BIOLOGY AND HYBRIDIZATION OF *APANTESIS PHALERATA* (HARRIS) AND *A. RADIANS* WALKER IN FLORIDA (LEPIDOPTERA : ARCTIIDAE)

by
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A Dissertation Presented to the Graduate Council of
The University of Florida
in Partial Fulfillment of the Requirements for the
Degree of Doctor of Philosophy

UNIVERSITY OF FLORIDA

1972

ACKNOWLEDGEMENTS

The author wishes to express sincere appreciation to Dr. D. H. Habeck, supervisory committee chairman, for his generous support, guidance, and patience throughout this study.

Gratitude is expressed to Dr. T. C. Emmel, Dr. R. M. Baranowski, Dr. F. W. Mead, and Dr. T. H. Patton, members of the supervisory committee, for their encouragement and for critical review of this work.

Specific acknowledgement is due Dr. Mead, Mr. D. P. Wojcik, and Mrs. Sandy Schuler for field-collected moths, and special thanks are extended to Mrs. Schuler for laboratory assistance.

The author wishes to thank Dr. Emmel for supervising research on 2 phases of the study and for access to his laboratory facilities.

To his wife, Jeanne, his deepest appreciation for her encouragement and the typing of this manuscript.

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June 1972

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Major Department: Entomology and Nematology

Biological and hybridization studies were conducted on *Apantesis phalerata* (Harris) and *A. radians* Walker, 2 closely related and often confused species of the *A. nais*-complex, from March 1969 through February 1972 in Gainesville, Florida.

Life histories of *A. phalerata*, *A. radians*, and a hybrid (*A. radians* male x *A. phalerata* female), reared on an artificial diet at 23±1°C, were nearly identical. The duration of the immature stages was longer for hybrid females than for males due to at least 1 extra instar. Both *A. phalerata* and *A. radians* males and females had 6, 7, or sometimes 8 larval instars.

The morphological difference between the genitalia of adults conformed to that found in other studies. Genitalia of hybrids were usually intermediate between those of the parents. No difference was found between the eggs, larvae, or pupae of the 2 species.

In laboratory studies involving 57 *A. phalerata* and 20 *A. radians* pairings, 58% and 70% successful matings occurred, respectively. Fifty-six hybrid pairings of *A. radians* males x *A. phalerata* females resulted

[illegible] successful matings, but 32 pairings of A. [illegible] males x A. radians females were unsuccessful.

Caged A. phalerata and A. radians virgin females attracted only males of their own species in nature. Nine of 17 caged hybrid females attracted A. radians males and 2 of these 9 also attracted A. phalerata males.

The haploid chromosome numbers of A. phalerata, A. radians, and A. radians male x A. phalerata female hybrids were 29, 30, and 29, respectively. These are the first counts of the genus Apantesis and include the first counts in the Lepidoptera between parents having a different chromosome number.

A rare, light wild strain of A. phalerata was found to be controlled by 2 unlinked sets of alleles. One gene controlled maculation and a second controlled hindwing color in females.

Male and female A. phalerata attracted to blacklight traps outnumbered those of A. radians by 7:1 and 3.5:1, respectively, from April 1968 through May 1970. Nine percent of wild A. phalerata females were unmated. Fifty-nine percent mated once, 22% twice, and the remainder 3 times. No A. radians were unmated. Seventy-five percent of A. radians females mated once, 18% twice, and the remaining 10% 3 times. The sex ratio of males to females was about 55:1 and 29:1 for A. phalerata and A. radians, respectively.

INTRODUCTION

Moths of the North American genus Apantesis Walker comprise a colorful and often rather variable group of approximately 30 species. Taxonomic confusion surrounds many moths of this genus, especially 4 sexually dimorphic and highly variable members, Apantesis nais (Drury), A. vittata (Fabricius), A. phalerata (Harris), and A. radians Walker, and total agreement on species designation in this complex is still lacking. Only the latter 2 species occur in northcentral Florida. Considerable confusion still exists as to the specific status of these 2 highly variable species.

Previous studies of A. phalerata and A. radians have been primarily morphological. The few biological studies that have been carried out were very limited in scope. There have been no detailed studies on the interrelationships between these species.

The present study was undertaken to gather detailed biological information about A. phalerata and A. radians and to determine if the 2 were reproductively isolated in northcentral Florida.

A. phalerata and A. radians are herein referred to as separate species in keeping with most current authors, despite this study's neutrality about their distinctness or synonomy.

LITERATURE REVIEW

Published material on the individual species of the Apantesis nais-complex is voluminous and confusing, as is the treatment of the complex as a whole.

The Apantesis nais-complex

Beutenmüller (1898) published short descriptions of Arctia (=Apantesis) nais, A. vittata, and A. phalerata; A. radians was not mentioned. Dyar (1900) also described the same 3 species as being distinct, but was uncertain about the specific status of A. nais. Hampson (1901) first dealt with all 4 moths of the complex; he accepted only 2 species, Arctia nais and A. vittata, synonymizing A. radians and A. phalerata with A. vittata. Holland (1903) regarded the complex as probably containing only 1 species, A. vittata, with which A. nais, A. radians, and A. phalerata were synonymized. Apantesis phalerata was elevated once again to specific status by Gibson (1903), who also recognized A. nais and A. vittata, but he did not mention A. radians.

In Florida, Grossbeck (1917) followed Hampson's classification, placing Apantesis phalerata and A. radians under A. vittata and keeping A. nais as distinct. Apantesis phalerata was again given specific status by Marchand (1917), who supported his position by unsuccessfully trying to cross A. phalerata with A. vittata in the laboratory. He also stated that A. nais was specifically distinct. Apantesis radians was not

mentioned. Strand (1919) employed the same classification used by Thompson and Crossbeck.

McDunnough (1938) first treated all 4 species as distinct. In an exhaustive look at the Apantesis nais-complex, Smith (1938) also listed the 4 species as distinct from each other. She listed the synonomy of each species, described larvae, pupae, and adults, and gave the distribution records of each. Her work is the most complete study of this group. Teitz (1952) also regarded the 4 species as distinct. He included a partial synonomy, cited literature to biological information, and gave food plants for each species.

Forbes (1960) regarded the Apantesis nais-complex as being composed of A. nais, A. phalerata, and possibly A. radians. He placed A. floridana Cassino, a synonym of A. radians, under A. phalerata. Forbes also regarded A. vittata of some authors and A. vittata females collected in Florida as A. phalerata. According to Forbes the figures of A. vittata (Plate XV; Fig. 22♂, 25♀) in Holland (1903), as well as the A. vittata of some collections, are actually A. nais. Also placed under A. nais is the form A. decorata Saunders (A. vittata of Smith). Although Forbes placed most specimens referred to as A. radians under either A. phalerata or A. nais, he still seemed to regard some specimens from Florida and Georgia as possibly belonging to A. radians.

Kimball (1965) listed 2 species in the A. nais-complex in Florida and credited Franclemont (personal communication) for this information. Franclemont viewed A. nais and A. phalerata as the 2 valid species, basing his decision on extensive rearing. Kimball had difficulty placing specimens labeled A. vittata or A. radians under A. nais or A. phalerata. He reported a Florida specimen of A. phalerata almost devoid of maculation.

Apantesis nais

Apantesis nais was described by Drury under the genus [illegible] (1773). The complete synonomy of the species, as well as descriptions of adults, genitalia, larvae and pupae, recorded food plants, distribution, and deposition of types, was given by Smith (1938). Teitz (1952) gave a more exhaustive list of food plants than Smith for the species of the complex. Forbes (1960) seemed to regard Apantesis vittata, or at least 2 forms of A. vittata, A. decorata (Saunders, 1863) and A. ochracea (Butler, 1881a), as A. nais.

A larval description of Arctia (=Apantesis) phalerata by French (1878) was corrected by the same author (1881) to refer either to Arctia decorata or A. nais. This description apparently referred to Apantesis vittata (Smith, 1938). A larval description of Arctia nais by French (1882) adds to the confusion. French reported rearing 2 larvae to adults; 1 adult female was reported as Arctia nais; the other, a male, was regarded as Arctia nais form phalerata. Dyar (1900) stated that French's former determination was doubtful and the latter was probably Arctia phalerata. Beutenmüller (1898) described the larvae of Arctia nais, but the description was very brief and generalized. Siefert (1902) gathered biological information on Arctia nais, including the effects of temperature on pupae, and parent vs. progeny variability in adults. Smith (1938) described the larvae of Apantesis nais in detail, reporting that they were indistinguishable from those of A. phalerata. Forbes (1960) also found no differences between the larvae.

Apantesis vittata

Apantesis vittata was described by Fabricius (1787) in the genus Bombyx. As with Apantesis nais, the complete synonomy and other

information on food plants, distribution, and descriptions for this species was given by Smith (1938).

A larval description of Arctia (=Apantesis) vittata by Beutenmüller (1898) is too brief and generalized to separate this species from closely related forms. Dyar (1900) compared mature larvae of Arctia (=Apantesis) phalerata and A. vittata and found no reliable character to separate them. Gibson (1900) described a last instar exuvium and pupa of Arctia vittata; they were virtually the same as those of A. phalerata, although the pupa of A. vittata was somewhat larger. Hampson (1901) regarded A. phalerata as a synonym of A. vittata, and the references on the larval stages of A. vittata in his catalogue refer rather to A. phalerata (Smith, 1938). Learned (1928) gave a brief description of the egg of A. vittata and a rather detailed description of the larval instars. However, Smith (1938) contends that the descriptions actually refer to Apantesis radians.

Apantesis radians

Apantesis radians was described by Walker (1855). As with the first 2 species the complete synonomy, food plants, distribution, etc., are given by Smith (1938). Cassino (1918) described a new species, Apantesis floridana, and a variety, A. floridana ochracea, both from Florida. The 2 were synonymized with A. radians by Smith, since both fell within the normal range of A. radians variability.

