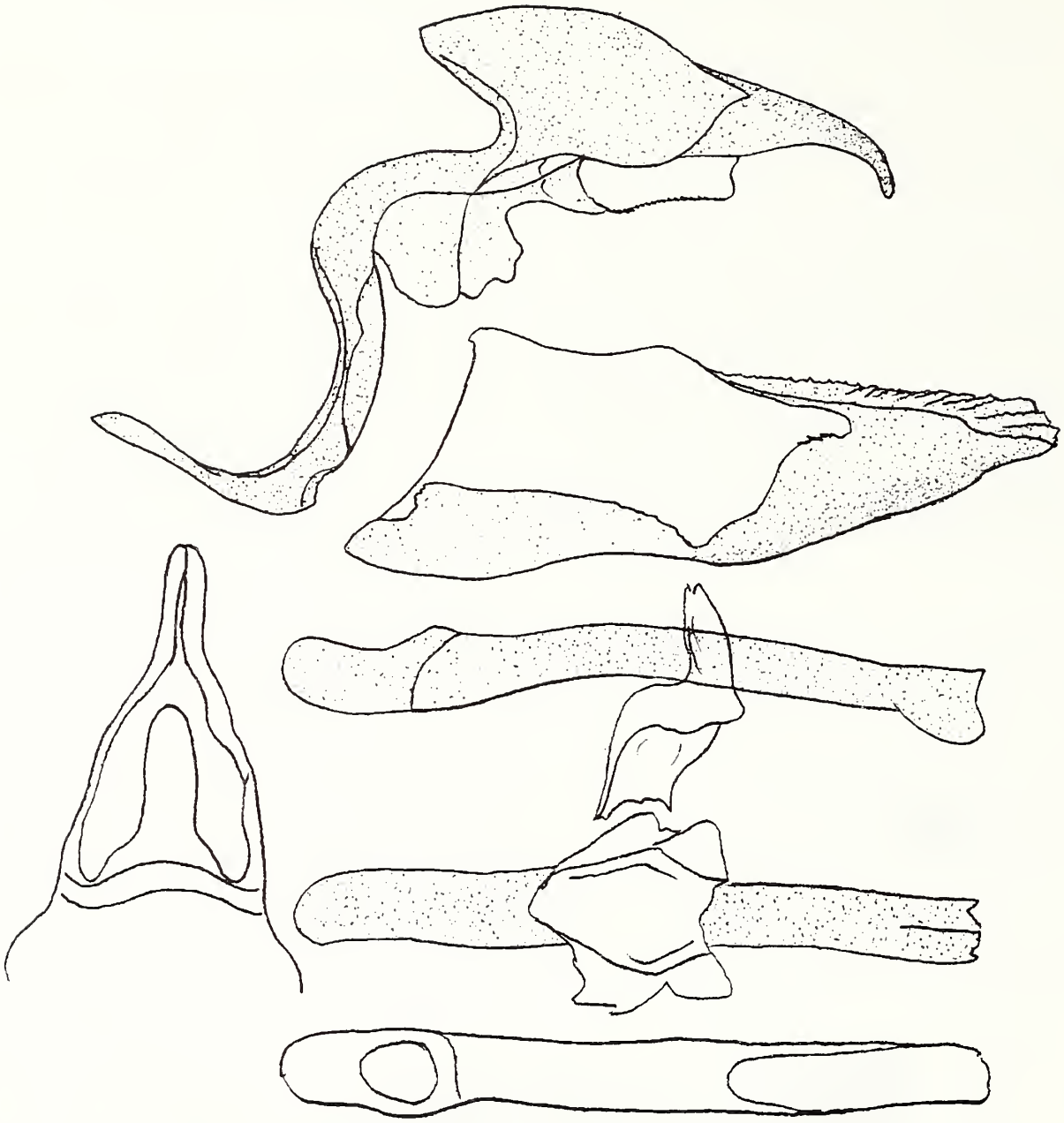


Fig. 3. *Speculum speculum* – genitalia (lateral view of tegumen, saccus, and associated structures; internal lateral view of valva; ventral view of uncus and gnathos; lateral ventral, and dorsal views of aedeagus)

FEMALE. Unknown.

Holotype. Male with the following labels: white, printed - / BRASIL: Rondonia / ca 70 km S / Ariquemes / B-80 between / lineas C-10 & 15 / 1 December 1991 / leg. G. T. Austin / (paper lures) /; white, printed and handprinted - / Genitalia Vial / GTA - 1676 /; white, printed and handprinted - / Genitalia Vial / SRS - 4383 / File No. /; red, printed and handprinted - / HOLOTYPE / *Speculum speculum* / Austin /. The holotype will be deposited at the Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil.

Paratype. BRAZIL: Rondônia; 65 km S Ariquemes, Linha C-20, 7 km E of B-65, Fazenda Rancho Grande, 10 Nov. 1994, at paper lures, 1330-1400 [local time] (1 male, GTA-7522). The paratype is at the McGuire Center for Lepidoptera and Biodiversity.

Type locality. BRAZIL: Rondônia; about 70 kilometers south of Ariquemes, road B-80 between linhas C-10 and C-15, ca. 200 meters elevation. This is approximately 15 km east of Cacaulândia in typical lowland tropical rainforest.

Etymology. The species is named as was its genus (see above).

Distribution and phenology. *Speculum speculum* is known only from its types taken in November and December.

Diagnosis and discussion. Both known specimens of *Speculum* were caught at paper lures indicating that the species is part of the guild that feeds on bird droppings and suggests it will be found associated with army ants (Austin *et al.* 1993, Vieira 2004). As noted above, *Speculum* appears to be allied to species within the tribe Erynnini of Pyrginae. Besides this tentative placement, little further speculation is possible at this time. The examination of a female could go far in elaborating its relationships. Females of most Erynnini have a gland at the seventh tergum (e.g., Burns 1964, de Jong 1975) that appears to be a synapomorphy (Warren 2006).

ACKNOWLEDGEMENTS

I thank V. Becker for making studies in Brazil possible and O.H H. Mielke and S.R. Steinhauser (SRS) for sharing data and knowledge with me. L.D. and J.Y. Miller and A.D. Warren graciously reviewed the manuscript and made helpful suggestions. J.M. Burns and an anonymous reviewer are thanked for suggestions that improved the manuscript. A. Sourakov kindly photographed the type. C. Eliazar is acknowledged for scanning the line drawings. The following supplied field assistance: R. and A. Albright, G. Bongiolo, J.P. Brock, O. Gomes, J.D. Turner, W. Ward, A.D. Warren, and F. and A. West. T.C. Emmel has continuously provided encouragement and support since inception of investigations in Rondônia. The Schmitz family at Fazenda Rancho Grande facilitated field studies in Rondônia by providing comfortable accommodations. The Conselho Nacional de Desenvolvimento Científico e Tecnológico issued the authorization permits from the Ministério da Ciência e Tecnologia for studies in Rondônia in collaboration with EMBRAPA/CPAC and the Universidade Federal do Paraná.

LITERATURE CITED

AUSTIN, G.T. 1993. A review of the *Phanus vitreus* group (Lepidoptera: Hesperiidae: Pyrginae). Trop. Lepid. 4 (suppl. 2):21–36.

_____. 1995. Hesperiidae of Rondônia, Brazil: comments on *Drephalys*, with descriptions of two new species (Lepidoptera: Hesperiidae: Pyrginae). Trop. Lepid. 6:123–128.

_____. 1996. Hesperiidae of central Rondônia, Brazil: three new species of *Narcosius* Steinhauser. J. Lepid. Soc. 50: 53–59.

_____., J.P. BROCK & O.H.H. MIELKE. 1993. Ants, birds, and skippers. Trop. Lepid. 4 (suppl. 2):1–11.

_____., T.C. EMMEL & O.H.H. MIELKE. In press. The tropical rainforest butterfly fauna of Rondônia, Brazil, species composition and richness. Mem. McGuire Center Lepid. Biodiv. 1.

_____. & O.H.H. MIELKE. 1997. Hesperiidae of Rondônia, Brazil: *Aguna* (Pyrginae), with a partial revision and descriptions of new taxa from Mexico, Panama, and Brazil. Revta bras. Zool. 14:889–965.

_____. & O.H.H. MIELKE. 2000. Hesperiidae of Rondônia, Brazil: *Cephise* Evans (Pyrginae), with descriptions of new species from Mexico and Brazil. Revta bras. Zool. 17:757–788.

_____. & S.R. STEINHAUSER. 1996. Hesperiidae of central Rondônia Brazil: *Celaenorrhinus* Hübner (Pyrginae), with descriptions of three new species and taxonomic comments. Insecta Mundi 10:25–44.

_____., O.H.H. MIELKE & S.R. STEINHAUSER. 1997. Hesperiidae of central Rondônia Brazil: *Entheus* Hübner, with descriptions of four new species (Lepidoptera: Pyrginae). Trop. Lepid. 8:5–18.

BROWN, K.S., JR. 1984. Species diversity and abundance in Jaru, Rondonia (Brazil). News Lepid. Soc. 1984(3):45–47.

_____. 1996. Diversity of Brazilian Lepidoptera: history of study, methods for measurement, and use as indicator for genetic, specific and system richness. Pp. 221–253. *In* C. E. M. Bicudo and N. A. Menezes (eds.), Biodiversity in Brazil: A First Approach. Proceedings Workshop Methods for the Assessment of Biodiversity in Plants and Animals. São Paulo: Instituto de Botanica/CNPq.

BURNS, J.M. 1964. Evolution in skipper butterflies of the genus *Erynnis*. Univ. Calif. Publ. Ent. 37:1–214.

_____. & D.H. JANZEN. 2005. What's in a name? Lepidoptera: Hesperiidae: Pyrginae: *Telemiades* Hübner 1819 [*Pyrdalus* Mabille 1903]: new combinations *Telemiades corbulo* (Stoll) and *Telemiades oiclus* (Mabille) – and more. Proc. Ent. Soc. Wash. 107:770–781.

DE JONG, R. 1975. An abdominal scent organ in some female Pyrginae. Ent. Ber. 35:166–169.

EMMEL, T.C. & G.T. AUSTIN. 1990. The tropical rainforest butterfly fauna of Rondonia, Brazil: species diversity and conservation. Trop. Lepid. 1:1–12.

_____., G.T. AUSTIN & H.H. SCHMITZ. In press. The tropical rainforest butterfly fauna of Rondônia, Brazil: current status of investigations and conservation. Mem. McGuire Center Lepid. Biodiv. 1.

EVANS, W.H. 1953. A catalogue of the American Hesperiidae in the British Museum (Natural History). Part III (groups E, F, G) Pyrginae. Section 2. London: British Museum (Natural History). 246pp.

MIELKE, O.H.H. 2005. Catalogue of the American Hesperioidea: Hesperiidae (Lepidoptera). Volume 3, Pyrginae 2: Pyrgini. Curitiba: Soc. Bras. Zool. pp. 413–771.

VIEIRA, R.S. 2004. Efeito da fragmentação florestal sobre borboletas (Lepidoptera, Hesperiidae) associadas à formiga-de-correição *Eciton burchelli* (Hymenoptera, Formicidae, Ecitoninae). Tese (Doutorado), Universidade Federal de São Carlos, São Paulo, Brazil. 166pp.

WARREN, A.D. 2006. The higher classification of Hesperiidae (Lepidoptera: Hesperioidea). PhD Dissertation, Oregon State Univ., Corvallis. 458pp.

Received for publication 20 June 2007; revised and accepted 4 December 2007.

Journal of the Lepidopterists' Society
62(1), 2008, 40–51

EARLY STAGES OF *MIRACAVIRA BRILLIANS* (BARNES) AND REASSIGNMENT OF THE GENUS TO THE AMPHIPYRINAE: PSAPHIDINI: FERALIINA (NOCTUIDAE)

DAVID L. WAGNER
Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269; email: david.wagner@uconn.edu

J. DONALD LAFONTAINE
Agriculture & Agri-Food Canada, Neatby Bldg., C.E.F., 960 Carling Avenue, Ottawa, ON K1A 0C6, Canada.

NOEL MCFARLAND
PO Box 277, Hereford, AZ 85615

AND

BRYAN A. CONNOLLY
Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269

ABSTRACT. The egg, larva, pupa, and male genitalia of *Miracavira brillians* (Barnes) are described and illustrated, and observations are provided on the insect's life history and larval biology. *Miracavira brillians* is transferred from the Acronictinae to the Amphipyrinae: Psaphidini: Feraliina based on numerous larval, pupal, and adult characters. Both larval and adult features support our arguments that the Amphipyrinae and Psaphidinae are synonyms.

