Volume 59 Number 1
8 April 2005
ISSN 0024-0966

Journal of the Lepidopterists' Society

8 April 2005

Published quarterly by The Lepidopterists' Society

THE LEPIDOPTERISTS' SOCIETY

Executive Council

Editorial Board

Honorary Life Members of the Society

Charles L. Remington (1966), E. G. Munroe (1973), Ian F. B. Common (1987),
Lincoln P. Brower (1990), Frederick H. Rindge (1997), Ronald W. Hodges (2004)

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
Airmail postage for the *News* $15.00

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: Hop Merchant, *Polygonia comma* (Harris), sunning on Halloween, 2004, central Illinois, USA. Photo by Peg Toliver

JOURNAL OF
THE LEPIDOPTERISTS' SOCIETY

Volume 59 2005 Number 1

Journal of the Lepidopterists' Society
59(1), 2005, 1 - 5

SPRING RECOLONIZATION RATE OF MONARCH BUTTERFLIES IN EASTERN NORTH AMERICA: NEW ESTIMATES FROM CITIZEN-SCIENCE DATA

ANDREW K. DAVIS
Dept. of Environmental Studies, Emory University, Suite E510, 400 Dowman Dr., Atlanta, GA 30322
AND
ELIZABETH HOWARD
Journey North 6234 Mt. Philo Road, Charlotte, Vermont 05445

ABSTRACT: Monarch butterflies in eastern North America return each year from their overwintering site in central Mexico to recolonize their range in the eastern US and Canada. Current knowledge of the spring recolonization rate (i.e the rate of advancement) comes from observations of eggs and larvae along a latitudinal gradient. Journey North is a website-based program whereby citizen-scientists report their first sightings of adult monarch butterflies each spring. We used 7 years of this sighting data combined with GIS technology to derive new estimates of the rate of monarch recolonization based on the cumulative area occupied and the rate of movement of the advancing wave front. We further used these data to examine differences between and within years (we divided each season into 12 time intervals) in the recolonization rate. Across all years, the average rate of recolonization was 71.6 km/d. We found no statistical difference between the annual (season average) estimates, which ranged from 66.6 to 78.1 km/d. Within seasons, we observed 4 distinct phases of the spring migration, consistent with previous work, and there was significant variation within years (i.e. between time intervals) in the rate of recolonization, with the migration wave front progressing the fastest (over 100 km/d) from 20 March to 9 April, and from 19 May to 29 May. Based on these new estimates, we conclude that the spring migration of monarch butterflies in eastern North America progresses faster than previously estimated, and the temporal patterns observed each year are remarkably constant.

Each spring, monarch butterflies (*Danaus plexippus*) in eastern North America return from their overwintering site in central Mexico to repopulate their breeding range, ultimately reaching most US states and Canadian provinces east of the Rocky Mountains. This fascinating journey is made even more complex by the fact that recolonization is completed by two successive generations of monarchs (Cockrell et al. 1993, Malcolm et al. 1993, Brower 1995). Many monarchs at the overwintering colonies mate before migrating north in the spring (Van Hook 1993, Oberhauser and Frey 1997). As they migrate northward, the mated females then lay eggs on the newly emerging milkweed plants. Although the exact distance traveled by these first-generation females is difficult to ascertain, evidence suggests that this recolonization process is accomplished in two or three phases. Adults returning from Mexico travel as far north as 35° latitude, or the southern portion of the United States (Cockrell et al. 1993) before they die. The offspring and grand-offspring derived from these eggs then complete the second and third phase of the journey northward to the northernmost areas of the monarchs' breeding range in the northern US and southern Canada. This recolonization process has been referred to as the 'successive brood' migration strategy (Malcolm et al. 1993).

Much of what is known about the timing of monarch recolonization is the result of a comprehensive study published by Barbara Cockrell, Stephen Malcolm and Lincoln Brower (Cockrell et al. 1993). In this study, detailed observations of spring oviposition timing were recorded over three successive years at many locations throughout the monarchs' eastern range. The authors provided evidence for the successive brood migration strategy, and demonstrated that the rate of recolonization northward does not proceed at a constant speed, but varies due to the lag of larval development of the second brood midway through the migration.

A decade later, our knowledge of the monarchs' spring migration has improved, largely due to the internet-based, citizen-science program called Journey North (http://www.learner.org/jnorth/). Established in 1994, Journey North is a web-based citizen science program where school children, educational groups and other volunteers throughout North America report the first sighting they make of an adult monarch butterfly each spring. The date and location of the sighting are recorded by the participants online and these data are archived by Journey North staff. At regular intervals during the spring, the sightings are plotted on a map of North America by Journey North staff, allowing the online participants to view their sighting along with other sightings from around North America. When all observations are combined and plotted by Journey North staff, viewers can see the northward progression of the monarchs' spring migration via the timing of participant sightings.

Although the Journey North program is used primarily as an educational tool for teachers, the data generated by the program have demonstrated their scientific value in increasing our knowledge of this critical phase of the monarch life cycle. We used the first 6 years of the Journey North data in a previous paper to document the state-by-state pattern of spring migration in the eastern North American population (Howard and Davis 2004). By using the timings and locations of monarch 'first sightings' reported by Journey North participants throughout the spring migration range we showed that there was an annual and nontrivial eastward movement of monarchs from southern Texas along the southeastern states before the migration wave front proceeds northward.

In the present paper, we used 7 years of Journey North data combined with GIS technology to derive updated estimates of the rate of spring recolonization based on both northward and eastward movement from southern Texas (which we used as the 'starting point' for the migration). We also used these revised rate data to determine if the rate of recolonization varies between and within years.

METHODS

Calculating recolonization rate. Journey North data consisted of citizen-science observations of first sightings of monarchs every year (usually between March and July for the spring migration), which includes the year, date and location (latitude, longitude) of the sightings. Further details of the Journey North data collection protocols have been addressed previously (Howard and Davis 2004) and are online at http://www.learner.org/jnorth/. We used data from 1997 to 2003 for this study. To measure the recolonization rate we used a method similar to that used by researchers to track the spatial spread of species invasions (reviewed in Shigesada and Kawasaki 1997) and infectious diseases (e.g. Dhondt et al. 1998). We calculated the area occupied by monarchs at successive time intervals during the spring to estimate the rate of expansion of the outer edge of the recolonized area. To derive time intervals we divided the Journey North data for each spring into 12 intervals of 10 days each. These intervals began and ended on the same julian dates each year (March 1 to July 28). We then digitally plotted the point locations of each Journey North monarch observation (based on the associated spatial coordinates of each sighting) onto a map of eastern North America using ArcView version 3.2a (Environmental Systems Research Institute, Inc., Redlands, CA, USA). For each 10-day interval in each year, we manually traced the smallest possible polygon around the outermost monarch observations that were made within that time interval (Fig. 1). Thus, each year as the migration expanded in each successive time interval, so did the size of the cumulative area within each successive polygon. We calculated the area of each polygon (in square kilometers) with a simple ArcView function. All polygons were drawn over land area only, and did not extend over ocean areas. Furthermore, to ensure that we were tracking the spread of monarchs that originated only in Mexico, we conservatively drew polygons over monarch sightings that took place only at 30 degrees north latitude and above.

To estimate the recolonization rate for each 10-day time interval we determined the amount of increase in polygon area from one 10-day interval to the next (km^2/d), then calculated the square root of this value to obtain an estimate of the linear rate of increase (km/d) over the 10-day interval. Dividing this value by 10 resulted in the rate (km/d) of recolonization per day. This value then represented our estimate of the speed (per day) at which the leading edge of the migration wave front progressed outward (which we infer to represent monarch recolonization) in all directions for each of our time intervals. Since we calculated the area of 12 time intervals, and our rate estimate is based on the difference in area between successive intervals, we ended up with 11 estimates of recolonization rate per season (or migration), over 7 seasons.

Statistical Analysis. To test for differences in the recolonization rate between intervals and years, we performed a univariate ANOVA using our recolonization rate estimates as the dependent variable, and using year as a fixed factor and time interval as a cofactor. An interaction effect between year and time interval was also included. This analysis was performed using SPSS software (SPSS 2001), and significance was accepted when $p<0.05$.

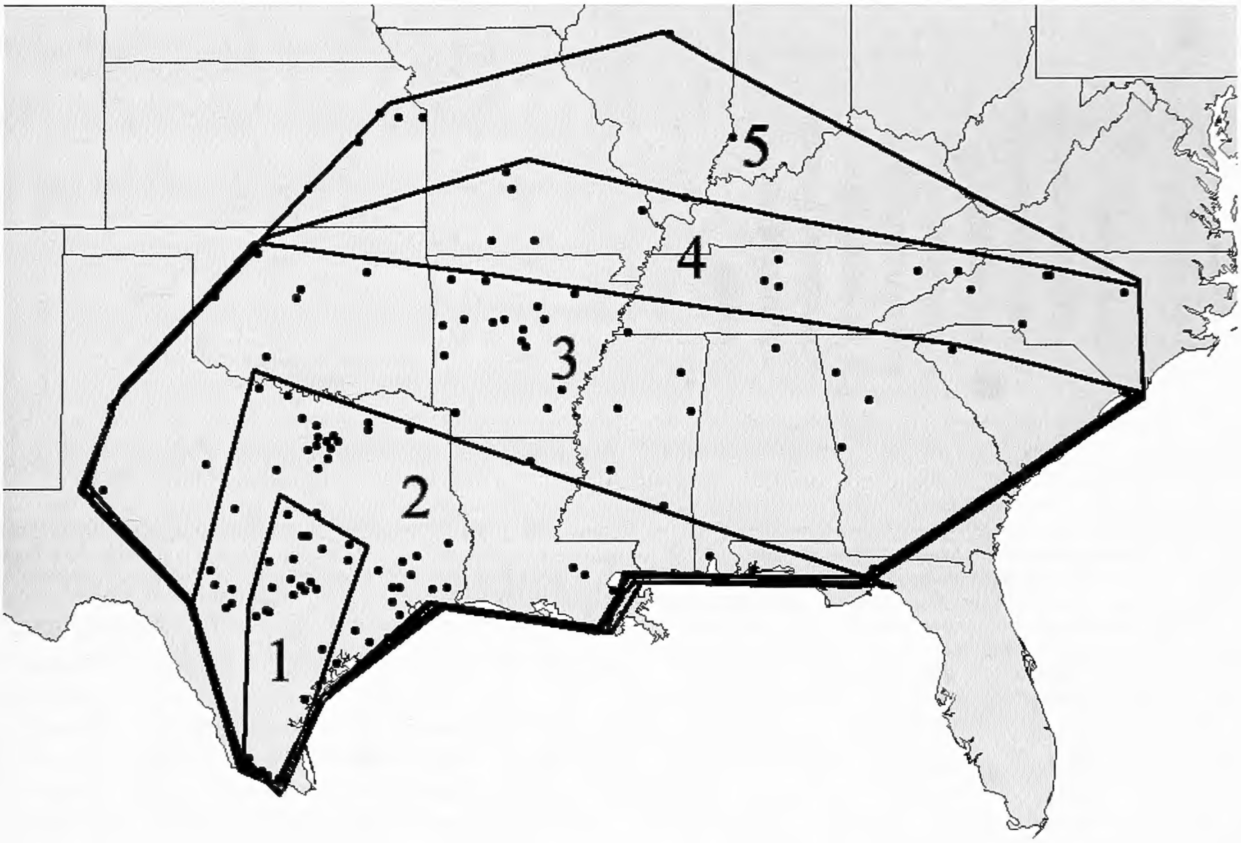


FIG. 1. Method used for assessing the recolonization rate of monarch spring migration using Journey North sightings. All monarch sighting locations (black dots) were plotted in Arcview (version 3.2). For each 10-day interval the smallest possible polygon was drawn around the sightings (dots) in that interval. The increase in area between successive polygons was calculated and the migration speed was calculated as the square root of this area increase. Numbers in figure denote successive 10-day time intervals.

RESULTS AND DISCUSSION

The average rate of recolonization across all years and all time intervals was 71.6 km/d, with the annual average ranging from 66.6 to 78.1 km/d over the 7 years examined in this study (Table 1). Maximum rates each year ranged from 111.0 to 165.9 km/d, and there was significant variation in the recolonization rate between intervals (df=1, F=20.1, p<0.001; Fig. 2). The 7-year average rates shown in figure 2 indicate that monarchs usually recolonized their range the fastest during the 3rd, 4th and 9th time intervals. We detected no significant effect of year on the recolonization rate with our analysis-of-variance test (df=6, F=0.101, p=0.996), nor was there a significant interaction between interval and year (df=6, F=0.155, p=0.987). The lack of a significant interaction effect between year and time interval in our ANOVA test indicates that there was little annual variation in this overall pattern (i.e. with respect to the rate) of spring recolonization. This result is not surprising, given the similar results we previously described, that there is little annual variation in the spatial pattern (i.e. state by state occupation) of migration (Howard and Davis 2004). Combined, these results speak to the consistent nature of the spring migration.

The estimates of recolonization rate we derived differ considerably from previous estimates. Before it was known that the spring migration is composed of two sets of cohorts, an early estimate of the spring recolonization rate was 4 km/day, assuming a constant rate of travel throughout the spring (Baker 1978). Cockrell et al. (1993) revised this estimate based on their observations of spring oviposition timing. They estimated a northward (only) rate of recolonization of 14 km/d, assuming a constant rate of travel. They also demonstrated how the spring migration can be divided into 4 time phases and calculated rates of 96.0, 12.4, 52.0, and 8.2 km/d for each phase, respectively (Fig. 3). Our maximum rate over all intervals in all 7 years was 165.9 km/d, considerably greater than the maximum

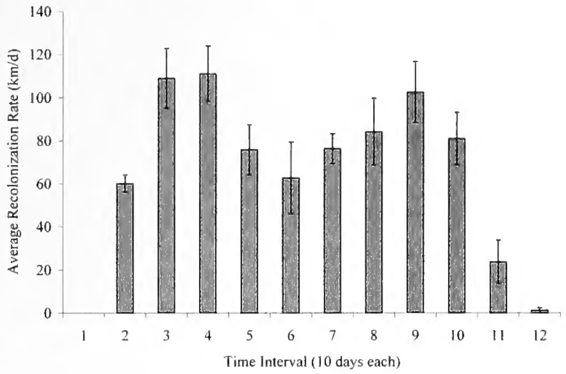


FIG. 2. Mean recolonization rate from one 10-day interval to the next over the 7 years studied. Standard error bars shown. Intervals begin on 1 March and end on 28 June.

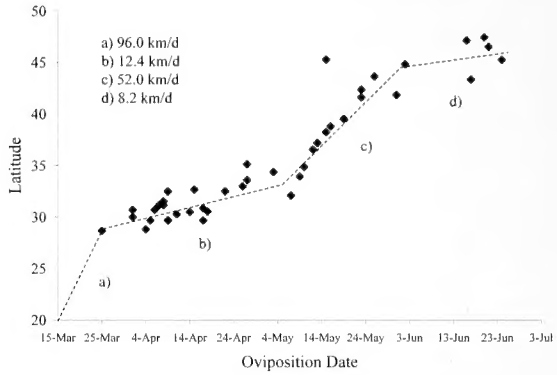


Fig. 3. Plot of timing of spring oviposition in relation to latitude, as shown in Cockrell et al. (1993). Reproduced with permission.

TABLE 1: Monarch spring recolonization rate estimates (in km/d) calculated for each 10-day interval in each year examined in this study. Rate calculated by determining the increase in geographic area occupied by the migration wave front from one time interval to the next (expressed in km2), deriving the square root of the increase (expressed in km), and dividing by 10.

Int[a]	Date[b]	1997	1998	1999	2000	2001	2002	2003	Average
2	10-Mar	61.3	75.9	52.4	53.1	61.2	46.3	70.9	60.2
3	20-Mar	157.8	69.7	98.8	102.2	63.5	150.9	119.7	108.9
4	30-Mar	110.1	128.0	165.9	133.1	94.6	71.0	74.5	111.0
5	9-Apr	46.8	105.9	53.0	81.9	127.8	55.4	59.5	75.8
6	19-Apr	0.0	29.9	29.7	82.9	126.6	77.3	92.2	62.7
7	29-Apr	94.6	58.3	86.4	93.4	54.4	58.0	88.9	76.3
8	9-May	62.2	153.7	66.5	43.5	126.5	53.0	83.0	84.1
9	19-May	77.6	38.5	108.2	107.6	96.4	147.7	141.2	102.4
10	29-May	129.1	26.2	101.5	94.0	66.3	72.5	76.8	80.9
11	8-Jun	49.6	61.2	0.0	11.8	0.0	0.0	43.3	23.7
12	18-Jun	0.0	0.0	0.0	0.0	0.0	0.0	8.7	1.2
Average		71.7	67.9	69.3	73.0	74.3	66.6	78.1	

[a] Interval - recolonization rates shown in each time interval are based on increases in migration wave front area between it and the previous time interval. Interval 1 not shown.

[b] date of the first day of each 10-day interval is show

rate obtained by Cockrell et al. (1993), of 96 km/d. However, despite being collected over a decade apart, and with two completely different methods, the data gathered by citizen-scientists in the Journey North program and that of Cockrell et al. (1993) show some remarkable similarities. For comparison with the results from that study, we plotted the area encompassed by the migration front at each time interval (Fig. 4). In this plot, one can distinguish the same 4 phases described by Cockrell et al. (1993; Fig. 3) in most years. For the most part, the spring recolonization (from Texas) begins with a rapid increase in area in intervals 2,3 and 4, which corresponds roughly to the first three weeks of April. The expansion then slows until interval 8, when it undergoes another rapid increase in area. The entire migration always slows and reaches a plateau by interval 11 (which begins on June 8). Interestingly, Fig. 4 also indicates that by the end of the migration each year, there is little variation in the size of the geographic range occupied by monarchs.

Since the Cockrell data is based on latitudinal movement, another useful comparison of these two data sets would be to create estimates based on latitudinal movement from the Journey North data. We did this by plotting the latitude of all 7 years of Journey North observations up to July 27 (2912 records) against its date (Fig. 5), which was done in the Cockrell paper. When a linear regression line is fitted to this data, the slope of the line indicates the overall rate of northward (latitudinal) recolonization, assuming a constant rate of

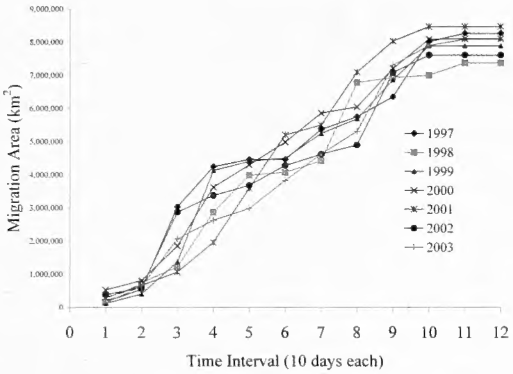


FIG. 4. Plot of the increase in area (km^2) occupied by the monarch migration in each 10-day interval for each year. Intervals begin on 1 March and end on 28 June.

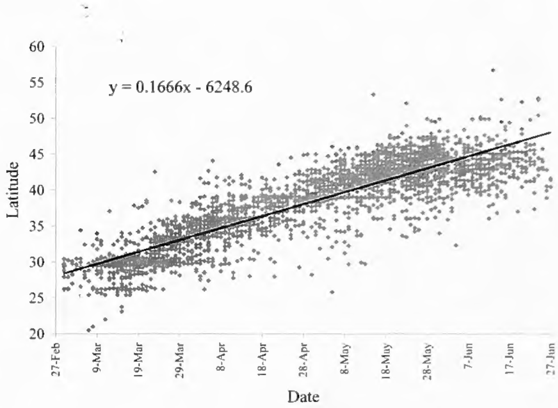


FIG. 5. Relationship between latitude and date using all Journey North spring monarch sightings from 1997-2003 up to July 27 (N=2912). The slope of the trendline (0.1666° lat./day) indicates a northward (only) recolonization rate of 18.4 km/day

progression throughout the migration. For the Journey North data, the slope of this line was 0.16 degrees of latitude per day, which translates to 18.4 km/d (1 degree latitude equals 110.6 km). The slope of the same regression line in Cockrell et al. (1993) indicated a rate of 14 km/d.

We conclude that the rate of advancement of the spring recolonization proceeds faster than previously described, although the overall pattern of recolonization is remarkably consistent year to year. Further, based on the similarities with previous results obtained, we conclude that the citizen-science based data gathered by Journey North is a valid scientific resource and is as accurate in tracking migration patterns as scientific observers.

ACKNOWLEDGEMENTS

This study could not have been completed without the thousands of dedicated citizen-scientists who contributed their observations each year to Journey North. We thank the Journey North staff for help in the data collection. Lincoln Brower provided advice on many occasions to the Journey North program. Sonia Altizer made helpful comments on all stages of this manuscript. Funding for Journey North has been provided in full by Annenberg/CPB.

LITERATURE CITED

BAKER, R. R. 1978. The evolutionary ecology of animal migration. Hodder and Stoughton, London.

BROWER, L. P. 1995. Understanding and misunderstanding the migration of the monarch butterfly (Nymphalidae) in North America: 1857-1995. J. Lepid. Soc 49:304-385.

COCKRELL, B. J., S. B. MALCOLM, AND L. P. BROWER. 1993. Time, temperature, and latitudinal contraints on the annual recolonization of eastern North America by the monarch butterfly. Pages 233-251 *In* S. B. Malcolm and M. P. Zalucki, editors. Biology and conservation of the monarch butterfly. Natural History Museum of Los Angeles County, Los Angeles, CA.

DHONDT, A. A., D. L. TESSAGLIA, AND R. L. SLOTHOWER. 1998. Epidemic mycoplasmal conjunctivitis in House Finches from eastern North America. J. of Wildl. Dis. 34:265-280.

HOWARD, E., AND A. K. DAVIS. 2004. Documenting the spring movements of monarch butterflies with Journey North, a citizen science program. Pages 105-114 *In* K. Oberhauser and M. Solensky, editors. The monarch butterfly. Biology and Conservation. Cornell University Press, Ithaca, NY.

MALCOLM, S. B., B. J. COCKRELL, AND L. P. BROWER. 1993. Spring recolonization of eastern North America by the monarch butterfly: successive brood or single sweep migration? Pages 253-267 *In* S. B. Malcolm and M. P. Zalucki, editors. Biology and conservation of the monarch butterfly. Natural History Museum of Los Angeles County, Los Angeles, CA.

OBERHAUSER, K., AND D. FREY. 1997. Coercive mating by overwintering male monarch butterflies. Pages 67-78 *In* W. A. Haber, L. Merino, K. Oberhauser, I. Pisanty, and T. Wilkinson, editors. 1997 North American conference on the monarch butterfly. Comission for Environmental Cooperation, Montreal, Quebec, Morelia, Michoacan, Mexico.

SHIGESADA, N., AND K. KAWASAKI. 1997. Biological Invasions: theory and practice. Oxford University Press, New York.

SPSS. 2001. Version 11.0.1. SPSS, Inc., Chicago.

VAN HOOK, T. 1993. Non-random mating in monarch butterflies overwintering in Mexico. Pages 49-60 *In* S. B. Malcolm and M. P. Zalucki, editors. Biology and conservation of the monarch butterfly. Publications of the Natural History Museum of Los Angeles County, Los Angeles, CA.

Received for publication 20 February 2004; revised and accepted 17 July 2004

Journal of the Lepidopterists' Society
59(1), 2005, 6 - 9

THE LIFE HISTORY OF *NOCTUANA HAEMATOSPILA* (HESPERIIDAE: PYRGINAE) IN ECUADOR

HAROLD F. GREENEY[1]
Yanayacu Biological Station and Center for Creative Studies, Cosanga, Ecuador,

AND

ANDREW D. WARREN[2]
Department of Zoology, Oregon State University, Corvallis, Oregon, 97331 USA

Noctuana Bell is a genus of about 6 medium-sized, rather similar pyrgine species, all of which are confined to the Neotropics. The genus was described primarily on the basis of its rather unique, "distinctly swollen" antennal clubs (Bell 1937:7). These skippers have rather long palpi, narrow wings with a pointed forewing apex, slightly to prominently scalloped wing margins, and are mottled on top with contrasting dark bands and indistinct smears. This mottled dorsal pattern gives these skippers a somewhat noctuid-like appearance, reflected in their generic name. Two species in the genus have striking, red to yellow markings contrasting against otherwise dark ventral hind-wings. One of these species, *Noctuana stator* (Godman & Salvin), has one or two rows of red to orange spots along the ventral hindwing margin; this species has recently been reported from south Hidalgo Co., Texas, USA (from a photograph), presumably as a stray individual (see Anonymous 2000). The other *Noctuana* species with red to yellow hindwing markings against an otherwise dark background is *N. haematospila* (C. Felder & R. Felder), the subject of this report.

Arguably the showiest of the *Noctuana* species, *N. haematospila* has been illustrated in color by Draudt in Seitz (1924:pl. 177), Lewis (1987:84) and Piñas & Manzano (1997:59), and was illustrated in great detail (although not in color) in its original description (C. Felder & R. Felder [1867:pl. 73]); also see Fig. 1 herein. *Noctuana haematospila* is distributed through the northern Andes Mountains, from Venezuela (its type locality) to Bolivia (Evans 1953), and it is widely distributed at elevations above 1000 m in Ecuador (Williams & Hawyard 1944). To date, no reports on adult behavior, larval food plants, or larval ecology have been published for any *Noctuana* species. Below we present notes on the adult and larval behavior and ecology of *N. haematospila* in an eastern Ecuadorian cloud forest.

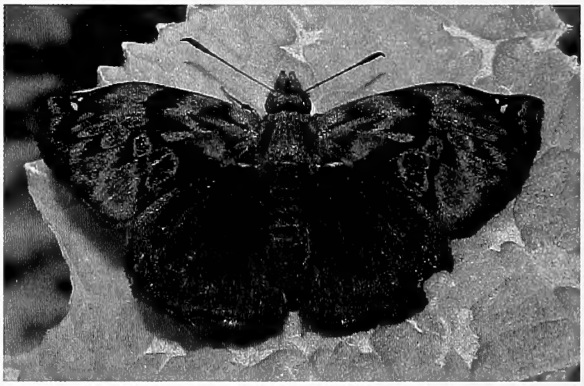


FIG. 1. Adult *N. haematospila* basking along roadside, at study site in Napo Province.

MATERIALS AND METHODS

All collections and observations of adults and immatures of *N. haematospila* were made at the Yanayacu Biological Station and Center for Creative Studies, located at an elevation of 2200 meters in the Quijos Valley of Napo Province in eastern Ecuador. The study site is situated approximately five kilometers west of the town of Cosanga, in Napo Province, and is composed of over 1500 hectares of primary cloud forest bordered by pastures, roads, farmland, and other disturbed habitats.

On 29 July 2000, 23 early instar larvae and one fourth instar larva were collected from *Rubus* L. (Rosaceae) plants along road margins adjacent to a disturbed habitat and cattle pasture at the study site. Larvae were transported in plastic bags to the Yanayacu Station and reared in separate, glass containers. Fresh food plant leaves were added daily and old leaves and frass were removed. The jars were wiped dry periodically to prevent build-up of pathogenic bacteria and fungi. Subsequently, numerous larvae were collected from similar situations at the study site, and observations were made on larvae of all instars in the field and in the lab. To avoid potential laboratory artifacts affecting shelter construction, all observations on shelter building behavior were made in the field prior to collection. A total of over 200 larvae of *N. haematospila* were

---

[1] c/o Carrion No. 21-01 y Juan Leon Mera, Quito, Ecuador

[2] Research Associate, Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México, Apdo. Postal 70-399, México, D.F. 04510 México

observed and tracked for this study, and great effort was made to study individual larvae in nature throughout their development. No oviposition events were witnessed, but over 100 partial egg shells and 17 eggs were encountered in the field. Two first instar larvae, newly hatched, were observed during shelter construction. Terminology for discussion and descriptions of larval shelters follows Greeney & Jones (2003). All voucher material is deposited in the collection of the senior author.

RESULTS

Adult *N. haematospila* are found sporadically throughout the year at our site. They are always associated with disturbed areas and are most common along road cuts where males guard low perches up to 1.5 m above the ground. Adults were active throughout the day during periods of sun, often sitting with wings spread in particularly sunny areas (Fig. 1). They evidently visit flowers only infrequently, and to date only one unsexed adult has been seen feeding at flowers of *Erato* sp. (Asteraceae). Most commonly, adults visit moist soil, dung, and carrion.

Larvae of *Noctuana haematospila* were found feeding on two species of *Rubus* L. (Rosaceae) at our study site in eastern Ecuador. These plants are common along roadsides, in pastures, and in other disturbed areas. First instar larvae were found from June to November. Larvae appeared to feed more frequently around dusk and dawn, but detailed periodicity of feeding has not been well documented. While not feeding, larvae rest in leaf shelters, and pupate in the last larval shelter constructed. All instars were observed to forcibly expel frass from the anus, later instars achieving a distance of over a meter. The one individual that was successfully followed from egg to eclosion took 134 days from the time the egg was found to complete development. Newly molted larvae have pale cream to bone colored head capsules prior to hardening.

Description of Early Stages: Egg. (n = 17, 1 mm diameter, Fig. 2c). Laid singly on dorsal surface of new or old and damaged leaves; brown, dome shaped with 14 irregular vertical ridges, darkening to nearly black before hatching.

Larva. First instar (n = 78) larva with head roughly heart shaped, shining black with sparse, short, pale setae visible under a dissecting scope; body dull, dark-orange, darkening to orange-brown or orange-green once feeding begins, sparsely covered with short, pale setae; pronotal shield poorly developed, distributed dorsally, shining black, elliptical when viewed from above. **Second instar** (n = 65) larva with head as described for first instar; body as described for post-feeding first instar, setae slightly denser, skin appearing granular with tiny pale spots; pronotal shield well developed, extending subdorsally, shining black, rectangular when viewed from above. **Third instar** (n = 35) larva with head similar to first instar but more angular, heart shape more pronounced, setae more evident; body as described for second instar but faint, thin, orange spiracular line running from A1 to A7 appearing as it nears molt. **Fourth instar** (n = 26) larva as described for third instar but thin spiracular line more evident, especially late in instar; pronotal shield extending to edge of subdorsal area. **Fifth instar** (n = 23, 48-50 days, Fig. 3) head (Fig. 2e) and body as described for fourth instar, spiracular line now more prominent but still thin, body turning dirty orange before pupation, making small pale spots more apparent; anal comb (Fig. 2d) broad basally, noticeably longer in the center than on the sides; central spines rounded and lateral spines sharper.

Pupa. (n = 8, 22-35 days, Fig. 2a). Robust with blunt head, all shining dark brown, intersegmental areas on abdomen bright orange-brown, dorsum with short, sparse, pale orange-brown setae.

Larval shelters. **First instars** (n = 78, Fig. 2b) begin shelter construction by making a roughly round or oval shaped cut starting away from the leaf margin. This man-hole cover-like section of leaf is then flipped onto the dorsal surface of the leaf and tightly silked. This shelter type has been described as a Group II, type five, center-cut fold (Greeney & Jones 2003). During construction of the first shelter, larvae appear not to ingest any leaf material. Small pieces of leaf were observed along the cut leaf edge and the gut did not darken with ingested material. Sealing silk was first laid down along the shelter bridge. This caused the lid to begin flipping towards the dorsal leaf surface. Subsequently, a series of multi-stranded ties were attached to the lid and the leaf surface, progressing away from the bridge along the lid margin as it was drawn closer to the leaf surface. In all, five such ties were used to seal the shelter. Once the shelter was constructed, resting silk was laid down in a circular pattern around the inside of the lid. Larvae rest on this while not feeding. **Second instar** (n = 47) larvae remain in the shelter built by first instars. Most **third instar** (n = 28) larvae built a second shelter as described for the first instars, but larger. Five larvae built roughly trapezoidal shelters cut from the edge of the leaf using two major cuts and folded along a broad bridge onto the dorsal surface of the leaf. This shelter type is known as a Group III, type nine, two-cut unstemmed fold. Early **fourth instar** (n = 16) larvae remain in the shelter built during the third stadium. Sometime during this stadium, larvae build a third shelter. In all observed larvae, late fourth instars built two-cut unstemmed folds as described for third instars. For this third shelter, however, the midvein at the base of the leaflet with the shelter was chewed so as to allow it to sag down, out of the plane of the leaf (Fig. 2f). Pale brown positioning silk was then laid along the ventral portion of this cut to hold the leaflet and shelter in a near vertical position. The portion of the leaf on which the shelters were built eventually died. Larvae left the shelters at night to feed on the remaining green parts of the leaf. Molting to **fifth instar** (n = 12) occurs within the third shelter. Sometime during the fifth instar, larvae build a fourth shelter. Based on observations in the field, it is suspected that fifth instar larvae often build a fifth, and even sixth shelter, all as described for fourth instars. In eight instances, the leaf petiole was cut and silked rather than the midvein of a single leaflet. This caused the entire three-part leaf to hang downward in a nearly vertical position. In one case, the main stem of the plant was severed near the apex, causing a cluster of three to four leaves to hang vertically. Eventually, the section of the plant severed turns brown and dries out. A few small, irregular perforations are cut in the lid and floor of the shelter. Resting silk is laid irregularly inside the shelter lid and floor, and larvae rest on both. All pupae (n = 8) encountered were found in shelters as described for fifth instars. The one larvae followed in the field from egg to eclosion pupated in its last larval shelter.

DISCUSSION

One proposed function of shelter building has been the chemical modification of leaf tissue by changing its exposure to sunlight (Sandberg & Berenbaum 1989). *Noctuana haematospila* larvae do not ingest leaf material during construction of their first shelter. While this suggests the possibility that unmodified leaf tissue may be unpalatable to young larvae, the fact that they soon commence feeding on nearby (and unmodified) leaf tissue, provides an alternative hypothesis which we feel is more likely. It is possible that ingesting material rather than simply cutting the leaf would take more

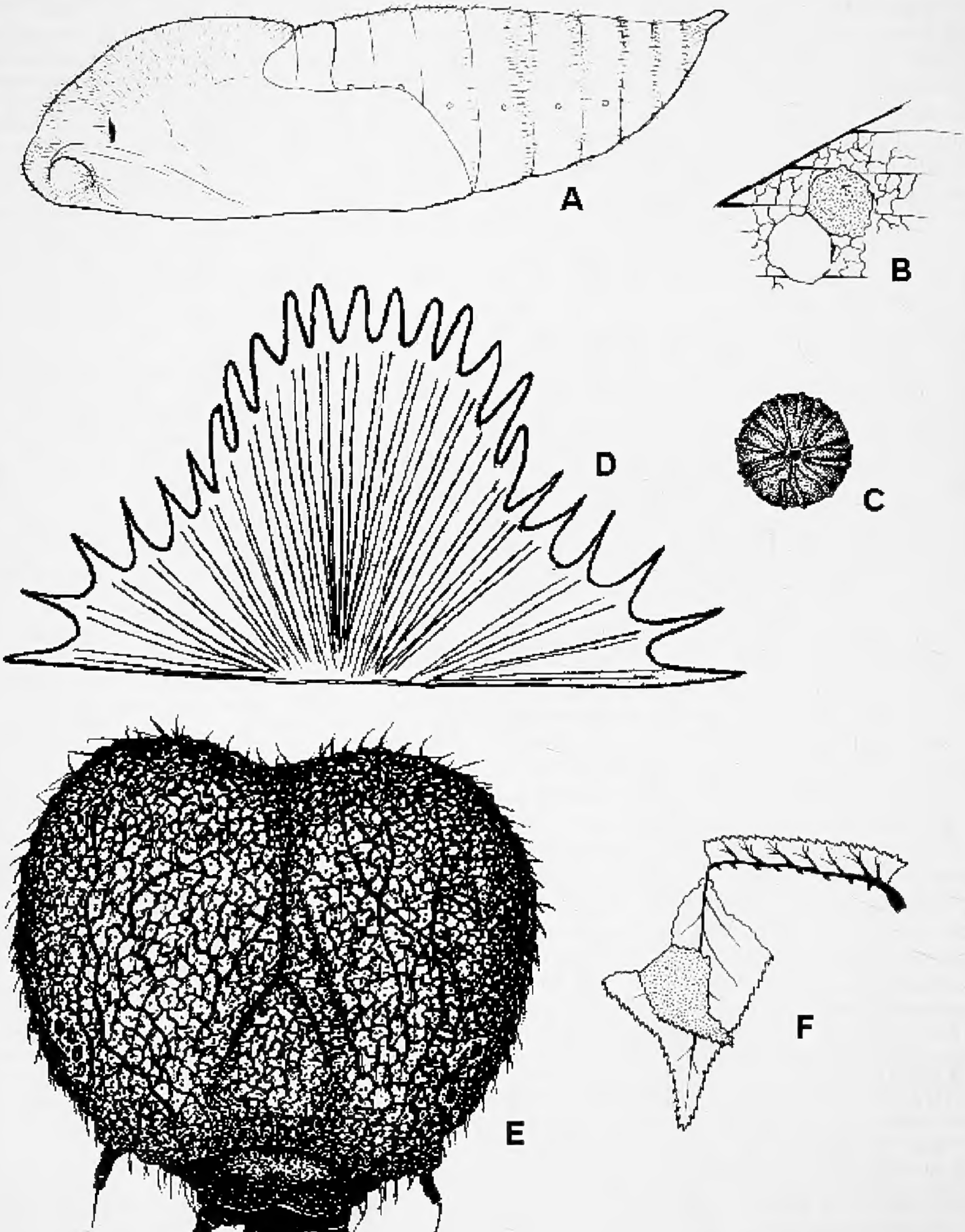


FIG. 2. Early stage morphology of *N. haematospila* and larval shelters from study site. A, Pupa; B, First instar shelter; C, Egg; D, Anal comb; E, Fifth instar head capsule; F, Fifth instar shelter before death of surrounding plant tissue.

FIG. 3. Fifth instar larva of *N. haematospila* at study site, resting on *Rubus* foodplant.

time and thus delay the shelter construction and the covering of the larva. All hatched eggs found in the field were partially consumed, and the energy provided by this first meal likely aids in allowing the young larva to avoid the need to feed during initial shelter construction. The center-cut fold shelter built by first instar larvae is similar to that built by many early instar pyrrhopygines, but is infrequently seen in the pyrgines (HFG unpubl. data). Across all hesperiids, in fact, this is an infrequently observed shelter type (Greeney & Jones 2003). As the initial cut does not begin from a leaf margin, and instead the larva's mandibles must pierce the leaf to initiate cutting, we suspect that accommodating modifications of the mandibles have accompanied the evolution of this shelter type. Detailed observations and careful comparisons of larval morphology across a wide taxanomic range are needed to elucidate this idea.

