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NEOTROPICAL NYMPHALIDAE
VII. REVISION OF *NESSAEA*

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A. INTRODUCTION

Nessaea is a small distinctive genus of colorful butterflies in the subfamily Eurytelinae. The male and female adults have a bright, turquoise blue, diagonal crossband on the dorsal forewing, and unique apple-green coloration on the ventral surfaces of the wings. The males are black above, and most species have some orange on the dorsal hindwings. The females are brownish above with a blue crossband. Striking differences in wing coloration and pattern appear to reflect a record of phylogenetic history in both species and subspecies.

Nessaea and *Catonephele* were previously combined in the genus *Epicalia*, and a revision by Stichel (1899) included *Nessaea* and *Myscelia* in the genus *Catonephele*. Röber, in Seitz (1915), and other authors have recognized *Nessaea* as a separate genus. Vane-Wright (1979) revised *Nessaea* based on specimens in European museums. He designated lectotypes, but did not formally recognize subspecies. He presented a cladistic study based on eight wing color/pattern elements. His revision was of great value in the present study.

A phylogenetic and biogeographic study of the subtribe Catonephelina (Jenkins, unpub.) indicates that it is comprised of four monophyletic genera, *Catonephele, Nessaea, Myscelia* and a new genus *Catocelia*. Cladistic analyses required morphological studies and a revision of *Nessaea* to allow morphological comparisons with *Myscelia* and *Catonephele* (revised by Jenkins, 1984 and 1985, respectively).

Nessaea is here revised based primarily on a new study of morphological characters of wing venation, male genitalia, the male hypandrium and rami (subgenital plate, modified 8th sternite), female genitalia, legs and palpi, as well as wing color/pattern elements previously used. Field studies and collecting by the author emphasized detailed study of local and phenotypic variation, and especially intergradation between subspecies. The sequence of species used in this revision of *Nessaea* is based on the phylogeny hypothesized in the cladistic study.

A biometric study was made by measuring forewing lengths of a large number of *Nessaea* adults. A comparison made with latitude and range shows that for *N. obrina* and *N. hewitsonii* there is a direct correlation of increase of wing length with increase of latitude, as stated in Bergmann's Rule.

Ten taxa are assigned to the genus, which includes four species and six subspecies.

Five taxa are newly synonymized in this study and the status is revised for several taxa including *N. regina* which is made a subspecies of *N. aglaura*.

D'Abrera (1987) illustrated species but not subspecies of *Nessaea*. Accurate identification of his pictures is difficult since all dorsal-ventral views of males are from different specimens (compare antennae and wing shape) and their localities are not given. Tentative identification of dorsal views of males are: *N. regina* = *N. aglaura regina*, *N. aglaura* = *N. aglaura aglaura*, *N. batesii* = *N. batesii magniplaga*, *N. obrinus* = *N. obrina faventia*, *N. hewitsoni* = *N. hewitsonii hewitsonii*. *N. aglaura thalia*, *N. o. obrina*, *N. o. lesoudieri*, *N. batesii batesii*, and *N. hewitsonii boliviensis* are not illustrated.

B. MATERIALS AND METHODS

Nessaea were collected and studied in the field by the author in many localities in six neotropical countries. Series of adult specimens were collected in the field to study the range of variation in a locality, especially in intergrade areas. Twenty nine museum and private collections were examined and the *Nessaea* were identified. Type specimens were studied in the British Museum (Natural History), London, and in the Museu Nacional, Rio de Janeiro, Brazil. The Stichel collection in the British Museum was especially valuable since he previously revised the genus in 1899. Slides of male genitalia of *Nessaea* that he prepared were also studied.

Male genitalia and hypandria were dissected in 24 specimens and genitalia in six female specimens. They were preserved in small glycerine vials that were numbered and deposited with their corresponding specimens.

The nomenclature of wing veins follows Miller (1970). The venation and nomenclature of *Nessaea* are shown in Fig. 1. The terminology for the male and female genitalia follows Klots (1970) and for the hypandrium or subgenital plate (8th sternite), including the postero-lateral appendages or rami, follows Tuxen (1970).

Keys are presented for identification of species of both males and females, and for male genitalia, hypandria and rami. Separate keys are presented for differentiating subspecies.

Data have been compiled for each specimen examined including sex, date, geographic locality, altitude and collection in which it is found. Full data are presented only for rare or new species or subspecies. The exact localities are presented but other data on sex, dates and altitude are summarized for more common taxa. These details are available from the author.

Distribution maps (Figs. 58-61) are based on specimens examined and determined by the author. Combined circles, triangles or squares indicate intergrades between subspecies at boundaries of ranges (or tension zones). An "X" after a locality name in the text indicates intergrades.

Over 1,400 specimens of *Nessaea* were studied and identified. Type specimens of twelve taxa were examined and compared with other specimens and the taxonomic implications are presented. Color photographs were made of the types and other critical specimens and the negatives and prints are deposited in the Allyn Museum. The holotype of one new subspecies described is in the Allyn Museum.

COLLECTIONS EXAMINED

AA - Allyn Museum of Entomology, Florida Museum of Natural History, Sarasota, FL (L. D. & J. Y. Miller)
AM - American Museum of Natural History, New York City, NY (F. H. Rindge)
BM - British Museum (Natural History), London, England (R. I. Vane-Wright, P. Ackery)
BO - Booth Museum, Brighton, England (G. Legg)
CA - California Academy of Sciences, San Francisco, CA (P. H. Arnaud)
CM - Carnegie Museum of Natural History, Pittsburgh, PA (J. E. Rawlins)
DB - Danny Burk Collection, South Bend, IN
DM - De la Maza Collection, México City, México
FL - Division of Plant Industry, Florida Dept. Agriculture, Gainesville, FL

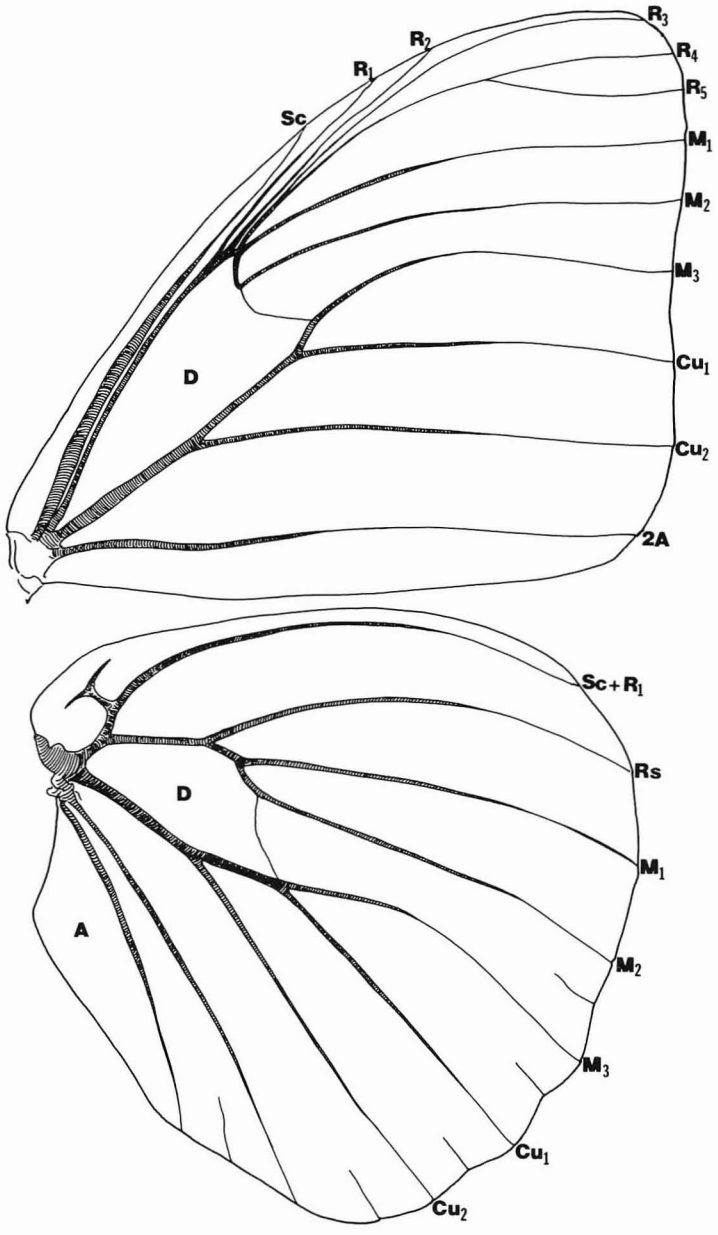


Figure 1. Wing venation of *Nessaea hewitsonii* showing nomenclature of veins.

GS - Gordon B. Small Collection, Balboa, Panamá (now in SI)
HD - Henri Descimon Collection, Marseille, France
JC - Dale and Joanne Jenkins Collection, Sarasota, FL
KB - Keith S. Brown Collection, Campinas, Brazil
LA - Los Angeles County Museum of Natural History, Los Angeles, CA (J. P. Donahue)
MM - Milwaukee Public Museum, Milwaukee, WI (A. M. Young & S. S. Borkin)
MN - Museu Nacional, Rio de Janeiro, Brazil (J. Cândido de Mello Carvalho)
MP - Muséum National d'Histoire Naturelle de Paris. Paris, France (G. Bernardi)
MZ - Museum of Comparative Zoology, Harvard University, Boston, MA (M. D. Bowers)
NC - James Neidhofer Collection, Milwaukee, WI (in MM)
PA - Philadelphia Academy of Sciences (in CM)
RO - Romero Collection, Maracay, Venezuela
SI - National Museum of Natural History, Smithsonian Institution, Washington, D. C. (J. F. Gates Clarke and R. Robbins)
SN - Stanley Nicolay Collection, Virginia Beach, VA (now in SI)
ST - Herman Strecker Collection (now in Field Museum of Natural History, Chicago, IL)
TE - Thomas Emmel Collection, Gainesville, FL
UC - Facultad de Agronomía, Universidad Central de Venezuela, Maracay, Venezuela (F. Fernandez & L. D. Otero)
UN - Universidad Nacional Mayor de San Marcos, Museo de Historia Natural, Lima, Perú (G. Lamas)
UP - Universidade Federal do Paraná, Curitiba, Brazil (O. Mielke)
VK - Harold L. King Collection, Sarasota, FL (now in FL)

C. BIONOMICS

Nessaea occur from Veracruz and Yucatán, México through Central America and throughout northern South America and the Amazon basin, south to Bolivia and Misiones, Argentina. They are found in evergreen tropical rain forest, in semi-deciduous tropical rain forest, or in semi-evergreen seasonal forest. DeVries (1987) states that in Costa Rica, *N. aglaura* is found only in swampy areas in primary rain forest.

I have studied the behavior of adult *Nessaea* in Panamá, Guyana, Venezuela, Brazil, Ecuador, and Perú. The data are similar for all species. These observations concur with those reported by Bates (1866), Davis (1928), Vane-Wright (1979), and DeVries (1987). The adults usually occur singly in forests that are undisturbed or with few trails and selective timber cutting. They may occur in forest openings where trees have fallen or at the edges of streams. However, I have collected *N. obrina* in cut-over heavily grazed areas in Guyana. Adult males alight on the upper surface of leaves in full sunlight with their bright blue and orange colors fully exposed. Collecting is difficult and netting from below the leaves is usually more successful. They are very wary and are readily disturbed by the slightest movement or noise. If only slightly excited they quickly fold their wings and show only the apple-green underwings and are difficult to distinguish from the leaves. If they are more disturbed, they fly very rapidly and usually alight nearby, but rarely return to the same resting place. In rainy or cloudy weather I have found them hanging from the ventral surface of leaves with only the green underwings exposed. Males are more commonly collected (998 males to 434 females).

Both male and female adults are highly attracted to baits of fermented fruit, especially banana and mango on tree trunks, leaves, or on the ground. They are also found at fermented sap runs on tree trunks, but respond only slightly to baits of fermented human or pig feces. They are attracted to bait traps but do not enter them readily, similar to *Myscelia*. According to DeVries (1987) the females are most active in the middle of the day, when they are ovipositing on seedlings of *Alchornea*, which occur in light gaps and along riparian edges. The eggs are yellow-green as in *Catonephele orites*, and are laid singly.

Stoll (1787) illustrated the larva of *Nessaea* with red lateral stripes. The larvae and pupae of *N. obrina* have been illustrated in color paintings by the Rev. A. Miles Moss and by Miss M. E. Fountaine, and were published in black and white with brief descriptions

by Vane-Wright (1979). A mature larva of *N. aglaura aglaura* is depicted in Fig. 2 (after DeVries, 1987) which shows the larval setal characteristics. He describes the larva and pupa as follows:

> "*Mature larva* — body a beautiful jade green with three spines per segment, each bearing five branches; spines amber; head the color of blue steel on the anterior half, amber on the posterior half; two long head horns bearing three sets of whorled spines on the shaft; posterior half of horns amber, the anterior half blue (Fig. 23). As in *Catonephele*, the larvae rest on the dorsal surface of leaves with the face down and the horns projecting forward and react violently when molested. *Pupa* — dark green, mottled with scaly brown on the wingpads. Pupation takes place on the dorsal surface of leaves with the body held horizontal to the substrate."

D. SYSTEMATICS

Nessaea Hübner, [1819]

Nessaea Hübner, [1819]. Verz. Bekannt. Schmett. (3): 41. Type-species by selection of Hemming, 1943. Proc. R. Ent. Soc. London. (B) 12: 28: *Papilio ancaeus* Linnaeus. Vane-Wright (1981) states: "*Papilio ancaeus* is currently considered to be a junior subjective synonym of *Papilio obrinus* Linnaeus, 1758: 470. (Clerck, 1764: Pl. 31; Stoll, 1787:31)."

Polychroa Billberg, 1820. Enum. Ins. Mus. Billb.: 78. The type species *Papilio obrinus* L. (Scudder, 1875. Proc. Amer. Acad. Arts Sci., 10: 253) is a junior objective synonym.

[*Catonephele*; Hübner auctt. (in part).]

[*Epicalia* Doubleday; auctt. (in part).]

The validity of *Nessaea* as a separate monophyletic genus has been confirmed by cladistic analysis (previously cited) of the subtribe Catonephelina. This analysis also shows that the problematic *Myscelia capenas* Hew. should be assigned to the genus *Catocelia* (cited above). It lacks the green underwing surface and the blue median diagonal crossband typical of *Nessaea*; however, it has a white crossband and other characters which also occur in some *Nessaea*.

The genus *Nessaea* is characterized as follows:

1. Adults contain a brilliant blue pterobilin pigment (Choussy & Barbier, 1973) exhibited in both sexes as a blue median diagonal crossband on the dorsal forewing.
2. The ventral surfaces of the wings of both sexes are predominently apple-green.
3. The male genitalia has a spindle-shaped saccus tapering to a point.