Additional key words: *Amphipyra*, *Apsaphida*, *Feralia*, *Paratrachea*, *Viridemas*, *Ptelea*, countershading, non-resemblance

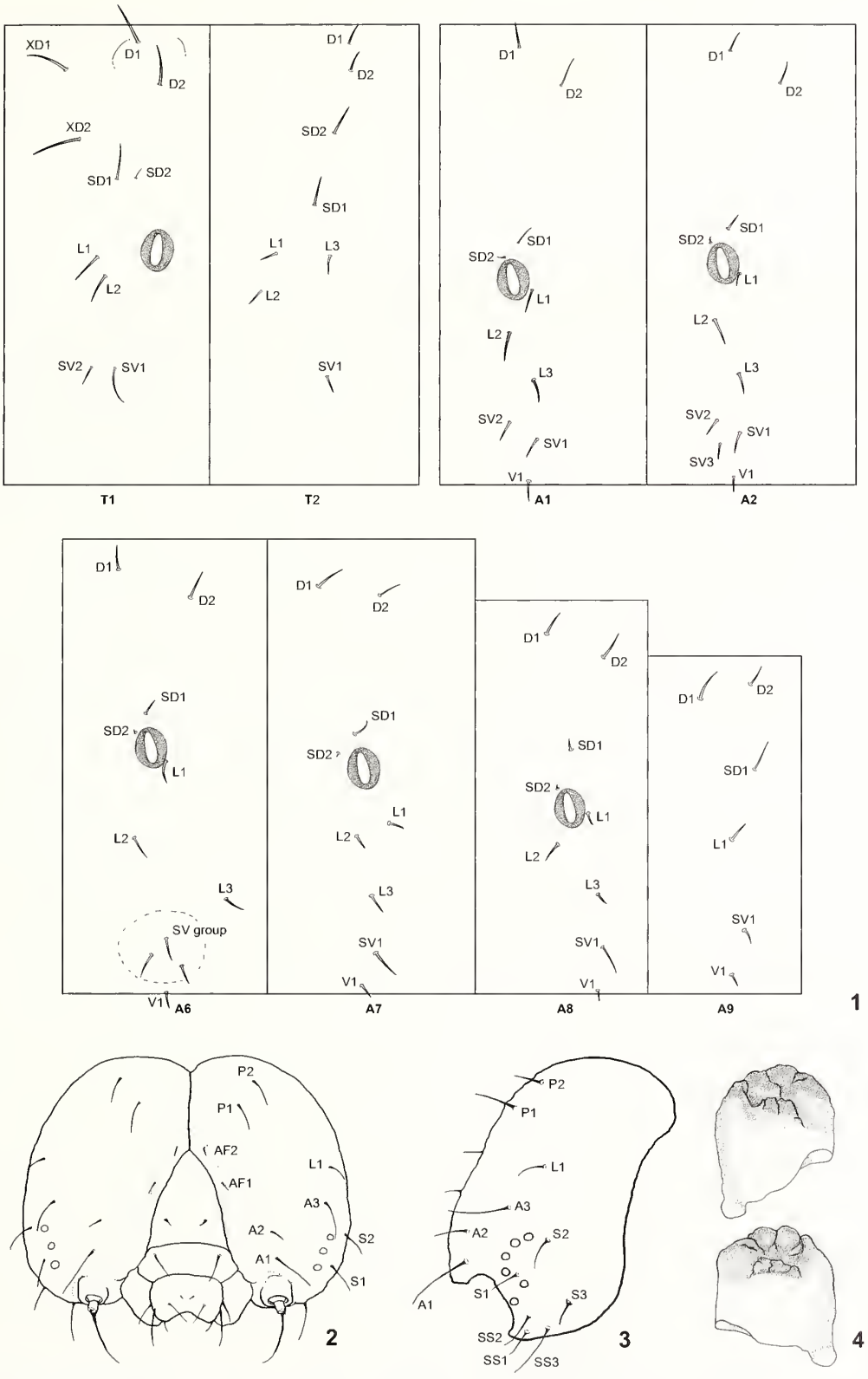
Miracavira brillians (Barnes, 1901), a handsome green moth with lichen-like patterning from the American Southwest, is a univoltine insect that flies during the summer-monsoon season. Barnes described *brillians* in the genus *Feralia* Grote from material collected in the Huachuca Mountains of southeastern Arizona. In 1937, Franclemont created the cuculliine genus *Miracavira* for moths that had been treated by earlier workers as members of the genus *Feralia* (or its synonym *Momaphana* Grote) that lacked (eye) lashes. He designated *Momaphana sylvia* Dyar as the type of the genus; although he did not specifically mention *brillians*, its membership was implied given its close similarity to *sylvia*. McDunnough (1938) continued to associate *Miracavira brillians* with *Feralia* Grote and placed it between *Psaphida* Walker and *Feralia* in his checklist of North American Macrolepidoptera. Franclemont and Todd (1983) moved *Miracavira* into the Apameini (Amphipyrinae), following the somewhat superficially similar genus *Phosphila* Hübner. Poole (1995) did not treat *Miracavira* in his monograph on the Psaphidinae. Recently Fibiger and Lafontaine (2005) moved the genus into the Acronictinae without explanation. Here we describe and figure the egg, larva, pupa, and male genitalia of *M. brillians*, provide notes on the insect's life history and larval biology, and transfer the genus into the Amphipyrinae: Psaphidini: Feraliina. In addition to *Miracavira*, the male genitalia of five additional psaphidine genera are figured and compared: *Apsaphida* Franclemont, *Feralia* Grote, *Paratrachea* Hampson, *Psaphida* Walker, and *Viridemas* Smith. The paper concludes with an enumeration of structural and behavioral similarities of *Miracavira* and *Amphipyra* Ochs. and a brief discussion suggesting that the Amphipyrinae and Psaphidinae are synonyms (with the latter given tribal status).

MATERIALS AND METHODS

Eggs of *Miracavira brillians* were obtained from a female collected at UV light by NMcF on 16 August, 2006: AZ: Cochise Co., Hereford, Ash Canyon, 5,170 ft, oak-manzanita woodland. The female began laying eggs on the first night of confinement. Larvae were reared to maturity on *Ptelea trifoliata* in Hereford by NMcF and at the University of Connecticut by DLW and BC.

One larva was prepared for SEM study by running it through a series of ethanol baths (70%, 80%, 90%, 95%, 100%) before it was dehydrated with hexamethyldisilazane. The caterpillar was then coated with gold-palladium for three minutes in a Polaron E 5100 sputter coater. Images were obtained with a Zeiss DSM-982 Gemini FE SEM at 3 kV.

Six larval and one adult specimen and 57 film slide vouchers have been deposited at the University of Connecticut. Nomenclature, and in particular circumscription of the Amphipyrinae and Psaphidinae, follow the works of Kitching and Rawlins (1998) and Fibiger and Lafontaine (2005).

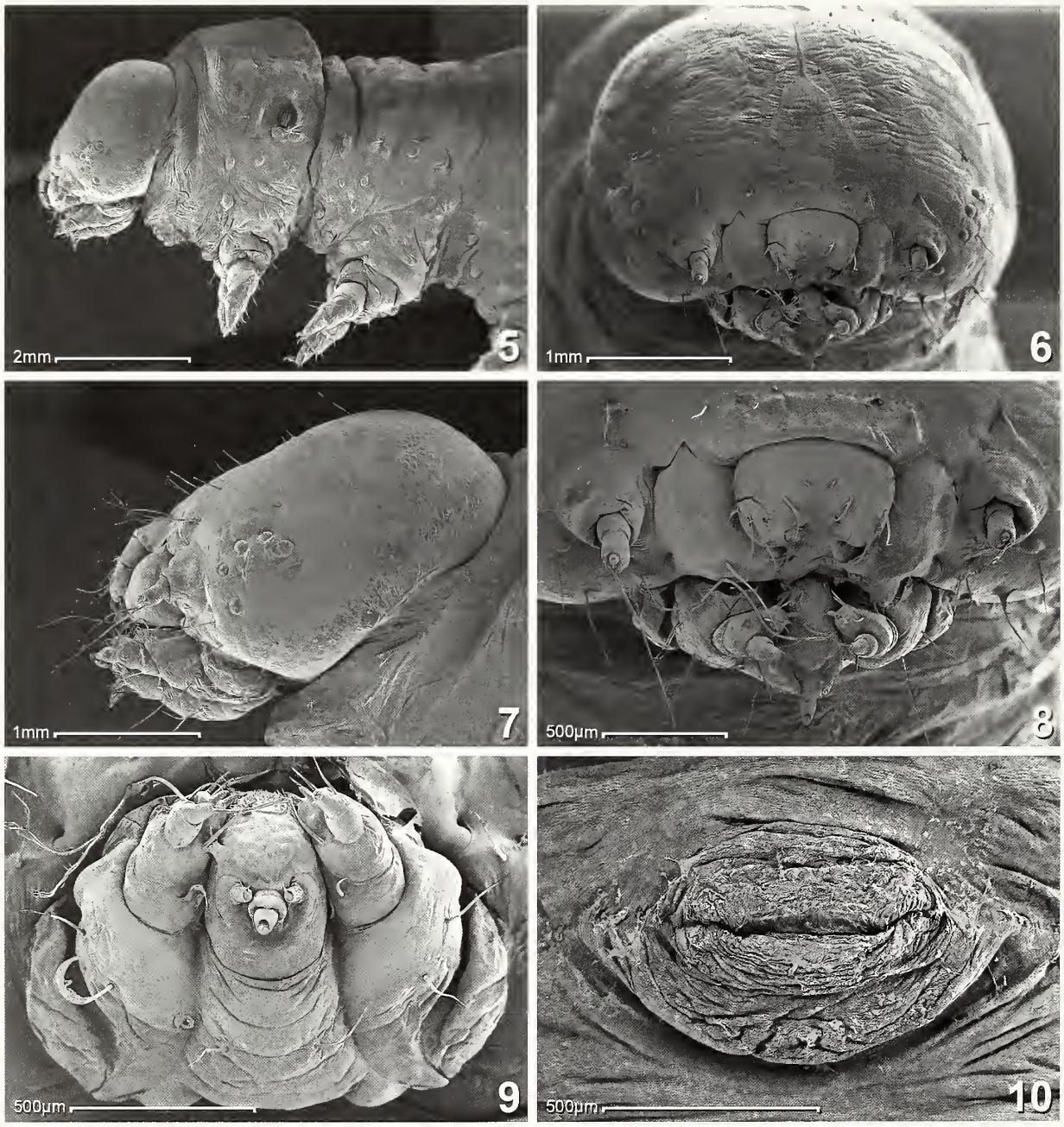


FIGS. 1–4. *Miracavira brillians* last instar. (**1**) Setal map. (**2**) Head, frontal (**3**) Head, lateral. (**4**) Mandibles, mesal surfaces.

RESULTS AND DISCUSSION

Description of immature stages. *Egg* (Figs. 15, 16). Round, nearly as high as wide with 19–20 ribs; fewer than half of the ribs reach the micropylar area (n=12).

First-fourth instars (Figs. 17–20). Prolegs on A3 and A4 reduced, especially in the first instar. First instar (Fig. 17): Body translucent, shiny, with ground yellowish but coloration strongly influenced by (green) contents of gut; no white or cream markings. Larger pinacula black. No hump. Head pale orange-tan. Second instar (Fig. 18): Body wall translucent, emerald green with numerous creamy to white spots; broken white middorsal stripe; thin continuous spiracular stripe; large; white spot below D1 and smaller creamy spot that includes D2 pinaculum. Larger pinacula black, thickened. Prothoracic ridge marked with white to creamy spots. Low hump over A8. Head subtly tinted with orange-tan. Third instar (Fig. 19): Emerald green, corrugated, with prominent creamy spotting; spiracular stripe much enlarged and fusing with lines that continue along leading edge of prothoracic and anal shields. Larger pinacula blackened. Spiracles without prominent black ring and halo of last two instars. Hump enlarged but without prominent middorsal protuberance. Head green with pale snowflake spotting and pale adfrontal edging along triangle.