The additional modification to the basic shelter plan seen in later instars of *N. haematospila* includes a positioning cut with corresponding positioning silk. The use of a positioning cut to modify the overall position of the shelter is widely used among the hesperiines (Greeney & Jones 2003, HFG unpubl. data). Its function remains unknown, but at least in the case of *N. haematospila*, such a modification caused the death of plant tissues surrounding the shelter and made the overall structure much better camouflaged.

We hope this brief note encourages others to report findings on this and other increasingly threatened tropical species.

ACKNOWLEDGEMENTS

We are greatly indebted to Chris Aldassay, Jennifer Butcher, Heidi Connahs, Jenny Getty, Paul Martin, Hannah Montag, Josh Richman, and Tina Sommer for countless hours spent helping to track larvae in the field. We also thank Richard S. Peigler for supplying some literature cited herein. This work could not have been completed without the tireless contributions and support of the PBNHS. This is publication number 10 of the Yanayacu Natural History Research Group.

LITERTURE CITED

ANONYMOUS, 2000. Run, don't walk, for stray adventures. American Butterflies. 8:43.

BELL, E. L. 1937. New genera and species of Neotropical Hesperiidae with notes on some others. Amer. Mus. Novit. No. 914:1-17.

DRUADT, M. 1917-1924. Grypocera. Pp. 833-1056 *In* Seitz (ed). Grossschmetterlinge der Erde. Vol. 5, Die Amerikanischen Tagfalter. Alfred Kemen, Stuttgart.

EVANS, W. H. 1953. A Catalogue of the American Hesperiidae indicating the classification and nomenclature adopted in the British Museum (Natural History). Part III (groups E, F, G), Pyrginae, section 2. British Museum, London. 246 pp.

FELDER, C. & R. FELDER. 1865-1875. Rhopalocera, 548 pp. *In* Reise der Österreichischen Fregatte "Novara" um die Erde in den Jahren 1857, 1858, 1859, under den Befehlen Commodore B. von Wüllerstorf-Urbair. Zoologischer Theil. Zweiter Band: Abtheilung. Vienna.

GREENEY, H. F. & M. JONES. 2003. Shelter building in the Hesperiidae: a classification scheme for larval shelters. J. Res. Lep. 37:27-36.

LEWIS, H. L. 1987. Butterflies of the World. Harrison House, New York. 312 pp.

PIÑAS, F. R. S. J. & I. P. MANZANO. 1997. Mariposas del Ecuador. Vol. 1, Géneros. Pontifica Universidad Católica del Ecuador, Quito. 115 pp.

SANDBERG, S.L. & M. R. BERENBAUM. 1989. Leaf tying by tortricid larvae as an adaptation for feeding on phototoxic *Hypericum perforatum*. J. Chem. Ecol. 15:875-885

WILLIAMS, R. C. & K. J. HAYWARD. 1944. Hesperiidarum rei publicae Aequatoris catalogus. Acta Zool. Lilloana. 2:63-246.

Recieved for publication 19 September 2003; revised and accepted 10 November 2004

Journal of the Lepidopterists' Society
59(1), 2005, 10 - 18

MOVEMENT AND MIGRATION PATTERNS IN *PIERIS RAPAE* (PIERIDAE)

N. GILBERT
Genetics Field Station, 219d Huntingdon Road, Cambridge CB3 0DL, U.K.

AND

D.A. RAWORTH
Agriculture and Agri-Food Canada, Pacific Agri-Food Research Centre, P.O. Box 1000, Agassiz, British Columbia, Canada V0M 1A0;
email: raworthd@agr.gc.ca

ABSTRACT. Non-migratory movement of the small white butterfly, *Pieris rapae* (L.), was studied in Australia to augment a set of rules developed in the 1970-1980s. Males, like females maintained a preferred direction. *Pieris rapae* was attracted to low vegetation (not necessarily host plants) at distances of 20 m or more. Although daily movement is highly directional, direction reversals occurred at vegetation boundaries. These, and other previously published characteristics of movement, account for many of the patterns of non-migratory movement of *P. rapae*. Migratory movement of *P. rapae* and *P. brassicae* (L.) was studied in the Pyrenees to determine if migration requires additional characteristics. The north-south migration in the central Pyrenees did not extend to adjacent plains. At the northern end of the migration a portion of the *P. rapae* population overwintered while the remainder migrated south. Autumn migrants, moving south, were new individuals of normal size (24.0 ± 0.20 mm wing length) while spring migrants, moving north, varied in age and were large (26.2 ± 0.14 mm wing length). More male than female *P. rapae* were observed in both north and southbound migrations. Migrating *P. rapae* and *P. brassicae* flew straight tracks 1-4 m above the ground at about 8 km/h. Migrants showed no special physiological adaptation for flight at low temperatures when compared with non-migratory individuals. Both migratory and non-migratory *P. rapae* displayed a circadian rhythm that cut off activity at about 1500 hrs even though conditions were suitable for flight. Spring migrants flew in all directions from W through N to E, average direction was away from the sun - but not directly away - and the hourly rate of change was less than the 15° celestial rotation. Non-migratory populations appear to be pre-adapted for migration, requiring only an exaggerated degree of bias in individual directions.

Additional key words: attraction, flight, orientation, *Pieris brassicae*

In 1970, the small white butterfly, *Pieris rapae* (L.) (Pieridae), was selected as a suitable organism for a study of insect movement (Gilbert et al. 1976). The object of the study was to assemble a set of 'rules' which describe patterns of movement, not in one particular environment, but in any environment which the insect normally encounters. A coherent account of several features of the non-migratory movement of *P. rapae* was developed (Jones et al. 1980). The present paper attempts to complete the work by studying several aspects not previously considered, including migratory movement.

NON-MIGRATORY MOVEMENT

The movement of *P. rapae* females during egg laying is an asymmetric two-dimensional random walk (Moran 1968) with two main characteristics (Jones et al. 1980, Root & Kareiva 1984): females are attracted to host plants at distances of about 1 m; and each female maintains a preferred direction of travel during her daily period of egg-laying - but different directions on different days. On some days, preferred directions show a bias, so that more individuals choose one direction than another (Jones et al. 1980). Here, we examine directionality of male movement, and attraction to host and non-host plants at distances greater than 1 m. These studies were carried out in Australia where *P. rapae* shows greater directionality and less attraction to host plants than in Canada or Britain (Jones 1977, 1987).

Male directionality. In February 1991, at Cockatoo Hill, Bruny Island, Tasmania, an isolated 34 ha paddock of rape (*Brassica napus* L., Brassicaceae) was divided into 40 x 40 m squares (Fig. 1). The paddock was surrounded by eucalypt bush, *Eucalyptus* spp. (Myrtaceae) which butterflies rarely enter (cf. Cromartie 1975). Three squares marked B, C, and D were used as catching sites. The butterfly density was about 60 adult males per square in late January, increasing to 150 on 9 February - about one male (+ one female) per 10 m^2. After a wet spring, there was a profusion of dandelions, (*Taraxacum* sp., Asteraceae), thistles (*Cirsium* sp., Asteraceae) and wild mustard (*Brassica* sp.) in flower. Butterflies were caught, marked with a felt pen and released in each of seven or more successive half-hour periods (recorded separately) per day, during 14 days from 20 January to 10 February. On other days, weather precluded flight. A different mark was used each day, but individuals were not distinguished. On each day, the mark-recapture procedure was conducted at one site only. A total of 1797 marked males were released, with 49% recaptures including multiples, on the same day, and 16% recaptures one or more days after marking, mostly at the same site.

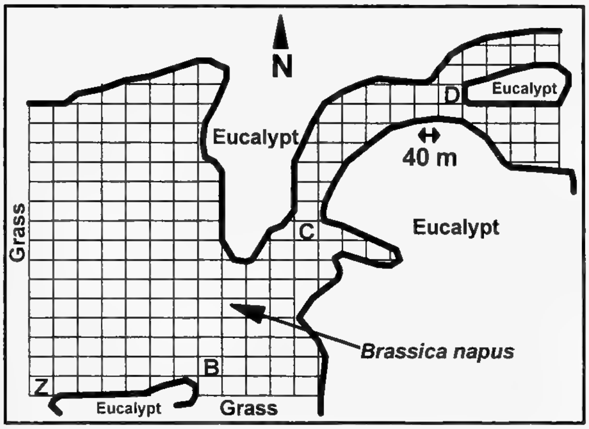


FIG. 1. Map of a paddock of rape, *Brassica napus*, with superimposed grid, February 1991, at Cockatoo Hill, Bruny Island, Tasmania; B, C, and D were mark-release-recapture sites (Table 1); Z was the observation site for *Pieris rapae* crossing marked lines (Fig. 3).

TABLE 1. Following-day recaptures of marked male *Pieris rapae*, Bruny Island, January-February 1991 (cf. Fig. 1).

Release site	Recapture site	No. released	No. recaptured
B	*C*	*67*	*2*
C	*B*	*102*	*1*
B	*C*	*139*	*1*
C	*D*	*102*	*2*
D	*C*	*120*	*3*
D	*C*	*167*	*9*

Same-day recaptures permitted maximum-likelihood estimation of N, the number of males present on the square, and q, the retention rate per half-hour within the capture square. The daily average values of q decreased as temperature increased (Fig. 2a), reflecting increased flight activity (Fig. 2b) and emigration. The effect of temperature on male activity is similar to that observed for females (Jones et al. 1980).

Monte Carlo simulations were used to examine directionality of male movements over the grid in Figure 1. Estimated values of q were incorporated into the simulations to account for the effects of temperature. Analyses assumed various degrees of directionality (i.e. of correlation between successive moves). The paddock was represented by numbering the squares and maintaining a list of the four squares adjacent to each square; barriers were represented by listing the same adjacent square twice for squares at the edge - thereby simulating reflection. The program predicted expected numbers of recaptures at different sites one day later. In the field, the highest number of recaptures on the following day arose for movements between sites C and D rather than sites B and C (Table 1, $\chi^2 = 5.6$, d.f. = 1, $p < 0.05$), reflecting the narrow channel between C and D (Fig. 1; Haddad 2000, Sutcliffe & Thomas 1996). A purely random walk, with no directionality, predicted no recaptures at all at different sites over a flight period of 1 day (cf. Fig 4, Jones et al. 1980). Therefore, the values in Table 1 are impossible unless the males maintained some directionality through the day. Simulation results best fit the observed data when the probability of movement from one grid square to the next in the same direction was 0.4. This degree of daily directionality is less than

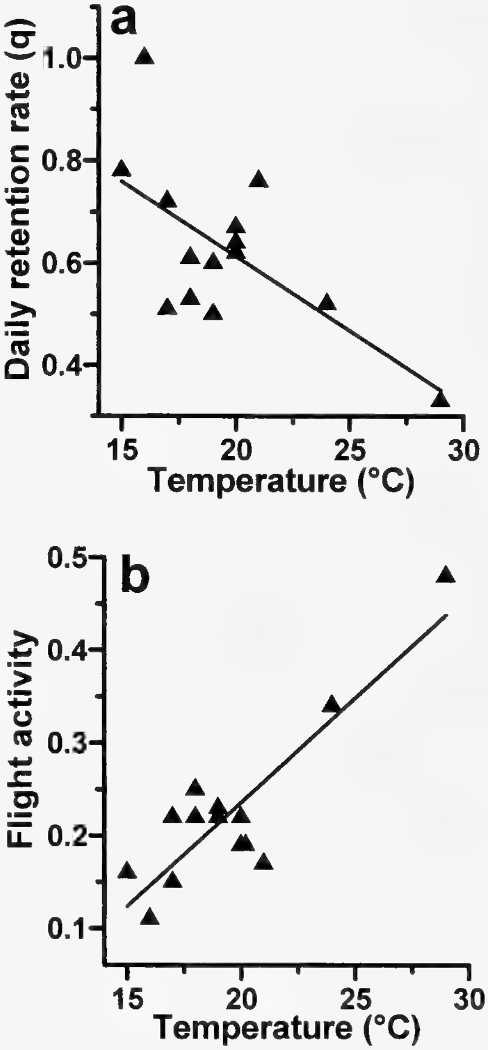


FIG. 2. Daily average retention rate (a), and flight activity (b), of male *Pieris rapae* per half-hour in a 40 x 40 m square within a paddock of rape, *Brassica napus*, at Cockatoo Hill, Bruny Island, Tasmania versus daily maximum temperature recorded at Hobart, Tasmania, February 1991. Flight activity was calculated as the daily average of number of males caught per half-hour, divided by N, the maximum-likelihood estimate of the number of males present. (a) $y = 28.5 - 14.4x$, $r^2 = 0.42$, $p < 0.05$; (b) $y = 11.8 + 34.2x$, $r^2 = 0.77$, $p < 0.001$.

0.6 determined for egg-laying females at Canberra (Jones 1977), but at high population densities, males are continually distracted by interactions with other individuals.

Long-distance attraction to host and non-host plants. The high population density on the Bruny Island rape paddock is typical of summer densities in *Brassica* fields elsewhere in Australia. But adult densities away from *Brassica* fields are much lower. Attraction to host plants at distances of 1 m cannot explain how *Brassica* plots maintain such high local densities. Many of the butterflies which cross the edge of a field in their chosen daily direction, must return.

The behavior of *P. rapae* was studied at the edge of a cabbage (*Brassica oleracea* var. *capitata*) field near Richmond, Tasmania on 22 February 1996. Adult density was similar to that on Bruny Island. Butterflies were observed which had flown at least 2 m over grass, outwards from the edge of the cabbage field. There were no flowers in the area. Of 87 individuals of both sexes, 59 turned back and returned to the cabbages before reaching a fence 20 m outside the edge. The average distance where they turned was 10.2 ± 5.92 (S.D.) m. The other 28 crossed the fence, where they could not be observed reliably. There was an attraction either back towards the cabbage plants, or back towards the resident butterflies at distances of 20 m or more.

Attraction to host plants at distances greater than 1 m was tested in another way. The theory of diffusion (Crank 1975) predicts that butterfly density should decrease rapidly with distance from the edge of a field of cabbages. On 21 February 1994, *Pieris rapae* were counted crossing two marked lines parallel to the edge of the paddock of rape at Cockatoo Hill, Bruny Island, Tasmania (site Z, Fig. 1), one line 60 m outside and the other 10 m inside the paddock. Observations were made during 15 alternating periods, 40 min at the outer line and 15 min at the inner line, throughout the 7 h of main butterfly activity. Counts of *P. rapae* decreased with distance from the paddock, and increasing temperature had less effect on counts outside than inside the paddock (Fig. 3). Egg laying on isolated plants placed at various distances from a cabbage paddock should therefore also decrease with increasing distance. To test this, 10 groups of four 8 week old potted kale (*Brassica oleracea* var. *acephala*) plants were placed in a line leading away from the cabbage field near Richmond, Tasmania on 23-24 February 1996. The first group was just inside the edge of the cabbage field, and successive groups were spaced 2.5 m apart. After two days, the eggs on each plant were counted. Instead of diminishing, the number of eggs increased with distance from the edge (Fig. 4). This does not reflect butterfly density, which decreased rapidly with distance. Rather, it reflects attraction of egg-laying females towards the cabbage field at distances of 15 m or more, which counteracted the local attraction to the kale plants. The attraction must have increased closer to the field.

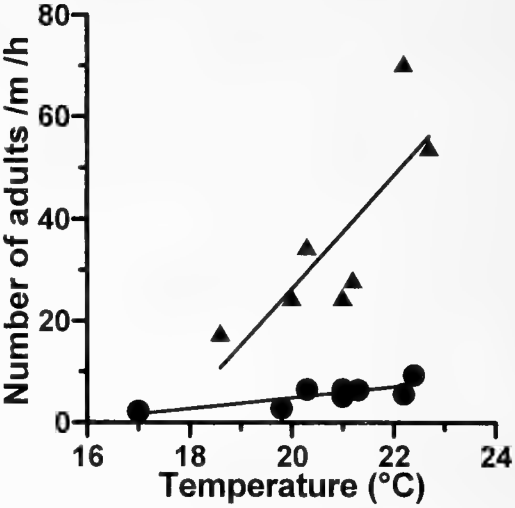


FIG. 3. Number of *Pieris rapae* crossing two marked lines parallel to the edge of a paddock of rape, *Brassica napus*, at Cockatoo Hill, Bruny Island, Tasmania, 21 February 1994 versus temperature. Triangles: line placed 10 m inside the paddock, $y = -195. + 11.1 x$, $r^2 = 0.65$, $p < 0.05$, slope S.E. = 3.65. Circles: line placed 60 m outside the paddock, $y = -16.4 + 1.06 x$, $r^2 = 0.65$, $p < 0.05$, slope S.E. = 0.322. Slopes are different, $t = 2.7$, $p < 0.05$.

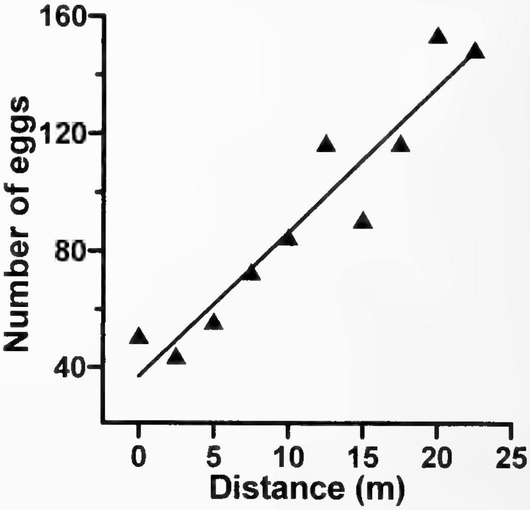


FIG. 4. Number of eggs laid on groups of four kale plants, *Brassica oleracea* var. *acephala* during a 2-day period versus distance from the edge of a field of cabbage, *B. oleracea* var. *capitata* near Richmond, Tasmania, 23-24 February 1996. $y = 37.0 + 4.95 x$, $r^2 = 0.90$, $p < 0.001$.

Attraction at distances greater than 1 m is, at least in part, towards vegetation rather than towards other butterflies. In January 1996, a 50-hectare paddock at

Missionary Creek, Bruny Island had recently been ploughed and seeded with rape. There was a 20 m wide stand of unploughed vegetation plus newly-germinated rape, along the creek; but the rest of the paddock was bare and dry. Very few wild butterflies were present. On 16 January, 68 marked adults were released along the creek. On the following day, 71% were recaptured at the same place between 0945-1315 hrs. By 13 February, after heavy rains, the entire paddock was covered in rape plants. Of 84 adults released in similar conditions, only 24% (the same for males and females) were recaptured the next day between 1015-1445 hrs, and catches on the following day confirmed that the butterflies had dispersed over the paddock. When the paddock was bare, they remained with the vegetation along the creek; but when the paddock was well covered with plants, they dispersed.

Two studies suggest that longer-distance attraction is towards scrub vegetation, not just Brassicaceae. First, 200 adults were released on 26 January 1991 in seashore vegetation at Adventure Bay, Bruny Island. Of 14 which subsequently flew out of the vegetation over sand dunes, all promptly returned. There appeared to be no Brassicaceae in the vegetation. Second, between 0915-1215 hrs on 1 and 2 November 1997 in clear sun, 22-27°C, at Atherton, N. Queensland, *P. rapae* adults were observed entering a 20 x 40 m vegetable patch containing no Brassicaceae, and an adjacent 16 x 40 m grass paddock (with 16 m common border). *Pieris rapae* was scarce in the area; sometimes one, never more than two butterflies were seen at a time. Females were caught and males were watched as they flew out of the area. Therefore, every observation represented a new arrival - if not a new individual. In 6 h, 19 *P. rapae* were observed in the grass paddock and 53 in the vegetable patch, significantly different from expected values given patch size and assuming no patch preference (χ^2 = 9.5, d.f. = 1, p < 0.01). Of the 19 butterflies observed in the grass paddock, 10 left for surrounding grassland, but 9 entered the vegetable patch, a disproportionately large number (χ^2 = 17.0, d.f. = 1, p < 0.01) given that only 16 m of the 112 m grass paddock perimeter was adjacent to the vegetables.

MIGRATORY MOVEMENT

Characteristics of *P. rapae* and *P. brassicae* (L.) movement were examined in the Pyrenees, over which these species migrate annually (Lack & Lack 1951, Williams et al. 1956), to determine what additional characteristics are needed to explain the movement pattern of migratory individuals. Because little is known of this migration we first consider the general features: taxonomy of the migrating species; geographical extent of the migration; proportion of the population that migrate rather than diapause; age and size of spring vs. autumn migrants; and sex ratio of the migrants. We then consider specifics of freely migrating butterflies: velocity, light and temperature required for flight; circadian rhythm for flight; and directionality.

General features of the migration. Williams et al. (1956) found that the most common migrating species were *P. rapae* and *Colias croceus* (Geoffroy); five other migrating species were abundant and four were rare. There has been some confusion, however, with respect to identification of *P. rapae*. In the Mediterranean, *P. rapae* is easily confused with *P. ergane* (Geyer), *P. mannii* (Mayer) or *P. napi* (L.). Whereas British *P. napi* always bear green wing markings, Mediterranean individuals lack this pigmentation if the pupae are exposed to high temperatures in the laboratory or in the field. Breeding experiments at 20°C confirmed that the trans-Pyrenean migratory species is *P. rapae*, not *P. ergane*, *P. mannii* or *P. napi*. Most of the following observations and catches were made at a level site at altitude 1630 m in the upper Ariege valley ('A', Fig. 5), where there are no resident populations of these species.

The migration is well documented along the middle length of the Pyrenees (Lack & Lack 1951, Williams et al. 1956). At either end, the situation is less clear. At the Atlantic end, Snow & Ross (1952) reported a migration of dragonflies, but no butterflies, near Hendaye. At the Mediterranean end, Williams et al. (1956) reported a southward migration of butterflies, including *P. rapae* in autumn, but noted "Whites" flying both north and south. Spieth and Kaschuba-Holtgrave (1996) reported an autumn migration of *P. brassicae* WSW at Perpignan (Fig. 5). Our observations at Carcassonne, and Rivesaltes near Perpignan (Table 2), when the autumn trans-Pyrenean migration was in full spate, do not confirm reports of a migration. Furthermore, on 23 September 1992, during the main migration, nine *P. rapae* were caught and marked in the morning at le Racou, Argelès, where Williams et al. (1956) made observations; five were recaptured that afternoon, and two the following day. There was no sign of migration at the eastern end of the Pyrenees. In the middle of the range, the migration of both *P. rapae* and *P. brassicae* appears confined to the Pyrenees. It did not extend to the adjacent plains where there were resident populations which showed no sign of migration (Table 2).

The trans-Pyrenean *P. rapae* and *P. brassicae* have the same temperature thresholds for larval development, 10°C and 9°C respectively (Gilbert & Raworth 1996), as their conspecifics elsewhere (Gilbert 1988, and

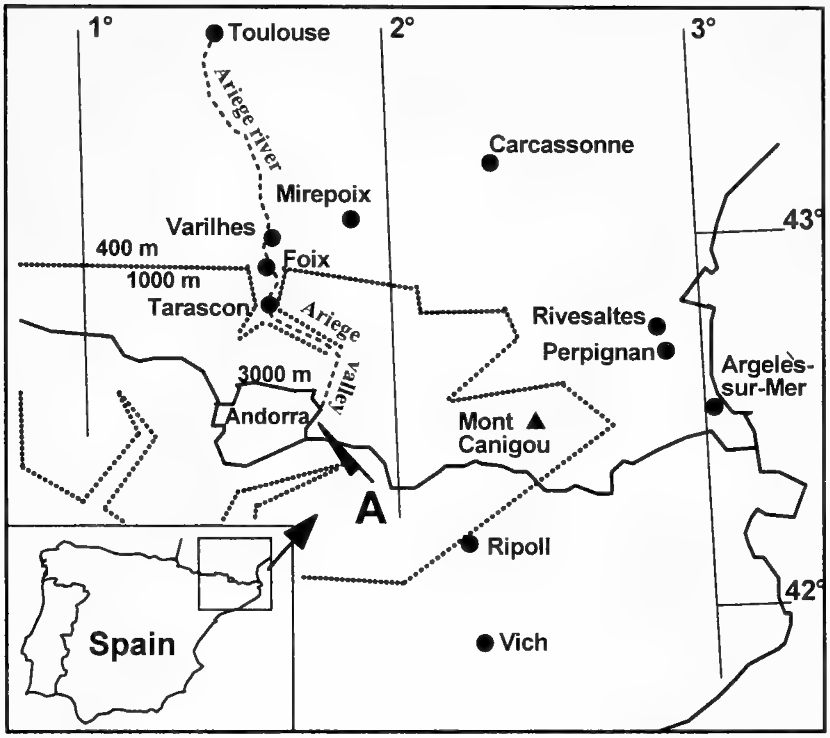


FIG. 5. Map of the Pyrenees and surrounding area; arrow at 'A' marks the sample site in the Ariege river valley at 1630 m altitude; Coll dels Clots, another sample site (Table 3), lies 1.5 km N of 'A' at 2170 m altitude. The fine dotted line marks ~1000 m elevation; 3000 m peaks generally run along the border between Andorra and France.

unpublished data). It follows that slow larval development in winter is possible at the south side of the Pyrenees, but not at the north. Therefore, *P. rapae* and *P. brassicae* which spend the summer on the north side of the Pyrenees can either pass the winter in diapause, or migrate south to produce an active generation through the winter. Migrant *P. rapae* were caught in June 1995 and bred through two generations under field conditions at Cambridge; second-generation eggs hatched 25 August and average pupation date was 20 September. When pupating at the September equinox, 23 of 33 pupae entered diapause and the rest emerged later in autumn - by contrast, all of 45 local Cambridge pupae diapaused. The proportion entering diapause *in situ* in the Pyrenees is unknown, but certainly some; for on 26 April 1996, 26 *P. rapae* (25 ♂; 1 ♀) and 23 P. brassicae (13 ♂; 10 ♀) were caught at Tarascon (480 m), long before the northwards migration (Ariege valley site 'A', Table 2) had begun.

The physical characteristics of spring and autumn migrants of *P. rapae* were different. During 4 consecutive years, 114 northbound and 40 southbound individuals of both sexes were caught and measured, and many more were observed in flight or feeding. Those going south in autumn were all new individuals with undamaged white wings and very black markings; old individuals have frayed, yellow-green wings and pale markings. They were of normal size with wing lengths 24.0 ± 0.20 (S.E.) mm, corresponding to average pupal weight of 150 mg (Jones et al. 1982), and some at least were not ready to lay eggs - determined by placing twelve females in several cages with kale plants. Those going north in spring were of varying ages, but exceptionally large with wing lengths 26.2 ± 0.14 (S.E.) mm, corresponding to average pupal weight of 180 mg, and the females were mated and ready to lay. When bred on kale at 20 and 26°C, the progeny of the large spring-migrant *P. rapae* were the same size as *P. rapae* elsewhere. During the spring migration, *P. rapae* are so large that they are difficult to distinguish from small *P. brassicae*.

Males always predominated in the migration. In samples collected in 4 successive years under clear sun at 16-19°C, totals were: northbound, *P. rapae* 101 ♂: 13 ♀, *P. brassicae* 9 ♂: 7 ♀; southbound, *P. rapae* 27 ♂: 13 ♀, *P. brassicae* 38 ♂: 21 ♀, *C. croceus* 15 ♂: 7 ♀. These ratios, which are significantly different from 50:50 (d.f. = 1, $p < 0.05$) for southbound ($\chi^2 = 4.9$) and northbound ($\chi^2 = 67.9$) *P. rapae* and southbound *P. brassicae* ($\chi^2 = 4.9$), are not artifacts of catching because males, being stronger fliers than females, are harder to catch. In contradiction, Gray et al. (1953) observed *C. croceus* 30

TABLE 2. Observations of the movement of *Pieris rapae* and *P. brassicae*, flying on clear sunny days in the Pyrenees and on adjacent plains to the north and south (Fig. 5).

Location[1]	No.	Movement[2]	Conditions
Carcassonne	15 *P. brassicae*	not migrating, flying NE	1000-1100h, 4 Oct. 1992
Rivesaltes	17	not migrating	29 Sept. 1996
Mirepoix	-	not migrating	p.m., 6 Oct. 1994
Varilhes	7 *P. rapae*	flying S, 9 flying N	1330-1500h, 27 Sept. 1994, max 21°C
Varilhes	-	not migrating	1100-1200h, 6 Oct. 1994, 17°C
Foix	4	migrating S	1100-1130h, 27 Sept. 1994, max 21°C
Ariege valley (site 'A')	6♂, 5♀ *P. brassicae* caught; 87♂, 8♀ *P. rapae* caught; 71 not caught	migrating N-NW:	27-28 Jun. 1996, max 19°C
Ariege valley (site 'A')	222	migrating (Tables 3, 4)	30 Jun.-1 Jul. 1996, max 19°C
Ripoll	-	not migrating	29 Jun. 1996, max 27°C
Vich (Vic)	>24 *P. rapae*	not migrating	29 Jun. 1996, max 27°C

[1] Varilhes is at the southern edge of the plain, Foix is just in the foothills.

[2] Butterflies flying straight tracks in a limited set of directions were defined as migrating; those flying non-linear tracks or where preferred directions were all round the compass, not migrating.

♂: 68 ♀, at another location. However, in their study, sex was determined while the butterflies were in flight - a difficult task. Egg-laying females are easily distinguished from prowling males but these behaviors do not apply during migration.

Characteristics of movement of migrating individuals. The main barrier to migration in the Pyrenees is the central chain of mountains 40 km wide which rise to altitudes of about 3000 m. Migrating *P. rapae* and *P. brassicae* (Table 3) flew in straight tracks 1-4 m off the ground, uphill or downhill, stopping to feed when they encountered flowers. Mean velocity, measured in calm conditions by running with the butterflies for 100 m on level ground with a stop watch, was about 8 km/h (n = 10); Williams et al. (1956) estimated flight speed at 8-16 km/h. One day therefore affords ample time to cross the central 40 km. However, the mountains are generally obscured by clouds. Migration continues when it is partly cloudy and some blue sky is visible, but stops when clouds completely cover the sky (Williams et al. 1956, confirmed by observations of migrations from 1994-97). The butterflies often have to wait several days for the sun.

At sea level, *P. rapae* flies at temperatures exceeding 15°C in sun, and exceeding 20°C under clouds (unpublished observations during 20 years). Between 15 and 20°C, the butterflies warm themselves by basking in the sun. This agrees with the observation that *P. rapae* caught in flight always have thoracic temperatures ≥ 20°C when measured with a thermocouple and electronic thermometer (n = 41, including 16 butterflies in Tasmania and 25 migrants in the Pyrenees, at 20°C and 15°C air temperature, respectively). But at 1630 m altitude, migrating butterflies fly in sun at air temperatures as low as 9°C (Williams et al. 1956, confirmed by observations of migrations from 1994-97). When 15 *P. rapae* of Pyrenean migratory stock were caged at sea level with 15 butterflies from Cambridge, individuals from both sources became active in sun at 15°C, which indicates that there is no physiological adaption to lower temperatures in trans-Pyrenean stocks. Presumably the greater irradiation at altitude enables the butterflies

TABLE 3. Counts of migrating *Pieris rapae* and *P. brassicae* (not distinguished, but mostly *P. rapae*) observed over 30 x 30 m areas, Ariege valley ('A', Fig. 5) at 1630 m, except Coll dels Clots at 2170 m (CdC); with sun times and air temperatures (T). Full sun, still days, 1996.

Sun time (hrs.)	0730-0830	0830-0930	0930-1030	1030-1130	1130-1230	1230-1330	1330-1430	1430-1530	1530-1630
28 June T(°C)	16	16.5	18	18	18.5	19.5	19.5	19	18.5
Migrants	4	5	13	17	21	36	29	11	0
30 June T(°C)		14.5	15.5	16	17	17.5	18	19	
Migrants		11	25	32	31	40	26	12	
1 July T(°C)		14	14.5		20		17.5		
Migrants		5	18	--	11(CdC)	-	22		

to warm up at air temperatures below 15°C. In June and October, temperatures in the Pyrenees at 1630 m exceed 9°C through most of the day in fine weather, so temperature is not a limiting factor.

Pieris rapae has a circadian rhythm. Its timing has been estimated by experiments on females caged at Hobart, Tasmania in clear sun at temperatures remaining above 20°C until 1800 hrs (sun time). Control females were free to lay all day (six gravid females in one cage and seven in another produced 79.8 eggs per female). Another 13 gravid females were deprived of host plants until specified times. After being presented with host plants at 1400 hrs, six of these females laid 63.8 eggs per female; when presented with host plants at 1500 hrs the remaining seven females laid 23.9 eggs per female, and very few eggs were laid after 1600 hrs. Counts of migrating *P. rapae* and *P. brassicae* in the Pyrenees also declined abruptly between 1500-1600 hrs (Table 3), even though conditions were suitable for flight.

Migrant *P. rapae* and *P. brassicae* were observed in the Ariege valley and surrounding hills ('A', Fig. 5) in June and July 1996. The Ariege valley runs SW - NE at the observation point. There was more scrub vegetation in the valley than on the surrounding hills. Migrant directions varied from W through N to E. Those which crossed the valley at right angles flew straight uphill NW, with no obvious tendency to deviate along the valley. The first 2 days of observation established the daily time pattern on the valley floor (Table 3). On the third day, the observer began on the valley floor, then climbed 500 m following the average direction of migration (NNE), and subsequently returned. There appeared to be more migrants in the valley (counts between 0830-1030 hrs and 1330-1430 hrs) than higher up (counts between 1130-1230 hrs), but the difference was not significant ($\chi^2 = 3.2$, d.f. = 1, $p > 0.05$). The average direction vectors of migrating *P. rapae* and *P. brassicae* followed the sun through the day (Table 4), but the average direction was not directly away from the sun, and the hourly rate of change was less than the 15° celestial rotation.

DISCUSSION

Non-migratory movement. Non-migrating male *P. rapae* exhibit some directionality. This directionality increases the radial distance moved, and may increase their chances of finding new mates, just as female directionality increases the chances of finding new host plants (Jones et al. 1980).

Jones et al. (1980) found that movement of non-migratory *P. rapae* is highly directional each day. Daily direction is, however, influenced by field boundaries because 70% of individuals that left a *Brassica* field in the current study, reversed direction at 20 m or more, and returned. Schtickzelle & Baguette (2003) observed similar direction reversals at boundaries in *Proclossiana eunomia* Esper (Nymphalidae), and found that patch area and landscape fragmentation affected emigration.

The probability of *P. rapae* emigrating from a field was not determined, but the relationship between egg-laying and distance from a field (Fig. 4) suggests that attraction to a field at 25 m is considerably less than at 1, or 10 m. Furthermore, 30% of *P. rapae* observed flying away from a field flew beyond a fence at 20 m. These observations suggest that there may be considerable patch-to-patch movement in *P. rapae*, as has been observed for *Hesperia comma* L. (Hesperiidae) (Hill et al. 1996) and *P. eunomia* (Baguette & Nève 1994). Attraction to low vegetation at distances up to 20 m

TABLE 4. Average directions of migration (S.E. ± 7.3°), Ariege valley ('A', Fig. 5), 30 June to 1 July 1996 (cf. Table 3). 0° is N, 90° is E. Individual directions varied from W through N to E.

Sun time (hrs)	0830-1030	1030-1230	1230-1330	1330-1530
Direction	21°	24°	52°	54°
n	59	63	40	60

would adapt *P. rapae* to finding host plants in patchy environments where mixes of host and non-host plants occur.

Five characteristics account for many of the patterns of local and long-distance (1-2 km) movement of non migratory *P. rapae*: daily directionality in males and females, sometimes biased (Jones et al. 1980, Root & Kareiva 1984); attraction to host plants at distances of about 1 m (Jones et al. 1980); attraction to flowers (Root & Kareiva 1984); attraction to low vegetation (not necessarily host plants) at distances of 20 m or more; and interactions with other individuals (Hertz 1927).

Migratory movement. The different physical characteristics of spring and autumn *P. rapae* migrants implicate different forces driving the two migrations. The autumn migrants, being of normal size and young, must experience warm summer temperatures as larvae (Gilbert & Raworth 1996), and on emergence immediately fly south. They thereby escape winter and produce the next generation in Spain while a portion of their cohort diapause north of the Pyrenees. The spring migrants, being large and old, must experience winter temperatures around 10°C as larvae (Gilbert & Raworth 1996), and spend some time as adults in Spain before migrating north. In southern France, including Tarascon at the northern edge of the Pyrenees, *P. rapae* emerges from winter diapause during April and May. There is then a period in June when adults and larvae are scarce or non-existent, despite the abundance of young *Brassica* plants. Therefore, the trans-Pyrenean migrant females find an empty niche, while the males must wait for the appearance of second-generation adult females, which at Tarascon begin to emerge around the end of June, very soon after the migration.

The orientation-navigation system for trans-Pyrenean *P. rapae* appears to be different from *Danaus plexippus* L. (Nymphalidae). Migrating *D. plexippus* use various cues, including the physiographic features of the Sierra Madre Oriental ranges (Calvert 2001), but the direction of migrant *P. rapae* varied from west through north to east and they did not appear to utilize the physiographic features. The direction vectors for trans-Pyrenean spring migrant *P. rapae* tended to move away from the sun. This suggests the lack of a sun compass, such as that observed in *D. plexippus* (Perez et al. 1997). The fact that Pyrenean migration continues under partly cloudy conditions but stops under complete cloud cover, suggests that the butterflies may use polarized light, and that an alternate system such as a magnetic compass (Etheredge et al. 1999), which would function under cloud cover, is not available to them. The short migration by Pyrenean butterflies relative to that of *D. plexippus* may explain the lack of multiple guidance systems, but the nature of the orientation-navigation system is unknown.

Migrating Pyrenean *P. rapae* require little energy for vertical movement. Based on the data of Marden (1987) and Ellington (1991), an adult *P. rapae* weighing 40 mg has $5x10^{-4}$ watts power during flight. Therefore, the work done to raise a butterfly 1000 m equals the power output during 13 minutes of flight. (This does not mean that the butterfly can ascend 1000 m in 13 minutes - it is a measure of the work done against gravity.) Therefore, assuming no wind, a butterfly which migrates 40 km across the central Pyrenees at a flight speed of 8 km/h devotes 5 hours' power to horizontal translation and perhaps 20 minutes' power to vertical ascent, and some of the work done against gravity can be recovered during subsequent descent. This explains why *P. rapae* can afford to fly over the Pyrenees rather than follow the valley bottom.

Pieris rapae in England and Australia are non-migratory, but the difference in the directional bias of individuals relative to migratory populations is a matter of degree. Baker (1978) observed that preferred directions of *P. rapae* in England are biased towards NNW in spring, and conversely in autumn. It is unclear whether the bias occurs on all days, or only on some. Similarly, Jones et al. (1980) observed a northward bias on some days at Canberra. In both cases, despite the bias, there were individuals with preferred directions all round the compass. Only a limited set of directions are followed during migration. However, the bias in the preferred direction of non-migrant populations suggests that non-migrant *P. rapae* are pre-adapted to migration.

