# BULLETIN OF THE ALLYN MUSEUM

## STUDIES IN THE LYCAENINAE (LYCAENIDAE)

### 4. The Higher Classification of the American Coppers

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Rothschild and Jordan (1906; 427) expressed a truth that has guided us in our systematic work for many years. They stated, "Classification has always suffered from the habit of systematists of studying the systematics of a district rather than concentrating their labours on certain families, taking into account all of the species of the globe." Sadly, this criticism may still be leveled at many of today's systematists, though the habit of doing "A Revision of (whatever group) of North America, North of the Rio Grande" is becoming less prevalent than in the past. It is, therefore, with some reluctance that we embark on a study of the Coppers of only the Western Hemisphere. We hope that we may be forgiven our chauvinism, since we have utilized material from the Old World for comparative purposes. We have limited our study because Dr. Sibatani (1974) has proposed a tentative classification of the world Lycaeninae and has promised further studies on the subfamily. We do not agree entirely with his handling of the Western Hemisphere species. We feel that a modification of his scheme for this part of the world may be useful toward the formulation of a unified world classification of the group.

With the notable exception of the Sibatani scheme, the Coppers have suffered as much as any other group from the provincialism that Rothschild and Jordan were so eloquently decrying. The lycaenines are represented on such diverse parts of the world as the Palearctic, Nearctic and northern Central America; eastern and southern Africa; the Malay Peninsula, New Guinea and New Zealand, but not Australia. Small wonder, then, that the Coppers have been treated on parochial grounds by many authors throughout the history of lepidopterology. Because of this, the classification of the Lycaeninae has differed greatly from one region to another. Workers have had difficulty equating these systematic treatments across geographical boundaries. The results have been of two types. Many workers have come reluctantly to the conclusion that all of the Coppers should be placed into the first named genus, *Lycaena* Fabricius. Others have decided that only those species in "their" areas warrant generic splitting,

despite equally impressive distinctions among species in other areas. In this instance one must side with the "lumper", rather than with the "splitter". The latter seems to be indicating that only the material from his own pet region is important, all the rest being less so. The "lumper" is stating that he either can see no generic differences among all of the material, or, that he is confused by these differences and does not choose to single some out for special treatment. We cannot accept either philosophy, and neither does Sibatani.

The Europeans were the first ones to subdivide the Lycaeninae; Dalman in 1816 described *Heodes* and others misapplied the Hübnerian genus *Chrysophanus* (now known to be a Hairstreak) to the Coppers.

Later, Scudder (1876) revised the butterflies of North America, describing four new genera in the Lycaeninae and retaining *Heodes* and *Chrysophanus*. His systematic characters were carefully developed, but they are not the ones used by most modern authors, so the work is largely ignored, despite its excellent attributes. The Scudder study was strictly a North American one. A few of his conclusions were based on gleanings from the literature about North American butterflies he was not familiar with: hence, some of his decisions are totally erroneous.

Several authors such as Tutt (1906) and Verity (1919 and 1943) further subdivided the Palearctic Coppers, and Draudt (1920) described a "subgenus" for the Central American "*Lycaena*" *pyrrhias* (Godman and Salvin). No study was made of the worldwide fauna. All suffer from the parochial bias mentioned earlier.

American workers by and large have ignored previous generic studies. Except for *Tharsalea*, Scudder's new genera uniformly have been synonymized with whatever monogenus was in vogue. Currently, authors on this side of the Atlantic use only *Lycaena* and the subgenus *Tharsalea*. They place only *phlaeas* Linnaeus and *cupreus* W. H. Edwards in *Lycaena* (*Lycaena*). The other species are considered part of *Lycaena* (*Tharsalea*). Variations in this pattern have been few; however dos Passos (1964), while placing all Coppers in *Lycaena*, restricts the subgenus *Tharsalea* to only its type-species, *arota* Boisduval. *Iophanus* Draudt, when it has been mentioned, has been relegated to subgeneric standing within *Lycaena*.

Meanwhile, the proliferation of genera in Europe has gone on unabated. Justification is given by such as Higgins (1975) for this generic splitting. One cannot look at those pages without becoming convinced that indeed something *is* going on with the Coppers. Why, then, have the American authors insisted on retaining the single megagenus *Lycaena* for all of our species? Perhaps this "lumping" best can be explained by tradition, but then what constitutes "tradition"? Tradition has been to follow the latest check-lister whether or not he has had expert knowledge to properly arrange a correct selection of taxa. Simple genitalic analysis will demonstrate to even the most cynical that "our" Coppers, too, have something "going on" with them. At least in part, Scudder was right over a century ago, certainly more correct than have been those American authors who followed him.

Sibatani (1974) dramatically has turned the parochial study of the Coppers into a scientific worldwide study utilizing modern characters. Fine as it is, his work suffers somewhat from "Old World thinking", especially as regards his treatment of the subgenus *Tharsalea* (*Tharsalea*). Higgins (1975) characterized the lycaenines, based on European material, as having the "...saccus always will developed." Sibatani does not contradict this statement, and includes all of the American Coppers save *phlaeas*, *cupreus* (as "*cuprea*") and *Iophanus pyrrhias* in *Tharsalea* (*Tharsalea*). This assignment ignores the fact that some members included in Sibatani's *Tharsalea* (*T.*) have a well developed saccus, and others have barely a vestige of this structure. If the saccus is so important in European Lycaeninae, surely its absence in some Nearctic ones is equally important. Nevertheless, the Sibatani arrangement of the Coppers is a good one — the best we have — and we do not presume to attack any portion of it save his treatment of the New World species. Accordingly, though we have looked at most of the species he mentions (Sibatani, 1974: 109-110) and have verified the genera he proposes (but does not name) as new, we do not propose names for any of these at this time. That is the pro-

vince of Dr. Sibatani, and we look forward to seeing his paper(s) on these genera.

This, then, is our justification for not treating the lycaenine fauna of the whole world, even though we have examined the vast majority of the species and their genitalia, both males and females. The notes which follow should be taken in conjunction with Sibatani's paper and hopefully will add to it.

Taxonomy at the specific level has been done in other parts of the series (Ferris, 1974, 1977; Johnson and Balogh, 1977), and more such studies will be forthcoming. The present paper will provide the basis for generic assignment of the New World species: no actual species-group taxonomy is provided herein.

## MORPHOLOGICAL CHARACTERS

Scudder (1876) relied chiefly on characters of the legs and wings, but oddly enough, he was not particularly concerned with the neuration. To distinguish the various genera he used wing shape, whether or not the hindwing was tailed, the relative length of the cell (especially of the forewing), the relative lengths of the legs, whether or not the mid- and hindtarsi were swollen and the distribution of pattern elements on the wings. He was led by this selection of characters into some strange alliances, but his underlying classification was surprisingly accurate. Perhaps it was the general vagueness of his classification that led later students to reject much of Scudder's generic work. Certainly only the genus *Tharsalea* has withstood the critical eyes of later lepidopterists, and that only has survived in most classifications as a subgenus. The Scudderian characters have been examined in the present study, and it would be simple to reject the Scudder classification based only on these characteristics. Scudder's work suffered greatly from his asumptions about species he had not seen. He placed *hermes* W. H. Edwards in *Tharsalea* on the basis of the hindwing "tail" at the end of Cu$_2$. Other characters examined by other workers, as well as by us, have shown this relationship of *hermes* and *arota* to be spurious. In common with other writers of the day, Scudder placed *heteronea* Boisduval, originally described in *Polyommatus* but now known to be a Copper, in the polyommatine genus *Cupido*.

