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## THE BUTTERFLIES OF ANEGADA, BRITISH VIRGIN ISLANDS, WITH DESCRIPTIONS OF A NEW *CALISTO* (SATYRIDAE) AND A NEW *COPAEODES* (HESPERIIDAE) ENDEMIC TO THE ISLAND

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This paper is dedicated to the memory of John Griffith of Jesus College, Oxford.

### INTRODUCTION

Anegada island is the northernmost member of the Lesser Antillean arc, situated at 18° 43'N and 64° 19'W. Its nearest neighbors are Anguilla, about 80 statute miles (127 km) across the Anegada Passage to the east-southeast and Virgin Gorda, about 13 miles (21 km) due south. Whereas the Virgin Islands are generally mountainous, Anegada reaches perhaps 18' above mean sea level and much of the island is considerably lower (D'Arcy, 1975). It is about 10 miles (16 km) in length, about 15 square miles (39 km<sup>2</sup>) in area, oriented along the east-west axis and is just over 2 miles (3.5 km) across the widest point (Fig. 16). From the south coast and into the Anegada Passage to the southeast extends the Horseshoe Reef, long a hazard to navigation. The island had a long history of pre-Columbian occupation and, at the time of writing, has a resident population of about 125, most living in the Settlement, near the south coast in the center of the island.

The eastern two-thirds of Anegada consists of limestone pavement, generally exposed but in places lightly covered with sand; in the west the sand cover is deep and more or less uninterrupted. A conspicuous feature of the western region of the island (Fig. 16) is a series of extensive shallow saline ponds, now open to the sea via a narrow bridged channel on the south coast, although a channel on the north coast was also present until closed by a hurricane in 1819 (Schomburgk, 1832). The eastern end of the island is more

or less isolated other than along the northern shore by wet saline flats, from which a series of small, isolated pools extend westwards, flanking the northern coast. In the past, large areas of the island were dissected into fields and corrals by dry stone walls; these have been generally abandoned and the areas formerly cleared have become covered in dense dry scrub (Fig. 17), while cattle, donkeys and goats roam at will. Several fresh water wells or 'slobs' are reported in the eastern half of the island: a pond on the limestone pavement (Locality 9; fig. 16) is the largest we have visited.

We have worked on the island on six occasions: 6-10 September 1989, 1-4 April, 19-21 June 1990 (FM), 3-9 July, 3-10 September and 10-13 December 1990. Localities worked are numbered 1-10 on the map (Fig. 16) and mentioned in the general listing of butterflies recorded on the island, but attention is first focused on a very restricted area in the northwest, where two undescribed butterflies were recently found.

A single female specimen of a *Calisto* was included in a small collection of butterflies made during a visit to the island by Dr. Scott Miller, in July 1986, and this specimen is housed in the National Museum of Natural History (Washington). One of us (DSS) searched for this insect, unsuccessfully, in September 1989 and April 1990, but when we learned of the locality citation of 'Bones Bight' on the original specimen, the colony was discovered in June 1990 (FM) and has been studied (DSS) on subsequent visits.

Bone's Bight is a bay about one mile in length on the northwest coast of Anegada (Locality 3). It is bordered by a wide beach of white sand, flanked by low dunes bearing a dense cover of sea lavender (*Tournefortia gnaphalodes*), a low sedge (*Fimbristylis spadicea*), clumps of bay cedar (*Suriana maritima*), occasional sea grape trees (*Coccoloba uvifera*) and other shoreline plants. On the landward side, the dune vegetation merges with xeric scrub on the more or less exposed limestone slab, apparently a westerly projection of that covering much of the eastern part of the island. The region flanking the central stretch of the Bight constitutes a narrow isthmus between the beach and one of the saline ponds, edged with flats bearing beds of *Batis maritima* and *Salicornia perennis*: to the east and west the isthmus ends as the strip of land broadens around the ends of the pond (Fig. 16).

Search for the *Calisto* was started at the eastern end of Bone's Bight, from the limit of the dunes into the fringing scrub; initially, not only was the satyrid not seen but the region seemed almost devoid of butterflies other than a few specimens of *Hemiargus thomasi* and very occasional *Ascia monuste*. Search was continued, fruitlessly, westwards along and into the scrub, on both sides of a track traversing the isthmus. Work in almost shadeless sun in a seemingly comprehensively hostile locality was about to be abandoned, with the conclusion that four specimens collected by FM the previous month represented a brood no longer on the wing, when the first *Calisto* was sighted. At this point, near the center of the isthmus, the vegetation is generally of low ground cover, interrupted by patches of shrubby growth with scattered trees and thickets, and areas of exposed limestone pitted with small and larger sinkholes. Cover is provided by bushes of *Croton discolor* and *Ernodea littoralis*, small plants of *Erithalis fruticosa* and *Dodonea viscosa* while on the rock surface are present isolated barrel cactus (*Melocactus intortus*), the conspicuously yellow-flowered *Urechites lutea*, and *Strumpfia maritima*. Towering over the low cover are the 2 m inflorescence spikes of the epiphytic orchid *Epidendrum* (= *Encyclia*) *bifidum* and, rooted in small sinkholes are stunted saplings of *Tabebuia heterophylla* and loblolly trees (*Pisonia subcordata*). Mature loblollies, up to 6 m in height, are spread thinly through the area, the broad leaves providing patches of deep shade; these form the center of thickets which include small trees of *Coccoloba uvifera*, *Zizyphus rignonii*, *Byrsonima cuneata*, *Acacia anegadensis* and *Cassine xylocarpa*, often with dense bushy aggregates of *Dodonea*, *Erithalis*, *Croton*, *Lantana* and *Cordia rupicola*. The only features obviously demarcating this region from land to the east and west are, firstly, the more frequent and extensive open areas and, secondly, the presence of a coarse grass (*Uniola virgata*) distributed as isolated tussocks along the track and in more contiguous patches on land sloping down to the saline flats to the south and the dunes to the north. Tussocks are also frequent around the shaded perimeter of loblolly thickets but do not extend into the patches of leaf litter surrounding each *Pisonia* trunk. Further east, all

of the above plants are present with the exception of *Uniola virgata*; to the west the grass soon dwindles as the open patches of limestone on which it seems to flourish become increasingly sand covered and the open vegetation becomes replaced by a more continuous and dense *Dodonea/Erithalis* scrub that dominates the western end of the island.

At the moment when the first *Calisto* was found, a small tawny skipper was seen flying along an outer blade of a *Uniola* tussock, in its slow progression yet rapid wingbeat calling to mind the flight of *Copaeodes minima* (W. H. Edwards, 1870). This proved to be an undescribed insect, with a range precisely coinciding with that of the *Calisto*, sharing the same center of abundance but differing markedly in its behavior. The habitat of these two butterflies has been described in some detail since neither has been found elsewhere on the island. The insects will be described below and notes on their field behavior included later, in the list of species known from Anegada.

*Calisto anegadensis*, new species

Figures 1a, 1b (♂), 1c, 1d (♀), 1e, 1f (♂ genitalia), 1g (♀ genitalia)

*Description:* FW length ♂ : mean 17.2 mm (16.5-18 mm n=31); ♀ : mean 19.5 mm (18.5-20.5 mm n=12).

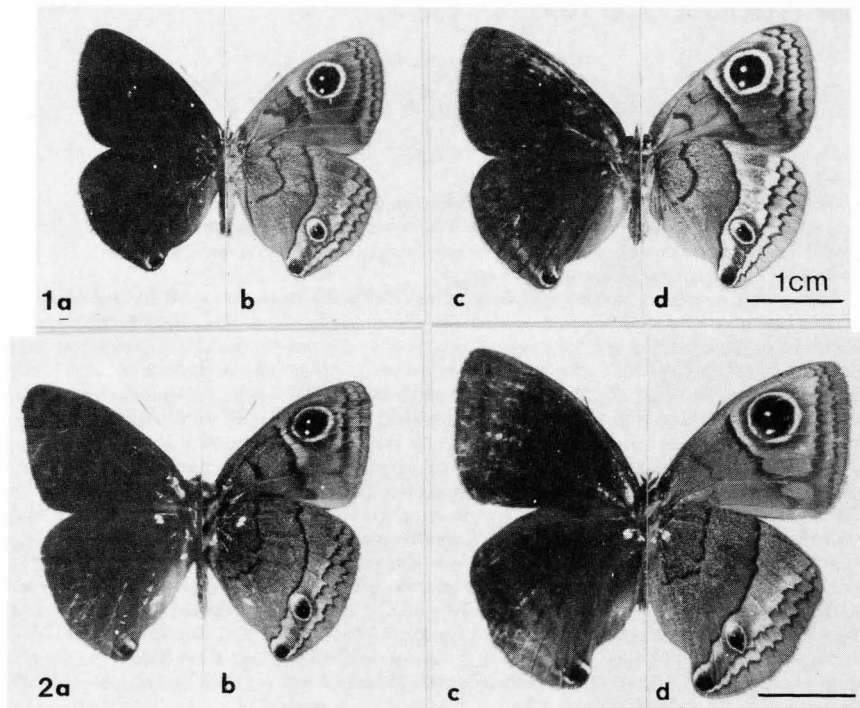
**Male:** *Upper surface,* FW rich dark brown-black, lateral area from anal angle to costa slightly paler; "androconial patch" not conspicuously darker than ground. HW uniformly brown-black with a well defined, intensely black tornal spot between short straight yellowish bars; tornal lobes well developed.