Very little has been published on the life history of A. radians. Siefert (1902) gave a detailed description of A. radians larval instars, stating that they do not deviate structurally from the other 3 closely related species. He also described the adults in some detail. In the

same paper, Siefert reported that female A. radians exposed at various locations in New Jersey and New York, where A. nais, A. virgata, and A. phalerata occurred, attracted no males. Apantesis radians females had attracted A. radians males in Florida. The biology of A. virgata cited by Learned (1928) refers to A. radians, according to Smith (1938).

Apantesis phalerata

Apantesis phalerata was first described by Harris in the genus Arctia (1835). Smith (1938) gave the synonomy, food plants, distribution, etc., of this species. She cited a reference by Butler (1881b), who described incompleta as a variety of Arctia (=Apantesis) phalerata. Her citation listed incompleta as a new species, instead of a variety of A. phalerata, as Butler intended. Siefert (1902) stated that Butler's description of incompleta agreed with several A. radians specimens he reared from a female collected in Florida. Teitz (1952) also placed this variety in synonomy with A. radians.

Beutenmüller's (1898) description of a mature larva of Apantesis phalerata was too brief and generalized to be of any diagnostic value. Gibson (1900) published the life history of A. phalerata, describing and giving the duration of each larval instar. He later gave additional notes on the variation of A. phalerata instars (1903). Barnes and McDunnough (1912) could find no difference between the eggs of A. phalerata, A. nevadensis (Grote), A. phyllira (Drury), and A. placentia (Abbot and Smith).

Corn Ear Worm

[illegible] species of the present study, [illegible] [illegible] Fabricius, seems to be of second importance. Forbes (1926) [illegible] A. phalerata as injurious to corn, but reported only slight damage. Anaresis phalerata is the most common and widely distributed species of the genus, occurring from southeastern Canada through Florida and Mexico (unconfirmed), and west to Texas (Smith, 1956; Teitz, 1952). Anaresis radians is restricted to the southern states, occurring west to Texas and north through North Carolina (Smith, 1938). Both species are very common in northcentral Florida where the present investigation was carried out.

METHODS AND MATERIALS

Rearing

Media

Larvae of Apantesis phalerata and A. radians (hereafter, both species are referred to only by their specific name in the text) were reared in the laboratory on an artificial diet (Table 1) slightly modified from that used by Shorey and Hale (1965).

The artificial diet was prepared by mixing all the dry ingredients except the agar, adding them to the soaked pinto beans and 1000 ml water and blending them in a 5 quart capacity Waring commercial blender. The agar was added to the remaining 800 ml of water (boiling) and, after it had thickened and become clear, was added to the media. The formaldehyde was added last, and the media poured into an approximately 10x12x5 inch plastic tub. Each batch poured into the tub was separated by a sheet of Alcoa polyvinyl chloride film (No. 5602). When the media had set sufficiently (usually overnight), they were cut into approximately 4x5x1 inch blocks (6 per batch), wrapped, and refrigerated at 10^{o}C for later use. Refrigerated media could be kept at least 2 months without spoiling.

Colonies

Eggs for colonies were obtained from females collected in blacklight traps. Females were individually put into $\frac{1}{2}$ pint cartons lined with

Table 1. Modified Snoey-...ie diet used to rear larvae of Aedes triseriatus and A. rudis.

Pinto beans (soaked overnight)	600 g
Brewer's yeast*	100 g
Ascorbic acid*	10 g
Sorbic acid*	3 g
Methyl p-hydroxybenzoate**	6 g
Formaldehyde (37%)	6 ml
Agar*	40 g
Water; with agar	800 ml
with dry ingredients	1000 ml

* Nutritional Biochemicals Corp., Cleveland, Oh.
** Fischer Scientific Co., Atlanta, Ga.

paper toweling. Standard petri dish bottoms were used as tops for the containers. The paper toweling was moistened daily. Eggs, usually laid on the side of the container, were left undisturbed until they hatched.

Larvae were mass reared at 23±1°C in ½ pint cartons containing about 20 g of medium pressed around the perimeter of the bottom. About 100 larvae could be reared through the early third instar before crowding became critical and thinning was necessary. About 20 late fourth and fifth instars could be maintained in a single carton without apparent crowding, and 8 last instars, usually sixth and seventh, could pupate in a carton with little or no cannibalism or stunted individuals.

Pupae were also transferred into ½ pint paper towel-lined cartons and covered with a petri dish bottom. The toweling was moistened daily. Forty to 60 pupae were sexed and placed into a single carton. Four to 6 pupae of each sex were preserved in 70% isopropyl alcohol from most colonies.

Adults were removed daily and either killed with ethyl acetate and mounted or used in 1 of several studies.

Field-collected females of the original colonies are shown in Table 2. This table gives the collection date and locality of females, whether larvae and pupae were preserved for each colony, and if a life history were carried out. All studies were either carried out with these original colonies or colonies resulting from self matings or matings between colonies, including hybrid crosses.

The capital letter D indicates a radians colony and L a phalerata colony. Missing colony numbers between 1 and 51 refer to 1970 colonies of either species outside the present study or females with inviable eggs. Colony numbers were arbitrarily started at number 60 in 1970 and missing numbers indicate field-collected females that did not result in colonies.

Table 2. Field collected ♀♀ and rearing data*

Stock ♀	Date found	Life history	Preserved instars: last	Preserved instars: all	Preserved pupae	Adults
A. phalerata						
L-524	?-III-69	-	-	-	-	+
L-4	17-IV-69	-	-	-	-	+
L-11	7-V-69	-	-	-	-	+
L-13	9-V-69	-	-	-	-	+
L-20	20-V-69	-	-	-	-	+
L-22	21-VI-69	-	-	-	-	+
L-33	26-III-70	+	-	+	-	+
L-34	28-III-70	+	-	+	-	+
L-36	1-IV-70	-	+	-	+	+
L-37	2-IV-70	-	+	-	-	+
L-40	18-IV-70	-	-	-	+	+
L-41	21-IV-70	-	-	-	+	+
L-42	20-IV-70	-	+	-	+	+
L-43	27-IV-70	+	-	+	+	+
L-46	11-V-70	-	+	-	+	+
L-47	11-V-70	-	+	-	+	+
L-48	12-V-70	-	+	-	+	+
L-50	14-V-70	-	+	-	+	+
L-60	3-III-71	+	+	-	+	+
L-61	14-III-71	+	+	-	+	+
L-63	13-IV-71	+	-	+	+	+
L-64	21-IV-71	-	-	-	-	+
L-65	19-IV-71	-	-	-	-	+
L-74	10-VI-71	-	-	-	-	+
A. radians						
D-3	17-IV-69	-	-	-	-	+
D-14	13-V-69	-	-	-	-	+
D-32	10-III-70	+	+	-	-	+
D-35	26-III-70	+	+	-	+	+
D-38	2-IV-70	-	+	-	+	+
D-39	15-IV-70	-	-	-	+	+
D-44	25-IV-70	+	+	-	+	+
D-45	8-V-70	-	+	-	+	+
D-49	12-V-70	-	+	-	+	+
D-51	28-V-70	-	+	-	+	+
D-62	14-III-71	+	+	-	+	+
D-66	26-IV-71	+	-	+	+	+

* All ♀♀ collected in Gainesville, Alachua County, Fl. except L-34 and D-33, found in Bradenton, Manatee County, Fl. and Quitman, Brooks County, Ga. respectively

\- indicates absence

\+ " presence

Number 524 in the table refers to a colony from a female which was collected before the present code numbers were in use. This stock was not used in the study at the outset and is referred to in detail later.

Life Histories

Females used in life history studies were collected and the larvae reared in the same manner as the colonies. Most life histories were undertaken in conjunction with colonies, the larvae from given females being used for both.

About 25 newly emerged first instar larvae for each life history were placed in a 1 ounce plastic cup into which about 3 g of medium had been pressed. The cup was covered with a paper top and the larvae allowed to feed for 3 days. Twenty of these first instar larvae were then placed individually into plastic cups with about 1 g of diet. Each larva was reared to the adult stage in the cup at $23\pm1^{\circ}C$.

Two phalerata, 2 radians, 3 hybrid (radians ♂ x phalerata ♀), and 1 hybrid x hybrid life histories were used in the present investigation.

A record was kept of the duration of each instar, number of instars, whether the head capsule and/or skin were eaten after molting, head capsule width, pupal duration, and sex of the resulting adult. Head capsules and larval and pupal skins were preserved in 70% isopropyl alcohol. Fresh medium was added ad libetum, about once a week for the first 3 instars and every 3 or 4 days for the last 2 instars. Frass was removed about every third day for early instars and daily for late instars.

Life histories for filial and hybrid generations were conducted in the same manner, except the females were mated in the laboratory.

Larval Preservation

Representatives of all larval instars of selected colonies were preserved. Larvae to be preserved were dropped into a beaker of boiling water. The beaker was then placed aside. After cooling, the larvae were transferred into 4 dram vials with 70% isopropyl alcohol, labeled, and filed. The label included the colony number, instar, and date of larval eclosion.

Morphology

General

The morphology of eggs, larvae, pupae, and adults was checked to determine characters which might be used to reliably separate the species involved in this study.

The height and width of eggs of F_1 phalerata and hybrid females were measured. Larval instars were carefully studied for morphological differences including such characters as number and placement of setae and verrucae, head capsule, hypopharynx and other mouthparts, larval pigmentation, and number and type of crochets. Pupae were also inspected for morphological differences, especially the cremaster and setae. Adult morphological studies were concentrated on male and female genitalia.

Genitalia

Moths used were provided with a number to correlate the genitalia with their specimens. One label was affixed to the specimen and the other was kept with its genitalia throughout preparation. Information included the colony number, individual moth number, time each abdomen was kept in potassium hydroxide, and the sex of the specimen.

The abdomens used for genitalia slides were cut behind the thorax of adult moths and placed into a solution of 10% potassium hydroxide for 2-4 days. Abdomens were rinsed several times with distilled water and placed into a 50 mm Syracuse watch glass. Dissection was done under a stereoscopic dissecting microscope in 30% isopropyl alcohol. Excision of the abdominal cuticle from the perimeter of the genitalia was facilitated in the male by squeezing the abdomen slowly, anteriorly to posteriorly, extruding the genitalia. The genitalia were then cut from the abdominal cuticle with iridectomy scissors. The excess cuticle and setae were carefully removed with jeweler's forceps and a small brush.

