

LEFT PAGE.— Fig. 1 (top left) *Catasticta* sp. (Pieridae), Boyacá, Colombia, A. R. Amarillo and C. E. Sarmiento (Bogotá, Colombia). 2. (top right) *Eligma narcissus* (Noctuidae), Vietnam, K. Spitzer (České Budějovice, Czechoslovakia). 3. (center left) *Thyridia* sp. (Nymphalidae: Ithomiinae), Rondonia, Brazil, D. Petr (Keene, Texas). 4. (center right) *Eumaeus atala florida* (Lycaenidae), Florida, USA, M. C. Minno (Gainesville, Florida). 5. (lower left) *Graphium agamemnon* (Papilionidae), Malaysia, H. H. Chuah (Houston, Texas). 6. (lower right) sp? (Dalceridae), Rondonia, Brazil, D. Petr (Keene, Texas).

RIGHT PAGE.— Fig. 7. (upper left) *Chrysocale* sp. (Arctiidae: Ctenuchinae), Boyacá, Colombia, A. R. Amarillo and C. E. Sarmiento (Bogotá, Colombia). 8. (upper right) *Dirphiopsis?* sp. (Saturniidae), Rondonia, Brazil, D. Petr (Keene, Texas). 9. (center left) *Cupha erymanthis* (Nymphalidae), Hong Kong, J. J. Young (Hong Kong). 10. (center right) *Lonomia cynira* (Saturniidae), San Luis Potosí, Mexico, J. K. Adams (Dalton, Georgia). 11. (lower left) *Crypsiphora ocellaris* (Geometridae), South Australia, N. McFarland (Hereford, Arizona). 12. (lower right) *Urania* sp. (Uraniidae), Rondonia, Brazil, L. Groce (Gainesville, Florida).

COVER PHOTOS: cover photographs (except front cover) are also honorable mentions from the Photo Contest.





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# LIFE HISTORY OF *ANETIA BRIAREA* AND ITS BEARING ON THE EVOLUTIONARY RELATIONSHIPS OF THE DANAINAE (LEPIDOPTERA: NYMPHALIDAE)

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**ABSTRACT.**— Wild captured *Anetia briarea* females oviposited on, and their larvae ate, *Cynanchum angustifolium*, a milkweed vine (Asclepiadaceae). Contrary to the early literature, 2nd through 5th instar larvae bear a pair of well developed dorsal tubercles on their mesothorax. This and several other larval and chrysalid characters question Ackery and Vane-Wright's (1984) placement of the genus *Anetia* in the largely Old World tribe Euploeini, as well as its relationship to the genus *Lycorea*. Several larval and chrysalid characters seem closer to those of the tribe Danaini. Forbes (1939) may well have been correct in placing *Anetia* at the base of the subfamily Danainae. The new findings have major evolutionary and taxonomic implications for the milkweed butterflies.

**KEY WORDS:** *Amauris*, Apocynaceae, Asclepiadaceae, behavior, biogeography, Central America, chemical defense, Danaina, Danaini, *Danaus*, Dominican Republic, *Euploea*, Euploeina, Euploeini, evolution, Greater Antilles, Hispaniola, hostplants, *Idea*, *Ideopsis*, immature stages, Ithomiinae, Itunina, larval morphology, *Lycorea*, Lycoreini, Mexico, milkweed butterflies, Neotropical, *Parantica*, parasites, Pinaceae, *Protoploea*, pupa, Taiwan, taxonomic characters, Theophrastaceae, *Tirumala*, West Indies.

A central unresolved question in Ackery and Vane-Wright's (1984, hereafter referred to as A&VW) comprehensive review of the Danainae is the systematic position of the genus *Anetia*. In addition, *Anetia* dominates New World Danaines in terms of the number of species in its genus: only 14 of the 157 known species of the Danainae occur in the New World, and five of these are within the genus *Anetia*. Despite this New World diversity and the systematic importance of the genus, practically nothing is known of the life histories of any of its members. A&VW and Kitching (1985) underscore the acute need for such information.