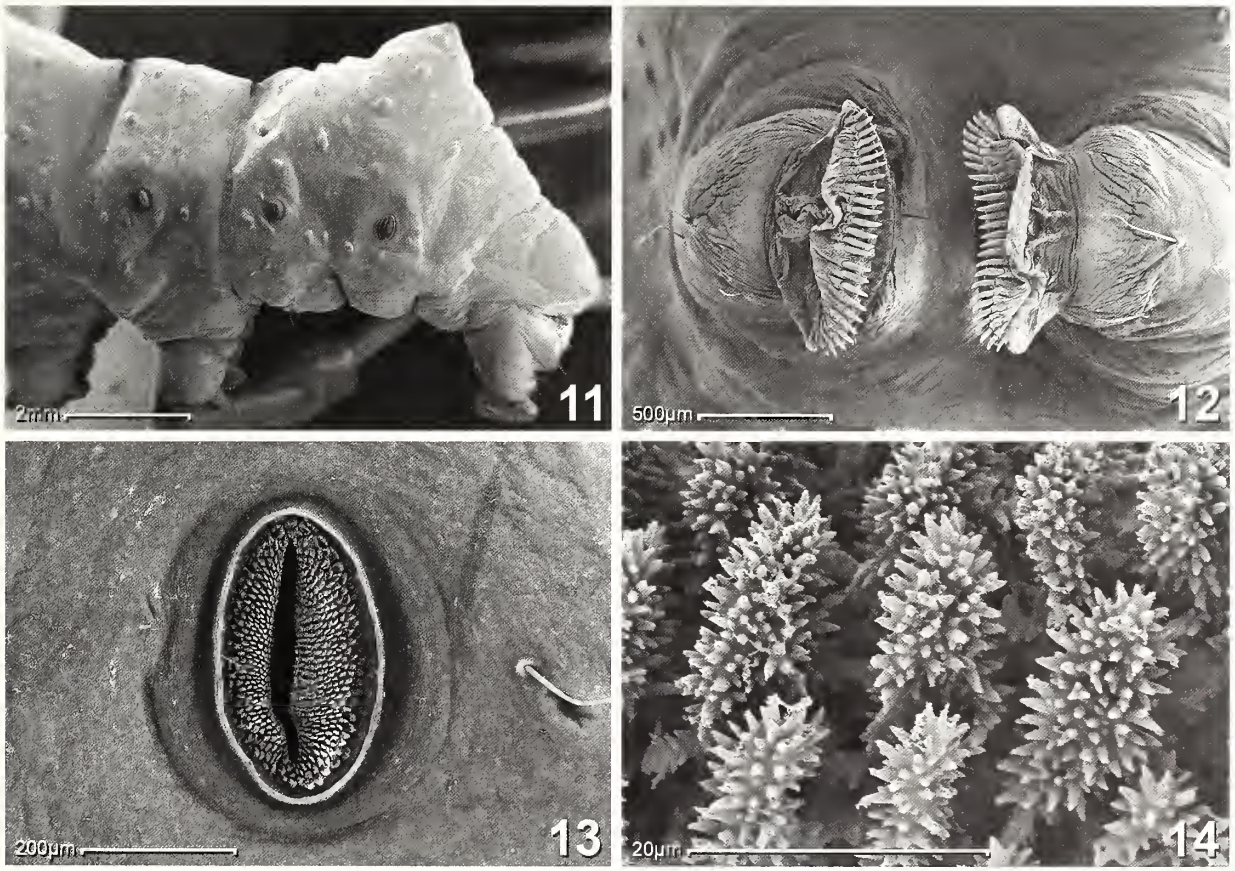
FIGS. 5–10. *Miracavira brillians* last instar. (**5**) Head to T2, lateral. (**6**) Head, frontal. (**7**) Head, lateral. (**8**) Mouthparts, frontal. (**9**) Maxillolabial complex. (**10**) Midsternal prothoracic gland.

Fourth instar (Fig. 20): Green with conspicuous, wart-like yellow spotting, and well-developed middorsal and spiracular stripes; prothoracic and anal shields thickened, edged with pale yellow. Spiracles ringed with black and outer diffuse halo of waxy-blue white. A8 with middorsal yellow knob at apex of hump. Bluish white waxy bloom added over duration of stadium.

Living fifth instar (Figs. 21–22). Waxy blue-green, especially above with subtle pink, violet, or maroon hues and strongly humped eighth abdominal segment bearing bright yellow middorsal wart (Fig. 21); integument spotted with oval, cream to yellow, slightly elevated spots; these largest over dorsum and bases of prothoracic legs; spot diameters reduced below spiracular stripe; prominent chalky white middorsal stripe frequently broken over thoracic segments and A10; spiracular stripe pale and thin, with numerous embedded yellow spots, continuing forward around anterior and posterior rims of prothorax and anal plates, respectively; upper edge running just below lower reach of spiracles; often broken and incomplete anterior to A4. Pinacula inconspicuous. Prominent white and black spiracles. Anal prolegs short and held back, scarcely extending beyond anal plate. Anterior edge of prothorax yellowed, forming raised lip over head. Head as in Fig. 22.

Preserved fifth instar (Figs. 1–14). Length: to 35 mm (n=4). Essentially unpigmented save for conspicuous enlarged and darkened peritreme around spiracles. Spiracular openings large with complex of echinoid-like papillae (Figs. 13, 14). Prothoracic shield, pinacula, and anal plate scarcely differentiated from adjacent cuticle. Thoracic and abdominal segments with scattered, clear warts or excrescences; these more pronounced in size on abdominal segments (Fig. 11); excrescences numerous below level of spiracles on both thorax and abdomen. Setae very short, thin and inconspicuous, few longer than height of spiracle, even those of anal plate scarcely longer than height of enlarged A8 spiracle (Figs. 5). Two SV setae on T1, one on T2 and T3, two on A1, three on A2–A6, and one on A7–A9. *Head* (Figs. 2, 3, 5–9): unpigmented, shallowly creased or roughened anteriorly with low warting rearward (Fig. 7); setae short and inconspicuous; frons extending about halfway to epicranial notch. Labrum narrow, less than twice as wide as deep, shallowly notched (Figs. 2, 6). Maxillolabial complex as in Figs. 7–9; labial palpus about half length of spinneret; pore apical (Fig. 9). Mandibles as in Fig. 4, with teeth poorly developed; unpigmented except for contrastingly blackened, toothed, distal margin. *Thorax* (Figs. 5): T1 swollen above, about 15% higher than T2 (receiving head in living larvae) (more pronounced in Fig. 5 than our other pickled individuals); well-developed cervical gland (Figs. 5, 10), everting in some pickled specimens). SD1 and SD2 subequal on T2 and T3, otherwise SD2 reduced, and closely positioned near spiracle on A1–A8. *Abdomen* (Figs. 1, 11–14): A8 with exaggerated hump, rising to a middorsal prominence crowned by single excrescence (Fig. 11). L1 closely set to spiracle on A1–A6 and A8, but sifted well downward on A7. SD1 on A9 of same thickness as other setae. Crochets uniordinal (Fig. 12); numbering 21–22, 23–24, 25–26, and 27–29 on A3–A6, respectively.

Pupa (Figs. 24–30). Length 13–14 × 5.5–6 mm (n=3). Elongate-oval, widest at A3 (Fig. 24) with distinctive ventral bulge (beyond mid length of wings) (Fig. 25) and dorsal bulge (over A1–A3) (Figs. 25, 28). Integument thick, dark brown with waxy bloom (when dry); surface heavily ornamented with creases and pits: thoracic segments



FIGS. 11–14. *Miracavira brillians* last instar. (**11**) A6–A10, lateral. (**12**) Prolegs on A6. (**13**) A8 spiracle, head to left. (**14**) Detail of 13.

deeply coriaceous with parallel creasing along axes of legs and antennae; abdominal segments with numerous, closely set, crater-like depressions; caudal transverse ridges on A4–A6 micropunctate. Setae minute, less than $^1/_2$ width of spiracle and difficult to locate except about cremaster on A10. Cremaster with horn-like spur directed laterad (Fig. 29). No mouthparts visible; wings ending at caudal reach of A4; legs and antennae as in Figs. 26, 27. Spiracles nearly elliptical; that on A8 rudimentary (Fig. 28).

Life Cycle. Eggs were laid individually with an adhesive (Fig. 15). Those held at ambient temperature at the collection site hatched after seven days (n>50). A portion of the chorion was consumed at eclosion. Larvae passed through five instars. The first three instars each lasted about 3–5 days, the fourth instar 6–8 days, and the final instar 7–14 days (Table 1). Most larvae matured in 4 weeks. Not surprisingly, given this rate of rapid development, larvae often fed both day and night (and remained at rest adjacent to feeding site). Prepupae tunneled into leaf litter or below ground, where they fashioned a loose cocoon of off-white silk. Pupation occurs 3–4 days after the cocoon is completed. Duration of the pupal stage is expected to be close to 10.5 months for those individuals hatching after a single year, although other psaphidines are known to overwinter multiple times and up to 7 years (Wagner et al. 2009, Dale Schweitzer unpublished data).

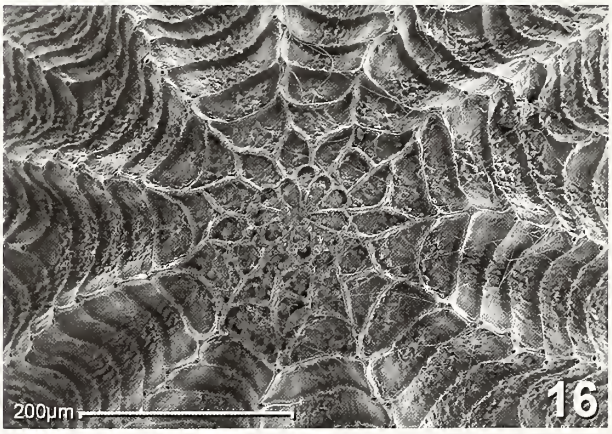
Life History Notes. *Miracavira brillians* is a specialist on *Ptelea trifoliata* (and perhaps other *Ptelea* in Mexico) (Family Rutaceae). While new foliage is preferred, especially by early instars, mature leaves, including those that are somewhat blighted, are ingested and satisfactory for development. Such is not the case for many eastern psaphidines which will struggle and starve if not offered young, not-yet-hardened foliage (Wagner 2005, Wagner et al. 2009).

The first through at least the third instars spin a thin sheeting of silk along a leaf edge and then feed on adjacent tissues, keeping the prolegs engaged in silk. Disturbed first instars may balloon downward on a line of silk. The first two instars skeletonize the upper side of the blade over and adjacent to a leaf edge, although towards the end of the second instar some larvae chew through the blade. Third instars largely confine their feeding to a leaf edge, either eating small holes through the blade or carving out cavities from a leaf edge. Some fourth instars also spin a silken sheet over the lamina into which the crochets are engaged, especially prior to

TABLE 1. Head capsule widths and development times for *Miracavira brillians*.

Stage/ Instar	Head capsule widths in mm: range, mean, # obs.	Approx. length in days; stragglers excluded[1]
Egg		Aug 16 – Aug. 23
1st	0.45–0.48, 0.47, 11	Aug. 23 – Aug.26
2nd	0.73–0.79, 0.77, 15	Aug. 26 – Aug. 31
3rd	1.14–1.18, 1.2, 9	Aug. 29 – Sept. 5
4th	1.82–1.98, 1.8, 18	Sept. 1 – Sept. 10
5th	2.88–2.90, 2.89, 2	Sept. 7 – Sept. 30
Pupa	8	Sept 15–

[1] Data combined from single clutch reared as two cohorts: one indoors in Hereford Arizona at ambient temperature and a second cohort reared at 23° C in a lab at the University of Connecticut. A third cohort of larvae from the same female sleeved (outdoors) in Hereford had accelerated development with larvae maturing after only 3–3.5 weeks.



FIGS. 15–16. *Miracavira brillians* egg. (**15**) Chorion sculpturing, note adhesive. (**16**) Micropylar area.

FIGS. 17–23. *Miracavira brillians* (**17–22**) and *Amphipyra* pyramidoides (**23**) larvae. (**17**) First instar. (**18**) Second instar. (**19**) Third instar. (**20**) Fourth instar. (**21**) Fifth instar. (**22**) Fifth instar, head. (**23**) Fifth instar *Amphipyra* pyramidoides.

a molt. Last instars typically rest off the blade, firmly grasping petioles or shoot tips.

Larvae of all instars are difficult to remove from their perch, either because they securely engage the prolegs into their silken sheet (first four instars) or because they hold onto the petiole or rachis tenaciously (last instar). Early instar caterpillars spin silk in advance of any change in position. Most remarkably, two of three preserved (boiled) last instars retained their grip on leaf tissue throughout a five-minute boiling period and to this writing remain firmly attached (in 70% alcohol) to the petiole to which they had initially secured themselves. It is remarkable that the larvae would hold on with such leviathan force, and one must wonder if this behavior has evolved, at least in part, to help the larvae maintain their purchase in the violent squalls of the American Southwest's monsoon season. Silk also aids molting as larvae secure the anal prolegs into the sheeting prior to molting. Almost without exception, cast skins are consumed following the molts.