Male genitalia required an extra step. The aedeagus was removed from the remainder of the genitalia by grasping the phallobase of the aedeagus with a pair of forceps and the base of the valves with a second pair and pulling gently. In this way the aedeagus was easily separated from the enclosing membrane. The vesica was inflated by slowly injecting 95% isopropyl alcohol into it from a #27 hypodermic syringe until it inflated and hardened. About 90 sec was usually adequate for hardening. The genitalia were then placed into Cellosolve® for about 20 min, transferred into clove oil containing a few drops of safranin stain for approximately 10 min, and placed into xylene for an additional 10 min.

The genitalia were removed from the xylene and placed lightly into a drop of Caedax® on a standard, clean microscope slide. A 22x22 mm^2 coverslip, usually supported by 3 or 4 chips of microscope slide glass, was then placed over the Caedax drop containing the genitalia. Additional Caedax was added under the coverslip until the cavity was filled. The slide was labeled, placed into a covered petri dish, and allowed to dry for about a week.

Chromosome Study

Dividing chromosomes of male testes were fixed and squashed to check for possible differences in chromosome numbers between the 2 species and resulting hybrids. A preliminary study had shown that germ cell division in _phalerata_ and _radians_ occurred during the penultimate instar.

Late penultimate _phalerata_, _radians_, and hybrid larvae were fixed by injecting a 3:1 ethyl alcohol:glacial acetic acid mixture into the sixth abdominal segment with a #27 hypodermic syringe. The injected larvae were placed into 4 ounce jars containing the same fixative, labeled, and refrigerated at about -10°C for later dissection.

For chromosome study the testes, usually found in the dorsal area of the sixth abdominal segment of male larvae, were removed with No. 5 watchmaker's forceps and placed onto a standard microscope slide. The testes were then macerated and a few drops of Lacto Orcein Stain added. This preparation was allowed to stand for about 10-12 min. The stained testes were next covered with a coverslip and the preparation squashed with about 400 lb/inch^2 pressure between 2 pieces of blotting paper. The perimeter of the coverslip was then sealed with clear lacquer.

Slides were inspected with a Zeiss research microscope STANDARD WL with plan-apochromatic field objectives. An oil immersion Planapo 100x objective was used for critical observations.

Chromosome counts were made during meiotic division when chromosomes were paired at meiosis I. Photographs were taken of unusually clear chromosome sets and of any interesting anomalies.

This technique basically follows that outlined by Emmel (1969).

Light Yellow Strain

Three pale males and several females rather devoid of pigmentation were noticed among the other typical adult progeny of a normal female (L-52), collected in March 1969. Each of the light males was mated to 1 of several sibling females with yellow hindwings. The larvae resulting from the 1 successful mating were reared through to adulthood. The adults were mounted, labeled, and stored for later analysis.

Mating Study

All matings were carried out in the laboratory at 23±1°C. Virgin male and female moths that had emerged on the same day were placed together into ½ pint paper cartons into which moist paper toweling had been placed. The cartons were covered snugly with petri dish bottoms and the paper toweling was moistened daily. The pairs remained in the cartons until the female died, then the moths were either mounted or placed into 1 ounce plastic cups, covered, and stored.

Eggs were allowed to hatch, and the first instar larvae were either reared for life histories and/or colonies, or left to die for later counting.

Three mating studies were undertaken, 1 in the summer of 1970 and 2 in the summer of 1971. In 1970, F_1 male and female moths of colonies 32 through 50 were mated. Pairs included phalerata males and females, phalerata males and radians females, radians males and phalerata females, and male and female radians. Pairs which included only phalerata or radians individuals were inter- and intracolony. Sixty-two matings were attempted.

In 1971, 70 mating attempts were carried out at [illegible] colonies 58 through 62. A second mating study was carried out in 1971 using colonies 64 through 66 in 53 mating attempts.

A mating was considered successful if the eggs laid by the female hatched. The females in the first 2 mating studies were dissected to check for spermatophores.

Attractant Studies

Attractant Cages

A series of studies was undertaken to demonstrate the presence of a sex pheromone and to determine the specificity of virgin female attractiveness to males under natural conditions.

Cages used to attract males were constructed of cylindrical, gallon cartons and standard #16 mesh aluminum screen. Two slightly different types were employed.

The bottom was first cut out of the carton and the top removed. The center area was cut out of the cover top. Two large pieces of the side were removed so that 2 strips connecting the top and bottom of the carton remained. Screen was cut to fit snugly around the outside of the carton and stapled to it. Two fairly shallow screen funnels were formed to fit into the open top and bottom of the carton. The funnels had diameters equal to that of the inside carton bottom and the outside of the carton top respectively. Both had a depth of approximately 3 inches. A 1 inch diameter hole was cut from the apex of each funnel. The bottom funnel was then stapled to the bottom of the carton, with its outside diameter flush with the carton bottom and the apex pointing inward. The

upper funnel was placed through the inside of the cover top and bottom and stapled to the outside of the top so that the top and funnel could be removed from the carton as a unit.

A 2x2 inch screen cage was also constructed. This cage was suspended by a screen bridge connected to the middle of opposite sides of the inside of the carton. One end of the inner cage, used as a door, was left unattached at 3 of its 4 sides.

A second closed-type cage was constructed as the first, except the side pieces were not cut out, thus no screen was placed around the circumference of the carton. A finished closed-type cage appears as in Fig. 1.

Female Attractant Study

Laboratory-reared, virgin female moths, used to attract males in the field, were placed singly into attractant cages. The top was then replaced and the cage hung from a string about 4 feet from the ground. Cages were suspended from about 10 locations around the laboratory, no more than 5 being used simultaneously.

Cages were inspected daily for male moths. Males were removed from the cages, mounted, labeled, and stored for later analysis. Each cage was left in its original location until the female died. In hot, dry weather, cages were sometimes brought into the laboratory ($23\pm1^{\circ}C$) in the morning, the females squirted with water, and the apparatus replaced at dusk.

Large Cage Study

On 9 September 1970, a newly emerged virgin female of stock DD-4949 (F_2 radians) and of LL-3646 (F_2 phalerata) were put separately into

Figure 1. Closed-type cage used to attract males

attractant cages suspended 8 feet apart, 4 feet above the ground, in a 4x12x8 foot outdoor screen cage. Ten newly emerged hybrid males (L-4x63) were then released into the screen cage. The attractant cages were checked for males after 3 and 7 days.

On 2 June 1971, 2 newly emerged virgin phalerata females (L-63) were put 1 each into 2 attractant cages and suspended from the large cage as above. Nine newly emerged L-63 males were released into the cage. The attractant cages were checked for males after 1, 2, and 7 days.

Marked, Released Males

A study was undertaken to determine if marked, released F_1 males would be attracted to caged females outdoors in numbers large enough to justify later releasing hybrid males to see if they would be attracted to the female of either type, a hybrid female, or some combination thereof.

On 12 June 1971, a virgin phalerata female from colony L-65 was placed into an open-type cage and the cage suspended from the top of a chain link fence in back of the laboratory. Two other open-type cages containing virgin females from colony L-63 had already been hanging in the vicinity for 4 and 9 days. Newly emerged virgin males from the L-65 colony were marked and released on 5 successive days, commencing 12 June. Males were marked with a Marks-A-Lot® felt tip pen. A small dot on the underside of the left hindwing indicated males released on the first day, a dot on the right hindwing the second day, the left forewing the third, the right forewing the fourth, and a dot on the underside of both hindwings designated the fifth day. All males were released approximately

midway between the 3 cages (about 100 feet apart) around 5:00 PM. Two blacklight traps were also operated about 150 feet from the cages and released males.

Seasonal Abundance

Two blacklight traps were run simultaneously in the vicinity of the laboratory. M. and female moths were collected approximately every week from 16 March 1968, to 31 May 1970. Moths were preserved in 70% isopropyl alcohol and identified, sexed, and counted later. Each female was also checked for spermatophores under a dissecting microscope.

RESULTS AND DISCUSSION

Rearing

Colonies

The artificial diet used in the present investigation seemed well suited for the rearing of these species. Larval and pupal duration and size were rather uniform. Reared and field-collected adults were comparable, both in color, maculation, and size.

Colonies were maintained through a second laboratory generation with no apparent decline in larval, pupal, or adult size or hardiness. In a study not connected with the present investigation, a decline was noted both in egg viability and larval survival after 4 or 5 laboratory generations. Only 1 small facet of the study herein utilized 3 laboratory generations; all others utilized 1 or 2.

Life Histories

Larval and pupal duration

No significant difference in larval or pupal duration was found between *phalerata*, *radians*, and hybrid colonies (Table 3).

When comparing larvae of the same sex that went through the same number of instars, there was a slight difference in total duration of the larval stage between *radians* colonies, colony D-62 taking longer than D-66 for both male and female larvae undergoing 6 or 7 molts.