We show here that the historical description of the larva of *A. briarea* (purported lack of tubercles, a black head, etc; see Poey, 1846-47; Gundlach, 1881; Brown and Heineman, 1972; Riley, 1975; A&VW, p. 244) is erroneous and that several new larval characters, together with the very *Danaus*-like morphology of the chrysalid, challenge A&VW's tentative systematic placement of the genus.

## REARING STOCK AND BIOLOGY

*Anetia briarea* Godart (Nymphalidae, Danainae) (Fig. 1) butterflies were collected in July 1992 from high altitude (3000m)

aggregations on *Pinus occidentalis* Swartz (Pinaceae) located on Pico Duarte in the Dominican Republic, Hispaniola. This area is described in detail by Ivie *et al.* (1990). Specimens were netted from a single aggregation, placed individually in glassine envelopes, and transported by mule back to base camp on 3 July, and then flown to Bozeman, arriving on 10 July. Ten females and 8 males were packed on artificial ice in an insulated box, and shipped overnight to Gainesville. Upon receipt at 3 PM (1500 hr) on 16 July, the butterflies were released into an outdoor 11m long x 5m wide x 4.5m high screened flight cage on a hot sunny day. The ambient shade temperature was 35°C. Unexpectedly, the butterflies entered heat shock and so were immediately transferred to an air-conditioned room with fluorescent lighting where they were held at approximately 25°C.

## INITIAL ATTEMPTS TO OBTAIN EGGS ON VARIOUS ASCLEPIADACEAE: *Asclepias*, *Cynanchum* and *Matelea*

We first tried to obtain eggs by enclosing one-three females in 3 x 5cm black silk organza bags over apical blooming stems of potted *Asclepias curassavica* L. plants in the air conditioned room. These plants were derived from the Miami, Florida area described in Malcolm and Brower (1986). Each day the butter-





Fig. 1. *Anetia briarea* from Pico Duarte, Dominican Republic (top = dorsal; bottom = ventral). Specimens collected by M.A. Ivie, 1988. © L.P. Brower 1992.

flies were removed and individually fed sucrose solution. Notwithstanding frequent agitation, the females exhibited no oviposition behavior from 16-19 July. On 19 July, we collected a flowering *Matelea sp.* vine from Gainesville (Alachua County, Florida), sealed its cut end in a vial of water and added it to one of the organza bags containing three females and *A. curassavica*. The females still laid no eggs.

On 20 July, we collected flowering *Asclepias lanceolata* Walt. plants growing in the freshwater marshy areas east of Cedar Key, Levy County, Florida. We also collected *Cynanchum angustifolium* Pers. at Cedar Key. The identification of *C. angustifolium* (Rosatti, 1989, p. 484) was verified by Kent Perkins of the University of Florida Herbarium, to which we donated three voucher specimens (Accession No. FLAS 175989); one of these will be sent to the British Museum (Natural History), London. According to Correll and Johnston (1970), *C. angustifolium* is synonymous with *C. palustre* (Pursh) Heller. At Cedar Key this small-leaved milkweed vine twines about the salt marsh grasses and grows in a narrow zone (about 10m in width) immediately above the high tide line. Burns (1988) reported this plant as a host of both *Danaus gilippus* (Cramer) and *D. plexippus* L. in North Carolina, and we saw several *D. g. berenice* ovipositing on it at Cedar Key. Several vines were collected that were flowering

and in bud. To avoid wilting, the bases of the cut stems of *Matelea*, *A. lanceolata* and *C. angustifolium* were wrapped in wet paper. These three asclepiads were then put inside a one gallon clear plastic bag that enclosed the apical flowering portions of the potted *A. curassavica* plant. Thus the three females had access to four diverse milkweed species. On 22 July, one female laid approximately five eggs on the *Cynanchum* leaves and stems.