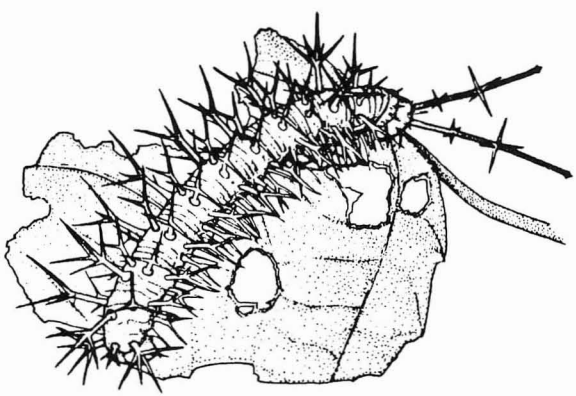


Figure 2. Larva of *N. aglaura aglaura*.

4. The male hypandrium has a broad bulbous base, greatly constricted at the middle and posterior, with small pointed postero-lateral projections.
5. The female corpus bursae has two elongate signa (composed of clusters of small chitinized teeth), with an anterior lateral projection pointed internally. This is unique to *Nessaea* and *Catonephele*.
6. The female lamella antevaginalis is broadly rectangular with two elongate pointed postero-lateral projections.
7. The presently known chromosome number is 11 (*Nessaea batesii*, deLesse, 1970) which is unique in Eurytelinae.

KEY TO ADULT MALE *NESSAEA*

Males.

1a. Dorsal hind wing (DHW) with submarginal blue cross band ..... *hewitsonii*
1b. DHW without blue cross band 2
2a. DHW with orange marking 3
2b. DHW without orange marking ..... *aglaura regina*
3a. DHW with orange marking restricted to costal area anterior to M_1; dorsal fore wing (DFW) with subapical blue marking, ventral hindwing (VHW) with blackish median line thin ..... *aglaura*
3b. DHW with orange marking extending posterior to M_1. DFW without blue subapical markings, VHW with reddish-brown median line broad and diffuse 4
4a. DHW with orange band broad, markings extending nearly to distal anterior margin in $Sc+R_1$ to Rs. VHW with postmedian ocelli joined proximally by a broken dark line ..... *obrina*
4b. DHW with orange band relatively narrow, restricted to median area; VHW with postmedian ocelli not joined proximally by a broken dark line ..... *batesii*

KEY TO ADULT FEMALE *NESSAEA*

1a. DFW without subapical blue maculae ..... *hewitsonii*
1b. DFW with subapical blue maculae 2
2a. DFW with three subapical blue maculae extending as a transverse row from veins R_3 to M_1; VHW without dark postmedian line connecting ocelli; median line narrow, blackish-brown ..... *aglaura*
2b. DFW with usually two subapical blue maculae between veins R_3-R_5 or with small blue spot in R_5-M_1; VHW with brown postmedian line or row of dashes or small crescents; median line diffuse reddish-brown 3
3a. VHW with brown postmedian line or row of nearly connected dashes proximal to ocelli; VFW without dark scales distal to blue cross bar ..... *obrina*
3b. VHW with a postmedian brown crescent proximal to each ocellus; VFW with dark scales distal to blue cross bar ..... *batesii*

KEY TO MALE GENITALIA AND HYPANDRIA OF *NESSAEA*

1a. Gnathos arm usually relatively narrow and more pointed in lateral view, in ventral view much longer than wide; valva without enlarged papilla at crista .... *aglaura*
1b. Gnathos arm broader, expanded and may be rounded in lateral view, in ventral view not elongate, may be wider than long 2
2a. Valva with papilla with many setae at crista; gnathos arm enlarged, rounded and blunt in lateral view, slightly longer in ventral view 3
2b. Valva without papilla at crista, gnathos arm enlarged but somewhat pointed in lateral view, ventral view gnathos arm much wider than long ..... *hewitsonii*
3a. Gnathos arm comparatively wider and more rounded; hypandrium quite constricted posteriorly with slightly concave margins at point of origin of rami; aedeagus straight ..... *batesii*

3b. Gnathos arm not as wide or expanded; hypandrium heavily constricted at middle, margins at origin of rami may be convex; aedeagus curved ..... *obrina*

Nessaea aglaura (Doubleday), [1848]

The taxonomy of *N. aglaura* is complicated by two major problems. Is *N. aglaura* a valid species separable from *N. obrina*? Second, is *N. regina* a subspecies of *N. aglaura*? (See Intergradation under *N. a. aglaura*.)

N. aglaura could be a distinct species or one of a number of subspecies of *N. obrina*. *Epicalia aglaura* was described by Doubleday (1848) as a distinct species, but Westwood (1850) recognized it as *Epicalia ancaea* var. *aglaura* and Kirby (1871) included it as *Catonephele obrinus* var. *aglaura*. Stichel (1899) recognized it as a separate species *Nessaea aglaura*, as have all following authors including Vane Wright (1979).

The ♂ and ♀ genitalia and ♂ hypandria of *N. aglaura* are quite similar, but are often separable from *N. obrina* by the relatively narrower and more pointed gnathos arm and lack of any enlarged papilla at the crista on the valva of *N. aglaura*. The ♂ hypandria and ♀ genitalia appear to be the same. The wing venation, palpi and other morphological characters do not differ significantly. The differences in wing coloration markings are not much more than between some subspecies. As shown in the key to males, there is a difference in the orange being limited to the costal area, some subapical blue on the DFW, and a thinner darker median line on the VHW in *N. aglaura*. Female differences are more subapical blue on the DFW and a thinner and darker median line and the postmedian line not connecting ocelli on the VHW in *N. aglaura*.

There is a trend or transformation series with decrease and loss of orange on the DHW of the ♂ and increase of blue in the subapical area of the DFW and blue apex on the DHW of ♂ and ♀, starting with *N. o. obrina*, *N. o. faventia*, *N. o. lesoudieri*, *N. a. thalia*, *N. a. aglaura* culminating in *N. a. regina*.

The distribution patterns of *N. aglaura* and *N. obrina* show that they adjoin each other and are completely allopatric. The boundaries of the ranges are in the Andean Cordilleras. Despite careful study I have not found any intergrades, which is considered to be an important factor in presently recognizing *N. aglaura* and *N. obrina* to be separate species. However, future studies may show *N. aglaura* and its subspecies to be part of *N. obrina*, or perhaps more probably semispecies of a widespread superspecies extending from México to Argentina.

Description: Male. The DFW is black and has a bright turquoise blue, median, diagonal cross band extending anterior to R_2; there are none to three blue subapical dashes; and there may be a red cross bar in the discal area. The DHW may have an orange marking in the costal area or may be absent; a blue apical marginal area may be present or absent; and there may be an anal red spot. The ventral forewing (VFW) is green with a light bluish-white median diagonal cross band extending anterior to R_2, with a dark umbral area distal to the crossband. The VHW has a row of four ocelli without a connecting stripe or other marks. The gnathos arm of the male genitalia is relatively pointed and narrow; the valva does not have a papilla or tooth.

Female. The DFW is brown with a turquoise, median, diagonal crossband extending anterior to R_2; there is a blue subapical band of three dashes; and there are basal and medial red bars in the discal cell. The DHW is brown and has a blue apical marginal area, and there may be one to four dark ocelli and a red anal spot. The ventral surface is similar to the male, but usually with more subapical blue dashes.

Key to Subspecies of *N. aglaura*

Males.

1a. DHW without orange bar; the apical marginal area is blue; prominent anal red macula(e) are present in Cu_2-A; DFW with submedian red bar in discal cell; three subapical blue dashes present ..... *regina*

1b. DHW with orange bar present from anterior margin to M_1; there is no blue apical

marginal area; anal red macula(e) are absent or reduced; DFW with one small or two (rarely three) subapical blue dashes 2

2a. DHW with orange bar terminating in diffuse irregular edge; anal red macula(e) absent; DFW with submedian red bar present in discal cell; two (or three) subapical blue dashes are present ..... *aglaura*

2b. DHW with orange bar terminating more abruptly; small anal red macula(e) usually present; DFW without any submedian red bar in the discal cell; one small (rarely two) subapical blue dashes are present, or may be nearly missing ..... *thalia*

Females.

1a. DFW with three blue subapical dashes forming a thin band separated by black veins. VHW without or with little white at the apical marginal area; submedian line with outward convex line in $Sc+R_1$ to Rs ..... *regina*

1b. DFW with subapical band not separated by black veins. VHW with white at apical marginal area 2

2a. DFW with three thick blue subapical dashes connected and forming a small band ..... *aglaura*

2b. DFW with three reduced and separate blue subapical dashes ..... *thalia*

Nessaea aglaura aglaura (Doubleday, [1848]

Figs. **2, 3-6, 49, 54, 58**

Epicalia aglaura Doubleday, [1848]. Gen. Diurn. Lepid. pl. 29, f. 3. TL: México, Oaxaca. Lectotype: 1 ♂ BM no. Rh. 9306, designated by Vane-wright (1979) (Examined).

Description: As in *N. aglaura* except for differences for *N. aglaura aglaura* listed in the key to subspecies. Average wing length ♂ (31-34)33.0 mm, ♀ (28-36)34.5 mm.

Distribution: The nominate form occurs from east-central México to Panamá and Colombia (Fig. 58), where it is found with intergrades of *N. aglaura regina* and *N. aglaura thalia*.

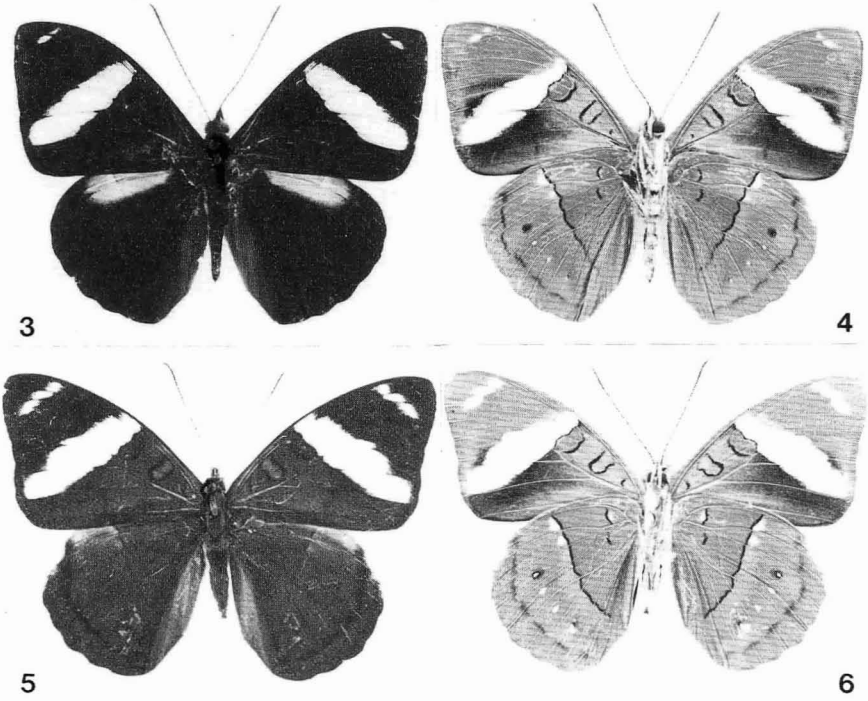
Taxonomy and Variation: The lectotype designated by Vane-Wright from Oaxaca, México in the BM was examined, and it is typical of the population from México to Costa Rica. There is much variation in size. The DFW in males usually has two blue subapical dashes, rarely three in México, and a red cross bar in the median area of the discal cell. In some Méxican males there is also a small red basal longitudinal stripe. Throughout the range there is a variable amount of white on the VHW distal to the median dark line. On the VHW of females there may be from one to usually four postmedian ocelli. The width of the blue crossband on the DFW is variable.

Intergradation: There is extensive intergradation of *N. a. aglaura* with *N. a. regina* and with *N. a. thalia* throughout most of Panamá and Colombia. I have carefully studied intergrades from seven localities in this region. PANAMA: *Colón*, Santa Rita Mts. 3 ♂ 2 ♀ (H. L. King); *Colón*, 5 ♂ 3 ♀ (G. Small, SI); *Panamá*, Cerro Campana, 1 ♂ 1 ♀ (G. Small, SI); *Darién*, San Blas Province, Puerto Obaldía (J. Mallet) 1 ♂ BM; COLOMBIA: *Chocó*, Solano, Quibdo 3 ♂ BM; *Valle*, Juntas, Río Cauca 1 ♂ BM; Río Dagua 5 ♂ BM. Total 19 ♂ and 6 ♀ specimens. Table 1 shows the critical characters of the three subspecies and also the range of variation in the intergrades between them. Every extreme of variation is found from no orange on the DHW (*Nessaea thalia* ab. "margaretha" Krüger) (Fig. 8), to a few orange scales (Fig. 7), to a small orange bar (Figs. 9-10) to full orange marking of *N. a. aglaura* and *N. a. thalia*. The same range of variation is found in most of the other eight characters. An unusual character found in two male intergrades from the Santa Rita Mts., Panama is pale green instead of blue crossbands on the DFW (Figs. 8-9). Six *N. thalia* ab. "margaretha" were found in four different intergrade areas. This is an extreme example of the range of intergradation with specimens having no basal orange on the DHW (as in *N. a. regina*), no blue apical area on the DHW, and reduced preapical blue

dashes on the DFW (as in *N. a. aglaura* and *N. a. thalia*). However, all of these characters are variable. Vane-Wright (1979; 1983) stated that more collecting is required to determine whether ab. "margaretha" is a distinct race or merely part of a cline. He recognized *N. a. regina* as a separate species. The male and female genitalia and the ♂ hypandrium of *N. a. aglaura*, *N. a. thalia*, and *N. a. regina* are indistinguishable from each other. This constitutes evidence, in addition to geographic ranges and extensive and widespread intergradation, that they are closely related subspecies. *N. obrina lesoudieri* shows considerable reduction of the posterior part of the DHW orange band approaching the costal orange band of *N. aglaura*.

Biology: Adults are found in evergreen tropical forest and in semi-deciduous tropical forest. Ross (1976) states that *N. aglaura* is typical of semi-evergreen seasonal forest in México, and according to DeVries (1987) it is found only in association with swampy areas in primary rain forest in Costa Rica. The adults are found from sea level to 1,000 m. They have been collected throughout the year indicating that there are several generations. Many records are from January to March and from July to September. In Costa Rica, DeVries (1987) states "At Finca La Selva it is present throughout the year, but undergoes wild fluctuations of abundance from month to month." In México, de la Maza and Turrent (1985) report that it is most common from May to September.

Immature Stages and Host Plants: The egg and mature larva and pupa have been described by DeVries (1987). The larval host plants are *Alchornea costaricensis* and *Plukenetia volubilis* (Euphorbiaceae) Vane-Wright (1983) and DeVries (1987).



Figures 3-6. *Nessaea aglaura aglaura* (Doubleday) ♂ dorsal (3), ventral (4) surfaces. MEXICO, *Oaxaca*, Río Sarabia (AA). ♀ dorsal (5), ventral (6) surfaces. MEXICO, *Veracruz*, Catemaco (AA).