Table 3. Duration of larval instars and pupae grouped by colony, number of instars, and sex of *Agrotis phalerata*, *A. radians*, hybrid (*A. phalerata* ♀ × *A. radians* ♂), and hybrid x hybrid at 25±1°C

Colony	Instars & sex	n	Stadia in days								Pupa	Total
			1	2	3	4	5	6	7	8		
A. phalerata												
L-63	6♂	11	4.4	4.0	4.9	4.9	5.5	9.2			10.7	43.6
	6♀	4	4.4	4.0	4.4	5.0	5.8	9.3			10.0	42.8
L-60	7♂	6	4.3	3.8	5.2	5.0	4.8	7.2	11.5		11.0	53.3
L-63	"	4	4.3	4.8	4.3	4.8	4.8	5.8	9.5		9.5	46.0
L-60	7♀	12	4.5	4.2	5.0	4.9	5.6	7.5	11.2		9.7	52.0
	8♂	2	5.0	4.0	5.0	5.0	5.0	6.5	7.0	12.0	10.5	55.5
A. radians												
D-62	6♂	9	4.7	4.2	4.7	6.0	6.4	10.3			10.7	45.4
D-66	"	9	4.2	3.7	3.0	6.1	5.7	10.0			11.4	44.3
D-62	6♀	7	4.7	4.1	4.7	5.7	6.7	10.0			9.4	45.3
D-66	"	2	4.0	4.0	3.0	6.0	6.0	10.0			10.0	43.0
D-62	7♂	1	4.0	4.0	4.0	5.0	6.0	6.0	10.0		12.0	51.0
D-66	"	2	4.0	4.0	3.0	6.0	5.0	6.0	9.5		12.0	49.5
D-62	7♀	2	5.0	4.0	5.0	6.5	7.5	8.5	11.0		10.0	57.5
D-66	"	5	4.2	3.8	3.2	5.8	5.0	6.0	9.6		11.2	48.6
D-62	8♀	1	5.0	4.0	5.0	6.0	7.0	9.0	6.0	12.0	7.0	61.0
hybrid												
DL-4446	6♂	14	5.1	4.0	4.9	5.0	5.6	9.3			10.7	44.4
DL-4941	"	15	5.2	4.6	5.0	6.5	6.0	11.1			12.3	51.0
DL-6261	"	6	5.0	4.0	4.0	4.2	6.0	8.7			11.2	43.2
DL-4446	7♀	6	5.8	4.0	5.7	5.7	7.8	9.3	13.0		11.5	62.0
DL-4941	"	4	5.8	4.5	5.0	6.5	6.0	10.0	16.0		11.5	64.0
DL-6261	"	11	5.1	4.4	4.0	4.9	6.8	8.0	12.5		10.1	56.0
DL-4941	8♀	1	6.0	5.0	5.0	6.0	7.0	9.0	14.0	15.0	13.0	80.0
DL-6261	"	3	5.0	4.7	4.3	5.0	6.0	7.3	8.7	12.3	10.7	64.0
hybrid x hybrid (DL-6664)[2]	5♀	3	4.0	4.0	3.7	4.7	10.0				10.0	36.4
	6♂	4	4.0	5.3	4.8	4.5	7.0	11.5			11.5	48.5
	6♀	5	4.0	5.0	4.2	4.0	6.4	10.0			9.8	43.4
	7♂	3	4.0	6.0	4.7	5.3	6.7	9.3	12.7		11.7	60.3
	7♀	3	4.0	5.3	5.0	5.3	7.0	9.7	14.7		10.7	61.3

The total duration of the larval stage of hybrid males [illegible] underwent 6 molts) in colony DL-4941 was greater than colony DL-4940 which was in turn greater than colony DL-6261. The same order of duration was present for hybrid females, all of which underwent either 7 or 8 [illegible].

The duration of the larvae and pupae of the hybrid x hybrid colony which underwent 6 or 7 molts was comparable to phalerata, radians, and hybrid colonies. However, the 3 female hybrid x hybrid larvae that underwent only 3 molts had a total average duration of only 36 days, about 7 days less than any other average duration.

Generally, no marked difference was found between the durations of the various instars, except the last. The duration of last instar larvae was typically equal to that of the pupae and about 1½ that of the penultimate instar.

Number of instars

A. phalerata and radians could not be separated on the basis of number of instars (Fig. 2). Both males and females of the 2 species had 6, 7, or sometimes 8 larval instars. Larvae in other colonies of both species, reared under different temperature conditions, had as many as 9 or 10 instars.

The instar distribution of the 3 hybrid colonies was radically different from that of either parent species. All 35 males of the hybrid colonies had 6 instars, the 25 females had 7 or 8 instars. The difference between the number of male and female instars accounts for the emergence of the last male before the first female adult. This was in contrast to the males and females of the parent species, which emerged at approximately the same time.

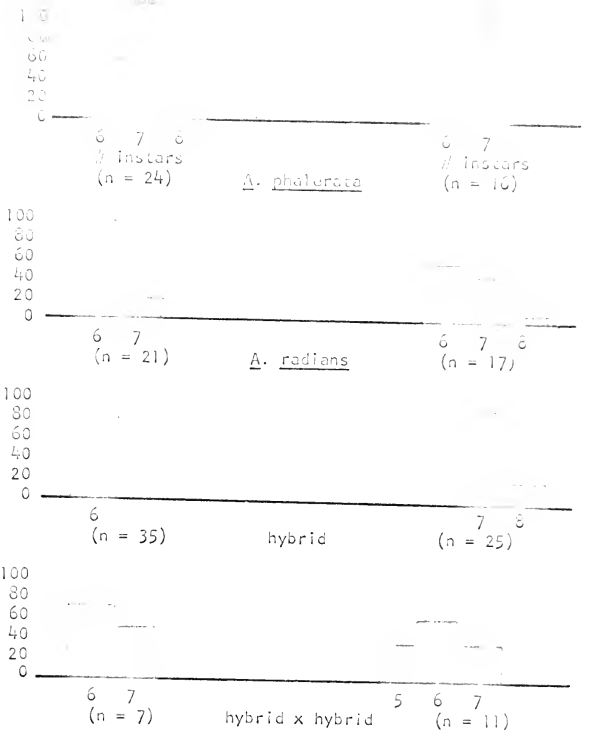

Figure 2. Number of instars of Apantesis phalerata (colonies L-60 and 63), A. radians (D-62 and 66), hybrid, A. radians ♂ x A. phalerata ♀ (DL-4446, 4941, and 6261), and hybrid x hybrid (DL-4446 x DL-4446) at 23±1°C

Three females of the hybrid x hybrid colony had 5 larval instars. No larvae of any of the other colonies underwent as few as 5 molts.

Although phalerata and radians were not separable on the basis of number of instars, the number of instars in the larvae of the hybrid cross of a female phalerata to a male radians suggests a specific distinctness between the parents. The crossing of a hybrid to a hybrid, with the resulting females undergoing only 5 instars, helps confirm this distinctness.

head capsule widths

The larvae of phalerata could not be separated from radians by mean head capsule width, with the possible exception of the first instar (Table 4). The head capsule width of first instar phalerata was almost always slightly smaller than radians, although there was some overlap. Through the remaining instars there was increasing overlap between measurements.

Mean head capsule widths of the hybrid larvae were not significantly different from those of either parent species. The second, third and fourth instar larvae of the hybrid x hybrid colony had mean head capsule widths larger than corresponding instars of either phalerata, radians, or the hybrid since these were the only larvae that went through only 5 instars.

The larvae which undergo fewer instars tend to have greater head capsule widths than the corresponding instar of larvae which molt more often. Thus, the adults whose larvae underwent 5 or 6 molts were similar in size to those whose larvae went through 7 or 8.

Table 4. Mean head capsule width of Apantesis phalerata, A. radians, hybrid (A. radians ♂ x A. phalerata ♀), and hybrid x hybrid larvae in mm

# instars	Sex	n	Instar 1	2	3	4	5	6	7	8
A. phalerata, colonies L-60, L-63 (n = 40)										
6	o	11	0.39(11)	0.59(11)	0.90(10)	1.38(10)	2.04(9)	2.82(5)		
6	o	5	0.39(5)	0.56(5)	0.86(4)	1.33(4)	1.96(4)	2.79(3)		
7	o	10	0.38(11)	0.56(9)	0.83(10)	1.25(9)	1.74(8)	2.31(10)	3.01(10)	
7	o	12	0.38(9)	0.53(9)	0.90(12)	1.18(4)	1.67(8)	2.28(8)	3.02(11)	
8	o	2	0.38(2)	0.54(1)	0.83(2)	1.20(2)	1.67(2)	2.21(1)	2.64(2)	3.10(2)
A. radians, colonies D-62, D-66 (n = 38)										
6	o	18	0.42(18)	0.60(12)	0.91(15)	1.35(15)	1.97(16)	2.78(16)		
6	o	9	0.42(8)	0.60(8)	0.91(6)	1.38(7)	1.99(7)	2.80(7)		
7	o	3	0.42(3)	0.59(2)	0.85(3)	1.33(2)	1.73(3)	2.29(3)	3.10(2)	
7	o	7	0.41(6)	0.57(4)	0.89(5)	1.28(7)	1.75(7)	2.28(6)	3.00(5)	
8	o	1	0.41(1)	0.61(1)		1.33(1)			2.57(1)	3.17(1)
hybrid, colonies DL-4446, DL-4941, DL-6261 (n = 60)										
6	o	35	0.42(35)	0.60(33)	0.92(29)	1.38(31)	1.95(31)	2.96(34)		
7	o	21	0.41(21)	0.58(20)	0.86(15)	1.25(20)	1.79(17)	2.47(15)	3.15(19)	
8	o	4	0.40(4)	0.56(4)	0.80(4)	1.18(4)	1.60(4)	2.20(3)	2.70(2)	3.23(3)
hybrid x hybrid, colony DL-4446 x DL-4446 (n = 18)										
5	o	3	0.43(2)	0.61(3)	0.95(2)	1.42(3)	2.24(3)			
6	o	4	0.42(2)	0.60(4)	0.93(3)	1.37(4)	1.95(2)	2.96(4)		
6	o	5	0.42(2)	0.58(5)	0.88(4)	1.30(5)	1.92(5)	2.78(4)		
7	o	3	0.42(2)	0.56(3)	0.87(2)	1.33(2)	1.82(2)	2.33(3)	3.13(3)	
7	o	3	0.41(2)	0.57(2)	0.88(3)	1.26(2)	1.86(3)	2.41(3)	3.16(2)	

Results

Eggs

Measurements revealed no differences between the eggs of parasites of phalerata and hybrid eggs. They were also indistinguishable in shape, color, and texture.

With 1 exception, no differences could be found between the larvae of phalerata and radians. Variation in the number and placement of setae on last instar head capsules was as great intraspecifically as interspecifically. The labrum, hypopharynx, epipharynx, mandibles, maxillae, and antennae also were inseparable. The number and placement of verrucae and setae on the body and prolegs, as well as the ground color of last instar larvae, were similar in both species.

