STUDIES ON RESTINGA BUTTERFLIES. I. LIFE CYCLE AND IMMATURE BIOLOGY OF MENANDER FELSINA (RIODINIDAE), A MYRMECOPHILOUS METALMARK

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This paper is the first of a series that deals with various aspects of the ecology of butterflies which inhabit the sandy coastal plains near the sea in southern Brazil. Called the "restinga" in Portuguese, it is an unique habitat that contains a large number of endemic plants and animals. Unfortunately, it is valuable land for real estate development and at present is being altered to make way for new residential and resort areas. Also, the new coastal highway from Rio de Janeiro to Santos, now under construction, is altering great expanses of restinga vegetation and in the process is opening up previously isolated areas to commercial exploitation. All this underlines the urgency with which the Brazilian coastal flora and fauna must be studied before their demise in the wake of "civilization."

The purpose of this paper is to describe the habitat and larval biology of *Menander felsina* (Hew.), an endemic resting butterfly. The discussion will include descriptions of oviposition, larval behavior, and relationships with ants. A future paper will deal with other aspects of adult behavior and population dynamics.

Published information on the larval biology of the neotropical riodinids is very scanty, especially considering that there are over 1500 recognized species. The majority of references deal with foodplant records or a description of larvae and pupae (Zikán, 1920, 1953; Stichel, 1920; Beutelspacher, 1972; Monte, 1934; Raymundo, 1907; Santos, 1931; Gomes, 1940; Biezanko, 1949; Bertels, 1954; Mabilde, 1896; Ronna, 1933; Mariconi, 1961; Brandão, 1942). To date, I know of only four studies on the relationship of riodinid larvae with ants, these being Ross (1966), Guppy (1904), Bruch (1926), and Bourquin (1953), which cover a total of six species. In contrast, there are 245 known myrmecophilous lycaenid larvae (Downey, 1961). In the present paper, the riodinid list is increased to seven species, a number which I suspect will grow in time with additional observations.

The range of *M. felsina* is coastal Brazil from Joinville, Santa Catarina to Rio de Janeiro, the latter being the type locality (Hewitson, 1863). Seitz (1916) gives the distribution as being southern Brazil, and Staudinger (1888) mentions a specimen from Santa Catarina. The male

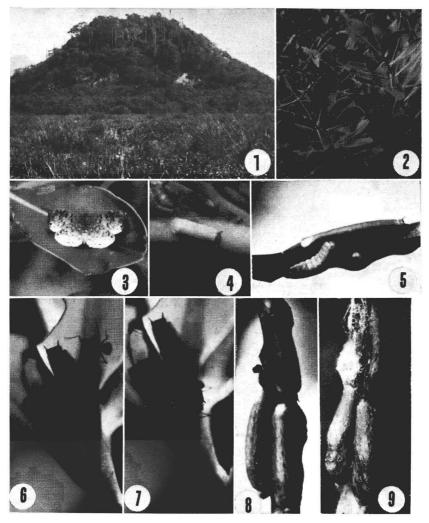
butterfly described by Butler (1877) is undoubtedly something else since it is nothing like those from southern Brazil. Certainly the confusion in this case resulted from Hewitson (1863–1878) illustrating only the female, leaving the male to the imagination. Material examined in the Museu Nacional and the Instituto Oswaldo Cruz collections indicates that the species is confined to the narrow coastal strip from Rio to Joinville, there being in addition to these localities specimens from Angra dos Reis between Rio and Santos.

Study Area and Methods

The study location is in a small woods at the base of a large rock (Fig. 1) some 20 m high called Pedra de Itauna at km 11 of the Rio-Santos highway. Here, the highway runs along a sand bar or "restinga" ca. 20 km long and 2 km wide that separates some small brackish water lakes from the open coast. An annual rainfall of ca. 1.5 m and an average temperature of 23°C place the area within the subtropical-humid classification of Holdridge (1967). The vegetation is not what one would expect in a subtropical-humid zone, however, since the sandy soils quickly drain moisture away, giving the landscape a rather desert-like appearance. The flats on the seaward side are covered with meter-high scrub that consists of bromeliads, cactus (Cerus sp.), and low deciduous bushes intermixed with grasses and other annuals such as Sporobohas virginicus and Panicum racemesum and with patches of low woods ca. 5 m high in protected localities. The vegetation in these latter areas is very dense, making penetration difficult except by man-made paths and in occasional sandy clearings, 5-10 m in diameter, which are encountered sporadically in the woods.