*Under surface* ground colour rich dark brown. FW with black marginal and submarginal lines, the latter obscure towards anal angle and veins between lines darker than spaces distal to ocellus; black bar from costa to cell end, — shaded distad with yellowish; a short dark bar from costa to mid-anterior cell margin and a curved dark bar from costa crossing cell near base, defining slightly reddish area to wing base. Large subapical round black ocellus within yellow ring slightly widened distad, with two small vertically placed white pupils, lower almost touching ring. HW with jagged black prediscal line through mid-cell and a curving black discal line from mid-costa to the inner margin slightly basad of tornus, dusted distad with light grey scales consolidated into concavo-convex line between ocellus and upper edge of tornal spot. Outer dark submarginal line from apex to tornus in regular arcs with apices towards vein ends; inner submarginal line less regularly arced and flanked basad above ocellus with three or four patches of greyish scales; spaces between submarginal lines scaled with light brown to grey towards tornus, ending in very narrow yellowish line in spaces  $Cu_2-3A$ , curving around outer margin of tornal spot; veins darkened between submarginal lines. Prominent slightly elliptical black ocellus in  $Cu_1-Cu_2$  outlined by yellow with some reddish scaling, then black; yellow ring slightly broadened basad and including small eccentric white pupil, sometimes with one or more minute axially placed white points in black ground of pupil. Two small white spots in spaces  $M_2-M_3$ ,  $M_3-Cu_1$ . Tornal spot black and ellipsoidal, narrowly edged with reddish. Fringes dark blackish brown above and beneath.

**Female:** *Upper surface* dark fuscous. FW slightly paler at base and beyond cell; HW with small black tornal spot flanked distad by narrow yellowish crescent in  $Cu_2-2A$  from which extends straight dark submarginal line, edged inwardly by lighter brown from  $M_2$  to tornus and flanked proximad by short yellowish line; tornal spot merges with similar sized patch of reddish scales posteriad of vein  $M_2$ ; tornal lobe well developed. *Under surface* FW ground color brown, darkest from ocellus to anal angle and faintly suffused with reddish from within basal area of cell to posterior margin. Two submarginal lines as in male but more clearly defined against pale grey-brown ground, especially towards apex and along anterior margin; three lines basad of ocellus as in male but more clearly defined, especially outermost crossing cell end, flanked distad by pale grey-brown line. Ocellus as in male but yellowish ring slightly wider and lower of two white pupils usually offset basad. HW similar to male but ground color distinctly reddish basad of black discal line; two submarginal lines conspicuous on pale grey-brown ground, outer arced as in male

and inner formed by series of offset dashes, flanked basad by four triangular grey-lilac patches. Black ocellus larger and more strongly elliptical than in male, defined by yellow then reddish ring, with small white pupil set in yellow ring basad and sometimes with minute white supplementary pupils as in male. Two small bluish white spots in spaces  $M_2$ - $M_3$ ,  $M_3$ - $Cu$ , on grey-lilac patches. Small black tornal spot with anterior reddish scaling confluent with that of outer ring of ocellus; fringes dark brown above, pale grey-brown beneath (Figs. 1a-1d; *C. nubila* Lathy, 1899 for comparison, Figs. 2a-2d).

The above descriptions are based on fresh specimens. As in other *Calisto* species, scale loss readily occurs before wing membranes sustain any damage in flight, resulting in marked changes in contrast and tint of markings. In this instance, upper surface ground color becomes paler in both sexes and, particularly on the HW under surface of the female,

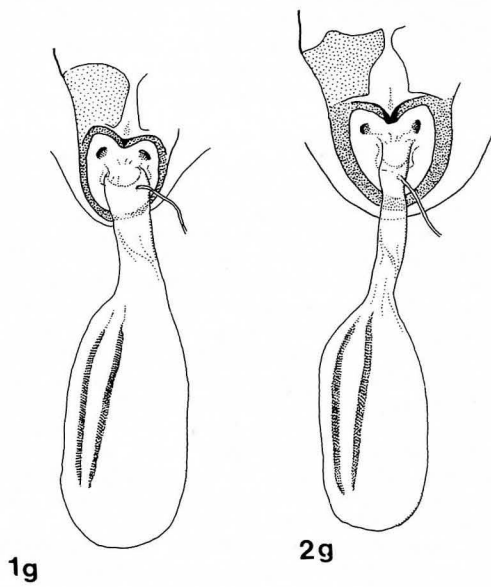
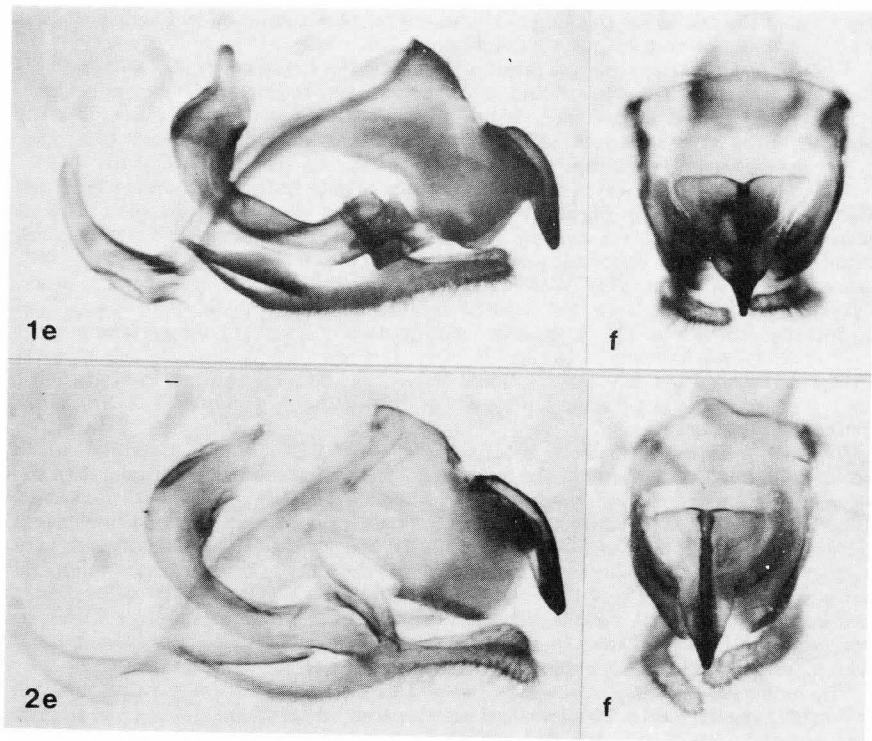


Figures 1-2. *Calisto anegadensis*: 1a male (Holotype) upper surface, 1b under surface; 1c female upper surface, 1d under surface. *Calisto nubila*: 2a male upper surface, 2b under surface; 2c female upper surface, 2d under surface. (El Junque, Puerto Rico, September 1986).

Figures 1-2 (cont.) *Calisto anegadensis* male genital capsule; 1e, lateral aspect, 1f, dorsal aspect including uncus and tegumen. *Calisto nubila* male genital capsule; 2e lateral aspect, 2f dorsal aspect including uncus and tegumen.

Female genitalia. Figure 1g, *Calisto anegadensis*, drawing of female genital plate and associated structures. Note that in this internal view (as in Fig. 2g), the signa lie at or slightly beneath the left margin of the corpus bursae, which has been rotated clockwise in this drawing. Figure 2g, *Calisto nubila* drawing of female genital plate and associated structures (for details see text).





the tints of the pale areas flanking the submarginal bands are soon lost and the extent to which they contrast with the ground diminishes.

**Variability:** Other than changes resulting from scale loss, neither sex shows appreciable individual variation. The relative placing of the two pupils within the FW ocellus beneath, vertically positioned in the male, is rather less constant in females where, in most specimens, the lower is variably offset towards the wing base with respect to the upper.

The specific name recognizes that this insect is known only from Anegada.

**Types:** Holotype ♂, N side of track through Bone's Bight isthmus, NW Anegada Island, British Virgin Islands, in flight, 1100 hrs July 5, 1990; allotype ♀, S side of track as above, nectaring on *Zizyphus rignonii*, 1200 hrs July 6 1990 (D. S. Smith and F. McKenzie), both deposited Hope Entomological Collections, Oxford, England. Paratypes, 1 ♀, Anegada: Bones Bight, July 1986 (S. Miller), National Museum of Natural History, Washington; data as above and September 3-10 1990: 2 ♂, 2 ♀, Allyn Museum of Entomology, Sarasota; 1 ♂, 1 ♀, American Museum of Natural History, New York; 1 ♂, 1 ♀, Carnegie Museum of Natural History, Pittsburgh; 1 ♂, 1 ♀, British Museum (Natural History), London; 1 ♂, National Museum of Natural History, Washington; 1 ♂, 1 ♀ collection Stuart Ramos, University of Puerto Rico, Mayaguez; 23 ♂, 5 ♀, Hope Entomological Collections.

**Genitalic features:** "The uncus is curiously modified into a blunt, curved rod, which seems to overlap the dorsum of the tegumen . . . the valves are much reduced, with the form of short, narrow rods": the features of the male genitalia of *Calisto nubila* Lathy, 1899 noted by Bates (1935) serve equally well for *C. anegadensis*, but the two insects differ, subtly but consistently (Figs. 1e, f; 2e, f). The valvae of *C. nubila*, though very similar to those of *C. anegadensis* in general form, are slightly more robust, the ventral contour is less straight and the caudal extremity of each valva is relatively slightly broadened or clubbed. A further difference is apparent from the dorsal aspect: the pair of symmetrical plates of the tegumen at the base of the uncus are slightly shorter (and hence less acute at their apex) in *C. anegadensis* than *C. nubila* (Figs. 1f, 2f).