TABLE 1. INTERGRADATION IN *N. AGLAURA*

Male	*aglaura*	Intergrades	*regina*	*thalia*
DHW orange bar in basal costal area to R_s	orange bar from costal margin to M_1 with diffuse irregular edge length (1.2-1.3) 1.2 mm	orange bar absent or variable width and length with either diffuse or abrupt termination, length (0.2-1.0) mm	no orange bar	orange bar to R_s terminates abruptly; may have reddish edge, length (1.0-1.2) 1.1 mm
DHW apical marginal area	blue absent	small blue area few blue scales, or none present	blue present	blue absent
DFW anal red macula in Cu_2-A_1	absent	present or absent	prominent red macula	small red macula present or absent
DFW submedian red bar in discal cell	red bar usually present	red bar usually small or absent	red bar present	no red bar in discal cell
DFW subapical blue dashes	2 (rarely 3)	1-2 (rarely 3) usually small blue dashes to only a few blue scales present	3	1 (rarely 2)
DFW blue crossband	blue	crossband blue, or pale greenish white in two specimens	blue	blue
Female				
DFW subapical blue dashes	3 thick blue dashes connected and forming a band crossed by black veins	3 reduced and separate blue dashes	3 blue dashes forming thin band crossed by black veins	3 reduced and separate blue dashes
VHW apical marginal area	white	with small white or greenish white area	without or with little white	greenish white
♂ genitalia and hypandrium and ♀ genitalia	No significant consistent differences among subspecies.			

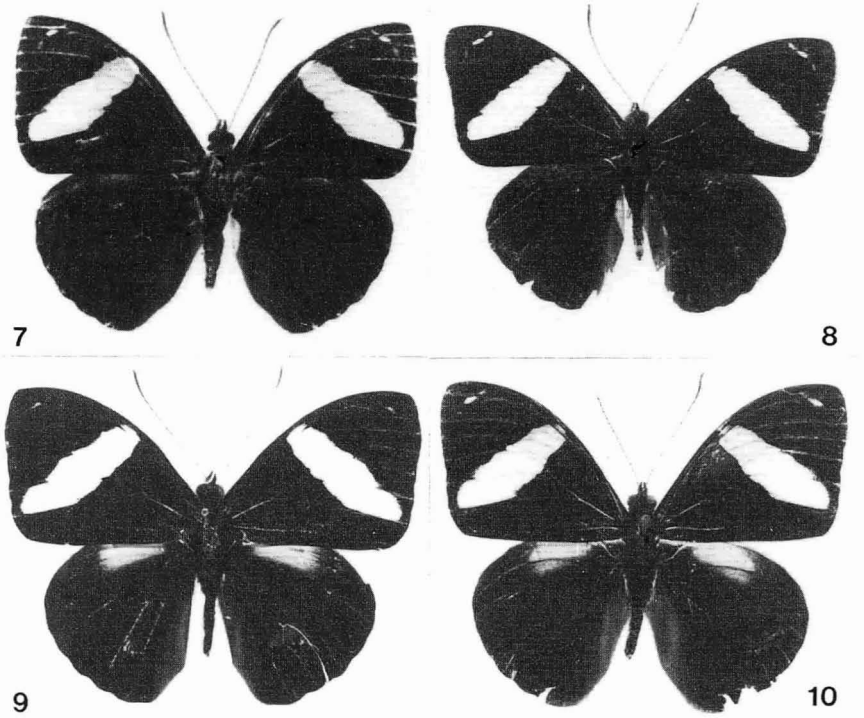
Specimens Examined: 89 ♂ 57 ♀

MEXICO: *Veracruz*, Catemaco; Tesonapa; El Chapo; Santiago Tuxtla; Uxpanapa; Presidio; *Tabasco*, Teapa; *Morelos*, Cuernavaca; *Oaxaca*, Río Sarabia; Jacatepec; Rancho San Carlos; El Naranjal; Chiltepec; Chimalapa; Tuxtepec; *Chiapas*, Santa Rosa Comitán; Chajul; Río Lacantún; Río Chixoy; Malpaso; Palenque; Bonampak; *Quintana Roo*, X-Can; *Yucatán*; GUATEMALA: *Alta Verapaz*, Polochic Valley; Cahabón; *Izabal*, Cayuga; *El Petén*, Sayaaxché; BELIZE: *Corozal*, Corozal; "British Honduras"; HONDURAS: *Cortes*, San Pedro Sula; La Cumbre; NICARAGUA: *Río San Juan*, Chontales; COSTA RICA: *Limón*, Río Sixola; Río Tortuguero; Puerto Viejo; Guápiles; Zent; *San José*, Parque Carrillo 300 m; *Puntarenas*, Punta Quepos; Osa Peninsula; Río Sarapiquí; *Heredia*, Finca La Selva; PANAMA: *Colón*, Colón X; Santa Rita Mts. X; *Panamá*, Cerro Campana; *Darién*, Puerto Obaldía X; COLOMBIA: *Chocó*, Solano, Quibdó X; *Cauca*, Juntas X; *Valle*, Río Dagua X.

Nessaea aglaura regina (Salvin), 1869 **[Stat. rev.]**

Figs. **11-14, 50, 54, 58**

Epicalia regina Salvin, 1869. Ann. Mag. Nat. Hist. 4(4): 178. TL: [Venezuela] "Caraccas". Lectotype: 1 ♂ BM. Rh. 9304, designated by Vane-Wright (1979). Paralectotype 1 ♀ BM, Rh. 9305, [Caracas]. Figs. **11-14.** (Examined)



Figures **7-10.** *Nessaea aglaura* intergrades. ♂ dorsal surface (**7**). PANAMA, *Colón*, Colón 500 m (SI). ♂ Dorsal surface (**8**). PANAMA, *Colón*, Santa Rita Mts. 700 m (VK). ♂ dorsal surface (**9**). PANAMA, *Colón*, Santa Rita Mts. 700 m (VK). ♂ dorsal surface (**10**). PANAMA, *Colón*, Santa Rita Mts. 700 m (VK).

Description: As in *N. aglaura* except for differences listed for *N. aglaura regina* in the key to subspecies. Average wing length ♂ (30-33)31.9 mm, ♀ (33-34)33.5 mm.

Distribution: This subspecies occurs in northern and western Venezuela and in northcentral and western Colombia (Fig. **58**). This is a considerable extension of the previously known range. Intergrades with *N. a. aglaura* are found in northwestern Colombia and Panamá, and with *N. a. thalia* in southwestern Colombia.

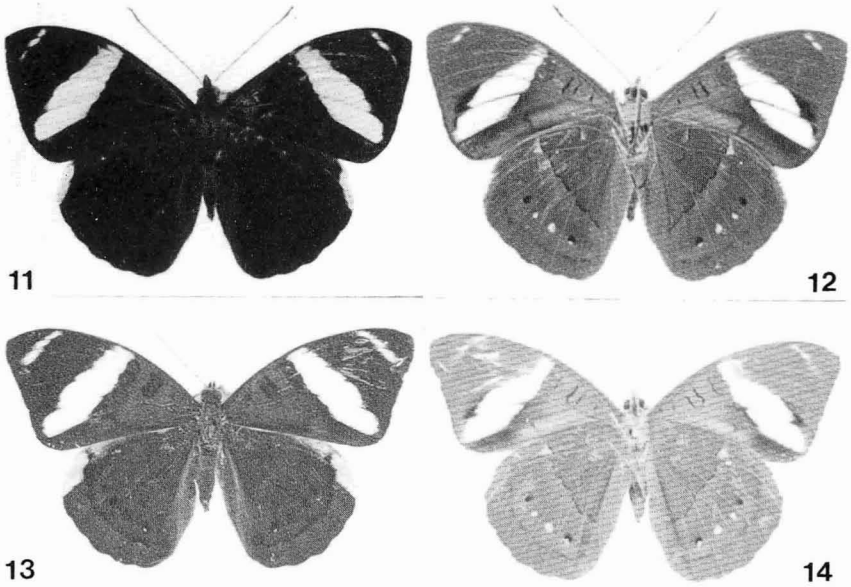
Taxonomy and Variation: The ♂ syntype was designated lectotype ♂, and a ♀ was designated paralectotype by Vane-Wright (1979) and were studied in the BM. The variation reported by him included slight differences in intensity of dark markings on the VHW, apical spots on the DFW, and a small triangular blue macula on the DFW of the male. There is considerable variation in nine characters in intergrades between *N. a. aglaura* and *N. a. thalia* as shown in Table **1**.

Biology: Nothing is known to have been reported on the behavior or early stages. Adults have been collected at altitudes from near sea level to 1,300 m in January, March, May, August, September and December.

Immature Stages and Host Plants: There are no known observations of larvae and host plants.

Specimens Examined: 33 ♂ 27 ♀

VENEZUELA: *Carabobo*, San Esteban Valley, over 200 m, 1 ♂ Dec. (Kaye) AA; 2 ♀



Figures **11-14**. *Nessaea aglaura regina* (Salvin). ♂ dorsal (**11**) ventral (**12**) surfaces. VENEZUELA, *Distrito Federal*, Caracas. Syntype *Epicalia regina* Salvin, and Lectotype (Vane-Wright, 1979) (BM). ♀ dorsal (**13**), ventral (**14**) surfaces. VENEZUELA, *Distrito Federal*, Caracas. Syntype *Epicalia regina* Salvin, and Paralectotype (Vane-Wright, 979) BM.

BM; Mar. Sep. 2 ♀ UC.; Las Quiguas 1 ♂ CM; (Vane-Wright, 1979); Puerto Cabello (Vane-Wright, 1979); Río Borburata 250 m Jan. 1 ♀ UC; *Aragua*, Maracay, Choroní, Río Aragua, 1,100 m Jan. 1 ♂ UC; 3 ♂ 2 ♀ RO; 800 m 2 ♂ 2 ♀ UC; Rancho Grande 750 m Sep. 4 M UC; *Distrito Federal*, Caracas (Vane-Wright, 1979); *Táchira*, La Morita 300 m May 1 ♀ UC; *Zulia*, Sierra de Perijá 1 ♀ UC; *Mérida*, Mérida 1 ♂ SI; No specific locality 5 ♂ 8 ♀ BM; 1 ♂ 1 ♀ SI; 3 ♀ CM; COLOMBIA: 1 ♂ (Ex Oberthur) BM; *Valle*, Cauca Valley 1 ♂ AM; *Boyacá*, Muzo 1 ♂ AM.

Nessaea aglaura thalia Bargmann, 1928 **[Stat. rev.]**

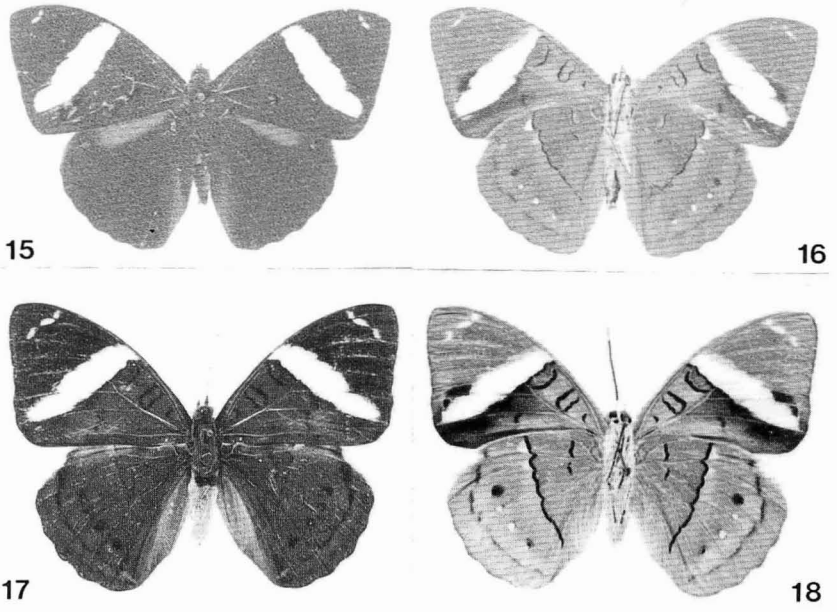
Figs. **15-18, 49, 54, 58**

Nessaea thalia Bargmann, 1928. Lepid. Rdsch. 2: 184. TL: COLOMBIA, [*Chocó*] Solano. Lectotype: 1 ♂ lectotype & 3 ♂ para-lectotypes including 1 ♂ cotype from Dagua, Colombia (Examined)

=*Nessaea aglaura ecuadorensis* Talbot, 1932. Bull. Hill Mus. Witley 4: 194. TL: ECUADOR, [*Los Ríos*] Santa Ana María, Quevedo. Holotype: 1 ♂ BM 1931-291, Joicey Coll. 3 ♂ paratypes (Examined) (2 ♂ paratypes also in Liverpool Mun. Mus.) Figs. **15-16 [Syn. nov.]**

=*Nessaea thalia* ab. "margaretha" Krüger, 1933. Ent. Zeit. Frankf. 46:240. TL: COLOMBIA, [*Valle del Cauca*] Río Dagua. Syntypes: 2 ♂ (probably in Coll. Biederman, Zurich) **[Syn. nov.]**.

Description: As in *N. aglaura* except for differences for *N. aglaura thalia* listed in the key to subspecies. Average wing length ♂ (29-33)31.2 mm, ♀ (34.5-35)34.9 mm.



Figures **15-18.** *Nessaea aglaura thalia* Bargmann. ♂ dorsal (**15**), ventral (**16**) surfaces. ECUADOR, *Los Ríos*, Santa Ana María, Quevedo. Holotype *Nessaea aglaura ecuadorensis* Talbot (BM). ♀ dorsal (**17**), ventral (**18**) surfaces. ECUADOR, *Pichincha*, Santo Domingo de los Colorados (AA).

Distribution: This subspecies occurs in its definitive form on the western slopes of the Andes mountains in Ecuador, and as intergrades with *N. a. aglaura* and *N. a. regina* in Colombia and Panamá (Fig. 58).

Taxonomy and Variation: *Nessaea thalia* Bargmann (1928) was described from six syntypes from Colombia. Vane-Wright (1979) designated a ♂ in the BM from Solano, Colombia, as lectotype and another ♂ from the same locality and a ♂ from Dagua, Colombia as paralectotypes. *Nessaea aglaura ecuadorensis* Talbot (1932) was described from five male specimens. Examination of type material shows that it is a synonym of *N. aglaura thalia*. *Nessaea thalia* ab. "margaretha" Krüger (1933) was described from two males from Río Dagua, northern Colombia, in which the orange on the DHW is absent. These were selected from a larger series in which the amount of orange was variable. I consider this to be part of an intergrade series as discussed previously under *N. a. aglaura*.

Biology: Vane-Wright (1983) quoted Mallet, that an adult was "sucking sap of *Castilla elastica* Cerv., [Moraceae]." Adults have been collected at altitudes from about 200 m to 1,000 m in January, April to June, November, and December.

Immature Stages and Food Plants: No data are available on the immature stages or food plants.

Specimens Examined: 22 ♂, 3 ♀
ECUADOR: *Manabí*, Palmar 200 m Apr.-Jun. 9 ♂ 1 ♀ AA; *Pichincha*, Napac 1,000 m Dec. 1 ♂ AA; Santo Domingo de los Colorados Jan. Nov. 1 ♂ 2 ♀ AA; *Los Ríos*, Santa Ana María, Quevedo 3 ♂ incl. M HT, BM; 2 ♂ paratypes (Liverpool Mun. Mus.) + 3 ♂ BM; Río Palenque Nov. 1 ♀ AA; *Chimborazo*, Chimborazo 1 ♂; Chimbo 1 ♂ BM.