Typical genera of trees and bushes are *Myrsine*, *Ocotea*, *Myrcia Tabebuia*, *Clusia*, *Eugenia*, and *Psidium*. The forest floor is packed knee deep in bromeliads, and the trees and bushes are festooned with mosses, lichens, and other epiphytic plants that take advantage of the frequent fogs which roll in from the sea. Bromeliads are represented by the genera *Nidularium*, *Billbergia*, *Aechmea*, *Vriesia*, and *Tillandsia*; Araceas by *Philodendron* and *Anthurium*; the Pteridophytes by *Lycopodium*, *Polypodium*, *Polystichum*, and *Elaphoglosum*; and the Gesneraceae by *Codonanthe* and *Hypocyrta* among others (Joly, 1970). Gallery forests with trees up to 10 m high are found in the better protected parts on the leeward side of the restinga. These support a flora and fauna similar to those farther inland, with *Heliconia* plants and other shade-loving varieties replacing the bromeliads on the forest floor.

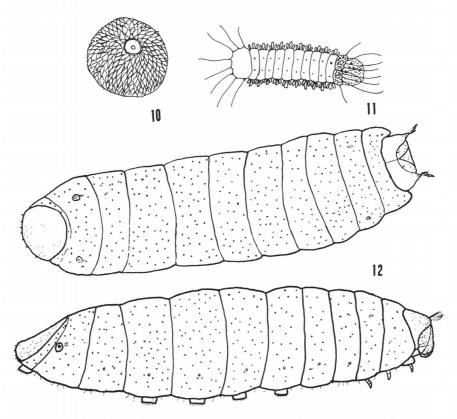
The habitat of M. *felsina* is the area of low woods just inside the seaward edge. Here, the adults can be found feeding on flowers and,



Figs. 1–9. 1, Habitat of *Menander felsina* showing woods at base of rock; 2, *Norantea brasiliensis*, foodplant of *M. felsina* larvae; 3, *M. felsina*, female on leaf of foodplant; *M. felsina*, third instar larva; 5, *M. felsina*, fifth and sixth instar larvae; 6, ant (*Camponotus crassus* ssp.) "drumming" on larva of *M. felsina*; 7, ant (*Camponotus crassus* ssp.) feeding at honey glands of *M. felsina*; 8, *M. felsina*, prepupal larva, note honeydew on upper part of larva; 9, *M. felsina*, pupa.

in the case of males, patrolling along paths and in the sandy clearings. The M. *felsina* will fly outside the woods on the flats for oviposition and feeding.

The observations that form the basis of this study were made over a



Figs. 10-12. Menander felsina: 10, egg; 11, first instar larva; 12, final instar larva, side and top views.

period of four years and some 46 visits. Ova were obtained after observing ovipositing females in the field and immatures were aquired by rearing them from eggs or collecting them on the foodplant, *Norantea brasiliensis* Choisy (Marcgraviaceae) (Figs. 2, 3). These were brought into the lab with the foodplant and raised in fruit jars. Attempts to induce females to oviposit on foodplant in the lab were unsuccessful; the insects remained in the corner of the cage nearest the light until dying three or four days after being caged. Of the 10 larvae brought in from the field, six pupated and four emerged as adults. Causes of death for larvae appeared to be injuries due to handling. The reasons for the pupae not emerging are unknown. In no case, however, were parasites found on larvae or pupae. Of eight eggs collected, five hatched and two larvae were raised to the third instar. Some larvae died in the first instar because we had no foodplant for them. Observations on ants were made both in the field and in the lab, and, in the latter case, on ants that were kept with the larvae.