The female genitalia of *C. nubila* and *C. anegadensis* are likewise similar, though differing in detail. Using the terminology proposed for other members of the genus (Johnson, Quinter and Matusik, 1987), the principal difference noted lies in the shape and degree of sclerotization of genital plate encircling the ostium, a narrow and ovoid hoop in *C. anegadensis* (Fig. 1g), substantially wider and more elliptical along the lower (ventral) border (Fig. 2g) in *C. nubila*. In each, the corpus bursae and ductus bursae are unsclerotized other than the paired signa bearing transverse rows of minute plates on the former, and in each the ductus seminalis joins the ductus bursae near its origin (Figs. 1g, 2g, dorsal views).

**Relationships:** In its restriction to a harsh, xeric habitat, and notably in its association with the grass *Uniola virgata*, this insect strikingly matches several species of the 'lyceius complex' of Hispaniola (Schwartz, 1989), *C. crypta* Gali, 1985, *franciscoi* Gali, 1985, *hendersoni* Gali, 1985 and *raburni* Gali, 1985. Members of this group share bright, richly tinted undersurface fields but are quite variable in position of the hindwing ocellar pupil and all but the anomalous *raburni* possess a full complement of small light spots above the HW ocellus. None of these shows a close resemblance to the Anegadan insect. In disposition and contrast of the underside pattern, including the presence of well defined subparallel hindwing marginal lines and in general appearance of the hindwing ocellus and pupil, *C. anegadensis* bears more resemblance to the primarily Cuban *C. sibylla* than to any Hispaniolan species, though differing in several respects. Notably, it differs in reduction in the number of spots in the postdiscal line above the hindwing ocellus.

At first sight, *C. anegadensis* seems very different from the endemic Puerto Rican *C. nubila*, in which the underside ground coloration is rich dark chestnut brown, largely obscuring the submarginal and postdiscal lines, especially in fresh specimens. Closer examination, however, suggests an underlying similarity between the two, including the following details of structure and pattern:

(i) In both, the forewing male "androconial patch" is diffuse, contrasting little with the ground, and in each sex of the two insects the forewing marginal area is only slightly

paler than the basal field.

(ii) The tornal lobe is pronounced in both; moreover, the intensely black tornal spot on upper and under surfaces is similar in size and shape and the pale capping of the spot on the upper surface of *C. nubila* is matched and accentuated in *C. anegadensis*.

(iii) The configuration of the light scaling between the submarginal lines and flanking the postdiscal line, together with the convergence of these light zones towards and around the tornal spot is very similar in the two insects, despite differences in tint.

(iv) The ellipsoidal contour of the hindwing ocellus is similar in each, likewise the placing of the pupil within reddish scaling, immediately inside the yellowish ocellar ring.

(v) The arcuate course of the outer submarginal line is approximately matched in the two species, likewise the stepped arrangement of the subparallel inner line.

(vi) The two insects are similar in the close juxtaposition of the submarginal line and the distal margin of the hindwing ocellus.

(vii) The two are closely matched in reduction in number of the small pale spots above the hindwing ocellus beneath, which in some species, as mentioned above, form a more or less complete postdiscal line. In *C. nubila* these are rarely absent and generally one or two in number; in all specimens of *C. anegadensis* examined, of both sexes, two such spots are present.

*C. nubila* is a rather larger insect in comparison to *C. anegadensis*; in the series which we have examined, the male and female forewing length is generally 18-21 mm and 20-24 mm respectively.

#### *Copaeodes eoa*, new species

Figures 3a, 3b (♂), 3c, 3d (♀), 3e, 3f (♂ genitalia)

**Description:** FW length ♂: mean 11.9 mm (11.1-12.6 mm n=36 SD=0.48); ♀: mean 12.5 mm (11.6-13.4 mm n=22 SD=0.47).

**Male:** *Upper surface* FW dark brown from mid-costa to apex and broadly along lateral margin and below cell, extending into distal area of cell in triangle directed basad; rest of cell and adjacent area to costa bright fulvous; narrow blackened stigma and area below more or less tinged with fulvous; veins obscured basad but blackened towards margin. HW fulvous, costa dark brown/black and straight black line from wing base to margin below costa; veins narrowly blackened distad with dark brown shading between vein ends. *Under surface* FW dull fulvous in cell and to costal margin; spaces dull fulvous but posterior margin of cell to anal margin black; veins Sc<sub>1</sub>, R<sub>1</sub>, R<sub>2</sub>, and R<sub>3</sub>, the same dull fulvous, the rest blackened. HW dull fulvous with diffuse dark shading towards costal margin; veins through Cu<sub>2</sub> narrowly blackened; anal vein only slightly darkened and rest of tornal area bright fulvous.

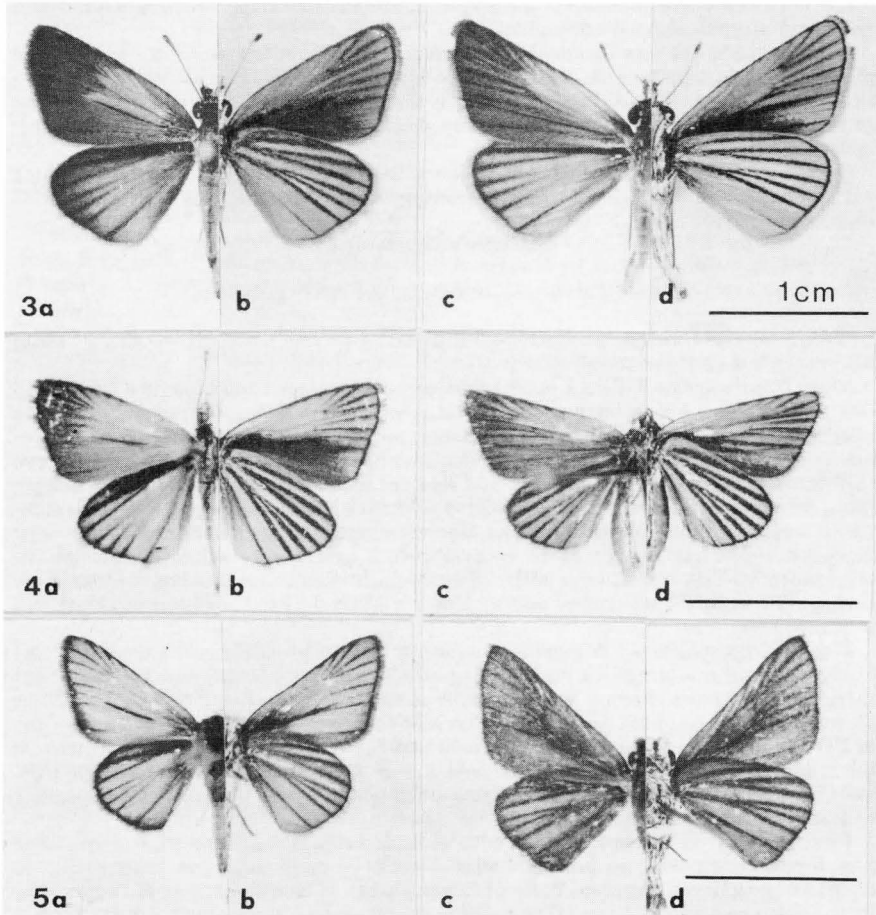
**Female:** *Upper surface* FW similar to male but fulvous precisely restricted to cell and above to costal margin; black scaling of veins slightly more prominent. HW as ♂ but marginal dark brown shading less obvious or absent. *Under surface* FW/HW as in ♂ but all fulvous areas brighter, black scaling on all veins narrower and black posterior area of FW reduced basad and not reaching anal angle. FW/HW margins with very narrow black line confluent with, but not broadened at vein ends. Black line delineating FW/HW margins slightly narrower than in ♂. Fringes fulvous in ♂ and ♀, duller in ♂ especially beneath; blackish distally in ♂, ♀ at FW apex.

**Both sexes:** Head dull brown/black with whitish scales along dorsal edge of eye, tufts of dull pale brown setae on frons and whitish setae on palpi and below head; each palp ends in non-recurved apiculus. Tufts of fulvous setae at lateral margins of thorax near wing bases and bright fulvous setae clothing dorsal surface of abdomen. Antenna short, without apiculus; dark brown above, slightly paler beneath especially on club. Nudum, seven segments. Legs brownish, pale setae along inner edges: foreleg epiphysis very reduced, fore- and mid-tibia spined; hind tibia with two pairs of long spines.

The specific name was suggested to us by our friend and colleague, the late Mr. John Griffith, of Jesus College, Oxford. It is a Latin form, derived from a Greek adjective, which was sometimes used poetically as a noun, particularly in a geographical context,

in the sense of 'the dawn' or of 'a dweller in the East', and as such appropriate to this outlying *Copaeodes*.

*Types*: Holotype ♂, N side of track through Bone's Bight isthmus, NW Anegada Island, British Virgin Islands, in flight around *Uniola virgata* grass, 1100 hrs. July 5 1990; allotype ♀, same data (D. S. Smith & F. McKenzie), both deposited Hope Entomological Collections, Oxford, England. Paratypes, similar data, July 5-9 and September 3-10 1990, N and S sides of track: 3 ♂, 3 ♀, Allyn Museum of Entomology, Sarasota; 2 ♂, 2 ♀, American Museum of Natural History, New York; 1 ♂, 1 ♀, Carnegie Museum of Natural History, Pittsburgh; 2 ♂, 2 ♀, British Museum (Natural History), London; 1 ♂, 1 ♀, National Museum of Natural History, Washington; 1 ♂, 1 ♀, collection Albert Schwartz, Miami;



Figures 3-5. *Copaeodes eoa*: 3a male (Holotype) upper surface, 3b under surface; 3c female upper surface, 3d under surface. *Copaeodes stillmani*: 4a male upper surface, 4b under surface; 4c female upper surface, 4d under surface. (Monte Cristi, Dominican Republic. coll. A. Schwartz). *Copaeodes j. jean*: 5a male upper surface, 5b under surface; 5c female upper surface, 5d under surface. (Imperatriz [Amazonas Province, Brazil] Coll. British Museum (Natural History)).