Migration appears to require no new characteristics of movement, only an exaggerated degree of bias in individual directions; but the cues which determine the sex ratio of migrants, and the start, end, and direction of migration remain unknown. Furthermore, general problems of migration remain unresolved. Although the trans-Pyrenean migration is two-way, different individuals travel north and south, so the origin of the behavior is hard to explain in terms of individual selection. Similarly, it is difficult to explain the movement of *P. rapae* in Florida which is predominantly northwards in the spring, with little autumn return (Williams 1958, Walker 1991).

ACKNOWLEDGEMENTS

We are indebted to CSIRO Entomology Division (Montpellier), Imperial College (Silwood Park), and University of Tasmania for facilities. We thank R. Utkhede and R.S. Vernon for helpful comments on the manuscript. Contribution No. 586, Agriculture and Agri-Food Canada, PARC - Agassiz, BC, Canada.

LITERATURE CITED

BAGUETTE, M., & G. NÈVE. 1994. Adult movements between populations in the specialist butterfly *Proclossiana eunomia* (Lepidoptera, Nymphalidae). Ecol. Entomol. 19:1-5.

BAKER, R. R. 1978. The Evolutionary Ecology of Animal Migration. Hodder and Stoughton, London. 1012 pp.

CALVERT, W. H. 2001. Monarch butterfly (*Danaus plexippus* L., Nymphalidae) fall migration: flight behavior and direction in relation to celestial and physiographic cues. J. Lep. Soc. 55:162-168.

CRANK, J. 1975. The Mathematics of Diffusion. Clarendon, Oxford. 414 pp.

CROMARTIE, W. J. 1975. Influence of habitat on colonization of collard plants by *Pieris rapae*. Environ. Entomol. 4:783-784.

ELLINGTON, C. P. 1991. Limitations on animal flight performance. J. Exp. Biol. 160:71-91.

ETHEREDGE, J. A., S. M. PEREZ, O. R. TAYLOR & R. JANDER. 1999. Monarch butterflies (*Danaus plexippus* L.) use a magnetic compass for navigation. P. Nat. Acad. Sci. USA 96:13845-13846.

GILBERT, N. 1988. Control of fecundity in *Pieris rapae*. V. Comparisons between populations. J. Anim. Ecol. 57:395-410.

GILBERT, N. & D. A. RAWORTH. 1996. Insects and temperature - a general theory. Can. Entomol. 128:1-13.

GILBERT, N.,) A. P. GUTIERREZ, B. D. FRAZER & R. E. JONES. 1976. Ecological Relationships. W. H. Freeman and Co., Reading. 157 pp.

GRAY, J. H., M. LOCKE & C. D. PUTNAM. 1953. Insect migration in the Pyrenees. The Entomologist 86:68-75.

HADDAD, N. 2000. Corridor length and patch colonization by a butterfly, *Junonia coenia*. Conserv. Biol. 14:738-745.

HERTZ, M. 1927. Bewegungen von Kohlweisslingen über einem Feld. Biol. Zentralbl. 47:569 570.

HILL, J. K., C. D. THOMAS & O. T. LEWIS. 1996. Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. J. Anim. Ecol. 65:725-735.

JONES, R. E. 1977. Movement patterns and egg distribution in cabbage butterflies. J. Anim. Ecol. 46:195-212.

JONES, R. E. 1987. Behavioural evolution in the cabbage butterfly (*Pieris rapae*). Oecologia 72:69-76.

JONES, R. E., N. GILBERT, M. GUPPY & V. NEALIS. 1980. Long-distance movement of *Pieris rapae*. J. Anim. Ecol. 49:629-642.

JONES, R. E., J. R. HART & G. D. BULL. 1982. Temperature, size and egg production in the cabbage butterfly, *Pieris rapae* L. Aust. J. Zool. 30:223-232.

LACK, D. & E. LACK. 1951. Migration of insects and birds through a Pyrenean pass. J. Anim. Ecol. 20:63-67.

MARDEN, J. H. 1987. Maximum lift production during takeoff in flying animals. J. Exp. Biol. 130:235-258.

MORAN, P. A. P. 1968. An Introduction to Probability Theory. Clarendon, Oxford. 542 pp.

PEREZ, S. M., O. R. TAYLOR & R. JANDER. 1997. A sun compass in monarch butterflies. Nature 387:29.

ROOT, R. B. & P. M. KAREIVA. 1984. The search for resources by cabbage butterflies (*Pieris rapae*). Ecology 65:147-165.

SCHTICKZELLE, N. & M. BAGUETTE. 2003. Behavioural responses to habitat patch boundaries restrict dispersal and generate emigration-patch area relationships in fragmented landscapes. J. Anim. Ecol. 72:533-545.

SNOW, D. W. & K. F. A. ROSS. 1952. Insect migration in the Pyrenees. Entomol. Mon. Mag. 88:1-6.

SPIETH, H. R. & A. KASCHUBA-HOLTGRAVE. 1996. A new experimental approach to investigate migration in *Pieris brassicae* L. Ecol. Entomol. 21:289-294.

SUTCLIFFE, O. L. & C. D. THOMAS. 1996. Open corridors appear to facilitate dispersal by ringlet butterflies (*Aphantopus hyperantus*) between woodland clearings. Conserv. Biol. 10:1359-1365.

WALKER, T. J. 1991. Butterfly migration from and to peninsular Florida. Ecol. Entomol. 16:241-252.

WILLIAMS, C. B. 1958. Insect Migration. Collins, London. 235 pp.

WILLIAMS, C. B., I. F. B. COMMON, R. A. FRENCH, M. MUSPRATT & M. C. WILLIAMS. 1956. Observations on the migration of insects in the Pyrenees in the autumn of 1953. T. Roy. Ent. Soc. London. 108:385-407.

Received for publication 25 February 2004, revised and accepted 20 October 2004

Journal of the Lepidopterists' Society
59(1), 2005, 19–34

PAN-NEOTROPICAL GENUS *VENADA* (HESPERIIDAE: PYRGINAE) IS NOT MONOTYPIC: FOUR NEW SPECIES OCCUR ON ONE VOLCANO IN THE AREA DE CONSERVACIÓN GUANACASTE, COSTA RICA

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

AND

DANIEL H. JANZEN
Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104, USA email: djanzen@sas.upenn.edu

ABSTRACT. Between 1995 and 2004, as part of an ongoing macrolepidopteran inventory of the Area de Conservación Guanacaste (ACG), Costa Rica, 327 adults of the hesperiid genus *Venada* were reared from 636 wild-caught caterpillars and pupae. Although *Venada* was thought to be monotypic over its wide range (Mexico to Bolivia), there are four **new species** on Volcán Cacao in the ACG: ***Venada nevada*, *V. daneva*, *V. cacao*,** and ***V. naranja*** — all described by **Burns**, using characters of adult facies, male and female genitalia, caterpillar color pattern, and ecologic distribution. These skippers inhabit both rain and cloud forest, but not dry forest. The caterpillars feed on mature leaves of saplings in five genera of Lauraceae: *Beilschmiedia*, *Licaria*, *Nectandra*, *Ocotea*, and *Persea*. Caterpillars of *Ridens* also eat plants in the family Lauraceae, and *Ridens* and *Venada* may be closely related.

Additional key words: caterpillars, foodplants (Lauraceae), genitalia (male and female), parasitoids, taxonomy, variation.

There are far more species of skipper butterflies in the neotropics than current literature suggests. DNA sequencing is not the only way of revealing them. Granted, DNA sequencing as minimal as barcoding (Hebert et al. 2003a, 2003b) indicates even more species in the common and widespread neotropical skipper *Astraptes fulgerator* (described by Walch in 1775) than does a synthesis of morphologic, ecologic, ethologic, larval dietary, and other nonmolecular data. But the *A. fulgerator* complex—with at least 10 species in the Area de Conservación Guanacaste (ACG) of northwestern Costa Rica (Hebert et al. 2004)—is somewhat exceptional. In any case, we show with *Venada* that a nonmolecular approach to detection of cryptic species still works well.

Evans (1952) erected the skipper genus *Venada* for just one species. Hence some might consider him a splitter. That would be ironic because, at and around the species level, Evans repeatedly lumped (see, for example, Burns 1964, 1994, 2000, Burns & Kendall 1969, Burns & Janzen 2001). *Venada* recalls *Cephise*, another of Evans's (1952) pan-neotropical and monotypic skipper genera. Within the last decade, *Cephise* has mushroomed to 12 species—some sprung from other genera, some new (Burns 1996, Austin & Mielke 2000)—with yet more to come. Here we add four new species to *Venada*, all of them present on Volcán Cacao in the ACG.

Oddly enough, adults of *Venada* and males of those species of *Cephise* that lack tails are superficially similar (compare Figs. 1–16 with Burns 1996:figs. 28, 29, 32–35 and with Austin & Mielke 2000:figs. 1, 2, 5, 6, 27–30, 33–36, 39, 40; and compare images in Janzen & Hallwachs 2005). *Venada* adults and tailless *Cephise* males are sometimes so similar that even skipper specialists have mistaken one for the other. Externally, the peculiar palpi of *Cephise* (Burns 1996:183 and figs. 24–27) at once distinguish these skippers from *Venada*; internally, the genitalia do so (compare Burns 1996:figs. 1–22 with Figs. 17–29).

In both sexes of *Venada*, four honey-colored spots on the forewing—in spaces 1b, 2 (by far the largest), 3, and the cell (second largest)—are in close contact with one another, forming a conspicuous, irregular patch or band from below mid-costa to above the tornus (Figs. 1–16). Males of *Venada* have a costal fold (Figs. 1, 3, 5, 7). Wingspreads of reared individuals range from about 40 to 50 mm, with males averaging a little less than females. Specimens reared in captivity have smaller wingspreads, on average, than those coming from wild-found pupae.

Although *Venada* is widely distributed, specimens are rare in collections. Adults of *Venada* are not strictly crepuscular or nocturnal (like those of various species in such other tropical skipper genera as *Bungalotis*, *Dyscophellus*, *Porphyrogenes*, and *Celaenorrhinus*). Three *Venada* adults were seen flying rapidly in full sun in the middle of a windless day (27 February 2004) at 1100 m elevation on Volcán Cacao.

MATERIALS AND METHODS

For a description of the large and growing ACG, and of the massive caterpillar rearing and inventory program expanding there over the past quarter-century, see Burns and Janzen (2001), Janzen (2004), and Janzen and Hallwachs (2005). Here we analyze rearing records and 327 adult specimens coming from 636 caterpillars and pupae of *Venada* found between 1995 and 2004. No adults have been netted in the ACG, and the three noted above are the only ones seen in the wild. Reared adults have been deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC, USA, and at INBio in Costa Rica.

At the ACG, each wild-caught caterpillar gets an individual code in which the last two digits of the year of collection and a unique number for that year embrace the acronym SRNP (Santa Rosa National Park) with hyphens (e.g., 02-SRNP-23364). The code extends to whatever that caterpillar may produce—i.e., pupa, adult, parasitoid(s). These rearing voucher codes started in 1977 at Santa Rosa National Park, which today is Sector Santa Rosa of the ACG. Skipper genitalia dissection codes (e.g., X-5390) constitute an ongoing, X-rated series begun in 1974 at the Museum of Comparative Zoology, Harvard University, and continued at the USNM. Any pinned adult whose abdomen has been removed for KOH-treatment to aid dissection, is cross-coded with the 1-dram vial of glycerol that holds both the dissected genitalia and the abdominal integument.

RESULTS

To promote brevity, comprehension, and comparison, the descriptions of the four ACG species of *Venada* are tabular. The table itself uses shortening devices: sex symbols; FW, HW for forewing, hindwing; and the vertebrate term "cheeks" for a pair of small, more or less triangular, posteroventrolateral areas on the head of the adult (posterior to the bases of the palpi and ventral to the eyes). When wingshape is described as "sexually dimorphic in the usual skipper fashion," the wings of males are noticeably narrower and more pointed than those of conspecific females.

In naming a new genus for the species originally called *Telegonus advena* Mabille (and soon after, *Nascus advena*), Evans (1952) made the anagram *Venada* of the specific name. Now, in a similar spirit, names of two new species of *Venada* are additional anagrams. The name of the third species is that of the volcano on which all four species live. This name, that of the fourth species, and one of the anagrams relate to color and, by extension, to color characters in the skippers (see Etymology in Table 1). Names of all *Venada* species are three syllables (with an accent on the middle one) and are meant to be euphonious.

DISCUSSION

Variation. Subtle interspecific differences in brown ground color—which are perceptible in series of fresh, reared adults—generally fade with both the wear and tear of living and the passage of time after death.

Of the four subapical, hyaline, white spots that dot the forewing in spaces 6–9 in the genus *Venada*, the spot in space 7 is the weakest and the least likely to be expressed (Figs. 1–7, 9–14). This subapical spot series may extend into spaces 5 and especially 4 in both sexes (more often females) of *V. naranja* and in females of *V. nevada*. Any such extended appearance in *V. nevada* females involves space 4 but rarely space 5. A spot in space 4 is vertically oriented in *V. naranja* (Figs. 8, 16) but angled inward from top to bottom in *V. nevada* (Figs. 2, 10).

The distal dark band on the ventral hindwing of species of *Venada* tends to be outlined distally with pale yellowish scales. This is most evident in *V. nevada*. The pale scaling is often hypertrophied in females of *V. nevada*, especially in space 2 (Fig. 10). On occasion, development is so extreme that an opaque, pale yellow spot appears on the brown hindwing dorsally at the very same position in space 2. This happens in about 15% of 125 *V. nevada* females.

About halfway along the anteroposterior length of the tegumen, a short, curved, middorsal, sclerotized sac projects dorsoposteriad, just over the roof of the tegumen, in three of seven genitalically dissected males of *V. naranja*: X-5055 (00-SRNP-9252), X-5684 (01-SRNP-6992), and X-5703 (00-SRNP-9469). Typically there is no such prominence in males of *Venada* (Figs. 17–24)—or, for that matter, in males of various related genera.

One of 14 genitalically dissected males of *V. nevada* (X-5709 [03-SRNP-4768]) has a tiny secondary cornutus. This is a sclerotized, sharply pointed spine terminating a short side-sac from the slender, membranous vesica that leads to the large, somewhat comb-like primary cornutus. Although a prominent comb-like cornutus occurs in three ACG species of *Venada* (Figs. 18, 20, 22), there is no trace of a cornutus in the seven dissected males of *V. naranja*.

Foodplants. Like the caterpillars of nearly all other pyrgine hesperiids, the caterpillars of *Venada* eat dicotyledonous plants. But they feed almost exclusively on the mature leaves of saplings in five (or more) genera

TABLE 1. New species of *Venada* reared from wild-caught caterpillars in the Area de Conservación Guanacaste, Costa Rica.

	***V. nevada* Burns, n. sp.**	***V. daneva* Burns, n. sp.**	***V. cacao* Burns, n. sp.**	***V. naranja* Burns, n. sp.**
FACIES:	Figs. 1, 2, 9, 10	Figs. 3, 4, 11, 12	Figs. 5, 6, 13, 14	Figs. 7, 8, 15, 16
Wingshape	sexually dimorphic in the usual skipper fashion	sexually dimorphic in the usual skipper fashion	sexually dimorphic in the usual skipper fashion	♂ with broader, rounder wings—hence very like ♀
Cheeks	white	white	almost entirely dark	almost entirely dark
Ground color (brown)	intermediate (lighter)	lightest (medium brown)	darkest (blackish brown)	intermediate (darker)
Overscaling	yellow; conspicuous	yellow; inconspicuous	yellow; inconspicuous	orange; very conspicuous
Visibility of paired dark bands on ventral HW	good	intermediate	poor	good
HW fringe	yellow to orange-yellow; narrow	pale yellow to light brown; narrow	light to medium brown; narrow	orange; wide
FW hyaline costal spots in spaces 11 & 12	♂ with dash in space 11, mostly or entirely distad of large cell spot; ♀ with pair of dashes in spaces 11 & 12 (like an = sign) more or less centered over large cell spot	♂ with 0 or 1 tiny spot in space 11, well distad of large cell spot; ♀ with 0 or 1 tiny point about at upper distal corner of large cell spot	♂ with small spots in spaces 11 & 12, about at upper distal corner of large cell spot; ♀ with 0, 1, or 2 tiny points at upper distal end of large cell spot	♂ with small spot in space 11, about at upper distal corner of large cell spot; ♀ with 0, 1, or 2 tiny points more or less centered over large cell spot
FW hyaline subapical spot expression	♂ in spaces 6-9 (7 rarely missing); ♀ in spaces 6-9, also often in 4 and rarely 5	♂ usually in spaces 6, 8, 9; ♀ usually in spaces 6-9; any spot in space 7 tiny	♂, ♀ usually in spaces 6-9	♂ usually in spaces 6-9; ♀ usually in spaces 4-9
♂ GENITALIA:	Figs. 17, 18	Figs. 19, 20	Figs. 21, 22	Figs. 23, 24
Valva: distal, upswept, dentate process:				
orientation	dorsad	dorsad to slightly anteriad	anteriad as well as dorsad	dorsad
base	long	long	short	intermediate
mass	intermediate to robust	most delicate	delicate	robust
anterior dentate surface	flattened and hollowed out, leaving dual dentate edges	flattened	flattened; slightly expanded at distal end (in posterior view)	not flattened, so forming single edge
gap between process and body of valva	wide	wide	narrow	usually narrow
dorsal margin in lateral view	about even or with slight hump posteriad	concave anteriad, then humped	slight hump posteriad	concave anteriad, then humped
Aedeagus:				
surface	smooth	smooth	finely dentate distally on right side	finely dentate distal swelling on right side
anterior opening	far anterior	far anterior	more posterior	more posterior
cornutus	short, narrow	intermediate, wider	long, narrow	lacking
Gnathos in dorsal view	wide	wide	wide	narrow
Number examined	14	7	6	7
♀ GENITALIA:	Figs. 25, 26	Fig. 27	Fig. 28	Fig. 29
Lamella antevaginalis: lateral plates of:				
proximity	far apart	far apart	intermediate	close together
anteroposterior length	short	intermediate to long	long	long
ventral surface	virtually bare	finely and densely hairy	finely and densely hairy	finely and densely hairy
central plate of (in ventral view)	like a volcano or a normal curve	relatively flat	like a normal curve	flattish to like a normal curve
Signum	finely dentate oval patch with longitudinal central ridge, on dorsal side of corpus bursae	finely dentate oval patch with longitudinal central ridge, on dorsal (or ventral) side of posterior corpus bursae	roundish patch of many small spines aligned and radiating in a bilaterally symmetrical pattern, on dorsal side of posterior corpus bursae	wide band of innumerable fine, mostly longitudinally oriented spines encircling posterior end of corpus bursae
Number examined	11	6	4	6

TABLE 1. New species of *Venada* (cont.)

	V. nevada **Burns, n. sp.**	*V. daneva* **Burns, n. sp.**	*V. cacao* **Burns, n. sp.**	*V. naranja* **Burns, n. sp.**
CATERPILLAR (ultimate instar):	Fig. 30	Fig. 31	Fig. 32	Fig. 33
Abdominal color pattern	6 lateral, vertical, yellow stripes on uniform ground	4 mid-lateral, yellow to orangish, ellipsoid to round spots on uniform ground	3 mid-lateral, yellow, round spots (each with noticeable black eye shadow) on finely white-dotted ground	3 mid-lateral, yellow, round spots on finely white-dotted ground
Head	orange ventrolateral eyespots on black ground; rusty tips to dorsal lobes	orange ventrolateral eyespots on black ground; rusty dorsal lobes	no noticeable eyespots; light rusty to pale orange ground	inconspicuous, reddish ventrolateral eyespots; dark rusty ground
Collar/Rump	red/red	red/red	black/pale orange	black/dull tannish
FOODPLANTS:				
Cunoniaceae:				
Weinmannia wercklei	3			
Lauraceae:				
Beilschmiedia pendula	4			
Beilschmiedia 13641	38			1
Beilschmiedia 14011	1			
Beilschmiedia sp.		1		
Licaria 13499	152		1	2
Licaria 13886	4			
Licaria 14999	1			
Nectandra hihua	2			
Nectandra martinicensis	4			
Nectandra purpurea	10			
Nectandra salicifolia	4		1	
Nectandra salicina	4			
Nectandra umbrosa		1		
Nectandra 13808	3			
Ocotea austinii			4	19
Ocotea dendrodaphne				7
Ocotea insularis	9			8
Ocotea mollifolia	1	25		
Ocotea nicaraguensis	2			
Ocotea veraguensis	74			2
Ocotea 13582	74			
Ocotea 13654	5			1
Persea americana (intro.)			2	1
Persea schiedeana		133		
Lauraceae 13487	3		7	14
Lauraceae 14087	1			
Lauraceae 16677	3	3		
Lauraceae 17369		1		
ELEVATION RANGE:	375-1460 m	620-700 m	1140-1460 m	950-1460 m
LARVAL HABITAT:	foliage of saplings in edge situations from cloud forest to piedmont rainforest	foliage of saplings in heavily shaded understory of old-growth piedmont rainforest	foliage of saplings in edge situations in cloud forest	foliage of saplings in edge situations in cloud forest

TABLE 1. New species of *Venada* (cont.)

	V. nevada **Burns, n. sp.**	***V. daneva*** **Burns, n. sp.**	***V. cacao*** **Burns, n. sp.**	***V. naranja*** **Burns, n. sp.**
HOLOTYPE MALE:	02-SRNP-23534 Volcán Cacao, 1185 m, ACG, Costa Rica Lat 10.92714 Long -85.46683	02-SRNP-20143 Volcán Cacao, 620 m, ACG, Costa Rica Lat 10.87868 Long -85.38963	02-SRNP-23364 Volcán Cacao, 1150 m, ACG, Costa Rica Lat 10.92691 Long -85.46822	03-SRNP-4740 Volcán Cacao, 1220 m. ACG, Costa Rica Lat 10.92918 Long -85.46426
DEPOSITION:	USNM	USNM	USNM	USNM
PARATYPES:	108 ♂, 125 ♀ Volcán Cacao, ACG, Costa Rica	37 ♂, 31 ♀ Volcán Cacao, ACG, Costa Rica	1 ♂, 3 ♀ Volcán Cacao, ACG, Costa Rica	11 ♂, 7 ♀ Volcán Cacao, ACG, Costa Rica
ETYMOLOGY:	anagram; Spanish for snowfall, which relates to white cheeks	anagram; the other species with white cheeks	known only from high on Volcán Cacao; chocolate relates to dark ground color	Spanish for orange, the distinctive color of wing fringes and overscaling

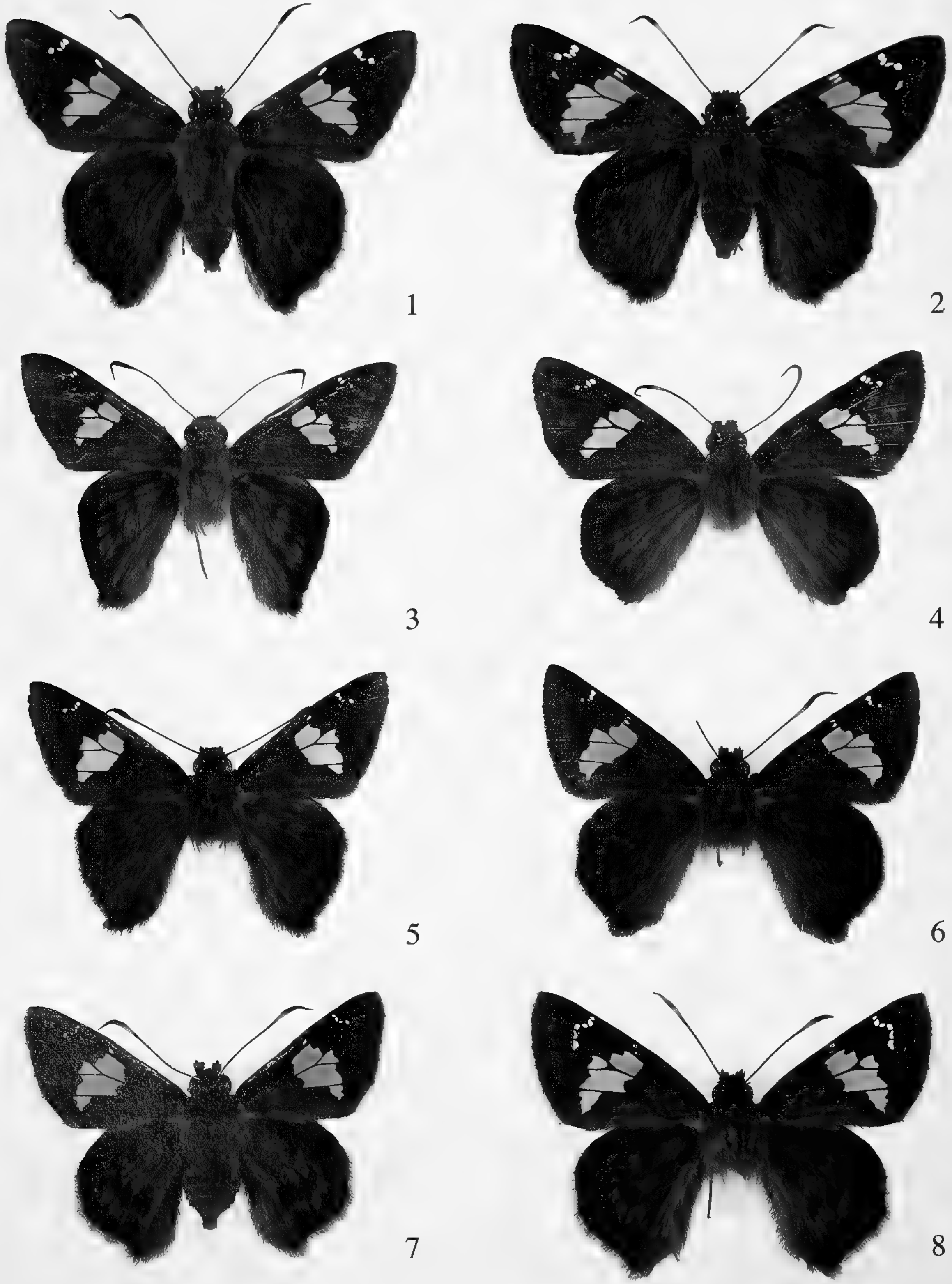
of the family Lauraceae: *Beilschmiedia*, *Licaria*, *Nectandra*, *Ocotea*, and *Persea* (Table 1). Both *V. cacao* and *V. naranja* also use the introduced lauraceous plant *Persea americana* Mill. However, three of 402 caterpillars of *V. nevada* (the only species of *Venada* reared in very large numbers) were found eating mature leaves of saplings of *Weinmannia wercklei* Standl. (Cunoniaceae) on the edges of the same forest in which the caterpillars are usually found feeding on Lauraceae. *Venada nevada* and *V. naranja* are more widespread and have more known foodplant species, while *V. daneva* and *V. cacao* appear to be using fewer of the species of lauraceous foodplants in their more restricted habitats. *Venada* is not found in the adjacent ACG dry forest even though *Ocotea veraguensis* (Meisn.) Mez, a foodplant of both *V. nevada* and *V. naranja* on Volcán Cacao, is common there (Janzen & Hallwachs 2005).

Only 10 other skippers occurring in the ACG eat leaves of Lauraceae: the pyrrhopygines *Jonaspyge aesculapus* (Staudinger) and *Jemadia pseudognetus* (Mabille); and the pyrgines *Zera hosta* Evans, two species of *Dyscophellus*, and five species of *Ridens* (Burns & Janzen 2001, Janzen & Hallwachs 2005). *Jonaspyge aesculapus* is noteworthy because, like *V. nevada*, it also eats *W. wercklei*. This pattern suggests similar chemical attractants in unrelated plants to which unrelated species of skippers convergently respond.

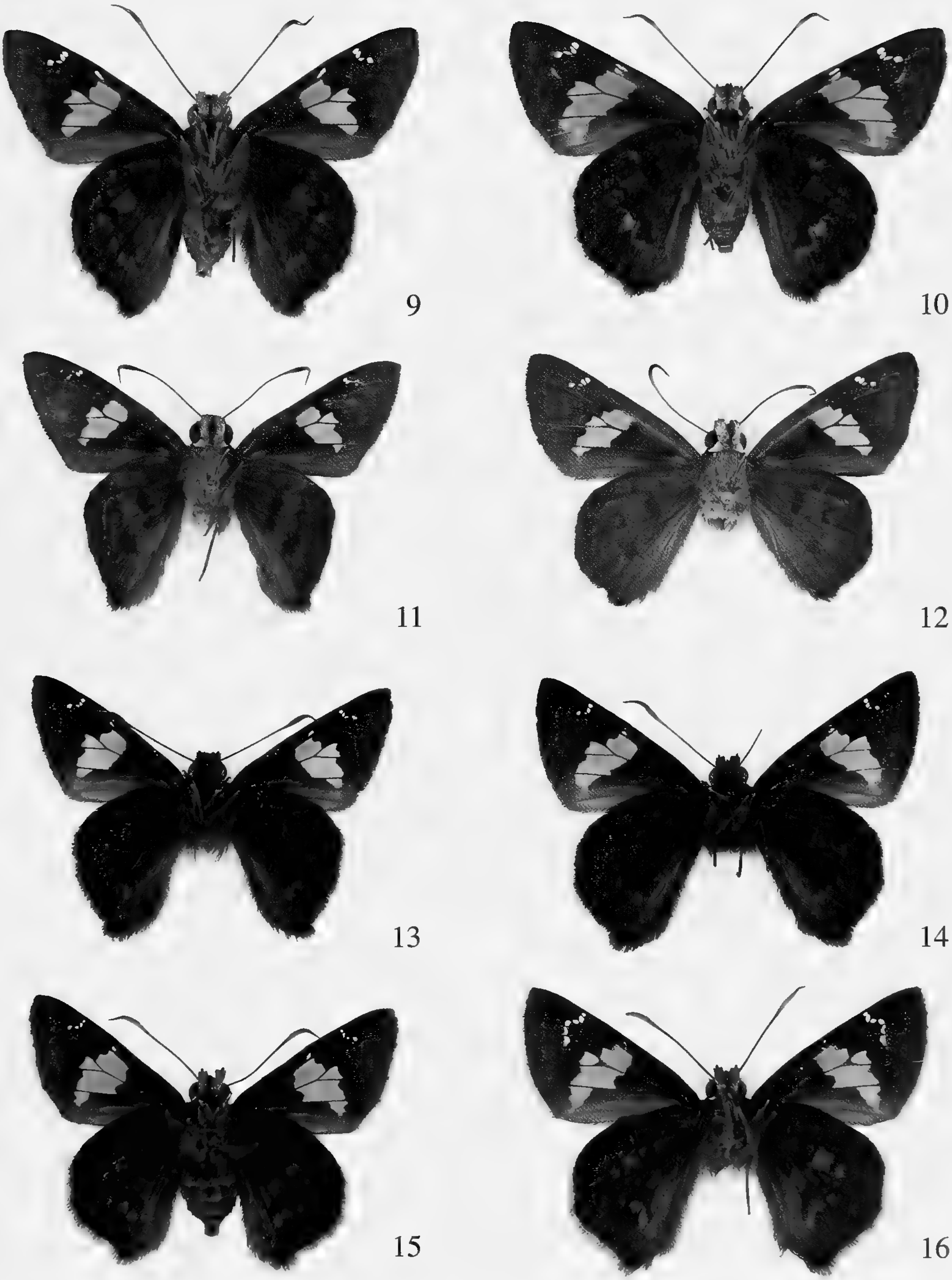
In contrast, selection of Lauraceae by *Ridens* and *Venada* probably reflects common ancestry. Although Evans (1952) described both *Ridens* and *Venada* and considered them related, he made them genera 12 and 18 in his *Urbanus* Group of 20 genera. Foodplants, caterpillar color patterns (Janzen & Hallwachs 2005), adult morphology, and mitochondrial DNA sequences of cytochrome *c* oxidase I suggest that *Ridens* and *Venada* are much closer. The DNA barcodes clearly distinguish the four ACG species of *Venada* from one another (Hajibabaei, Hebert, Burns, Janzen & Hallwachs, unpublished). This may be helpful in the future given the superficial similarity of *Venada* adults. (The caterpillars, however, have distinctive color patterns [Figs. 30–33]).

Foodplants of ACG *Venada* are too limited taxonomically (five genera of Lauraceae) and too shared by these skippers to be of much use in separating them, except in the case of *V. daneva* whose specific foodplant choices are almost unique (Table 1). The antithesis is the *Astraptes fulgerator* complex, most of whose 10 ACG species are defined by their disparate larval foodplants—chiefly in the families Sterculiaceae, Malvaceae, Ulmaceae, Fabaceae, Rhamnaceae, Sapindaceae, and Trigoniaceae (Hebert et al. 2004). On the other hand, male and female genitalia do not vary significantly among species of the *A. fulgerator* complex but clearly distinguish the species of *Venada* (Figs. 17–29).

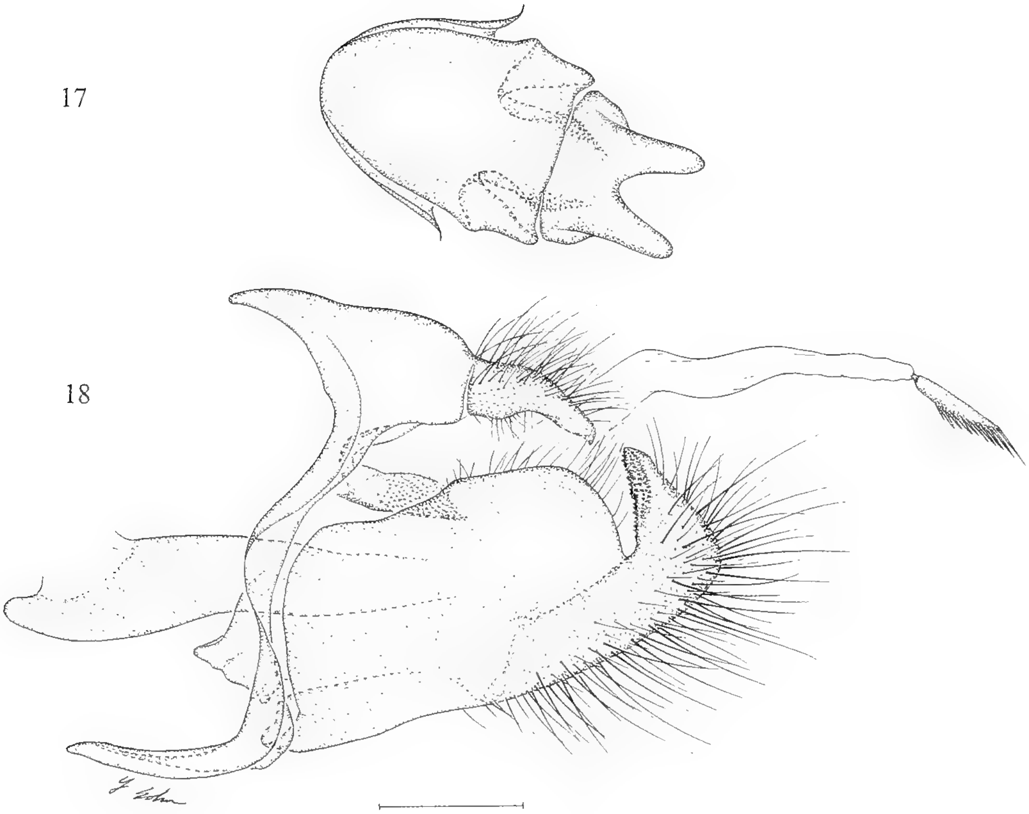
Geographic distribution. With four species on one volcano in the ACG, a pan-neotropical distribution (Mexico [Veracruz] to Bolivia), and paucity in collections, the formerly monotypic genus *Venada* will likely be found to contain a substantial number of species. Owing to their presumed similarity, series of specimens like those produced by the ACG bioinventory will be desirable for their detection and characterization. The present general scarcity of *Venada* in museums precludes much meaningful extrapolation. Genitalic dissections of a few miscellaneous specimens suggest additional species in Mexico and Guatemala, on the one hand, and Panama, on the other; but more material is needed. *Venada advena* was briefly described (Mabille 1889) from a single female from Chiriqui (western Panama). The scant verbal and visual portrayal of her facies does not exactly fit the facies of any of our ACG species. It seems



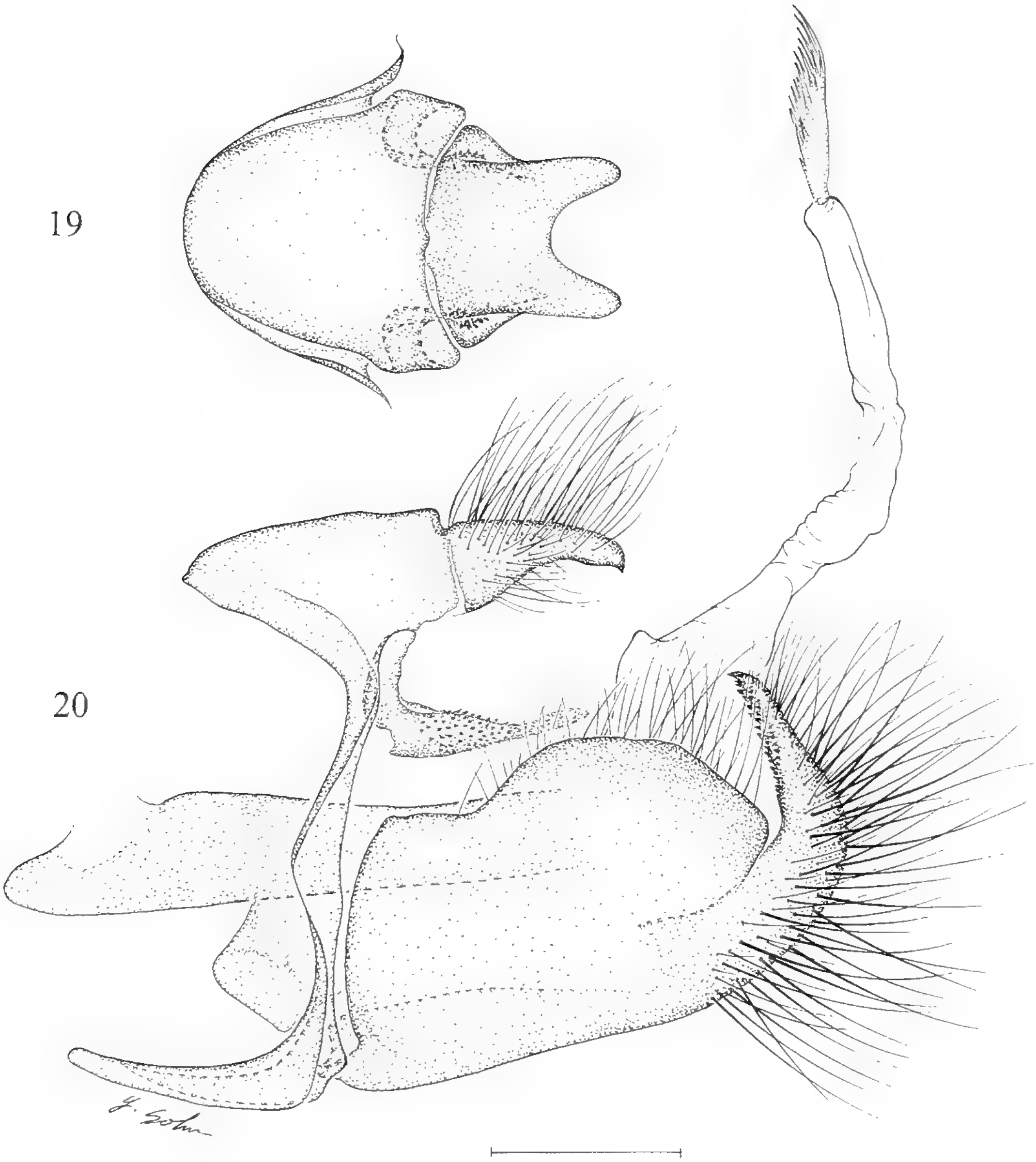
FIGS. 1–8. Adults in dorsal view (holotype males left, paratype females right) of four species of *Venada* from Volcán Cacao in the ACG, COSTA RICA (×1.4). **1, 2,** *V. nevada*, ♂ 02-SRNP-23534, ♀ 02-SRNP-23499. **3, 4,** *V. daneva*, ♂ 02-SRNP-20143, ♀ 01-SRNP-2550. **5, 6,** *V. cacao*, ♂ 02-SRNP-23364, ♀ 02-SRNP-23324. **7, 8,** *V. naranja*, ♂ 03-SRNP-4740, ♀ 01-SRNP-7133.