Description of Immature Stages

Egg (Fig. 10). About 0.4 mm in diameter, flattened above and below, giving it the appearance of a rounded tire, covered with network of lines. Micropyle a small circle with a dot in the middle. Color brown, matching stem on which egg is laid. Duration: 10-11 days.

First instar larva (Fig. 11). Newly hatched larva 1.3 mm in length; light green in color except for head and prothorax, which are dark brown. Forward edge of prothorax with 10 long, flexible setae extending over head. Rest of thoracic and abdominal segments have scaly lateral protrusions, three to a segment, the middle one being the largest, and a double row of black spots on dorsum. A transparent carapace attached to anal segment and extending past the rear of the larva has six long, flexible setae along its edge similar to those on prothorax. Very small, inconspicuous spiracles located along sides of abdominal segments 1–8 and on suprapedal lobe of prothorax. Duration about 6 days; head capsule width 0.2 mm.

Second instar larva. Coloring as in first instar but with scattered green specks on body. Setae of the prothorax same as in first instar only with two having developed into flattened lobes reaching the length of head. The scaly lateral protrusions present but folded under body. Plate at end of abdomen has setae as in the first instar, though proportionally reduced in length. Spiracles as in first instar. Duration 4 days; total body length 3 mm; head capsule width 0.3 mm.

Third instar larva (Fig. 4). Coloring as in second instar. Head brown with white specks on face. Setae of prothorax reduced to two lobes with one long seta coming from base of each and with two shorter ones on the sides. Tail plate setae reduced to small projections, and protrusions on sides of body missing. Honey glands on eighth abdominal segment well-developed with spiracles immediately above them. Other spiracles as in first instar. A small slit found on upperside of metathorax, corresponding to the tubercles mentioned by Ross (1966). Duration 5 days; total body length 5 mm; head capsule width 0.5 mm.

Fourth instar larva. Color as in third instar. Setae of prothorax consist of two groups of three, flat, elongated lobes, one larger than the other two. Two large setae found on sides of prothorax. Legs bear tufts of setae, otherwise similar to third instar. Duration 4 days; total body length 7 mm; head capsule width 0.9 mm.

Fifth instar larva (Fig. 5). Similar to fourth instar. Duration 5 days; total body length ca. 16 mm; head capsule width 1.2 mm.

Sixth instar larva (Figs. 5, 12). Similar to fourth and fifth instars only larger. Four days after molting larva enters into prepupal stage, the body turning mottled brown, except for patch of original green color dorsally. Prepupa (Fig. 8) lasts for 5 days, after which the pupa is formed. Length of prepupal larva 22 mm; head capsule width 1.8 mm.

Pupa (Fig. 9). Light to dark brown mottled with greenish shading dorsally, attached by thin girdle passing over middle of body and by silk pad under last segment. Wing cases extend halfway along sides. Duration 22 days; total length 21.5 mm; width at widest part of body 5 mm.

DISCUSSION

The foodplant (*Norantea brasiliensis*) of M. felsina at the study location is woody with rounded succulent leaves growing alternately around stems that spread out in all directions from the base of the plant to a maximum height of 1.5 m. The flowers appear from late

September–January in the form of small red balls with nectar caps hanging below them growing off an extension of the stem. Individual plants are widely but sparingly distributed around the restinga, generally in the protection of clumps of larger bushes. All plants discovered in the study area showed signs of larval damage.

Oviposition occurs from 1230–1400. The female alights near the end of a stem of N. *brasiliensis* and walks down it in a spiraling motion exploring the surface with her abdomen. A single egg is quickly deposited on the main stem near the base of a leaf. She then flies a short distance away to rest on the upper surface of a leaf, wings outspread. Within two minutes she returns to the food plant, depositing another egg on a different stem of the same plant or on a second plant if there is one in the same vicinity. One female was observed placing four eggs within 12 min. A total of five ovipositions were observed, and in no case were more than four eggs deposited by any one female in any given session.