First through third instars, when disturbed, sometimes vibrate rapidly from side to side. This behavior was most often noted in first instars and could sometimes be induced with a wisp of air. Vibrating was not observed in fourth and fifth instars.

As in other trifid noctuids, the early instars scarcely use the first two pairs of abdominal prolegs when crawling. The anterior pair (on A3) is only about half the size of those on A5 and A6. Prolegs on A4 are also reduced in size. Even while perched, first, and to some

extent second instars, elevated the anterior end of the body such that the first two pairs of prolegs were either not in contact with the leaf/silk or only weakly secured.

Miracavira is exceedingly sedentary, often occupying the same perch for three instars. The caterpillar's site fidelity contrasts markedly with *Amphipyra pyramidoides* Guenée, a familiar eastern species that *Miracavira* somewhat resembles. *A. pyramidoides* was cited by Heinrich (1979) as a species that plays "the shell game" with its (avian) predators by frequently changing its location, especially after feeding, and in so doing, removing itself from leaves that it has damaged and which might reveal its whereabouts to natural enemies.

The first two instars perch extended along a leaf margin where their coloration is stunningly cryptic (we found it difficult to accurately count larvae without the aid of reading glasses or a lens). Fourth and fifth instars perch with the head, partially drawn into the prothorax, craned back over and held above or pressed against the abdomen; the forelegs are commonly folded across the mouthparts. In middle instars the head is held over the dorsum of the middle abdominal segments. In the last instar the head is pushed even farther rearward, and in the extreme, the frons is held against the anterior face of the abdominal hump (segments 7 and 8) (Fig. 21) or drawn to one side. Again, the first two pairs of legs are held forward and flat against the body; the metathoracic legs are held outward. The anal prolegs are mostly covered by the anal plate. This resting (not alarm) posture presumably provides a case of protection through non-resemblance—the larva is most uncaterpillar-like in appearance. In the fourth and especially fifth instars, the larva becomes increasingly blue-green and a whitish bloom develops over the dorsum, enhancing the insect's countershading (Cott 1940, Edmunds 1974, Ruxton et al. 2004) (the caterpillar's pale dorsum is directed downward when the insect is perched on a petiole or twig). Whether *Miracavira*, in fact, enjoys the evolutionary benefits of non-resemblance and/or countershading will require testing, but there can be little argument that the insect's posture protects the head from direct strikes: at rest the head is pulled beneath the horn-like rim of the prothorax and the front is held proximate to the abdominal hump.

Taxonomic Placement. In 2005 Fibiger and Lafontaine transferred *Miracavira* into the Acronictinae on the basis of the heavily sclerotized, apically positioned clasper, and pattern similarities with the Old

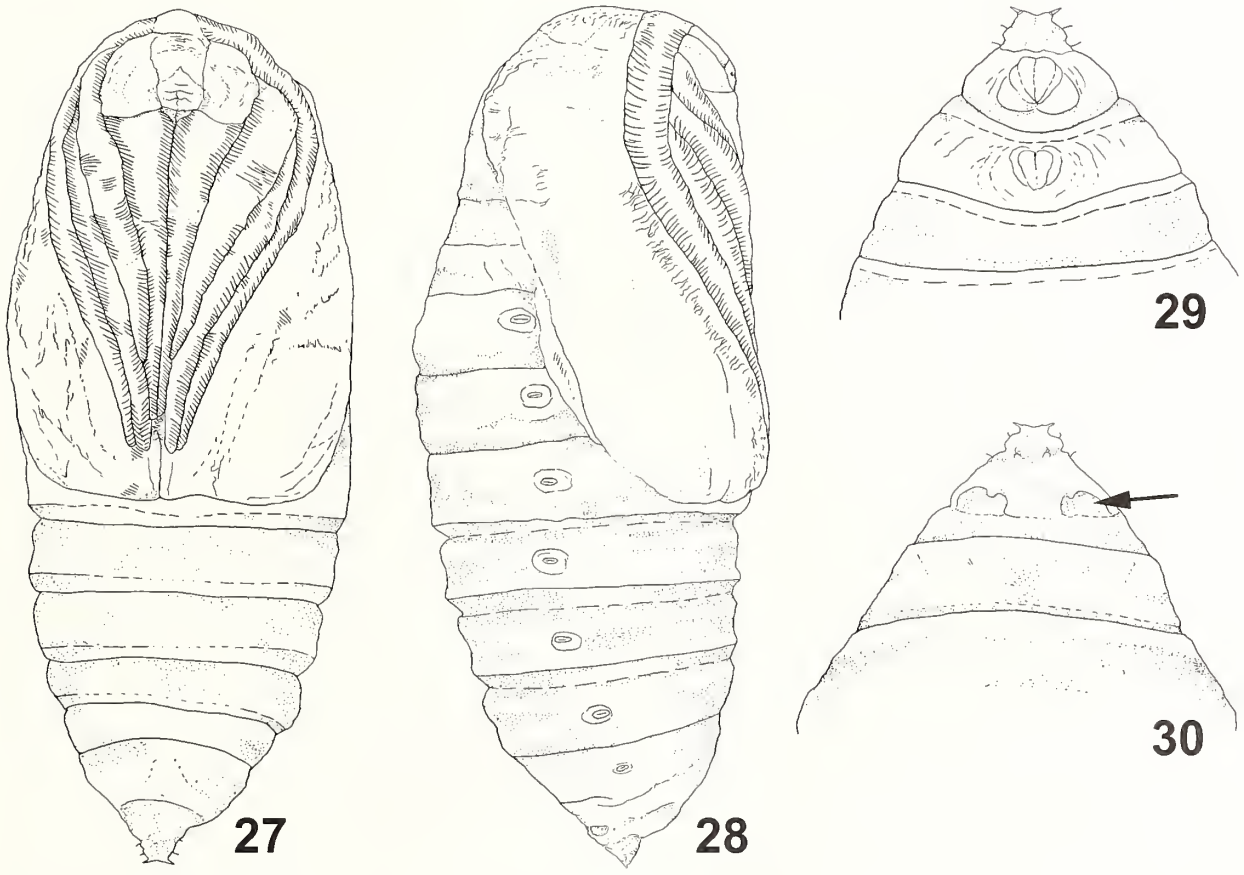
FIGS. 24–26. Pupa of *Miracavira brillians*. (**24**) dorsal. (**25**) lateral. (**26**) ventral.

World acronictine genera *Nacna* Fletcher and *Diphtherocome* Warren. Neither author had early stages of the insect for examination. The larva of *M. brillians* lacks acronictine features as defined by Crumb (1956), Kitching and Rawlins (1998), and Wagner (2007a, 2007b): i.e., *Miracavira* bears only primary setae, verrucae are absent, there is only one seta on the L3 pinaculum on A1–A8, and the dorsal pinacula are distant on both the meso- and metathorax.

The caterpillar of *Miracavira* shares a number of features common to the Psaphidinae (and Amphipyrinae): A8 is humped, the spiracular stripe continues around the anal plate, the dorsal pinacula are whitened, and the head is partially retracted into the thorax (Wagner et al. 2009). The pupa of *Miracavira* possesses dorsal pits on A10 (Fig. 30), a feature regarded to be synapomorphic for the subfamily Psaphidinae by Kitching and Rawlins (1998). Below we expand on our argument that *Miracavira* is a Amphipyrinae: Psaphidini, and best fits within the subtribe Feraliina.

Poole (1995) tentatively associated the Psaphidini and Feraliini on the basis of four characters: the thick, hairy vestiture of the adults; spring flight of the adults; irregular spining of the tarsi; and enlarged bulla posterior to the tympanal hood. The first of these are common among spring-flying noctuids; the fourth character also was noted by Poole (1995: 162) to occur in other subfamilies. Kitching and Rawlins (1998) identified the shared dorsal pits A10 of the pupa as an additional feature strengthening the association between the two tribes. Many of the genera that we examined over the course of this study were found to possess a dorsally lengthened, almost hood-like tegumen. Beyond these few characters, the Psaphidini and Feraliini are rather structurally divergent.

Psaphidini have a "claw" at the apex of the foretibia (actually a spine-like seta), a character common



FIGS. 27–30. Line drawings of female pupa. (**27**) ventral. (**28**) lateral. (**29**) A8–A10, ventral. (**30**) A8–A10, dorsal: arrow points to A10 pits.

throughout the Oncocnemidinae, Psaphidinae, and Stiriinae, but frequently lost secondarily (the tibial "claw" in the Cuculliinae is a spine not a seta). The male abdomen has the seventh tergite greatly enlarged and heavily sclerotized, a peculiar character shared with two other psaphidine tribes, Nocloini Poole and Triocnemidini Poole (but absent in the Feraliini). In the male genitalia (e.g., Fig. 31), the uncus is simple, tapered at the apex into a spine; the coronal setae at the valve apex are weak; the clasper is a slightly more heavily sclerotized area on the ventral margin of the valve with an elongated, lightly sclerotized, setose ampulla; the vesica is a simple expanded tube covered with spike-like cornuti with a single larger cornutus at the apex in most species. We consider most of these features to be plesiomorphic within the Psaphidinae because they are also present in the Oncocnemidinae and Stiriinae.

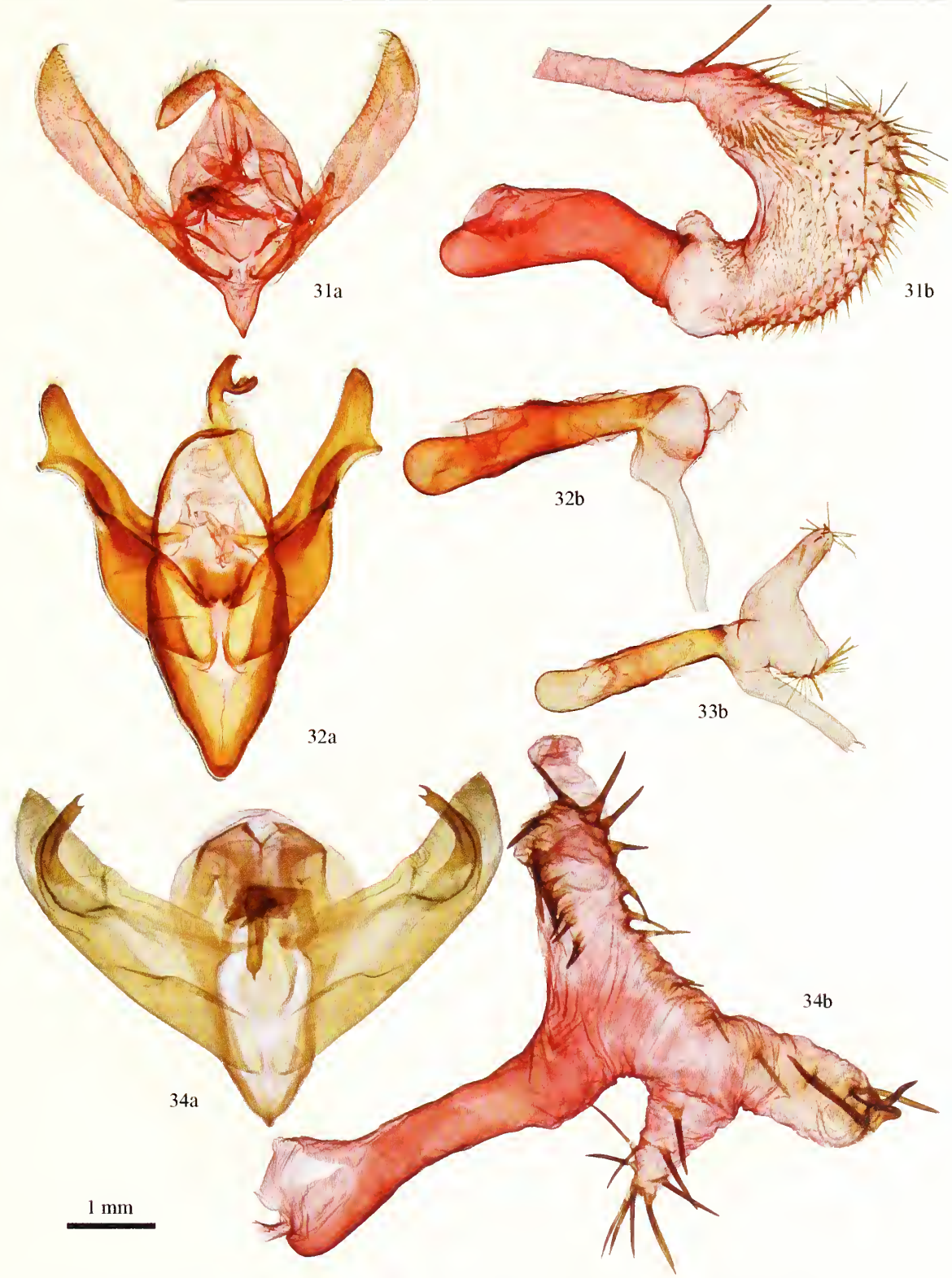
Typical Feraliini (only the genus *Feralia*, Figs. 32, 33) depart from the Psaphidini in several ways: the apical spine on the tibia is lost; the uncus is divided apically into a pincer-like structure; the apical corona on the valve is weak or absent; the clasper and ampulla are absent; a heavily sclerotized, tapered digitus is fused to the inner surface of the valve and narrows into a subapical pollex-like process; the vesica typically is rounded with two diverticula (e.g., Fig. 33b), each covered with long spike-like cornuti. In some species one or both of these diverticula are reduced (e.g., Fig. 32b).