1 ♂, 1 ♀, collection Stuart Ramos, University of Puerto Rico, Mayaguez; 24 ♂, 10 ♀, Hope Entomological Collections.

**Relationships:** This insect closely resembles the Hispaniolan endemic skipper cited by Evans (1955), Riley (1975) and Schwartz (1989) as *Oarisma stillmani*, though described by Bell and Comstock (1948) as a member of *Copaeodes*. The two insects, however, differ in several respects (Figs. 3 a-d, 4 a-d):

(i) *C. eoa* is consistently larger than *C. stillmani*. The forewing length of the holotype (♂) of the latter is 10 mm and of the allotype 11 mm and from long series Schwartz (1989) cites a length of 10-11 mm for both sexes. In *C. eoa*, the *minimum* forewing length of the ♂ and ♀ is 11 and 11.6 mm respectively and the virtual absence of size overlap is striking in series of two rather small butterflies.

(ii) **Upper surface:** On the ♂ forewing above the fulvous scaling is less extensive in *C. stillmani*, the dark border meeting the costa one-quarter to one-third basad of the apex; in the Anegadan insect the basal half of the costa is dark. The dark scaling at the forewing base of *C. eoa* is reduced or absent in *C. stillmani*.

(iii) In *C. stillmani* the area posteriad of the stigma is only slightly darker than anterior of it, leaving the stigma more clearly defined in the fulvous field.

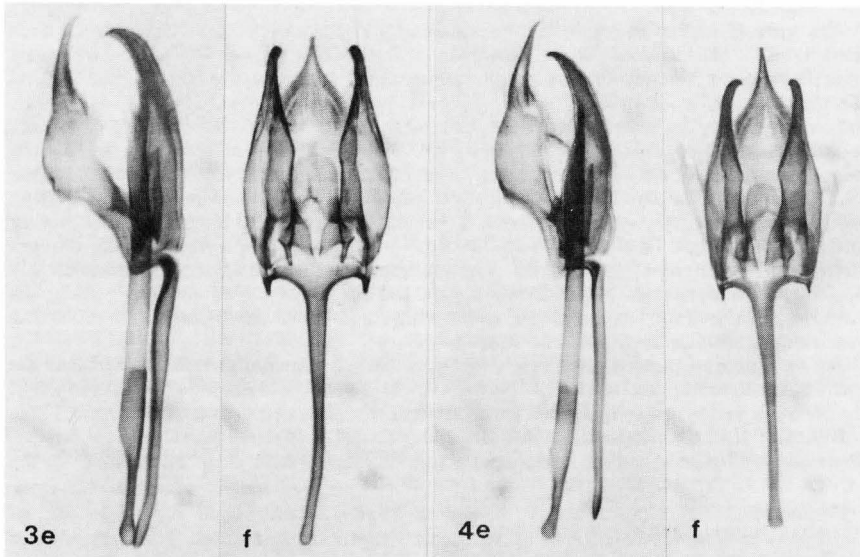
(iv) On the ♂ hindwing dark marginal shading is reduced or absent in *C. stillmani*, leaving the vein ends more crisply defined.

(v) In *C. stillmani* all veins are blackened from origin to margin. In the ♀ the forewing is similar in the two insects but dark shading in  $R_1-R_2$ ,  $R_2-R_3$  near the costa is absent in *C. stillmani*, extending the distal edge of the fulvous patch.

(vi) **Under surface:** In the ♂ the fulvous ground color is brighter in *C. stillmani*, particularly through absence of dark scaling anterior of  $Cu_2$  and distal to cell end.

(vii) Black scaling on hindwing veins is broader and less sharply traced in *C. stillmani*.

Furthermore, the stigma of the ♂ forewing is consistently shorter in *C. stillmani* than in *C. eoa*: mean length 3.06 mm ( $n=5$  S.D.=0.21) and 3.84 mm ( $n=36$  S.D.=0.21), respectively. The morphology of the stigma is considered further, below.



Figures 3-4 (cont.) *Copaeodes eoa* male genital capsule; 3e lateral aspect, 3f, ventral aspect with aedeagus removed. *Copaeodes stillmani* male genital capsule; 4e, lateral aspect, 4f, ventral aspect with aedeagus removed.

*Genitalia:* Our assessment of the male genitalic structures is based on dissection of 13 specimens of *C. eoa* and two of *C. stillmani*. The two are not identical, although differences noted are not dramatic:

1. In all specimens of *C. eoa* examined, the tip of the uncus extends only slightly, if at all, beyond the ends of the underlying valvae, while in *C. stillmani* it is somewhat more slender and the tip extends a little further beyond the valvae. (This feature is not apparent in Bell and Comstock's line drawing (1948: Fig. 15). The entire genital capsule is broader in *C. eoa* than in *C. stillmani* (Figs. 3e, 4e).

2. The juxta is similar in length in the two insects but is rather broader in *C. eoa* than in *C. stillmani* (Figs. 3f, 4f).

3. The shaft of the aedeagus is slightly more robust in *C. eoa* than in *C. stillmani*. Moreover, the cephalad extremity of the aedeagus of the two differs in contour: in *C. eoa*, the coecum is followed by a short, very slender section of uniform diameter before the shaft widens at the entry of the ductus ejaculatorius, a section that tapers from the coecum in *C. stillmani* (Figs. 3e, 4e).

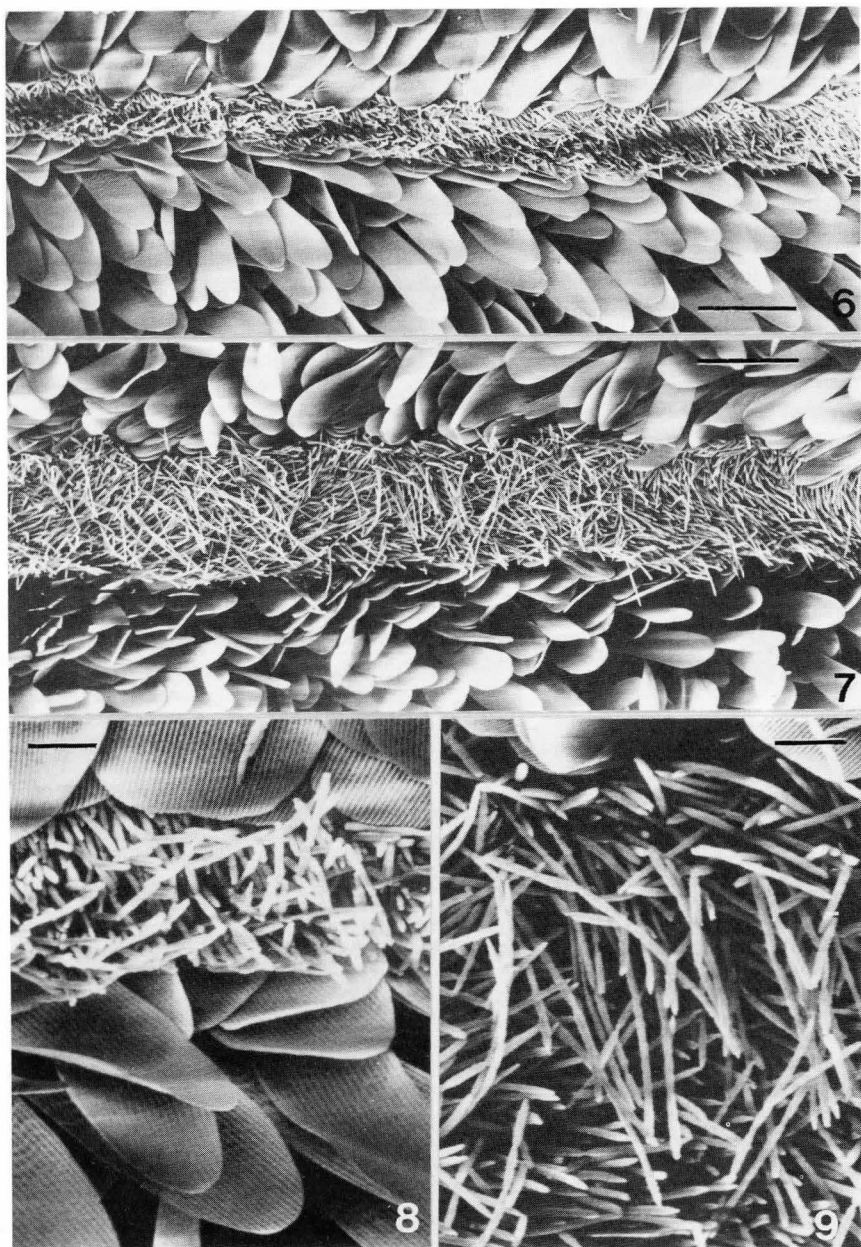
*Stigma:* In their generic assignment of *stillmani*, Bell and Comstock (1948) noted that "the short antennae and the antennal clubs, the palpi and the stigmata of the male primaries appear to be quite the same as those of other species placed in the genus *Copaeodes*". However, Evans (1955) removed the species to *Oarisma* primarily on grounds of wing shape, noting that two (of six) species of his *Oarisma*, *boeta* (Hewitson, 1870) and *stillmani* have a ♂ forewing stigma, while *O. powesheik* (Parker, 1870), *garita* (Reakirt, 1866), *edwardsii* (Barnes, 1897) and *nanus* (Herrich-Schaffer, 1865) lack this androconial brand. However, for all *Copaeodes* (*sensu* Evans) he stressed the presence of "... a peculiar stigma, consisting of a long narrow slit, surrounded by modified scales, running nearly parallel to the dorsum under the cubitus between the origins of veins 2 and 3" [i.e. Cu<sub>2</sub> and Cu<sub>1</sub>]. Moreover he included as a key feature of *stillmani* "upf with a linear stigma as in *Copaeodes*, while that of *boeta* differs in position and structure, consisting of a bar of black scales arising beneath the origin of vein 3 [Cu<sub>1</sub>] angled downwards to end in space 1b" [Cu<sub>2</sub>-2A].