The tiny larvae hatch 10-11 days after oviposition and immediately move up to the leaf buds of the plant, where they begin to feed. They spend their time hidden inside the curled portion of the bud, betraving their presence only by the frass that they leave outside the opening. After the second molt they move out and start feeding on the older leaves as well as the buds, always eating the edges and ends of the leaves. Feeding is during the early morning, late afternoon, and evening hours and on cloudy days. During the hot part of the day the larvae move to cooler spots under leaves or near the stem of the plant and remain motionless, their flat profiles and green color allowing them to blend in perfectly with the leaves on which they rest. To determine whether they were active at night, two visits were made to the foodplant after dark. Using a flashlight with a piece of red plastic over the lens, two larvae were located resting on the plant. They showed no interest in feeding or any other activity during the 2 hours they were watched. This inactivity during the night was noted with larvae raised in the lab. However, molting, entering into the prepupal stage, and pupation all took place during the night in the lab. Larvae of about the same size will remain together for feeding and pupating. However, it was more common to find solitary larvae, one to a stem of foodplant. When larvae of different instars were raised together, they showed no interest in each other and always fed separately on different leaves. No cannibalism was observed. When moving onto a leaf the first time, they always laid down a trail that consisted of strands of silk with a weaving motion of the head. This trail was used to maintain a grip on the surface of the leaf. If knocked off, the larvae would invariably remain dangling by a thread of silk.

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Starting with the third instar, the *M. felsina* larvae are myrmecophilous, being attended by ants that are a subspecies of *Camponotus crassus*. The early instars are completely ignored by ants. Upon encountering a larva, the ants will caress it with their antennae, rapidly alternating the strokes, first with one antenna and then the other, much as one would play a drum (Fig. 6). The larva responds to this "drumming" by extending two small glands located on the eighth abdominal segment from which is emitted a small quantity of clear liquid that the ants eat (Fig. 7). The ants remain in the vicinity of the larva for some time, returning now and then for more "drumming" and liquid. In the lab, I tickled a larva with a hair, ant fashion, and managed to get it to extend the glands. But these were quickly withdrawn and the larva started to move off, showing signs of being disturbed. Undoubtedly the larva was able to distinguish between ants and other stimuli.

In fact, an ant need not actually caress the larva; its mere presence nearby is enough to cause the larva to protrude the organs, an action that may serve as an attractor for the ants. The means by which the larvae know when an ant is near could not be determined during the study.

The honey glands located on the eighth abdominal segment were the only active myrmecophilous structures observed. On the metathorax are two slits high on the back corresponding to the lateral tubercles of Ross (1966), but prolonged observation of these under magnification failed to show any physiological change in them, even with ants in attendance. This is in contrast to the protrusion of the lateral tubercles noted in various other riodinid larvae such as Lemonias rossi (Ross, 1966) and Audre sp. (Callaghan, in prep.); these tubercles possibly serve to attract ants or frighten predators (Ross, 1966). Likewise, the "horns" of the prothorax in M. felsina appeared completely passive in relation to ants, unlike the vibrating pupilla of L. rossi. When disturbed, the *M. felsina* larvae nod the head rapidly up and down, creating vibrations inaudible to the human ear, but this seemed not to be directly related to the relationship with ants. The function of the "horn" structures in *M. felsina* remains a mystery, though, since ants were observed stroking the head and neck area, they could have an attractive or sensitive role.

The ants frequent the N. *brasiliensis* plants, eating plant secretions. When a larva is located, the discovering ant will communicate this information to nearby ants. An attendant ant was observed leaving a larva, walking over to another ant with whom it touched antennae, and being followed back to the larva, where both ants commenced "drumming" and partaking in the larva's fluids. Soon the first ant left, and the second

remained in attendance. Similar observations were made by Ross (1966), though in this case one ant passed honeydew to the other to communicate the presence of larvae.