#### SUCCESSFUL OVIPOSITION METHOD

On 23 July, we put three, two, and one female in separate plastic bags, each containing at least one stem with leaves, buds and flowers of each of the above four milkweed species. One bag at a time, with an inserted thermometer, was then taken into full sunlight and allowed to heat to  $<35^{\circ}\text{C}$ . As the females warmed, they were gently shaken and prodded so that their tarsi would contact the leaves and stems. When  $35^{\circ}\text{C}$  was reached, the plastic bag was moved to the shade to allow the butterflies to cool, and the operation was then repeated several times. On July 23-24th, we obtained approximately 24 eggs, all laid on the *Cynanchum* flowers, buds, leaves, or stems, from at least two of the females. On July 25th, using the same methodology but not including other milkweeds in the bag, a third female laid five eggs on *Cynanchum*. The eggs, still on the vegetation, were





Fig. 2. Early fifth instar larva (#7) feeding on a leaf of *Cynanchum angustifolium*. Total length = 3.1cm. © L.S. Fink 1992.

transferred to half pint clear plastic containers to which wet paper wads were added to prevent desiccation.

#### LARVAL REARING AND SURVIVAL

The first egg hatched on 24 July and was given a fresh *Cynanchum* stem and a fresh apical cutting of *A. curassavica*. Both plants had leaves, buds and flowers. This larva became cataleptic (*cf.* Zalucki and Brower, 1992) after nibbling one or the other of the foodplants and thereafter refused to eat. On 25 July, five eggs hatched and were given one fresh leaf each of *A. curassavica*, *A. incarnata* L., *A. tuberosa* L., and *Cynanchum*, as before. The *A. incarnata* plants were from Miami stock (Malcolm and Brower, 1986) and the *A. tuberosa* were commercially obtained nursery stock. One larva which nibbled *A. curassavica*, and another which sampled *A. incarnata*, went cataleptic, but a third began eating the *Cynanchum* stem and produced normal looking frass. By 26 July, three larvae were successfully eating *Cynanchum* leaves, buds, and/or stems. We then removed all the *Asclepias* leaves because the larvae did not eat them and we expected them to die if they attempted to do so. On 28 July we had five first instars. By 29 July, two of these apparently had

been cannibalized. All remaining larvae were therefore isolated. Several eggs failed to hatch and probably were infertile.

On 29 July we had six first through fourth instar larvae feeding on *Cynanchum*, maintained at approximately 24°C under a 16hr light/ 8hr dark regimen. Plant consumption was slow, and several first and second instar larvae stopped eating and died, suggesting that *C. angustifolium* is marginal as an *A. briarea* foodplant. We successfully reared two larvae through the fifth instar. One (hereafter called Larva #3) that hatched on 27 July (day 1) was second instar on day 3, third on day 5, fourth on day 9, and fifth on day 14. It spun up to form its chrysalid late on day 19 and was preserved early in its prepupal stage on the morning of day 19. Figures 4 and 5 show Larva #3 in its late fourth instar on day 13. The frontispiece is Larva #3 late in its fifth instar on day 18, one day before its prepupal stage. The second larva (hereafter called Larva #7) became fourth instar on 29 July, and fifth on 6 August. Figures 2 and 7 are Larva #7 photographed on 8 August, and Fig. 6 and 8 are Larva #7 photographed on 9 August. The prepupa formed from Larva #7 on 12 August (Fig. 9), and formed its chrysalid on 13 August. Figures 10-12 are this chrysalid photographed on 15 August, and Fig. 13 is the same individual (backlit) photographed on 16 August. Based on the size of *A. briarea* as an adult, we judged that the fifth instar larvae and the chrysalid were about 2/3 of the size they would have attained had they been reared on their native Hispaniolan foodplant(s). The three day old chrysalid was preserved on 16 August.

The larvae, prechrysalid, and chrysalid were photographed using a Nikon 8008 with a 105mm Micro Nikkor lens and through-the-lens flash or natural lighting, using Fujichrome 50 or 100 film. The egg was photographed with a Wild M-32 microscope, artificial lighting, and Kodachrome 64 film. The adults were photographed in natural sunlight on Kodachrome 25 with a Leicaflex R-3 and a 60mm Macro-Elmarit lens.