Nessaea obrina (Linnaeus), 1758

N. obrina is a widespread species distributed from Colombia and the Guianas to the mouth of the Amazon and south to Central Bolivia, and Mato Grosso, Brazil, extending to northern Argentina. It is common, and 422 ♂ and 200 ♀ have been identified.

The close relationship between *N. aglaura* and *N. obrina* has been discussed under *N. aglaura*.

In this revision three subspecies of *N. obrina* are recognized including the nominate form. Vane-Wright (1979) states that on present evidence it "might be possible to recognise four subspecies," and quotes K. S. Brown that a fifth subspecies could merit recognition. Detailed study of 622 specimens shows that three subspecies, *N. o. obrina*, *N. o. faventia*, and *N. o. lesoudieri* can be identified. There is considerable intergradation between *faventia* and *lesoudieri* mainly at the relatively broad tension zones or boundaries between the subspecies.

Description: Male. The DFW is black with a turquoise blue median diagonal cross band extending only to R_2; there are no subapical blue maculae. The DHW is black with bright orange from the anterior margin posteriorly to the anal vein. The VFW has a pale bluish-white, medial, diagonal cross band extending to R_2; there is no dark umbral area distal to the crossband. The VHW is leaf green with two dark and two white ocelli, with an ochre-brown linear band immediately basal to the ocelli. The male genitalia has the gnathos arm broad, expanded and rounded; the valva has a papilla with many setae at the crista.

Female. The DFW is brown with a blue crossband and one or two subapical blue maculae. The DHW is brown with a blue apical area and from one to four dark ocelli. The ventral surfaces are similar to those of the male.

Key to Subspecies of *N. obrina*

Males.

1a. DHW with two reddish anal spots (tornus) in Cu_2-A_1 usually present; there is a dull orange or orange-brown band with diffuse edges; the relatively narrow band is slightly constricted posteriorly ..... *obrina*
1b. DHW without two reddish anal spots in Cu_2-A_1; the orange band may be broad and dull and not constricted posteriorly, or bright orange-yellow and strongly constricted posteriorly 2
2a. DHW with broad orange bands usually dull with diffuse margins, broad entire length, not strongly constricted posteriorly ..... *faventia*
2b. DHW with bright orange-yellow bands with relatively sharp margins; very broad anteriorly and strongly constricted posteriorly ..... *lesoudieri*

Females.

1a. DHW usually with reddish anal markings at Cu_2-A; usually one small postmedian dark ocellus or with one or two faint ocelli visible ..... *obrina*
1b. DHW rarely with reddish anal markings; usually with three or four postmedian ocelli, mostly two large dark and two smaller ocelli ..... *faventia and lesoudieri*

Nessaea obrina obrina (Linnaeus), 1758

Figs. **19-22, 47, 51, 55, 59**

Papilio obrinus Linnaeus, 1758: Syst. Naturae. 490. TL: ♀ "India" [Surinam]. Syntype(s): Swedish Museum of Natural History, Sweden ♀
= *Papilio ancaeus* Linnaeus, 1758: Syst. Naturae. 486. TL: ♀ India [Surinam] Syntype(s): Swedish Museum of Natural History, Sweden ♀. Junior subjective synonym of *Papilio obrinus* Linnaeus, 1758 (Clerck, 1764: Pl. 31; Stoll, 1787: 31).

Description: As in *N. obrina* except for differences listed for *N. obrina obrina* in the key to subspecies. Average wing length ♂ (25-34)31.7 mm, ♀ (26-33)30 mm.

Distribution: The nominate form is found throughout the Guianas and in eastern Venezuela (Fig. **59**). Intergrades with *N. obrina faventia* were collected in Pará, Brazil.

Taxonomy and Variation: The name *Nessaea ancaea* (Linnaeus) was used by Hemming (1967) and by Vane-Wright (1979) following Hübner (1819) as the First Reviser. However, Vane-Wright (1981) changed the name to *Nessaea obrina* (Linnaeus) after Clerck (1764) and Stoll (1787) who used *obrinus*, and designated *N. anceaus* to be a junior subjective synonym of *Papilio obrinus* (Linneaus). For *N. obrina* Vane-Wright (1979) states, "I have seen a single male with a posterior red spot in cell Cu_2 on the hind wing upperside, as found in males of *N. regina*." Two red anal spots in Cu_2-A of the DHW are typical for the nominate subspecies and are present in nearly all of the 55 males examined by the author. They may be present, reduced or absent in intergrades in Pará. More collecting is required to determine the exact boundary between *obrina* and *lesoudieri* in Venezuela and northern Brazil. The orange marking on the DHW is somewhat variable. While it always has diffuse and usually irregular margins, the width and shape are somewhat variable. It is always narrower and often more constricted posteriorly in comparison with *N. o. faventia*. No measurements were made to compare widths of orange markings since specimens from Guyana and Venezuela are smaller than those from Brazil, especially in Mato Grosso (see Sec. E).

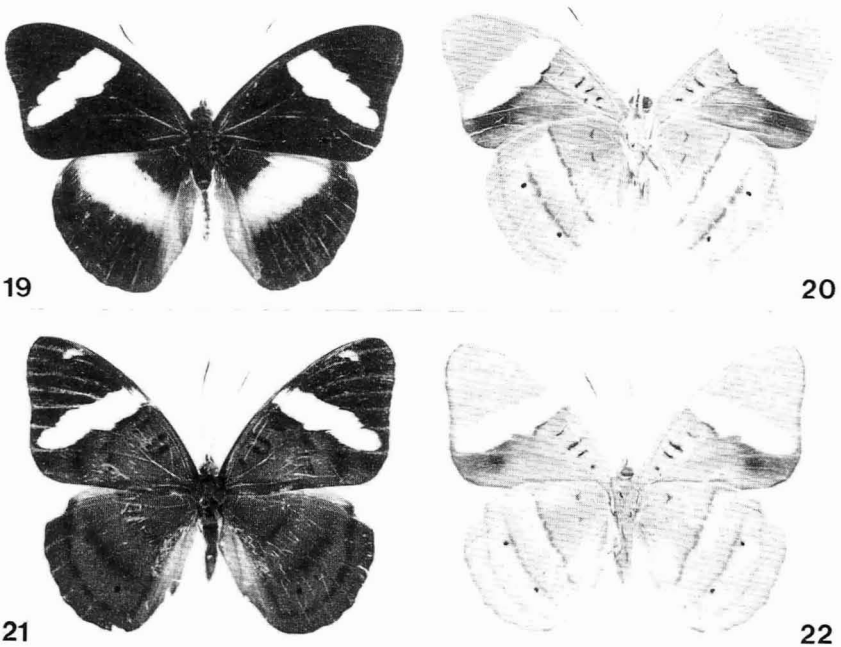
Biology: This subspecies occurs primarily in semi-deciduous tropical forest in openings and partially cut-over areas. I have collected males and females in partially cut-over and heavily grazed forests at Parika, Guyana.

The adults have been found at lower altitudes, especially in river valleys in the Guyanas. They have been collected in January and July to November.

Immature Stages and Host Plants: No observations on immature stages or host plants are known.

Specimens Examined: 55 ♂ 31 ♀

GUYANA: *West Demerara-Essequibo*, Upper Essequibo River 1 ♂ BM; Parika Oct. 2 ♂ 2 ♀ JC; 1 ♂ BM; *Mazaruni-Potaro*, Bartica 1 ♂ AA; *E. Demerara-W.C. Berbice*, Demerara River 1 ♂ AA; 1 ♀ SI; *Berbice*, New River Triangle, Camp Jaguar Nov. 2 ♂ 3 ♀ AA; *E. Berbice-Courantyne*, Berbice River 1 ♀ AA; 1 ♂ BM; "British Guiana" 3 ♂ AA; 1 ♂ SI; King Frederick William IV Falls 1 ♂ BM; Confluence Oronoque and New River, Aug. 1 ♂ BM; SURINAM: *Nickerie*, Nickerie 5 ♂ CM; Kabalebo River Jul. 2 ♂ CM; *Surinam*, Geldersland 1 ♂ SI; "Oova el Moroni" 1 ♂ 1 ♀ MP; Albina Jan. 1 ♀ BM; No specific locality 1 ♂ BM; 3 M, 1 ♀ AM; GUYANE: *Guyane*, St. Jean du Maroni 1 ♀ AA; Cayenne 2 ♂ BM; 1 ♀ AM; VENEZUELA: *Bolívar*, Uruyén 1 ♂ UC; Río Cuchivero, Mantecal 2 ♂ UC; El Peru 1 ♂ CM; Suapure 1 ♂ CM; Kanarakuni 2 ♂ 1 ♀ UC; Bochinche 1 ♂ UC; Centella 1 ♀ UC; El Dorado Aug. 1 ♀ UC; El Pao, Jul. 2 ♀ UC; 3 ♂ 3 ♀ RO; BRAZIL: *Pará*, Obidos Sep. 1 ♂ 2 ♀ SI.



Figures **19-22.** *Nessaea obrina obrina* (L.) ♂ dorsal (**19**), ventral (**20**) surfaces. GUYANA, *West Demerara-Essequibo,* Parika (JC). ♀ dorsal (**21**), ventral (**22**) surfaces. GUYANA, *Berbice,* New River Triangle, Camp Jaguar (AA).

Nessaea obrina faventia Fruhstorfer, 1910

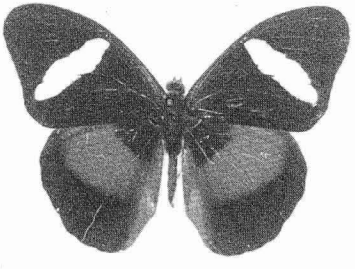
Figs. **23-26, 47, 51, 55, 59**

Nessaea obrinus faventia Fruhstorfer, 1910: Ent. Zeit. Frankf. 194. TL: Brazil, Mato Grosso. Syntype: 1 ♂ BM 1937-285 in BM, designated lectotype by Vane-Wright (1979) Figs. **23-24.** (Examined)

= *Nessaea obrinus latifascia* Röber, 1928: Intern. Ent. 68. TL: Bolivia, [*Santa Cruz*] Buenavista - 75 km N.W. Santa Cruz, 450 m. Coleção Julius Arp. Holotype: 1 ♂ HT, 1926-7 Bolivien/no. 20/415. In Museu Nacional, Rio de Janeiro. Vane-Wright (1979) designated this specimen lectotype. (Examined) **[Syn. nov.]**

Description: As in *N. obrina* except for differences listed for *N. obrina faventia* in the key to subspecies. Average wing length ♂ (30-40)34.8 mm, ♀ (28-41)37 mm.

Distribution: Occurs in the lower Amazon valley in Maranhão, Pará, eastern Amazonas, Mato Grosso, Rondônia and Bolivia (Fig. **59**). Hayward (1973) reports *N. obrina* is very rare and accidental in Misiones, Argentina. This subspecies intergrades with *N. o. obrina* in the lower Amazon, and with *N. o. lesoudieri* in northern Bolivia and in Rondônia, Brazil. A specimen with a locality label "Guatemala" in the Museum of Paris is certainly mislabeled.



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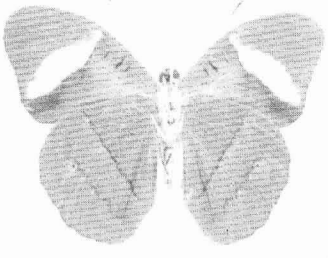

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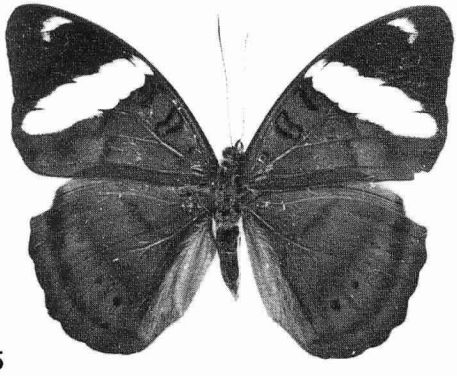

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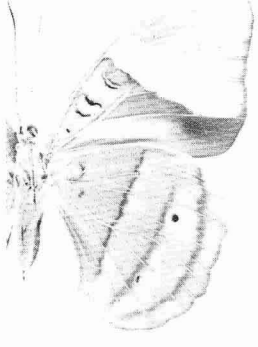

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Figures **23-26.** *Nessaea obrina faventia* Fruhstorfer. ♂ dorsal (**23**), ventral (**24**) surfaces. BRAZIL, *Mato Grosso.* Syntype *Nessaea obrinus faventia* Fruhstorfer and Lectotype (Vane-Wright, 1979) (X 0.8) (BM). ♀ dorsal (**25**), ventral (**26**) surfaces. BRAZIL, *Amazonas,* Manicoré (AA).

Taxonomy and Variation: The lectotype ♂ of *N. obrinus faventia* Fruh. designated by Vane-Wright (1979) in the BM was examined and compared and it is typical of the subspecies population of *faventia*. I have examined the lectotype ♂ of *N. obrinus latifascia* Röber designated by Vane-Wright (1979) in the Museu Nacional, Rio de Janeiro, and it is typical *N. obrinus faventia* and is synonymized.

There is some variation in the width of the orange marking of the DHW of the male in the intergrade areas. It is somewhat narrower in Obidos and Itaituba, Pará, Brazil where it intergrades with *N. o. obrina*. In some localities in Rondônia, Brazil and along the border of Perú and Bolivia the DHW orange marking becomes somewhat constricted posteriorly where *N. o. faventia* intergrades with *N. o. lesoudieri*. An interesting aberration of this intergrade was found at the Perú-Bolivian boundary. The DFW has a white diagonal crossband in place of the blue cross band. The DHW has a broad dull orange band with diffuse margins, and the band is somewhat constricted posteriorly. Hayward (1964) illustrated only the ventral surface of *N. obrina* in color. Although it is not possible to determine the subspecies, it is probably *N. o. faventia*. This locality of Misiones, Argentina is over 1000 km from the nearest other recorded locality for *N. obrina*.

Biology: This subspecies occurs in the lower Amazon valley in evergreen and semi-deciduous tropical forests in openings and trails. It has habits very similar to the other subspecies of *N. obrina*.

The adults have been collected mostly at lower altitudes, and the highest reported altitude is 400 m. in Bolivia. They have been found throughout the year but mostly from June to October.

Immature Stages and Host Plants: The larvae and pupa of *N. o. faventia* have been painted in color by Rev. A. Miles Moss and by Miss M. E. Fountaine. The pictures are on file at the BM and were reproduced by Vane-Wright (1979). The host plants were not stated.