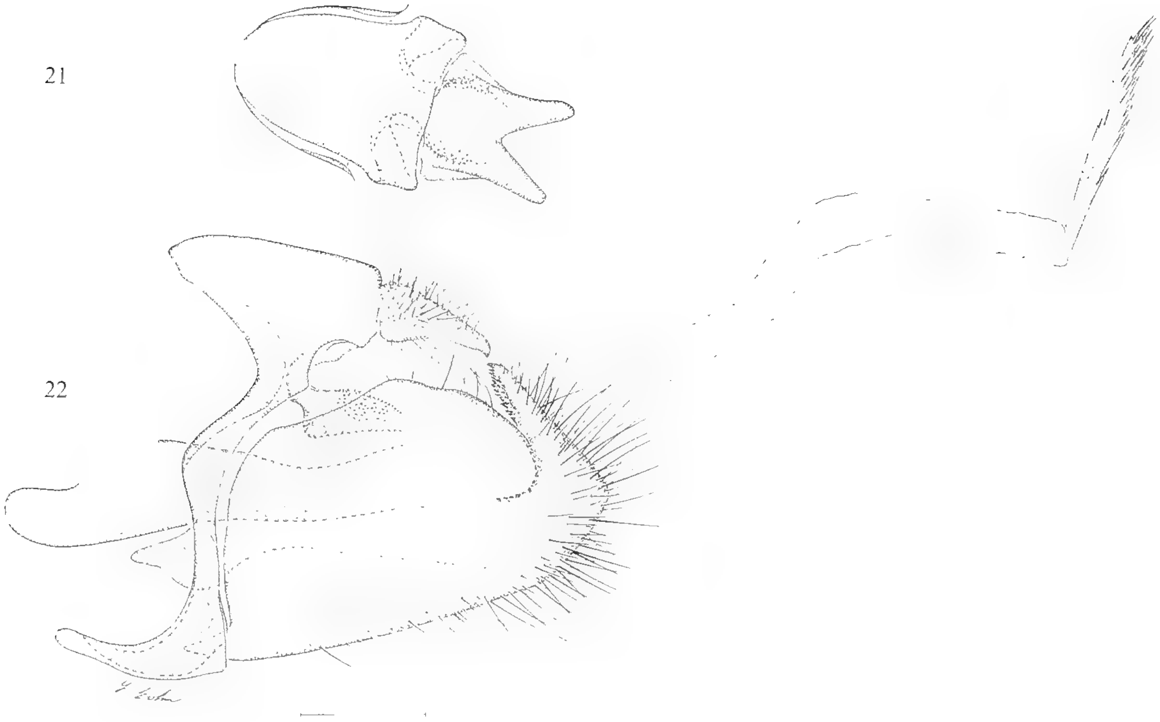
FIGS. 9–16. Adults in ventral view (holotype males left, paratype females right) of four species of *Venada* from Volcán Cacao in the ACG, COSTA RICA (×1.4). **9, 10,** *V. nevada*, ♂ 02-SRNP-23534, ♀ 02-SRNP-23499. **11, 12,** *V. daneva*, ♂ 02-SRNP-20143, ♀ 01-SRNP-2550. **13, 14,** *V. cacao*, ♂ 02-SRNP-23364, ♀ 02-SRNP-23324. **15, 16,** *V. naranja*, ♂ 03-SRNP-4740, ♀ 01-SRNP-7133.



FIGS. 17, 18. Male genitalia of *Venada nevada* from Volcán Cacao in the ACG, COSTA RICA, X-5693, 02-SRNP-8926 (USNM); scale = 1.0 mm. **17,** Tegumen, uncus, and gnathos in dorsal view. **18,** Complete genitalia (minus right valva), with vesica everted, in left lateral view.



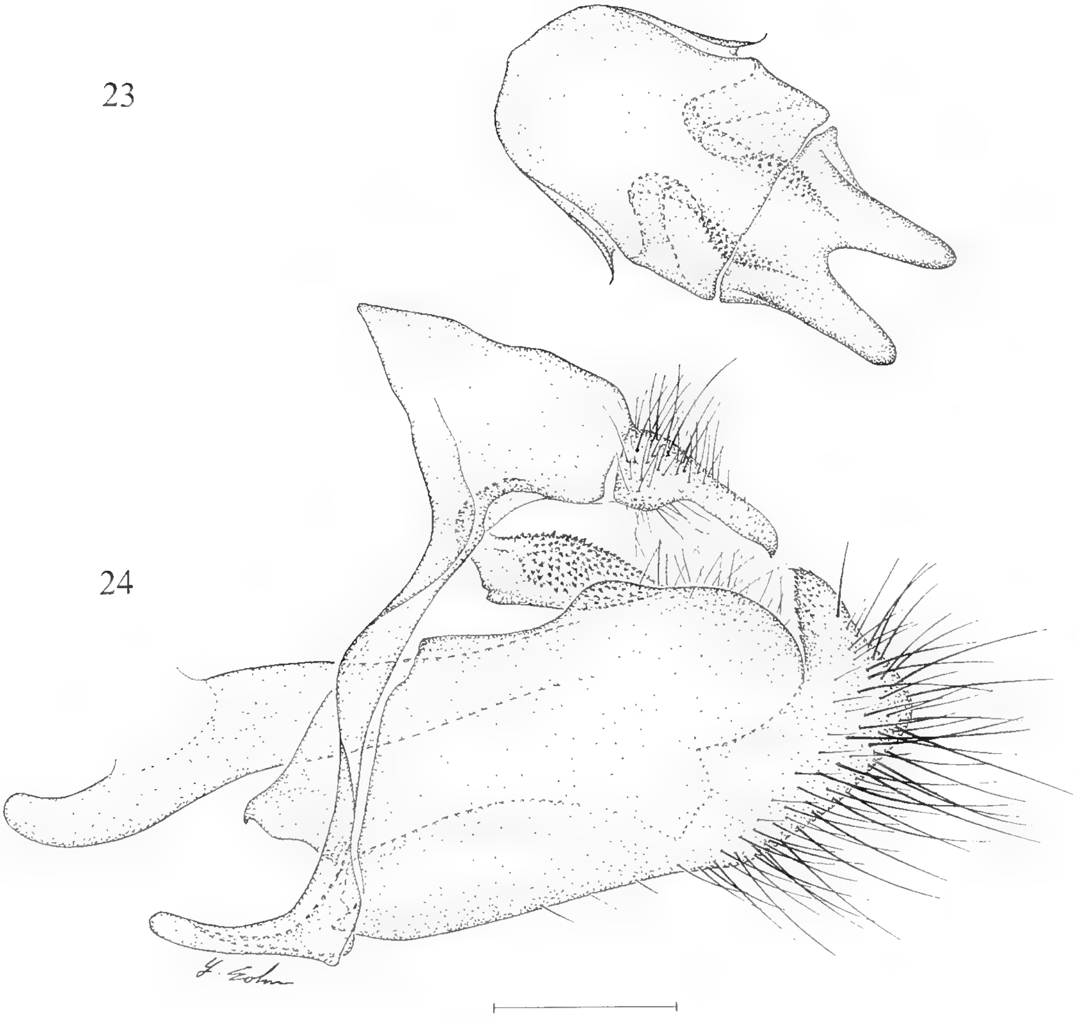
FIGS. 19, 20. Male genitalia of *Venada daneva* from Volcán Cacao in the ACG, COSTA RICA, X-5706, 03-SRNP-5862 (USNM): scale = 1.0 mm. **19,** Tegumen, uncus, and gnathos in dorsal view. **20,** Complete genitalia (minus right valva), with vesica everted, in left lateral view.



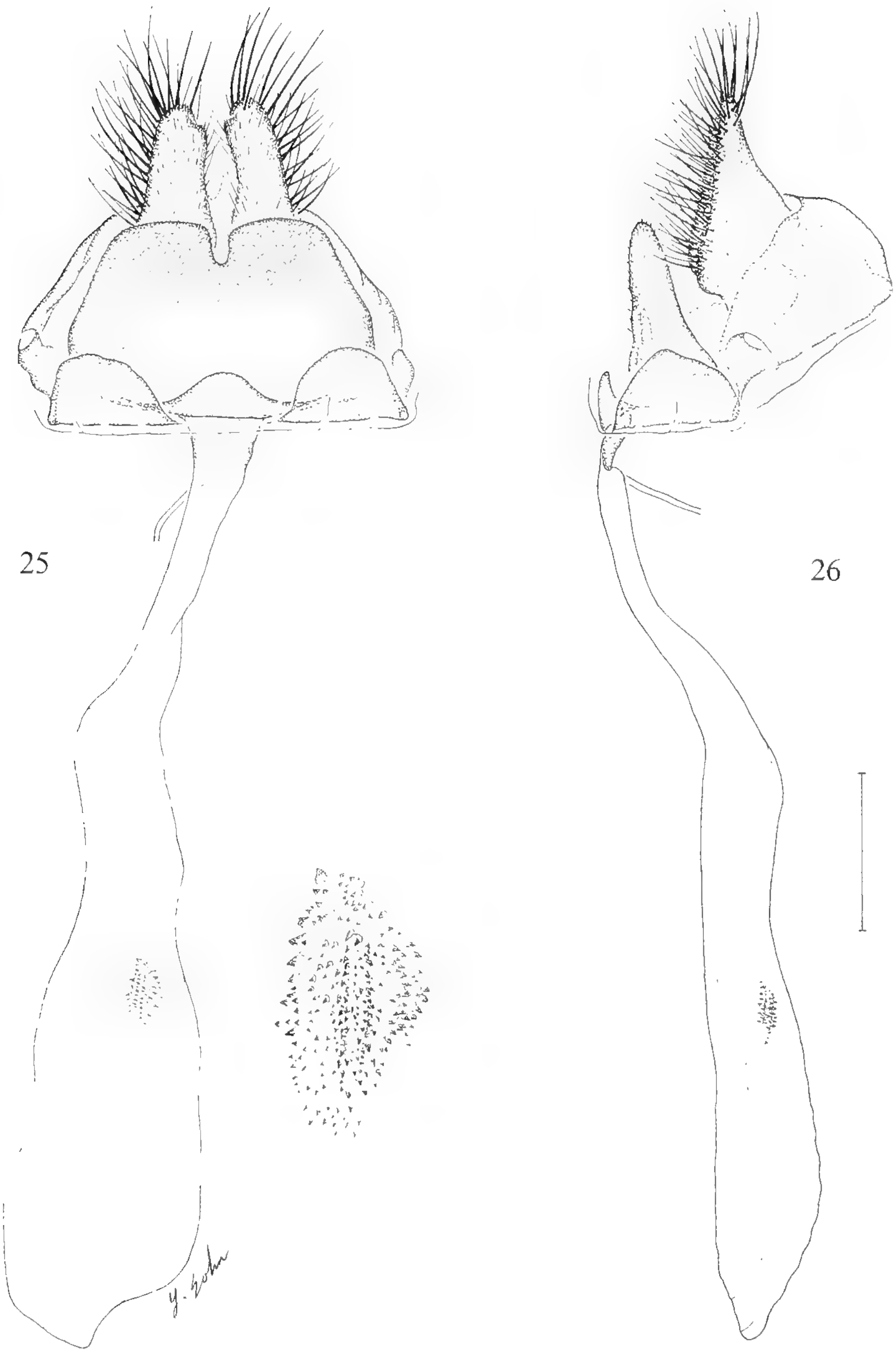
21

22

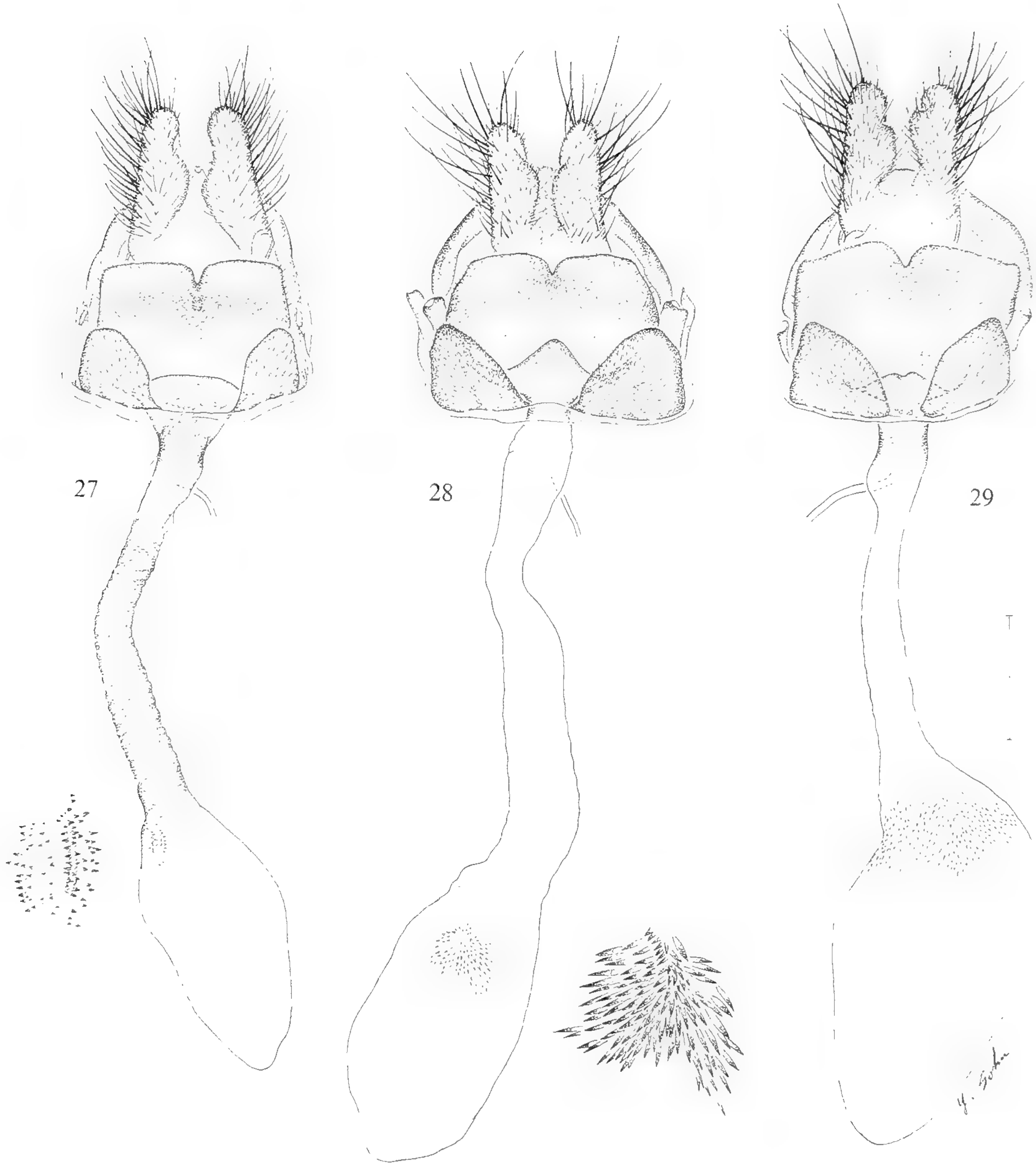
FIGS. 21, 22. Male genitalia of *Venada cacao* (holotype) from Volcán Cacao in the ACG, COSTA RICA, X-5390, 02-SRNP-23364 (USNM); scale = 1.0 mm. **21,** Tegumen, uncus, and gnathos in dorsal view. **22,** Complete genitalia (minus right valva), with vesica everted, in left lateral view.



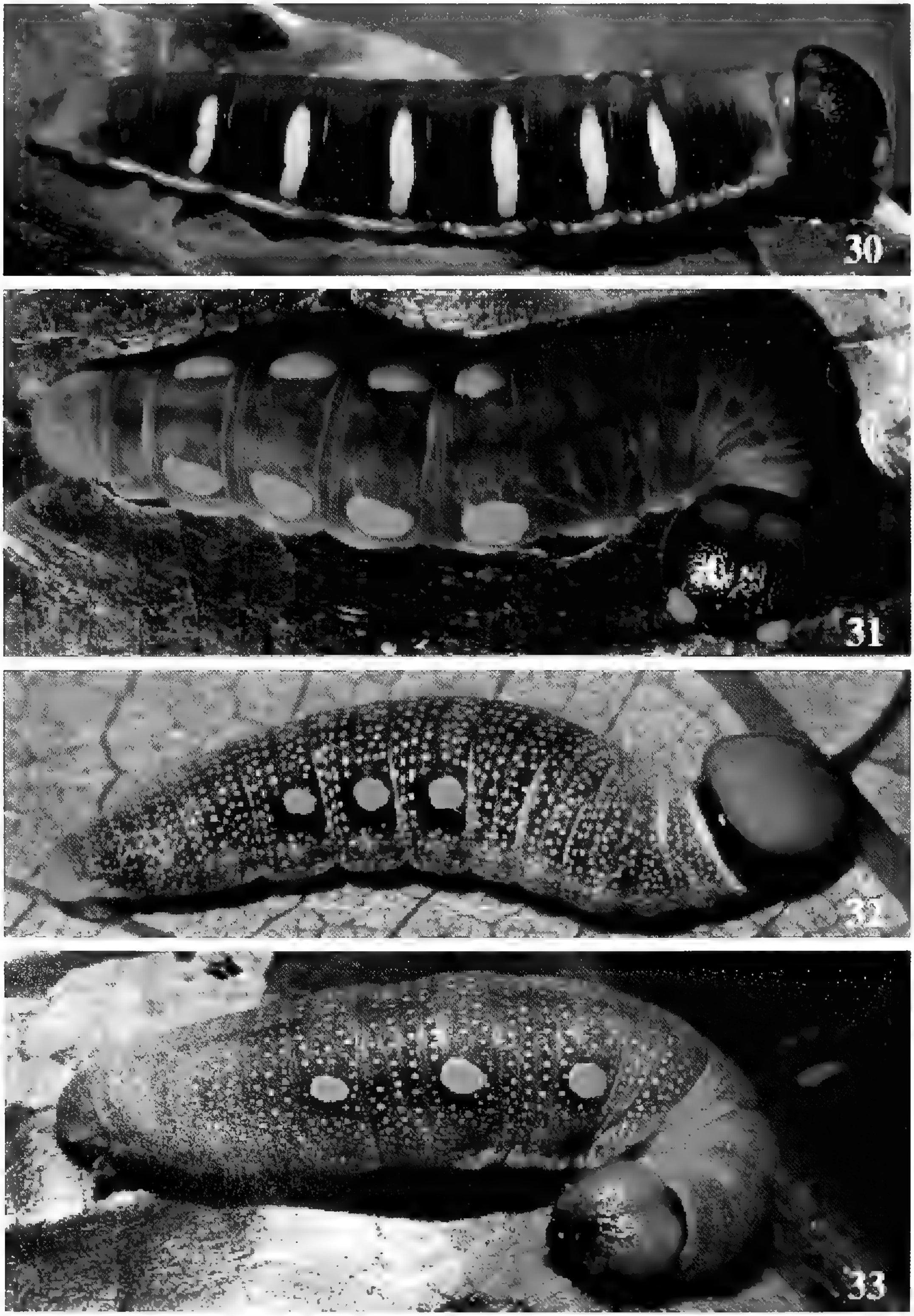
FIGS. 23, 24. Male genitalia of *Venada naranja* from Volcán Cacao in the ACG, COSTA RICA, X-5685, 02-SRNP-8086 (USNM); scale = 1.0 mm. **23,** Tegumen, uncus, and gnathos in dorsal view. **24,** Complete genitalia (minus right valva) in left lateral view.



FIGS. 25, 26. Female genitalia of *Venada nevada* from Volcán Cacao in the ACG, COSTA RICA, X-4604, 97-SRNP-11146 (USNM); scale = 1.0 mm. **25,** Ovipositor lobes, sterigma, bursa copulatrix, and part of ductus seminalis in ventral view, plus enlargement of signum. **26,** The same in right lateral view.



FIGS. 27–29. Female genitalia of three species of *Venada* from Volcán Cacao in the ACG, COSTA RICA. Ovipositor lobes, sterigma, bursa copulatrix, and part of ductus seminalis in ventral view; scale = 1.0 mm. **27,** *V. daneva*, with enlargement of signum, X-5691, 03-SRNP-6535 (USNM). **28,** *V. cacao*, with enlargement of signum, X-5688, 02-SRNP-23004 (USNM). **29,** *V. naranja*, X-5687, 01-SRNP-7133 (USNM).



FIGS. 30–33. Caterpillars (last instars) of four species of *Venada* from Volcán Cacao in the ACG, COSTA RICA. **30**, *V. nevada*, 97-SRNP-11042. **31**, *V. daneva*, 98-SRNP-6010. **32**, *V. cacao*, 99-SRNP-552. **33**, *V. naranja*, 00-SRNP-9050.

closest to that of *V. daneva*, but the whitish wing fringes and ash gray palpi ascribed to *V. advena* in its original description are not evident in *V. daneva*.

What can be offered at this time is the unsurprising fact that at least three of the ACG species range more widely in Costa Rica, as shown by the following museum specimens. *Venada nevada*: San Vito, 1150 m, Puntarenas, 31-XII-1976, 1 ♂, G. B. Small (USNM). *Venada cacao*: Juan Viñas, Cartago, ?-I-?, 1 ♂ (USNM); Monteverde, Puntarenas, 4 & 6-VII-1985, 1 ♂ 1 ♀, W. A. Haber (USNM); Buen Amigo, San Luis, Monteverde, 1000–1350 m, Puntarenas, ?-III-1995, 1 ♂, Z. Fuentes (INBio). What appears to be *Venada daneva*: Rancho Quemado, Osa Peninsula, Puntarenas, ?-IV-1991, 1 ♀, J. C. Saborio (INBio).

Venada cacao also occurs in Panama. Williams and Bell (1934:132, pl. VIII, fig. 4) described and illustrated (in left lateral view) the male genitalia of "*Nascus advena*." The genitalia of this "Panama" male (no further data given) clearly correspond to those of *V. cacao* (Fig. 22).

The male of "*Nascus advena*" illustrated dorsally and ventrally by Godman and Salvin (1893:vol. 3, pl. 79, figs. 6, 7) is not *V. advena*. If it belongs to any of the ACG species of *Venada*, it is *V. cacao*. This is because the hyaline costal spots, in spaces 11 and 12 of the forewing, are two in number and are located at the upper distal corner of the large cell spot. Judging from the text (Godman & Salvin 1893:vol. 2, p. 323), this illustrated male came either from Chiriqui or from Chontales, Nicaragua.

Parasitoids. None of the 15 reared caterpillars of *V. cacao* has been parasitized. Only one of 55 reared caterpillars of *V. naranja* and six of 164 reared caterpillars of *V. daneva* have produced parasitoids, and these have not yet been determined. The 402 rearings of *V. nevada* have yielded parasitoids in just 14 cases: five are the large tachinid *Chlorohystricia* sp. 1, a fly that also attacks *Yanguna cosyra* (H. Druce) and an undescribed species of *Ridens* in the same cloud forest habitat on Volcán Cacao; two are the generalist tachinid *Patelloa xanthura* (Wulp), which has been reared from caterpillars of 43 species of ACG hesperiids throughout dry, rain, and cloud forest; one is an as yet unidentified tachinid from cloud forest; two are unidentified ichneumonids, one from rain forest and one from cloud forest; and four are the ichneumonid *Casinaria* sp. 9 from both rain and cloud forest—a wasp that, in the same habitats, also attacks *Y. cosyra*, *Creonpyge creon* (H. Druce), *Phocides nigrescens* Bell, the above-mentioned undescribed *Ridens*, *Achlyodes busirus* (Cramer), *A. thraso* (Hübner), and *A. pallida* (R. Felder) (but mostly *Y. cosyra* and *Ridens*). *Venada* apparently lacks parasitoids that are host-specific, but occasionally supports parasitoids that live mainly on a small number of other medium-to-large, dicot-eating species of hesperiids.

ACKNOWLEDGEMENTS

We thank E. Araya, C. Cano, E. Cantillano, M. Carmona, O. Espinosa, R. Espinosa, R. Franco, D. Garcia, W. Hallwachs, C. Moraga, R. Moraga, G. Pereira, M. Pereira, J. Perez, F. Quesada, H. Ramirez, L. Rios, P. Rios, G. Sihezar, and F. Vargas for caterpillar hunting and husbandry; R. Espinosa, J. Gonzales, A. Guadamuz, B. Hammel, N. Zamora, and the herbarium staff at INBio for foodplant identifications; I. Chacon for locating specimens of *Venada* in the INBio collections; I. Gauld and D. M. Wood for wasp and fly identifications; P. Gentili and D. J. Harvey for dissecting skipper genitalia; J. Steiner for Figs. 1–16; and Y. Sohn for Figs. 17–29. The ACG caterpillar inventory has been variously supported by NSF grants BSR 90–24770, DEB 93–06296, DEB 94–00829, DEB 97–05072, and DEB 00–72730 and by the Area de Conservación Guanacaste, CONICIT, INBio, and the government of Costa Rica.

LITERATURE CITED

AUSTIN, G. T. & 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.

BURNS, J. M. 1964. Evolution in skipper butterflies of the genus *Erynnis*. Univ. Calif. Publ. Entomol. 37:1–217.

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

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

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

BURNS, J. M. & R. O. KENDALL. 1969. Ecologic and spatial distribution of *Pyrgus oileus* and *Pyrgus philetas* (Lepidoptera: Hesperiidae) at their northern distributional limits. Psyche 76:41–53.

BURNS, J. M. & D. H. JANZEN. 2001. Biodiversity of pyrrhopygine skipper butterflies (Hesperiidae) in the Area de Conservación Guanacaste, Costa Rica. J. Lepid. Soc. 55:15–43.

EVANS, W. H. 1952. A catalogue of the American Hesperiidae indicating the classification and nomenclature adopted in the British Museum (Natural History). Part II. Pyrginae. Section 1. British Museum, London. 178 pp., pls. 10–25.

GODMAN, F. D. & O. SALVIN. 1879–1901. Biologia Centrali-Americana. Insecta. Lepidoptera—Rhopalocera. Vol. 2, 782 pp. Vol. 3, 113 pls.

HEBERT, P. D. N., A. CYWINSKA, S. L. BALL & J. R. DEWAARD. 2003a. Biological identifications through DNA barcodes. Proc. Roy. Soc. Lond. B 270:313–321.

HEBERT, P. D. N., S. RATNASINGHAM & J. R. DEWAARD. 2003b. Barcoding animal life: cytochrome *c* oxidase subunit 1 divergences among closely related species. Proc. Roy. Soc. Lond. B 270:S596–S599.

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

JANZEN, D. H. 2004. Ecology of dry forest wildland insects in the Area de Conservación Guanacaste, pp. 80–96. *In* Frankie, G. W., A. Mata & S. B. Vinson (eds.) Biodiversity conservation in Costa Rica. Univ. Calif. Press, Berkeley.

JANZEN, D. H. & W. HALLWACHS. 2005. Philosophy, navigation and use of a dynamic database ("ACG Caterpillars SRNP") for an inventory of the macrocaterpillar fauna, and its food plants and parasitoids, of the Area de Conservacion Guanacaste (ACG), northwestern Costa Rica (http://janzen.sas.upenn.edu).

MABILLE, P. 1889. Diagnoses de Lépidoptères nouveaux. Le Naturaliste 11(2):59.

WALCH, J. E. I. 1775. Beyträge zur Insecten-Geschichte. Naturforscher 7:113–116, pl. 1.

WILLIAMS, R. C., JR. & E. L. BELL. 1934. Studies in the American Hesperioidea, Paper III (Lepidoptera). Trans. Am. Entomol. Soc. 60:121–132, pl. VIII.

Received for publication 11 June 2004; revised and accepted 9 February 2005

Journal of the Lepidopterists' Society
59(1), 2005, 35–37

IMMATURE STAGES OF *NAPEOGENES SULPHURINA* BATES, 1862 (NYMPHALIDAE, ITHOMIINAE) FROM NORTHEASTERN BRAZIL

Additional key words: Alagoas, life cycle, Lycianthes, Napeogenini, Solanaceae.

Although the immatures of Ithomiinae have been described for representatives of most genera (DeVries 1987, Brown & Freitas 1994 and references therein), little information is available for many basal groups and highly diversified genera (Freitas & Brown 2002). The tribe Napeogenini includes the genera *Hypothyris* (16 species), *Napeogenes* (23) and *Hyalyris* (12), plus the monotypic *Epityches, Aremfoxia, Garsauritis* and *Rhodussa* (Lamas 2004 as modified by Willmott & Freitas in prep.). Immatures have been described for species in all Napeogenini genera except *Aremfoxia* (Brown 1980, Brown & Freitas 1994), but additional information about species in the large genera is still needed. In the largest genus of this tribe, *Napeogenes*, immatures of only three species have been described (Brown & Freitas 1994:14, including partial information for *N. sulphurina* in Table 1). The present paper describes in details the immature stages of *Napeogenes sulphurina* Bates, 1862 (Nymphalidae, Ithomiinae), and compares their morphological characters with those of other known Napeogenini.

Adults and immatures of *Napeogenes sulphurina* were collected near Usina Serra Grande, Ibateguara, Alagoas, about 70 km from the Atlantic coast (08∞58'S, 36∞03'W) and about 500 m above sea level. This region contains many fragments of dense lower montane rain forest. The mean annual temperature is 24°C, and the annual rainfall has been near 3000 mm in some recent years (M. Tabarelli, pers. comm.). Most observations were made in the Coimbra forest fragment (3400 ha), from 3 to 5 August, 2003, in the Sede region, Cavalo Morto Road, Varjão and Road to Petrópolis. Immatures and host plant were found in the forests near the Road to Petrópolis (09°00'S, 35°53'W), where a large Ithomiinae "pocket" was present. Additional specimens used for descriptions were collected by KSB in Ipojuca, Pernambuco (about 120 km NE from Usina Serra Grande), in 1970 (see Table 1 in Brown & Freitas 1994). Data were recorded on behavior and development times for all stages, and dry head capsules and pupal castings were kept in small glass vials. When there was sufficient material, immatures were fixed in Kahle solution (AVLF collection). All measurements were made using a microscope fitted with a calibrated micrometric ocular. Egg size is presented as height and diameter of field-collected eggs, and head capsule size is the distance between the most external stemmata (as in Freitas 1991).

DESCRIPTION OF EARLY STAGES

Egg (Fig. 1a,b). White, spherical, with 14-15 longitudinal ridges and 8-9 transverse ridges; height and diameter 0.7 mm. Duration 4-5 days, n = 4

Larvae: first instar (Figure 1c,d). Body white, turning green after first meal; legs, prolegs and anal plate without pigmentation. Head light yellow; average width 0.43 mm (SD = 0.012, n = 4). Maximum length 2 mm. Duration 2-3 days, n = 2.

Second instar. Similar to previous instar except for the following characters. Head yellow; average width 0.57 mm (SD = 0.009, n = 4). Maximum length 3.5 mm. Duration 2-3 days, n = 4.

Third instar. Similar to previous instar except for the following characters. Body light green; conspicuous sublateral semicircular tubercles; a lateral yellow mark in A1 and a pair of yellow lateral protuberances in A8. Head cream with a frontal transverse black band; average width 0.85 mm (SD = 0.035, n = 4). Maximum length 7 mm. Duration 3-4 days, n = 4.

Fourth instar (Fig. 1e). Similar to previous instar except for the following characters. Body dark gray; legs black; lateral yellow stripe broad and including sublateral tubercles and spiracles. Average head width 1.23 mm (SD = 0.039, n = 6). Maximum length 10 mm. Duration 2-4 days, n = 4.

Fifth instar (Fig. 1f,g). Body dark greenish gray; legs black; prolegs with lateral black plates; conspicuous sublateral semicircular tubercles; anal plate same color as the rest of the body (without black); a lateral dark yellow mark in A1 and a pair of dark yellow protuberances in A8; lateral yellow stripe broad and including sublateral tubercles and spiracles. Head cream with a frontal transverse black band; average width 1.82 mm (SD = 0.059, n = 5). Maximum length 17 mm. Duration 5 days, n = 3.

Pupa (Fig. 1, h-i). Short, slightly bent, beige after pupation, with many brown markings on the abdomen and wing cases; becoming entirely reflective after two days; cremaster dark red; ocular caps short and pointed. Length 9 mm (n = 2). Duration 8-9 days (n = 2).

HOST PLANTS OVIPOSITION, AND IMMATURE BEHAVIORS

Adults (Fig. 1j) were common in most of the habitats in the study area, including primary and secondary forests, visiting flowers early in the morning on forest edges. Adults were observed feeding on flowers of Asteraceae, and also on bird droppings inside the forest. Adults were especially abundant (more than 200 adults in an area of about 200 m2) together with their co-mimics *Scada reckia* (abundant) and *S. karschina delicata* (rare, local) in a large ithomiine pocket near the Road to Petrópolis, the place where the host plant was found. The host plant is a small scandent vine in the genus *Lycianthes* (Solanaceae), very similar to that used by this species in Ipojuca (Drummond & Brown 1987: 350). Ovipositions were not observed, but all eggs found (n = 10) were laid singly under leaves. After hatching, caterpillars first ate part of the egg shell, and then began to eat the leaves by chewing small holes in

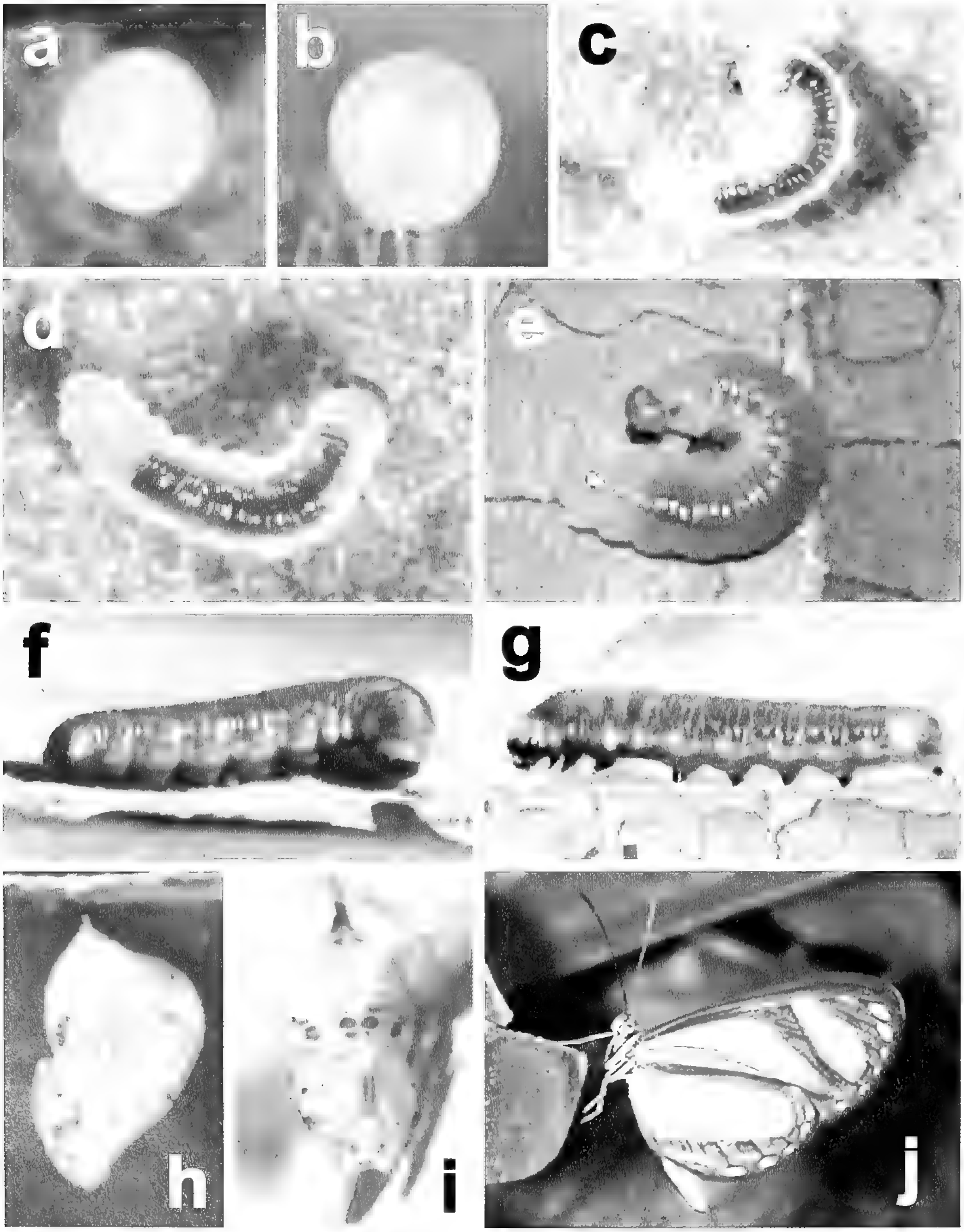


FIG. 1 - Immature stages of *Napeogenes sulphurina*; a,b, egg; c, first instar; d, second instar; e, fourth instar; f,g, fifth (last) instar; h,i, pupa (h, lateral; i, dorsal); j, adult male.

the blade. Larvae were not cannibalistic, and rested in a J-shaped position on the underside of the leaves; when disturbed, they dropped off the leaf suspended by a silk thread.