Last instar phalerata larvae usually had more crochets than radians. This was particularly true of the long, central crochets of the heteroideous series of each species. Although the number of crochets sometimes varied from proleg to proleg on a given larva, the difference was uncorrelated.

The mean number of central crochets of a last instar phalerata representative from each of 13 different colonies was 19.3, with an average range of 18.1 to 20.8, and a total range of 15 to 24. The mean number of radians central crochets of 6 colonies was 15.8, with an average range of 14.7 to 16.8, and a total range of 13 to 18.

Although the preceding crochet counts separated most last instars, some overlap was present, with the 3 lowest mean phalerata counts below the highest mean radians count.

Genitalia

The differences in genitalia used by Learned (1927) and Smith (1936) to separate male and female phalerata from radians generally applied to Florida specimens. However, a few radians males were found with only 1 spine on the aedeagus instead of 2 to 4 as cited by Learned and Smith. Female genitalia conformed to the description by Smith.

The genitalia of hybrid females were intermediate. The lips of the ostium, used by Smith to separate the females of phalerata and radians, were intermediate in hybrid specimens, both in size and crenulation. The lips of phalerata are larger and more crenulated than radians. The aedeagus of some hybrid males had 2 large posteriorly projecting spines characteristic of phalerata, others had a large lateral spine with small basal ones characteristic of radians, and some had spines intermediate between the 2 species with 1 spine projecting posteriorly as in phalerata and the second projecting somewhat laterally. The genitalia of all hybrid males inspected were intermediate in size between the larger phalerata and smaller radians.

Chromosome Study

Definitive chromosome counts with photographic confirmation were obtained from microscopic slide examination of phalerata, radians, and hybrid testes squashes. The haploid chromosome numbers of phalerata, radians, and the hybrid cross are n = 29, 30, and 29 respectively (Fig. 3). Since no other counts have been reported in the genus, the chromosomal evidence for the phylogenetic relationship between these 2 species is here speculated upon for the first time.

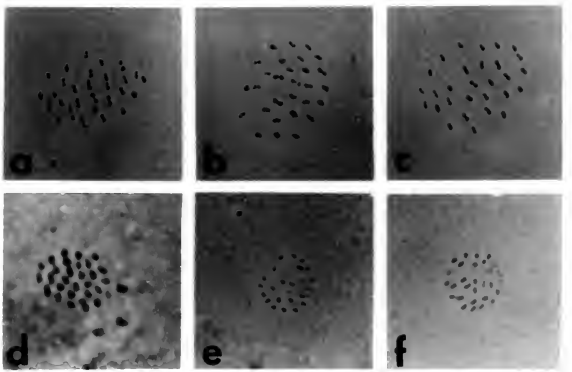

Figure 3. Photomicrograph of testes squashes at 1110 mag.; chromosomes at first meiotic division during metaphase. (a-c) Apantesis phalerata, F_1 L-60 (n = 29); (d) A. radians, F_1 D-62 (n = 30); (e,f) A. radians ♂ x A. phalerata ♀, DL-6261 (n = 29)

The karyotype and origin of [illegible] could have resulted from the fusion of 2 of radians' (ancestor of radians) 30 chromosomes, or a loss of 1 ancestral chromosome. A departure downward in chromosome number from a mean of [illegible] is common in the arctiids and closely related noctuids. In counted species of both families the mean haploid number is 31 chromosomes (Robinson, 1971). The reported arctiid counts show 1 species with a haploid number of 26, 4 with 28, 1 with 29, 2 with 30, 17 with 31, and 1 species with a number varying between 30 and 33. The noctuids show the same apparent tendency toward reduction in chromosome number from the probable ancestral number of 31, with 7 species having less than 31 and 3 exceeding 31.

It is possible that radians resulted from the fusion of 2 chromosomes in an n = 31 ancestor, and that phalerata was the result of a further fusion of 2 radians chromosomes. These fusions would limit the amount of genetic recombination and thus the general adaptation of the species. But fusion would be favorable to a well adapted species where the need for genetic recombination would be minimal, in fact, probably at a selective disadvantage.

If phalerata had evolved from an ancestor with a haploid number of 30, such as radians, microscopic examination of its 29 chromosomes might show 1 double-sized or exceptionally large chromosome. However, photographic examination did not disclose a significantly larger chromosome, although many of the uniformly sized chromosomes were rather unclear.

The possibility also exists that phalerata (or an n = 29 ancestor of phalerata) gave rise to radians (or an ancestor of radians) by fragmentation of 1 of its chromosomes. The evolution of many lepidopteran species has been accompanied by an increase in chromosome number (Emmel,

1972: submitted for publication). Thus, 1 of the 29 chromosomes could have split, with both parts being retained in the new karyotype, resulting in a new chromosome complement of 30. The potential value of this fragmentation would be increased potential for genetic recombination, allowing the species to be more generally adaptable.

There is some support for the above fragmentation hypothesis in phalerata and radians. If radians had resulted from the fragmentation of 1 of an ancestral phalerata's (or similar n = 29 species) chromosomes, 2 smaller chromosomes might be found among the 30. Two chromosomes (Fig. 3G) do appear smaller than the others. However, this could be due to orientation in the case of the larger of the 2 and some other reason in the smaller.

If radians had evolved from phalerata, one probably would expect radians' range to be more restricted, having split rather recently (suggested by their almost identical morphology, life history, and occasional hybridizing). Such is the case, with radians occupying about 1/3 the area that phalerata does.

If one accepts the ancestral fragmentation hypothesis as more likely, the hybrid chromosome number of 29 is most easily explained by the 2 short chromosomes of radians pairing with their "former" chromosome in phalerata at fertilization. The hybrid count of 29 would result from the loss of 1 of the 2 small chromosomes after pairing in meiosis I (the loss of both small chromosomes would have meant the additional loss of the unpaired phalerata chromosome, resulting in a hybrid count of 28). If one follows the fusion hypothesis, the picture would be similar, only the 2 complete chromosomes of radians would pair with the large, "fused" chromosome of phalerata at fertilization.

Since adult hybrid did result from the cross of the 2 species, the small lost chromosome seems relatively unimportant. The unusual hybrid male and female larval instar distribution might indicate that 1 or both of the small ruficans chromosomes (and thus the formerly analogous phalerata chromosome) affect larval development. However, simply crossing 2 distinct species with the same chromosome number has, in many instances, resulted in more numerous and radical developmental anomalies than that observed in the hybrids of the present study.

Light A. phalerata Strain

Thirty-nine males and 35 females resulted from the successful mating of 1 of the light males to a light female sibling. Female adults were of 2 patterns. The first pattern was that of a typical phalerata female, except the normally red secondaries and abdominal area were light yellow. All 30 females displaying this pattern were uniform. In the second pattern the red areas were again replaced by yellow, but, additionally, there was a loss of black maculation, resulting in females that were nearly all yellow. The typically black marginal and submarginal spots of the secondaries were absent and the black costal margin faded slightly proximally. One female of the 6 showing this loss of maculation had traces of submarginal spots. Only traces of postcostal maculation remained on the primaries. The patagium was entirely yellow, 1 female having a trace of the typical black spot. The tegulae were likewise yellow, devoid of the usual black bands. The antennae and underside of the abdomen had a few yellow scales. Both are normally black. The black dorsal abdominal stripe was considerably reduced. The 2 patterns are shown in Fig. 4c.

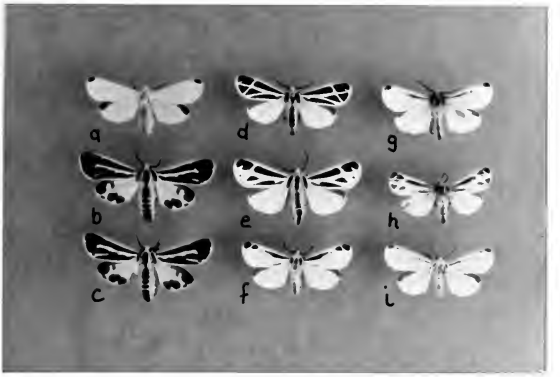

Figure 4. Various forms of Apantesis phalerata found in the light strain. (a) light, homozygous female; (b,c) dark females with full maculation; (d) dark male with full maculation; (e) heterozygous male showing partial expression of maculation; (f,g) light, homozygous males; (h) wild male collected in Gainesville, Florida, heterozygous for maculation; (i) light, homozygous male reported by Kimball

About [illegible] of the 43 [illegible] males to those almost completely devoid of maculation. The other 4 were normal. In the transition through the [illegible] costal stripe and postmedian transverse, subterminal W-shaped, and submedian longitudinal bands widened and fused. The black spots of the patagium, tegulae, and dorsal abdominal stripe also were reduced through the series. Four males in this transition are shown in Fig. 4a-g.

A discontinuity was noted among males which exhibited a gradation between absent maculation and normal marking. The lighter forms of 1 class retained most of the dark, posterior forewing band, some of the marginal spot enclosed by the W and the wing margin, and a distinct dorsal abdominal stripe as in normal males. The second class, containing all light forms, lacked the forewing band and marginal spot, and the dorsal abdominal stripe was reduced. The abdominal stripe easily separated the males into 2 distinct classes. The light male successfully mated in the laboratory belonged to the first class.

Kimball (1965) reported an aberrant male almost devoid of maculation from Gainesville, Florida, in 1959. This specimen appears identical to several in the L-524 series of males. Another light male was found in July 1968 in Gainesville. It also fits well into the series, but at a slightly different point. These 2 are shown in Fig. 4h-i. A third light male was found in Bradenton, Florida, in 1970. These aberrations were the only noticeably light phalerata found among more than 2,000 males collected during this study.

The rearing of this aberrant series shows that this light form is hereditary. The 74 progeny of the successful cross showed the range of variation expressed by the controlling gene(s). When this rare aberration

of [illegible] is collected in the future, it is hoped that [illegible] of the simple mutant character of this strain will avoid taxonomic confusion and the naming of unnecessary "forms" or "species."

Genetic analysis

One autosomal gene appears to control maculation. A simple dominant allele at this locus causes maculation and its recessive allele accounts for the rare, light forms. In males, expression of the heterozygote is variable.