Specimens Examined 166 ♂ 58 ♀

BRAZIL: *Maranhão*, Fazenda Terrasse; Imperatriz; Montes Aúreos; *Pará*, Anajás; Aveira; Paragominas; Água Azua; Rurópolis; Itaituba X; Rio Tapajós; Guamá; Belém; Rio Belém; Utinga; Obidos X; Santarém; Pernambuco; Urumanza; Rio Curuá-Una; *Amazonas*, Manicoré; Maués; Igarapé Preto; Ticunas; Conceição; Rio Tapajós; *Amapá*, Porto Santana; *Mato Grosso*, Vera; Cáceres; Diamantino; Barra do Bugres; Salto do Céu; Cuiabá-Corumba; Cuiabá-Santarém km 1666; km 715; *Rondônia*, Rio Verde; Jaru X; Cachoeira do Samuel X; Guajará-Mirim; Costa Marques; BOLIVIA: *Santa Cruz*, Buenavista (type of *latifascia*) Surutu; *Cochabamba*, Chapare 400 m; Bolivia-Perú boundary X; ARGENTINA: *Misiones* (Hayward, 1973). GUATEMALA: No specific locality, 1 ♂ MP [Error].

Nessaea obrina lesoudieri Le Moult, 1933 **[Stat. rev.]**

Figs. **27-30, 47, 51, 55, 59**

Nessaea lesoudieri Le Moult, 1933 Novit. Ent. (3): 18, pl. 2, figs. 5 & 6. TL: Brazil, Manaus. Holotype: 1 ♂ BM 1968-155. Synonymized by Vane-Wright, (1979) (Examined) **[Stat. rev.]**

=*Nessaea obrinus* ♀ ab. "coniuncta" Krüger, 1933. Intern. Ent. Zeit. 27: 176-178. TL: Brazil: "Upper & Lower Amazons; Rio Madeira". Syntypes: 4 ♀ coll. Krüger, Leipzig **[Syn. nov.]**

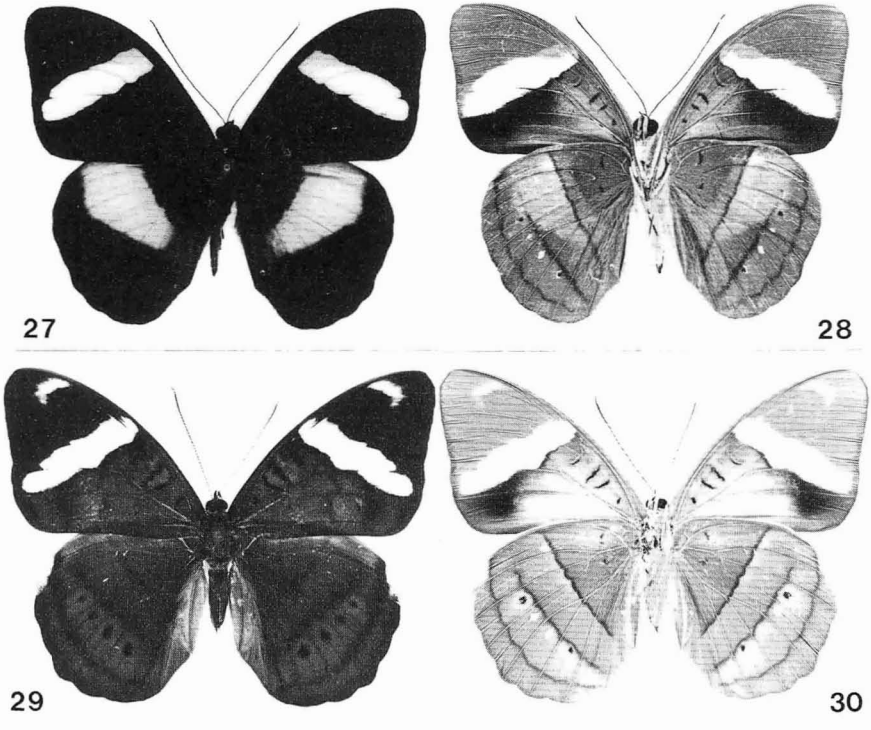
=*Nessaea obrinus romani* Bryk, 1953. Ark. Zool. 5: 103. TL: Brazil, Amazonas, São Gabriel, Rio Negro. Holotype: 1 ♂ Swedish Mus. Nat. Hist., Stockholm **[Syn. nov.]**

Description: As in *N. obrina* except for differences listed for *N. obrina lesoudieri* in the key to subspecies. Average wing length ♂ (32-40)36 mm, ♀ (35-40)37 mm.

Distribution: This subspecies is found in southern and eastern Colombia, Ecuador, and Perú and extends eastward in the Amazon valley to Manaus, Brazil (Fig. **59**). It intergrades with *N. o. faventia* in Rondônia, Brazil and in northern Bolivia.

Taxonomy and Variation: This upper Amazon population of *N. obrina* has been described from two different aberrations. *N. lesoudieri* was described from a single male with white in place of blue crossbands on the DFW. The underside is not green but yellow as illustrated by Vane-Wright (1979). This specimen lacking the blue pterobilin pigment has been examined in the BM. It was described as a species and the name is available for the subspecies. Vane-Wright (1979) placed this taxon in synonymy. *N. obrinus* ab. "coniuncta" Krüger, is based on four females from the Rio Madeira and the upper and lower Amazon. Between the subapical blue dashes and the blue crossband on the DFW there are small blue spots between M_1 and M_3. It is a described aberration and not a valid trinomial and is a synonym of *N. o. lesoudieri*. *N. obrinus romani* Bryk has the orange marking on the DFW narrowed posteriorly and is typical of the *N. o. lesoudieri* population. The type ♂ and ♀ are from São Gabriel on the Rio Negro, Amazonas, Brazil. *N. o. romani* is synonymized.

There is some variation in the width and shape of the orange marking of the DHW of males. The width of the orange band posteriorly is always much narrower than anteriorly, but it may vary from 0.5 to 0.7 times the width anteriorly. Narrow and wider posterior markings may occur in specimens from the same locality, especially in intergrade areas.



Figures **27-30**. *Nessaea obrina lesoudieri* Le Moult. ♂ dorsal (**27**), ventral (**28**) surfaces. PERU, *Madre de Dios*, Puerto Maldonado (AA). ♀ dorsal (**29**), ventral (**30**) surfaces. PERU, *San Martín*, Juanjui (AA).

Some males from Perú and Bolivia have some blue scales in the subapical area of the DFW. Females may have a subapical broad or narrower blue elongate macula sometimes with a separate posterior blue spot.

Biology: *N. o. lesoudieri* adults are found in tall evergreen tropical forest and in semi-deciduous tropical forest. They occur in forest openings, trails and at the edge of forest, and in forest clearings inhabited by indians. I have found adults flying in openings in logging areas where selected trees have been felled. They fly rapidly and settle on leaves in the sun about 2-4 meters in height. They were highly attracted to fermented banana baits in Ecuador and Perú. The adults are not common but the males are so brightly colored they are readily seen. They are difficult to catch except on banana baits or when found hanging below leaves during cloudy or rainy weather.

The adults occur mostly at low altitudes often in river valleys, up to an altitude of about 800 m. They have been collected every month of the year, with no observed peak of abundance.

Immature Stages and Host Plants: There is nothing known to be reported on the immature stages or host plants of this subspecies.

Specimens Examined: 201 ♂ 111 ♀

VENEZUELA: *Amazonas*, Cerro Duida; Maco; Río Ventuari; La Esmeralda; COLOMBIA: *Amazonas*, Florida; Río Putumayo; *Putumayo*, Río Putumayo; *Caquetá*, Río Ortegueza; ECUADOR: *Napo*, Puerto Misahualli; *Pastaza*, Canelos; Sarayacu; *Azuay*, Cuenca; PERU: *Loreto*, Iquitos; Pebas; Upper Río Tapiche; Mazán; Explorama; Sarayacu; Nauta; Río Cachiacu; San Roque; Río Mishuayacu; *Ucayali*, Pucallpa; *Huánuco*, Tingo María; Previsto; Tournavista; *Ayacucho*, Hacienda Candalosa; *Junín*, Chanchamayo; Satipo; Río San Pedro; *San Martín*, Juanjui; *Madre de Dios*, Puerto Maldonado; BRAZIL: *Amazonas*, São Paulo de Olivença; Tefé; Manaus; Puraquequara; Manacapuru X; Humaitá; Manicoré; Balbina; Fonte Boa; Jauaretê; São Gabriel da Cachoeira (Bryk, 1953); *Acre*, Alto Juruá; Xapuri; Brasiléia; Rondônia, Porto Velho; Jaru X; BOLIVIA: Border of Perú and Bolivia.

Nessaea batesii (Felder & Felder), 1860

This species has a relatively restricted distribution in eastern Venezuela, the Guianas and the lower Amazon in Brazil. It appears to form a transition species between *N. obrina* and *N. hewitsonii* with a strong reduction of the median orange marking on the DHW in the male, especially in the nominate subspecies *N. batesii batesii*. The subspecies *N. b. magniplaga* differs only in the width of this orange marking so that the subspecies are quite closely related. No differences were found to consistently separate the females. Future studies may show a clinal relationship between the two populations.

Key to Subspecies of *N. batesii*

Male.

1a. Median orange marking of DHW narrower 4.55 (±S = 0.45) mm. Lower Amazon, Brazil ..... *batesii*

1b. Median orange marking of DHW broader from 7.11 (± S = 0.68) mm in Guyana to 6.38 (± S = 0.35) mm in Guyane ..... *magniplaga*

Description: Male. The DFW is black except for a turquoise blue, median, diagonal cross band extending to R_2. There are no blue subapical maculae. The DHW has a relatively narrow, median, orange discal macula or band from the costal area which is quite narrowed posteriorly to a point at Cu_2 or 2A. There is no blue apical margin. The VFW has an oval bluish-white area extending anteriorly as a white band to Sc. There is a dark umbral area

distal to the blue marking. The VHW has two black and two white ocelli each with a brownish crescentic or half-circular line proximal to each ocellus. The male genitalia has an expanded and rounded gnathos arm. The valva has an expanded papilla at the crista, but lack chitinous teeth.

Female. The DFW is brown with a blue median diagonal crossband. There is a blue subapical macula, and a red median bar in the discal cell. The DHW is brown with a blue apical margin and there are two to rarely four dark ocelli. The ventral surface is similar to the male.

Nessaea batesii batesii (Felder & Felder), 1860

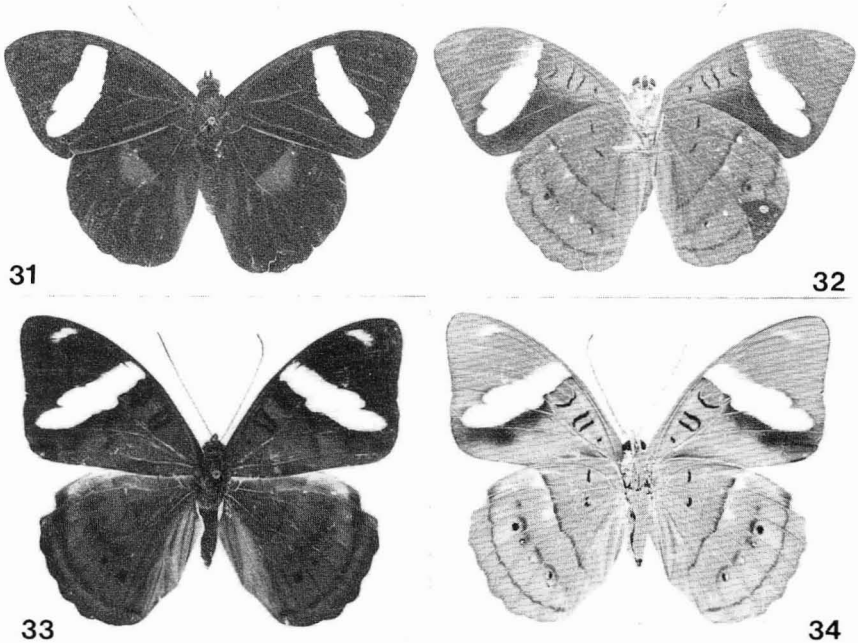
Figs. **31-34, 52, 56, 60**

Epicalia batesii Felder & Felder, 1860. Wien. Ent. Monat. 4:237. TL: Brazil [Belém]. Lectotype: BM, 1 ♂ Bates type (114) designated by Vane-Wright (1979) Figs. **31-32.** (Examined)

Nessaea batesii aestherica Fruhstorfer (label on specimen). TL: Surinam. Type: BM 1 ♂ labeled TYPE. Martin, 1923: 52. unpub. ms. name. (Examined) **[Nomen nudum]**.

Description: As in *N. batesii* except for differences listed for *N. batesii batesii* in the key to subspecies. Average wing length ♂ (29-36)33.6 mm, ♀ (32-40)37.1 mm.

Distribution: Occurs in the lower Amazon valley, eastern Brazil, in Amapá, Pará, Piauí and Maranhão (Fig. **60**). There is a male of this subspecies labeled "Chiriquí" [Panamá] in the Museum of Paris, a ♀ from Río Napo, Ecuador in the Museum of Paris, and a



Figures **31-34.** *Nessaea batesii batesii* (Felder & Felder). ♂ dorsal (**31**), ventral (**32**) surfaces. Brazil [Pará, Belém]. Syntype *Epicalia batesii* Felder & Felder and Lectotype (Vane-Wright, 1979) (BM). ♀ dorsal (**33**), ventral (**34**) surfaces. No locality (AA).

♂ from the Cauca Valley, Colombia in the Museum of Comparative Zoology, Harvard University. These specimens are probably mislabeled.

Taxonomy and Variation: The Felder type of *N. batesii* in the BM has been designated lectotype by Vane-Wright (1979). I have examined this specimen and it is illustrated in Figs. **31-32**. The width of the median orange marking on the DHW of males in specimens of *N. b. batesii* from Para is 4.55 ± S = 0.45 mm (Vane-Wright, 1979); the Felder type is 4.5 mm. I have studied the "aberrations" mentioned by Vane-Wright (1979), two ♀ from Belém lacking blue in the crossband on the DFW and appearing white. A male from Anajás, Isla de Marajó, Pará, Brazil in the KB collection has the DHW median marking pale yellow instead of bright orange.

Biology: The nominate subspecies is relatively uncommon in museum collections. It has been collected only at low elevations below 200 m. A pair of adults were taken in copula by A. Miles Moss at Belém (Vane-Wright, 1979). Most specimens in collections do not have dates, but there are records of February, May, July, August and October.

Immature Stages and Host Plants: No records of immature stages or host plants are known.

Specimens Examined: 33 ♂ 14 ♀

BRAZIL: *Amapá*, Serra do Navio 1 ♂ Feb. MN; *Pará*, Altamira, Rio Xingu 2 ♂ 3 ♀ MN; Ponte Nova, Guamá 1 ♀ MN; Belém 1 ♀ MN; Benevides Oct. 1 ♂ CM; Utinga 1 ♂ Aug. MN; Anajás 1 ♂ Aug. KB; Maranhão 2 ♀ BM; 1 ♂ AM; *Piauí*, Grande Fazenda 3 ♂ 1 ♀ MN; *Maranhão*, Montes Aúreos 1 ♂ BM; No recorded localities 22 ♂ 6 ♀ BM.

Nessaea batesii magniplaga Röber, 1928

Figs. **35-38, 52, 56, 60**

Nessaea batesi magniplaga Röber, 1928. Intern. Ent. Zeit. 22: 67-71. TL: "Bolivia, Buenavista - 75 km nordwestl. Santa Cruz - 450 m." [Error, probably mislabeled, from Guyana]. Holotype: red type label 1 ♂ "*brevifascia*, type/Coleção Julius Arp" (MN). (Examined).