The immatures of *N. sulphurina* are very similar to those of other Napeogenini species (D´Almeida 1938, Brown 1980, Brown & Freitas 1994: 14), including the presence of sublateral semicircular tubercles and a lateral stripe in the 4th and last instar larvae, and the shape and color of the pupa (except for *Epityches*, which has a green pupa similar to those of the Dircennini and Godyridini; Brown & Freitas 1994). Prolegs with lateral black plates (a feature most common in species belonging to the basal tribes of Ithomiinae such as Tithoreini and Melinaeini) are known in *Napeogenes* and *Rhodussa*, but are absent in *Garsauritis* and all known immatures of *Hypothyris* and *Hyalyris*. The frontal transverse black band on the head capsule, shared with most known *Ithomia* (Brown & Freitas 1994:14, Srygley & Penz 2000), is known only in the genus *Napeogenes* within the Napeogenini (*N. sylphis, N. inachia*, Brown & Freitas 1994:14, and *N. apulia* [unpublished data, K. R. Willmott]); additional information about other species of *Napeogenes* is needed to confirm this pattern.

Marcelo Tabarelli, Inara Leal, André Santos and Antônio Aguiar greatly helped in field work in Alagoas and provided information on the study site in Serra Grande. This study was funded by Fapesp (grants 00/01484-1 and 04/05269-9 to AVLF) and is part of the project "Lepidoptera of São Paulo State" (BIOTA-FAPESP program - grant 98/05101-8). André V. L. Freitas thanks also the National Science Foundation (DEB-0316505).

LITERATURE CITED

BROWN JR., K. S. 1980. A review of the genus *Hypothyris* Hübner (Nymphalidae), with descriptions of three new subspecies and early stages of *H. daphnis*. J. Lepid. Soc. 34: 152-172.

BROWN JR., K. S. & A. V. L. FREITAS. 1994. Juvenile stages of Ithomiinae: overview and systematics (Lepidoptera: Nymphalidae). Trop. Lepid. 5: 9-20.

D'ALMEIDA, R. F. 1938. Estudo sobre três gêneros da sub-família Ithomiinae (Lepid.: Rhop.). Mem. Inst. Oswaldo Cruz 33: 231-247.

DEVRIES, P. J. 1987. The butterflies of Costa Rica and their natural history. Papilionidae, Pieridae, Nymphalidae. Princeton University Press, Princeton, NJ.

DRUMMOND, B. A., III & K. S. BROWN JR. 1987. Ithomiinae (Lepidoptera: Nymphalidae): summary of known larval host plants. Ann. Mo. Bot. Gard. 74: 341-358.

FREITAS, A. V. L. 1991. Variação morfológica, ciclo de vida e sistemática de *Tegosa claudina* (Eschscholtz) (Lepidoptera: Nymphalidae, Melitaeinae) no Estado de São Paulo. Rev. Bras. entomol. 35: 301-306.

FREITAS, A. V. L. & K. S. BROWN JR. 2002. Immature stages of *Sais rosalia* (Nymphalidae, Ithomiinae). J. Lepid. Soc. 56: 104-106.

LAMAS, G. 2004. Ithomiinae, pp. 172-191. *In*: Lamas, G. (Ed.), Checklist: Part 4A. Hesperioidea-Papilionoidea. In: Heppner, J.B. (Ed.), Atlas of Neotropical Lepidoptera. Vol. 5A. Gainesville, Association for Tropical Lepidoptera/Scientific Publishers.

SRYGLEY, R. B. AND C. M. PENZ. 2000. Larval description and host-plant record for *Ithomia diasia* Hewitson (Nymphalidae: Ithomiinae) in Panama. J. Lepid. Soc. 54: 145-146.

ANDRÉ VICTOR LUCCI FREITAS, KEITH S. BROWN JR., *Museu de História Natural and Departamento de Zoologia, Instituto de Biologia, Universidade Estadual de Campinas, CP 6109, Campinas, São Paulo, 13083-970, Brazil*

Received for publication 7 April 2004, revised and accepted 10 December 2004

Journal of the Lepidopterists' Society
59(1), 2005, 37–39

NOTES ON THE LIFE HISTORY OF *DYNASTOR DARIUS DARIUS* (FABRICIUS) (NYMPHALIDAE: BRASSOLINAE) FROM VENEZUELA

Additional key words: Biology, development, host plants, immature stages

Three *Dynastor* species are known to occur in South America (Urich & Emmel 1991a, 1991b). *Dynastor darius* (Fabricius), is a common, though usually not abundant, fast-flying, crepuscular butterfly, active at dawn as well as dusk. It has been reported from Brazil to Guatemala, including Trinidad (Aiello & Silberglied 1978, Urich & Emmel 1991b). Two subspecies are commonly recognized: *darius* from Mexico to the Amazon basin, and *stygianus* (Butler) from Guatemala to Ecuador (De Vries 1987). In Venezuela, subspecies *darius* inhabits semi-deciduous forests between 100 and 1000m.

This butterfly has been reported as a minor pest of pineapple crops (*Ananas comosus* (L.) Merr., Bromeliaceae) (Araque 1961, Petty et al. 2002). Host records include also different Bromeliads in the genera *Aechmea*, *Billbergia*, *Bromelia*, *Ortgiesia* and *Tillandsia* (De Vries 1987, Penz et al. 1999). In natural conditions, adults rest on soil where they are well camouflaged among dry leaves. However, we have seen some quietly resting on plant trunks close to the ground. M. Cock (personal communication) was able to easily catch a specimen that was resting on a thin palm trunk. Though it has been reported that the adults of *D. d. stygianus* and *D. d. darius* do not visit rotting fruit or other sources of nutrition (DeVries 1987, Urich & Emmel 1991b), we have seen them occasionally feeding on rotten mangoes (*Mangifera indica* L. Anacardiaceae) at dusk in at least two Venezuelan localities (Palmichal, Carabobo and Choroní, Aragua).

TABLE 1: Time and day of emergence of 37 adults of *Dynastor darius* Fabricius from same egg batch. Rearing locality: Maracay, Aragua, Venezuela (450 m). Rearing period: July - October. Mean Temp: 24.3 °C; Mean RH: 98.2 %

Emergence (Days)	1100 - 1200 h	1200 - 1300h	1300 - 1400 h	1400 - 1500 h	1500 - 1600 h
1 (Sept. 22, 1996)		2 ♂♂			
2 (Sept. 23, 1996)					1 ♂
3 (Sept. 24, 1996)		1 ♂			
4 (Sept. 25, 1996)	1 ♂	1 ♀		1 ♀	
5 (Sept. 26, 1996)	1 ♂				
6 (Sept. 27, 1996)	1 ♂	1 ♀	1 ♂	1 ♂	
7 (Sept. 28, 1996)	1 ♂		2 ♀♀	1 ♀	
8 (Sept. 29, 1996)		1 ♂	1 ♀	3 ♀♀	
9 (Sept. 30, 1996)			2 ♂♂	1 ♀	1 ♀
10 (Oct. 1, 1996)					
11 (Oct. 2, 1996)	1 ♂		1 ♀		
12 (Oct. 3, 1996)					
13 (Oct. 4, 1996)		2 ♂♂		2 ♀♀	1 ♀
14 (Oct. 5, 1996)					
15 (Oct. 6, 1996)	1 ♂	1 ♂		1 ♀	1 ♀
16 (Oct. 7, 1996)	1 ♂				
(Total adults emerged / Time period)	7 ♂♂	7 ♂♂; 2 ♀♀	3 ♂♂; 4 ♀♀	1 ♂; 9 ♀♀	1 ♂; 3 ♀♀

Rearing notes. On 6 July 1996, a female was captured at 1830 h in Los Cerritos, Choroní, Aragua (200 m), along the coastal border of Henri Pittier National Park, Venezuela, and taken to Maracay (450 m; annual mean temp: 24.6 °C (24.3 °C Jul - Oct); mean RH: 97% (98.2 % Jul - Oct). There it was placed in a 50 X 75 X 50 cm cage with a plant of *Bromelia plumieri* (E. Morren) L. B. Sm. (Bromeliaceae), and, fed fermented mango and sugar-water (about 30 % sugar). The butterfly was observed to feed on both. It deposited a total of 42 eggs in various spots inside the cage and on the leaves of *B. plumieri*, from 7 to 12 July 1996, after which it stopped laying.

All the eggs proved viable, and the 42 larvae were transferred to separate cages, where they were fed leaves of five Bromeliaceae [*Aechmea aquilega* (Salisb.) Griesb.; *A. lasseri* L.B. Sm.; *B. plumieri*, *B. chrysantha* Jacq.; and *Quesnelia arvensis* (Vell.) Mez, depending upon availability], and larval development observed and recorded. Plant identifications were made using Oliva Esteva & Steyermark (1987). Of the five plant species offered to them, only *B. plumieri* had been reported previously as a larval food plant of this brassolid (DeVries 1985, 1987, Penz et al. 1999).

Development. A thorough description of eggs, larvae and pupae were made by Aiello & Silberglied (1978), who reared the species on *Ananas comosus* from eggs obtained from a captured female in Panama. Other details of the life history of ssp. *darius* were also given by Urich & Emmel (1991b) from a larva reared on *Aechmea nudicaulis* (L.) Griseb. (Bromeliaceae) in Trinidad. In our experience, the egg stage lasted about 12 days; the first instars emerged between 19 and 22 July and lasted between 10 to 12 days; the duration of the five larval stadia was 45 to 50 days; and the pupal stage lasted 11 to 31 days. These development times are consistent with previously reported data (Aiello and Silberglied 1978, Urich & Emmel 1991b), except for the pupal duration. Even though the mean pupal duration of 15 days was similar to the 13–17 days reported by Aiello & Silberglied (1978) and Urich & Emmel (1991b), some of our pupae took much longer to develop.

Larvae and pupae. The larvae fed at night, a behavior we have observed in the field. During the day, they remained hidden, resting at the base of the plant, with the head down.

Though the larvae accepted all five of the above-mentioned bromeliads, we noticed that they ate *B. plumieri* more quickly. On several occasions we have found two or three larvae on *B. plumieri* plants in the Choroní area where the plant is quite common, while we have found at least one larva on the other four bromeliads used in our rearing in the same area. A. Aiello (personal communication) found a final instar *D. d. stygianus* on *B. plumieri* in Panama (late August 1995), so both subspecies probably have a similar range of food plants.

The larvae were very aggressive and territorial and five of them were damaged during fights and failed to complete development. The remaining 37 larvae all reached the pupal stage. Two days before pupation, each larva changed color (green to pale brown) and looked for a place to transform. Once a place was located the larva produced a silk support to which it attached, head down and remained quiescent for about three days. On the fourth day, the larva began moving with up and down and semicircular motions, and secreted a viscous, yellow, liquid that was originated from the pre-pupa. After moving and shaking strongly in circles, the larval skin was shed. Initially, the pupa was gelatinous and had an amorphous shape. Contractions slowed, and in a period of about five minutes, the pupa acquired its final form. The final coloration developed a few hours later. The pupa clearly resembled a cryptic *Bothrops* snake (Aiello & Silberglied 1978, DeVries 1987, Mallet & Joron 1999, Urich & Emmel 1991b), which are of common occurrence among plants of *B. plumieri* in the Choroní area.

Adults emerged from all 37 reared pupae, during a 16 day period, and all emergences occurred between 1100 and 1500 h (TABLE 1); most males emerged in late morning (1100 -1200 h), whereas most females emerged in the afternoon (1300-1500 h) (TABLE 1). The sex ratio was 1:1 (19 males and 18 females) (TABLE 1).

We would like to express our deepest appreciation to Annette Aiello for insightful comments and corrections to the original manuscript. We thank also Matthew Cock and Gerardo Lamas for comments and suggestions on the latest version. Ana Fernández (Maracay) and Pedro Infante (Choroní) provided us with some of the plants used to rear the butterflies.

LITERATURE CITED

AIELLO, A., & R. E. SILBERGLIED. 1978. Life history of *Dynastor darius* (Lepidoptera: Nymphalidae: Brassolinae) in Panama. Psyche 85(4): 331 - 345.

ARAQUE, R. 1961. El cultivo de la piña en Venezuela. Caracas, Consejo de bienestar Rural.

DE VRIES, P.J. 1985. Hostplant records and Natural history notes on Costa Rican butterflies (Papilionidae, Pieridae & Nymphalidae). J. of Res. Lepid. 24(4): 290 - 333.

DE VRIES, P.J. 1987. The Butterflies of Costa Rica and their Natural History, Papilionidae, Pieridae, Nymphalidae. New Jersey, Princeton University Press.

MALLET, J., & M. JORON. 1999. Evolution of diversity in warning color and mimicry: polymorphisms, shifting balance, and speciation. Ann. Rev. of Ecol. and Syst. 30: 201 - 233.

OLIVA ESTEVA, F., & J.A. STEYERMARK. 1987. Las Bromeliáceas de Venezuela. Caracas, Editorial Armitano.

PENZ, C.M., A. AIELLO, & R.B. SRYGLEY. 1999. Early stages of *Caligo illioneus* and *C. idomeneus* (Nymphalidae, Brassolinae) from Panamá, with remarks on larval food plants for the subfamily. J. Lep. Soc. 53(4): 142 - 152.

PETTY, G.J., G.R. STERLING, & D.P. BARTHOLOMEWW. 2002. Pests of Pineapple. Pp. 157 - 195. *In* Peña, J.E., J.L. Sharp, & M. Wysoki (eds.), Tropical Fruit Pests and Pollinators. UK, CABI Publishing.

URICH, F.C., & T. EMMEL. 1991a. Life history of Neotropical butterflies from Trinidad. 4. *Dynastor macrosiris* (Lepidoptera: Nymphalidae: Brassolinae). Trop. Lepid. 2(2): 141 - 144.

URICH, F.C., & T. EMMEL. 1991b. Life history of Neotropical butterflies from Trinidad. 5. *Dynastor darius darius* (Lepidoptera: Nymphalidae: Brassolinae). Trop. Lepid. 2(2): 145 - 149.

FRANCISCO ROMERO M., *Colección Entomológica Familia Romero. Urb. Las Acacias, Vereda 12, # 13, Maracay, Aragua, Venezuela*; PEDRO BERMÚDEZ, *Urbanización Mata Redonda, 2da. Transversal, Manzana 17, No 189-A, Maracay, Aragua, Venezuela*; AND JORGE M. GONZÁLEZ*, *University of Georgia, Department of Entomology, Athens, Georgia, 30602, USA; email: jmgonzal@uga.edu*

*To whom all inquiries should be sent.

Received for publication 15 May 2004; revised and accepted 9 November 2004

Journal of the Lepidopterists' Society
59(1), 2005, 40–43

GREGARIOUS OVIPOSITION IN BUTTERFLIES

Additional key words: *Heliconius*, *Aglais*, clutch size.

Here I compile and discuss records of gregarious oviposition in butterflies. There have been field observations of this behavior in seven species of butterflies, all from the nymphalid genera *Heliconius*, *Aglais*, and *Euphydryas*. This concentration of observations in only a few unrelated genera suggests that the behavior has evolved multiple times in butterflies. It appears that in most cases described, multiple females aggregated together to oviposit over a short period of time, even when host plants may not have been a limited resource. Some possible adaptive functions of this behavior are discussed.

Most butterfly examples of gregarious oviposition are from the genus *Heliconius*, with four different species in the genus having been observed to aggregate while laying eggs. Mallet and Jackson (1980) observed two individuals of *Heliconius xanthocles* contributing to a collective egg clutch of 41 eggs over a 25 min period. During this time the authors also captured a third female who appeared to be ready to contribute to the clutch. A published photograph illustrates the two females ovipositing simultaneously on the tip of *Passiflora praeacuta* shoot. On a separate occasion, Mallet and Jackon (1980) also observed two individuals of *Heliconius* (*Laparus*) *doris* contributing to a collective clutch of more than 200 eggs over a period of 50 min on the upper surface of a young, folded leaf of *P. praeacuta*. Further circumstantial evidence for gregarious oviposition by *H. doris* include Benson et al.'s (1975) discovery of a clutch of over 800 eggs and J. Mallet's remarkable observation of a cluster of over 1200 pupae (pers. comm.). Turner (1971) reported observing two wild females of *Heliconius sara* "taking turns at laying their eggs in a shared batch". Jocelyn Crane also observed two *H. sara* ovipositing together in an insectary (Mallet & Jackson 1980), although captive observations may not be representative of behavior in nature.

Of all butterflies, the most data for gregarious oviposition are from *Heliconius hewitsoni*. Regarding this species, Longino (1984) reported "more than one female may contribute eggs simultaneously to the same egg cluster" and Duckett (1989) that "more than one female often will lay her eggs on the same shoot." L. Gilbert (pers. comm.) has consistently observed gregarious oviposition by *H. hewitsoni* in the field for over 15 years, indicating that the behavior is not a seasonal aberration or a rare chance event. In Costa Rica during the summer of 2001 I personally observed 12 cases of gregarious oviposition by *H. hewitsoni* (Fig. 1A-D) and found that an average of 4.5 females would contribute to a single collective clutch over an average of 1.1 h, even when local host plant was abundant (Reed 2003). In one particularly extreme example of the behavior, I observed 10 females contributing to a single clutch of 156 eggs. Longino (1984) noted "Interaction of *H. hewitsoni* females at oviposition appears to be aggressive. Females on the shoot hold their wings down over the shoot, as if fending off approaching females", a behavior I have also observed and photographed (Fig. 1B). Interestingly, male *H. hewitsoni* guarding potential pupal mates display an identical wing stance (Deinert et al. 1994).

Sourakov (1997, 1998) photographed two females of *Aglais cashmirensis* simultaneously contributing to a single, discrete egg cluster. Within 20 min the females produced a "multilayered heap" of approximately 100 eggs before being interrupted by the observer. This occurred when there were large patches of *Urtica* host plant in the vicinity that were not hosting eggs or larvae, suggesting that aggregation during oviposition was due to choice, as in *H. hewitsoni*. Thomas and Lewington (1991) described reports of multiple females of *Aglais urticae* contributing to collective clutches of up to a thousand eggs. Regarding *A. urticae*, they further stated "it is not unusual to find two females laying simultaneously on the same leaf." Unfortunately, however, their report did not include any quantitative data or specific observations.

R. Rutowski (pers. comm.) photographed two females of *Euphydryas chalcedona* ovipositing on a single host plant (Fig. 1E), although specific data were not taken regarding the collective clutch size or duration of the oviposition event. In this case, the females produced separate, discrete egg clutches that were located near each other. This should be contrasted with the *Heliconius* and *Aglais* examples where multiple females contributed eggs to a single collective clutch. On several occasions Rutowski (pers. comm.) has observed collections of several hundred *E. chalcedona* eggs on a single host plant, a number that far exceeds the expected clutch size of a single female. A

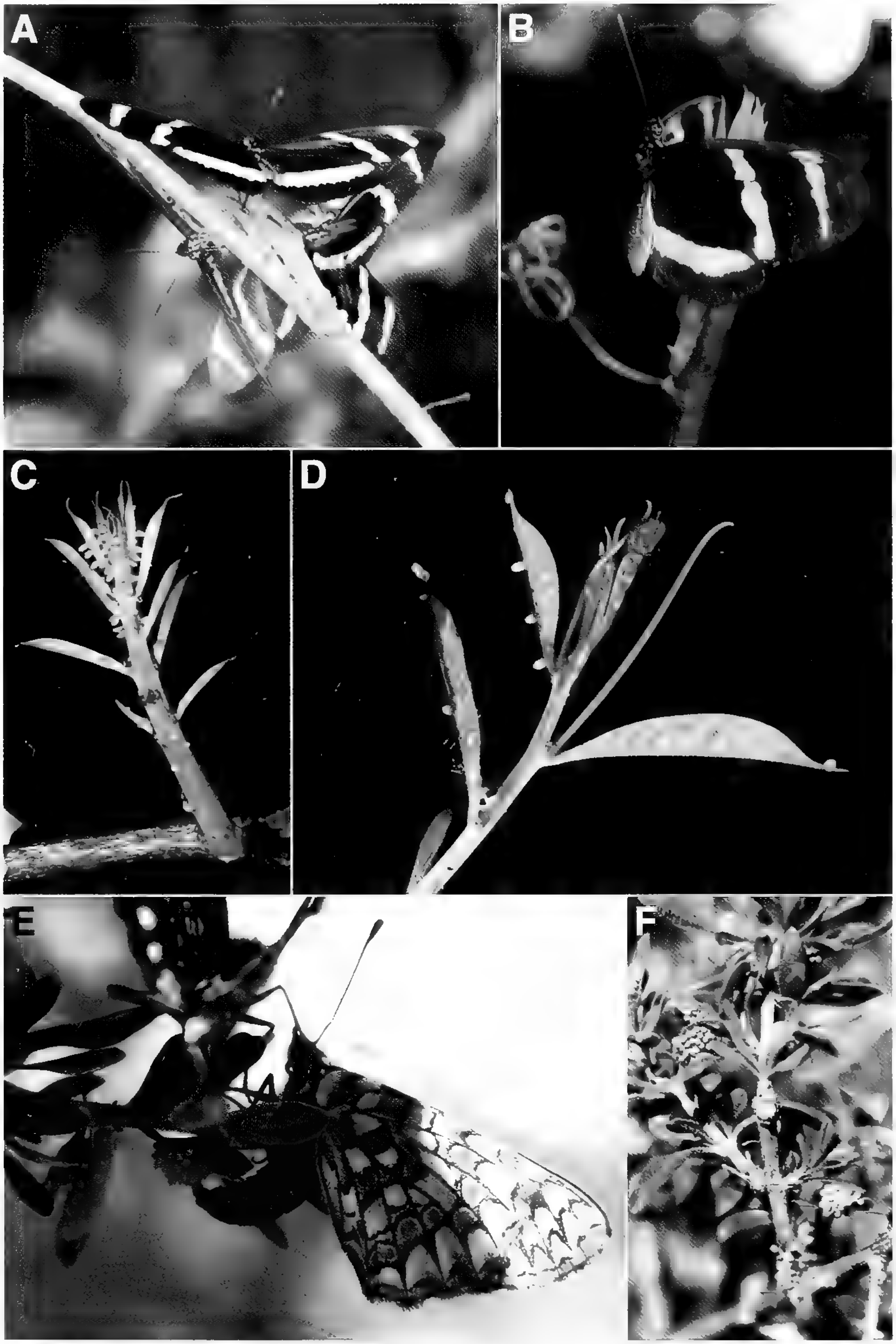


FIG. 1. Gregarious oviposition in *Heliconius hewitsoni* and *Euphydryas chalcedona*. A, four *H. hewitsoni* showing oviposition behavior on a young *Passiflora pittieri* (Passifloraceae) shoot near Sirena Biological Station, Costa Rica, July 2001; B, *H. hewitsoni* female perched on a young *P. pittieri* shoot; C, a cluster of 63 *H. hewitsoni* eggs that has been slightly spaced due to shoot growth. The number of eggs in this clutch suggests that three or four females contributed to it (Reed 2003); D, aggregation of newly hatched *H. hewitsoni* larvae on a host plant shoot tip, note the wide spacing of the egg shells; E, two *E. chalcedona* showing oviposition behavior on *Keckiella antirrhinoides* (Scrophulariaceae) near Sunflower, Arizona, Spring 1985; F, multiple discrete *E. chalcedona* egg clutches (red arrows) in close proximity on *K. antirrhinoides*. The color differences between egg masses suggest they were laid at different times. (E and F photos courtesy of R. L. Rutowski).

photograph of multiple *E. chalcedona* clutches on a single host plant shows that the clutches are of slightly different colors (Fig. 1F). These color differences may indicate that the clutches were laid at different times, which again contrasts with the *Heliconius* and *Aglais* examples where females tended to aggregate temporally.

There is circumstantial evidence for gregarious oviposition from several other butterflies. Stamp (1980) reported observing multiple *Euphydryas phaeton* clutches on single host plant leaves, but it was unknown if these clutches were from multiple females. Likewise, in *Eueides vibilia unifasciatus* multiple clutches have been observed on single leaves, although oviposition was not directly observed (K.S. Brown Jr., pers. comm.). Also, in *Pieris brassicae* egg clusters appear to attract conspecific females (Mitchell 1977). While this suggests a possible mechanism for gregarious oviposition, I am unaware of published records of multiple *P. brassicae* females contributing to egg clusters.

Is gregarious oviposition a common behavior among butterflies? Unfortunately there are too few data to address this. The serendipitous nature of observing oviposition in the field hinders any kind of quantitative conclusion in this respect. Repeated observations of gregarious oviposition in *H. hewitsoni* (L.E. Gilbert pers. comm., Reed 2003) and *A. urticae* (Thomas & Lewington 1991) indicate that the behavior may be common in these species. While most observations of gregarious oviposition are anecdotal, the phylogenetic clustering of observations in the genera *Heliconius* and *Aglais* suggests that the behavior may be an important life history trait within these groups. In fact, there seems to have been at least two independent origins of gregarious oviposition in *Heliconius*; one origin in the *xanthocles / doris* clade, and one or two origins in the clade that includes *sara*, *hewitsoni*, *sapho*, and *eleuchia* (see phylogeny by Brower & Egan 1997). Both *Aglais* and *Heliconius* contain multiple clutch-laying species, and it is reasonable to speculate that the evolution of clutch laying behavior is a prerequisite for developing a gregarious oviposition strategy. I am unaware of reports of gregarious oviposition in species that are single-egg layers.

When considering adaptive explanations for gregarious oviposition in butterflies it is important to separate hypotheses into two categories: (1) the basic advantages of clutch-laying, and (2) the advantages of clutches of mixed relatedness. There is a literature on the evolution of clutch-laying in butterflies, much of which cites Stamp's (1980) comparative review. Some hypotheses that have been proposed to account for the evolution of clutch-laying in general include prevention of egg dessication (Stamp 1980), enhancement of egg aposematism (Stamp 1980), decrease of exposure to predators and parasitoids (Stamp 1980), minimization of female search time (Stamp 1980), evolutionary response to increased fecundity (Courtney 1984), and the facilitation of larval aggregation (Stamp 1980). Gregarious oviposition could quantitatively enhance most of these effects.

The dessication, aposematism, and anti-predation hypotheses rely on eggs being in close proximity to each other, with eggs on the outside of clusters acting as "insulation" for more internal eggs (Stamp 1980, Clark & Faeth 1998). While it is possible that gregarious oviposition could enhance these specific effects in gregarious *Aglais*, it would probably have little influence in *Heliconius* or *E. chalcedona*. The fast growth rate of young *Passiflora* shoots often results in clustered *Heliconius* eggs being well spaced within a day or two of being laid (Fig. 1C, D), while *E. chalcedona* apparently do not combine clutches (Fig. 1E, F).

Stamp (1980) proposed that females might lay eggs in clusters in order to minimize personal exposure to predators and other hazards. This may be plausible for *E. chalcedona* or gregarious *Aglais*, however it may not be as applicable to *Heliconius*. *Heliconius* butterflies, being relatively unpalatable Müllerian mimics, possess a modicum of protection from predators such as birds (eg. Kapan 2001). Furthermore, prolonged daily shoot inspections (Reed 2003) suggest that females may not be overly concerned with minimizing their oviposition-related flight time.

All Lepidoptera known to have gregarious larvae are also clutch-layers (Sillén-Tullberg 1988), supporting the idea that a primary function of clutch-laying is to facilitate larval aggregation. Several adaptive hypotheses have been proposed to explain larval aggregation in insects, including enhancement of larval aposematism (Stamp 1980), group defensive strategies (Hamilton 1971), enhancement of larval feeding efficiency by increased thermoregulatory ability (Casey 1993), increased social stimulation to feed (Long 1953), and increased ability to overcome leaf toughness (Ghent 1960). These hypotheses are plausible as selective forces playing a role in the evolution of gregarious oviposition in various cases.

Beyond the general benefits of aggregation described above, the formation of aggregations of mixed relatedness through gregarious oviposition adds a new dimension to adaptive interpretations of clutch-laying. Evidently there is a selective advantage to large larval aggregations that outweighs the cost of intraspecific competition. Sourakov (1997) suggested that gregarious oviposition could be a way to minimize the number of clutches in a locality in order to decrease egg apparency to parasitoids. Another possibility is that large aggregations of conspecifics result in a prey dilution effect (Turner & Pitcher 1986, Vulinec 1990), decreasing the probability of a female's offspring being lost per predation event. There is evidence from *H. hewitsoni* that variation in the number of females contributing to a clutch may be a mechanism for host quality-dependent clutch size adjustment (Reed 2003), an effect that has also been observed in parasitic mantispids that communally adjust clutch size in respect to the concentration of their spider hosts (Rice 1986). Whatever their benefits may be, mixed-relatedness aggregations are possibly a widespread phenomenon in Lepidoptera, as examples have also been described from some moth species (Porter et al. 1997, Costa & Ross 1993). Future work that explicitly tests some of the adaptive hypotheses outlined above would be helpful for understanding why gregarious oviposition has arisen repeatedly during butterfly evolution.

I thank Larry Gilbert for first alerting me to gregarious oviposition in *H. hewitsoni*, and Keith Brown, Jim Mallet, and Ron Rutowski for sharing unpublished observations. I also thank an anonymous reviewer for comments.

LITERATURE CITED

BENSON, W. W., K. S. BROWN, & L. E. GILBERT. 1975. Coevolution of plants and herbivores: passion flower butterflies. Evolution 29:659-680.

BROWER, A.V.Z, & M.G. EGAN. 1997. Cladistic analysis of *Heliconius* butterflies and relatives (Nymphalidae: Heliconiiti): A revised phylogenetic position for *Eueides* based on sequences from mtDNA and a nuclear gene. P. Roy. Soc. Lond. B Bio. 264:969-977.

CASEY, T.M. 1993. Effects of temperature on foraging of caterpillars, pp. 5-28. *In* N.E. Stamp and T.M. Casey (eds.), Caterpillars. Ecological and Evolutionary Constraints on Foraging. Chapman & Hall, New York

CLARK, B.R. & S.H. FAETH. 1998. The evolution of egg clustering in butterflies: A test of the egg dessication hypothesis. Evol. Ecol. 12:543-552.

COSTA, J.T. III, & K.G. ROSS. 1993. Seasonal decline in intracolony genetic relatedness in eastern tent caterpillars: Implications for social evolution. Behav. Ecol. Sociobiol. 32: 47-54.

COURTNEY, S.P. 1984. The evolution of egg clustering by butterflies and other insects. Am. Nat. 123:276-281.

DEINERT, E. I., J. T. LONGINO, AND L. E. GILBERT. 1994. Mate competition in butterflies. Nature 370: 23-24.

DUCKETT, C. N. 1989. Natural history of *Pedilia* sp. A and its interactions with other herbivores of *Passiflora pittieri*. Entomography 6:381-189.

GHENT, A.W. 1960. A study of group-feeding behavior of larvae of the jack-pine sawfly *Neodiprion pratti banksianae* Roh. Behavior 16:110-148.

HAMILTON, W.D. 1971. Geometry for the selfish herd. J. Theoret. Biol. 31:295-311.

KAPAN, D.D. 2001. Three-butterfly system provides a field test of mullerian mimicry. Nature 409:338-340.

LONG, D. 1953. Effects of population density on larvae of Lepidoptera. Trans. Roy. Entomol. Soc. London 104:543-585.

LONGINO, J. T. 1984. Shoots, parasitoids, and ants as forces in the population dynamics of *Heliconius hewitsoni* in Costa Rica. Ph.D. Dissertation. University of Texas, Austin.

MALLET, J. L. B. & D. A. JACKSON. 1980. The ecology and social behavior of the Neotropical butterfly *Heliconius xanthocles* Bates in Colombia. Zool. J. Linn. Soc. 70:1-13.

MITCHELL, N. 1977. Differential host selection by *Pieris brassicae* (the large white butterfly) on *Brassica oleracea* (the wild cabbage). Entomol. Exp. Appl. 22:208-219.

PORTER, A.H., S.J. CADARET, S.A. JOHNSON, H. MIZOHATA, A.I. BENEDETTER, C.L. BESTER, J.L. BORSAH, S.D. KELLY, G.S. BUEHNER, & M.L. SHERMAN. 1997. Relatedness and gregariousness in the Orange Striped Oakworm, *Anisota senatoria* (Saturniidae). J. Lepid. Soc. 51: 208-217.

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

RICE, M.E. 1986. Communal oviposition by *Mantispa fuscicornia* (Neuroptera: Mantispidae) and subsequent larval parasitism on spiders (Arachnida: Araneidae) in South Texas USA. J. Kansas Entomol. Soc. 59:121-126.

SILLÉN-TULLBERG, B. 1988. Evolution of gregariousness in aposematic butterfly larvae: A phylogenetic analysis. Evolution 42:293-305.

SOURAKOV, A. 1997. "Social" oviposition behavior and life history of *Aglais cashmirensis* from Nepal (Lepidoptera: Nymphalidae). Holarctic Lepid. 4:75-76.

SOURAKOV, A. 1998. "Social" egg-laying in *Aglais cashmirensis*, the Indian Tortoiseshell. News Lepid. Soc. 40:28.

STAMP, N. E. 1980. Egg deposition patterns in butterflies: why do some species cluster their eggs rather than deposit them singly? Am. Nat. 115:367-380.

THOMAS, J. & R. LEWINGTON. 1991. The butterflies of Britain and Ireland. Kindersley, London. 124 pp.

TURNER, G. F. & T. J. PITCHER. 1986. Attack abatement: a model for group protection by combined avoidance and dilution. Am. Nat. 128:228-240.

TURNER, J. R. G. 1971. Studies of Müllerian mimicry and its evolution in burnet moths and heliconid butterflies, pp. 224-260. *In* R. Creed (ed.), Ecological Genetics and Evolution. Blackwell Scientific Publication, Oxford and Edinburgh.

VULINEC, K. 1990. Collective security: Aggregation by insects as a defense, pp. 251-288. *In* D.L. Evans and J.O. Schmidt (eds.), Insect defenses. Adaptive mechanisms of prey and predators. State University of New York, Albany, New York.

ROBERT D. REED, *Department of Biology, Duke University, Durham, North Carolina 27708, USA*

Received for publication 17 February 2004; revised and accepted 1 September 2004

Journal of the Lepidopterists' Society
59(1), 2005, 44

ROLAND TRIMEN'S OBSERVATIONS ON TOUGHNESS IN UNPALATABLE AFRICAN BUTTERFLIES: A HISTORICAL ANNOTATION TO DEVRIES 2003

Additional key words: aposematism beak mark Danainae Heliconiinae

DeVries' (2003) recent experimental demonstration that the unpalatable danaine *Amauris albimaculata* Butler has significantly tougher wings than its palatable nymphaline mimic *Pseudacraea lucretia* Neave is an elegant study in comparative functional morphology. However, the observation that unpalatable models' wings are tough with respect to other species was discussed by Roland Trimen (1870), in one of the first papers documenting aposematism and mimicry among African butterflies. The relevant passage is quoted here in its charming entirety:

> "Most species of *Danais* (sic) and *Acraea* feign death very readily; and they possess another means of defence which, as far as I am aware, has not hitherto been recorded, viz. the remarkable elasticity of their entire structure. No pressure of the thorax, short of absolute crushing of the tissues, suffices to kill or even paralyze these Butterflies; and the collector who treats them as he would species of other families soon finds his collecting-box alive with its struggling occupants. So flexible are their wings, that the insect generally succeeds in withdrawing them from the crossed fences of pins which form a complete barrier to any motion on the part of ordinary Butterflies; and however bent and distorted the wings may become in such exertions, I have never known a fracture of nervures or membrane to result, the organs resuming their natural position even after having been bent double for some hours. While entomologizing in Natal, my Kafir collector used often to bring me numerous examples of the commonest species in his box, and when engaged in the necessary work of rejection, I constantly found the limp-winged Danaidae and Acraeidae, as soon as they were released from the transfixing pin, fly off with perfect ease and apparent nonchalance.
>
> It is not difficult to perceive how important, as a reserve means of defence, this unusual elasticity of structure may prove. That birds, and other eaters of insects, may occasionally capture a Butterfly of these malodorous tribes before discovering its distasteful character is not an unreasonable supposition, especially in seasons when an exceptional scarcity of some favourite food may prevail. In such a case it may be safely stated that the chances are very greatly in favour of a *Danais* or an *Acraea* escaping, if not wholly unhurt, yet without serious injury, after rough treatment that would have proved fatal to a harder but less elastic animal."

If, as Smith (1979) suggested, beak marks are the result of intentional release of bad-tasting butterflies, then it would be surprising if Batesian mimics in general had tougher wings than their non-mimetic close relatives, unless the adaptation in question is the weakening, rather than the toughening, of the wings, to improve the probability of escape. Perhaps Batesian mimics can afford to have tougher wings, which would likely be advantageous in the absence of predators, because they are less likely to be sampled and therefore do not need to escape by tearing away parts of their wings. In any event, this is a rich area for further empirical study, and will be particularly illuminating if conducted in a phylogenetic context (cf. Brower 1995).

LITERATURE CITED

BROWER A. V. Z. 1995. Locomotor mimicry in butterflies? A critical review of the evidence. Phil. Trans. R. Soc. Lond. B 347: 413-425.

DE VRIES, P. J. 2003. Tough African models and weak mimics: new horizons in the evolution of bad taste. J. Lepid. Soc. 57: 235-238.

SMITH, D. A. S. 1979. The significance of beak marks on the wings of an aposematic, distasteful and polymorphic butterfly. Nature 281: 215-216.

TRIMEN, R. 1870. On some remarkable mimetic analogies among African butterflies. Trans. Linn. Soc. Lond. 26: 497-522; 2 plates.