Hindwing color is controlled by a second gene locus. The dominant allele, responsible for red hindwings, is expressed only in the female. Male hindwings are yellow, regardless of the presence of this dominant gene. The homozygous recessive state of this gene in the female results in yellow hindwings.

In the following analysis, D represents the dominant gene for expression of maculation and d its recessive allele. R designates the gene for red hindwings and r its recessive allele for yellow.

The male and female successfully crossed in the laboratory can each have only 1 genotype. The parental genotypes, their observed and expected offspring, and X^2 values are shown below.

Parents: ♂ × ♀

♂ Ddrr (Dark partly expressed) × ♀ Ddrr (Dark; yellow hindwings)

Offspring:

	Genotype	Class	Expected ratio	# observed	# expected
♀♀	DDrr or Ddrr	Dark	3	29	26.25
	ddrr	Light	1	6	8.75
			Totals	35	35

$X^2 = 0.770$

	Genotype	Phenotype	Expected ratio	Observed	Expected
♂♂	DDrr or Ddrr	Dark	3	30	29.25
	ddrr	Light	1	9	9.75
			Totals	39	39

$X^2 = 0.017$

The observed and expected numbers for both male and female moths of the laboratory cross do not differ significantly from a 3:1 ratio. The X^2 value of 0.770 in the female moths means that a 0.25 to 0.50 probability exists that the number of observed moths would differ from the number expected by more than the experimental results. This probability is between 0.75 and 0.90 in the males.

The genotype of the original field-collected (dark, red hindwings) female was undoubtedly DdRr. If it were homozygous for maculation, no light offspring would have resulted, and if it were homozygous recessive, its phenotype would have been light. Likewise, if it were homozygous for red hindwings, none of the offspring would have had yellow hindwings, and if it were homozygous recessive it would have had yellow hindwings.

The light aberrant male reported by Kimball was undoubtedly a recessive homozygote for maculation while the light males found in Gainesville and Bradenton were heterozygotes.

Mating Study

All 3 mating studies indicated that the *rediens* male and *phalerata* female can mate successfully in the laboratory, viable eggs being the criterion of a successful mating (Table 5). In contrast, not 1 *phalerata* male mated successfully with a *rediens* female out of 32 pairings.

Table 5. Number of attempted and successful matings for *Apanteles phalerata* and *A. radians* combinations for each of three mating studies, colonies D-33 - L-50, L-60 - D-62, and L-64 - D-66 at 23±1°C

	phalerata ♂ × ♀			*phalerata* ♂ × *radians* ♀			*radians* ♂ × *phalerata* ♀			*radians* ♂ × *radians* ♀		
	# successful matings	total pairs (n)	%	# s. m.	(n)	%	# s. m.	(n)	%	# s. m.	(n)	%
Mating study 1 1970 D-33 - L-50 colony	12	19	63.2	0	11	0	6	23	26.2	6	9	66.7
Mating study 2 1971 L-60 - D-62 colony	18	32	56.3	0	13	0	3	22	13.6	1	3	33.3
Mating study 3 1971 L-64 - D-66 colony	3	6	50.0	0	8	0	5	11	45.4	7	8	87.5
Total	33	57		0	32		14	56		14	20	
% successful mating; 3 study ave.			56.5			0			28.4			62.5
Total ave. %; studies grouped			57.9			0			25.0			70.0

The frequency at which [illegible] successfully [illegible] their [illegible] indicates that deviations for mating probably were not [illegible]. Fifty-six, or ca. 70% of 57 [illegible] and 20 [illegible] pairings, respectively, were successful. The frequency of [illegible] male x [illegible] female matings was less than ½ that of species with their own kind.

In the 51 phalerata x phalerata pairings checked for spermatophores, each female that mated successfully contained at least 1 spermatophore. Of the 21 phalerata pairings that were unsuccessful, only 1 female contained a spermatophore.

Likewise, in 12 radians x radians pairings checked for spermatophores, each female that mated successfully contained at least 1 spermatophore. Of the 5 radians pairs that were unsuccessful, only 1 female contained a spermatophore.

In the 45 radians male x phalerata female pairings checked, every female which mated successfully contained a spermatophore. As in the first 2 types of pairings, there was 1 case out of the 36 unsuccessful matings of a female that contained a spermatophore. This indicates that the lower mating success of the radians male x phalerata female pairing is not due to the passing of inviable sperm but rather to the pairs not mating at as great a frequency as either of the parent species.

None of the 24 checked phalerata females that were paired with a radians male contained a spermatophore. This indicates, as above, that the pairs simply were not mating, at least to the point when the spermatophore was passed.

[illegible]

[illegible]

The female attractant research was probably the most important facet of study. Unlike the laboratory matings this study [illegible] what males the female attracts in nature. If phalerata and radians males were distinct species, the female should just attract her own type of male.

Females of phalerata attracted only phalerata males (Table 6). Of the 33 caged virgin females, 24 attracted 51 males and 9 attracted none. Six of the 33 females were removed from the attractant cages before death. Two caged females were eaten by ants. The remainder died in their cages. Attracted adult males showed no significant preference between open- and closed-type cages. Disregarding females that were removed early, peak attraction seemed to occur on the second through fourth nights. One female attracted a male 11 days after emergence.

Females of radians likewise only attracted males of the same type (Table 7). Sixty-seven males were attracted to 15 of the 24 females. Nine females attracted no males. Ten of the 24 females were removed from the attractant cages before death. In 4 instances it was not noted if the female had died before being removed. The remaining 10 females died in their cages.

Disregarding the females which were removed alive, peak attraction seemed to occur on the second and third night after emergence. Two females attracted 5 and 14 males from 8 to 11 days after emergence. As with phalerata, radians males showed no cage preference.

Table 3. Number of wire [illegible] to catch, Virginia [illegible]

Stock	Date out	Day attracted ♂ ( )	♂♂ died	♂♂ removed alive from cage	♂♂
	1970				
L-33					
(#1)	31-V		8		0
(#2)	31-V		8		0
(#3)	12-VI		10		0
L-34	23-VI	3(1) 4(1)		5	2
L-36					
(#1)	16-VI		5*		0
(#2)	14-VI	1(1)		1	1
L-37	22-VI	5(1)	7		1
L-40	10-VII			4	0
L-41	4-VII			3	0
L-43	4-VII	3(1)		3	1
L-46	7-VII		3		0
L-47	8-VII	3(2)		3	2
L-48	14-VII		6*		0
	1971				
L-60					
(#1)	30-IV	1(1) 3(2) 8(3)	11		6
(#2)	1-V		6		0
(#3)	2-V	2(1) 4(3) 5(1) 6(4)	14		9
(#4)	18-V		5		0
L-61					
(#1)	7-V	2(1) 3(3)	7		4
(#2)	12-V		6		0
(#3)	18-V	2(1)	8		1
L-63					
(#1)	3-VI	3(2)	5		2
(#2)	8-VI	1(1) 2(6) 5(1) 8(1)	13		9
(#3)	10-VI	5(1)	10		1
L-65	12-V	4(9) 6(1) 7(4) 11(1)	16		15

* ♀ killed by ants

Table 7. [illegible] attracted to [illegible] in F and F [illegible] in Anaheim

Stock	Date out	Day attracted & (#)	Q♂ died	Q♂ removed from Box	Total Q♂
	1970				
D-32					
(#1)	12-V	2(5) 6(3) 9(2)		*	10
(#2)	12-V	1(1) 3(5)	3		6
D-55					
(#1)	20-VI		8		0
(#2)	15-VI	1(1) 2(4)	2		5
D-56					
(#1)	4-VII		5		0
(#2)	11-VII	3(3)		3	3
D-45	7-VII	3(2)		5	2
D-51					
(#1)	29-VII		6		0
(#2)	26-VII			3	0
(#3)	26-VII	3(1)		3	1
(#4)	29-VII	2(1) 6(2)			3
(#5)	29-VII	2(2)	6		2
(#6)	29-VII	2(1)	6		1
D-32F_2col.1					
(#1)	1-VII			3	0
(#2)	7-VII			3	0
(#3)	30-VI	5(1)		5	1
D-32F_2col.2					
(#1)	16-VII			4	0
(#2)	23-VII		6		0
(#3)	14-VII			6	0
	1971				
D-62					
(#1)	6-V	5(1) 6(3)	6		4
(#2)	7-V	2(1) 4(1)	7		2
(#3)	18-V	2(2) 5(1) 6(3) 8(5) 9(9) 10(2)	16		20
(#4)	23-V	4(1) 8(2) 9(1) 10(1) 11(1)	14		6
D-66	18-VI	5(1)	15		1

* Date ♀ removed unknown

Seventeen female hybrids (phalerata ♀ x radians ♂) from 5 different colonies attracted a total of 42 males (Table 8). Three males were phalerata, the remainder radians. One female attracted a phalerata male on the second night and 2 radians males on the third night; another attracted 2 phalerata and 3 radians males on the first night and an additional 9 radians males in the next 6 days. One male was attracted to a hybrid female after 11 days. Peak attraction seemed to occur during the first 4 nights.

The female attractant studies strongly suggest that the 2 species of moths are in fact separate interbreeding populations in nature. The problem of whether the 2 species are separated by morphological and/or behavioral differences is apparently academic to the species question since males do not appear to be attracted to females of the other species. The problem of a chance male "finding" a virgin female of the other species seems to be fairly well resolved, despite the 2 species being able to mate successfully in the laboratory. The probability of the 2 types occurring together in nature and going through the correct behavioral sequences through mating, and this mating occurring often enough to sustain a hybrid population, seems extremely remote. More than 1000 males collected in light traps were examined and none had genitalia intermediate between the 2 types as had those of the laboratory hybrids, as would be expected if hybrid males were present in nature.