Eliot (1973) and especially Sibatani (1974) laid the groundwork for truly modern revisionary treatment of the Coppers, a treatment that includes not only wing, leg and antennal characters, but also male and female genitalic ones. These are the basic characteristics that we have attempted to use in the present study, and it seems to us that only such multivariat studies can elucidate relationships. It is as bad to use only genitalic characters as to rely entirely on pattern of venational characteristics. Higgins (1975) has utilized all possible characters in his analysis of the European species, and while some may criticize his acceptance of so many genera in the Lycaeninae, these detractors should consider these characters carefully before dismissing the conclusions out of hand.

### Analysis of Characters

Naturally, characteristics will be found that separate or group species, and we here are attempting for Lycaeninae to differentiate between the taxonomically important and unimportant ones. The pattern can be very confused, but some generalities may be drawn from examination of as many attributes as possible from the largest possible number of species.

One of the obvious characteristics of some Coppers is the presence, absence or indication of a "tail" at the end of hindwing vein Cu$_2$. This structure is well shown in the Old World *Heliophorus* section (Seitz, 1908-1928: pl. 160) *Melanolycaena* (Sibatani, 1974: fig. 1), *Phoenicurusia* Verity and "*Lycaena*" *li* (Oberthür) and its relatives (Seitz, 1906-1910: pl. 77). Too much emphasis should not be placed on this attribute, since some populations of *Lycaena phlaeas* are tailed, others not, and among *Thersamonia thetis* (Klug) it may even be a brood characteristic (Higgins and Riley, 1970: 248; pl. 51). In the New World there are only three "tailed" Coppers, *Iophanus pyrrhias* (Fig. 1),

*Tharsalea arota* (Fig. 6) and *"Lycaena" hermes* (Fig. 59). This "tail" is hinted at in some populations of *Gaeides xanthoides* (Boisduval) (Fig. 22) and California *L. phlaeas*, but most populations of the latter have no indication of this structure. In the absence of any other differences, the presence of "tails" cannot be considered a good taxonomic trait; too great emphasis of the presence of these structures led Scudder (1876: 125) to some spurious conclusions.

The presence of a hindwing tornal lobe is a character given some weight by Sibatani (1974: 96; fig. 1). It is shown by *Melanolycaena, Thersamonia* Verity (Higgins and Riley, 1970: pl. 51), the *Heliophorus* section and *"Lycaena" li* and its relatives (see "Seitz" plates listed above) in the Old World. This tornal lobe is well developed in *Iophanus pyrrhias* (Fig. 1) and moderately in the other two "tailed" American Coppers (Figs. 6 and 59). The presence or absence of the tornal lobe is somewhat more important taxonomically than is the "tailed" condition, but certainly not so diagnostic as some venational, genitalic or biological parameters.

Characters of wing venation long have been used (overused?) in butterfly taxonomy. The venation among Lycaeninae is remarkably similar; only four factors have been found that will differentiate species or genera. The discocellulars ($m_1$-$m_2$ and $m_2$-$m_3$) of both wings are uniformly weakly developed in all but four species examined (Old and New World). In *Gaeides xanthoides* (Fig. 22), *Lycaena phlaeas* (Fig. 11), *L. cupreus* (Fig. 12) and *Epidemia helloides* (Fig. 46) at least $m_2$-$m_3$ of the hindwing is absent. Other *Gaeides* and *Epidemia* have full complements of discocellulars; hence, the conditions of these veins is more a curiosity than a taxonomically significant phenomenom.

The relative positions of the veins offer more significance. Three parameters in particular vary more or less with genitalic ones and aid in what seems to be a consistent taxonomy of the group. 1) The relative positions of forewing veins $R_{4+5}$ and $M_1$ are informative. These veins may be well separated, as in *Gaeides* (Fig. 22), nearly connate, as in *(Epidemia epixanthe*, Fig. 45), connate on a short stalk *(Epidemia helloides*, Fig. 46) or connate on a long stalk *("Lycaena" hyllus*, Fig. 33). 2) Hindwing veins Rs and $M_1$ may arise well separated, as in *Epidemia* (Fig. 45) to nearly connate, as in *Iophanus pyrrhias* (Fig. 1). 3) The hindwing veins $M_3$ and $Cu_1$ also vary from nearly connate at their origins, as in *I. pyrrhias* (Fig. 1) to well separated, as in *Epidemia epixanthe* (Fig. 45).

Scudder (1876) made much use of the inflation of the mid- and hindtarsal basal segments. Only *L. phlaeas* (Fig. 18) and *Gaeides gorgon* (Boisduval) among the American lycaenines display this character. Several other species have this segmental modification indicated, but not to the extent of the two noted species. Far more information may be gleaned from examination of the forelegs of both sexes. The relative lengths of the segments, especially the difference between male foretibia and foretarsus, varies more or less along phyletic lines. In *Iophanus* (Fig. 2) the tibia is longer than the femur (the only Copper sampled in which this was true), and the tibia is significantly longer than is the foretarsus. In most other genera (for example, Fig. 15) the femur is longer than the tibia, which in turn is longer than the tarsus. An exception is *Gaeides* (Fig. 25, for example) and its relatives in which the foretibia and foretarsus are subequal. The female foreleg varies from heavily spined in *Gaeides xanthoides* (Fig. 26) to very lightly spined, as in *"Lycaena" hermes* (Fig. 61). The relative lengths of the segments in the female varies systematically in much the same ways as do the segments in the male. The male foretarsus bears a distinct claw in most Palearctic species, as well as most in the Nearctic. Perhaps the most poorly defined tarsal claws are in *Gaeides* (Fig. 26) and especially *Epidemia* (as Fig. 49). The miniaturization and tendency toward loss of parts is perhaps the most potent taxonomic characteristic yet discussed here, no doubt on a par with genitalic and behavioral traits described below.

The palpi show very little usable variation Most species have the second segment about twice the length of the third, but some Nearctic species (*"L." hermes, Epidemia nivalis, "L." hyllus, Gaeides xanthoides* and *Iophanus pyrrhias*) have the third segment somewhat longer than this, and only in *Lycaena cupreus* (Behr) and *Epidemia nivalis* (Boisduval) is the second segment more than twice as long as is the third.

The antennae also are less useful than had been hoped. The number of segments in the antenna vary from 30 to 40, the Old World species tending to exhibit more segments than material from the Western Hemisphere. The club, which occupies the distal 25 to 40 percent of the antenna, is usually rather gradually and moderately developed. The stoutest clubs were observed in the Palearctic *Heodes tityrus* (Poda), the New Zealand *"Lycaena" salustius* (Fabricius) and the Nearctic *Epidemia dorcas* (W. Kirby). The first and last named species are congeneric with members having more typical antennae, however, and we believe that the antennal characteristics are of little use for classification. The genus *Epidemia* seems to have the greatest development of the antennal club among New World Coppers, though that of *"Lycaena" hyllus* is fairly stout.

The genitalia, both male and female, demonstrate a great number of usable characteristics for classification of the Coppers, as so often among most other butterflies. One is tempted to use *only* genitalic characters for classification, but this would be to err nearly to the same degree as if one ignored the genitalia entirely. Nonetheless, some of the most powerful systematic characteristics are located in the genitalia.