Description: As in *N. batesii* except for differences listed for *N. batesii magniplaga* in the key to subspecies. Average wing length M 33.57 (± S = 1.29) mm, ♀ 37.09 (± S = 1.73) mm (Vane-Wright (1979).

Distribution: Occurs in the Guyana shield highlands area from eastern and southern Venezuela through all of the Guianas (Fig. **60**).

Taxonomy and Variation: Vane-Wright (1979) has published a photograph of a type labeled "*brevifascia*" which he considered to be the type of *Nessaea batesii magniplaga* Röber (1928). I have examined this type carefully in the MN in Rio de Janeiro and agree with Vane Wright that it is a mislabeled male specimen probably from Guyana. The name "*brevifascia*" is apparently an unpublished manuscript name for the subspecies *magniplaga*. The width of the median orange marking on the DHW of males in *N. b. magniplaga* is: Venezuela and W. Guyana (8.0-9.5 mm) (Jenkins); Guyana 7.11 (± S = 0.68) mm; Surinam 6.73 (± S = 0.45); and Guyane 6.38 (± S = 0.35) mm (Vane-Wright 1979). Additional measurements confirm these data. I have studied several "aberrations" in the BM, a ♀ from Guyana with the DFW blue crossband on the left wing is nearly lacking, there is a ♂ with the band very narrowed anteriorly, and a ♂ with the DHW orange almost absent on the right wing.

The distribution of *N. batesii* in Venezuela and northern Brazil needs to be studied in

more detail, especially the intergradation zone between *N. b. magniplaga* and *N. b. batesii*.

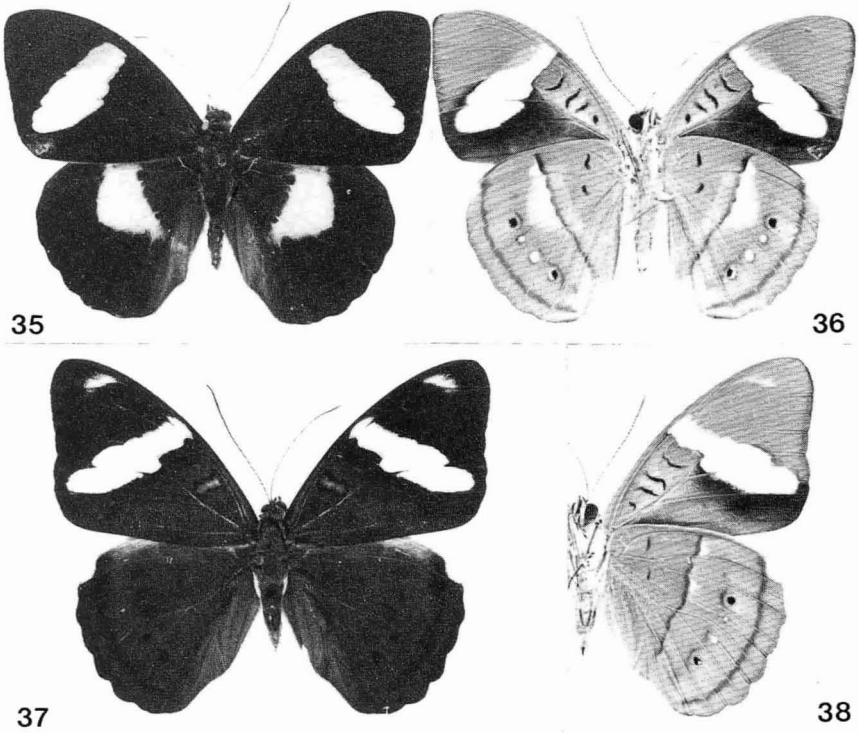
Biology: *Nessaea b. magniplaga* occurs in openings and trails in tall evergreen tropical forest and in semi-deciduous partly open tropical forest. I have collected this subspecies in semi-deciduous forest along trails baited with fermented bananas near El Dorado in eastern Venezuela. In Kamarung, Guyana, I collected males in openings in heavy evergreen forest without using fruit bait. A pair were collected in copula in Guyana (Bates, 1866).

This subspecies occurs from near sea level to about 300 m elevation. It has been collected from July to December.

Immature Stages and Host Plants: No observation records are known for immature stages or host plants.

Specimens Examined: 77 ♂ 42 ♀

GUYANA: *Rupunini*, Rupununi Trail; Kassikaityu; *North-West*, Baramita; *Mazaruni-Potaro*, Bartica; Kamarung; Takutu Mts.; Kartabo; Demerara River; *Berbice*, New River Triangle, Camp Jaguar; Kutari; SURINAM: No specific locality; GUYANE: *Guyane*, Bas-Maroni; Maroni River; St. Laurent; St. Jean du Maroni, Cayenne; *Inini*, Orapu; VENEZUELA: *Bolívar*, El Dorado, El Pueblita; El Bochinche; Imataca; Río Caura; El Playón; *Amazonas*, Alto Orinoco.



Figures 35-38. *Nessaea batesii magniplaga* Röber. ♂ dorsal (35), ventral (36) surfaces. SURINAM, "interior Surinam" (AA). ♀ dorsal (37), ventral (38) surfaces. GUYANA, *Berbice,* New River Triangle, Camp Jaguar (AA).

Nessaea hewitsonii (Felder & Felder), 1859

N. hewitsonii has no orange coloration and has a distinctive blue postmedial cross band on the DHW as well as a blue apical area. The species has a wide distribution in the upper Amazon basin and on the eastern slopes of the Andes mountains. It is relatively common locally and I have collected many specimens at fermenting fruit baits in Ecuador and Perú. Two subspecies are recognized, the nominate form and a new subspecies from Bolivia. Vane Wright (1979) observed the differences in Bolivian specimens from the nominate population.

Description: Male. The DFW has a black background with a turquoise blue (or whitish blue) median diagonal crossband that extends anteriorly to R_2. There are no subapical blue maculae. The DHW has a turquoise blue submarginal crossband extending from M_1 to 2A; the posterior marking may be divided at Cu_2 and narrowed. There is a blue apical area. The VFW is similar to *batesii* except that there is no dark umbral area or dark scales distal to the bluish crossband. The VHW has two black (and often a small posterior) and two white ocelli. These are located on the distal side of a continuous reddish-brown narrow band. The male genitalia has an enlarged or expanded and slightly pointed gnathos arm. The valva does not have a papilla at the crista.

Female. The DFW is brown with a blue median crossband with a red second discalis. The DHW is brown and has two to four dark ocelli and a blue apical area. The VFW and VHW are similar to the male.

Key to Subspecies of *N. hewitsonii*

Males.

1a. The VFW has a light blue median crossband with the anterior part of the band (R_3-M_2) whitish 2-3 mm in diameter. The DHW has a dark blue cross band which is broad (3.3-5.0 mm) with no detached macula posterior to Cu_2. The VHW has two large black postmedian ocelli and two conspicuous bluish-white ocelli, which may have dark centers ..... *hewitsonii*

1b. The VFW median crossband is white or white with pale blue shading, with the anterior part (R_3-M_2) of the band white and narrower (1.0-1.5 mm in diameter). The DHW has a blue or pale blue cross band narrower (3.0-3.5 mm) and tapered, with an elongate triangular separate macula posterior to Cu_2. The VHW has two small or incomplete dark postmedian ocelli and two small white ocelli ..... *boliviensis*

Females.

1a. The VFW has a relatively broad white median band (2-2.5 mm) from R_3 to M_2. The DFW has a median cross band that is bright blue. The VHW has two large dark postmedian ocelli and two white ocelli which may have dark central spots. ..... *hewitsonii*

1b. The VFW has a narrow (or missing) median band (1 mm) from R_3 to M_2. The DFW median crossband may be paler blue. The VHW has two small or partial postmedian dark ocelli and two very reduced white ocelli ..... *boliviensis*

Nessaea hewitsonii hewitsonii (Felder & Felder), 1859

Figs. **1, 39-42, 48, 53, 57, 61**

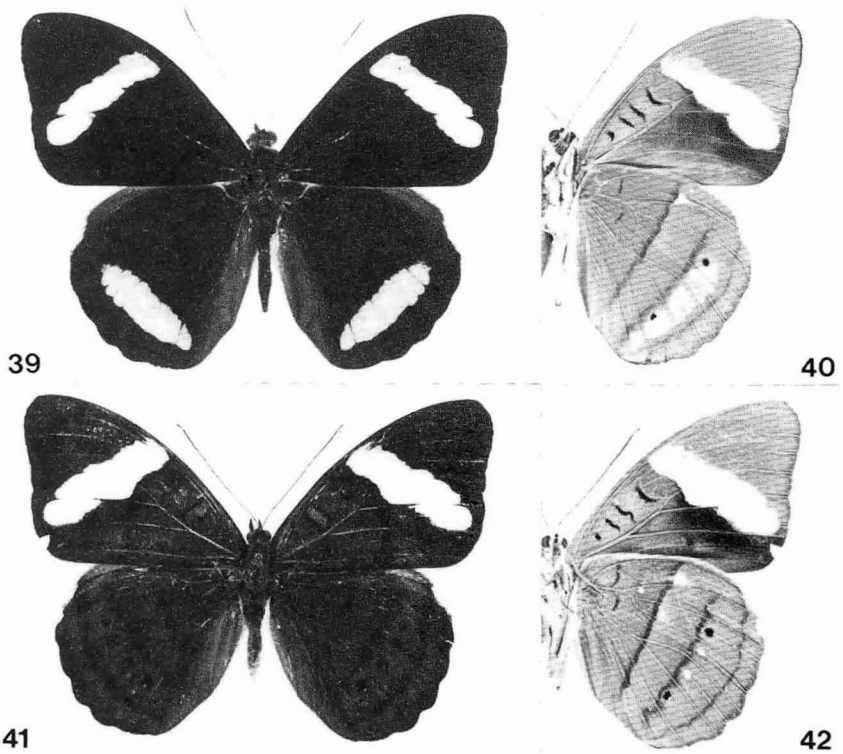
Epicalia hewitsoni Felder & Felder, 1859. Wien. Ent. Monat. 3: 263-273, 1 pl. TL: Brazil [São Paulo de Olivença region]. Syntypes: 1 ♂ BM designated lectotype by Vane-Wright (1979). (Examined). [The illustration by Felder and Felder (1859) pl. 5, f. 1 states

hewitsonii and was adopted by Felder and Felder (1862) first revisers].

Description: As in *N. hewitsonii* except for differences listed for *N. hewitsonii hewitsonii* in the key to subspecies. Average wing length ♂ (33-40)36.1 mm, ♀ (37-41)38.8 mm.

Distribution: This subspecies is widespread, occurring from Colombia, Ecuador and Perú extending eastward into the Amazon valley, (questionably to Obidos, Pará) and south to Rondônia, Brazil (Fig. **61**). Intergrades occur in southern Perú with *N. hewitsonii boliviensis*.

Taxonomy and Variation: A syntype specimen in the BM collected by Bates was designated lectotype by Vane-Wright (1979). I have studied this specimen and it is typical of nominate *N. hewitsonii*. There is very little variation in *N. h. hewitsonii* except for size related to latitude. There is some variation in the width of the blue median crossband on the DFW, but this varies within a series from the same locality. I have examined a specimen in the MN which appears to be a hybrid of *N. hewitsonii* with a species with orange on the DHW. This was illustrated in Vane-Wright (1979) as a presumed hybrid *obrina* (=*ancaea*) X *hewitsonii*. It is from São Paulo de Olivença, Brazil which is in the range of *N. obrina*. However, the orange marking is more typical of *N. batesii* which does not occur in this region. The blue postmedian band on the DHW was reduced to three



Figures **39-42**. *Nessaea hewitsonii hewitsonii* (Felder & Felder). ♂ dorsal (**39**), ventral (**40**) surfaces. PERU, *Amazonas*, Yurimaguas (AA). ♀ dorsal (**41**), ventral (**42**) surfaces. ECUADOR, *Pastaza*, Puyo (AA).

blue maculae. There is also a blue apical area on the DHW typical of *N. hewitsonii*. The postmedial dark line on the VHW is more typical of *N. obrina* than *N. batesii*.

Biology: *N. hewitsonii* occurs fairly commonly in a broad range of the Amazon basin including the eastern slopes of the Andes mountain range. It is found in high evergreen tropical forest, semi-deciduous tropical forest, and riverine forest. I have collected adults in openings where trees have fallen or been cut, along forest trails, and at the edges of forests. They fly very fast in an erratic fashion and land suddenly on leaves, or on the ground if decaying fruit is present. They are readily identified by the bright blue bands on the front and hind wings. I have found them highly attracted to fermented bananas and other fruit baits in various localities in Ecuador and Perú. They are also attracted to human perspiration (Vane-Wright, 1979).

The adults occur at near sea level to about 1,500 m in altitude on the eastern slopes of the Andes. They have been collected in every month of the year.

Immature Stages and Host Plants: No records are known of the immature stages or host plants.

Specimens Examined ♂ 276, ♀ 77

COLOMBIA: *Santander*, Landázuri; Medina; *Cundinamarca*, Bogotá; *Valle*, Cauca Valley; *Meta*, Villavicencio 400 m; San Martín; Río Meta; *Putumayo*, Florida; Condagua; Río Caqueta; Río Putumayo; Mocoa; Villa Garzón 300 m; ECUADOR: *Napo*, Río Arajuno; Curaray; Río Coca 300 m; Puerto Misahualli; Tena; Río Napo; Limoncocha; Cotapino; *Zamora-Chinchipe*, Zumbi; *Pastaza*, Canelos, Río Bobonaza; Puyo; Río Pununo; Sarayacu; *Bolívar*, Balzapamba; *Tungurahua*, Topo; PERU: *Loreto*, Iquitos; Balsapuerto; Nauta; Pebas; Río Humayta; Yurimaguas; Río Paranapura; Lower Río Ucayali; *Ucayali*, Pucallpa; *Amazonas*, Pongo de Manseriche; *Huánuco*, Tingo María; Río Huallaga; *Junín*, Satipo; Chanchamayo; La Merced; Río Toro; Río Perené; *Pasco*, Palcazu; Chuchurras; *Cuzco*, Río Colorado; *San Martín*, Chambirayacu; *Madre de Dios*, Shintuya X; BRAZIL: *Amazonas*, Benjamin Constant; São Paulo de Olivença; Rio Madeira; Manicoré; Tefé; Igarapé Preto; Ticunas; Lago Acará; *Pará*, Obidos (?) *Rondônia*, Jaru; São Carlos; *Acre*, Rio Juruá, Alto Rio Juruá.

Nessaea hewitsonii boliviensis Subsp. nov.

Figs. **1, 43-46, 48, 53, 57, 61**

Description: Male. The DFW has a black background with a turquoise blue or whitish-blue, median, diagonal crossband that extends anteriorly to R_2. There are no subapical blue maculae. The DHW has a turquoise blue or pale blue crossband (3.0-3.5 mm at widest point), with a separate triangular blue macula (separated at Cu_2). The VFW median crossband is white or white with pale blue shading with the anterior part (R_3-M_2) of the band white (1.0-1.5 mm in diameter). The VHW has two small or partial dark and two small white postmedian ocelli distal to a continuous reddish-brown narrow band. The male genitalia and hypandria are the same as *N. h. hewitsonii*.