The attraction of wild males of both species to the caged hybrid females indicates that an intermediate pheromone (or possibly 2 pheromones) is produced by the hybrid genotype. The "hybrid" pheromone attracted males of both species in 2 cases, 1 female attracting both species on the same night. In both cases the female attracted more radians than phalerata males (2:1 and 12:2 radians to phalerata). This was not due to

Table 2. [illegible] of Anopheles [illegible] and [illegible] attracted to cages, [illegible] by [illegible]

Stock	Date out	♂♂ attracted ♀ (♂)	♂♂ died	♀♀ (♂) [illegible]	[illegible]
	1970				
DL-4446					
(#1)	22-IX		7		0
(#2)	22-IX		7		0
DL-4445col.2					
(#1)	13-X		4		0
(#2)	25-XI		10		0
(#3)	6-XI		11		0
	1971				
DL-6260					
(#1)	21-VII	2(1)* 2(4) 3(2) 6(1)	13		5
(#2)	23-VII	8(1) 10(1) 11(1)	14		3
DL-6261col.7					
(#1)	23-VII	4(1) 8(2)	12		3
(#2)	24-VII	3(1) 9(1) 10(1)	16		3
(#3)	3-VII	1(1)		1	1
(#4)	4-VII	1(2)		1	2
(#5)	4-VII	1(2)* 1(3) 2(1) 3(3) 7(5)	13		14
(#6)	12-VIII		6		0
(#7)	22-VIII	2(1) 4(6)	15		7
(#8)	21-VIII		14		0
DL-6261col.11					
(#1)	5-VIII	4(1)	15		1
(#2)	8-IX		10		0

* A. phalerata ♂; all others A. rediens

a lack of phalerata males since large numbers of offspring were collected in the light traps at the same time the females were out. A few phalerata males were attracted to the hybrid females on the first or second day. Apparently, in these 2 females the pheromone for both species was present and the pheromone attractive to phalerata was emitted early and only for a short time.

These results do not preclude the possibility of some of the females being only able to attract radians males.

Two females which attracted radians males were mated to those males. One pair mated successfully, the majority of the eggs hatching. This would indicate that if hybrid females occurred in nature they could potentially interbreed with at least radians males. However, one would suspect that neither the offspring of this cross nor the hybrids themselves would be well adapted to separate microhabitats in which phalerata and radians have each evolved, having a morphology and behavior different from that of either parent. Since both parent species are separate in nature they fulfill at least slightly different roles. The 2 species have been subject to selection as distinct species for probably thousands of years. To have an intermediate type (i.e., hybrid) instantaneously fit into some unique new microhabitat and not be selected against is difficult to imagine.

Large Cage Study

Neither the virgin phalerata or radians female attracted any DL-4446 hybrid males in the field cage. Finding males in the attractant cages would have shown that the hybrid males could respond to the pheromone of the phalerata and/or radians females.

No flying males in the attractant cages provided [illegible]. The males could have been preyed upon. The cage was not completely predator free; 2 tiger beetles (Cicindelidae) and 5 spiders (4 Linyphiidae, 1 Lycosidae) were killed within about 10 min when the attractant cages were being suspended. There were undoubtedly other potential predators present. However, the possibility of a rather low number of predators accounting for loss of most or all of the male moths seems slight. A few small tears and areas where the screen had pulled away from the sides could have provided a means of escape, but this possibility seems remote as most of these openings were repaired and the remainder were very tiny.

The screen sides might have interfered with the flight of the male moths orienting to the caged females. Any arc greater than a few feet would have sent the male moth into the side of the screen cage. Also, any orientation in a given constant direction (i.e., flying perpendicular to the wind until the pheromone is sensed) would be prohibited.

The environment of the screen cage might have been unnatural (for instance, males being on the sides of the cage) so that the males could not respond properly to the females.

Additionally, laboratory-reared males might not have been attracted as were wild males.

Finally, the females simply might not have been attractive to the hybrid males. If this explanation were so, to the exclusion of the aforementioned explanations, then males should be attracted to caged females of their own species in the screen cage.

The second experiment tested this hypothesis. No L-63 males were found in the attractant cages with a female of their own species.

[illegible]ly, the screen cage conditions [illegible] nature of the males themselves account for the males not [illegible] with the caged females.

Marked, Released Males

Of the 34 F_1 phalerata males (L-65) released, only 3 were attracted to a caged virgin female and none to the light traps during the 2-week period (Table 9). All 3 males were attracted to the L-65 female. This female also attracted 6 wild males. The other 2 females attracted 0 and 2 wild males. Twenty-six wild males were attracted to the 2 light traps.

The capturing of 3 marked males did not seem to justify releasing hybrid males. Releasing hybrid males could have introduced some introgression between the gene pools of the 2 species, hindering further study. If both radians and phalerata females attracted released males of their own species in great numbers, hybrid males might have been released to see whether they were attracted to either of the parent species.

The study does show, however, that laboratory reared males are attracted to virgin females. This was not known when the hybrid attraction experiment was carried out in the preceding study.

Seasonal Abundance

The relative abundance of phalerata and radians males is shown in Fig. 5.

Males of phalerata outnumbered radians males by about 7:1. Males of phalerata were abundant throughout the summer months, peaking in

Table 5. [illegible] (L-65) and wild ♂♂ attracted to sticky traps baited with virgin ♀♀

Date June 1971	No. of marked ♂♂ released	Marked (and unmarked) ♂♂ attracted to sticky traps baited with virgin ♀♀			
		L-65 ♀ out 3 June	L-65 ♀ out 8 June	L-65 ♀ out 12 June	L-65 ♀ out 16 June trap
12	6(m^1)*	-	-	-	1(w)
13	9(m^2)	-	1(w)**	-	1(w)
14	5(m^3)	-	-	-	3(m^1)
15	7(m^4)	-	1(w)	-	3(w)
16	7(m^5)	-	-	2(m^2)	5 w)
17		-	-	1(m^2)	2(w)
18		-	-	6(w)	11(w)
Total	34(m)		2(w)	6(w) 3(m)	26(w)

(m^1 through m^5)* L-65 males released on 12 through 16 June 1971

(w)** Wild males

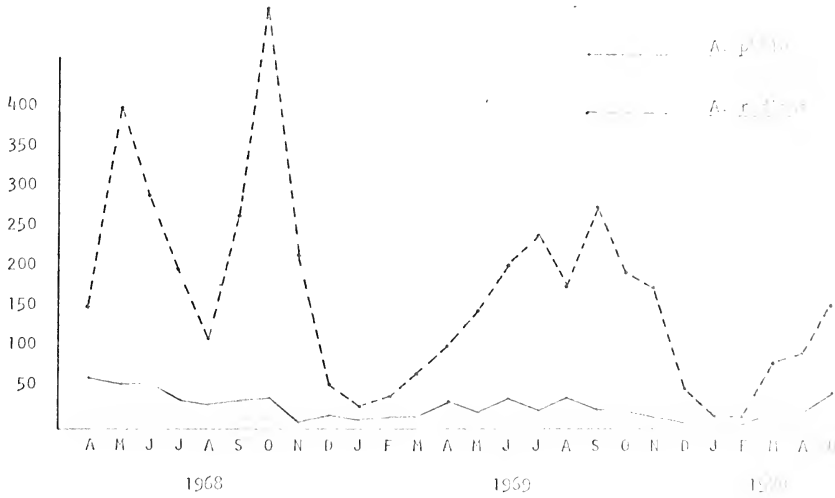

Figure 5. Abundance of male Apantesis phalerata and A. radians from 1 April 1968 through May 1970, in Gainesville, Florida

October. Their numbers [illegible] the winter months, then increased again in March.

Males of radians also were most abundant during [illegible], peaking in April in 1968, and in August in 1969, and [illegible] throughout the winter months until March.

Females of phalerata outnumbered those of radians by about 3.5:1. Females of phalerata were most abundant in October, the peaks coinciding with those of the male. Nine percent of the phalerata females were unmated. Fifty-nine percent mated once, 27% twice, and the remaining 5% mated three times (Fig. 6).

The relative yearly abundance of radians females probably cannot be stated accurately since their numbers were so low. However, the 1968 peak of April coincides with that of the male. No unmated radians were found. Seventy-five percent of the females mated once, 15% twice, and the remaining 10% mated 3 times (Fig. 7).

The sex ratio of phalerata males to females, as collected by blacklight, was about 55:1; the ratio for radians was about 29:1. The former contrasts sharply with the approximately equal numbers of phalerata males and females in Highlands County, Florida, reported by Frost (1963). Turner (1918) found a male to female ratio of about 48:1 in Agrotis vittata, a closely related species, attracted to blacklight in Hagerstown, Maryland. Bryant Mather (personal communication, 1971) found a male to female ratio of about 40:1 in phalerata attracted to blacklight traps in Mississippi. Although not computed many times more phalerata males than females were found by the author in the Florida State Division of Plant Industry blacklight samples over the past 3 years in Gainesville,

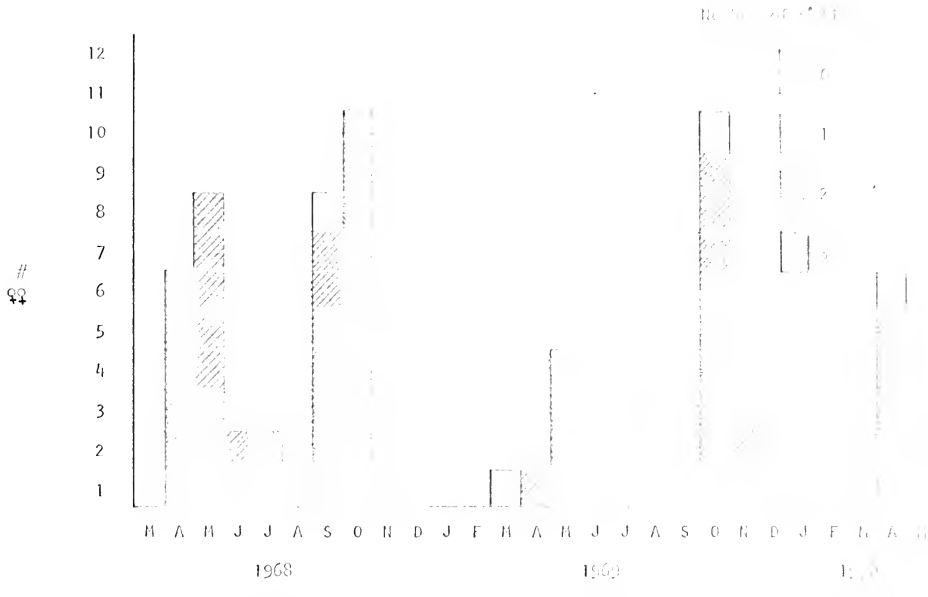

Figure 6. Female *Agantesis phalerata* collected in Gainesville, Florida, from 16 M[illegible] through 31 May 1970, showing number of matings per female

Figure 7. Female *Apentesis radiosa* collected in Gainesville, Florida, from [illegible] through 31 May 1970, showing number of matings per female.