The uncus is well developed and bilobate with the lobes rather widely separated. The uncus shows far more resemblance to that of the Blues (Polyommatinae) than to the Hairstreaks (Theclinae). The lobes themselves appear to sit on the tegumen rather like caps and are slightly curved ventro-distad. The lobes may be more or less downturned in a few genera (for example, *Tharsalea*, Fig. 9). In all other New World genera the strong curving is not shown. The lobes are more or less divergent, though detection of this trait may be governed by the angle from which the observer is looking.

Much has been made of the development of the saccus by Eastern Hemisphere workers (Higgins, 1975; Eliot, 1973), but were one to consider this character of overriding subfamilial importance, many of the New World species could not be considered "Coppers". *Thersamonia thersamon* (Esper) (Fig. 64) and to a lesser degree *Phoenicurusia phoenicurus* (Lederer) (Fig. 65) share the poorly developed saccus with many of our species, but in other respects all of these butterflies are perfectly "good" Coppers. We find the configuration of the saccus to be an important generic character.

Higgins (1975: 98-103) shows the penis of most European Coppers as a straight organ: the exception being that of *Thersamonia* (pp. 102-103) which is slightly bent downward. Those of most Asiatic species examined are also straight with the exception of that of *Phoenicurusia* (Fig. 65) which is strongly diverted ventrad, as are most of the typically New World lycaenines. The coupling of this characteristic with the abortive saccus and a few other characteristics mentioned later, suggest a systematic relationship between *Phoenicurusia* and many of the wholly American genera (but not *Tharsalea*, as suggested by Sibatani, 1974: 109). The development of the penis appears to be of great systematic importance in the Coppers.

The furca is much used in Higgins' (1975) classification of the European Coppers, and indeed this structure is quite variable within the subfamily. It appears to be one of the best generic discriminators of any characteristic, though again it is better developed in Old World material. Such wholly American genera as *Epidemia* (Fig. 51, for example) and *Chalceria* (for example, Fig. 41) have the furca least developed.

The valvae show great variability throughout the Lycaeninae, much of it correlating with other variation thus suggesting the generic assignment of many species. One character that was used profitably by Johnson and Balogh (1977) is the presence or absence of internal teeth on the valvae. These occur not only in *Chalceria rubidus* (Fig. 41) and *ferrisi*, as those authors suggested, but also in *C. heteronea* (Fig. 42), *Gaeides xanthoides* (Fig. 28) and *editha* (Fig. 29), *"Lycaena" hermes* (Fig. 62) and *Heodes virgaureae* (Linnaeus) (Higgins, 1975: fig. 114, but not other *Heodes*) among the species examined.

In most Old World Coppers the valvae are rather massive (Eliot, 1973: fig. 69), but the Palearctic *Phoenicurusia* (Fig. 65) shares the rather finely drawn valvae associated with most of the New World species, a characteristic that may have led Sibatani (1974: 109) to place *Phoenicurusia* as a Palearctic subgenus of the American *Tharsalea*. *Thar-*

*salea arota* (Fig. 6) actually has rather massive valvae for a New World Copper. As mentioned above, however, *Phoenicurusia* has the poorly developed saccus more associated with *"L."hyllus* (Fig. 36) and *Epidemia* (Fig. 51, for example). Therefore, if subgeneric asignment is to be made with the American Coppers and *Phoenicurusia*, it would appear that the latter would have to be a subgenus of *Epidemia* or *Chalceria*, rather than *Tharsalea*. Massive valvae are shown in the American Lycaeninae by *T. arota*, *Iophanus pyrrhias* (Fig. 4) and *"Lycaena" hyllus* (Fig. 35), as well as the two species with Palearctic affinities, *Lycaena phlaeas* (Fig. 19) and *cupreus* (Fig. 20).

The falces in most species are curved, as shown by Eliot (1973: Fig. 69) for the New Zealand *"Lycaena" salustius*, but in a few species they are rather "elbowed", while in a few others they are straighter than shown in the cited figure. The picture of the falces, then, is one of almost continuous variation, and the character is not considered here to be especially important in higher classification.

The female genitalia of most Nearctic species were diagrammatically portrayed by Johnson and Balogh (1977: figs. 10-11). These structures vary chiefly in the posterior elements (sterigma, ductus bursae and to a lesser degree, in the configuration of the papillae anales). These structures especially demonstrate the systematic proximity of *Gaeides* (Fig. 31, for example) and *Chalceria* (Fig. 43, for example), but they certainly suggest the limits of other Nearctic genera as well.

Two sets of biological data were analyzed, voltinism and foodplant preference. The data on voltinism suggest that Coppers are rather more opportunistic than are some butterflies, with multivoltine species frequently found in generic association with univoltine ones. Foodplant preference is similarly confused. By far the majority of Coppers feed as larvae on Polygonaceae *(Rumex, Polygonum, Oxyria, Eriogonum)*, but a few species have entirely different preferences: *Tharsalea arota* feeds on gooseberry (Saxifragaceae), *Epidemia epixanthe* (Boisduval and Leconte) on cranberry (Rosaceae) and *E. dorcas* on cinquefoil (Rosaceae). Still others utilize Rhamnaceae, Rubiaceae, etc. It appears that Polygonaceae is the ancestral foodplant of the Coppers, but individual species by be opportunistic and able to shift to other plant groups, presumably those with biochemical affinities to the docks, *etc.* Foodplant specificity does not seem to be strongly developed in the dock feeders, although apparently when species shift away from polygonaceous plants they become highly host-specific.

The ova of Coppers have been examined to a much less extensive degree, but they do show possible generic characteristics (Figs. 58-59, *Epidemia; 66, Lycaena*), and at least one closely allied species-pair, *Epidemia helloides* (Fig. 58) and *dorcas* (Fig. 59), have different micropylar configurations. Females of these two species are almost more separable by the eggs they carry than by their morphological characteristics.

## SYSTEMATIC REVIEW OF THE GENERA

The species in the New World show certain affinities with one another and others with Palearctic ones. These relationships suggest that the Coppers of the Western Hemisphere might predate the splitting of the Palearctic from the Nearctic in the Mesozoic, whereas in a few instances Coppers have arrived in the Americas rather recently from the Palearctic (see Phylogenetic and Zoogeographic Considerations, later in this paper). The implied taxonomic sequence for the American Coppers is given below.

### Iophanus Draudt, 1920

*Iophanus* Draudt, 1920: 814. Type-species by monotypy *Chrysophanus* (?) *pyrrhias* Godman and Salvin, [1887] (1879-1901), 2: 101. Proposed as a subgenus of *Chrysophanus*.

Included species: only the type.

This genus is characterized as follows:

Antenna about half length of forewing; comprised of 31-32 segments; club gradual and moderate, occupying terminal two-fifths of antenna. Palpi rather long, shaggy and semierect; third segment four-sevenths length of second.

♂ foreleg (Fig. 2) miniaturized but with a tarsal claw; femur shorter than tibia, but longer than tarsus; tarsus fringed throughout, but tibia almost nude. ♀ foreleg (Fig. 3) likewise rather miniaturized with moderately well developed spines on tibia and especially tarsus; femur longer than tibia, which in turn is longer than tarsus. First mid-tarsal subsegment not inflated.