Female. The DFW has a brown background with a blue or pale blue median crossband. There are no subapical blue maculae. The DHW has two to four dark ocelli, and there is a blue apical area. The VFW and VHW are similar to the male.

Average wing length ♂ (35-40)37.5 mm, ♀ (36-41)38.8 mm.

HOLOTYPE ♂: BOLIVIA: *Beni*, Trinidad. JC to AA.

PARATYPES 19 ♂ 6 ♀: BOLIVIA: *Beni*, Trinidad 1 ♂ HD; 1 ♂ BM; Reyes 1 ♂ BM; *Santa Cruz*, Buena Vista 12 ♂ 4 ♀ BM; 17° S 61° W. 1 ♂ SI; No specific locality 2 ♂ 1 ♀ DB; *Cochabamba*, El Palmar, Chapare 1 ♀ AA.

Deposition of type material: Holotype ♂ and 1 ♀ paratype in AA; 1 ♂ paratype in HD; 1 ♂ in SI; 14 ♂ and 4 ♀ in BM and 2 ♂ and 1 ♀ in DB.

Distribution: This subspecies is presently known to occur in Bolivia and in Southern Perú where intergrades occur in Madre de Dios and Junín provinces (Fig. **61**).

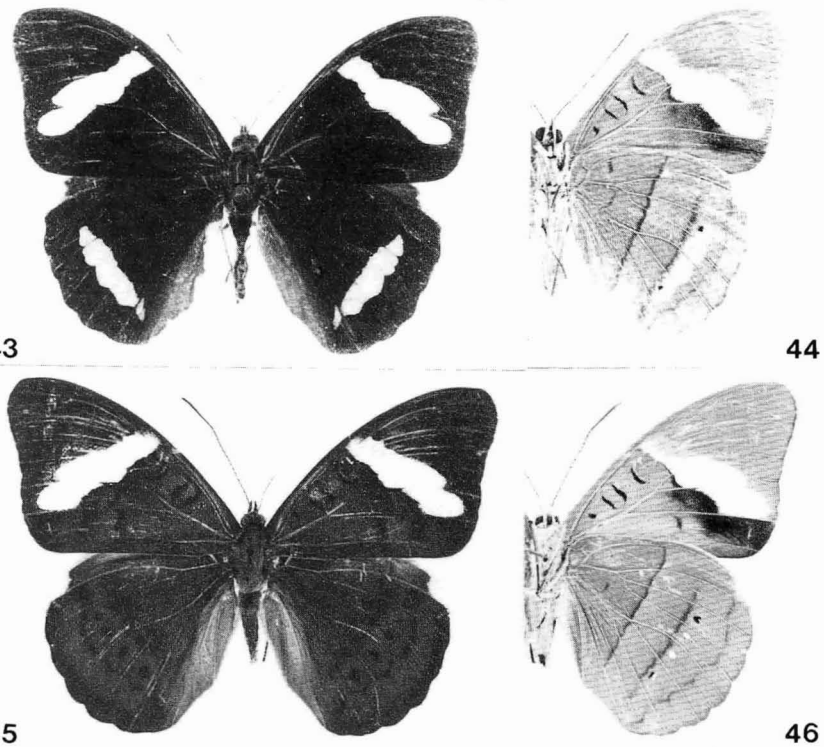
Taxonomy and Variation: Diagnostic characters are presented in the key to subspecies. There is some variation in the coloration of the blue cross bands on the fore and hind wings. The bands may be almost pure white to partially white or washed with pale blue to pale greenish-blue. Some specimens have white only on the DFW or part white on any of the bands.

Biology: Adults are found in tropical forests in openings or trails. They have been collected from about 500 to 1,000 m elevation. Adults have been found from July to April.

Immature Stages and Host Plants: The immature states and host plants are unknown.

Specimens Examined: 46 ♂ 17 ♀

BOLIVIA: *Beni*, Trinidad 1 ♂ HD, 1 ♂ JC; 1 ♂ BM; Reyes 1 ♂ BM; *Santa Cruz*, Buenavista 750 m Aug.-Apr. 12 ♂ 4 ♀ BM; Apr.-Jul. 450 m 9 ♂ 6 ♀ CM; Santa Cruz de la Sierra 5 ♂ 1 ♀ BM; 1 ♂ SI; 1 ♂ MP; Río Surutu 1 ♂ Apr. CM; Prov. Sara 3 ♂



Figures **43-46.** *Nessaea hewitsonii boliviensis* Jenkins. ♂ dorsal (**43**), ventral (**44**) surfaces. BOLIVIA, *Beni*, Trinidad. Holotype *Nessaea hewitsonii boliviensis.* Jenkins (JC) deposited in (AA). ♀ dorsal (**45**), ventral (**46**) surfaces. BOLIVIA, *Santa Cruz* (no specific locality). Paratype (DB).

4 ♀ CM; Portachuela Apr. 2 ♂ 1 ♀ CM; No specific locality 1 ♂ AM; 2 ♂ 1 ♀ DB; Río Juntas 1 ♂ BM; 17° S, 61° W SI; *Cochabamba*, Cochabamba 2 ♂ BM; Chapare Apr. 1 ♀ AA; PERU: *Junín*, La Merced X 1 ♂ BM; *Madre de Dios*, Shintuya 460 m, July X 2 ♂ AA.

E. WING LENGTH OF *NESSAEA* IN RELATION TO LATITUDE

The remarkable difference in wing length of specimens of *Nessaea* suggests that there may be environmental factors involved, perhaps related to latitude. Bergmann's Rule states: "The smaller-sized geographic races of a species are found in the warmer parts of the range, the larger-sized races in the cooler districts." Ray (1960) stated that this rule expresses fundamental size, growth and form relationships with relation to temperature and is applicable to both poikilotherms and homiotherms.

Vane-Wright (1979) noted the difference in wing sizes of *Nessaea* and made wing measurements of each species. He concluded "that the biometric data essentially reflect the phylogenetic sequence proposed (*regina*→*aglaura*→*batesii*→[*obrina*] = *ancaea*→*hewitsoni*, insofar as no other single sequence of species would give such orderly trends as those shown." He states that while Bolivian specimens of *N. hewitsonii* "are also the largest, little should be made of this. As shown by Vane-Wright, Ackery and Smiles (1975), the size of Andean butterflies may vary in a way analogous to 'Bergmann's Rule'... We might expect Bolivian *hewitsoni* to be the largest." They showed that there was a direct correlation of increased wing length with increased latitude for *Heliconius telesiphe* and *Podotricha telesiphe* in the Andean region. For *Hamadryas februa*, Jenkins (1983) stated that the smallest wing lengths in males occurred in Trinidad, Venezuela, and Colombia (ave. 27.6 mm) [10° N Lat.], while in northern México the length was ave. 40.0 mm [25° N. Lat.] and in Argentina the length was ave. 42.0 mm [30° S. Lat.]. A similar increase in wing length with latitude was shown in both males and females for both *H. februa* and *H. feronia*. However, it was not observed in several other species of *Hamadryas*.

Measurements were made of forewing lengths of the four species of *Nessaea*. Since males are usually smaller than females the data for the two sexes were analysed separately. Measurements were made with dial calipers or a millimeter rule (accurate to 0.5 mm) from the base of the wing to the extreme tip. Data on wing lengths in Vane-Wright (1979) were used when it was possible to assign latitude to his localities. (Since his study was not made to compare with latitude, some data were lumped, for example, Table 1 for *hewitsonii* (4) N. Andes-Ecuador, Colombia and Peru [10° N. Lat. to 16° S. Lat.] and could not be used.) The forewing measurement data combined with data from Vane-Wright (1979) are presented in Table 2 for *N. obrina* and *N. hewitsonii*. There were insufficient data available for *N. aglaura* and *N. batesii* to make valid comparisons and the few data analysed for these species showed little significance.

Regression analyses were conducted. The data are plotted for wing length vs. latitude in Fig. 47 for *N. obrina* and in Fig. 48 for *N. hewitsonii*. For male *N. obrina* the calculated regression line slope was 0.345 with a correlation coefficient of 0.866 showing good direct correlation of wing length vs. latitude. (The mean was 34.50 mm and the SD was 2.41 and variation 5.44.) For female *N. obrina*, the slope was 0.479 and the correlation coefficient was 0.924. (The mean was 36.17 mm with the SD 2.76 and variation 7.026.)

For male *N. hewitsonii* the calculated regression line slope was 0.176 and the correlation coefficient was 0.845. (The mean was 36.59 mm and the SD 1.26 with a variance of 1.465.) For females the slope was 0.127 and the correlation coefficient was 0.698. (The mean was 38.53 mm with the SD 1.14 and a variance of 1.18.)

These analyses show that there is a statistically significant direct linear correlation indicating that with increase of latitude there is an increase of wing length for *N. obrina* and *N. hewitsonii*. However, the decrease is not at a minimum at the equator but occurs at between 5° to 10° N Latitude. This is the same phenomenon observed with *Hamadryas* species (Jenkins, 1983). The smallest specimens of *Nessaea* occur at about 10° N. latitude in northern Colombia, Venezuela and into the northern part of the Guyanas. At present

there does not appear to be a logical explanation. When data on wing length are compared for correlation with elevation or longitude, there does not appear to be any significant correlation. However, this has not been studied with sufficient comparable data to be statistically certain.

TABLE 2. WING LENGTH OF NESSAEA VS. LATITUDE

Locality	° Lat.	Males mm	Males No.	Females mm	Females No.
NESSAEA OBRINA					
Guyana (V)	N. 5	30.88	21	32.19	15
Guyana	N. 5	30.40	15	31.18	9
E. Venezuela	0	33.0	1	34.5	2
Obidos	S. 2	32.61	8	35.8	5
Ecuador	2	33.05	4		
Lower Amazon (V)	3	33.31	41	35.04	34
Tefé, Maués	3.5	33.8	13	35.1	9
Iquitos (V)	4	35.5	44	37.74	27
Iquitos	4	34.78	9	36.82	3
Upper Middle Amazon (V)	4	35.55	34	37.9	19
Manicoré	5.5	35.0	3	35.05	6
Tingo María	9	35.6	10	39.8	3
Satipo & Rondônia	11	37.33	9	39.2	5
Madre de Dios	13	37.71	15	40.1	3
Bolivia	15	39.5	2		
NESSAEA HEWITSONII					
Colombia	N. 5	35.0	6		
Colombia	N. 3			37.5	3
Ecuador	S. 2	35.5	18	37.8	8
São Paulo Olivença (V)	3.5	36.14	17	38.03	4
São Paulo Olivença	3.5	35.3	6	37.0	1
Iquitos	4	35.5	21	39.0	1
Iquitos (V)	4	36.72	28	38.69	10
Rio Madeira (V)	4	35.01	12	37.06	5
Tingo María	9	37.2	12	39.5	2
Jaru, Rondônia	10	37.0	2		
Satipo, Perú	11	38.6	10	40.1	4
Madre de Dios	13	38.0	2		
Bolivia (V)	16	37.69	23	38.97	6
Bolivia	16	38.0	4	40.2	2

(V) = Vane-Wright (1979)

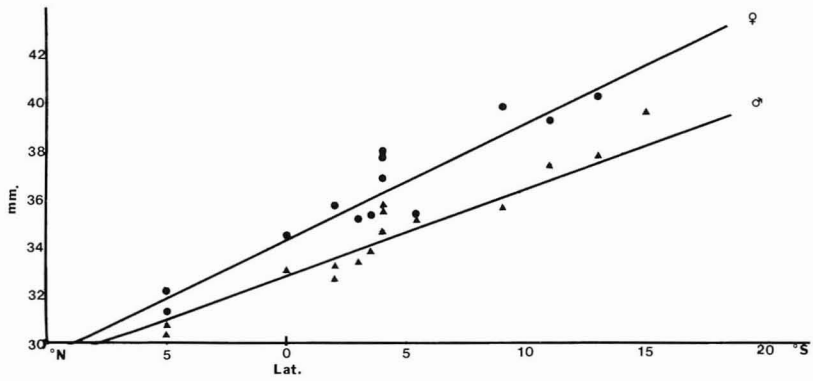


Figure 47. Relationship of wing size to latitude in *Nessaea obrina.*

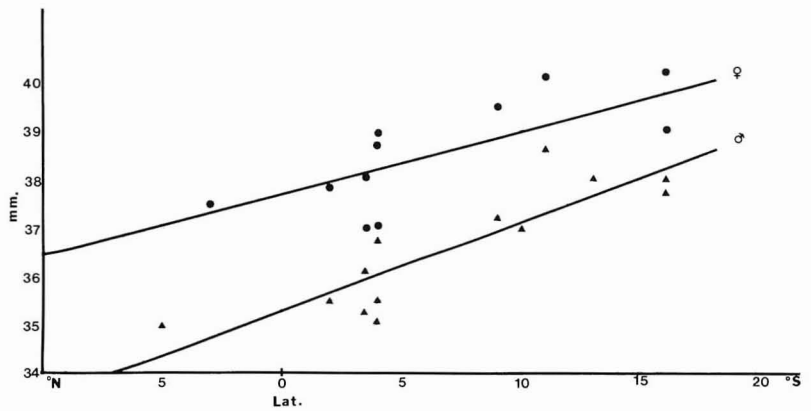


Figure 48. Relationship of wing size to latitude in *Nessaea hewitsonii.*

F. ACKNOWLEDGMENTS

I am pleased to acknowledge the kind assistance of persons who have helped with this revision of *Nessaea.* Mr. Richard I. Vane-Wright was most helpful in discussions. His revision (1979) served as a valuable starting point for this study. This manuscript was reviewed and helpful suggestions were made by Drs. Lee D. Miller, Jacqueline Y. Miller, Gerardo Lamas M., John C. Downey and Keith S. Brown. Many museum curators, as listed under collections examined, were very helpful in permitting study and photographing of their collections and loan of specimens. Dr. J. Y. Miller helped with photographic illustrations. Fig. 2 is reprinted with permission of Princeton University Press.