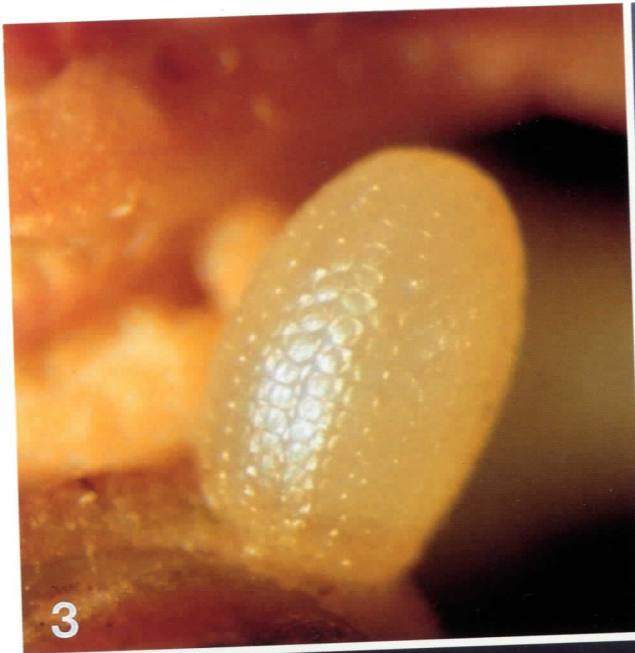
Unhatched eggs, first, second, and fourth instar larvae that died, one late fifth instar larva (Larva #3) and one chrysalid (Larva #7) were preserved in ethanol and shipped to the British Museum for cladistic analyses. Several second through fourth instar larval head capsules were also preserved and included in the shipment.

#### POSSIBLE FOODPLANTS IN HISPANIOLA

One reason for the uncertain systematic position of the genus *Anetia* within the Danainae is the lack of documented foodplants (review in A&VW, 1984). Our success in inducing *Anetia briarea* to oviposit on *Cynanchum angustifolium* and in rearing two of about 25 larvae successfully on this milkweed bolsters the weak evidence that supports the Asclepiadaceae as *Anetia* foodplants (*A. thirza*, A&VW, p. 243; DeVries, 1987, p. 214; *A. briarea*, Wetherbee, 1989; *A. pantheratus*, Wetherbee, 1991). As noted above, *A. briarea* did not accept *Matelea* sp., *Asclepias curassavica*, *A. incarnata*, *A. lanceolata*, or *A. tuberosa*, either for oviposition or as a larval foodplant, and the two *Asclepias* species that they nibbled (*A. curassavica* and *A. incarnata*) seemed toxic to the first instar larvae.

Many larvae failed to develop successfully on *Cynanchum angustifolium*. This strongly suggests that different non-*Asclepias*







milkweeds serve as foodplants for *A. briarea* in their native habitats. According to Moscoso (1943), approximately 31 endemic species in nine genera of the Asclepiadaceae occur on Hispaniola, together with six introduced species in five genera. The endemics include two species of *Asclepias* (*A. curassavica* and *A. nivea*), one *Astephanus*, one *Funastrum* (= *Sarcostemma*), three *Gonolobus*, one *Ibatia* (= *Cynanchum*?), seven *Marsdenia*, twelve *Metastelma*, three *Poecilopsis*, and one *Tainionema*; the introduced species are in *Calotropis*, *Hoya*, *Cryptostegia*, *Stapelia*, and *Stephanotis*.

Sorting out which of these asclepiads are natural *Anetia* foodplants will require further field research. Since the generic classifications of these milkweeds are in flux (cf. Correll and Johnston, 1970; Long and Lakela, 1971; Wunderlin, 1982; Clewell, 1985; Judd, 1987; Rosatti, 1989), the task will be formidable. It is essential that the plant specimens upon which oviposition occurs and upon which larvae feed successfully be pressed, documented, and deposited in appropriate museum herbaria.

Our new data render dubious the often quoted *A. briarea* larval foodplant as *Jacquinia* in the family Theophrastaceae. It is likely that *Jacquinia* was the substrate bush upon which an asclepiad vine was growing (Ivie, personal observations).

### SYSTEMATIC IMPLICATIONS

Although the most probable systematic placement of *A. briarea* based on characters of the immatures will have to wait for analysis of the material that we have forwarded to the British Museum (Natural History), London (Kitching *et al.*, in prep.), our preliminary examination allows us to comment on several questions raised in the literature.