Both larval and adult characters indicate that *Miracavira* has a close phylogenetic affinity to the Feraliini Poole. The emerald green and, more importantly, transparent, second and third instars of *Miracavira* resemble those of *Feralia*. Like *Miracavira*, larvae of *Feralia* are exceedingly sedentary in habit (McFarland 1963), and at least in later instars, caterpillars of both genera accept older foliage, a trait not shared with spring-active genera of Psaphidini. Adult coloration of *Miracavira* and *Feralia* are similar—both *M. brillians* and *M. sylvia* (Dyar) were originally described as members of the genus *Feralia* (or its synonym *Momaphana*); evidently, the principal reason that the two species were removed by Franclemont (1937) was because the adults lacked eye lashes. Adults lack the apical digging claw on the foretibia common to Psaphadini.

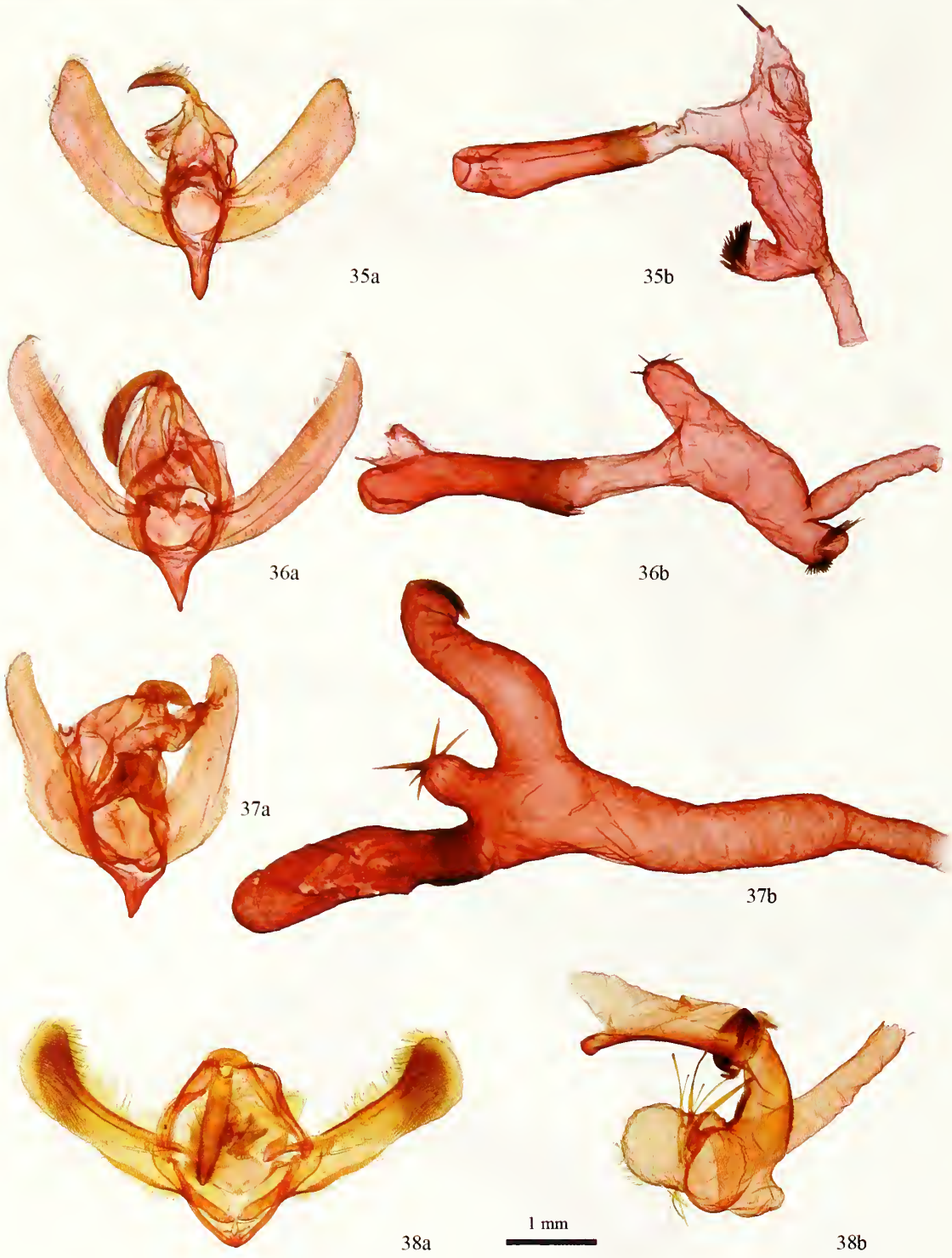
Miracavira has highly divergent male genitalia (Fig. 34, note we figure *M. sylvia*, the type species of the genus), but within the psaphidine is structurally more similar to genera in the Feraliini than to those in the Psaphidini. *Miracavira* and other genera have diverticula in the vesica covered with spike-like cornuti (in *Miracavira* the vesica has three large diverticula, each covered with long spike-like cornuti). In both *Feralia* and *Miracavira* the ampulla of the clasper and the corona are lost. Differences in genitalia between the two genera are extreme and seem to overshadow the similarities: *Miracavira* has no trace of a digitus, the uncus is typical of other psaphidines, not highly modified as in *Feralia*, the dorsal part of the tegument is highly modified, and the clasper is massive (lost in *Feralia*).

We associate three other genera (*Paratrachea* Hampson, Fig. 35; *Apsaphida* Franclemont, Fig. 36; and *Viridemas* Smith, Fig. 37) with the Feraliini on the basis of the loss of the tibial "claw," the loss of the clasper and ampulla on the valve, the dorsally expanded tegumen, and the presence of two cornuti-covered diverticula in the vesica. These three genera can be associated with each other by a brush-like structure formed by a tight clustering and reduction in length of the cornuti at the apex of the diverticulum closest to the ductus ejaculatorius. Two of these genera, *Paratrachea*, based on *P. viridescens* (B. & McD.), and *Apsaphida*, can be associated as sister taxa by the close similarity of the shape of the vesica.

Connections to the Amphipyrinae. Intriguing are the similarities between the larvae of *Miracavira brillians* and *Amphipyra pyramidoides* (Amphipyrinae) (Figs. 21, 23). Shared features include the raised and rather angulate eighth abdominal segment; a yellow middorsal wart on A8; a similar set of middorsal, subdorsal, and spiracular stripes, with the latter weakening over the anterior abdominal segments; and bulging yellow excrescences (Fig. 11) over the upper half of the body and smaller warting below the level of the spiracles. *Miracavira* caterpillars and those of some *Amphipyra* (including the Palearctic species *A. pyramidea* L. and *A. berbera* Rungs) often have a decided blue-green aspect to the ground color—an unusual coloration among caterpillars. In both genera the head is partially retracted into the thorax (as is the case with many psaphidines). An especially striking similarity is the spiracular coloration: both *Miracavira brillians* and *Amphipyra pyramidoides* have a broad black ring (?peritreme) about the spiracle that, in turn, is surrounded by a pale halo (Figs. 21, 23). Late instars of the two genera rest with the anterior end of the body lifted and well removed from the perch (Figs. 21, 23). Members of both *Amphipyra* and *Feralia* also bridge the phenotypic gap between the Amphipyrinae and Psaphidinae. The larval coloration and patterning of *Amphipyra tragopoginis* (Clerck), and in particular its striping and humped eighth abdominal segment are reminiscent of North American *Feralia* species. *Feralia*



FIGS. 31–34. Male genitalia: (a) genital capsule; (b); aedeagus with vesica everted. (**31a, b**) *Psaphida resumens* Walker. (**32a, b**) *Feralia jocosa* (Guenée). (**33b**) *Feralia sauberi* (Graeser). (**34a, b**) *Miracavira sylvia* (Dyar).



FIGS. 35–38. Male genitalia: (a) genital capsule; (b) aedeagus with vesica everted. (**35 a, b**) *Paratrachea viridescens* (Barnes & McDunnough). (**36 a, b**) *Apsaphida eremna* Franclemont. (**37 a, b**) *Viridemas galena* Smith. (**38 a, b**) *Amphipyra tragopoginis* (Clerck).

februalis Grote, a western oak-feeding member of the genus, has an exaggerated, sharply angulate, hump on A8, comparable to that of *Miracavira brillians* and *Amphipyra pyramidoides*.

The male genitalia of the Amphipyrinae and Psaphidinae also share many characters. In the Amphipyrinae the clasper and ampulla may be lightly sclerotized with the ampulla finger-like and setose (e.g., *Amphipyra tragopoginis*, Fig. 38); or similar to those of the Psaphidinae with the ampulla large, spike-like, and heavily sclerotized (e.g., *Pyrois effusa* (Boisduval)); or lost (e.g., *Amphipyra pyramidoides* and many Feraliini). Also, in both the Amphipyrinae and Psaphidinae the vesica is covered with long, spike-like cornuti arising from stout bases. Two derived amphipyrine character states (not shared by Psaphidinae) are the large, broad, flat pleural sclerite and the disproportionately massive uncus.

In sum the similarities between the Amphipyrinae and Psaphidinae show that the Psaphidinae would be best subsumed within the Amphipyrinae as the tribe Psaphidini, and the Feraliine as a subtribe of the latter. Evolutionary relationships among the currently recognized amphipyrine-psaphidine tribes, and inparticular the Nocloini and Triocnemidini, need study. Towards this end, we encourage others to secure and preserve early stages of the Nocloini and Triocnemidini (which are all but unknown) and preserve tissue for molecular studies.

ACKNOWLEDGEMENTS

George Godfrey alerted us to the fact that he and Jack Franclemont had reared *Miracavira* on hop tree (*Ptelea trifoliata*) in 1967 from the Chiricahuas. Jim Romanow assisted with the scanning microscopy. Andrea Farr and René Twarkins prepared the line art. René Twarkins cleaned the images, "inked" the setal map, and assembled the plates. Jocelyn Gill prepared the male genitalia plate. Pupae of *Feralia* and *Amphipyra* were sent to us by Ben D. Williams and Steven Passoa, respectively. Glenn Dryer and the Connecticut College Arboretum supplied *Ptelea* leaves to BC and Clinton Morse of the University of Connecticut Greenhouse propagated seedlings for DLW. Financial support came from the U.S. Department of Agriculture, Forest Services, Forest Health Technology Enterprise Team, cooperative agreement number 01-CA-11244225-215 to DLW.

LITERATURE CITED

BARNES, W. 1901. Descriptions of some new species of North American Lepidoptera. Canad. Entomol. 33: 53-57.

COTT, H.B. 1940. Adaptive coloration in animals. Methuen, London, England. 508 pp.

CRUMB, S.E. 1956. The caterpillars of the Phalaenidae. Technical Bulletin 1135. USDA, Washington, DC. 356 pp.

EDMUNDS, M. 1974. Defence in animals. Longman, England. 357 pp.

FIBIGER, M. & J.D. LAFONTAINE. 2005. A review of the higher classification of the Noctuoidea (Lepidoptera) with special reference to the Holarctic fauna. Esperiana. Buchreihe zur Entomologie. Volume 11: 1-205.

FRANCLEMONT, J.G. 1937. Descriptions of new genera (Lepidoptera, Noctuidae, Cuculliinae). J. New York Entomol. 69: 127-130.