Forewing (Fig. 1) apex rather acute; veins Rs and $M_1$ connate on a short stalk; $Cu_1$ closer to $M_3$ than to $Cu_2$ at origins. Hindwing (Fig. 1) with a well developed "tail" at end of $Cu_2$; tornal lobe well developed; veins Rs and $M_1$ approximate at their origins; $M_3$ and $Cu_1$ nearly connate at origins.
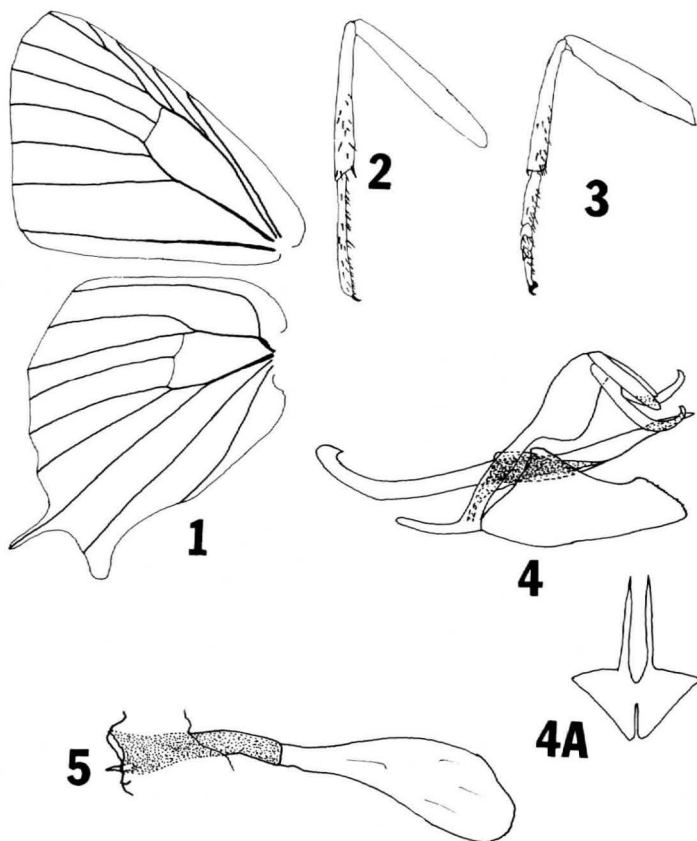


Figures 1-5: *Iophanus pyrrhias* (Godman and Salvin). 1, ♀ venation; GUATEMALA: CHIMALTENANGO: Quisache (Slide M-3077, Lee D. Miller). 2, ♂ forefemur + -tibia + -tarsus; same data as Fig. 1. 3, ♀ forefemur + - tibia + - tarsus; MEXICO: CHIAPAS: Mt. Huitepec (Slide M-3103, Lee D. Miller). 4, ♂ genitalia (preparation M-3198-V, Lee D. Miller); same specimen as Fig. 1. 4A, dorsal view of furca of same preparation as Fig. 4. 5, ♀ genitalia (preparation M-3609-V, Jacqueline Y. Miller); same data as Fig. 3. Venation drawings approx. 3.5x; leg and genitalic drawings approx. 12x. All specimens in Allyn Museum of Entomology collection.

♂ genitalia (Fig. 4) with rather divergent uncus lobes; saccus long and straight; penis long, slightly upturned; furca rather modestly developed; valvae broad and massive with moderate terminal teeth and no internal teeth.

♀ genitalia (Fig. 5) with sterigma and ductus bursae strongly sclerotized, but relatively unornamented; vaginal plate heavily sclerotized.

Larval foodplant a species of *Rumex* (J. F. Emmel, personal communication).

Wing pattern linear, reminding one far more of a Hairstreak than of either a normal Copper or a Blue. This characteristic, as much as any other, led Sibatani (1974: 110) to place *Iophanus* in the *Heliophorus* section of the Lycaeninae.

*I. pyrrhias* is a highly aberrant Copper, and one that is difficult to place within the subfamily. In venation it is rather "modern" since a number of veins are anastomosed, or at least connate at their origins. Genitalically, however, the pattern is one referable to the more "primitive" Coppers, having massive valvae, the well developed saccus and poorly developed furca in the male, and the simple but well sclerotized sterigmal elements of the female. On balance, however, *Iophanus* appears to be a more primitive lycaenine, and it distribution sugests that it is the most primitive survivor of the Cretaceous-Tertiary invasion of the New World. It is found in the same region where *Anetia* (the most primitive danaid) and *Baronia* (the most primitive papilionid, and one that is represented by North American Eocene fossils) may be found today.

The male is purplish-brown above, while the female is blue-purple basally with some distal copper-colored patches distad on the upper surface. The under surface of both sexes recalls the "*Thecla*" *loxurina* Hewitson group and *Micandra* Staudinger, both of the Eumaeini, far more than any New World lycaenine.

### Tharsalea Scudder, 1876

*Tharsalea* Scudder, 1876: 125. Type-species by original designation *Polyommatus arota* Boisduval, 1852: 293-294.

Included species: only the type[1].

The genus *Tharsalea* is characterized as follows:

Antenna about half length of forewing; comprised of 30-32 segments; club gradual and moderate, occupying terminal third of antenna. Palpi long, shaggy and semi-erect; third segment about half as long as second.

♂ foreleg (Fig. 7) miniaturized, but with a tarsal claw; tarsus fringed and tibia lightly spined in distal half; femur longer than tibia, which in turn is longer than tarsus. ♀ foreleg (Fig. 8) not greatly miniaturized with fairly heavy spines on entire tarsus and distal half of tibia; femur longer than tibia, which in turn is longer than tarsus. Basal midtarsal subsegment not at all inflated.

Forewing (Fig. 6) apex pointed; veins Rs and $M_1$ approximate, but not connate, at origins; $Cu_1$ arises closer to $M_3$ than to $Cu_2$. Hindwing (Fig. 6) with well developed "tail" at end of $Cu_2$; tornal lobe moderately well developed; vein Rs arises well back from $M_1$; $M_3$ and $Cu_1$ arise approximate, but separate.

♂ genitalia (Fig. 9) with uncus lobes not divergent, but strongly downturned distally; saccus long and upturned; penis long and more or less straight; furca rather well developed and heavily sclerotized (Fig. 9A); valvae simple, not so massive as in *I. pyrrhias* and lacking terminal or internal teeth.

♀ genitalia (Fig. 10) with a narrow, well sclerotized Jterigmal region.

Larval foodplants are various *Ribes* (Saxifragaceae), according to Opler (1975: 310) and others.

Wing pattern linear, but less like that of a Hairstreak than is that of *I. pyrrhias*. One must suspect that the general pattern is related strongly to the general form of the wing in this instance — a linear pattern converging on the "tail" tending to divert a

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[1]In his original description of this genus, Scudder included not only *arota*, but also *Chrysophanus virginiensis* W. H. Edwards (a subspecies of *arota*) and *Chrysophanus hermes* W. H. Edwards, a species having nothing whatsoever to do with *Tharsalea* (see below).

predator's attention from the body.

T. *arota* is perhaps the second most primitive Copper in the New World. Genitalically it is not so primitive as is *I. pyrrhias*, these structures (with the exception of the downturned uncus lobes) being closer the the "main line" lycaenine configurations. With regard to wing venation and the morphology of the legs, though, *arota* is more like what we would expect the ancestral Copper to be. We suspect that *arota* became established in the New World as soon as, or at most only slightly later than did *pyrrhias*, probably in the Cretaceous-Tertiary division of the Holarctic. The present species' ancestor was certainly here before the vast majority of progenitors of the groups that follow.