**A. Is *Anetia* a Danaine?** Early authors vacillated over whether *Anetia* should be included with or excluded from the Danainae (A&VW, pp. 2-7, 60). Although a general consensus has converged on including the genus, A&VW note that as recently as the 1970's lepidopterists were not consistent in their recognition of this. A&VW (p. 17) include the genus on the basis of the male hair pencils. Our rearings of *A. briarea* confirmed two additional larval features consistent with their placement in the Danainae:

**1) Larval tubercles:** *Anetia briarea* larvae have a pair of tubercles on the mesothorax (postcephalic segment 2), but none on any other segments (Fig. 2, 4-9, frontispiece). The question of whether *Anetia* had any tubercles or not has been equivocal since Forbes (1939) interpreted earlier reports to indicate that the genus lacked them. Because this absence was unlike all other known Danaine larvae, Forbes placed the genus at the base of the Danainae. Our discovery indicates that larval tubercles almost certainly characterize the entire subfamily Danainae and remove what was a major taxonomic inconsistency in defining the subfamily. (The first instar larvae of *A. briarea* did lack tubercles and had completely black, shiny head capsules; perhaps

the early report cited by Forbes was of a first instar larva.)

**2) Larval foodplant:** Oviposition and larval feeding on a member of the Asclepiadaceae (*Cynanchum angustifolium*) support the placement of *Anetia* within the Danainae.

**Adult aggregation behavior:** Ivie *et al.* (1990) recently discovered remarkable aggregations of *A. briarea* high in the central montane region of the Dominican Republic and the species appears to have a vertical migration and diapause syndrome reminiscent of the migration and overwintering behavior of *Danaus plexippus* (Brower, 1985; see also Schwartz, 1989 for possible vertical migrations in other *Anetia* species). Wang and Emmel (1990) also recently found that 9 Danaine species in 5 genera (*Euploea*, *Tirumala*, *Ideopsis*, *Parantica*, and *Danaus* (*Salatura*)) exhibit migratory and aggregation behavior in Taiwan. This common behavior in divergent species groups of the Danainae suggests that the migration-aggregation syndrome may be an ancient character of the subfamily.

**B. Within the Danainae, where does *Anetia* belong?** Forbes (1939) placed *Anetia* as the ancestral stem group of the rest of the Danainae, which he then divided into three tribes: the Lycoreini (New World only), Euploeini (Old World only), and Danaini (Old and New World). Based largely on adult characters, A&VW (p. 6, 12) revised Forbes' classification by eliminating the tribe Lycoreini, and moving *Lycorea* and *Anetia* into the New World subtribe Itunina alongside the Old World subtribe Euploeina containing *Euploea*, *Idea* and *Protoploea*. These five genera in two subtribes together constitute the Tribe Euploeini. A&VW acknowledge (p. 61) that new evidence, such as that recently produced by Kitching (1985), may lead to different groupings. Thus Kitching, evaluating egg, larval, and pupal characters of a subset of Danainae (but not including any *Anetia*), disagreed with A&VW's placement of *Lycorea* (and, by extension, *Anetia*) close to *Euploea*. Both A&VW and Kitching repeatedly assert that *Anetia*'s life history is critical to resolving the higher-level classification of the Danainae.

**1) Larval tubercles (filaments):** *Anetia briarea* is similar to *Lycorea*, and unlike all other known Danaine larvae, in having a single pair of tubercles on the 2nd thoracic segment and lacking them on any other segments (Fig. 2, 4-9, frontispiece). This supports A&VW's (pp. 12, 23, 62) contention that *Anetia* is most similar to *Lycorea*.