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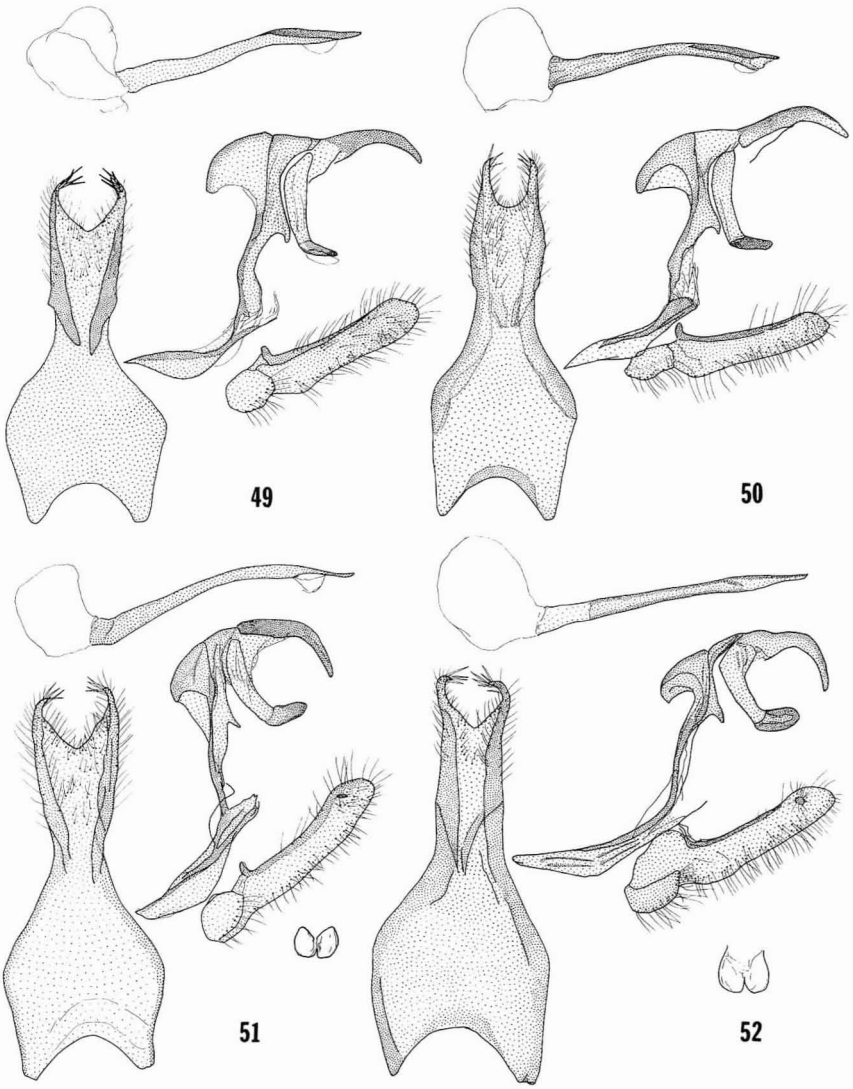
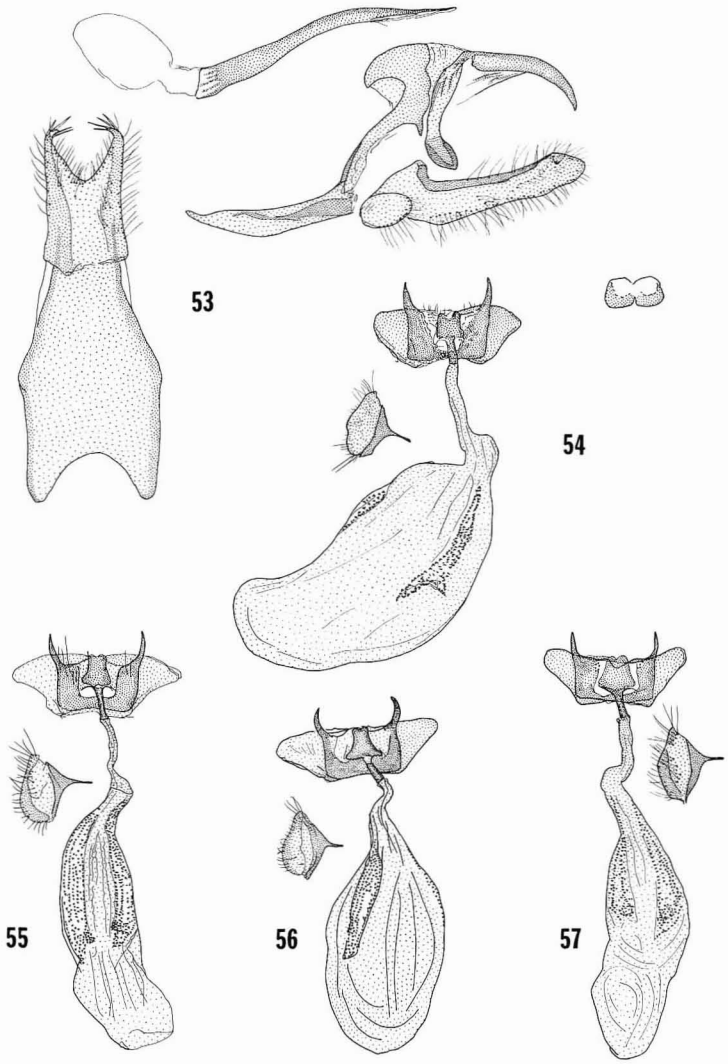


Figure 49-52. ♂ genitalia and hypandria of *Nessaea*. **49** *Nessaea aglaura aglaura*. **50** *Nessaea aglaura regina*. **51** *Nessaea obrina*. **52**, *Nessaea batesii*.



Figures 53-57. 53. ♂ genitalia and hypandrium of *Nessaea hewitsonii*. 54-57. ♀ genitalia of *Nessaea* showing sterigma and associated structures, corpus bursae with signa and papillae anales. 54. *Nessaea aglaura*. 55. *Nessaea obrina*. 56. *Nessaea batesii*. 57. *Nessaea hewitsonii*.

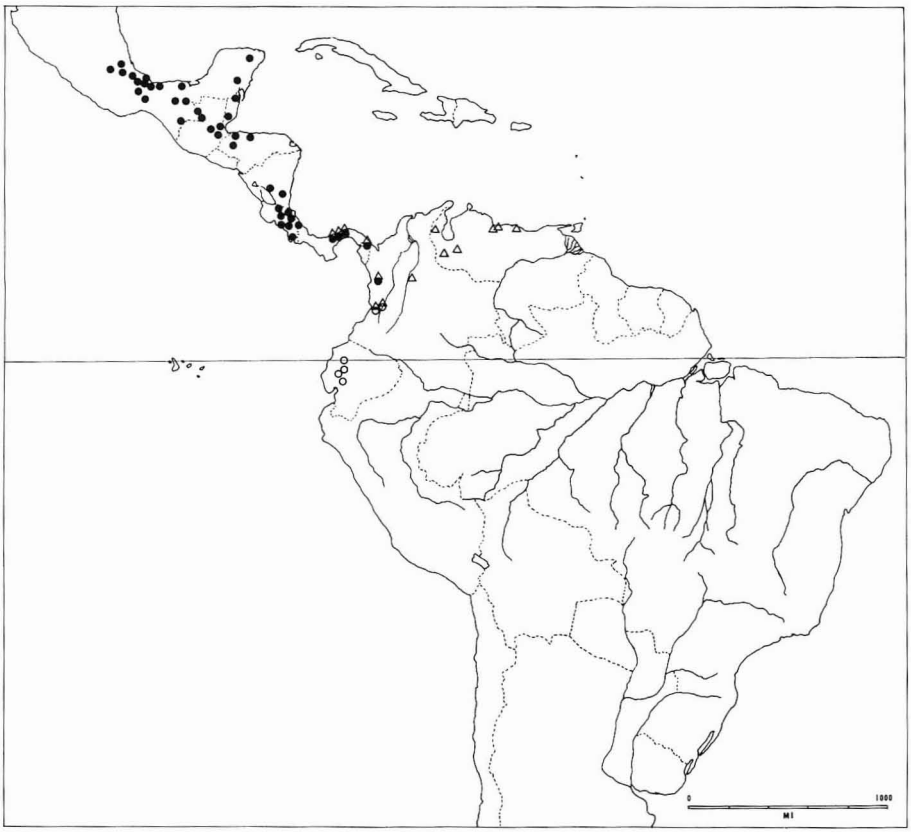


Figure 58. Distribution of subspecies of *Nessaea aglaura* ● = *a. aglaura*, △ = *a. regina*, ○ = *a. thalia*.

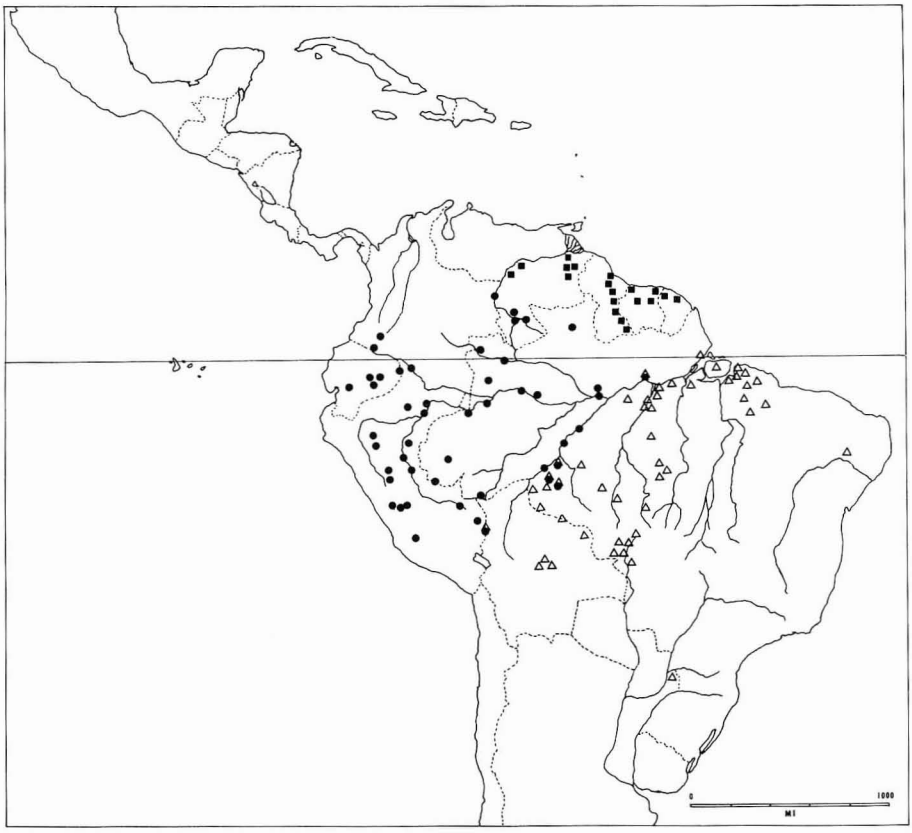


Figure 59. Distribution of subspecies of *Nessaea obrina*. ■ = *o. obrina*, Δ = *o. faventia*, ● = *o. lesoudieri*.

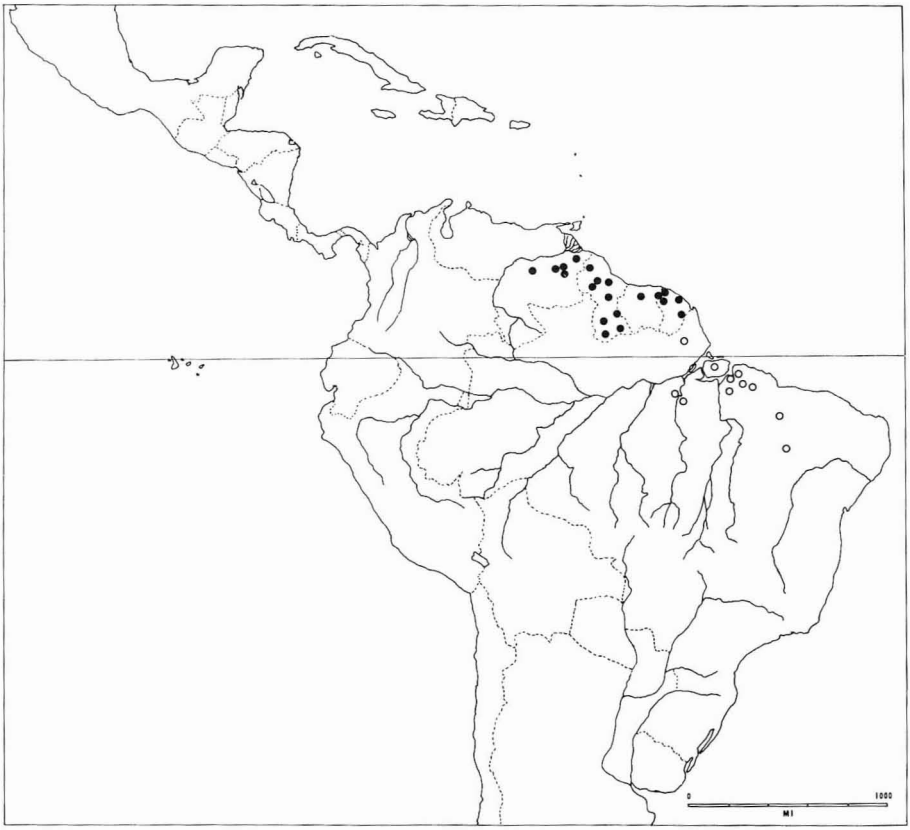


Figure 60. Distribution of subspecies of *Nessaea batesii*. O = *b. batesii*, ● = *b. magniplaga*.

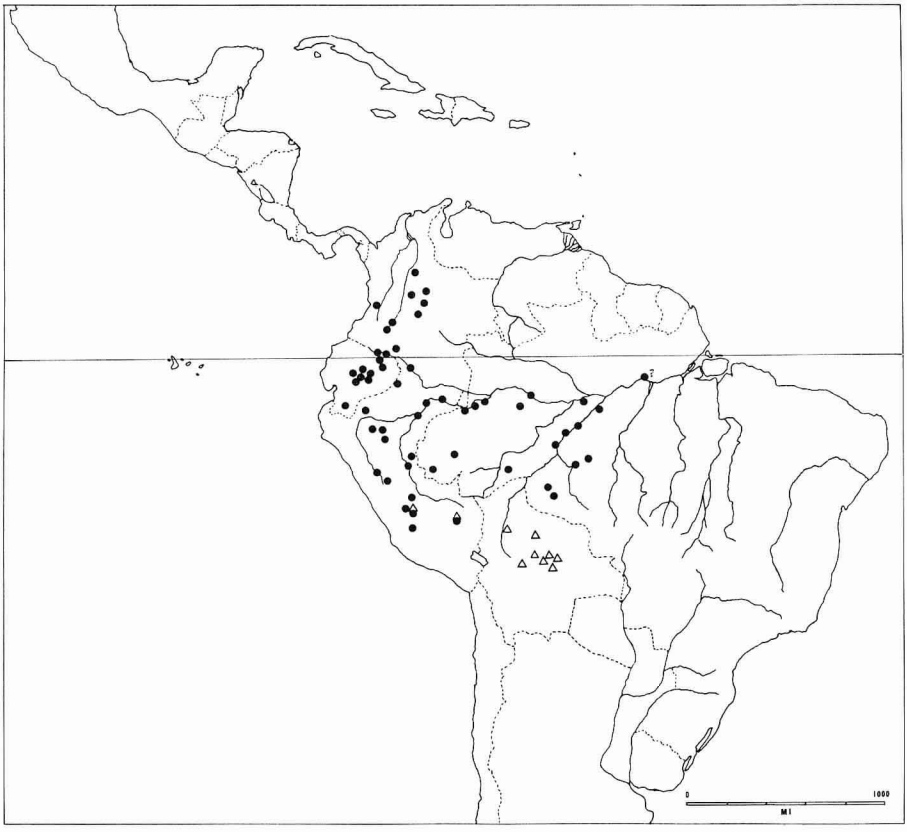


Figure 61. Distribution of subspecies of *Nessaea hewitsonii.* ● = *h. hewitsonii,* △ = *h. boliviensis.*

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