The male looks like no other Copper in this hemisphere. It is tailed, dark coppery brown above and warm to gray-brown beneath. The female has a more typical "Copper" pattern on the dorsal surface (Howe, 1975: pls. 55-56), but the under surface pattern is
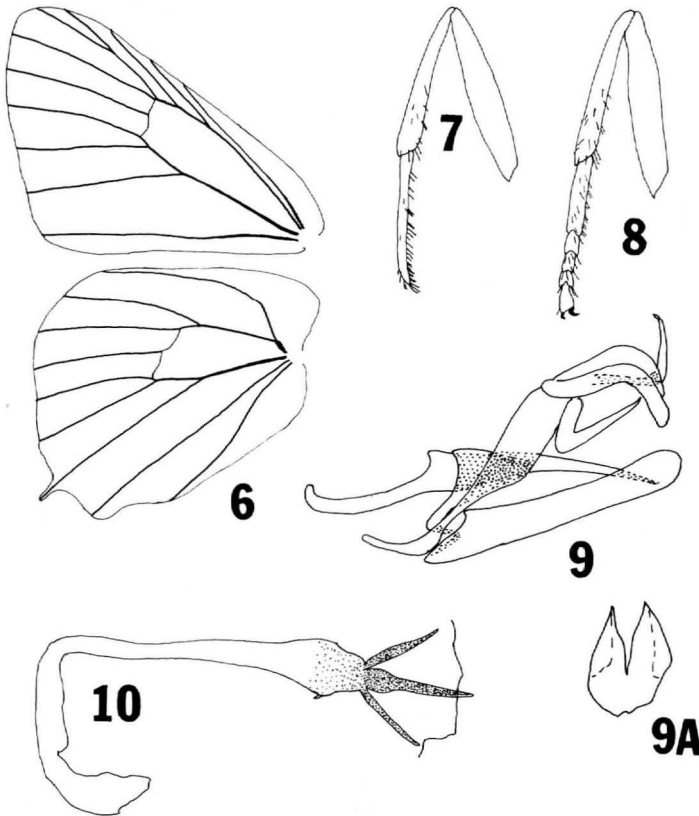


Figures 6-10: *Tharasalea arota arota* (Boisduval). 6, ♂ venation; CALIFORNIA: Arroyo Bayo, Mt. Hamilton (Slide M-3078, Lee D. Miller). 7, ♂ forefemur + -tibia + -tarsus; same data as Fig. 6. 8, ♀ forefemur + -tibia + -tarsus; CALIFORNIA: Los Angeles Co.: NE of Sandberg (Slide M-3104, Lee D. Miller). 9, ♂ genitalia (preparation M-3100-V, Lee D. Miller); same specimen as Fig. 6. 9A, dorsal view of furca of same specimen as Fig. 9. 10, ♀ genitalia (preparation M-3318-V, Lee D. Miller); same data as Fig. 8. Magnifications as in Figs. 1-5.

linear, as in the male. The pattern of the male led Sibatani (1974: 109-110) to associate *Tharsalea* with the Old World genus *Phoenicurusia*. The male genitalia of *P. phoenicurus* (Fig. 65), however, bear little resemblance to those of *T. arota* (Fig. 9). The saccus is shorter and the valvae are more finely drawn in the former. *Phoenicurusia* seems to be a highly modified genus more closely related to *Thersamonia* of the Old World, or even the Nearctic *Epidemia* and *Gaeides,* than to the more "primitive" *Tharsalea,* superficial similarities notwithstanding.
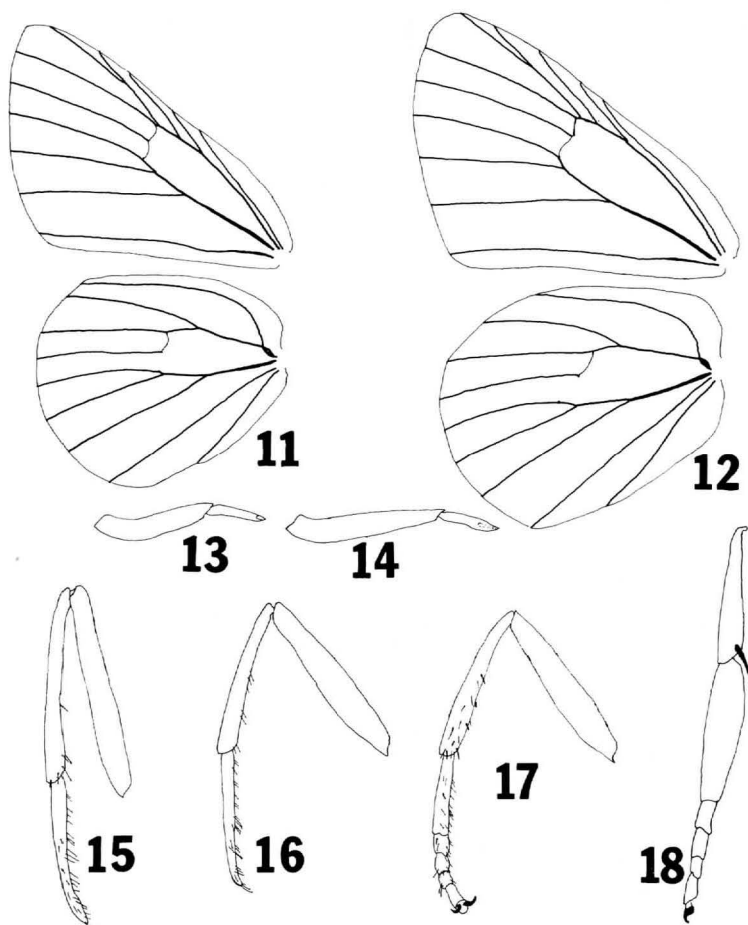


Figures 11-18: appendages of Nearctic *Lycaena* species. 11, *L. phlaeas americana* Harris, ♂ venation; NORTH CAROLINA: Cumberland Co. (Slide M-3085, Lee D. Miller). 12, *L. cupreus cupreus* (W. H. Edwards), ♂ venation; CALIFORNIA: Tuolumne Co.: Tioga Pass (Slide M-3086, Lee D. Miller). 13, *L. p. americana*, Palpus; same data as Fig. 11. 14, *L. c. cupreus*, palpus; same data as Fig. 12. 15, *L. p. americana*, ♂ forefemur + -tibia + -tarsus; same data as Fig. 11. 16, *L. c. cupreus*, ♂ forefemur + -tibia + -tarsus; same data as Fig. 12. 17, *L. c. cupreus*, ♀ forefemur + -tibia + -tarsus; CALIFORNIA: Tuolumne Co.: Tioga Pass (Slide M-3112, Lee D. Miller). 18, *L. p. americana*, ♂ midtibia + -tarsus; same data as Fig. 11. Magnifications as in Figs. 1-5.

## Lycaena Fabricius, 1807

*Lycaena* Fabricius, 1807: 285. Type-species by designation of Curtis, 1828: pl. 12, *Papilio phlaeas* Linnaeus, 1761: 285.
=*Lycia* Sodovskii, 1837: 81. Type-species, as replacement name, *Papilio phlaeas* Linnaeus, 1761: 285. Preoccupied by *Lycia* Hübner, [1825]: 319.
=*Migonitis* Sodovskii, 1837: 82. Type-species, as replacement name, *Papilio phlaeas* Linnaeus, 1761: 285. Preoccupied by *Migonitis* Rafinesque, 1815: 147.
=*Rumicia* Tutt, 1906: 131. Type-species by original designation *Papilio phlaeas* Linnaeus, 1761: 285.
=*Chrysophanus* of authors, not Hübner, 1818, 1: 18.
=*Heodes* of authors, not Dalman, 1816: 63.

Included species: *Papilio phlaeas* Linnaeus (1761: 285); *Chrysophanus abottii* Holland (1892: 90), extralimital; *Chrysophanus cupreus* W. H. Edwards, (1870: 20-21).