**2) Larval head capsule coloration:** Kitching (1985, pp. 37, 58) identifies three major color patterns in the fifth instar head capsules of the Danainae: (i) uniformly dark as in *Lycorea*; (ii) black with white spots as in *Amauris* and *Parantica*; and (iii) and black with white stripes as in *Tirumala* and *Danaus*. The striped head is considered a unique derived character (an apomorphy) of Kitching's subtribe Danaina. The fifth instar head capsule of *A. briarea* is striped black and white; see Fig. 4 (fourth instar), Fig. 8 and frontispiece (fifth instar). This suggests that either head capsule stripes have evolved more than once, or that both Kitching's and A&VW's placements are incorrect: one interpretation is that *Anetia* is at the base of the Danainae as Forbes

Fig. 3-8.— 3. Egg of *A. briarea* (actual size = 0.8mm x 1.3mm) (© L.P. Brower 1992); 4. Lateral view of a late fourth instar larva (#3); total length = 2cm; the larva is inverted from its normal position (© L.S. Fink 1992); 5. Dorsal view of a late fourth instar larva (#3) (© L.S. Fink 1992); 6. Dorsal view of larva #7, fifth instar (total length approx. 3.2cm) (© L.S. Fink 1992); 7. Lateral view of larva #7, early fifth instar; the larva is inverted from its normal position (© L.S. Fink 1992); 8. Ventral view of larva #7, fifth instar (© L.S. Fink 1992).