ANDREW V. Z. BROWER, *Department of Zoology, Oregon State University, Corvallis, OR 97331; Email: browera@science.oregonstate.edu*

Received for publication 13 October 2003; revised and accepted 9 January 2004

Journal of the Lepidopterists' Society
59(1), 2005,

HUGH AVERY FREEMAN (1912 - 2002): REFLECTIONS ON HIS LIFE AND CONTRIBUTIONS TO LEPIDOPTEROLOGY

ANDREW D. WARREN
Department of Zoology, Oregon State University, Corvallis, Oregon, 97331 USA

Few individuals in recent decades can match Hugh Avery Freeman's contributions to the study of Lepidoptera. Our current knowledge of Mexican hesperiid diversity is based on Freeman's groundbreaking research, as is our knowledge of the butterfly fauna of the lower Rio Grande Valley of Texas. Freeman also created what can be considered a subdiscipline out of the study of the Giant Skippers, or Megathymini. His early publications on the group generated much excitement among his colleagues, and provided the initial stimulus for decades of additional exploration and research. Freeman described 107 new species and subspecies of butterflies (including 4 new forms) and 5 new genera, and authored 111 scientific publications. His collections of Lepidoptera were extensive, and these were important and significant additions to various institutional collections as they were sold or donated. Extensive material from Freeman's collections can be found in the American Museum of Natural History, New York (AMNH), Carnegie Museum of Natural History, Pittsburgh (CMNH), United States National Museum, Washington D.C. (USNM), and Allyn Museum, Florida State University (AME in literature, now FSMC). Freeman was an active member of the Lepidopterists' Society, and was well known to all researchers of Hesperiidae and *Catocala* (Noctuidae), as well as Texan Lepidopterists.

Hugh Avery Freeman was born on October 7th, 1912, in Conway, Faulkner Co., Arkansas. His father, George Allen Freeman, was a Methodist minister who grew up in Vermont. His mother, Stella Freeman, grew up on the Hope Hill Farm in Faulkner County, Arkansas, where Avery (as he was known to his family and friends) spent most of his childhood. George and Stella had two other children, Joy Bates Freeman and Moore Freeman, and adopted a third child out of a Methodist home, Dorothy Freeman. Avery attended North Little Rock High School, and graduated in the class of 1932.

Avery grew up on his parents' acreage, the Hope Hill Farm. This setting was rich in lepidopteran species, which caught Avery's attention. At age 15, after reading Gene Stratton-Porter's *A Girl of the Limberlost*, Lepidoptera became subjects of scientific interest. Between 1927 and 1930, Avery's interest in Lepidoptera was general, although he paid special attention to the Sphingidae (no doubt due to Stratton-Porter's influence), which were the subject of his first entomological publication, an annotated list of the Sphingidae of Arkansas (ref. 1). Avery quickly became fascinated with small butterflies, especially the Lycaenidae, Riodinidae and Hesperiidae, and by 1930, Avery's interest in Lepidoptera had become focused on the Hesperiidae (but see refs. 26, 28, 32, 33 and 56). Early collecting efforts at the Hope Hill Farm proved to be important, providing new data on the distribution of various species in Arkansas (refs. 18, 33), and type material for two of Avery's new skipper taxa (*Polites verna sequoyah*, ref. 7; *Amblyscirtes linda*, ref. 8).

Avery received his B.A. in biology from Hendrix College (Conway, Arkansas) in June 1936 and he was elected to Phi Beta Kappa. He then moved to Dallas (Texas) to attend Southern Methodist University (SMU). There, he earned a M.S. in entomology in June 1938, and published a list of the Hesperiidae of Dallas County in 1939 (ref. 2). Plans to pursue a Ph.D. in entomology were interrupted by the economic strains of the Depression. In 1938, Avery began teaching biology and chemistry at Lancaster High School (Lancaster, Texas) for $90 a month. Avery found more than a job in Lancaster, and in 1939 married Erna Louise Morris, a native of Lancaster living with her parents at the time. Their happy marriage of 62 years lasted until Avery's passing on February 19th, 2002, and produced three children, Linda Louise Freeman (born 1940; now Linda Stafford), Julia Anne Freeman (born 1945; now Julia Matthews), and Avery Gilbert Freeman (born 1955). Avery was very proud of his family, and named new species and subspecies of skippers after each of his family members: *Amblyscirtes linda* (ref. 8), *Lerodea julia* (ref. 19), *Agathymus gilberti* (ref. 57), *Astraptes gilberti* (ref. 77), *Amblyscirtes erna* (ref. 8), *Megathymus yuccae louiseae* (ref. 52) and *Astraptes louiseae* (ref. 77). Louise was a very supportive wife, and spent much time working on Avery's Lepidoptera-related projects "behind the scenes." In addition to collecting specimens from the yard and elsewhere while Avery was teaching (she collected the allotype female of *Celaenorrhinus stallingsi*, ref. 21), Louise dispatched many of Avery's reared Megathymini, which would emerge and expand their wings, almost invariably, while Avery was away teaching.

While Avery proved to be an excellent educator, his true passion remained in the study of Lepidoptera. In an effort to build his collection of Texas species, he sought a teaching position in west Texas, having mastered the butterfly fauna of the Dallas area. Between 1941 and 1944, Avery taught biology and chemistry at White Deer High School (White Deer, Carson County, Texas), spending his weekends and holidays collecting all over north and west Texas. During this period, Avery discovered several new taxa of Hesperiidae in Texas (refs. 8, 9) and developed a very strong interest in the Megathymini (ref. 14). It was also during this time Avery developed a strong interest in the Neotropical Hesperiidae, and largely because of this, sought a teaching position in the lower Rio Grande Valley of Texas in 1944.

From 1944 to 1948, Avery taught biology and coached track and football at the Pharr-San Jacinto-Alamo High School (Pharr, Texas). He spent most of his free moments collecting butterflies, especially skippers. During these four years of intensive collecting activities in the valley, Avery contributed a tremendous amount of new information on the butterfly fauna of the region, and reported over two-dozen butterfly species from the United States for the first time (refs. 6, 16, 17, 19, 20, 21, 22, 23, 25, 26, 29, and 32), some of which were new to science. During the period of Avery's collecting activities in the valley, large areas of native habitat remained, including some dense subtropical forest lining the Rio Grande river, where Avery found several species of shade-loving skipper species for new US records, and even saw (but could not collect) the only blue morpho (probably *Morpho peleides* Kollar) ever reported north of the Mexican border (ref. 44, also Stallings & Turner 1946). Indeed, since 1948, no single person has contributed such a wealth of new information on the butterflies of south Texas.

In 1948, Avery was offered a job at the Southern Methodist University, and the Freeman's moved back to the Dallas area. From 1948 to 1951, Avery worked as a biology instructor at SMU. From 1951 to 1954, Avery taught chemistry at Forest Avenue High School in Dallas, and from 1954 to his retirement in 1981, he taught biology and chemistry at Hillcrest High School in Dallas. He was honored as Teacher of the Year at Hillcrest in 1963. During this long teaching career, when not busy with family activities, Avery worked in the evenings, and on rainy weekends, writing up the results of his research on Lepidoptera for publication.

In 1943, Avery published his first paper on *Megathymus* Scudder (ref. 10), which was followed over the next 23 years by 18 additional publications on the Megathymini, naming 3 genera, 14 species, 7 subspecies and one form. These publications laid the foundation upon which all subsequent studies on the Giant Skippers (or "Megs") have been based. The excitement generated in the community of North American lepidopterists by Avery's early publications on Megs cannot be overstated; lepidopterists were literally leaving their nets in the truck and going into the field with a shovel and knife (Remington 1961). Upon learning of Avery's techniques for collecting and rearing immatures, and reading about the various new species and subspecies he was describing from the southwestern United States and Mexico, the study of Giant Skippers became a serious interest of several lepidopterists, including (among others) Don B. Stallings and family, J. R. Turner and family, Charles L. Remington and family, C. F. Harbison, R. S. Wielgus and family, and Kilian Roever. By the time he started working with Megs, Avery had developed a close relationship with Don Stallings and J. R. Turner, of Caldwell, Kansas, as evidenced by the naming of his first two new *Megathymus* taxa, in 1943, after Don Stallings' son, Don B. (Dee) Stallings, Jr. (ref. 10). Indeed, one of the first new butterfly taxa described by Stallings and Turner, *Neonympha gemma freemani*, was named to honor Avery (Stallings & Turner 1947). While Avery never coauthored scientific papers with the Stalling and Turner clan, they clearly discussed Megs on a frequent basis and kept up a regular and cordial correspondence as evidenced by archived correspondence, at the CMNH. Avery is mentioned and gratefully acknowledged in essentially every paper published by Stallings and Turner and colleagues (see Huber (1999) for a nearly complete list of publications by D. Stallings and coauthors). Avery, the Stallings' and the Turners' described as separate species the various allopatric populations of *Megathymus* or (after 1959) *Agathymus* that they found on different *Agave* species, when coupled with morphological differences. In 1969, Avery published his last paper on Megs, an exhaustive review of the entire group, where a total of 48 species of Megs were recognized, in 5 genera; 32 of these were *Agathymus*, and 20 of these *Agathymus* species were residents of the United States (ref. 76). Shortly afterward, Avery donated his entire collection of Megs to the AMNH (Rindge 1970). In 1975, Roever treated the North American complex of *Agathymus* taxa as 10 geographically and ecologically variable species, and that arrangement has been generally followed since, despite little or no actual justification for the nomenclatural changes made. The question of relationships between these taxa requires a careful reexamination, including a phylogenetic study using morphological and molecular character data.

Throughout Avery's career as a teacher from 1938 to 1981, he spent his summers collecting extensively over Arkansas, Texas, New Mexico, Arizona and Mexico (e.g., ref. 44). He made 34 collecting trips to Mexico, mostly funded by grants from the Carnegie Institute, United States National Science Foundation, American Philosophical Society and the National Geographic Society. During these travels, Avery amassed what is undoubtedly the largest and most complete and important single collection of Mexican Hesperiidae ever assembled. He made frequent trips to the Hotel Covadonga, south of Ciudad Valles, San Luis Potosí, to play golf and collect butterflies around the golf course that was literally carved out of the jungle. These trips clearly had a lasting impressing on Avery, for he named a new skipper, *Poanes benito*, after Benito Reycendes, one of his favorite caddies at Hotel Covadonga (ref. 96), and named several other new species after various close friends in Ciudad Valles (refs. 77, 84, 93, 96). Avery published 27 papers dealing primarily with Mexican Hesperiidae, in which he described 69 new species, one new subspecies, and two new genera. Between 1949 and about 1969, Avery was the only researcher seriously studying the Mexican fauna of Hesperiidae. He purchased hundreds of specimens from Eduardo C. Welling, and named a new species, *Thoon wellingi*, after his long-time friend and fellow collector (ref. 74). During this period, Avery also acquired Mexican skipper specimens from various other individuals, naming new species after each of them, including Robert Wind, Peter Hubbell, Don Stallings, Tarsicio Escalante, Kent Wilson, and Wilbur McAlpine.

In 1980, Avery sent reprints of his papers on Mexican Hesperiidae to Kikumaro Okano, of Mishima City, Japan. This act served as an introduction to the study of Mexican Hesperiidae for Japanese readers, once Okano (1981, 1982) published summaries of Freeman's research and descriptions. Okano's 1981 paper included a listing of all Mexican skipper species known at that time, from literature reports, listing bibliographic citations and type localities for essentially all included species. Freeman's name appears on almost every page of this report. Okano's 1982 paper was dedicated almost entirely to Freeman's publications, as it reproduced (in English) the original descriptions of 61 of Avery's new skipper species described from Mexico, as well as copies of the illustrations of genitalia provided in Avery's original publications.

Avery was a charter member of The Lepidopterists' Society, and was a regional coordinator of the Annual Season Summary for 32 consecutive years, from 1951 to 1983 (Stanford 2001, 2002). No Season Summaries were published from 1953 to 1958, but an unpublished report for 1954 was found in Avery's files (archived at the CMNH), with reports by himself (from Texas), William Howe (from Kansas), Don B. Stallings (from Kansas and Texas), J. R. Turner (Texas), W. J. Reinthal (Texas) and Lowell Hulbirt (Texas). A copy of Avery's unpublished 1953 report may exist in C. L. Remington's files (records were contributed by William Howe and Edward Welling, at least); it is unknown if Avery prepared reports between 1955 and 1958. Avery contributed records to the Season Summaries every year the reports appeared between 1947 and 1989 (a total of 43 years), as well as during 1953 and 1954 (at least) when no Summaries appeared. He served on the editorial committee of the News from 1959 to at least 1977, was a member-at-large of the Executive Council from 1962-1964, was the Society's 1st Vice President in 1971, and Vice President in 1972 (Kendall 1977).

From an early age, Avery was a prolific correspondent. He was never bashful about seeking determinations on his collected material from experts, for example J. F. G. Clarke, Ernest L. Bell, Arthur W. Lindsey, R. C. Williams, W. H. Evans, E. Murray-Aaron and F. M. Brown for his early studies. Ernest Bell, of the AMNH, was an especially important mentor to Avery, a fact evident by the name Avery chose for the first undescribed species of skipper he discovered and named in 1941: *Amblyscirtes belli* (ref. 5). A large percentage of Avery's collections were built through specimen exchanges with his many friends and colleagues; indeed his collections were more diverse than most institutional collections. Some, but certainly not all, of the individuals who corresponded with Avery about Hesperiidae, or provided specimens of Hesperiidae for Avery's collections (either directly or indirectly) include the following: Arthur C. Allyn, Paul H. Arnaud, Jr., Andrew Atkins, George T. Austin, James Baker, David L. Bauer, Dean Berry, T. B. Blevins, James P. Brock, Auburn E. Brower, Otto Buchholz, John M. Burns, John V. Calhoun, Sergio Carmelo, Steven J. Cary, Franklin H. Chermock, F. E. Church, Dale Clark, W. Judson Coxey, Ken Davenport, Jack Dennis, Philip J. DeVries, E. A. Dodge, Julian P. Donahue, Cyril F. dos Passos, Malcom Douglas, John C. Downey, Joseph F. Doyle, III, Bastiaan M. Drees, T. M. Dunkle, James Donald Eff, Tarsicio Escalante, Clifford D. Ferris, R. J. Fitch, Don P. Frechin, Valerie H. & Albert C. Frederick, Alma Garcés, A. García, H. A. Gibbon, Carl W. Gottschalk, Nancy Greig, Lionel Paul Grey, John E. Hafernik, F. Haimbach, Charles F. Harbison, Chuck Harp, Victor Hellebuyck, E. Henao, John B. Heppner, Carlos C. Hoffmann, William H. Howe, H. A. Howland, Peter Hubbell, Lowell Hulbirt, J. K. Jacob, Daniel H. Janzen, Peter M. Jump, John Kemner, Roy O. Kendall, R. Kergosien, H. L. King, Edward C. Knudson, J. A. Kusche, Richard A. Leussler, Jorge E. Llorente, Ralph W. Macy, John H. Masters, Bryant Mather, Rudi Mattoni, H. Elliot McClure, Nadine M. & William W. McGuire, R. M. McKenzie, Lee D. & Jacqueline Y. Miller, Arthur H. Moeck, Rudolph C. de Mordaigle, Herbert K. Morrison, Douglas D. Mullins, C. O. Neumann, Berthold Neumoegen, William W. Newcomb, Stanley S. Nicolay, Kikumaro Okano, William A. Palmer, Ricky L. Patterson, Otto C. Poling, Floyd W. & June D. Preston, Homer F. Price, Alan Probert, J. Puig, C. & O. Querci, Marco Rangel, George W. Rawson, Walfried J. Reinthal, Abraham Ramirez, Charles L. Remington, P. S. Remington, S. N. Rhodes, Frederick H. Rindge, Ronald Rockwell, Kilian Roever, E. Romei, Frank Sala, Julian A. Salazar, Patrick J. Savage, James A. Scott, William E. Sieker, Arthur C. Sheppard, P. J. Sheppard, John A. Shuey, Ernest M. Shull, Henry Skinner, C. P. Slater, Annie T. Slosson, Jeffrey R. Slotten, Marion E. Smith, Michael J. Smith, Thomas U. Spalding, R. B. Srygley, Don B. Stallings, Ray E. Stanford, F. Steinbach, Stephen R. Steinhauser, J. W. Tilden, J. E. Turner, John R. Turner, A. Vázquez, M. L. Walton, Andrew D. Warren, Robert J. Warren, Eduardo C. Welling, Kent H. Wilson, Robert G. Wind and John Woodgate. Avery's complete correspondence files (including correspondence with many additional individuals) have been archived at the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Avery worked closely with Roy O. Kendall of San Antonio, Texas, for several years, researching the Papilionoidea and Hesperioidea of Texas. The two of them published a list of Texas butterflies together in 1963 (ref. 51), and exchanged much correspondence on the Texas fauna. Avery agreed to prepare genitalia drawings of all Texas Hesperiidae for Roy Kendall's massive project on the butterflies of Texas, which were completed in 1980; however, these drawings have not yet been published.

After donating his collection of Mexican Hesperiidae to the AMNH in March, 1981, and retiring from Hillcrest High School shortly after, Avery became impressed with the diversity of *Catocala* species he found attracted to a mercury vapor light in his back yard in Garland, and began the process of building a collection of North American *Catocala*. Avery amassed long series of *Catocala* specimens from his yard for exchange (collected at light and at bait), and supplemented this material with large series he was obtaining from John Kemner in Dripping Springs, Texas. During Avery's "*Catocala*-years", roughly 1982 through 1988, Avery corresponded with, and exchanged specimens with numerous individuals (in addition to many of those listed above), including, among others, David Baggett, Carlos R. Beutelspacher, Vernon A. Brou, Jr., Charles T. Bryson, Robert W. Cavanaugh, John M. Coffman, James P. Fitter, Mecky Furr, Lawrence F. Gall, Bonnie Gibbons, James E. Gillaspy, Richard M. Gilmore, David C. Hawks, F. W. Hedges, J. Richard Heitzman, Parker & Donna Henry, Katsumi Ishizuka, Joel M. Johnson, John W. Johnson, Samuel A. Johnson, John C. Jordison, Peter W. Kovarik, Ross Layberry, Ron H. Leuschner, Eric H. Metzler, Stephen Miller, Wayne A. Miller, James Muow, Kenneth Neil, Jim Oberfoell, Craig Odegard, Leo J. Paulissen, Robert W. Poole, C. Stephen Quelch, Eric L. Quinter, S. Roman, Richard C. Rosche, Theodore D. Sargent, Dale F. Schweitzer, Mack Shotts, Terry W. Taylor, Erich Walter, Ronald S. Wilkinson, Benjamin D. Williams and Michael Zappalorti. Through many exchanges (he even traded Hesperiidae for *Catocala* specimens on several occasions), Avery amassed a nearly complete collection of North American *Catocala* species, and published one note on *Catocala* (ref. 111),

While Avery's passion with *Catocala* was intense, it was not permanent, since the relationship he formed with John Kemner would eventually lead him back into the study of Mexican skippers. After several years of collecting in North America, mostly Texas and Florida, Kemner started making collecting trips into Mexico, and by 1987, had located several very productive sites in Oaxaca State. At one of these sites, ca. 5 miles north of Oaxaca City on Hwy. 175, Kemner found an unusual suite of skippers that proved to be of major interest to Avery. Among this lot were several species of *Piruna* Evans, including two undescribed species. After reviewing this material, Avery "officially" returned to studying skippers, initiated a large project revising the genus *Piruna*, and started borrowing all the holotypes and other *Piruna* specimens that he could locate. A short time later, Avery donated his entire collection of *Catocala* to the AMNH. In 1990, Avery named the first of these two new species *Piruna kemneri* (ref. 106), after his good friend and colleague. This not only provided additional stimulation to fuel Kemner's collecting efforts, but also irreversibly cemented Avery's return to skipper study. While Avery only described a total of 4 new taxa discovered by Kemner, he initially identified and spread many other new skipper taxa discovered by Kemner before forwarding these on to his colleagues for subsequent description (e.g. Burns 1992b, 1994, Steinhauser 1991, 1996, Steinhauser & Warren 2002), though not all of these have yet been formally described. Avery was an inspiration to

Kemner, and Kemner was an inspiration to Avery- they made a perfect team. While Kemner was selling specimens to various collectors to cover the costs of his collecting activities, he never charged Avery a cent for all the skippers he gave him; to Kemner, obtaining species determinations and knowledge of his new discoveries was compensation enough. Through material donated to Avery by Kemner, Jim Brock, Michael J. Smith and Douglas D. Mullins, Avery also returned to the study of one of his long-time favorite genera, *Amblyscirtes* (refs. 5, 8, 84), and described two new taxa of *Amblyscirtes* initially discovered by Brock (refs. 109, 110).

Illegal collecting eventually caught up with Kemner, once the U.S. Fish and Wildlife Service learned that his Mexican material was being collected and sold without necessary permits. On August 16, 1991, Special Agents for the Fish and Wildlife Service arrived at Avery's home and confiscated all 1796 Mexican specimens collected by Kemner in Avery's possession. These specimens were subsequently deposited in the CMNH in April, 1996. This event ended the collaboration that Avery and Kemner had developed, and dealt a devastating blow to both of them, although they maintained a regular correspondence until Avery's passing.

For Avery, the loss of Kemner's collaboration was indeed discouraging, but he was still being inundated with skipper specimens for determination. From August 1989 until 1998, Avery determined large lots of specimens for the CMNH, at the request of Dr. John Rawlins, Curator of Invertebrates. Between August 1989 and January 1998, Avery determined over 7000 specimens of Hesperiidae for the CMNH, and in recognition of his contributions, he was appointed as Research Associate in 1991. Most specimens of Nearctic and Neotropical skippers in the CMNH bear Avery's determination label. The CMNH material kept Avery busy dissecting, determining, labeling, listing and writing, without having to leave Garland. Avery returned the last batch of specimens to the CMNH in 1998, when, due to failing health, he felt he was no longer able to work with the material.

In conclusion, Avery Freeman contributed to the study of Lepidoptera in every possible manner. He collected and reared scientific specimens now available to future generations in museums. Avery furthered the science by publishing new methods for collecting and rearing skippers. He wrote prolifically about new faunas and species. He also inspired a new generation of skipper workers through his work and correspondence. An active member of the Lepidopterists' Society, Avery embodied fully the enthusiasm of the amateur and the careful work of the professional. He will be missed, but never forgotten for all his contributions.

COLLECTIONS

Megathyminae. Collection of 2353 specimens to AMNH before August 1970, see Rindge (1970).

Mexican Hesperiidae. Entire collection of several thousand specimens mailed to AMNH in March, arrived at AMNH in April, 1981; completely curated into AMNH collection by August 1981 (ref. 104). Material acquired after about 1987, mostly from John Kemner, deposited at the FSMC (at least 56 specimens), CMNH (roughly 1800 specimens deposited by April 1996) and USNM (at least 225 specimens, including several from north of Mexico).

North American Hesperiidae. Several thousand specimens to A. Warren in June 1998; the remaining several thousand to the CMNH in 2000.

Lycaenidae and Riodinidae. Donated 1453 specimens of Mexican Lycaenidae and Riodinidae to CMNH before November 1972, on several occastions: 1st and 2nd lots in August 1968, 3rd lot in September 1968, 4th lot in January 1970, 5th lot in December 1970, 6th lot in early 1972. Subsequently donated 2231 additional hairstreak specimens, including complete holdings of North American taxa, to the CMNH on December 1st, 1972. Lists of donated specimens were compiled by H. K. Clench for each lot and sent to Freeman; these are archived at the CMNH.

Catocala. Donated 2878 specimens to AMNH in November, 1990, entirely curated into AMNH collection by November 1992 (ref. 111).

Avery also donated various Hesperiidae specimens to Michigan State University (in November 1965), the USNM (at least 225 specimens on various occasions including April 1988, May 1988, September 1989, December 1989, September 1990, December 1990, February 1990, June 1991, January 1992, February 1992, July 1992) and various holotypes (as stated in their original descriptions), and other specimens to the FSMC. As noted in ref. 104, Freeman holotypes that were said to have been deposited in the USNM in ref. 77 are actually at the AMNH.

PATRONYMS

Neonympha gemma freemani Stallings & Turner, 1947. Canadian Ent. 78(7-8):134-137. TL: Pharr, [Hidalgo Co.], Texas. Holotype male, 28 October 1944, H. A. Freeman collector, in USNM. Currently placed in the genus *Cyllopsis* R. Felder, see Miller (1974)

Agathymus freemani Stallings & Turner, 1960. Ent. News 71(5):109-115. TL: near Bagdad, [Yavapai Co.], Arizona. Holotype female, 10 October 1957, J. R. Turner collector, in YPM. Currently considred a subspecies of *Agathumus baueri* (Stallings & Turner), see Roever (1975)

Vinius freemani L. Miller, 1970. J. Lepid. Soc. 24(2):120-124. TL: 2 mi. SE Coatzacoalcos, Veracruz, Mexico. Holotype male, 18 January 1966, H. K. Clench and L. D. Miller collectors, in CMNH. Currently placed in *Vinpeius* Austin, and considered a synonym of *V. tinga* (Evans), see Austin (1997).

Calephelis freemani McAlpine, 1971. J. Res. Lepid. 10(1):1-125. TL: Davis Mtns., about 12 mi. NW Alpine, St. Hwy. 118, Jeff Davis Co., Texas. Holotype male, H. A. Freeman collector, in USNM.

Mellana balsa freemani Steinhauser, 1974. Bull. Allyn Mus. 22:1-38. TL: Santa Tecla, El Salvador, 900m. Holotype male, 27 June 1972, S. R. & L. M. Steinhauser collectors, in FSMC. Currently placed in *Quasimellana* Burns, and considered a synonym of *Q. balsa* (Bell), see Burns (1994).

Dalla freemani A. Warren, 1997. Trop. Lepid. 8(1):35-37. TL: Olas de Moka, Dept. Solola, Guatemala. Holotype male, September

1808(?), ex colln. Geo. P. Engelhardt, in AMNH.

Freemania A. Warren, 2000. Boletín Científico, Mus. Hist. Nat., Univ. Caldas 5:138-153. Type species: *Freemania rawlinsi* A. Warren, 2000. Generic name preoccupied, see Warren (2001).

Freemaniana A. Warren, 2001. Proc. Ent. Soc. Wash. 103(4):1028-1029. Type species: *Freemania rawlinsi* A. Warren, 2000. Replacement name for *Freemania*.

Halotus jonaveriorum Burns 1992. J. Lepid. Soc. 46(3):182-194. TL: La Soledad - Buena Vista, 1525m., Sierra Madre del Sur, Oaxaca, Mexico. Holotype male, 12 April 1990, John Kemner collector, in USNM. Named for John Kemner and Avery Freeman.

Annotated Bibliography of Publications by Hugh Avery Freeman

This bibliography includes all of Hugh Avery Freeman's entomological publications known to this author, listed chronologically. All publications have been personally examined. Two additional manuscripts have been drafted, that will be finished and coauthored by A. Warren; one is a taxonomic revision of the genus *Piruna*, the other describes new species of *Staphylus*.

1. 1938. Notes on the Sphingidae (Lepidoptera) of Arkansas. Field and Lab. 6(2):33-43. {Apr 1938} [Survey from 1926 to 1937; distributional data by county; months of capture; larval food plants; adult nectar sources, behavior; *Herse cingulata, Protoparce sexta, P. quinquemaculatus, P. rustica, Chlaenogramma jasminearum, Dolba hylaeus, Ceratomia amyntor, C. undulosa, C. catalpae, Isoparce cupressi, Atreus plebeia, Sphinx chersis, S. gordius, Smerinthus jamaicensis, Paonias exaecata, P. myops, Cressonia juglandis, Pachysphinx modesta, Erinnyis ello, E. obscura, Aellopos titan, Haemorrhagia thysbe, H. diffinis, Pholus satellita, P. achemon, P. fasciatus, Ampeloeca versicolor, A. myron, Darapsa pholus, Amphion nessus, Xylophanes tersa, Celerio lineata*]

2. 1939. The Hesperiidae of Dallas County, Texas. Field and Lab. 7(1):21-28. {Jan 1939} [Survey from September, 1936 to June, 1937; September, 1937 to April, 1938; distributional data; *Epargyreus tityrus, Goniurus proteus, Achalarus lyciades, Thorybes pylades, T. daunus, T. confusis, Urbanus syrichtus, U. tessellata, Pholisora catullus, P. hayhurstii, Erynnis brizo, E. persius, E. juvenalis, E. horatius, E. tristis, E. funeralis, Ancyloxypha numitor, Copaeodes aurantiaca, C. minima, Hylephila phyleus, Polites verna, P. themistocles, Atalopedes campestris, Catia otho, Atrytone logan, A. arogos, A. vestris, Poanes viator, P. zabulon, Amblyscirtes vialis, A. celia, A. comus, Lerema accius, Lerodea eufala, Calpodes ethlius, Megathymus yuccae*; adult nectar sources]

3. 1941. Hermaphroditism among the Hesperiidae (Lepidoptera, Rhopalocera). Field and Lab. 9(1):27-28. {Jan 1941} [(*Atalopedes campestris, Polites manataaqua*), *Pyrgus communis*]

4. 1941. Distributional notes on *Atrytone dion* race *alabamae* Lindsey (Lepidoptera, Rhopalocera, Hesperiidae). Field and Lab. 9(1):29. {Jan 1941} [(Mobile Co., Alabama; Chikasaw, Alabama); Dahl Swamp, Accomac, Virginia; Dismal Swamp, Virginia; North Little Rock, Arkansas]

5. 1941. A new species of *Amblyscirtes* from Texas (Lepidoptera, Rhopalocera, Hesperiidae). Ent. News. 52(2):50-51. {[21] Feb 1941} [*Amblyscirtes belli* n. sp. (TL: two miles west of Vickery, Dallas Co., Texas. Holotype male, H. A. Freeman collector, in AMNH)]

6. 1941. *Lerodea tyrtaeus* (Ploetz), new to the United States (Lepidoptera, Rhopalocera, Hesperiidae). Field and Lab. 9(2):45. {May 1941} [Recorded from one mile north of West Columbia, Brazoria Co., Texas]

7. 1942. Notes on some North American Hesperiidae with the description of a new race of *Polites verna* (Edwards) (Lepidoptera, Rhopalocera). Ent. News. 53(4):103-106. {[20] Apr 1942} [Distributional data; *Erynnis burgessi, E. baptisiae, Hesperia uncas, H. meskei, Polites verna sequoyah* n. ssp. (TL: Hope Hill Farm, Faulkner Co., Arkansas. Holotype male, H. A. Freeman collector, in AMNH), *Atrytone dion alabamae, A. dukesi, Amblyscirtes belli, Lerodea tripunctus* (confirmed from U.S. at Miami, Florida)]

8. 1943. Two new species of *Amblyscirtes* from Texas and Arkansas (Lepidoptera, Rhopalocera: Hesperiidae). Ent. News. 54(1):14-20. {Jan [6 Feb], 1943} [*Amblyscirtes erna* n. sp. (TL: Palo Duro Canyon, Texas. Holotype male, 25 April 1942, H. A. Freeman collector, in AMNH), *A. linda* n. sp. (TL: Hope Hill Farm, Faulkner Co., Arkansas. Holotype male, 6 July 1942, H. A. Freeman collector, in AMNH)]

9. 1943. New Hesperioidea, with notes on some others from the United States (Lepidoptera, Rhopalocera). Ent. News. 54(3):72-77. {Mar [7 Apr], 1943} [Distributional data; *Thorybes pylades albosuffusa* n. form (TL: Fort Davis [Jeff Davis Co.], Texas. Holotype male, H. A. Freeman collector, in AMNH), *Erynnis persius persius, E. p. pernigra, E. p. avinoffi, E. p. fredericki* n. ssp. (TL: near Lead, Spearfish Canyon, [Lawrence Co.], South Dakota. Holotype male, V. H. & A. C. Frederick collectors, in AMNH), *Amblyscirtes simius, M. yuccae alabamae* n. ssp. (TL: Anniston, [Calhoun Co.], Alabama. Holotype male, 12 April 1937, M. E. Smith collector, in AMNH)]

10. 1943. Notes on and redescriptions of *Megathymus yuccae* (Boisduval & LeConte) and its subspecies (Lepidoptera, Rhopalocera, Hesperioidea). Ent. News. 54(9):211-217. {[11] Nov 1943} [Distributional data; *Megathymus yuccae yuccae* (TL restriction: South Carolina to the southern tip of Florida), *M. y. coloradensis, M. y. navajo, M. y. alabamae, M. y. stallingsi* n. ssp. (TL: Caldwell [Sumner Co.], Kansas. Holotype male, emg. 11 April 1943, D. B. Stallings collector, in AMNH), *M. y. stallingsi*, form *dee*, n. form (TL: Caldwell [Sumner Co.], Kansas. Holotype female, emg. 12 April 1943, D. B. Stallings collector, in AMNH)]

11. 1944. A new form of *Hesperia metea* Scudder from Texas (Lepidoptera Hesperiidae). Field and Lab. 12(1):20-22. {Jan 1944} [*Hesperia metea belfragei* n. form (TL: Cedar Hill, Dallas Co., Texas. Holotype male, H. A. Freeman collector, in AMNH)]

12. 1944. A new form of *Hesperia leonardus* (Harris) from the middle western United States (Lepidoptera, Rhopalocera, Hesperiidae). Bull. Brooklyn Ent. Soc. 38(5):153-154. {14 Mar 1944} [*Hesperia leonardus stallingsi* n. form (TL: Blendon, Franklin Co., Ohio. Holotype male, 24 August 1935, G. W. Rawson collector, in AMNH)]

13. 1944. A new subspecies of *Polites themistocles* (Latreille) from British Columbia, Canada (Lepidoptera, Rhopalocera, Hesperioidea). Ent. News. 55(2):47-48. {Feb [17 Mar], 1944} [*Polites themistocles turneri* n. ssp. (TL: Jesmond, British Columbia. Holotype male, 9 July 1937, J. K. Jacob collector, in AMNH)]

14. 1944. Notes on the *streckeri* group of the genus *Megathymus* (Lepidoptera, Rhopalocera). Ent. News. 55(4):103-105. {Apr [3 May], 1944} [Distributional data; *Megathymus streckeri, M. texana* (= *leussleri*), *M. texana* form *albocincta*]

15. 1944. Further notes on the Hesperioidea of Dallas County, Texas. Field and Lab. 12(2):56-58. {Jun 1944} [Distributional data; *Urbanus dorantes, Cogia outis, Pyrgus communis albescens, Erynnis burgessi, E. baptisiae, E. martialis, E. propertius, Hesperia viridis, H. metea belfragei, H. meskei, Polites vibex brettoides, P. verna sequoyah, Wallengrenia otho egeremet, Atrytone logan lagus, A. dion alabamae, A. ruricola* form *immaculatus, Amblyscirtes belli, Megathymus yuccae stallingsi, M. y. stallingsi* form *dee, M. texana*]

16. 1945. Notes on some North American Hesperiidae, with two new records for the United States (Lepidoptera, Rhopalocera). Ent. News. 56(1):4-5. {Jan [16 Feb], 1945} [Distributional data; *Urbanus eurycles, Astraptes fulgerator, A. anaphus* (first U.S. record from Pharr [Hidalgo Co.], Texas), *Lerodea tyrtaeus, Perichares phocion dolores* (first U.S. record from Pharr, Hidalgo Co., Texas)]

17. 1945. Notes on some Hesperiidae, with new records for the United States (Lepidoptera, Rhopalocera). Ent. News. 56(4):102-104. {Apr [25 May], 1945} [Distributional data; *Aguna asander* (first U.S. record from Pharr [Hidalgo Co.], Texas), *Astraptes hopfferi* (first U.S. record from Pharr [Hidalgo Co.], Texas), *Spathilepia clonius* (first U.S. record from Pharr [Hidalgo Co.], Texas), *Lerodea edata* (first U.S. records from Brownsville [Cameron Co.] and Pharr

[Hidalgo Co.], Texas), *Godmania malitiosa* (first U.S. record from Pharr [Hidalgo Co.], Texas), *Perichares phocion dolores*]

18. 1945. The Hesperiidae (Lepidoptera) of Arkansas. Field and Lab. 13(2):60-63. {Jul 1945} [Based on 19 years of collection and study; distributional data; *Proteides clarus, Urbanus proteus, Achalarus lyciades, Autochton cellus, Thorybes bathyllus, T. confusis, T. pylades, Pyrgus syrichtus* form *montivagus, P. communis, Pholisora catullus, P. hayhurstii, Erynnis icelus, E. brizo, E. persius, E. baptisiae, E. martialis, E. juvenalis, E. funeralis, Ancyloxypha numitor, Copaeodes aurantiaca, C. minima, Hesperia metea belfragei, H. meskei, H. leonardus stallingsi, Hylephila phyleus, Polites themistocles, P. manataaqua, P. vibex, P. verna sequoyah, Wallengrenia otho, W. otho egeremet, Poanes hobomok, P. zabulon, Atrytone logan, A. dion alabamae, A. ruricola, Lerema accius, Amblyscirtes vialis, A. nysa, A. linda, A. belli, Lerodea eufala, L. l'herminier, Calpodes ethlius, Panoyuina* [sic] *ocolo* [sic]]

19. 1945. A new species of *Lerodea* from Texas (Lepidoptera: Hesperiidae). Ent. News. 56(8):203-205. {[19] Oct 1945} [*Lerodea julia* n. sp. (TL: Pharr [Hidalgo Co.], Texas. Holotype male, 15 October 1944, H. A. Freeman collector, in AMNH); male genitalia illustrated]

20. 1946. Notes on some skippers, with new records for the United States (Lepidoptera, Hesperiidae). Canadian Ent. 77(11):201-203. {18 Apr 1946} [Distributional data; *Urbanus doryssus* (first U.S. record from Pharr [Hidalgo Co.], Texas), *U. auginus auginulus* (first U.S. record from Pharr [Hidalgo Co.], Texas), *Aguna asander, Pellicia bromias* (first U.S. record from Pharr [Hidalgo Co.], Texas), *Carrhenes canescens* (first U.S. record from Pharr [Hidalgo Co.], Texas), *Celaenorrhinus fritzgaertneri* (first U.S. record from the Pharr-San Jacinto-Alamo High School campus, just outside of Pharr [Hidalgo Co.], Texas), *Synapte malitiosa* (first U.S. record from Pharr [Hidalgo Co.], Texas)]

21. 1946. Two new species of skippers from North and Central America (Lepidoptera: Hesperiidae). Ent. News. 57(8):185-187. {Oct [20 Dec], 1946} [*Celaenorrhinus stallingsi* n. sp. (TL: Monterrey, N[uevo] L[eón], Mexico. Holotype male, 28 May 1941, D. B. Stallings collector, in YPM), *Calpodes evansi* n. sp. (TL: Pharr [Hidalgo Co.], Texas. Holotype male, 21 October 1944, H. A. Freeman collector, in AMNH); genitalia illustrations of males]

22. 1947. New skipper records for the United States. Ent. News. 58(7):184-186. {Jul [27 Oct], 1947} [*Aguna asander* form *panthius, Pellicia costimacula* (first U.S. record from Pharr [Hidalgo Co.], Texas), *Gorgythion begga pyralina* (first U.S. record from Pharr [Hidalgo Co.], Texas); summary of native and stray skippers in the Rio Grande Valley]

23. 1948. Notes on some North American skippers, with the description of a new species from Kansas (Lepidoptera: Hesperiidae). Ent. News. 59(8):203-206. {Oct [23 Dec], 1948} [Distributional data; *Urbanus undulatus* (first U.S. record from Pharr [Hidalgo Co.], Texas), *Hesperia metea licinus* (= *belfragei* n. syn.; = *horus* n. syn.), *Atrytone eulogius* (first U.S. record from Brownsville [Cameron Co.], Texas), *Atrytonopsis turneri* n. sp. (TL: Barber Co., Kansas. Holotype male, 5 May 1946, in AMNH), *Cobalus percosius* (first U.S. record from between Brownsville and Southmost [Cameron Co.], Texas)]

24. 1949. Notes on some tropical American skippers (Lepidoptera, Rhopalocera, Hesperiidae). Field and Lab. 17(3):75-81. {Jun 1949} [Distributional data, Texas, Mexico, Central America; *Urbanus doryssus, Chioides zilpa, Astraptes anaphus, Proteides mercurius, Cabares potrillo, Cogia calchas, Spathilepia clonius, Grais stigmaticus, Timochares ruptifasciatus, Pyrgus domicella, Pholisora mazans, Chiomara asychis, Calpodes sylvicola, C. nyctelius, C. evansi, Lerodea edata*]

25. 1949. A summary of new butterflies from Texas. Texas J. Sci. 1(3):40-41. {30 Sep 1949} [New records for North America recently found in Texas: *Papilio lycophron pallas, Heliconius petiveranus, Biblis hyperia aganisa, Cyclogramma asteria, Adelpha fessonia, Chlorippe pavon, Apodemia walkeri, Emesis emesia, Thecla bazochii, T. cestri, Strymon yojoa, S. spurina, Urbanus doryssus, U. undulatus, U. auginus auginulus, Aguna asander, A. asander* f. *panthius, Astraptes anaphus, A. hopfferi, Pellicia bromias, P. costimacula, Spathilepia clonius, Celaenorrhinus fritzgaertneri, Carrhenes canescens, Gorgythion begga pyralina, Atrytone eulogius, Cobalus percosius, Lerodea tyrtaeus, L. edata, Synapte malitiosa, Perichares phocion dolores*; New species and subspecies from Texas: *Euptychia gemma freemani, Asterocampa clyton louisa, Celaenorrhinus stallingsi, Thorybes pylades albosuffusa, Lerodea julia, Amblyscirtes belli, A. erna, Calpodes evansi, Megathymus yuccae stallingsi*]

26. 1950. A new species of hairstreak and new records for the United States (Lepidoptera, Rhopalocera, Lycaenidae). Field and Lab. 18(1):12-15. {2 Jan 1950} [*Strymon buchholzi* n. sp. (TL: Pharr [Hidalgo Co.], Texas. Holotype male, 24 November 1946, H. A. Freeman collector, in AMNH); distributional data; *Strymon zebina* (first U.S. report from Pharr [Hidalgo Co.], Texas), *S. rufofusca* (first U.S. report from eleven miles south of Pharr [Hidalgo Co.], Texas), *S. cyphara* (first U.S. report from eleven miles south of Pharr [Hidalgo Co.], Texas), *S. echion* (first U.S. report from eleven miles south of Pharr [Hidalgo Co.], Texas), *Thecla facuna* (first U.S. report from near Hidalgo [Hidalgo Co.], Texas); adult nectar sources]

27. 1950. Further observations on *Calpodes evansi* Freeman (Lepidoptera, Rhopalocera, Hesperiidae). Field and Lab. 18(1):15-17. {2 Jan 1950} [Distributional notes; photographs of holotype male]

28. 1950. The distribution and flower preferences of the Theclinae of Texas (Lepidoptera, Rhopalocera, Lycaenidae). Field and Lab. 18(2):65-73. {3 Apr 1950} [Survey period of 8 years; phenological and geographical distributions; *Atlides halesus corcorani* form *estesi, Strymon maesites telea, S. simaethis sarita, S. pastor, S. zebina, S. spurina, S. yojoa, S. cyphara, S. cecrops, S. beon, S. echion, S. clytie, S. azia, S. rufofusca, S. columella istapa, S. laceyi, S. buchholzi, S. melinus, S. melinus pudica, S. melinus franki, S. ontario, S. ontario autolycus, S. polingi, S. alcestis, S. alcestis oslari, S. titus watsoni, S. edwardsii, S. falacer, Mitoura siva* (first report from Texas), *M. xami, M. damon castalis, Incisalia irus, I. hadros, I. henrici solatus, I. henrici turneri, Thecla bazochii, T. cestri, T. facuna*]

29. 1950. The distribution of *Wallengrenia otho* (Abbot & Smith) and its subspecies in the United States (Lepidoptera, Rhopalocera, Hesperiidae). Field and Lab. 18(2):78. {3 Apr 1950} [*Wallengrenia otho otho, W. otho egeremet, W. otho curassavica* (first U.S. records from "Del Rio, through Laredo on down to Brownsville, Texas, along the Rio Grande River;" common around Pharr, Hidalgo Co.)]