[illegible] by Frost could also not [illegible] discrepancy).

[illegible] 5-year ecological study of [illegible] forest fire with [illegible] Burton (published as [illegible] Florida, Rhoades (1985) used Agaristia virgo (Linnaeus) as 1 of 20 indicator species. These non-target species showed the effect of insecticides on population size. The average number of A. virgo per light trap per year was 160.

The average number of phalerata and raptans per light trap per year in the present study was 970 and 145 respectively. The average number of A. virgo per light trap per year was less than 2 in Gainesville.

A. virgo is not common anywhere in Florida and it is probable that these specimens were actually phalerata, raptans, or A. phyllira (Drury) that were misidentified.

SUMMARY

Biological and hybridization studies were conducted on phalerata and radians from March 1969 through February 1972 in Gainesville, Florida. The life histories, morphology of immature stages, attractiveness of females to males, number of chromosomes, and seasonal abundance were investigated and compared.

The life histories of phalerata, radians, and a hybrid (radians ♂ x phalerata ♀), reared on an artificial diet at 23±1°C were nearly identical. No difference in larval or pupal duration was found between phalerata, radians, or hybrid colonies. Hybrid females had a longer immature stage than males since female larvae underwent at least 1 additional instar. Both phalerata and radians males and females had 6, 7, or sometimes 8 larval instars.

The 2 species could not be separated by mean head capsule width, with the possible exception of the first instar. The head capsule of the first instar larvae of phalerata was almost always wider than that of radians.

The morphological difference between the genitalia of adults conformed to that found in other studies. The genitalia of hybrids were intermediate between the parent species. No difference was found between the eggs, larvae, and pupae except that last instar phalerata larvae generally had more proleg crochets than radians.

In 3 separate laboratory studies, involving 57 [illegible] on 26 [illegible] pairings, 58% and 70% successful matings occurred, respectively. Fifty-six hybrid pairings of rediens male x phalerata female resulted in only 25% successful matings, and all 32 pairings of phalerata male x rediens female were unsuccessful.

Caged phalerata and rediens virgin females attracted only males of their own species in nature. Nine of 17 caged hybrid females attracted rediens males and 2 also attracted phalerata males.

The haploid chromosome numbers of phalerata, rediens, and the rediens male x phalerata female hybrid cross were 29, 30, and 29, respectively. These are the first counts of the genus Agonopsis and include the first count in the Lepidoptera of a hybrid between parents having different chromosome numbers.

A rare light strain of phalerata was found to be controlled by 2 sets of alleles at different loci. One gene controlled maculation, with the homozygous recessive condition accounting for the extreme light forms. Heterozygotes vary in their expression of maculation. Normally marked adults with full maculation are homozygous dominants. The rare yellow hindwinged females found in this strain are explained by the occurrence of the homozygous recessive state of a second gene.

Blacklight trap collections from April 1968 through May 1970 indicated that both species show increased abundance in March, relatively high numbers during summer months, and a trailing off in November and December. Male and female phalerata outnumbered those of rediens by 7:1 and 3.5:1, respectively. Nine percent of the wild phalerata females were unmated. Fifty-nine percent mated once, 27% twice, and the

LITERATURE CITED

Barnes, M. D., and J. McDunnough. 1912. On the larval stages of certain Arctian species. Can. Entomol. 44:132-136, 188-191.

Butler, A. G. 1881a. Descriptions of some apparently new species of Arctiidae from North America. Entomol. Mon. Mag. 18:136.

_____. 1881b. On some North-American sphinges and bombyces. Ann. Mag. Nat. Hist. 5:311.

Beutenmüller, W. 1898. Descriptive catalogue of the Bombycine moths found within 50 miles of New York City. Bull. Amer. Mus. Nat. Hist. 10:353-448.

Cassino, S. E. 1918. A new Apantesis. Lepidopterist 2:2-4.

Drury, D. 1770. Illustrations of natural history. White, London, England. 132p.

Dyar, H. G. 1900. Preliminary notes on the larvae of the genus Arctia. J. N.Y. Entomol. Soc. 8:34-47.

Emmel, T. C. 1969. Methods for studying the chromosomes of Lepidoptera. J. Res. Lepid. 7:23-28.

Fabricius, J. C. 1787. Mantissa insectorum. Part II. Hafniae, Proft, Germany. 374p.

Forbes, S. A. 1920. A monograph of insect injuries to Indian corn. Tewnty-third report of the state entomologist on the noxious and beneficial insects of the state of Illinois. State Printers, Springfield, Illinois. 280p.

Forbes, W.T.M. 1960. Lepidoptera of New York and neighboring states. Part IV. Agaristidae through Nymphalidae including butterflies. Cornell Univ. Agric. Exp. Sta. Mem., 271.

French, G. H. 1878. Lepidoptera or butterflies and their larva, or caterpillars. Part II. Econ. Entomol. of Ill., 181-182. In Seventh report of the state entomologist on the noxious and beneficial insects of the state of Illinois.

_____. 1881. Notes on the larvae of some moths. Papilio 1:81-82.

_____. 1882. The preparatory stages of Arctia nais Drury. Papilio 2:176-179.

Frost, S. W. 1963. Winter, insect-light trapping at the Archbold Biological Station, Florida. Fla. Entomol. 46:23-43.

Gibson, A. 1900. The life-history of Arctia phalerata Harr. Can. Entomol. 32:369-376.

_____. 1903. Notes on Canadian species of the genus Apantesis (Arctia). Can. Entomol. 35:111-123, 143-154.

Grossbeck, J. A. 1917. Lepidoptera of Florida. Bull. Amer. Mus. Nat. Hist. 37:54-55.

Hampson, G. F. 1901. Catalogue of the Lepidoptera Phalaenae. Part III. British Mus. Nat. Hist., London, England. 625p.

Harris, T. W. 1835. List of the insects of Massachusetts. Part IV, p. 595. In R. Hitchcock (ed.), Catalogue of the animals and plants of Massachusetts. Univ. of Massachusetts, Amherst, Mass., 595p.

Holland, W. J. 1903. The moth book. Doubleday, Page and Co., New York, 479p.

Kimball, C. P. 1965. The Lepidoptera of Florida. Div. Plant Industry, Fla. Dept. Agric., Gainesville, 363p.

Learned, E. T. 1927. A study of the male abdominal appendages of the nais group of Apantesis Walker (Lepidoptera : Arctiidae). Psyche 34:135-147.

_____. 1928. The early stages of Apantesis vittata (Lepidoptera : Arctiidae). Entomol. News 39:9.

Marchand, W. 1917. The specific differences between Apantesis nais Drury, A. vittata Fabr. and A. phalerata Harris. Psyche 24:59-60.

McDunnough, J. 1938. Checklist of the Lepidoptera of Canada and the United States of America. Mem. Southern Calif. Acad. Sci. 1:51.

Rhoades, W. C. 1963. A synecological study of the effects of the imported fire ant eradication program. Fla. Entomol. 46:301-310.

Robinson, R. 1971. Lepidoptera genetics. Pergamon Press, New York. 688p.

Saunders, W. 1863. On some hitherto undescribed Lepidopterous larvae. Proc. Entomol. Soc. Phila. 2:28-30.

Siefert, O. 1902. Contributions to the knowledge of North American Arctiidae. III. J. N.Y. Entomol. Soc. 10:82-89.

Shorey, H. H., and R. L. Hale. 1965. Mass-rearing of the larvae of nine noctuid species on a single medium. J. Econ. Entomol. 58: 522-524.

Smith, M. E. 1938. A revision of the genus Apantesis Walker (Lepidoptera, Arctiidae). Ph.D. Thesis. Univ. Illinois. 212p. Univ. Microfilms. Ann Arbor, Mich. (Diss. Abstr. 1:173).

Strand, E. 1919. Pars 22: Arctiidae: subfam. Arctiinae, p. 285, 295. In H. Wagner (ed.), Lepidopterorum Catalogus. W. Junk, Berlin, Germany.

Teitz, H. M. 1952. The Lepidoptera of Pennsylvania, a manual. Penn. State Coll. Sch. Agric. Penn., 194p.

Turner, W. B. 1918. Female Lepidoptera at light traps. J. Agric. Res. 14:135-149.

Walker, F. 1855. Catalogue of Lepidoptera Heterocera in the British Museum. Part III. British Mus. Nat. Hist., London, England. 775p.

BIOGRAPHICAL SKETCH

Jack Stangl Bacheler was born 30 December 1943, in Washington, D.C. In June 1962, he graduated from Birmingham Seaholm High School in Birmingham, Michigan. In June 1966, he received the degree of Bachelor of Arts with a major in Zoology from Miami University in Oxford, Ohio. In 1966, he enrolled in the Graduate School of the University of Florida. He worked as a research assistant in the Department of Entomology until June 1968, when he received the degree of Master of Science. From June 1968 until the present time he has pursued his work toward the degree of Doctor of Philosophy.

Jack Stangl Bacheler is married to the former Joanne Anne Elce and is the father of one son. He is a member of Omicron Delta Kappa, The Newell Entomological Society, The Florida Entomological Society, and The Lepidopterists' Society.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Dale H. Habeck, Chairman
Associate Professor of Entomology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Thomas C. Emmel
Assistant Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Thomas H. Patton

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This dissertation was submitted to the Dean of the College of Agriculture and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

June 1972

Dean, College of Agriculture

Dean, Graduate School