—— & E.L. TODD. 1983. Noctuidae, pp. 120-159. *In* Hodges, R.W. et al. (eds.), Check list of the Lepidoptera of America north of Mexico, E.W. Classey Ltd. & The Wedge Entomological Research Foundation, Cambridge Univ. Press, Cambridge, United Kingdom.

HEINRICH, B. 1979. Foraging strategies of caterpillars: leaf damage and possible predator avoidance strategies. Oecologia 42: 325-337.

KITCHING, I.J. & J.E. RAWLINS. 1998. The Noctuoidea. pp. 355-401. *In* Kristensen, N. P. (ed.), Lepidoptera, moths and butterflies. Volume 1: Evolution, Systematics, and Biogeography. Handbook for Zoology. Volume IV. Arthropoda: Insecta, Walter de Gruyter, Berlin, Germany.

MCDUNNOUGH, J. 1938. Checklist of the Lepidoptera of Canada and the United States of America. Part 1. Macrolepidoptera. Mem. Southern Calif. Acad. Sci. 272 pp.

MCFARLAND, N. 1963. The Macroheterocera (Lepidoptera) of a mixed forest in Western Oregon. Oregon State University, Corvallis. Unpublished Ph.D. Thesis. 154 pp.

POOLE, R.W. 1995. Noctuoidea. Noctuidae (Part), Cuculliinae, Stiriinae, Psaphidinae (Part). *In* Dominick, R. B. et al. (eds.), The Moths of America north of Mexico. Fasc. 26.1, Wedge Entomological Foundation, Washington DC. 249 pp.

RUXTON, G.D., M.P. SPEED, & D.J. KELLY. 2004. What, if anything, is the adaptive function of countershading? Anim. Behav. 68: 445-451.

WAGNER, D.L. 2005. Caterpillars of eastern North America: A guide to identification and natural history. Princeton University Press, Princeton, New Jersey. 512 pp.

——. 2007a. Larva of *Cerma* Hübner and its enigmatic linkages to the Acronictinae (Lepidoptera: Noctuidae). Proc. Entomol. Soc. Wash. 109: 198-207.

——. 2007b. Barking up a new tree: Ancient pupation behavior suggests *Cerma* Hübner is an acronictine noctuid (Lepidoptera). Syst. Entomol. 32: 407-419.

——, D.F. SCHWEITZER, J.B. SULLIVAN, & R.C. REARDON. 2009. Caterpillars of eastern North American Noctuidae. Princeton University Press.

Received for publication 25 April 2007; revised and accepted 28 September 2007.

Journal of the Lepidopterists' Society
62(1), 2008, 52–53

SUMMER AZURE (*CELASTRINA NEGLECTA* W. H. EDWARDS, LYCAENIDAE) NECTARING ON POISON IVY (*TOXICODENDRON RADICANS*, ANACARDIACEAE)

The purpose of this communication is to report on the ecological relationship between poison ivy (*Toxicodendron radicans* [L.] Kuntze) and Summer Azure (*Celastrina neglecta*, W. H. Edwards; Papilionoidea: Lycaenidae) as discovered during a systematic survey of poison ivy pollination during the summer of 2005.

Daily observations of at least one hour in length were conducted at a central Iowa site (East River Valley Park/Carr Woods, Ames, Iowa; Story County) from June 6–June 20, 2005. June 6 was the day of the first recorded open inflorescence and pollination event and June 20 the last recorded pollination event. This site harbors both climbing and nonclimbing individuals of eastern poison ivy (*Toxicodendron radicans* subsp. *negundo*, Anacardiaceae; Gillis 1971). Each pollination event was photographed using an Olympus D-540 (either still shots or video) and was accompanied by field notes indicating length of visit and time of day.

Celastrina neglecta visited inflorescences on three of the fifteen days that viable inflorescences were available (Fig. 1). Five distinct nectaring observations were recorded on June 8, eleven on June 9, and one on June 10. All events occurred between 13:00 and 18:00 hours, and the observation period on each of the three days was approximately the same (~2 h). These days were towards the beginning of the flowering period when inflorescences were most abundant throughout the population (pers. obs.). Multiple individuals were observed visiting the same plants simultaneously on both June 8 and 9, indicating visits were not by a single butterfly that repeatedly visited the same site.

Fig. 1. *Celastrina neglecta* nectaring at an inflorescence of poison ivy (*Toxicodendron radicans*) on June 8, 2005.

Total length of time spent per visit on a single inflorescence was recorded on both June 9 and June 10 (n = 12). Mean time per visit was 39.3 s (standard deviation = 38 s; median = 37.6 s). During this observation period, *Celastrina neglecta* would only nectar at an inflorescence if it was the sole visitor; when a competing visitor (such as a bee) alighted on the same inflorescence, the butterfly would immediately leave. *Celastrina neglecta* was persistent in its visits even when strong wind was present.

Previously, the only known relationships between Lepidoptera and poison ivy and its relatives (*Toxicodendron* section *Toxicodendron*, Anacardiaceae) were for larval feeding and shelter (Criddle 1927; Dyar 1904; Eastman and Hansen 1991; Gillis 1971; Richers 2007; Robinson *et al.* 2007; Tietz 1972). Nectar-seeking at poison ivy (*T. radicans*) by *Celastrina neglecta* represents a novel relationship between adult Lepidoptera and poison ivy previously unrecognized, and enhances our understanding of Lepidoptera-*Toxicodendron* interactions. This observation also adds to our understanding of the diversity of plant lineages for which Lepidoptera may provide pollination service. Insects from two other orders are also known to pollinate poison ivy, including multiple coleopteran families (*e.g.*, Cantharidae, Cerambycidae, and Cleridae; Senchina 2005) and the ubiquitous honeybee (*Apis mellifera*, Hymenoptera:Apidae; Gillis 1971; Lieux 1981). The identification of *Celastrina neglecta* as a poison ivy floral associate suggests that adults from multiple insect orders may be important in poison ivy pollination ecology.

LITERATURE CITED

CRIDDLE, N. 1927. Lepidoptera reared in Manitoba from poison ivy. Can. Entomol. 59: 99–101.

DYAR, H.G. 1904. Poison ivy caterpillars. J. New York Entomol. Soc. 12: 249–250.

EASTMAN, J. AND A. HANSEN. 1991. The book of forest and thicket: trees, shrubs, and wildflowers of eastern North America. Stackpole, Mechanicsburg. xi + 212pp.

GILLIS, W.T. 1971. The systematics and ecology of poison-ivy and the poison-oaks (Toxicodendron, Anacardiaceae). Rhodora 73: 72–159, 161–237, 370–443, 465–540.

LIEUX, M.H. 1981. An analysis of Mississippi USA honey: pollen, color, and moisture. Apidologie 12: 137–158.

RICHERS, K. 2007. California Moth Specimen Database. Accessed on July 11, 2007. http://bscit.berkeley.edu/eme/cal-moth_species_list.html.

ROBINSON, G.S., P.R. ACKERY, I.J. KITCHING, G.W. BACCALONI, AND L.M. HERNANDEZ. HOSTS – A Database of the World's Lepidopteran Hostplants. Accessed on July 11, 2007. http://www.nhm.ac.uk/research-curation/projects/hostplants.

SENCHINA, D.S. 2005. Beetle interactions with poison ivy and poison oak (Toxicodendron P. Mill. sect. Toxicodendron, Anacardiaceae). Coleopt. Bull. 59: 328–334.

TIETZ, H.M. 1972. An index to the described life histories, early stages and hosts of the Macrolepidoptera of the continental United States and Canada, vol. II. A. C. Allyn; Sarasota. 1041pp.

DAVID S. SENCHINA, *2507 University Ave., Biology Department, Drake University, Des Moines, IA 50311-4516*, email: dssenchina@drake.edu.

Received for publication 26 June 2006, revised and accepted 6 December 2007.

Journal of the Lepidopterists' Society
62(1), 2008, 53–56

ROAD CROSSING BEHAVIOR OF AN ENDANGERED GRASSLAND BUTTERFLY, *ICARICIA ICARIOIDES FENDERI* MACY (LYCAENIDAE), BETWEEN A SUBDIVIDED POPULATION

Additional key words: conservation, *Lupinus*, Oregon.

As high quality grasslands dwindle from degradation, habitat fragmentation increases, and urbanization expands butterflies must cope with the encroachment of human modified landscapes if they are to survive. Some butterflies have incorporated exotic larval host plants and non-native nectar resources to survive in urbanized habitats (Shapiro 2002, Graves & Shapiro 2003) while others occupy the isolated vestiges of historically dominant habitats (Severns *et al.* 2006). For butterflies to survive in human modified habitats they must successfully navigate amongst an array of unnatural physical structures like residential areas, roads, vacant lots, agricultural fields, orchards, to find adult resources, mates, and larval host plants. While some vagile, polyphagous butterflies appear to be successful in urban situations (Blair & Launer 1997) others with narrow host plant breadth and specific habitat requirements suffer as habitat modification increases. If we are to conserve, create, and maintain areas for butterflies with specialized habitat requirements, then understanding how these species respond to human modified habitats is important for conservation planning.

Fig. 1. Photograph of narrow, two-lane paved road, and hedgerow (3m - 5m tall x 100m long) separating the southern subpopulation habitat (left) and the northern subpopulation (behind the hedgerow).

Icaricia icarioides fenderi Macy (Lycaenidae), hereafter Fender's blue, is an endangered, endemic species to remnant Willamette Valley upland prairies of western Oregon, U.S.A. Fender's blue is presently known from about 15 remnant upland prairie sites (Wilson *et al.* 2003) and most of these are fragmented and isolated. About half of the remaining Fender's blue butterflies are located within the city limits and just west of Eugene, Oregon (Schultz *et al.* 2003), suggesting that conservation of this species will likely involve butterfly movement through human modified habitats (McEntire *et al.* 2007). Furthermore, Fender's blue appears to be limited to primarily local movements (Schultz 1998) and its primary larval host, *Lupinus sulphureus* Dougl. ex Hook. ssp. *kincaidii* [C.P. Smith] Phillips (Fabaceae), Kincaid's lupine, is also a locally restricted, threatened species that can be difficult to establish (Schultz 2001, Severns 2003). In the near future, Fender's blue will face the pressures of navigating through a matrix human modified habitats as open areas surrounding remnant native prairies are becoming increasingly urbanized. An understanding of how Fender's blue responds to roads and physical barriers that isolate butterfly populations and suitable grassland habitat will contribute important information to aid landscape level butterfly conservation planning.

I selected a population of Fender's blue butterfly that occupies remnant upland prairie in western Oregon, USA to study if a road and hedgerow were barriers to butterfly movement. This study site, ≈10km west of Eugene, contains one of the larger remnant butterfly populations that is bisected by a paved, narrow two-lane road, bordered on the east side by a 3–5m tall

hedgerow that extends for circa 100m (Fig. 1). On either side of the road habitat conditions are similar, excepting that host plant abundance in the southern subpopulation is about 10 times greater than in the northern subpopulation. Both subpopulations are surrounded by residential areas, open water, and *Populus balsamifera* L. ssp. *trichocarpa* [Torr & Gray ex Hook] Brayshaw (Salicaceae) forests. In the spring of 2007, I recorded butterfly behavior on four separate occasions on the 7th, 8th, 26th, and 28th of May on clear, sunny days above 22°C, totaling 2 hrs and 35 minutes of observation. I recorded butterfly sex and the height from the ground, <1m and ≥ 1m, that butterflies flew as they left the southern subpopulation and crossed the road. Since all but three of the butterflies that I observed flying onto the road also crossed the width of the road (≈ 8m), I recorded the flight behavior of the butterflies when they reached the hedgerow (≈100m long x 3m–5m tall). I grouped the behavior into three flight patterns; 1) those individuals that immediately returned across the road to the prairie after encountering the hedgerow (immediate returns), 2) individuals that flew over the top of the hedgerow into the next field (emigrants), and 3) those individuals that when encountering the hedgerow tracked the length of the hedgerow for at least 5 meters before returning across the road to the original field (eventual returns). Additionally, I noted the flight heights of individuals flying from the northern subpopulation (over the hedgerow) as they flew across the road (immigrants). It is likely that individual butterflies were observed more than once and that the lack of independence was likely to be substantial enough that any statistical tests on butterfly road crossing behavior would be inappropriate, so I present the percentage of observations having recorded behaviors.