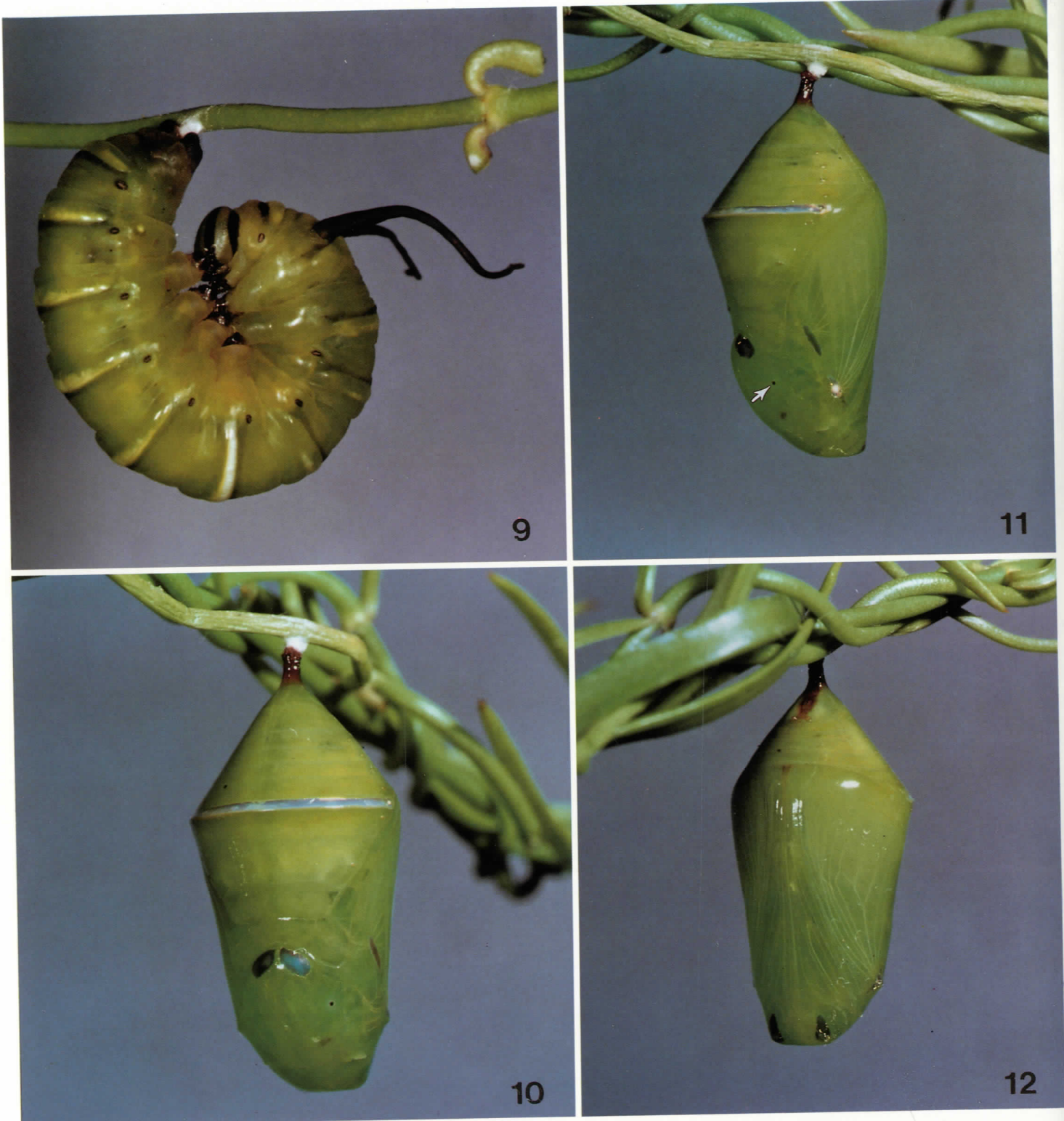


Fig. 9-12.— Fifth instar larva #7 hanging from its silk pad about 12 hours before metamorphosis to the chrysalid; 10. Dorsal view of chrysalid formed from larva #7, two days old; note the two large dorsal gold spots and the general *Danaus*-like shape (total length, head to base of cremaster = 1.7cm); 11. Lateral view of same chrysalid as in Fig. 10; note two gold spots at the base of the developing wings (the small white arrow points to scar due to neogregarine protozoan infection); 12. Ventral view of same chrysalid as in Fig. 10; note ocular gold spots (all © L.S. Fink 1992).

thought; a second is that it belongs in the Tribe Danaini.

3) **Larval pigment pattern:** Kitching (1985, p. 34) gives four basic pigment patterns for the fifth instar larvae of the Danainae. These are the presence of transverse stripes with or without spots

(considered plesiomorphic), spotted only, uniformly pale, or longitudinally striped. To this we add a fifth pattern which characterizes *A. briarea*: transverse stripes together with a single ventrad longitudinal stripe (see Fig. 2, 4, 6-7). Two species of





Fig. 13. Pre-eclosion chrysalid of *Anetia briarea*. © L.S. Fink 1992.

*Tirumala* share this pattern, arguing for *Anetia*'s placement with the Danaini, rather than with *Lycorea* (see A&VW's color Pl. IV and VI, Fig. 33, 34, and 52). However, the water is muddied because *Euploea core amymone* (Godart) has a somewhat similar pattern (see A&VW's color Pl. VI, Fig. 47).

**4) Chrysalid shape and gold markings:** The shape of the *A. briarea* chrysalid is more similar to *Danaus* than to *Euploea* (compare our Fig. 10-13) to A&VW's color Pl. I-III, Fig. 7-24). The *A. briarea* chrysalid is green with gold spots and a transverse gold-banded ridge on abdominal segment 3. Kitching (*l.c.*) considers the transverse ridge on the abdomen (his character P20) as an apomorphic character of the tribe Danaini, and the gold spots (his character P26) as an apomorphic character of the subtribe Danaina (*Tirumala*, *Danaus*). These traits, therefore, again link *Anetia* to A&VW's tribe Danaini rather than to the Euploeini. Note also that the *Anetia* chrysalid is far more *Danaus*-like in shape than *Lycorea*-like (A&VW color Pl. III, Fig. 24).

**5) Gregarine parasites:** The *Anetia* chrysalid had a black spot caused by cuticular erosion, bleeding and clotting indicative of the neogregarine protozoan parasite, *Ophryocystis elektros-cirra* McLaughlin and Myers (see small white arrow, Fig. 11; the same wound is visible in Fig. 10). This protozoan was first described from Queen butterflies (*Danaus gilippus berenice*

Cramer) reared in south Florida by McLaughlin and Myers (1970) and repeatedly infected stocks of monarch butterflies reared at Amherst College in Massachusetts. Infection of overwintering monarch butterflies has also been noted in California (John Dayton and Elisabeth Bell, personal communication; Leong *et al.*, in press). Although the degree of host specificity of this species of neogregarine is unknown, its ability to cross-infect *Anetia* further suggests a close relationship between *Anetia* and *Danaus*.