30. 1950. Notes on *Megathymus*, with description of a new species (Lepidoptera, Rhopalocera, Megathymidae). Field and Lab. 18(4):144-146. {11 Dec 1950} [*Megathymus neumogeni* (= *aryxna*, = *drucei*), *M. evansi* n. sp. (TL: Ramsey Canyon, Cochise Co., Arizona. Holotype male, 11 September 1950, H. A. Freeman collector, in AMNH)]

31. 1951. Notes on the *Agave* feeders of the genus *Megathymus* (Lepidoptera, Rhopalocera, Megathymidae). Field and Lab. 19(1):26-32. {18 Jan 1951} [Larval food plants, descriptions of immatures, larval behavior and habits, female oviposition behavior; *Megathymus neumogeni, M. evansi, M. polingi, M. stephensi, M. neumogeni, M. mariae, M. smithi*]

32. 1951. Distributional notes on *Papilio palamedes* Drury and its subspecies *leontia* [sic] R.&J. (Lepidoptera, Rhopalocera, Papilionidae). Field and Lab. 19(1):32. {18 Jan 1951} [Arkansas, Texas; *P. palamedes, P. palamedes leontia* [sic] (first U.S. record from Rockport, [Aransas Co.], Texas)]

33. 1951. Distributional notes on the Theclinae of Arkansas. Field and Lab. 19(1):36-39. {18 Jan 1951} [Survey period of 24 years; taxonomic and biological notes; *Atlides halesus, Strymon cecrops, S. m-album, S. melinus, S. ontario, S. titus mopsus, S. edwardsii, S. falacer, S. liparops strigosa, Mitoura damon, Incisalia irus, I. niphon*]

34. 1951. Notes on the genus *Yvretta* Hemming with a new record for the United States (Lepidoptera, Rhopalocera, Hesperiidae). Field and Lab. 19(1):45-46. {18 Jan 1951} [Distributional data; key to adults; *Yvretta citrus* (first U.S. report from near Fort Davis [Jeff Davis Co.], Texas), *Y. rhesus* (= *axius*, = *subreticulata*), *Y. carus*]

35. 1951. New skipper records for Mexico (Lepidoptera, Rhopalocera, Hesperiidae). Field and Lab. 19(1):46-48. {18 Jan 1951} [*Thorybes bathyllus* (from southeast of Monterey, N[uevo] L[eón]), *Heliopetes sublinea, Atrytone ruricola metacomet* form

immaculatus (from Monterrey, N[uevo] L[eón]), *Amblyscirtes celia* (from Monterrey, N[uevo] L[eón])]

36. 1951. Ecological and systematic study of the Hesperioidea of Texas (Lepidoptera, Rhopalocera, Hesperioidea). Southern Methodist University Studies 6:1-67. {1951} [study period from 1936 to 1949; distributional data; adult habits and nectar sources; keys to adults; *Apyrrothrix araxes arizonae, Phocides lilea, P. urania, Nascus euribates, Polygonus lividus arizonensis, Aguna asander, A. asander* form *panthius, Proteides clarus, P. mercurius, Urbanus proteus, U. dorantes, U. eurycles, U. simplicius, U. undulatus, U. doryssus, U. auginus auginulus, Chioides albofasciatus, C. zilpa, Codatractus alcaeus* (first U.S. record from the Davis Mountains, Texas), *C. melon arizonensis, Astraptes fulgerator, A. anaphus, A. hopfferi, Zestusa dorus, Achalarus lyciades, A. casica, A. coyote, Autochton cellus, Thorybes bathyllus, T. confusis, T. pylades, T. pylades albosuffusa, T. drusius, Cogia calchas, C. outis, C. hippalus, Cabares potrillo, Spathilepia clonius, Pellicia bromias, P. costimacula, Grais stigmaticus, Carrhenes canescens, Timochares ruptifasciata, Celaenorrhinus fritzgaertneri, C. stallingsi, Achlyodes thraso, Xenophanes tryxus, Chiomara asychis, Gorgythion begga pyralina, Pyrgus philetas, P. syrichtus, P. communis, P. communis albescens, P. domicella, Heliopetes laviana, H. macaira, Antigonus evansi, A. pulverulenta, Celotes nessus, Pholisora catullus, P. mejicanus, P. ceos, P. hayhurstii, P. mazans, P. alpheus, Erynnis brizo, E. burgessi, E. gesta, E. persius, E. baptisiae, E. juvenalis, E. meridianus, E. horatius, E. funeralis, E. tristis, E. scudderi, Oarisma edwardsii, Adopaeoides simplex, Ancyloxypha numitor, A. arene, Copaeodes aurantiaca, C. minima, Yvretta carus, Hylephila phyleus, Hesperia uncas, Hesperia metea licinus, H. woodgatei, H. viridis, H. pahaska williamsi, H. meskei, H. attalus, Atalopedes campestris, Ochlodes morrisoni, Polites themistocles, P. vibex brettoides, P. vibex praeceps, P. verna sequoyah, Wallengrenia otho, W. otho egeremet, Poanes viator, P. hobomok, P. zabulon, Atrytone arogos iowa, A. logan, A. logan lagus, A. eulogius, A. dion alabamae, A. ruricola metacomet, A. r. metacomet* form *immaculatus, Atrytonopsis vierecki, A. python margarita, A. edwardsii, A. pittacus, Cobalus percosius, Lerema accius, Amblyscirtes vialis, A. alternata, A. belli, A. celia, A. nysa, A. nereus, A. eos, A. aenus, A. erna, A. texanae, A. oslari, A. simius, A. phylace, Lerodea eufala, L. edata, L. tyrtaeus, L. l'hermenier, L. julia, Synapte malitiosa, Thespieus macareus* (reported from San Antonio [Bexar Co.], Texas), *Calpodes ethlius, C. evansi, C. sylvicola, C. ocola, Panoquina panoquinoides, P. nyctelius, Perichares phocion dolores, Megathymus yuccae stallingsi, M. texana, M. texana* form *albocincta, M. mariae, M. stephensi, M. smithi*]

37. 1952. Notes on *Megathymus yuccae* (Boisduval & LeConte), with description of a new subspecies (Lepidoptera, Rhopalocera, Megathymidae). Field and Lab. 20(1):29-33 {Jan [29 Feb] 1952} [Distributional data; larval food plants; *Megathymus yuccae* (= *alabamae* n. syn.); *yuccae* neotype designation (TL: Aiken Co., South Carolina. 7 April 1951, H. W. Eustis collector, in AMNH), *M. y. buchholzi* n. ssp. (TL: Jupiter [Palm Beach Co.], Florida. Holotype male, 13 March 1947, O. Buchholz collector, in AMNH), comparison with *M. y. yuccae*]

38. 1952. 4. Great Plains - Texas and eastern plains of Rocky Mts. states to Saskatchewan and Manitoba. Pp. 95-97 in: The field season summary of North American Lepidoptera for 1951. Lepid. News. 5(8):81-110. {1951 [15 Apr 1952]} [Distributional data]

39. 1952. Two new species of *Megathymus* from Texas and Mexico (Lepidoptera, Rhopalocera, Megathymidae). Amer. Mus. Novit. 1593:1-9. {29 Oct 1952} [*Megathymus chisosensis* n. sp. (TL: Chisos Basin, Chisos Mountains, Texas. Holotype male, emg. 22 September 1951, H. A. Freeman collector, in AMNH), *M. hoffmanni* n. sp. (TL: Valle de Mexico. Holotype female, October 1916, C. C. Hoffmann collector, in AMNH); photographs of types; male and female genitalia illustrations]

40. 1953. 4. Great Plains - Texas and eastern plains of Rocky Mountain states to Saskatchewan and Manitoba. Pp. 90-93 in: The field season summary of North American Lepidoptera for 1952. Lepid. News. 7(3/4):66-118. {16 Nov 1953} [Distributional data]

41. 1955. Four new species of *Megathymus* (Lepidoptera, Rhopalocera, Megathymidae). Amer. Mus. Novit. 1711:1-20. {11 Mar 1955} [Larval food plants; *Megathymus harrisi* n. sp. (TL: Stone Mountain [Dekalb Co.], Georgia. Holotype male, 17 July 1953, L. Harris, Jr. collector, in AMNH), *M. belli* n. sp. (TL: La Bequilla, Durango, Mexico. Holotype male, 29 July 1902, Batty collector, in AMNH), *M. mcalpinei* n. sp. (TL: 5.1 miles north of Marathon [Brewster Co.], Texas. Holotype male, emg. 26 September 1953, H. A. Freeman collector, in AMNH), *M. smithi, M. maculosus* n. sp. (TL: Kingsville, [Kleberg Co.], Texas. Holotype male, emg. 21 September 1952, H. A. Freeman collector, in AMNH); photographs of types; male and female genitalia illustrations]

42. 1956. A new species of *Hesperia* from California (Hesperiidae). Lepid. News. 9(6):196-198. {16 Apr 1956} [*Hesperia tildeni* n. sp. (TL: Cherry Flat Reservoir, Santa Clara Co., California. Holotype male, 27 August 1949, J. W. Tilden collector, in AMNH); photographs of types; male genitalia illustration]

43. 1959. A revision of the genera of the Megathymidae, with the description of three new genera. Lepid. News. 12(3/4):81-92. {26 Jan 1959} [*Aegiale* (= *Teria*, = *Acentrocneme*), *Agathymus* n. gen. (TS: *Megathymus neumogeni*), *Turnerina* n. gen. (TS: *Megathymus hazelae*), *Megathymus, Stallingsia* n. gen. (TS: *Megathymus maculosus*); keys to genera; illustrations of antennae and tarsi; bibliography of the Megathymidae]

44. 1960. Butterfly collecting in Texas and New Mexico. J. Lepid. Soc. 13(2):89-93. {12 Feb 1960} [East Texas (Tyler State Park), central Texas (Buckner Blvd., Dallas; Lancaster, 10 miles south of Dallas), Pharr area (along Rio Grande River; La Reforma ranch north of Hidalgo; six miles north of McAllen), southwestern Texas (Fort Davis; Mt. Locke), Texas panhandle (Palo Duro Canyon; Gray's ranch north of Skellytown), New Mexico (Canadian River south of Tucumcari; Raton; between Rodeo and Lordsburg; Carlsbad; Santa Fe; Albuquerque; Folsom; Ft. Wingate; Zuni Mountains; Silver City; Santa Rita; Gallup)]

45. 1960. 3. Zones III and IV: Rocky Mountains and Great Plains. Pp. 6-8 in: Season's summary for 1959. News Lepid. Soc. 1960(3):1-17. {15 Apr 1960} [Distributional data]

46. 1960. Notes on *Agathymus* in Texas, and the description of a new species from Mexico (Megathymidae). J. Lepid. Soc. 14(1):58-62. {15 Dec 1960} [Larval food plants; distributional data; *Agathymus estelleae* (first U.S. records), *A. mariae, Agathymus fieldi* n. sp. (TL: Guadalajara, Mexico, Jalisco Highway 15, Kilometer 724, 4400'. Holotype female, emg. 30 September 1957, Stallings and Turner collectors, in AMNH); photographs of types, cremaster, male and female genitalia]

47. 1961. Zone IV: Great Plains - Canada to Texas in the Plains Region. Pp. 6-7 in: Season's summary, 1960. News Lepid. Soc. 1961(4):1-13. {1 Jun 1961} [Distributional data]

48. 1962. Zone IV. Great Plains - Canada to Texas in the Plains Region. Pp. 6-7 in: Season's summary, 1961. News Lepid. Soc. 1962 (3):1-14. {15 Apr 1962} [Distributional data]

49. 1962. A new species of *Agathymus* from Texas (Lepidoptera, Rhopalocera, Megathymidae). Amer. Mus. Novit. 2097:1-8. {27 Jun 1962} [Larval foodplants; *Agathymus diabloensis* n. sp. (TL: 5 miles west of Victoria [sic] Canyon, Diablo Mountains, Hudspeth Co., Texas. Holotype female, emg. 13 September 1960, H. A. Freeman collector, in AMNH), photographs of types; illustrations of male and female genitalia, cremaster]

50. 1963. Zone IV: Great Plains - Canada to Texas in the Plains Region. Pp. 6-7 in: Summary, 1962 season. News Lepid. Soc. 1963 (4):1-15. {1 Jun 1963} [Distributional data]

51. 1963. The butterflies and skippers of Texas, a tentative list. (with R. O. Kendall, senior author). Authors, San Antonio and Garland, Texas. 5pp. {1 Jul 1963} [distributional data, months of occurrence; list of 326 species plus dubious species; map; the publication of this list was supported by the Rob and Bessie Welder Wildlife Foundation, Sinton, Texas, an organization that has elsewhere been cited as the publisher of the list.]

52. 1963. *Megathymus yuccae* in Texas, with the description of two new subspecies. J. Lepid. Soc. 17(2):89-99. {8 Nov 1963} [Distributional data; *Megathymus yuccae reinthali* n. ssp. (TL: two

miles west of Ben Wheeler, Van Zandt Co., Texas. Holotype female, emg. 28 March 1961, H. A. Freeman collector, in AMNH), *M. y. coloradensis, M. y. stallingsi, M. y. louiseae* n. ssp. (TL: 16 miles north of Del Rio [Val Verde Co.], Texas. Holotype female, emg. 5 May 1960, H. A. Freeman collector, in AMNH), *M. y. wilsonorum*; photographs of types; keys to adults]

53. 1963. Type localities of the Megathymidae. J. Res. Lepid. 2(2):137-141. {Sep [30 Dec], 1963} [References; larval food plants; soil pH; *Aegiale hesperiaris, Agathymus neumogeni, A. carlsbadensis, A. florenceae, A. judithae, A. diabloensis, A. mcalpinei, A. chisosensis, A. juliae, A. hoffmanni, A. evansi, A. belli, A. aryxna, A. baueri, A. freemani, A. fieldi, A. mariae, A. micheneri, A. stephensi, A. comstocki, A. remingtoni, A. estelleae, A. polingi, A. alliae, A. indecisa, A. rethon, Turnerina mejicanus, T. hazelae, Megathymus yuccae yuccae, M. y. buchholzi, M. y. stallingsi, M. y. wilsonorum, M. y. coloradensis, M. y. navajo, M. y. arizonae, M. y. martini, M. y. browni, M. cofaqui, M. harrisi, M. streckeri, M. texanus texanus, M. t. leussleri, M. ursus, M. violae, M. beulahae, Stallingsia smithi, S. maculosus*; some type localities restricted]

54. 1964. The effects of pH on the distribution of the Megathymidae. J. Res. Lepid. 3(1):1-4. {Mar [9 May] 1964} [*Agathymus mariae, A. estelleae, A. florenceae, A. carlsbadensis, A. judithae, A. diabloensis, A. mcalpinei, A. chisosensis, A. aryxna, A. polingi, A. remingtoni, A. micheneri, Megathymus yuccae stallingsi, M. y. reinthali, M. y. wilsonorum, M. y. louiseae, M. y. reubeni, M. texanus, M. violae, M. ursus, Aegiale hesperiaris*]

55. 1964. Zone IV: Great Plains - Canada to Texas in the Plains Region. Pp. 7-9 in: North American season summary for 1963. News Lepid. Soc. 1964 (4):3-17. {1 Jun 1964} [Distributional data]

56. 1964. A new species of *Apodemia* from Texas (Riodinidae). J. Lepid. Soc. 18(2):75-77. {28 Aug 1964} [*Apodemia chisosensis* n. sp. (TL: Chisos Mountains, 5400', [Brewster Co.], Texas. Holotype male, 3 August 1962, H. A. Freeman collector, in AMNH); photographs of types; illustrations of male genitalia]

57. 1964. Four new species of *Agathymus* from Texas (Megathymidae). J. Lepid. Soc. 18(3):171-185. {2 Nov 1964} [Distributional data; larval food plants; soil pH; *Agathymus chinatiensis* n. sp. (TL: 2.7 miles south of Shafter [Presidio Co.], Texas. Holotype female, emg. 5 October 1960, H. A. Freeman collector, in AMNH), *A. lajitaensis* n. sp. (TL: 10 miles west of Lajita [sic] [Presidio Co.], Texas. Holotype female, emg. 2 October 1961, H. A. Freeman collector, in AMNH), *A. gilberti* n. sp. (TL: 14 miles north of Bracketville [sic] [Kinney Co.], Texas. Holotype female, emg. 22 October 1961, H. A. Freeman collector, in AMNH), *A. rindgei* n. sp. (TL: 14 miles north of Bracketville [sic] [Kinney Co.], Texas. Holotype female, emg. 23 October 1961, H. A. Freeman collector, in AMNH); photographs of types; illustrations of male and female genitalia, and cremasters]

58. 1965. Larval habits of *Agathymus mariae* (B. & B.). J. Res. Lepid. 3(3):145-147. {Sep 1964 [14 Apr 1965]} [Larval food plants, behavior, pupation]

59. 1965. Zone IV: Great Plains - Canada to Texas jin [sic] the Plains Region. Pp. 7-9 in: North American season summary for 1964. News Lepid. Soc. 1965 (3):2-14. {15 Apr 1965} [Distributional data]

60. 1965. Two new subspecies of *Megathymus yuccae* (Bdv. & LeC.) from Texas. J. Lepid. Soc. 19(2):83-90. {15 Jul 1965} [*Megathymus yuccae kendalli* n. ssp. (TL: San Antonio, Bexar Co., Texas. Holotype female, emg. 12 March 1957, H. A. Freeman collector, in AMNH), *M. y. winkensis* n. ssp. (TL: Wink, Winkler Co., Texas. Holotype female, emg. 16 March 1964, H. A. Freeman collector, in AMNH); photographs of types]

61. 1966. Zone IV: Great Plains. Canada to Texas in the Plains Region. P. 7 in: North American annual summary for 1965. News Lepid. Soc. 1966 (3):4-12. {15 Apr 1966} [Distributional data]

62. 1966. A new species of *Agathymus* from Texas (Megathymidae). J. Lepid. Soc. 20(3):181-185. {25 Aug 1966} [*Agathymus valverdiensis* n. sp. (TL: 28 miles north of Del Rio, Val Verde Co., Texas. Holotype female, emg. 16 September 1963, H. A. Freeman collector, in AMNH); photographs of types; illustrations of male and female genitalia, cremaster; larval biology and food plants]

63. 1966. New Hesperiidae records for Mexico. J. Lepid. Soc. 20(4):226-228. {30 Nov 1966} [Distributional data; *Elbella dulcinea* n. stat. (from Sierra Blanca and Presidio, Veracruz), *E. patrobas* (from Catemaco, Veracruz and Chimalapa, Oaxaca), *Urbanus esma* (from Catemaco, Veracruz), *Astraptes colossus* (from Paraje Nuevo, Veracruz and Chimalapa, Oaxaca), *Damas clavus* (from Catemaco, Veracruz), *Panoquina evansi* (from Acahuizolta, Guerrero and Catemaco, Veracruz), *Aides aegita* (from Catemaco, Veracruz), *Xeniades orchamus* (from Mante, Tamaulipas), *Saliana antonius* (from Valles, San Luis Potosí)]

64. 1967. New skipper records for Mexico. J. Res. Lepid. 5(1):27-28. {1 Mar 1966 [5 Apr 1967]} [Distributional data; *Astraptes helen* (from Paraje Nuevo, Veracruz), *Cogia mala* (from Acahuizolta, Guerrero and north of Tehuacán, Puebla), *Ouleus cyrna* (from Sta. Rosa, Comitán, Chiapas), *Carystoides lila* (from Tamazunchale, San Luis Potosí)]

65. 1967. Zone IV: Great Plains. Canada to Texas in the Plains Region. Pp. 8-9 in: North American annual summary for 1966. News Lepid. Soc. 1967 (3):4-17. {15 Apr 1967} [Distributional data]

66. 1967. Three new species of Hesperiidae from Mexico. J. Lepid. Soc. 21(2):115-119. {26 May 1967} [*Astraptes escalantei* n. sp. (TL: Ocozingo [sic], Chiapas, Mexico. Holotype male, August 1948, T. Escalante collector, in AMNH), *A. catemacoensis* n. sp. (TL: Catemaco, Veracruz, Mexico. Holotype male, September 1964, T. Escalante collector, in AMNH), *Euphyes donahuei* n. sp. (TL: 4 miles east of San Blas, Nayarit, Mexico. Holotype male, 17 July 1963, J. P. Donahue collector, in AMNH); photographs of adults; male genitalia illustrations]

67. 1967. On the status of *Heliopetes sublinea* (Hesperiidae). J. Lepid. Soc. 21(3):205-206. {21 Aug 1967} [Distributional data: Tamaulipas, Nuevo León, San Luis Potosí, Mexico]

68. 1967. Remarks on the genus *Zera* in Mexico with a new record. J. Res. Lepid. 5(3):181-184. {Sep 1966 [Sep 1967]} [Distributional data; *Zera nolckeni, Z. hosta* (first Mexican record from Sta. Rosa, Comitán, Chiapas), *Z. hyacinthinus, Z. tetrastigma, Z. eboneus*; key to adults]

69. 1967. *Polythrix octomaculata*, not *procerus*, in Texas (Hesperiidae). J. Lepid. Soc. 21(4):278. {28 Nov 1967} [Corrects previous records of *Urbanus auginus auginulus* and *Polythrix procerus* to *P. octomaculata*]

70. 1967. Speciation in the *Agathymus* (Megathymidae). J. Res. Lepid. 5(4):209-214. {Dec 1966 [29 Nov 1967]} [Discussion of the *Agathymus neumogeni, mariae*, and *remingtoni* complexes of species, *A. hoffmanni, A. aryxna, Aegiale hesperiaris*; larval food plants and habits]

71. 1968. Zone IV: Great Plains, Canada to Texas in the Plains Region. Pp. 11-12 in: North American annual summary for 1967. News Lepid. Soc. 1968 (3):6-19. {15 Apr 1968} [Distributional data]

72. 1968. New records, and notes on the status of some Hesperiidae from Mexico. J. Res. Lepid. 6(1):59-64. {Mar 1967 [Sep 1968]} [*Bolla cyclops* (from Sta. Rosa, Comitán, Chiapas; suggests *sonda* is a separate species from *cyclops*), *Piruna cyclosticta* (confirmation of species-status), *Dalla dividuum* (confirmation of species-status), *Mellana mulleri* (confirmation of species-status), *M. fieldi* (from Sta. Rosa, Comitán, Chiapas)]

73. 1969. *Polyctor polyctor* (Prittwitz) in Mexico (Hesperiidae). J. Res. Lepid. 6(3):195-196. {Sep 1967 [Dec 1968/Jan 1969]} [from Acahuizolta, Guerrero; all other records from Mexico refer to *P. cleta*, a separate species]

74. 1969. New species and records of Hesperiidae from Mexico (Lepidioptera). J. New York Ent. Soc. 76(4):267-277. {Dec 1968 [14 Feb 1969]} [*Urbanus hubbellus* n. sp. (TL: Sinaloa, Sinaloa, Mexico. Holotype male, March-April 1964, P. Hubbell collector, in AMNH), *Astraptes talthybius* (from Soyolapan el Bajo, nr. Comaltepec, Oaxaca), *Potamanaxas unifasciata* (from Chiltepec, Oaxaca), *Cycloglypha tisias* (from Puerto Eligio, nr. Comaltepec, Oaxaca), *Camptopleura oaxaca* n. sp. (TL: Soyolapan el Bajo, nr. Comaltepec, Oaxaca, Mexico. Holotype male, 13 August 1961, E. C. Welling collector, in AMNH), *Aecas aecas* (from Chiltepec, and Yelta, nr. Valle Nacional, Oaxaca), *Nastra l'herminieri* [sic] (from Colima, Colima),

Cymaenes laureolus (from Coatapec and Fortin de los Flores, Veracruz, and Xicotepec de Juarez, Puebla), *Thoon wellingi* n. sp. (TL: Yelta, nr. Valle Nacional, Oaxaca, Mexico. Holotype male, 13 September 1961, E. C. Welling collector, in AMNH), *Decinea rindgei* n. sp. (TL: Soyolapan el Bajo, nr. Comaltepec, Oaxaca, Mexico. Holotype male, 5 August 1961, E. C. Welling collector, in AMNH), *Halotus angellus* (from Rancho Santa Lucia, Sinaloa), *Atrytonopsis zweifeli* n. sp. (TL: 1 mile south Cedritos, Coahuila, Mexico. Holotype male, 23 June 1957, R. Zweifel collector, in AMNH); photographs of types; illustrations of male genitalia]

75. 1969. Zone IV: Great Plains, Canada to Texas in the Plains Region. Pp. 10-12 in: North American annual summary for 1969 [sic, 1968]. News Lepid. Soc. 1969 (3):5-21. {15 Apr 1969} [Distributional data]

76. 1969. Systematic review of the Megathymidae. J. Lepid. Soc. 23(suppl. 1):1-59. {1969} [Megathyminae: *Stallingsia smithi, S. maculosus, S. jacki, Megathymus yuccae yuccae* (= *alabamae*), *M. y. buchholzi, M. coloradensis coloradensis, M. c. elidaensis* n. comb., *M. c. navajo* n. comb., *M. c. browni* n. comb., *M. c. stallingsi* n. comb., *M. c. reinthali* n. comb., *M. c. martini* n. comb., *M. c. maudae* n. comb., *M. c. arizonae* n. comb., *M. c. reubeni* n. comb., *M. c. winkensis* n. comb., *M. c. wilsonorum* n. comb., *M. c. louiseae* n. comb., *M. c. kendalli* n. comb., *M. cofaqui, M. harrisi, M. streckeri, M. texanus texanus* (= *albocincta*), *M. t. leussleri, M. ursus, M. violae, M. beulahae, M. gayleae*; Aegialinae: Aegialini: *Aegiale hesperiaris* (= *kollari*, = *agavis*), *Turnerina mejicanus, T. hazelae*; Agathymini: *Agathymus neumogeni, A. carlsbadensis, A. florenceae, A. judithae, A. diabloensis, A. macalpinei* [sic], *A. chisosensis, A. hoffmanni, A. aryxna, A. baueri, A. freemani, A. juliae, A. evansi, A. belli, A. ricei, A. mariae, A. chinatiensis, A. lajitaensis, A. rindgei, A. gilberti, A. micheneri, A. remingtoni, A. estelleae, A. valverdiensis, A. fieldi, A. stephensi, A. comstocki, A. dawsoni, A. polingi, A. alliae, A. rethon, A. indecisa*; keys to subfamilies, tribes, genera, species complexes, species and subspecies; restriction and confirmation of many type localities; chromosome numbers; 4 photographs]

77. 1969. Records, new species, and a new genus of Hesperiidae from Mexico. J. Lepid. Soc. 23(suppl. 2):1-62. {1969} [*Pyrrhopyge tzotzili* n. sp. (TL: Ocozingo [sic], Chiapas, Mexico. Holotype female, July 1942, T. Escalante collector, in AMNH), *Mysoria wilsoni* n. sp. (TL: Mexcala, Guerrero, Mexico. Holotype male, 23 July 1956, K. Wilson collector, in AMNH), *Epargyreus windi* n. sp. (TL: Ajijic, Jalisco, Mexico. Holotype male, 3 October 1965, R. Wind collector, in AMNH), *E. brodkorbi* n. sp. (TL: Unión Juárez, Chiapas, Mexico. Holotype male, 19 March 1939, R. Brodkorb collector, in AMNH), *Astraptes louiseae* n. sp. (TL: Presidio, Veracruz, Mexico. Holotype male, August 1951, T. Escalante collector, in AMNH), *A. gilberti* n. sp. (TL: seven miles south of Valles, San Luis Potosí, Mexico. Holotype male, 1 August 1966, H. A. Freeman collector, in AMNH), *Polythrix mexicanus* n. sp. (TL: seven miles south of Valles (grounds of Hotel Covadonga), San Luis Potosí, Mexico. Holotype male, 2 August 1966, H. A. Freeman collector, in AMNH), *Ridens crison* (from Comitán, Chiapas), *Urbanus albimargo* (from Catemaco, Veracruz, Santa Rosa, Comitán, Chiapas and seven miles south of Valles, San Luis Potosí), *Aethilla chiapa* n. sp. (TL: Ocozingo [sic], Chiapas, Mexico. Holotype male, August 1958, T. Escalante collector, in AMNH), *Mimia chiapaensis* n. sp. (TL: Santa Rosa, Comitán, Chiapas, Mexico. Holotype male, May 1965, T. Escalante collector, in AMNH), *Windia* n. gen. (TS: *Windia windi*), *Windia windi* n. sp. (TL: Salada, Colima, Mexico. Holotype male, 13 June 1967, R. Wind collector, in AMNH), *Staphylus veytius* n. sp. (TL: Cintalapa, Chiapas, Mexico. Holotype male, 17 August 1964, H. A. Freeman collector, in AMNH), *S. zuritus* n. sp. (TL: Cintalapa, Chiapas, Mexico. Holotype male, 17 August 1964, H. A. Freeman collector, in AMNH), *Quadrus francesius* n. sp. (TL: Santa Rosa, Comitán, Chiapas, Mexico. Holotype male, May 1965, T. Escalante collector, in AMNH), *Enosis matheri* n. sp. (TL: Catemaco, Veracruz, Mexico. Holotype male, December 1963, T. Escalante collector, in AMNH), *Dalla ramirezi* n. sp. (TL: Catemaco, Veracruz, Mexico. Holotype male, August 1958, A. Ramírez collector, in AMNH), *Vettius argentus* n. sp. (TL: Santa Rosa, Comitán, Chiapas, Mexico. Holotype male, May 1965, T. Escalante collector, in AMNH), *Niconiades comitana* n. sp. (TL: Comitán, Chiapas, Mexico. Holotype male, July 1964, T. Escalante collector, in AMNH), *Anthoptus macalpinei* n. sp. (TL: Fortin de las Flores, Veracruz, Mexico. Holotype male, 26 September 1966, W. S. McAlpine collector, in AMNH), *Pheraeus covadonga* n. sp. (TL: seven miles south of Valles, San Luis Potosí, Mexico. Holotype male, 10 June 1966, H. A. Freeman collector, in AMNH), *Cynea nigricola* n. sp. (TL: Santa Rosa, Comitán, Chiapas, Mexico. Holotype male, May 1965, T. Escalante collector, in AMNH), *Methionopsis typhon* (from seven miles south of Valles, San Luis Potosí), *Moeris duena* (from Santa Rosa, Comitán, Chiapas), *Carystoides escalantei* n. sp. (TL: Villa Juárez, Puebla, Mexico. Holotype male, August 1954, T. Escalante collector, in AMNH), *C. abrahami* n. sp. (TL: Catemaco, Veracruz, Mexico. Holotype male, July 1951, A. Ramírez collector, in AMNH), *C. floresi* n. sp. (TL: seven miles south of Valles (jungle section of the grounds of Hotel Covadonga), San Luis Potosí, Mexico. Holotype male, 4 August 1966, H. A. Freeman collector, in AMNH), *Carystoides mexicana* n. sp. (TL: seven miles south of Valles, San Luis Potosí, Mexico. Holotype male, 5 August 1966, H. A. Freeman collector, in AMNH), *Atrytone mazai* n. sp. (TL: Mexcala, Guerrero, Mexico. Holotype male, 13 July 1956, K. Wilson collector, in AMNH), *Atrytone potosiensis* n. sp. (TL: seven miles south of Valles, San Luis Potosí (grounds of Hotel Covadonga), Mexico. Holotype male, 4 August 1966, H. A. Freeman collector, in AMNH), *Mellana montezuma* n. sp. (TL: seven miles south of Valles (grounds of Hotel Covadonga), San Luis Potosí, Mexico. Holotype male, 27 July 1966, H. A. Freeman collector, in AMNH), *Euphyes peneia* (from Catemaco, Veracruz), *E. chamuli* n. sp. (TL: Santa Rosa, Comitán, Chiapas, Mexico. Holotype male, May 1965, T. Escalante collector, in AMNH), *Tirynthia huasteca* n. sp. (TL: seven miles south of Valles (grounds of Hotel Covadonga), San Luis Potosí, Mexico. Holotype male, 7 August 1966, H. A. Freeman collector, in AMNH); photographs of types; illustrations of male genitalia; holotypes at AMNH, not USNM as stated in text, see ref. 104]

78. 1970. Notes on the genus *Cephise* Evans, with a new record for Mexico (Hesperiidae). J. Lepid. Soc. 24(1):68-69. {26 Mar 1970} [Distributional data; *C. cephise* from six miles south of Ciudad Valles, S[an] L[uis] P[otosí]); notes on systematic position of the genus]

79. 1970. Zone IV: Great Plains, Canada to Texas in the Plains Region. Pp. 11-12 in: North American annual summary for 1969. News Lepid. Soc. 1970 (3):6-19. {15 Apr 1970} [Distributional data; first U.S. record for *Aguna metophis* from Bentsen - Rio Grande Park, [Hidalgo Co.], Texas]

80. 1970. A new genus and eight new species of Mexican Hesperiidae (Lepidoptera). J. New York Ent. Soc. 78(2):88-99. {19 Oct 1970} [*Urbanus viridis* n. sp. (TL: Fortin de los Flores, Veracruz, Mexico. Holotype male, 15 August 1967, H. A. Freeman collector, in AMNH), *Zobera* n. gen. (TS: *Zobera albopunctata*), *Z. albopunctata* n. sp. (TL: Salada, Colima, Mexico. Holotype male, 13 June 1967, R. Wind collector, in AMNH), *Piruna maculata* n. sp. (TL: Durango - Villa Unión Hwy, Rte. 40, 6500', Sinaloa, Mexico. Holotype male, 29 April 1966, P. Hubbell collector, in AMNH), *Piruna sina* n. sp. (TL: Durango - Villa Unión Hwy, Rte. 40, 6500', Sinaloa, Mexico. Holotype male, 29 April 1966, P. Hubbell collector, in AMNH), *Piruna ajijiciensis* n. sp. (TL: Ajijic, Jalisco, Mexico. Holotype male, 20 July 1966, R. Wind collector, in AMNH), *Piruna milpa* n. sp. (TL: Milpillas, Guerrero, Mexico. Holotype male, 6 July 1956, K. Wilson collector, in AMNH), *Amblyscirtes immaculatus* n. sp. (TL: Salada, Colima, Mexico. Holotype male, 4 June 1967, R. Wind collector, in AMNH), *Aedes* [sic] *brilla* n. sp. (TL: Catemaco, Veracruz, Mexico. Holotype male, January 1953, T. Escalante collector, in AMNH); photographs of types; illustrations of male genitalia]