The unusual stigma shown by all species assigned by Evans to *Copaeodes*: *auriantiacae* (Hewitson, 1868), *minima* (W. H. Edwards, 1870) and *jean* Evans, 1955, is shared by *stillmani* and *eoae*. We have examined the fine structure of the stigma by scanning electron microscopy in *C. minima* and *C. eoa* and the comparison is illustrated in Figs. 6-11. While the stigmata vary considerably in width, that of *eoae* being the broader, they are identically constructed with respect to the morphology of the androconial scales which provide the 'black' reflectance of the stigma, viewed by eye. In each, the cylindrical scales of the stigma are slender (ca. 2-3 μm in diameter) and show helically arranged and cross-ribbed fluting, each scale apparently equipped with a terminal aperture. Micrographs at higher magnification (Figs. 10-11) are shown for *C. eoa* but comparable scales of *C. minima* are structurally identical. Moreover, the irregular disposition of the wing scales immediately flanking the androconial bar and, notably, in the orientation of many scales along the posterior margin of the stigma normal to the wing surface, features resolved in a dissecting microscope, are similar in the two insects.

Following reassignment of *stillmani* to *Copaeodes*, its Anegadan relative becomes the second Antillean representative of the genus, which elsewhere extends through much of the Nearctic and south to Brazil. Of the Neotropical representatives, *C. jean* Evans, 1955, and notably the nominate subspecies *jean*, is most similar, in wing facies, to these insects. The male of *C. j. jean* is even more lightly marked above than *C. stillmani* while in the

Figures 6-11 SEM preparations. 6, central region of stigma of right forewing of *Copaeodes minima* (apex towards upper right). Stigma is represented by a narrow band of slender cylindrical scales. (Scale bar: 0.1 mm). 7, similarly oriented area including stigma in *Copaeodes eoa*: the band of cylindrical scales is wider than in *C. minima* but of similar construction. (Scale bar: 0.1 mm). 8, 9, illustrating the similarity in organization of the stigma of *C. minima* (8) and *C. eoa* (9). (Scale bars: 20 μm).





♀ forewing/hindwing spaces are heavily suffused with dark scales and in both sexes the black scaling along the veins resembles that of the Antillean species (Figs. 5a-5d).

The similarity in wing facies, and notably in the black tracing of the hindwing veins beneath, between *C. eoa* and *C. stillmani* and the Cuban endemic species *Oarisma nanus* deserves comment. This last species lacks a forewing stigma and, as Bates (1935) noted, cannot be included in *Copaeodes* as outlined above. In this context it may be noted that several members of the *Thymelicus* sub-group show more or less prominent light or dark scaling on or between the veins; *Ancyloxypha melanoneura* (C. & R. Felder, 1867), for example, possesses heavily blackened veins on both surfaces. We have not examined specimens of the rare Cuban endemic *Oarisma bruneri* Bell, 1959, an insect that lacks a *Copaeodes*-like stigma and has the hindwing veins beneath obscured by dark brown scaling (Alayo & Hernández, 1989; Pl. 46, figs. H-I) and, again, we have no reason to suppose that its generic placement is inappropriate.

*List of butterflies recorded from Anegada*

DANAIDAE

[*Danaus plexippus* (Linnaeus, 1758)]

We have not encountered this insect on Anegada, but a single specimen was seen by a visitor in a garden on the south coast in April 1990 and is reported from the Settlement by Mr. Aaron Soares, a resident of the island. It is present on Culebra and occurs elsewhere in the Virgin Islands but is not known to have established a breeding population on Anegada at the present time: no sign of immature stages were seen on *Asclepias curassavica* at The Slob (Locality 9; fig. 18). D'Arcy (1975) mentions two other asclepiads on the island, *Cryptostegia grandiflora* cultivated in the Settlement and *Cynanchum anegadensis*, available as potential larval foodplants.

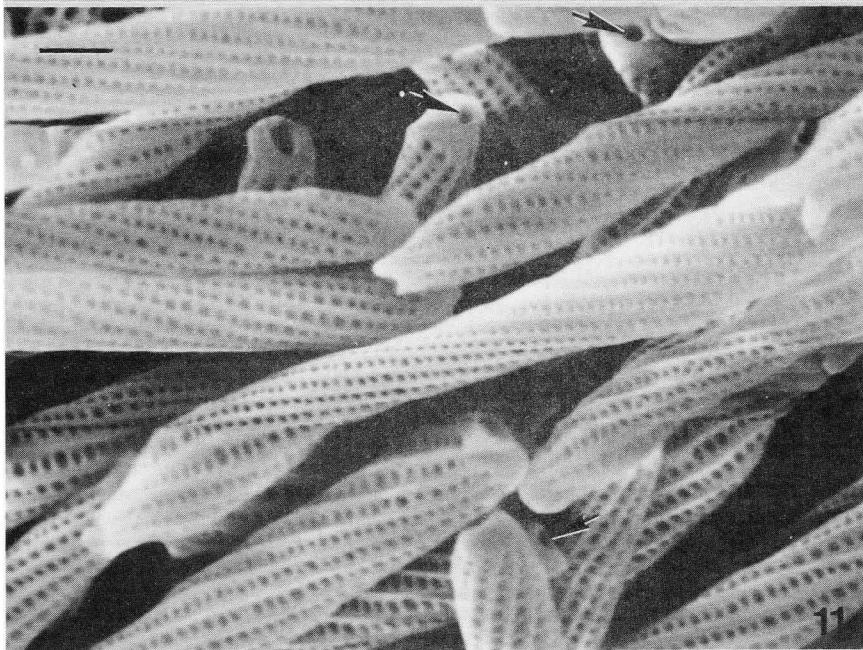
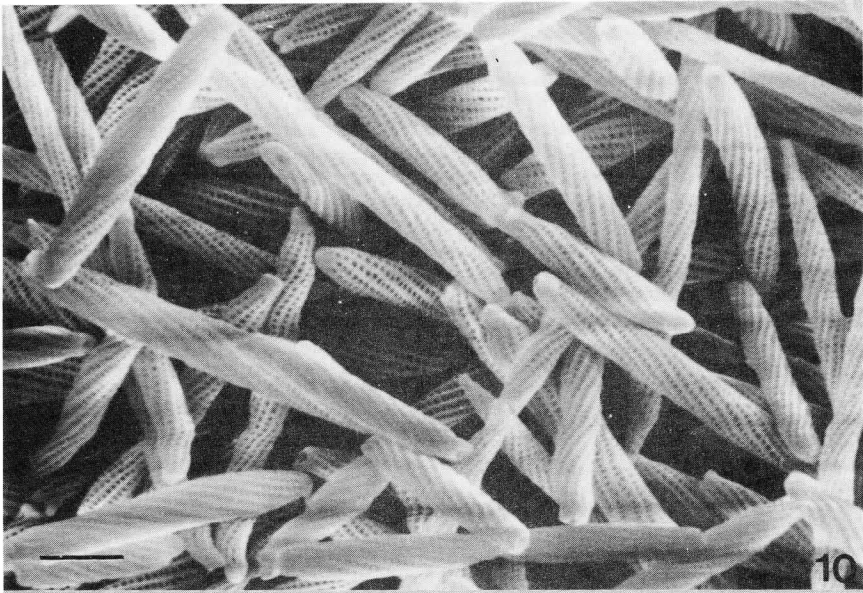
SATYRIDAE

*Calisto anegadensis* (see above)

This is a remarkably inconspicuous butterfly within its very restricted habitat, since much of its flight activity takes place within the tortuous avenues of partial shade afforded by the ground cover, just above the sand or limestone surface. Where stands of *Uniola virgata* are more dense (Fig. 19), it generally flies at the level of the contorted mass of dead blades at the base of each tussock. Its flight is generally quite swift, seen briefly in full sun as it leaves a patch of cover before it reenters the vegetation to pursue its irregular, concealed and always unpredictable course.

In July, an abrupt change in flight behavior was seen within the thickets developed around the larger *Pisonia* trees; the butterflies often darted upwards from the low understory and flew swiftly and directly to the small rhamnaceous tree *Zizyphus rignonii*, here reaching a height of about 4 m. The butterflies, of both sexes, alighted on the inconspicuous greenish white inflorescences, generally between 2 m above the ground and the tree crown, pausing to take nectar, for a few seconds, with closed wings before flying to another cluster of flowers. Care was taken not to disturb the nectaring insects, but individuals stayed at a tree for no more than a minute; on leaving the blossoms the butterflies swooped down to the tree base and resumed their low flight, sometimes flying across the open shaded area beneath the *Pisonia* canopy and settling for an instant on

Figures 10-11. Androconial scales of stigma of *C. eoa*; these are inserted on the wing surface but are readily detached. Each scale is cylindrical (10), the wall is regularly fluted and each bears a terminal aperture (Scale bar: 5µm). 11, illustrates the terminal apertures (arrows) of scales of the stigma of *C. eoa* and further details of the cross-ribbed fluting of the scale wall. (Scale bar: 2µm).



the leaf litter (Fig. 20). Up to eight *Calisto* were seen at one time at a *Zizyphus* tree; elsewhere, other than occasional pairs (of undetermined sex) engaged in brief whirling flight above the ground cover, the butterflies were always seen singly. The butterflies were very occasionally seen at flowers of *Lantana involucrata*, but only a single *Strymon acis* (Drury, [1773]) was noted with *Calisto* at *Zizyphus*.