*Lycaena* is characterized as follows:
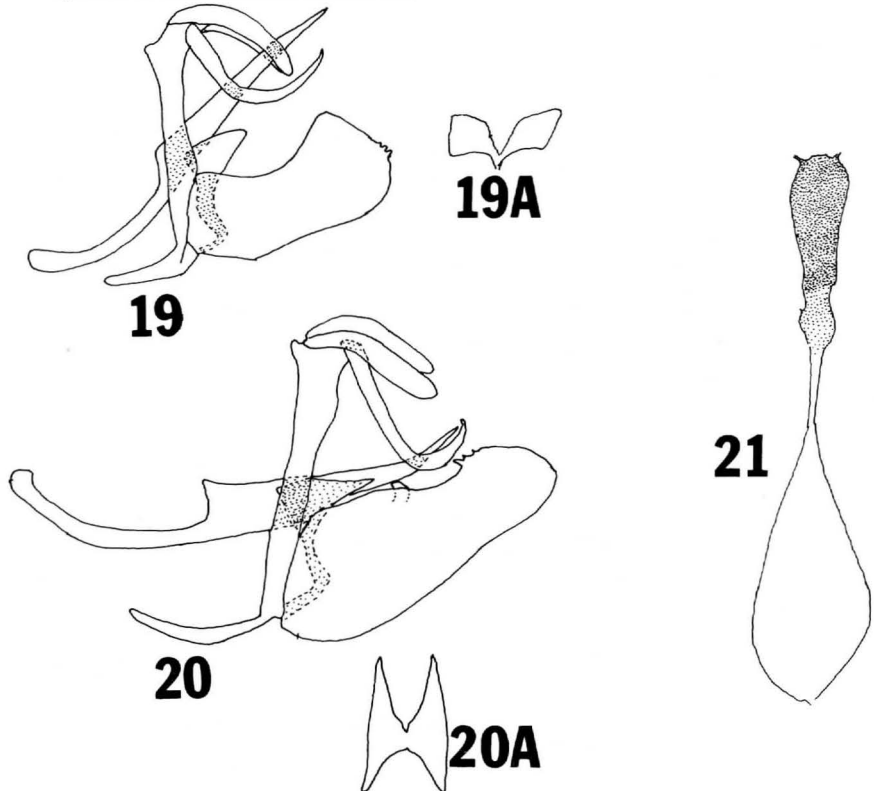


Figures 19-21: genitalia of Nearctic *Lycaena* species. 19, *L. phlaeas americana* Harris, ♂ genitalia (preparation M-3305-V, Lee D. Miller); same data as Fig. 11. 19A, dorsal view of furca of same preparation as Fig. 19. 20, *L. cupreus cupreus* (W. H. Edwards), ♂ genitalia (preparation M-3306-V, Lee D. Miller); same data as Fig. 12. 20A, dorsal view of furca of same preparation as Fig. 20. 21, *L. p. americana*, ♀ genitalia (preparation M-3323, Lee D. Miller); ILLINOIS: Cook Co.: Willow Springs. Magnifications as in Figs. 1-5.

Antenna less than half length of forewing; comprised of 30-32 segments; club gradual and moderate, occupying terminal three-tenths to one-third of antenna. Palpi shaggy, moderate and semi-erect; third segment from half (*phlaeas;* Fig. 13) to three-eighths (*cupreus,* Fig. 14) length of second.

♂ foreleg (Figs. 15 and 16) miniaturized (more so in *cupreus* than in *phlaeas* or *abottii*) with rather well developed tarsal claw; tarsus spined and tibia lightly fringed in distal half; femur longer than tibia, which in turn is longer than tarsus. ♀ foreleg (Fig. 17) almost as greatly miniaturized with tibia and tarsus moderately to lightly spined; femur longer than tibia, which is in turn equal in length to tarsus. First midtarsal subsegment somewhat inflated (Fig. 18).

Forewing (Figs. 11 and 12) apex more or less pointed in ♂, rounded in ♀; veins Rs and $M_1$ approximate (*cupreus*) to nearly connate (*phlaeas*) at origins; $Cu_1$ arises somewhat nearer to $M_3$ than to $Cu_2$. Hindwing (Figs. 11 and 12) with "tail" suggested at end of $Cu_2$ in Eurasian *phlaeas* (hinted at in California *L. phlaeas hypophlaeas* (Boisduval) ), but not in other Nearctic species; tornal lobe not developed (except hinted at in *abottii*); vein Rs arises well separated from $M_1$; $M_3$ and $Cu_1$ arise approximate (*phlaeas, abottii*) to well separated (*cupreus*).

♂ genitalia (Figs. 19 and 20) with uncus lobes divergent (*cupreus*) to moderately divergent (*phlaeas, abottii*) and straight; saccus long and more or less straight; penis long and straight; furca well developed and massive; valvae massive with well developed terminal (*phlaeas, abottii*) or dorsal (*cupreus*) teeth; no internal teeth.

♀ genitalia (Fig. 21) with a "necked" bursa; sterigma simple and well sclerotized; ductus bursae straight and strongly sclerotized.

Larval foodplants are various Polygonaceae, especially *Rumex* and *Polygonum.*

Wing pattern strongly polyommatine with very little tendency toward linear arrangement of elements.

There is no question that *L. abottii* belongs in the same genus as *phlaeas* (in fact, the former may be the East African subspecies of *phlaeas*), but there is some question about *cupreus*. Scudder (1876: 125), strictly on the basis of its fiery red coloration above, placed *cupreus* in his genus *Chalceria.* Structurally it simply does not belong there. Sibatani (1974: 109) places it in an unnamed subgenus of *Lycaena* with *L. alciphron* (Rottemburg) and possibly *aeolus* Wyatt (both Palearctic). He may be correct, but for the time being it is thought best to place *cupreus* in *Lycaena* without further subdivision.

## Gaeides Scudder, 1876

*Gaeides* Scudder, 1876: 126. Type-species by original designation *Chrysophanus dione* Scudder, 1868: 330 (=*Polyommatus xanthoides* Boisduval, 1852: 292, subspecies).

Included species: *Polyommatus xanthoides* Boisduval, (1852: 292); *Chrysophanus editha* Mead (1878: 198); *Polyommatus gorgon* Boisduval (1852: 292).

*Gaeides* may We characterized as follows:

Antenna about half length of forewing; comprised of 32-34 segments; club gradual and moderate, occupying terminal quarter (*editha*) to three-tenths (*xanthoides, gorgon*) of antenna. Palpi long, shaggy and semi-porrect to semi-erect; third segment from half to as much as three-fifths (*xanthoides*) length of second.

♂ foreleg (Figs. 24 and 25) relatively more miniaturized than in previous genera with moderately well developed tarsal claw; tibia and tarsus moderately fringed and spined; femur longer than tibia, which in turn is equal to (*gorgon*) to longer (*xanthoides, editha*) than tarsus. ♀ foreleg (Figs. 26 and 27)with tarsus and lower half of tibia spined (especially heavy in *xanthoides*); femur longer than tibia, which in turn is longer (*gorgon*) or shorter (*xanthoides, editha*) than tarsus. First midtarsal subsegment slightly inflated in *gorgon*, but not in others.