It is apparent that the ants protect the larvae. In no case were larvae found parasitized by wasps, tachinid flies, or fungi, the constant attention of the ants undoubtedly serving to discourage this type of predation (Edwards, 1878). Norantea brasiliensis frequented by ants were largely free of other insect life, the exceptions being flying insects visiting the flowers and another lepidopterous larva found feeding on the leaves, but not attended by the ants. In contrast, other kinds of plants had numerous spiders and other small insects. To test the reaction of the ants to intruding organisms, small spiders were released on the *N. brasiliensis* near ants attending larvae. Upon discovering the intruders, the ants took up a defensive position, typical of *Camponotus*, by rearing up on the hind legs with the abdomen tucked between them. The intruders always beat a hasty retreat under these circumstances.

Observations of *M. felsina* indicate that the larvae remain on the foodplant 24 hours a day from hatching until pupal diapause, always with the ants nearby. The only time when larvae were discovered without ants was on one particular plant during a rainstorm.

Shortly after the fifth instar, the larva moves off the leaf where it had fed and crawls down the stem to the lower part of the plant. Here, it takes a head-down position on the stem or among the leaf litter nearby and assumes the mottled brown-green color of the prepupa. Observations of specimens in the lab indicate that this takes place at night. If disturbed, the larva will move off to find a more suitable spot. During this stage, the honey glands often secrete large quantities of honeydew, thus attracting the ants, which can always be found around the prepupal larvae. This undoubtedly provides protection during a very vulnerable period in the larva's life. After 5 days, the larval skin is shed and the chrysalid case hardens, again taking place during the night-time hours. The ants at this point lose interest and abandon the pupa. The imago emerges 21 days later.

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NOTES AND NEWS

Letters to the Editor

Dear Mr. Godfrey,

Referring to the article of Mr. Hans Epstein in "Notes and News" in the Journal of the Lepidopterists' Society, vol. 31, number 1, pp. 73–74, I have to protest strongly against Epstein's remark that "F. Bryk and C. Eisner . . . are heavily responsible for the oversplitting; for instance, by now 200 odd subspecies of Palaearctic *P. apollo* L. have been described." I regard it as a malicious remark. Objectively, many more *apollo* subspecies have been described by other authors than Bryk and myself.

Sincerely yours, Curt Eisner

Dear Dr. Godfrey:

The repeated recent mentioning of *Papilio xuthus* occurring in Hawaii (vol. 30: 149 and vol. 31: 75) and the conjecturing about from where it may have immigrated needs a clarification from local Hawaiian records. The first specimen was recorded during April 1971 at Salt Lake, Honolulu, near Hickam Air Force Base. The species spread rapidly in the following years over all the Islands: 1972 Kauai, 1974 (June) Maui and Hawaii, 1974 (August) Molokai, 1974 (September) Lanai. Hawaiian entomologists are convinced that it came here by means of military planes, probably from Guam where it previously had its easternmost distributional limit. It is not alone in its way of immigration. Over the last few years we got also from Guam the banana skipper (*Erionota thrax*), the first specimen of which was caught at Hickam Air Force Base in August 1973. Three recent newcomers among the Sphingidae were also first recorded around Hickam Air Force Base. Their easternmost distributional limit before they came here was Okinawa: Theretra nessus (August 1974), Deilephila nerii (September 1974), Macroglossum pyrrhostictum (July 1976). Very often live specimens are intercepted by the quarantine service of the Department of Agriculture. So was recently recorded a \mathcal{Q} of *Psilogramma menephron* on a military plane from the West Pacific (Guam?). Also commercial planes occasionally bring in interesting species: in a PAN AM plane from Pago Pago (Samoa) came a live 3 of Deilephila torenia, a beautiful and rare, dark olive-green phenotype. One of the latest live interceptions on a military plane was a 3 of Hippotion boerhaviae from Guam. Among the butterflies there suddenly appeared this year (January) large numbers of the gulf fritillary (Agraulis vanillae), and nobody has an explanation how that may have happened.

> Sincerely, J. C. E. RIOTTE