At the time of the above observations, the *Pisonia* trees on the Bone's Bight isthmus were not in flower. To the west, and outside the area occupied by *C. anegadensis*, a flowering specimen was very attractive to *Hemiargus thomasi* Clench, 1941 and in April, on the central plain, *Pisonia* blossoms were much visited by this lycaenid, by *Wallengrenia drury* (Latreille, [1824]), *Ephyriades arcas* (Drury, [1773]) and by a range of Diptera and Hymenoptera and may, at times, provide *Calisto* with an abundant nectar source. Similarly, the yellow-flowered endemic *Acacia*, attractive to lycaenids in April, was not in flower in July while flowering of *Croton discolor* and *Lantana involucrata* was just starting. Further field work will establish the selective or opportunistic nectaring of *Calisto* on Anegada; flower visiting was not observed in September or December.

Flight activity of *C. anegadensis* starts soon after 0800 hr., reaches a peak between 1100 hr. and 1300 hr. and continues until after 1700 hr. In July, during the hottest time of day, 20-30 individuals were seen per hour, in undisturbed flight and excluding the nectaring assemblies, and the butterflies were at least as common in the previous month (FM). Adult numbers were decreased in September but in December had regained the mid-summer levels. In July, most specimens were fresh, displaying the full range and intensity of coloration (see above); while most were worn in September and December, some were recently emerged in each of these months, suggesting that the insect is at least trivoltine through the second half of the year and it may well prove to be continuously brooded. Particularly noteworthy was the virtual absence of symmetrical wing damage through unsuccessful bird or lizard attack; a single male showed such damage near the forewing ocellus. Anole lizards were infrequent in a habitat where they might be expected in abundance and small birds that might include butterflies in their diet were rarely seen. In this respect, the adult Anegadan *Calisto* seems to enjoy a less threatened life than *C. nubila* in the rain forest and woodlands of Puerto Rico, in which such damage is commonplace.

## NYMPHALIDAE

### *Junonia genoveva* (Cramer, 1780)

West of the Settlement, this species has been recorded very occasionally on each visit, along roads and tracks through the scrub. In June and July it was more frequent on the thinly vegetated limestone pavement and along the mud flats bordering the saline ponds between the Settlement and East End near the south coast (Localities 7 to 8), nectaring at flowers of buttonwood (*Conocarpus erectus*) with *Strymon acis*, virtually the only other butterfly flying in the area.

### [*Junonia evarete*] (Cramer, 1779)

In December, a few specimens of a *Junonia* were seen on the northeastern coast between Crazy Pond and East End (Locality 5) which, from their sustained flight and dark, featureless underside hindwing seen when at rest on bare ground were tentatively identified as this species, rather than *J. genoveva* (see Turner & Parnell, 1985). No specimens were collected.

### *Hypolimnias misippus* (Linnaeus, 1764)

A male was collected on 10 November 1990 by Mr Aaron Soares and two others seen in a grassy field at the Neptune's Treasure property (Locality 1), on the southwest coast. This may represent a new record for the Virgin Islands and is certainly the first record

from Anegada. In December, two more males were seen in the same area but whether this species is present as a vagrant or as a breeding resident remains unknown; we know of no likely breeding colony nearer than Puerto Rico or Antigua.

### HELICONIIDAE

*Agraulis vanillae insularis* (Maynard, 1891)

Sparsely distributed in all regions of the island except for the southeastern flats, where it was not recorded, this butterfly is perhaps more frequent along the coasts than in the interior. Nectaring has not been noted and *A. vanillae* is no more common in gardens than elsewhere.

### LYCAENIDAE

*Strymon acis mars* (Fabricius, 1777)

The distribution of this species matches that of its presumed larval foodplant, *Croton discolor*, rare or uncommon on the sandy ground of the West End (Locality 2) and on the bare sparsely vegetated limestone near the south coast east of the Settlement (Localities 7 to 8). Over much of the island it is second only to *Hemiargus thomasi woodruffi* Comstock and Huntington, 1943 in abundance and its catholic use of available nectar sources is noteworthy. In September 1989 it was very common on newly opened *Croton* flowers; a year later few of these plants were in flower and *S. acis* (Drury, [1773]) congregated at *Lantana camara* and *L. involucrata* and, in large numbers around The Slob pond (Locality 9) on *Asclepias curassavica* (Fig. 14) and *Pluchea odorata*. In April, when *Croton* was again unavailable, this hairstreak nectared on *Pluchea* in preference to *Asclepias* and was most abundant at low trees of the endemic *Acacia anegadensis*, at the time in full bloom. In July *S. acis* was less common and visited loblolly trees (*Pisonia cordata*), *Lantana* and *Cordia ruplicola*. In December the insect was generally scarce; newly opened *Croton* flowers and occasionally *Amyris elemifera* were attractive while most other nectar sources were unavailable and it was common only along the northeast coast, on the low beachside crucifer *Cakile lanceolata* and particularly on *Suriana maritima*.

The island races of this species in the eastern Antilles are at present under study. Subspecies *mars* is generally regarded as representing the insect on Puerto Rico and the Virgin Islands (Riley, 1975), nominate *acis* occurring on several islands of the Lesser Antilles from Barbuda and Antigua (the designated type locality) south to Dominica. However, the long series obtained from Anegada differs consistently in underside hindwing pattern from specimens of *mars* from western Puerto Rico and Mona Island.

*Strymon bubastus ponce* (Comstock & Huntington, 1943)

A few worn specimens were seen in grass plots in gardens and on *Pluchea* flowers at The Slob (Locality 9, fig. 18) in April and September 1989 and a single worn example was collected in December.

*Strymon columella columella* (Fabricius, 1793)

This species was first recorded in September 1989 from a single specimen at The Slob, where it was moderately common a year later, emerging during the period of the visit and flying with the far more abundant *Strymon acis* and nectaring on *Pluchea odorata*. Absent from this locality in December, it was found only along the northeast coast (Localities 4 to 6) but was there very common, nectaring on *Suriana maritima* and occasionally on *Cakile lanceolata*.

*Leptotes cassius catilina* (Fabricius 1793)

A single female of this subspecies, occurring elsewhere in the Virgin Islands and west



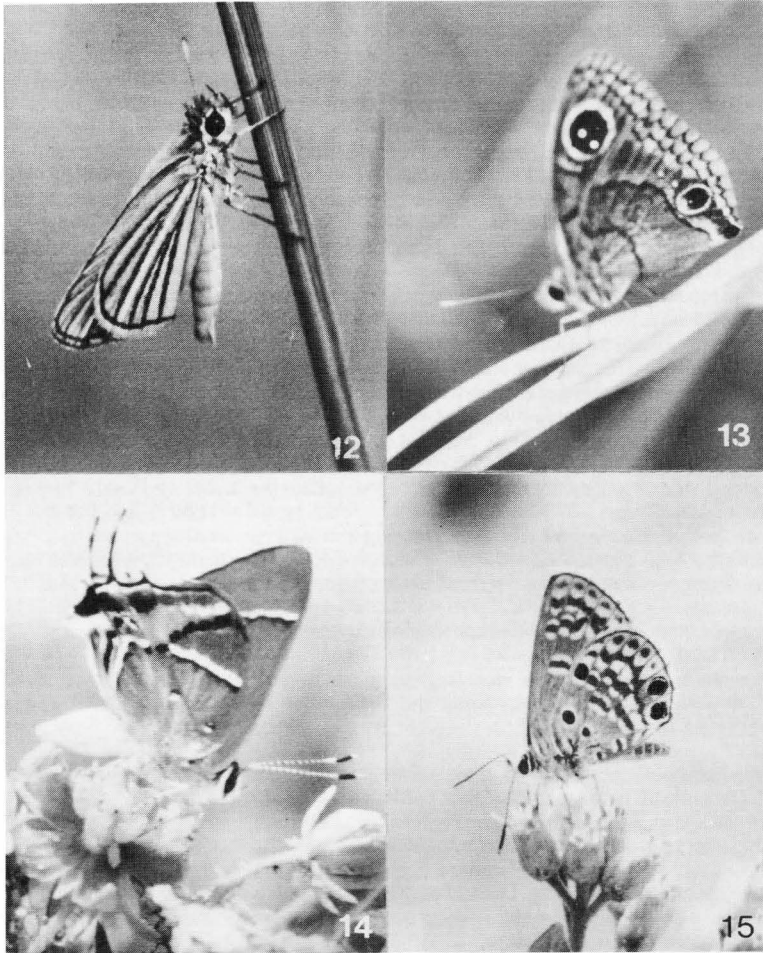
to Culebra, was collected in the garden of the hotel (Locality 10), on the southwest coast, in September 1989.

*Hemiargus hanno watsoni* Comstock & Huntington, 1943

Two males were collected in garden scrub (Locality 10) on the southwest coast in September 1989. While this and the last species might well be overlooked where *Hemiargus thomasi* Clench, 1941 is common, repeated sampling on each subsequent visit failed to reveal further specimens of either.