Forewing (Figs. 22 and 23) apex quite pointed; veins Rs and $M_1$ nearly connate at

origins (actually connate on a very short stalk in *gorgon*); $Cu_1$ equidistant from $M_3$ and $Cu_2$ in *gorgon*, closer to $M_3$ in other species. Hindwing (Figs. 22 and 23) with "tail" only slightly indicated at end of $Cu_2$ in *xanthoides* and *editha* only; no tornal lobe; Rs and $M_1$ arise separate from one another, closest together in *xanthoides*, furthest apart in *gorgon*; $M_3$ approximate to, but separate from, $Cu_1$ at their origins.

♂ genitalia (Figs. **28, 29** and **30**) with somewhat divergent uncus lobes, not downturned; saccus very short (almost absent in *gorgon*); penis long and slightly downturned; furca massive, well developed and diverted both anteriad and posteriad; valvae broad at base, tapering distad (especially in *gorgon*); internal teeth strong in *xanthoides* and *editha*, fine in *gorgon*.

♀ genitalia (Figs. **31** and **32**) with bulbous sclerotized sterigma ornamented caudally; ductus bursae rather constricted medially and well sclerotized. These structures suggest close relationship with *Chalceria* (see below).

Larval foodplants various, mostly Polygonaceae (Opler, 1975).

Wing pattern clearly polyommatine, but wing shape more produced than in most Blues.

There is no question about the congenericity of *editha* and *xanthoides* (indeed, some authors consider them to be conspecific), but *gorgon* is something of a puzzle. It does not entirely fit *Gaeides* with respect to wing venation or ♂ genitalia, but the ♀ genitalia show a close affinity with *xanthoides*, *editha* and members of *Chalceria*. Scud-
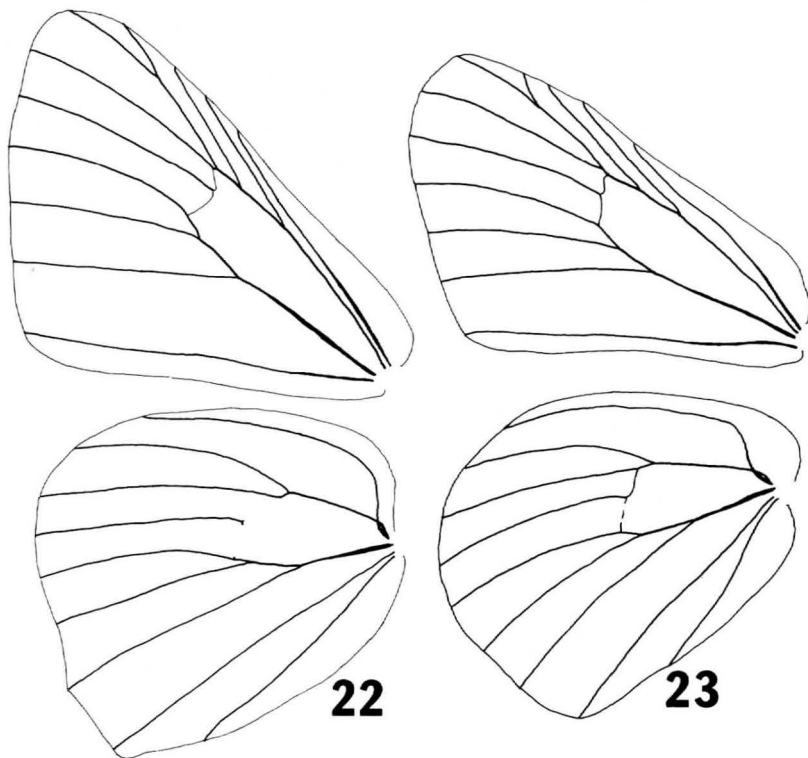


**22**　　　**23**

Figures 22-23: ♂ venation of *Gaeides*. 22, *G. xanthoides xanthoides* (Boisduval); CALIFORNIA: Inyo Co.: SW of Independence (Slide M-3055, Lee D. Miller). 23, *G. gorgon* (Boisduval); CALIFORNIA: Contra Costa Co.: Mt. Diablo (Slide M-3090, Lee D. Miller). Magnifications as in Figs. 1-5.

der (1876: 126) placed *gorgon* in *Gaeides*, but as "Division 2". Perhaps that species tends to unite *Gaeides* and *Chalceria*, but other characteristics such as the ♂ genitalia tend to separate the two. The solution of considering the two genera separate, though closely related, seems best.
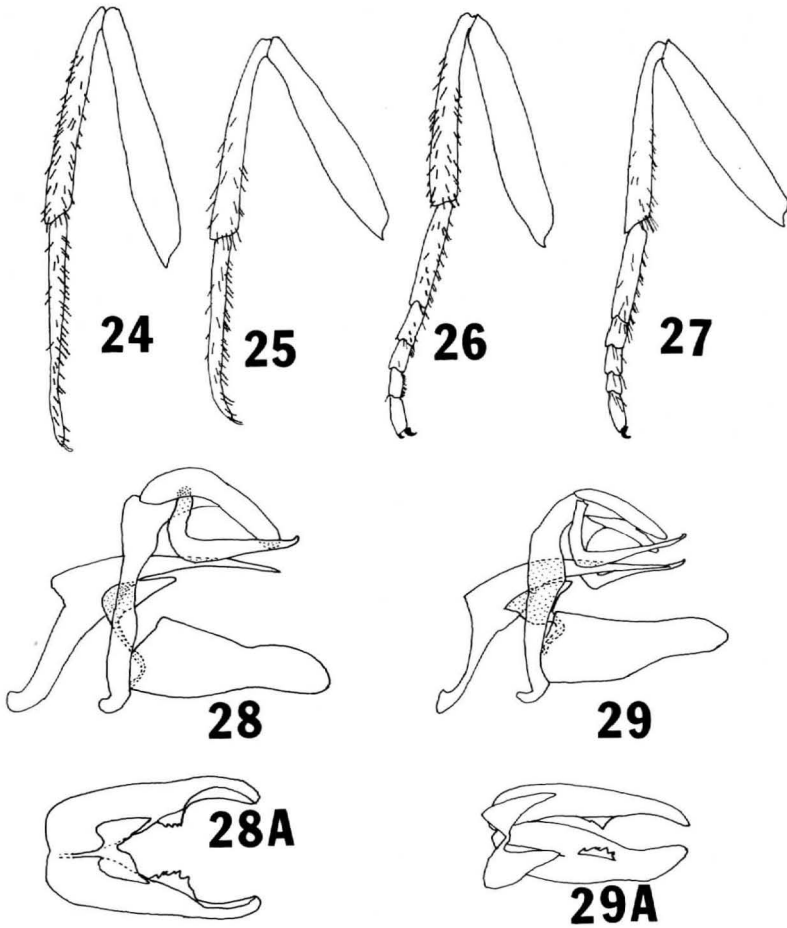


Figures 24-29: forelegs and ♂ genitalia of *Gaeides* species. 24, ♂ forefemur + -tibia + -tarsus of *G. xanthoides xanthoides* (Boisduval); same data as Fig. 22. 25. *G. gorgon* (Boisduval), ♂ forefemur + -tibia + -tarsus; same data as Fig. 23. 26, *G. x. xanthoides*, ♀ forefemur + -tibia + -tarsus; CALIFORNIA: Inyo Co.: SW of Independence (Slide M-3108, Lee D. Miller). 27, *G. gorgon*, ♀ forefemur + -tibia + -tarsus; CALIFORNIA: Contra Costa Co.: Mt. Diablo (Slide M-3116, Lee D. Miller). 28, *G. x. xanthoides*, ♂ genitalia (preparation M-3055-V, Lee D. Miller); same data as Fig. 22. 28A, dorsal view of furca and valvae of same preparation as Fig. 28. 29, *G. editha* (Mead), ♂ genitalia (preparation M-3311-V, Lee D. Miller); OREGON: Crook Co.: Big Summit Prairie. 29A, dorsal view of furca and valvae of same preparation as Fig. 29. Magnifications as in Figs. 1-5.