In the combined observation time of 155 minutes there were 185 road-crossing events, 161 occasions were by males and 21 occasions by females (Table 1). Under the observation conditions and duration, a Fender's blue butterfly crossed the road about once every 50 seconds. Most of the butterflies observed crossing the road from the southern subpopulation also returned to the source field when encountering the hedgerow (Table 1). All of the immigrating males that flew over the hedgerow (from the north) did not turn around when they crossed the road to head back towards the hedgerow, but rather continued on into the southern subpopulation. Most males and females from the southern subpopulation flew along the base of the hedgerow for at least 5 m before returning across the road to the original field (Table 1). Since less than 10% of females and 2% of males flew over the hedgerow from the south (Table 1), it appears that hedgerow was a more substantial barrier to movement between the two subpopulations than the road. Several other studies have demonstrated that roads do not appear to substantially restrict butterfly movement (Mungira & Thomas 1992, Ries & Debinski 2001, Ries *et al.* 2001, Saarinen *et al.* 2005, Valtonen & Saarinen 2005). However, in these studies butterflies with different dispersal tendencies also differed in their behavioral response to road edges. The more vagile, strong-flying species were less sensitive to road barriers (Mungira & Thomas 1992, Ries & Debinski 2001) than butterflies that were either habitat specialists (Ries & Debinski 2001) or those that were not efficient dispersalists (Mungira & Thomas 1992, Valtonen & Saarinen 2005). Although I did not directly measure the proportion of Fender's blue butterflies that turned before encountering the road habitat, the high frequency of road crossings suggests that the road at the study site is not likely to impact dispersal, but the hedgerow was a substantial barrier to dispersal. Since grassland butterflies have been demonstrated to be sensitive to linear objects like lines of flagging (Dover & Fry 2001), forest edges (Haddad 1999), and abrupt changes in vegetation structure (Summerville *et al.* 2002, Ries & Debinski 2001), it is not surprising that the hedgerow was a substantial barrier to emigration.

One of the primary concerns with roads, besides being a potential barrier to movement, is that roads may lead to significant butterfly mortality (Munguira & Thomas 1992, Mckenna *et al.* 2001, Ries *et al.* 2001). I only observed three occasions when cars were present on the road simultaneously with Fender's blue butterflies. On all three occasions the vehicles were traveling around 40km/hr and butterflies detected the

Table 1. Summary of male and female Fender's blue flight behavior while road crossing.

	♂	♀
total observation #	161°	21
% emigrants (southern subpopulation to north)	1.2 %	9.5 %
% immediate returns	1.9 %	4.8 %
% eventual returns	96.9 %	85.7 %
% road crossing flights <1m in height	98.2 %	100 %
% road crossing flights ≥1m in height	1.8 %	–
% immigrants crossing flights < 1m in height	94.7 %	–

° three males were observed crossing the road with oncoming cars, they flew out of the road way before crossing and are not included in this table.

movement of the cars and flew to either side of the road about 10 meters before the cars reached the vicinity of the butterflies. I also checked the road and verges on each observation date for dead butterflies and found none. When it has been measured, usually < 10% of butterflies from study populations experience direct vehicle mortality (Mungira & Thomas 1992, Ries *et al.* 2001, Valtonen & Saarinen 2005), although Mckenna *et al.* (2001) suggest that a greater proportion of mortality is possible. Anecdotal Fender's blue observations suggest that the road at the study site may not be associated with a high incidence of mortality. Since this road does not have frequent vehicle traffic, generally from 30–60 cars/day, and is relatively narrow compared with other local roads, a low incidence of vehicle-associated mortality seems reasonable. However, Fender's blue flight behavior while crossing the road suggests a greater potential for mortality on wider roads with heavier traffic and greater vehicle speeds.

Nearly all of the Fender's blue butterflies observed crossing the road did so at a height <1m from ground level, regardless of whether they were emigrants or immigrants (Table 1). It appeared that most of the individuals flew within 0.5m of the ground while crossing the road. Butterflies also made many small turns, appearing to zigzag and retrace areas of the road previously covered. This type of flight is characteristic for Fender's blue while searching for resources, especially when compared to the relatively straight, higher elevation flight when butterflies encounter unsuitable habitat (Schultz 1998, Schultz & Crone 2001). It is concerning that the butterflies in this study appeared to treat the road as a habitat with potential resources when it is clearly devoid of both nectar and larval host plants. The apparent search behavior by Fender's blue butterfly while crossing the road may place more individuals in jeopardy of vehicle mortality on busier, wider roads if the behavior documented at my study site is representative of butterfly behavior while crossing most types of paved roads. Prior studies on butterfly behavior crossing roads did not focus on the flight behavior while crossing the road but rather on whether or not the butterflies crossed the road (Mungira & Thomas 1992, Mckenna *et al.* 2001, Ries *et al.* 2001, Saarinen *et al.* 2005, Valtonen & Saarinen 2005). Height from the ground and resource searching flight behavior while road crossing is likely an important determinant in the incidence of vehicle induced butterfly mortality. Mungira and Thomas (1992) witnessed butterflies being sucked down to the level of the road by passing vehicles, which were then subsequently hit by oncoming traffic, suggesting that butterflies crossing the road at shorter distances off the ground may experience a greater chance of mortality.

Given the threats of increased habitat loss through urbanization, fragmentation of remaining habitat, and overall habitat degradation by exotic species (Severns 2007), implementation of the stepping stone reserve design for the southern Willamette Valley (Schultz 1998, McEntire *et al.* 2007) should consider the position of roads and barriers to movement. Barriers to movement, like the hedgerow in this study, are not necessarily detrimental to conservation but their impacts depend upon the landscape situation in which they occur. For example, an opaque hedgerow lining a butterfly population from a busy road may decrease mortality by encouraging butterflies to fly back into the prairie habitat when encountering the habitat edge instead of crossing a road. Hedgerows or trees lining a site may be beneficial if the butterfly population is relatively large and isolated from other suitable habitat but may be detrimental if the population is small and the physical barriers restrict local butterfly colonization. Since hedgerows can be modified through cutting/planting, ephemeral vegetation barriers could be created to aid reintroduction efforts so that dispersing butterflies are forced back into the target site, increasing site residency times of reproducing individuals. These same barriers to dispersal could also be removed or modified when the target population is considered large enough to be a stable source population, for example. The successful management and conservation of Fender's blue butterfly and perhaps many other butterfly species will rely on our understanding of how adult butterflies interact within the matrix of human modified, degraded, and higher-quality remnant habitat. Clearly the study I have presented is limited in the number of study sites that prevents a more broad set of recommendations for butterfly conservation. However, Fender's blue flight behavior suggests how butterflies cross roads may be just as important to their conservation as the choice to cross or not cross roads. Studies that compare how butterflies interact with human and natural physical barriers may prove invaluable towards conserving rare and common butterflies inhabiting a mosaic of natural and urban habitats.

ACKNOWLEDGMENTS

The U.S. Army Corps of Engineers, Willamette Valley Projects, funded this project and I thank J. Matthews, K.S. Summerville, and one anonymous reviewer for their thoughtful comments that helped improve this manuscript.

LITERATURE CITED

BLAIR, R.B. & A.E. LAUNER. 1997. Butterfly diversity and human land use: species assemblages along an urban gradient. Biol. Conserv. 80:113–125.

DOVER, J.W. & G.L.A. FRY. 2001. Experimental simulation of some visual and physical components of a hedge and the effects of butterfly behavior in an agricultural landscape. Entomol. Exp. et Appl. 100:221–233.

GRAVES, S.D. & A.M. SHAPIRO. 2003. Exotics as host plants of the California butterfly fauna. Biol. Conserv. 110:413–433.

HADDAD, N.M. 1999. Corridor use predicted from behaviors at habitat boundaries. Am. Nat. 153:215–227.

MCENTIRE, E.J.B., C.B. SCHULTZ, & E.E. CRONE. 2007. Designing a network for butterfly habitat restoration: where individuals, populations and landscapes interact. J. Appl. Ecol. 44:725–736.

MCKENNA, D.D., K.M. MCKENNA, S.B. Malcom, & M.R. Berenbaum. 2001. Mortality of Lepidoptera along roadways in central Illinois. J. Lepid. Soc. 55:63–68.

MUNGIRA, M.L. & J.A. THOMAS. 1992. Use of road verges by butterfly and burnet populations, and the effect of roads on adult dispersal and mortality. J. Appl. Ecol. 29:316–329.

RIES, L. & D.M. DEBINSKI. 2001. Butterfly responses to habitat edges in the highly fragmented prairies of central Iowa. J. Anim. Ecol. 70:840–852.

_____, D.M. DEBINSKI, & M.L. WIELAND. 2001. Conservation value of roadside prairie restoration to butterfly communities. Conserv. Biol. 15:401–411.

SAARINEN, K., A. VALTONEN, J. JANTUNEN, & S. SAARNIO. 2005. Butterflies and diurnal moths along road verges: does road type affect diversity and abundance? Biol. Conserv. 123:403–412.

SCHULTZ, C.B. 1998. Dispersal behavior and its implications for reserve design in a rare Oregon butterfly. Conserv. Biol. 12:284–292.

_____. 2001. Restoring resources for an endangered butterfly. J. Appl. Ecol. 38:1007–1019.

_____ & E.E. Crone. 2001. Edge-mediated dispersal behavior in a prairie butterfly. Ecology 82:1879–1892.

_____, P. HAMMOND, & M.V. WILSON. 2003. Biology of the Fender's blue butterfly (*Icaricia icarioides fenderi* Macy), an endangered species of western Oregon native prairies. Nat. Areas J. 23:61–71.

SEVERNS, P.M. 2003. Propagation of a long-lived and threatened prairie plant, *Lupinus sulphureus* ssp. *kinc---aidii*. Restor. Ecol. 11:334–342.

_____, L. BOLDT, & S. VILLEGAS. 2006. Conserving a wetland butterfly: quantifying early lifestage survival through seasonal flooding, adult nectar, and habitat preference. J. Insect Conserv. 10:361–370.

_____. 2007. Exotic grass invasion impacts fitness of an endangered prairie butterfly. J. Insect Conserv. DOI 10.1007/s10841–007-9101-x.

SHAPIRO, A.M. 2002. The Californian urban butterfly fauna is dependent on alien plants. Divers. and Distrib. 8:31–40.

SUMMERVILLE, K.S., J.A. VEECH, & T.O. CRIST. 2002. Does variation in patch use among butterfly species contribute to nestedness at fine spatial scales? Oikos 97:195–204.

VALTONEN, A. & K. SAARINEN. 2005. A highway intersection as an alternative habitat for a meadow butterfly: effect of mowing, habitat geometry and roads on the ringlet (*Aphantopus hyperantus*). Ann. Zool. Fennici 42:545–556.

WILSON, M.V., T. ERHART, P.C. HAMMOND, T.N. KAYE, K. KUYKENDALL, A. LISTON, A.F. ROBINSON, JR., C.B. SCHULTZ, & P.M. SEVERNS. 2003. Biology of Kincaid's lupine (*Lupinus sulphureus* ssp. *kincaidii* [Smith] Phillips), a threatened species of western Oregon native prairies. Nat. Areas J. 23:72-83.

PAUL M. SEVERNS, *Oregon State University, Department of Botany and Plant Pathology, 2082 Cordley Hall, Corvallis, OR 97331;* email: severnsp@onid.orst.edu.

Received 26 June 2007; revised and accepted 1 November 2007

Journal of the Lepidopterists' Society
62(1), 2008, 57

THE LEPIDOPTERA OF THE BRANDBERG MASSIF IN NAMBIA, Part 2, Lepidoptera Africana 4, volume editor: Wolfram Mey. 303 pages, 22 color plates. 2007. *Esperiana*, Buchreihe zur Entomologie, Memoir 4, series editor Hermann H. Hacker, ISBN 3-938249-07-2. Hardbound. Copies of *Esperiana* can be ordered from the homepage at www.esperiana.net. Euro 99 (~ $144).

Because many lepidopterists, particularly in North America, may be unfamiliar with the relative new Lepidoptera journal, *Esperiana*, a review of one of the most recent issues should be of interest. The journal is named in honor of the early German lepidopterist, Eugen Johann Christoph Esper (1742-1810). First issued in 1990, *Esperiana* now comprises 13 volumes devoted primarily to the Palearctic Lepidoptera. A memoir series focused on monographs of the African fauna was initiated in 2004.