## TENTATIVE CONCLUSIONS

Taken together, the new larval and chrysalid characters suggest that *Anetia* cannot be included in the tribe Euploeini, and may not belong close to *Lycorea*. Some characters place it close to the Danaini. Forbes (1939) may well have been correct in placing the genus *Anetia* as a relict Antillean stem group of the whole subfamily Danainae.

If *Anetia* is in fact at the stem of the Danainae, new evidence that *A. briarea* contains cardenolides (Brower *et al.* in prep.) may be a major challenge to the view that cardenolide sequestration for chemical defense is a specialized and recent character (Ackery and Vane-Wright, 1985; Ackery, 1988, in press; Vane-Wright, 1991). We wait with bated breath the outcome of further cladistic analyses, as well as new life history and cardenolide data on other *Anetia* species.

## BIOGEOGRAPHIC SPECULATIONS

If *Anetia* is at the stem of the Danainae, major biogeographic questions emerge. Only one species, *A. thirza* Geyer, occurs on the mainland (in Central America northward to Mexico), while the four other species occur in the Greater Antillean Islands. Three are on Cuba (*A. cubana* Salvin, *A. briarea* Godart, and *A. pantheratus* Martyn), three are on Hispaniola (*A. jaegeri* Ménétriés, *A. briarea*, and *A. pantheratus*) and one is on Jamaica (*A. jaegeri*). A sixth, as yet undescribed species, may also occur on Jamaica (Brown and Heineman, 1972; Vane-Wright *et al.*, in press).

Is this Greater Antillean Danaine fauna a relict of an ancient pantropical distribution (cf. Liebherr, 1988)? Did the Danainae originate from *Anetia* ancestors in the New World, and spread to the Old, or *vice versa* (Brown and Heineman, 1972)? Did the presence of the Apocyanaceous-feeding Ithomiinae limit the adaptive radiation of the Danainae in the New World tropics? Likewise, did the absence of the Ithomiinae permit the Danaine adaptive radiation into the 125 known species in the Indo-Pacific region (cf. Poulton, 1908; A&VW, *l.c.*, p. 61, 106, 116; Kitching *et al.*, in press)?

The absence of an adequate fossil record of butterflies and the current incomplete state of our knowledge of the geological history of the West Indies in relation to Central America make it difficult to answer these questions (cf. Rosen, 1975; Pindell and Dewey, 1982; Donnelly, 1988; Liebherr, 1988; Miller and Miller, 1989). Nevertheless, the somewhat similar Old and New World distributions of Danaines and the *Pseudodiyastata* group of relict Drosophilid flies (Grimaldi, 1988) suggests a general biogeographic pattern. It is just possible that Central America was the



place of origin of the Danainae. Perhaps *Anetia* survived as a relict genus as a result of continental drift and island formation dating back to the late Cretaceous that isolated the genus from mainland competition on the Greater Antilles (*cf.* Miller and Miller, p. 244, *l.c.*).

#### ACKNOWLEDGMENTS

We thank the persons and organizations who made field work possible including J. and M. Brodzinsjy, K. Guerrero, J. Lambertus, and The National Parks of the Dominican Republic. C. Canelo, V. Peralta, D. Sikes, W. Lamier, T. McNary and R. Ivie assisted with permits, logistics or actual field work, and R. Miller, L. Ivie, and R. Grubb assisted with laboratory expertise. We also thank Professor Albert S. Ae of Nanzan University for describing the plastic bag method of inducing oviposition in recalcitrant butterflies, Professor Dana Griffin for leading us to *Cynanchum angustifolium* on Cedar Key, Kent Perkins of the University of Florida Herbarium for verifying its identification, Professor Walter Judd for insights into the West Indies milkweed flora, Marc Minno for locating *Matelea*, Daryl Harrison for help with the artwork, and L. McEdward for use of the Wild microscope. Dick Vane-Wright, Phil Ackery, and Tom Turner kindly allowed us to see their in press paper on Jamaican Danaines. The research was supported by NSF Grant DEB-9213266 to M. A. Ivie, by a University of Florida DSR grant to L. P. Brower, and by the Ulrich-Hana Foundation.

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