*Hemiargus thomasi woodruffi* Comstock & Huntington, 1943

The most widespread and in most localities the most common butterfly on Anegada,



Figures 12-15. 12, *Copaeodes eoa* male at rest on stem of *Uniola virgata*. 13, *Calisto anegadensis* female at rest in leaf litter. 14, *Strymon acis mars* nectaring on *Asclepias*. 15, *Hemiargus thomasi woodruffi* male nectaring on *Cordia*.



this species is nevertheless seldom seen far from nectar sources. It is the only species occurring regularly with *Calisto anegadensis* and *Copaodes eoa* on the Bone's Bight isthmus and one of the few seen in the West End scrub (Locality 2) and on the barren limestone flats bordering the southeastern coast (Localities 7 to 8). It is particularly common around *Acacia anegadensis* and other leguminous trees, when in flower, and has also been seen nectaring at loblolly trees (*Pisonia subcordata*), sea grape (*Coccoloba uvifera*) and West Indian almond (*Terminalia catappa*), at the exotic flowering tree *Moringa oleifera* and at *Cakile lanceolata*, *Amyris elemifera*, *Croton discolor*, *Suriana maritima*, *Serjania polyphylla*, *Asclepias curassavica*, *Cordia rupicola* (Fig. 15), *Lantana camara*, *L. involucrata*, *Erithalis fruticosa* and *Pluchea odorata*. This species is probably continuously brooded and worn and fresh adults have flown together on each visit.

#### PIERIDAE

*Ascia monuste* (Linnaeus, 1764)

Although seen in all parts of the island on each visit, this butterfly is very thinly distributed. In the Bone's Bight area, for example, fewer than 10 specimens were recorded during each day in the field. A small group of puddling males was seen at The Slob in April when very little water remained in the pool; otherwise it has been seen most frequently along the southwestern dunes (Localities 1, 10), occasionally visiting flowers of *Borrhchia arborescens* and in gardens, nectaring on *Gomphrena* and other ornamental flowers.

*Appias drusilla* (Cramer, 1777)

A single male was seen near The Slob in a shady thicket in September 1989 and two males were collected in December 1990, one in the same locality and one in the thick scrub bordering the southern edge of Flamingo Pond.

*Eurema elathea* (Cramer, 1775)

Locally frequent in disturbed land and especially in grassy gardens (Localities 1, 10 and elsewhere), this species has been recorded on each visit. Prior to December 1990, all specimens collected were of the dry season form 'elatides' but on that occasion about half represented the wet season morph 'elathea' in which the sandy hindwing ground scaling of the underside is replaced by glossy white.

*Eurema lisa euterpe* (Ménétriés, 1832)

This species sometimes flies with the last but is far less frequent; it is less restricted to inhabited areas, also occurring very sparsely in open patches within dry scrub along the southern coast.

*Phoebis sennae sennae* (Linnaeus, 1758)

As widely, though more sparsely distributed throughout the island than *Ascia monuste*, this insect has been seen infrequently and generally singly, though in September 1990 several were noted nectaring at *Coccoloba uvifera* at The Slob.

#### HESPERIIDAE

*Polygonus leo savigny* (Latreille, [1824])

With the exception of *Copaodes eoa* in its restricted habitat, we have found this species to be the commonest hesperiid on Anegada. It has been recorded on each visit, flying

within the woody thickets on the central plain, around the scattered *Pisonia* trees growing on land formerly divided into fields and cattle corrals. As elsewhere it flies rapidly, settling often beneath leaves of terminal twigs. In September 1990 it was seen nectaring on flowers of *Pluchea odorata* at The Slob and elsewhere on *Coccoloba uvifera* and *Terminalia catappa*. It has been noted most regularly at flowers of an exotic tree *Moringa oleifera* on the Neptune's Treasure property on the southwest coast (Locality 1) where 10-20 individuals have often been seen at one time, generally nectaring with closed wings but occasionally with wings held fully open. Nectaring at this tree started before 0800hr and continued until just after sunset; *P. leo* was joined occasionally by *Wallengrenia drury* and by *Hemiargus thomasi* and throughout the day by an abundance of the strikingly effective polistine wasp-mimicking ctenuchine moth *Horama grotei* Butler 1876, by day-flying sphingids (*Aellopos tantalus* (Linnaeus 1758)), by xylocopid and other bees and a range of Diptera; for this island a quite remarkable wealth of insects.

*Urbanus dorantes cramptoni* Comstock, 1944

In our experience a rare species on Anegada; a single specimen of a tailed skipper (either this insect or *U. proteus* (Linnaeus, 1758) was seen in scrub west of the Settlement in September 1989 and another single sighting was reliably made of *U. dorantes* (Stoll, [1790]) in December 1990, in the scrub near West End (Locality 2). Collected specimens will presumably prove to represent the subspecies *cramptoni*, widespread and generally common from Hispaniola and Puerto Rico to the Virgin Islands.

*Ephyriades arcas* (Drury, [1773])

This skipper has been found on each visit, widely if sparingly distributed on the central plain and along the southern and northeastern coast. It is most often seen within and around thickets, flying with, but less frequent than *Polygonus leo* (Gmelin, [1790]). Females have not been seen visiting flowers, while males have been noted taking nectar at *Croton discolor*, *Coccoloba uvifera*, *Terminalia catappa* and *Pisonia cordata* when their open winged posture renders them very conspicuous. In December this species was much attracted to the white-flowered vine *Serjania polyphylla* in inland scrub.

*Pyrgus oileus oileus* (Linnaeus, 1767)

An extremely local insect; very few specimens have been recorded, in September 1989 and 1990 and in December 1990, and found only in the grassy garden area of the hotel, on the southwest coast (Locality 10).

*Wallengrenia drury* (Latreille, [1824])

Although recorded on each visit, this is another sparsely distributed butterfly, occurring on the central plain and on the south coast, west of the Settlement. Isolated specimens have been seen at infrequent intervals on flowers of *Dodonea viscosa*, *Erithalis fruticosa* and beachside *Borrchiea arborescens* and *Suriana maritima* and somewhat more often at flowers of *Coccoloba uvifera*, *Terminalia catappa*, *Pisonia subcordata* and *Moringa oleifera* trees.

*Hylephila phyleus* (Drury, [1773])

In April 1990 this skipper was not uncommon around The Slob, visiting flowers of *Pluchea odorata*, but was seen neither there nor elsewhere on other occasions.

*Copaodes eoa* (see above)

While the distribution of this skipper precisely matches that of *Calisto anegadensis* on the Bone's Bight isthmus, its use of the habitat is quite different. It flies around and

within tussocks of *Uniola virgata*, occasionally settling on a stem or blade (Fig. 12); while at rest the forewings generally remain tightly apposed and the hindwings are flexed slightly apart, at intervals. While the association between the insect and the grass was obvious, its flight pattern takes it away from the tussocks as it moves, very slowly, over the ground cover and the exposed limestone surface, sometimes abruptly leaving this course and ascending quite rapidly to over 2 m to pass between or above clumps of *Dodonea* and *Erithalis*. Unlike the *Calisto*, it seldom enters the low vegetation and flies in full sun. While flying around tussocks near loblolly trees it avoids those within the shade.

Nectaring was observed only occasionally, butterflies pausing, at times for over a minute, at flowers of *Cordia rupicola*, *Croton discolor* and *Lantana involucrata*. In July, it was never seen to join *Calisto* at flowers of *Zizyphus*. The period of flight activity matched that of *C. anegadensis*; counts made between 1100 hr. and 1300 hr. suggested that the two insects were present in comparable numbers. The two were often included within a field of view, a circumstance accentuated by the virtual absence of other butterflies in this generally very inhospitable terrain. It appears to be multivoltine, at least during the second half of the year, fresh specimens being noted on each visit and pairs *in copula* were seen in July and December.

## DISCUSSION

The butterfly fauna of Anegada is unusual in composition and distribution. On each of six visits, we have found that on large tracts of the island butterflies are virtually absent, that species abundant on many Antillean islands have been recorded only rarely, yet that two of the commonest, albeit extremely local butterflies are previously undescribed. We have only on single occasions found *Leptotes cassius*, *Hemiargus hanno* and *Hylephila phyleus*, the female of *Appias drusilla* has never been seen and the presence of *Urbanus dorantes* was confirmed only on our sixth visit. The distribution of the common species, *Hemiargus thomasi*, *Strymon acis* and *Strymon columella* moves with the flowering of nectar sources. The roadsides and pathways of Anegada lack *Bidens*, *Stachytarpheta* and other low plants attractive to butterflies elsewhere; a single flowering bush of *Croton* or *Lantana*, or an isolated *Pisonia* tree often represents an oasis to the observer, as to the assembled insects, and we have seen more specimens of *Polygonus leo* at a *Moringa* tree or of *Wallengrenia drury* at a West Indian almond in one minute than encountered in a day on the central plain. Yet on each visit a few butterflies have been locally common; on an island for which seasonality is minimal, none of our visits has followed a period of prolonged or considerable rainfall, when the pattern of butterfly distribution and frequency may differ markedly from the picture we have drawn, which probably fairly represents the usual situation on this very dry island.

The presence of two endemic butterflies in a very small area of an ecologically rather monotonous island, an area inhospitable to other species and in numbers that have not fluctuated greatly during our periods of observation from June to December, is remarkable. The precise coincidence in distribution of *Uniola virgata* and of *Calisto anegadensis* and *Copaeodes eoa* suggests that this grass serves as larval foodplant for each and that neither butterfly strays appreciably from its breeding ground. The apparent restriction of *Uniola* and its attendant insects to the limestone tongue of the Bone's Bight isthmus is as striking as it is puzzling: the area is about 0.8-1.0 mile in length, and at its narrowest point the width of the isthmus between the dunes and the Bone's Bight pond is no more than 200 yards, somewhat wider at the western end. Thus the land area occupied by the butterflies, and by the grass, is no more than 100 acres (ca. 40 ha.), perhaps considerably less since the seaward limit of *Uniola* into the dunes was not systematically determined.