The Ethiopian Region has seldom received the attention it deserves in most areas of entomology, particularly in the more primitive, usually smaller species generally referred to as Microlepidoptera. This lack of attention, of course, is largely the result of the paucity of researchers focused on this enormous region. The pioneering works by A. J. T. Janse over many years on the South African Lepidoptera and the most recent Catalogue of the Lepidoptera of southern Africa (Vari et al. 2002) have provided valuable introductions to this fauna. The latest effort to increase our knowledge of the Ethiopian Region was initiated by Wolfram Mey of the Museum für Naturkunde, Humboldt Universität, Berlin, Germany, and several collaborators, with an entomological survey of one of the most poorly known areas in Namibia, the Brandberg Massif. The first report on the three Brandberg expeditions (Mey 2004) provided a general introduction to their survey including an itinerary, description of collecting sites, and list of participants. It also provided the taxonomic treatment of 28 families of Lepidoptera. The present volume comprises the second and final report, with treatments for approximately 30 additional families. The taxonomic studies in both reports include related material from other areas of southern Africa in addition to the Brandberg. Of particular significance in Part 2 are the list of all species studied and the summaries of the Lepidoptera diversity of the Brandberg Massif compared with three other areas of Africa.

Most of Part 2 consists of 20 sections by 13 authors treating in varying detail the systematics of approximately 30 families. A few sections (e.g., Noctuidae by H. Hacker) are supplements to Part 1. All are written in English except for the section on Pyralinae in French by P. Leraut. Each section begins with a brief introduction to the subject taxonomic group and includes paragraphs on general biology, materials and methods, often comments or lists on African diversity, a review of the species studied, illustrations of morphology, and references. Complete taxonomic descriptions usually are provided only for new taxa, occasionally supplemented with descriptions of previously named genera. Previously known and undetermined species are provided with only collecting data and summaries of general distribution. Treatments of the various families vary largely according to their relative diversity and degree of familiarity, as well as to the specialties of the authors. For example, the only section that includes species keys is the one by Mey on the small, but well sampled, southern hemisphere family Cecidosidae. The genitalia of all new taxa and most of the undetermined or named species are illustrated by either line drawings or photographs. Good quality color photographs are likewise provided for all new taxa and most of the undetermined or named species whenever possible.

In the final chapter of Part 2, appropriately titled "Epilogue", Mey summarizes the major findings of the entire project. A total of 58 families and 683 species of Lepidoptera are treated to some degree in both volumes from the general region around the Brandberg. The actual number of species from the three Brandberg expeditions was 611, with the Noctuidae being the most species-rich (134 species). Nine new genera and 124 new species were described. In an appropriate conclusion, undoubtedly based upon what was learned from the Brandberg survey, Mey proposes several other areas in the Afrotropical region now in need of attention.

Because several poorly known families are reviewed and illustrated in both volumes of this series, most Lepidopterists should find something of interest within the Memoirs. Wolfram Mey and his colleagues should be congratulated, not only for their fine efforts to collect and report on this previously poorly known fauna, but also for completing the entire task through to publication only five years after cessation of fieldwork.

LITERATURE CITED

MEY, W. (ed.). 2004. The Lepidoptera of the Brandberg Massif in Namibia, part 1. Lepidoptera Africana 4. *Esperiana*. Memoir 1, 333pp., 14 plates.

VARI, L., D.M. KROON, AND M. KRUGER. 2002. Classification and checklist of the species of Lepidoptera recorded in southern Africa. Simple Solutions Australia Ltd., Chatswood, XXI + 384pp.

DONALD R. DAVIS, *Department of Entomology, P.O. Box 37012, Smithsonian Institution, Washington, D.C. USA. 20013-7012. email: davis.don@nmnh.si.edu.*

Journal of the Lepidopterists' Society
62(1), 2008, 58–59

CHRYSALIS: MARIA SIBYLLA MERIAN AND THE SECRETS OF METAMORPHOSIS. By Kim Todd. 330 pages, 8 black-and-white and 8 color plates; 8 x 5.25 in.; ISBN 978-0-15-603299-5 (paperback), ISBN 978-0-15-101108-7 (hardcover); US$15 (paper). A Harvest Book of Harcourt, Inc., Orlando, New York and London. Publication date: 2007.

As a penurious graduate student 40 years ago, I spent a significant amount of my savings on a full-size facsimile edition of Maria Sibylla Merian's "Insects of Surinam." Many years later my wife surprised me with an authentic Merian butterfly plate, which hangs proudly in our living room. It shows the familiar Gulf Fritillary, *Agraulis vanillae*. That plate lies at the very heart of a mystery about Madame Merian. I read this book hoping it would solve that mystery. But it didn't.

"That curious Person Madam Maria Sibylla Merian," as her contemporary and patron James Petiver famously styled her, was just that. Reared in Frankfurt in a family and social circle of publishers, printers, artists, craftsmen and engravers, she found her vocation in collecting, rearing and painting caterpillars and what issued from them: butterflies and moths, but also parasitoids. "She was," as a tropical biologist quipped to me recently, "the Dan Janzen of her day." Married at 16, mother of two daughters, she eventually tired of her domestic arrangements and left her husband in order to join a religious commune. He tracked her to the commune's door and camped outside, but she refused to see him and eventually he went away and secured a divorce. But she tired of the pietistic discipline and moved to the bustling capital of Amsterdam, where, as a 52-year-old divorcee, she conceived the notion of traveling to the Dutch colony of Surinam on the north coast of South America to rear and paint tropical insects. And that is exactly what she did, setting sail in June 1699, accompanied by her 21-year-old daughter Dorothy. They spent two years in Surinam. The resulting artworks made her reputation.

In writing a biography of this strong-willed, independent, fearless woman, Kim Todd has done her scholarly homework. Because so little tangible evidence of Merian's life exists, she artfully fills in the blank spaces with vignettes of life in the intellectual circles of Germany and Holland, in the commune founded by Jean de Labadie, and in the sultry backwaters of the Guianas where slavery was an omnipresent evil. She attempts to make a case that Merian was in fact a major innovator insofar as she attempted to pursue the life histories of Lepidopterans as integrated wholes and to represent them artistically in an "ecological" way, on their host plants and in the company of their natural enemies. She suggests that Merian helped significantly in banishing the outlandish notions of spontaneous generation and transformism that had colored zoology right into the seventeenth century. In her Epilogue, she attempts to tie her fascination with metamorphosis to contemporary research in developmental genetics, insect hormones, and phenotypic plasticity. I think it is fair to say that while she may have contributed some to the emergence of such science, her contemporary Swammerdam, for one, contributed quite a bit more. Merian's achievement is extraordinary enough without having to stretch to tie her to the latest stuff in "evo-devo."

Which brings us to the mystery.

There is no doubt that Maria Merian reared many Lepidopterans to the adult, both in Europe and in Surinam. Her extant notes and her illustrations make that clear. But from the very beginning, the composition of her paintings shows more "art" than "science." Her Book of Flowers, published in three volumes between 1675 and 1680, portrays European garden and wild flowers, often (usually!) accompanied by meticulously-rendered insects, including Lepidoptera—some of the most subtle representations I know of that fauna. But the insects bear no "ecological" relationship to the flowers; they are clearly there only for artistic reasons. Thus the Peony plate has a lovely female *Lycaena phlaeas* which, however, would have nothing to do with a Peony since it is neither a nectar source nor a larval host. Likewise the Magpie Moth (*Abraxas grossulariata*) shown with a garden hyacinth…and so on. The seemingly random placement of insects with plants becomes a real problem, however, when it comes to her Surinam work. Here, because almost everything illustrated was new to science, the assumption that she was in fact giving an integrated "ecological" view of the life history was not only natural, and seemingly encouraged by her; it was frequently unjustified. Todd attempts to excuse the problem in terms of material lost in shipment and so forth (p. 206). She also acts as if it is a minor problem. But it isn't, and that takes us back to the Gulf Fritillary plate in my living room.

Have you ever wondered why the Gulf Fritillary is named *vanillae* when it has nothing to do with vanilla (which comes from an orchid)? The name is Linnean, from the Systema Naturae, 10th edition (1758), p. 482. If you go to p. 482 (which you can do on-line, since the entire work has been digitized and posted), you find

Linnaeus gives the reference "Merian Surin. 25 t.25.—Habitat in Epidendro vanilla. Americes." And there is the plate, with upper and under surfaces of the butterfly, somebody else's caterpillar, and a cast skin of what appears to be a Papilionid pupa, all on a vanilla orchid, just as the text says. The story is perfectly clear. Linnaeus described and named the animal from Merian's plate—there never was a type-specimen—and he inferred that it lived on vanilla. (Johannes Fabricius knew that the bug eats *Passiflora* and tried to rename it *passiflorae*. But that's another story.

Another familiar tropical American butterfly, the White Peacock (*Anartia jatrophae*) presents an identical tale. Todd actually reproduces the guilty plate, representing the butterfly together with Cassava, *Manihot esculenta*, but then called *Jatropha manihot*. Once again the describer (Linnaeus' pupil Johansson, in his thesis which forms part of the compilation Amoenitates Academicae) cites "Merian Surin. 4 t.4—Habitat in Jatropha. Americes (p.408)." Again no type specimen, only an illustration and an unwarranted assumption. *Anartia jatrophae* does not eat Cassava. It eats a bunch of other things, none of them in the Euphorbiaceae like Cassava.

So if Merian was so dedicated to working out the secrets of metamorphosis, why are so many of her plates deceptive? (The one reproduced on the cover has a *Morpho*, a non-morphid caterpillar, another Papilionid pupal case, and a flowering and fruiting branch of pomegranate—not a Surinam native.) Clearly, Kim Todd cannot tell us.

Postscript: In 1999 Prestel-Verlag (Munich) published a lovely facsimile edition of (selected pages from) Merian's Book of Flowers. It contains an outstanding short biography of Merian by Thomas Buerger (1999), which is not cited by Todd. If you would like the solid story in concise form, shorn of its background color but with an art historian's slant, you might prefer it to Chrysalis. But Buerger doesn't solve the mystery either.

LITERATURE CITED

BUERGER, T. 1999. Stations of an artist in the Baroque Age: Frankfurt am Main, Nuremberg, Amsterdam, Surinam. Pp. 82–88. in: M.S. Merian. New Book of Flowers. Prestel-Verlag, Munich.

ARTHUR M. SHAPIRO, *Center for Population Biology, University of California, Davis, CA 95616. e-mail: amshapiro@ucdavis.edu.*

Journal of the Lepidopterists' Society
62(1), 2008, 60

MANUSCRIPT REVIEWERS FOR 2007 (VOLUME 61)

Manuscript reviewers are anonymous contributors to the scientific rigor, clarity, and quality of text and illustrations in the papers published by the Journal of the Lepidopterists' Society. The reviewers' input is invaluable and always welcomed by authors, editors and readers. We hope their careful work continues to allow the Journal to increase quality and readership. On behalf of all the authors and the editorial staff of the Journal, respectful acknowledgement is given to the reviewers for contributions published in Volume 61.

James Adams, Calhoun, GA
Susan Borkin, Milwaukee, WI
Lincoln Brower, Roseland, VA
John Brown, Washington, DC
Richard Brown, Missisippi State, MS
John Burns, Washington, DC
Michael Collins, Nevada City, CA
Thomas Dimock, Ventura, CA
Robert Dirig, Ithaca, NY
Marc Epstein, Sacramento, CA
Todd Gilligan, Columbus, OH
Paul Goldstein, Gainesville, FL
James Hayden, Ithaca, NY
Ronald Hodges, Eugene, OR
Jean-Francois Landry, Ottawa, ON, Canada
Ron Leuschner, Manhattan Beach, CA
Tim McCabe, Albany, NY
Eric Metzler, Alamogordo, NM
William Miller, St. Paul, MN
David Nunalee, Sammamish, WA
Karen Oberhouser, St. Paul, MN
Harry Pavulaan, Herndon, VA
Richard Peigler, San Antonio, TX
Michael Pogue, Ellicott City, MD
Greg Pohl, Edmonton, AB, Canada
Jerry Powell, Berkeley, CA
Robert Robbins, Washington, DC
Brian Scholtens, Mt. Pleasant, SC
Art Shapiro, Davis, CA
John Shuey, Indianapolis, IN
Jeff Slotten, Gainesville, FL
John Snyder, Greenville, SC
Ann Swengel, Baraboo, WI
Felix Sperling, Edmonton, AB, Canada
James Troubridge, Ottawa, ON, Canada
Jim Tuttle, St. Kilda, Victoria, Australia
Andrew Warren, Gainesville, FL
Susan Weller, St. Paul, MN
Wayne Whaley, Orem, UT
Ernest Williams, Clinton, NY

Date of Issue (Vol. 62, No.1): 6 May 2008

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 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.

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