81. 1970. A new species of *Piruna* from Texas (Hesperiidae). J. Lepid. Soc. 24(4):247-249. {16 Nov 1970} [*Piruna haferniki* n. sp. (TL: Green Gulch, Big Bend National Park, Brewster Co., Texas. Holotype male, 4 August 1968, J. E. Hafernik collector, in AMNH); photographs of holotype; illustration of genitalia]

82. 1971. Zone 4 [Saskatchewan, North Dakota, South Dakota, Nebraska, Kansas, Oklahoma, Texas]. P. 3 in: Annual field season summary for 1970. News Lepid. Soc. 1971(3):1-9. {15 Apr 1971}

[Distributional data]

83. 1972. Zone 4: Saskatchewan, Manitoba, The Dakotas, Nebraska, Kansas, Oklahoma and Texas. Pp. 6-7 in: 1971 Field season summary. News Lepid. Soc. 1972 (2):1-16. {15 Mar 1972} [Distributional data]

84. 1973. A review of the *Amblyscirtes* with the description of a new species from Mexico (Hesperiidae). J. Lepid. Soc. 27(1):40-57. {23 Feb 1973} [Key to adults; distributional data; synonymies; *Amblyscirtes* (= *Stomyles*, = *Mastor*, = *Epiphyes*), *A. folia* (= *tutolia*), *A. raphaeli* n. sp. (TL: Salada, Colima, Mexico. Holotype male, 7 August 1969, E. C. Welling collector, in AMNH), photographs of type, male gelitalia illustrated, *A. immaculatus, A. nisulae-pinorum, A. exoteria* (= *nanno*, = *marcus*), *A. simius, A. cassus, A aenus, A. erna, A. linda, A. oslari, A. fluonia, A. elissa, A. samoset* (= *hegon*, = *nemoris*, = *argina*), *A. texanae, A. tolteca, A. prenda, A. aesculapius* (= *textor*, = *oneko*, = *wakulla*), *A. carolina, A. reversa, A. nereus, A. nysa* (= *similis*), *A. eos* (= *comus*, = *nilus*, = *quinquemacula*), *A. vialis* (= *asella*), *A. celia, A. belli, A. alternata* (= *meridionalis*), *A. florus* (= *mate*), *A. anubis, A. phylace, A. fimbriata* (= *bellus*)]

85. 1973. Zone 4: Saskatchewan, Nebraska, Kansas, Oklahoma, and Texas. Pp. 9-10 in: The 1972 field season summary. News Lepid. Soc. 1973 (2):1-19. {15 Mar 1973} [Distributional data]

86. 1974. Zone 4: Great Plains: Saskatchewan, Manitoba, North Dakota, South Dakota, Nebraska, Kansas, Oklahoma, and Texas. Pp. 6-8 in: The 1973 field season summary. News Lepid. Soc. 1974 (2):1-18. {25 Jun 1974} [Distributional data]

87. 1975. Zone 4: Great Plains: Saskatchewan, Manitoba, Oklahoma, and Texas. Pp. 7-8 in: The 1974 field season summary. News Lepid. Soc. 1975 (2/3):1-17. {1 Jun 1975} [Distributional data]

88. 1975. A new species of *Euphyes* Scudder from Texas (Hesperiidae). J. Lepid. Soc. 29(4):227-229. {24 Nov 1975} [*Euphyes macguirei* n. sp. (TL: Benbrook Res., Tarrant Co., Texas. Holotype male, emg. 6 October 1973, W. W. McGuire collector, in AMNH); photographs of types; illustration of male genitalia]

89. 1976. New Hesperiidae records for Mexico. J. Lepid. Soc. 30(1):62-67. {22 Apr 1976} [Distributional data; *Tarsoctenus praecia* (from "Mexico"), *Drephalys dumeril* (from Candelaria Loxicha, Oaxaca), *D. oria* (from Rancho San Carlos, Oaxaca), *Aguna aurunce* (from Tenosique, Tabasco), *Zestusa staudingeri* (from 20 km south of San Cristóbal, Chiapas), *Ridens philia* (from Santa Rosa, Comitán, Chiapas and Candelaria Loxicha, Oaxaca), *Astraptes fulgor* (from Campeche, Campeche), *A. tucuti* (from Rancho Dos Amatos [sic], Veracruz), *A. samson* (from Presidio, Veracruz and Muste, Chiapas), *Calliades zeutus* (from X-Cán, Quintana Roo), *Thorybes albosuffusa* (from Cedritos, Coahuila and "Colima"), *Bungalotis erythus* (from X-Cán, Quintana Roo), *Dyscophellus ramon* (from Presidio, Veracruz), *Nascus broteas* (from Tenosique, Tabasco), *Gindanes brontinus* (from Pisté, Yucatán), *Pythonides assecla* (from Tenosique, Tabasco and X-Cán, Quintana Roo), *Ebrietas livius* (from Tenosique, Tabasco), *Pyrgus oileus orcus* (from Tapachula, Chiapas), *Synapte puma* (from Candelaria Loxicha, Oaxaca), *Thargella caura* (from Tenosique, Tabasco and Orizaba, Veracruz), *Lerema lumina* (from San Carlos, Chiapas), *Onophas columbaria* (from Kabah Ruins, Yucatán), *Turesis theste* (from Tenosique, Tabasco), *Vertica grandipuncta* (from Tenosique, Tabasco), *Talides alternata* (from Candelaria Loxicha, Oaxaca), *Telles arcalaus* (from "Ochls north Mexico"), *Carystoides orbius* (from Tenosique, Tabasco), *Mellana balsa freemani* (from Candelaria Loxicha, Oaxaca), *M. tecla* (from Candelaria Loxicha, Oaxaca), *Panoquina panoquinoides* (from Progresso, Yucatán), *Xeniades pteras* (from Muste, Chiapas), *Saliana hewitsoni* (from Catemaco, Veracruz)]

90. 1976. Zone 4: Great Plains: Manitoba, North Dakota, South Dakota, Nebraska, Kansas, Oklahoma, and Texas. Pp. [7] - [8] in: The 1975 field season summary. News Lepid. Soc. 1976 (2):[1]-[18]. {15 May 1976} [Distributional data]

91. 1977. *Staphylus azteca*, new record for the United States (Hesperiidae). J. Lepid. Soc. 31(1):62. {30 Mar 1977} [Distributional data in Mexico and Central America; one female, Alpine, Brewster Co., Texas, 2 June 1940, H. A. Freeman collector; specimen later determined to be *Staphylus ceos* (W. H. Edwards, 1882), see Opler & Warren (2002)]

92. 1977. Zone 4: Great Plains: Saskatchewan, Manitoba, South Dakota, Nebraska, Oklahoma, and Texas. Pp. 9-10 in: Field summary 1976. News Lepid. Soc. 1977 (2):3-15, 18-21. {Mar/Apr 1977} [Distributional data]

93. 1977. Six new species of Hesperiidae from Mexico. J. Lepid. Soc. 31(2):89-99. {30 Jun 1977} [*Pyrrhopyge hoffmanni* n. sp. (TL: Tenosique, Tabasco, Mexico. Holotype male, 3 September 1962, E. C. Welling collector, in AMNH), *Epargyreus deleoni* n. sp. (TL: X-Cán, Quintana Roo, Mexico. Holotype male, 13 June 1969, E. C. Welling collector, in AMNH), *Typhedanus salas* n. sp. (TL: Pisté, Yucatán, Mexico. Holotype male, 26 August 1968, E. C. Welling collector, in AMNH), *Polythrix guatemalaensis* n. sp. (TL: Sayaaxche, El Petan [sic], Guatemala. Holotype male, 23 August 1963, E. C. Welling collector, in AMNH), *Codatractus yucatanus* n. sp. (TL: Pisté, Yucatán, Mexico. Holotype male, 1 September 1967, E. C. Welling collector, in AMNH), *Bungalotis milleri* n. sp. (TL: Candelaria Loxicha, Oaxaca, Mexico. Holotype male, 22 September 1968, E. C. Welling collector, in AMNH); photographs of types, illustrations of male genitalia]

94. 1978. Zone 4: Great Plains: Saskatchewan, Manitoba to Texas. Pp. 8-9 in: Field summary for 1977. News Lepid. Soc. 1978 (2):3-16. {Mar/Apr 1978} [Distributional data]

95. 1979. Zone 4: Manitoba, North Dakota, South Dakota, Nebraska, Oklahoma, Texas. P. 8 in: Field summary for 1978. News Lepid. Soc. 1979 (2):3-18. {Mar/Apr 1979} [Distributional data]

96. 1979. Nine new species and seven new records of Mexican Hesperiidae. Bull. Allyn Mus. No. 52:1-13. {20 Jul 1979} [Distributional data; *Ridens allyni* n. sp. (TL: Candelaria Loxicha. Oaxaca, Mexico. Holotype male, 30 September 1968, E. C. Welling collector, in FSMC), *Myrinia raymundo* n. sp. (TL: Tenosique, Tabasco, Mexico. Holotype male, 4 September 1962, E. C. Welling collector, in FSMC), *Pythonides mundo* n. sp. (TL: Candelaria Loxicha, Oaxaca, Mexico. Holotype male, 14 March 1969, E. C. Welling collector, in FSMC), *Zobera marginata* n. sp. (TL: Candelaria Loxicha, Oaxaca, Mexico. Holotype male, 12 August 1971, E. C. Welling collector, in FSMC), *Piruna mexicana* n. sp. (TL: 9 miles east of Querétaro, Querétaro, Mexico. Holotype male, 25 August 1967, J. A. Scott collector, in FSMC), *P. sombra* (from Ochuc, and Tuxtla Gutierrez, Chiapas), *Dalla lathaea* (from Ochus [sic], Chiapas). *Turesis tabascoensis* n. sp. (TL: Tenosique, Tabasco, Mexico. Holotype male, 28 August 1962, E. C. Welling collector, in FSMC), *Vertica ibis* (from Tenosique, Tabasco), *Decinea mustea* n. sp. (TL: Muste, Chiapas, Mexico. Holotype male, 19 July 1968, E. C. Welling collector, in FSMC), *Poanes benito* n. sp. (TL: La Calera, 10 miles south of Cumbre de Autian [sic], Jalisco, Mexico. Holotype male, July-August 1967, P. Hubbell collector, in FSMC), *Mellana oaxaca* n. sp. (TL: Candelaria Loxicha, Oaxaca, Mexico. Holotype male, 14 September 1971, E. C. Welling collector, in FSMC), *Euphyes ampa* (from Candelaria Loxicha, Oaxaca), *Amblyscirtes simius* (from 18 miles southeast of Saltillo, Coahuila), *Saliana severus* (from Chimalapa, Oaxaca), *Neoxeniades posta* (from Tehuantepec, Oaxaca); photographs of types; illustrations of male genitalia]

97. 1979. Review of the Mexican *Polythrix* Watson 1893 (Hesperiidae). J. Lepid. Soc. 33(2):124-128. {20 Jul 1979} [key to adults; distributional data; *Polythrix octomaculata* (= *decurata*, = *calenus*, = *elegans*, = *alciphron* n. syn.), *P. asine, P. mexicanus, P. procerus* (= *aelius*, = *auginulus*), *P. guatemalaensis, P. caunus* (= *lindora*); illustrations of male genitalia]

98. 1980. Zone 4: Saskatchewan, Manitoba, N. & S. Dakota, Nebraska, Kansas, Oklahoma, Texas. Pp. 18-19 in: Season summary, 1979. News Lepid. Soc. 1980 (2):13-27. {Mar/Apr 1980} [Distributional data]

99. 1981. Zone 4: Saskatchewan, Manitoba, N. & S. Dakota, Nebraska, Kansas, Oklahoma, Texas. P. 20 in: Season summary, 1980. News Lepid. Soc. 1981 (2):13-28. {Mar/Apr 1981} [Distributional data]

100. 1982. Zone 4: Manitoba, S. Dakota, Nebraska, Kansas & Texas. Pp. 21-22 in: Season summary, 1981. News Lepid. Soc. 1982 (2):13-31. {Mar/Apr 1982} [Distributional data]

101. 1982. Notes on some species of *Astraptes* Hübner, 1819 (Hesperiidae). J. Lepid. Soc. 36(3):236-237. {14 Dec 1982} [*Astraptes fulgerator* (= *mercatus*, = *fulminator*, = *misitra*, = *albifasciatus*, = *catemacoensis* n. syn.), *A. crana* (= *escalantei* n. syn.)]

102. 1983. Zone 4: Manitoba, North Dakota, South Dakota, Nebraska, Kansas, and Texas. Pp. 22-24 in: Season summary, 1982. News Lepid. Soc. 1983 (2):13-35. {Mar/Apr 1983} [Distributional data]

103. 1984. Zone 4. Great Plains: Saskatchewan, Manitoba, North Dakota, Nebraska, Kansas, Oklahoma and Texas. Pp. 23-26 in: Season summary, 1983. News Lepid. Soc. 1984 (2):13-36. {Mar/Apr 1984} [Distributional data]

104. 1989. On the location of some H. A. Freeman skipper holotypes (Hesperiidae). J. Lepid. Soc. 43(3):244. {7 Sep 1989} [All in AMNH: *Pyrrhopyge tzotzili, Mysoria wilsoni, Epargyreus windi, E. brodkorbi, Astraptes louiseae, A. gilberti, Polythrix mexicanus, Aethilla chiapa, Mimia chiapaensis, Windia windi, Staphylus veytius, S. zuritus, Quadrus francesius, Enosis matheri, Dalla ramirezi, Vettius argentus, Niconiades comitana, Anthoptus macalpinei, Cynea nigricola, Pheraeus covadonga, Carystoides escalantei, C. abrahami, C. floresi, C. mexicana, Atrytone mazai, A. potosiensis, Mellana montezuma, Euphyes chamuli, Tirynitha huasteca*]

105. 1989. Four new skipper records for Mexico (Hesperiidae). News Lepid. Soc. 1989(6):79. {Nov/Dec 1989} [*Hyalothyrus neleus pemphigargyra* (from Agua Azul, Chiapas), *Bolla saletas* (from 5 miles north of Oaxaca, Oaxaca), *Mycteris caerula* (Palenque - Ocosingo Hwy., km. 95, Chiapas), *Paratrytone niveolimbus* (from Road to Tenejapa, San Cristóbal, Chiapas]

106. 1990. A new species of *Piruna* from Mexico (Hesperiidae). J. Lepid. Soc. 44(1):28-31. {5 Jun 1990} [*Piruna kemneri* n. sp. (TL: 5 miles north of Oaxaca, Hwy. 175, ca. 1800m., Oaxaca, Mexico. Holotype male, 21 July 1987, John Kemner collector, in AMNH); photographs of type; illustration of male genitalia]

107. 1991. A new species of *Piruna* from Oaxaca, Mexico (Hesperiidae). J. Lepid. Soc. 45(1):42-45. {14 Aug 1991} [*Piruna mullinsi* n. sp. (TL: 8 km north of Oaxaca, Hwy. 175, ca. 1800m., Oaxaca, Mexico. Holotype male, 17 August 1988, John Kemner collector, in AMNH); photographs of type; illustration of male genitalia]

108. 1991. A new species of *Dalla* from Mexico (Lepidoptera: Hesperiidae). Trop. Lepid. 2(1):65-67. {[28] Aug 1991} [Distributional data; *Dalla bubobon, D. ligilla, D. dividuum, D. mentor, D. lalage, D. lethaea, D. faula, D. ramirezi, D. curiosa, D. steinhauseri* n. sp. (TL: Km 95, La Esperanza, Cerro Pelón, ca. 2100m., Sierra Juárez, Oaxaca, Mexico. Holotype male, 28 May 1990, John Kemner collector, in FSMC); *Niconiades vista* (first Mexican record from road to Telea [sic] de Castro, 2250m., Oaxaca)]

109. 1992. A new species of *Amblyscirtes* from Mexico (Hesperiidae). J. Lepid. Soc. 45(4):291-295. {1991 [19 May 1992]} [*Amblyscirtes brocki* n. sp. (TL: Trinidad - Yecora Road, 16 km NW Yecora, Sonora, Mexico. Holotype male, 21 July 1985, Jim P. Brock collector, in AMNH); photographs of type, illustration of male genitalia]

110. 1993. Notes on *Amblyscirtes* Scudder, with the description of two new subspecies (Insecta: Lepidoptera: Hesperiidae: Hesperiinae). Ann. Carnegie Mus. 62(4):341-350. {29 Nov 1993} [Distributional data; *Amblyscirtes tolteca tolteca*, *A. t. prenda* rev. stat., *A. elissa elissa*, *A. e. arizonae* n. ssp. (TL: 0.5 mi W Kino Springs, Santa Cruz Co., Arizona. Holotype male, 20 July 1986, Jim P. Brock collector, in CMNH), *A. fimbriata fimbriata* (= *bellus*), *A. f. pallida* n. ssp. (TL: 64 km W Toluca 9300', Mexico, Mexico. Holotype male, 10 June 1989, John Kemner collector, in CMNH); photographs of types; checklist of *Amblyscirtes* species and synonyms]

111. 1995. Underwing moths (Noctuidae: *Catocala*) in my Texas residential lot. News Lepid. Soc. 1995(4):94. {Oct 1995} [Survey period from 20 May 1982 to 6 October 1989; list of 30 *Catocala* species taken at Garland, Dallas Co.: *agrippina, alabamae, amatrix, amica, carissima, consors, dejecta, delilah, epione, ilia, innubens, insolabilis, jair, junctura, lacrymosa, lineela, maesitosa, micronympha, minuta, mira, muliercula, neogama, piatrx, sappho, texarkana, texanae, titania, ulalume, ultronia, vidula*; *Catocala* collection to the AMNH]

112. (un-dated, un-published manuscript). The distribution of Hesperiidae in Mexico. 142pp. [Compiled before or during 1981 and distributed to various colleagues for comments; lists 696 species from Mexico, giving type localities and Mexican distribution for each. This list was frequently consulted during the preparation of Llorente et al. (1990) and Warren (2000), and was cited by Warren (2000)]

NEW GENERA, SPECIES, SUBSPECIES AND FORMS

Names are arranged alphabetically, and keyed to numbered entries in the bibliography above. The current subfamilial or tribal placement for each taxon is listed (following Opler & Warren 2002). In all cases where the status of a taxon has changed from that originally proposed by Freeman, references have been provided for further information.

New genera.
Agathymus Megathymini 43
Stallingsia Megathymini 43
Turnerina Megathymini 43
Windia Pyrginae 77
Zobera Pyrginae 80

New Species.
abrahami, Carystoides Hesperiinae 77
ajijiciensis, Piruna Heteropterinae 80
albopunctata, Zobera Pyrginae 80
allyni, Ridens Pyrginae 96
argentus, Vettius Hesperiinae 77
belli, Amblyscirtes Hesperiinae 5
belli, Megathymus Megathymini 41 Placed in *Agathymus* Freeman, see 43.
benito, Poanes Hesperiinae 96 See Burns (1992a) for taxonomic notes.
brilla, Aides Hesperiinae 80
brocki, Amblyscirtes Hesperiinae 109
brodkorbi, Epargyreus Pyrginae 77
buchholzi, Strymon Eumaeini 26 Synonym of *S. bebrycia* (Hewit.), see Robbins & Nicolay (2001).
catemacoensis, Astraptes Pyrginae 66 Synonym of *A. fulgerator azul* (Reak.), see 101.
chamuli, Euphyes Hesperiinae 77
chiapa, Aethilla Pyrginae 77
chiapaensis, Mimia Pyrginae 77
chinatiensis, Agathymus Megathymini 57 Subspecies of *A. mariae* (Barnes & Benjamin), see Roever (1975).
chisosensis, Apodemia Riodinidae 56
chisosensis, Megathymus Megathymini 39 Possible subspecies of *Agathymus neumogeni*, see Roever (1975), 43.
comitana, Niconiades Hesperiinae 77
covadonga, Pheraeus Hesperiinae 77
deleoni, Epargyreus Pyrginae 93
diabloensis, Agathymus Megathymini 49 Subspecies of *A. neumogeni* (W. H. Edw.), see Roever (1975).
donahuei, Euphyes Hesperiinae 66 Synonym of *E. peneia* (Godm.), see Mielke (1972).
erna, Amblyscirtes Hesperiinae 8 Subspecies of *A. aenus* (W. H. Edw.), see Scott (1977).
escalantei, Astraptes Pyrginae 66 Synonym of *A. creteus crana* Evans, see 101.
escalantei, Carystoides Hesperiinae 77
evansi, Calpodes Hesperiinae 21 Placed in *Panoquina* Hemming, see Evans (1955).
evansi, Megathymus Megathymini 30 Placed in *Agathymus*

Freeman, see 43.

fieldi, Agathymus Megathymini 46

floresi, Carystoides Hesperiinae 77

francesius, Quadrus Pyrginae 77

gilberti, Agathymus Megathymini 57 Possible subspecies of *A. mariae* (Barnes & Benjamin), Roever (1975).

gilberti, Astraptes Pyrginae 77 Synonym of *A. alector hopfferi* (Plötz), see Warren (2000).

guatemalaensis, Polythrix Pyrginae 93 Placed in *Cephise* Evans, see Burns (1996).

haferniki, Piruna Heteropterinae 81

harrisi, Megathymus Megathymini 41 Synonym of *M. cofaqui* (Strecker), see Gatrelle (1999).

hoffmanni, Megathymus Megathymini 39 Placed in *Agathymus* Freeman, see 43.

hoffmanni, Pyrrhopyge Pyrrhopyginae 93 Placed in *Melanopyge* Mielke, see Mielke (2002).

huasteca, Tirynthia Hesperiinae 77 Subspecies of *Decinea decinea* (Hewit.), see Mielke (2004).

hubbellus, Urbanus Pyrginae 74 Synonym of *U. prodicus* Bell, see Steinhauser (1981).

immaculatus, Amblyscirtes Hesperiinae 80 Synonym of *A. patriciae* (Bell), see Warren (1996).

julia, Lerodea Hesperiinae 19 Placed in *Nastra* Evans by Evans (1955).

kemneri, Piruna Heteropterinae 106

lajitaensis, Agathymus Megathymini 57 Subspecies of *A. mariae* (Barnes & Benjamin), see Roever (1975).

linda, Amblyscirtes Hesperiinae 8

louiseae, Astraptes Pyrginae 77 Synonym of *Narcosius parisi helen* (Evans), see Steinhauser (1986).

macalpinei, Anthoptus Hesperiinae 77

macguirei, Euphyes Hesperiinae 88 Synonym of *E. dion* (W. H. Edw.), see Shuey (1989).

maculata, Piruna Heteropterinae 80

maculosus, Megathymus Megathymini 41 Placed in *Stallingsia* Freeman, see 43.

marginata, Zobera Pyrginae 96

matheri, Enosis Hesperiinae 77

mazai, Atrytone Hesperiinae 77 Placed in *Anatrytone* Dyar, see Burns (1994).

mcalpinei, Megathymus Megathymini 41 Subspecies of *A. neumogeni* (W. H. Edw.), see Roever (1975), 43.

mexicana, Carystoides Hesperiinae 77

mexicana, Piruna Heteropterinae 96 Subspecies of *P. aea* (Dyar), see Warren (2000).

mexicanus, Polythrix Pyrginae 77

milleri, Bungalotis Pyrginae 93

milpa, Piruna Heteropterinae 80 Synonym of *P. penaea* (Dyar), see Warren (2000).

montezuma, Mellana Hesperiinae 77 Synonym of *Quasimellana fieldi* (Bell), see Burns (1994).

mullinsi, Piruna Heteropterinae 107

mundo, Pythonides Pyrginae 96

mustea, Decinea Hesperiinae 96

nigricola, Cynea Hesperiinae 77

oaxaca, Camptopleura Pyrginae 74

oaxaca, Mellana Hesperiinae 96 Synonym of *Quasimellana eulogius* (Plötz), see Burns (1994).

potosiensis, Atrytone Hesperiinae 77 Placed in *Anatrytone* Dyar, see Burns (1994).

ramirezi, Dalla Heteropterinae 77

raphaeli, Amblyscirtes Hesperiinae 84

raymundo, Myrinia Pyrginae 96

rindgei, Agathymus Megathymini 57 Possible subspecies of *A. mariae* (Barnes & Benjamin), see Roever (1975)

rindgei, Decinea Hesperiinae 74

salas, Typhedanus Pyrginae 93

sina, Piruna Heteropterinae 80

stallingsi, Celaenorrhinus Pyrginae 21

steinhauseri, Dalla Heteropterinae 108

tabascoensis, Turesis Hesperiinae 96

tildeni, Hesperia Hesperiinae 42 Subspecies of *H. colorado* (Scudder), see Opler & Warren (2002).

turneri, Atrytonopsis Hesperiinae 23 Subspecies of *A. hianna* (Scudder), see dos Passos (1960).

tzotzili, Pyrrhopyge Pyrrhopyginae 77 Placed in *Jonaspyge* Mielke, see Mielke (2002).

valverdiensis, Agathymus Megathymini 62 Subspecies of *A. estelleae* (Stallings & Turner), see Roever (1975).

veytius, Staphylus Pyrginae 77 Synonym of *S. tierra* Evans, see Warren (2000).

viridis, Urbanus Pyrginae 80

wellingi, Thoon Hesperiinae 74 Synonym of *Arita arita* (Schaus), see Mielke (2004).

wilsoni, Mysoria Pyrrhopyginae 77 Synonym of *M. affinis* (Herr.-Sch.), see Warren & Mielke (2004).

windi, Epargyreus Pyrginae 77

windi, Windia Pyrginae 77

yucatanus, Codatractus Pyrginae 93

zuritus, Staphylus Pyrginae 77 Synonym of *S. iguala* (R. C. Williams & Bell), see Warren (2000).

zweifeli, Atrytonopsis Hesperiinae 74

New Subspecies and Forms.

alabamae, Megathymus yuccae Megathymini 9 Synonym of *M. y. yuccae* (Boisd. & Leconte), see 37.

albosuffusa, Thorybes pylades Pyrginae 9

arizonae, Amblyscirtes elissa Hesperiinae 110

belfragei, Hesperia metea Hesperiinae 11 Synonym of *H. m. licinus* (W. H. Edw.), see Miller & Brown (1981).

buchholzi, Megathymus yuccae Megathymini 37

dee, Megathymus yuccae stallingsi Megathymini 10

fredericki, Erynnis persius Pyrginae 9

kendalli, Megathymus yuccae Megathymini 60

louiseae, Megathymus yuccae Megathymini 52

pallida, Amblyscirtes fimbriata Hesperiinae 110

reinthali, Megathymus yuccae Megathymini 52

sequoyah, Polites verna Hesperiinae 7 Placed in *Pomepius* Evans, see Evans (1955).

stallingsi, Hesperia leonardus Hesperiinae 12 Synonym of *H. l. leonardus* Harris, see Miller & Brown (1981)

stallingsi, Megathymus yuccae Megathymini 10

turneri, Polites themistocles Hesperiinae 13

winkensis, Megathymus yuccae Megathymini 60

ACKNOWLEDGEMENTS

Many people contributed to this report. Hugh Avery Freeman provided reprints of most of his papers, specimens of many taxa, valuable information on Hesperiidae, and was a close friend of and mentor to the author for 10 years. Thanks to Dale Clark, Louise Freeman and John Kemner for providing literature and information after February, 2002. Ray Stanford, Jonathan Pelham, Larry Gall, June and Floyd Preston, Ernst Brockmann and Bob Robbins provided important citations or literature. Thanks to Susan Weller, Louise Freeman, Larry Gall, Olaf Mielke, John Kemner, Nick Grishin, Jonathan Pelham and Ray Stanford for comments on early versions of this paper.

LITERATURE CITED

AUSTIN, G. T. 1997. Notes on Hesperiidae in northern Guatemala, with descriptions of new taxa. J. Lepid. Soc. 51(4):316-332.

BURNS, J. M. 1992a. Genitalic recasting of *Poanes* and *Paratrytone* (Hesperiidae). J. Lepid. Soc. 46(1):1-23.

——. 1992b. Genitalic characterization, enlargement, and reassociation of the Neotropical Hesperiine genus *Halotus* (Hesperiidae). J. Lepid. Soc. 46(3):182-194.

——. 1994. Genitalia at the generic level: *Atrytone* restricted, *Anatrytone* resurrected, new genus *Quasimellana*- and yes! we have no *Mellanas* (Hesperiidae). J. Lepid. Soc. 48(4):273-337.

——. 1996. Genitalia and the proper genus: *Codatractus* gets *mysie* and *uvydixa*- in a compact *cyda* group- as well as a hysterectomy, while *Cephise* gets part of *Polythrix* (Hesperiidae: Pyrginae). J. Lepid. Soc. 50(3):173-216.

Dos Passos, C. F. 1960. Taxonomic notes on some Nearctic Rhopalocera. 1. Hesperioidea. J. Lepid. Soc. 14(1):24-36.

Evans, W. H. 1955. A Catalogue of the Hesperiidae indicating the classification and nomenclature adopted in the British Museum (Natural History). Part IV. Hesperiinae and Megathyminae. London, British Museum. 499 pp. + pls. 54-88.

Gatrelle, R. R. 1999. Subspecific status of southeastern U.S. *Megathymus cofaqui* and *M. yuccae*: renaming of the Florida subspecies of *M. cofaqui*. Taxonomic Rep. 1(4):1-6.

Huber, R. 1999. We remember *Viola*. News. Idalia Soc. 10(6)3-4.

Kendall, R. O. (compiler). 1977. The Lepidopterists' Society Comemerative Volume. Mem. Lepid. Soc. 1:xvii + 374pp.

Llorente, J. B., A. M. Luis & I. F. Vargas. 1990. Catalogo sistematico de los Hesperioidea de Mexico. Publ. Esp. Mus. Zool. 1:[iv], 1-70.

Mielke, O. H. H. 1972. As espécies Sul-Americanas do gênero *Euphyes* Scudder, 1872 (Lepidoptera: Hesperiidae). Bol. Univ. Paraná, Zool. 5:175-222.

——. 2002. Pyrrhopyginae: gêneros novos e revalidados (Lepidoptera, Hesperiidae). Revta. Bras. Zool. 19(1):217-228.

——. 2004. Hesperiidae, in: Lamas, G. (Ed.). Checklist: Part 4A. Hesperioidea - Papilionoidea, in: Heppner, J. B., (Ed.). Atlas of Neotropical Lepidoptera. Scientific Publishers, Gainesville. xxxvi + 439 pp.

Miller, L.D. 1974. Revision of the Euptychiini (Satyridae). 2. *Cyllopsis* R. Felder. Bull. Allyn Mus. 20:1-98.

Miller, L. D. & F. M. Brown. 1981. A Catalogue/Checklist of the Butterflies of America North of Mexico. Mem. Lepid. Soc. 2:vii, 1-280.

Okano, K. 1981. Studies on the Mexican butterflies (1). Additions and revisions to the Hoffmann's "Catalogo Sistematico y Zoogeografico de los Lepidopteros Mexicanos". Part I: Hesperiidae (Lepidoptera: Rhopalocera). Tokurana (Acta Rhopalocera) 1:23-139.

——. 1982. Studies on the Mexican butterflies (2). Notes on the Mexican skippers (Hesperiidae). Tokurana (Acta Rhopalocera) 4:23-56.

Opler, P. A. & A. D. Warren. 2002. Butterflies of North America. 2. Scientific Names List for North American Butterfly Species of North America, north of Mexico. Contrib. Gillette Mus. Colo. St. Univ. 79pp. http://www.biology.ualberta.ca/old_site/uasm//Opler&Warren.pdf

Remington, P. S. 1961. An expedition to Mexico for Megathymidae. J. Lepid. Soc. 15(1):65-72.

Rindge, F. H. 1970. Freeman collection of Megathymidae donated to the American Museum of Natural History. J. Lepid. Soc. 24(3):208.

Robbins, R. K. & S. S. Nicolay. 2001. An overview of *Strymon* Hübner (Lycaenidae: Theclinae: Eumaeini). J. Lepid. Soc. 55(3):85-100.

Roever, K. 1975. Megathymidae. Pp. 411-422, in: Howe, W. H. The Butterflies of North America. Doubleday & Co., Inc., Garden City, New York. 633pp.

Scott, J. A. 1977. *Amblyscirtes "erna,"* a form of *Amblyscirtes aenus*. J. Res. Lepid. 15(2):92.

Shuey, J. A. 1989. The morpho-species concept of *Euphyes dion* with the description of a new species (Hesperiidae). J. Res. Lepid. 27(3-4):160-172.

Stallings, D. B. & J. R. Turner. 1946. Texas Lepidoptera (Rhopalocera: Papilionoidea). Ent. News 57(2):44-49.

——. 1947. New American butterflies. Canadian Ent. 78(7-8):134-137.

Stanford, R. E. 2001. The season summary: 55 years, going strong. News Lepid. Soc. 43(3):75

——. 2002. The season summary: 55 years, going strong (continued). News Lepid. Soc. 44(1):6,22.

Steinhauser, S. R. 1981. A revision of the *proteus* group of the genus *Urbanus* Hubner. Lepidoptera: Hesperiidae. Bull. Allyn Mus. No. 62:1-41.

——. 1986. A review of the skippers of the *narcosius* group of species of the genus *Astraptes* Hubner (sensu Evans, 1952) and erection of a new genus. Lepidoptera: Hesperiidae. Bull. Allyn Mus. No. 104:1-43.

——. 1991. Six new species of skippers from Mexico (Lepidoptera: Hesperiidae: Pyrginae and Heteropterinae). Insecta Mundi 5(1):25-44.

——. 1996. Three new species of skippers from Mexico (Hesperiidae: Lepidoptera). Bull. Allyn Mus. 141:1-11.

——. & A. D. Warren. 2002. A new species of *Euphyes* Scudder from western Mexico (Hesperiidae: Hesperiinae). J. Lepid. Soc. 55(4):164-168.

Warren, A. D. 1996. Notes on *Amblyscirtes patriciae*: Description of the female and notes on its synonymy, behavior, habitat and distribution in Mexico (Lepidoptera: Hesperiidae: Hesperiinae). Trop. Lepid. 7(2): 127-132.

——. 2000. Hesperioidea (Lepidoptera), pp. 535-580. In: Llorente, J. E., E. González & N. Papavero (eds.). Biodiversidad, Taxonomía y Biogeografía de Artrópodos de México: Hacia una Síntesis de su Conocimiento. Volumen II. Universidad Nacional Autónoma de México, Mexico City. xvi + 676pp.

——. 2001. A replacement name for *Freemania* A. Warren, with notes on the higher classification of the genus (Lepidoptera: Hesperiidae). Proc. Ent. Soc. Wash. 103(4):1028-1029.

——. & O. H. H. Mielke. 2004. *Mysoria affinis* (Herrich-Schäffer): morphological variation and synonymy (Lepidoptera, Hesperiidae, Pyrrhopyginae). Revta. Bras. Zool. 21(2):309-314.

Received for publication 4 July 2004; revised and accepted 8 October 2004

Journal of the Lepidopterists' Society
59(1), 2005, 59

MANUSCRIPT REVIEWERS FOR 2004 (VOLUME 58)

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 all of us. Let us hope that their careful work continues to allow the *Journal* to grow in quality and readership. On behalf of all authors and editorial staff of this Journal, respectful acknowledgements are given to the reviewers for contribtuions published in volume 58.

Adamski, David; Washington, DC
Aiello, Annette; Panama City, Panama
Austin, George; Gainesville, FL
Berenbaum, May; Urbana, IL
Brower, Andrew; Corvallis, OR
Brown, John; Washington, DC
Brown, Keith; Sao Paulo, Brazil
Davis, Don; Washington, DC
Donahue, Julian; Los Angeles, CA
Freitas, André; Campinas, Brazil
Fuller, Edward; Edmonton, Alberta, Canada
Funk, Chris
Gall, Larry; New Haven, CT
Heath, Alan; Hertfordshire, England
Heffernan, Emily; Gainesville, FL
Hodges, Ron; Eugene, OR
Holloway, Jeremy; London, England
Jeffords, Mike; Urbana, IL
Lafontaine, J. D.; Ottawa, Ontario, Canada
Lamas, Gerardo; Lima, Peru
Landry, Bernard; Geneva, Switzerland
Miller, Jackie; Gainesville, FL
Miller, Lee; Gainesville, FL
Otero, L. Daniel; Venezuela
Peigler, Richard; San Antonio, TX
Penz, Carla; New Orleans, LA
Poole, Robert; Rockville, MD
Powell, Jerry; Berkeley, CA
Raguso, Robert; Columbia, SC
Robbins, Robert; Washington, DC
Rubinoff, Daniel; Honolulu, HI
Schick, Kathy; Stockton, CA
Solis, Alma; Washington, DC
Spector, Sasha; Washington, DC
Summerville, Keith; Des Moines, IA
Viloria, Angel; Caracas, Venezuela
Wagner, David; Storrs, CT
Warren, Andy; Corvallis, OR
Weiss, Martha; Washington, DC
Weller, Susan; St. Paul, MN
Willmott, Keith; London, England
Wright, David; Lansdale, PA
Young, Allen; Milwaukee, WI

Journal of the Lepidopterists' Society
59(1), 2005, 60

THE 2005 MEETING OF THE LEPIDOPTERISTS' SOCIETY

The 56th annual meeting of The Lepidopterists' Society will be held during 2–7 August 2005, at the Windemere Hotel and Conference Center in Sierra Vista, Arizona (USA). It will be jointly sponsored by the Pacific Slope Section of the Lepidopterists' Society and the SouthEastern Arizona Butterfly Association (SEABA). There will be field trips to nearby mountain ranges.

Visit: http://alpha.furman.edu/~synder/snyder/lep/meet.htm

Date of Issue (Vol. 59, No. 1): 8 April 2005

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: miketol@eureka.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: pjd@mpm.edu). Short manuscripts concerning new state records, current events, and notices should be sent to the *News*, Phil Schappert, Dept. Zoology, University of Texas, Austin, TX 78712, USA (or electronically to: philjs@mail.utexas.edu). ***Before submitting manuscripts or electronic files,*** consult instructions in volume 55(1):46–49 or the Society's web site at http://www.lepsoc.org/.

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 a diskette 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 the following format and without underlining:

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: Illustrate only half of symmetrical objects such as adults with wings spread, unless whole illustration is crucial. Mount photographs and drawings on stiff, white backing, arranged in the desired format. 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). Illustrations larger than letter-size are not acceptable and should be reduced photographically to that size or smaller. On the back of each illustration, print the author's name and figure numbers as cited in the text. 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 small caps (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

General Notes

Obituary