In a survey of the plants of Anegada, D'Arcy (1975) lists *Uniola* (as *Leptochloopsis virgata*) as present in "isolated clumps, mostly near the sea [along] various parts of the coastline" and as "wandering onto the plain from nearby shoreline habitats". Firstly, this does not accurately describe the distribution of the grass at the Bone's Bight site, where it is absent from the shoreline and most abundant on the adjacent strip of limestone pavement. Secondly, we have searched unsuccessfully for this conspicuous grass elsewhere around the island; of particular interest is a small zone of open wood of wind-shaped loblolly

trees and thickets on the limestone in the extreme northeast (near locality 5), visited in December, much resembling the Bone's Bight locality except for the absence of *Uniola* and of the two butterflies elsewhere associated with it. This grass has a wide if local distribution in the West Indies, occurring in the Bahamas, Jamaica and the Greater Antilles (Adams 1972) in arid, rocky lowlands, but Little, Woodbury & Wadsworth (1976) do not list it for Virgin Gorda, Anegada's nearest neighbor. Its apparently restricted presence on Anegada is paralleled by that of *C. anegadensis* and *C. eoa* but factors determining their restriction on the island remain obscure.

Much of Anegada has been farmed in the past, but the extent to which the Bone's Bight isthmus has been modified is undetermined; one homesite, the Faulkner property, lies at the eastern end of the locality and no trace of dry stone walling, very extensive on the central plain, has been found on the land where *Uniola* flourishes. It is possible that this area represents a tiny enclave, less modified over the period of human presence than much of the surface of the island. Further information on the field biology of the endemic butterflies is needed and, if our expectation that *Uniola virgata* serves as larval foodplant proves correct, then protection of the grass becomes a matter of importance. The biological interest of the region is already established since it encompasses, in part, the breeding ground of the endemic iguana, now considerably rarer than formerly.

The similarity between the Anegadan locality and xeric areas of Hispaniola harboring some members of the *Calisto lyceus* complex and *Copaodes stillmani*, as described by Schwartz (1989), faithful even to comparable exclusion of widely distributed and elsewhere common butterflies, is remarkable and provides an appropriate point for consideration of the biogeographical affinities and relationships of *Calisto anegadensis* and *Copaodes eoa*.

The distribution and diversity of members of the endemic West Indian genus *Calisto* has been considered in a vicariance model by Miller and Miller (1989) that traces their lineage from the separation of the proto-Greater Antillean block from Central America, its fragmentation and eventual accretion *inter alia* into the present islands of Cuba and Hispaniola, during the mid- to late Tertiary. This means of distribution of continental antecedents of *Calisto* satisfactorily accounts for the subsequently evolved range and variety of the genus on these islands, notably the presence of two evolutionary lines resulting in presumably plesiomorphous forms, with pronounced tornal lobes, principally in the lowlands, and smaller, more round-winged and more apomorphic forms arising primarily in the mountains.

The presence of one extant *Calisto* on Puerto Rico, structurally aligned with its plesiomorphous congeners elsewhere on the Antillean islands may be accounted for by envisaging the presence of an archetype on the southern part of the fragmenting block that became the easternmost of the Greater Antilles and also contributed to the formation of Hispaniola. If Puerto Rico received the two lines that diverged on Cuba and Hispaniola, the smaller, more apomorphic forms did not survive to the present day and the island is now graced, as is Jamaica, only by a single large and distinctive endemic species. It is the Puerto Rican *C. nubila* to which the Anegadan representative is clearly most closely related, and the similarity in habitat occupied by *C. anegadensis* and lowland xerophiles on Hispaniola, and notably their probable common use of *Uniola virgata*, reflects parallel ecological specialization rather than close phylogenetic relationship.

Miller and Miller (1989) suggest that "the Virgin Islands and northern Lesser Antilles are faunistically related to Puerto Rico . . . probably through dispersal" and we consider this to hold for *Calisto*, among the least effective dispersalists. The present island of Anegada is about 82 miles (131 km) east of Puerto Rico, divided into much smaller intervals by the intervening islands of Culebra and the Virgin Islands other than St. Croix, the widest gap now being the 18 miles (29 km) between eastern Puerto Rico and western Culebra. During the Pleistocene, between 3 million and 10,000 years B.P., numerous glaciation cycles are thought to have occurred, variably lowering the sea level and at times probably providing land links between Puerto Rico, Culebra and at least some of the present Virgin Islands north of St. Croix (Heatwole & McKenzie 1967; Little, Woodbury & Wadsworth 1976; Heatwole, Levins & Byer 1981), allowing the hypothetical progenitor

of *C. anegadensis* to disperse eastwards overland, either without interruption or at a time when the challenge of over water movement was greatly lessened. Two of the present authors (DSS, FM) have worked on Culebra and the nearby islets of Cayo Lobo, Cayo Norte, Cayo Luis Peña and Culebrita, where no habitat resembling the Bone's Bight isthmus has been encountered and where it seems unlikely that a relict *Calisto* population is present. Before it is concluded that the population on Anegada is the sole survivor of the far eastern range of the genus, the small, rocky and dry members of the British Virgins group must be surveyed.

No *Calisto* has been found on Anguilla, Anegada's nearest neighbor to the southeast (LDM), nor would it be expected there; the geological separation of the Virgin Islands and Lesser Antilles would have made entry of the genus into the latter very improbable.

We suggest that the presence of *Copaeodes eoa* on Anegada may be accounted for by much the same argument as followed above for the *Calisto* with which it flies; vicariant apportioning of an ancestral continental stock to Hispaniola and/or Puerto Rico and easterly movement from the latter across the transient Pleistocene overland route. This insect is clearly closely related to the Hispaniolan *C. stillmani*. Genitalic similarity alone might suggest that the two could be considered as island races of a single species, but we consider that structural features and differences in wing facies, mentioned above, between insects physically separated by about 400 miles (640 km), justifies our viewing them as specifically distinct. If *C. eoa* was derived directly from *C. stillmani* or from a common ancestor, divergence could be envisaged as having occurred *in situ* on Anegada, on Puerto Rico or on land in between; only discovery of this or a similar butterfly elsewhere along its putative dispersal route might serve to favor one possibility over another.

It may be noted that the proposed reassignment of *stillmani* and its Anegadan relative to *Copaeodes* rather than than to *Oarisma* neither materially assists nor hinders our view of their possible origin and biogeographical relationships. The present continental ranges of the two genera is quite similar; each is widely distributed in North America, through Central America and in South America respectively to Brazil and Peru. With respect to the Antillean representatives, were *nanus* and *stillmani* viewed as closely related, it might be supposed that they shared a common ancestor derived from Central America and distributed to Cuba and Hispaniola by tectonic land movements, as argued for other butterflies by Miller and Miller (1989). As members of *Oarisma* and *Copaeodes*, a similar derivation from the proto-Greater Antillean block may be envisaged, the resemblance between the *stillmani* and *nanus* lines reflecting merely convergence of wing pattern in allied but distinct genera, each prone to contrasting hindwing coloration and each with comparably distinct extant continental congeners.

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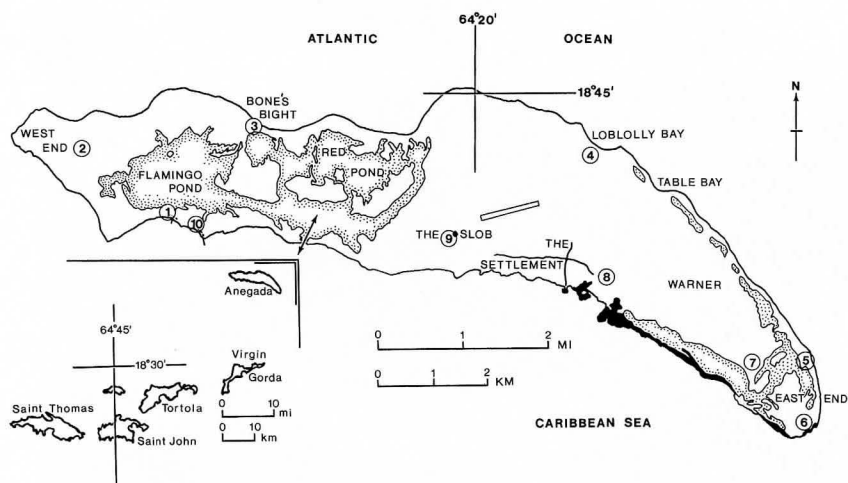


Figure 16. Map of Anegada and (inset) its relationship to other islands of the group. Collecting sites (1-10) are indicated and mentioned in the text. Note: solid black indicates fringing mangrove; double arrow indicates channel linking western saline ponds with the sea: the airport is shown by the rectangle in the center of the island.



Figures 17-18. 17, edge of quarry near airport; note the limestone substrate covered with dense low scrub and isolated *Pisonia subcordata* tree. 18, The Slob (Locality 9), a freshwater pond on the central plain including *Pluchea* and *Asclepias* at the edge and the sparsely vegetated limestone plate.



Figures 19-20. 19, limestone plate and associated vegetation at Bone's Bight (Locality 3), the habitat of *Calisto anegadensis* and *Copaeodes eoa*. Note tussocks of the grass *Uniola virgata* in foreground. 20, shaded understory within a *Pisonia* thicket at Bone's Bight. Tussocks of *Uniola virgata* extend to the shady perimeter.

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