## Hyllolycaena, new genus

*Chrysophanus* Scudder, 1876: 127, not Hübner, 1818: 18.
Type-species and only species included *Papilio hyllus* Cramer, [1775]: 67-68.

Antenna nearly half length of forewing costa; comprised of 32-34 segments; club fairly stout and occupying terminal three-tenths of antenna. Palpi long and semi-porrect; third segment about five-eighths length of second.

♂ foreleg (Fig. 34) quite miniaturized with a weak claw; tarsus lightly fringed, but tibia poorly spined; femur slightly longer than subequal tibia and tarsus. ♀ foreleg (Fig. 35) with moderately heavily spined tibia and tarsus; femur longer than tibia, which in turn is about equal to tarsus. First midtarsal subsegment not appreciably inflated, if at all.

Forewing (Fig. 33) with a rounded apex; veins Rs and $M_1$ connate at origin on a rather long stalk; $Cu_1$ arises much closer to $M_3$ than to $Cu_2$. Hindwing (Fig. 33) without "tail" or tornal lobe; vein Rs arises well separate from $M_1$; $M_3$ and $Cu_1$ arise well
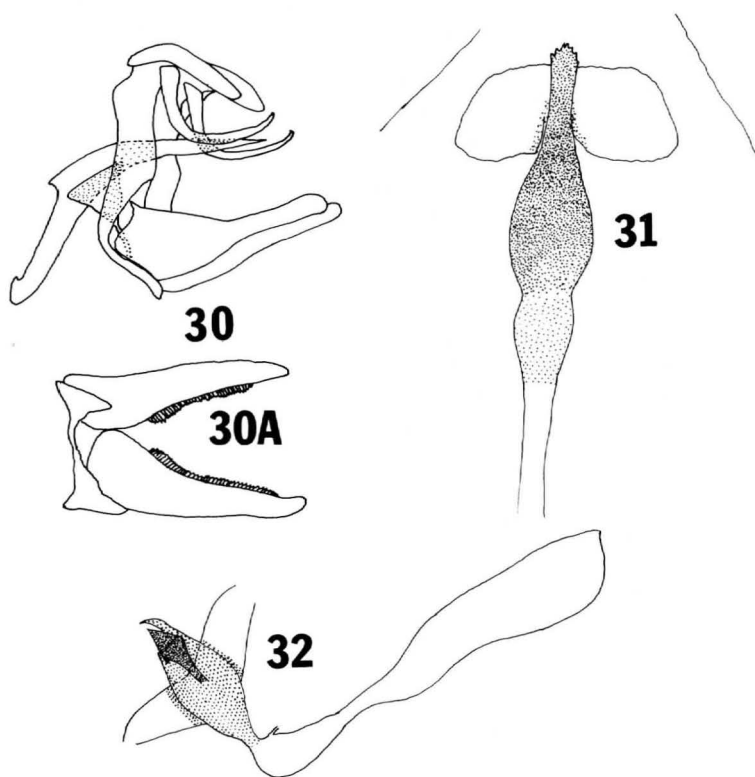


Figures 30-32: genitalia of *Gaeides* species. 30, *G. gorgon* (Boisduval), ♂ genitalia (preparation M-3073-V, Lee D. Miller); same data as Fig. 22. 30A, dorsal view of furca and valvae of same preparation as Fig. 30. 31, *G. xanthoides xanthoides* (Boisduval). ♀ genitalia (preparation M-3321-V, Lee D. Miller); same data as Fig. 26. 32, *G. gorgon*, ♀ genitalia (preparation M-3617-V, Jacqueline Y. Miller); same data as Fig. 27. Magnifications as in Figs. 1-5.

separated.

♂ genitalia (Fig. 36) with slightly divergent straight uncus lobes; saccus almost non-existent; penis long and sharply bent downward; furca small, heavy and well developed; valvae simple and of much the same thickness throughout slightly humped dorsad and lacking terminal or internal teeth.

♀ genitalia (Fig. 37) with strongly sclerotized bulbous sterigma; ductus bursae expanded about its middle.

Foodplant chiefly *Rumex crispus* (Opler, 1975).

Wing pattern and shape very much polyommatine with no linear elements whatsoever.
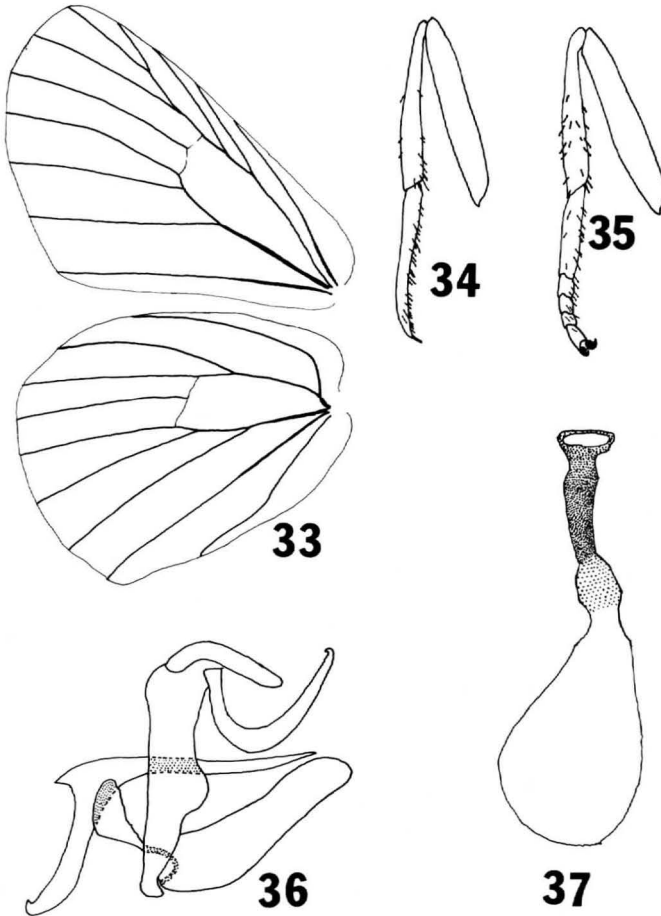


Figures 33-37: *Hyllolycaena hyllus* (Cramer). 33, ♂ venation; ILLINOIS: Cook Co.: Chicago (Slide M-3083, Lee D. Miller). 34, ♂ forefemur + -tibia + -tarsus; same data as Fig. 33. 35, ♀ forefemur + -tibia + -tarsus; ILLINOIS: Cook Co.: Chicago (Slide M-3110, Lee D. Miller). 36, ♂ genitalia (preparation M-3303-V, Lee D. Miller); same data as Fig. 3. 37, ♀ genitalia (preparation M-3611-V, Jacqueline Y. Miller); same data as Fig. 35. Magnifications as in Figs. 1-5.

Superficially *H. hyllus* rather closely resembles *Rapsidia dispar* (Haworth), but surprisingly the genitalia of the two species are not at all comparable. The present species has almost no saccus, whereas that of *dispar* is long and well developed; the valva of *dispar* is of the *Heodes-Lycaena* type (see Higgins, 1975), whereas that of *Hyllolycaena* is more of the *Gaeides* type. The venation suggests a dervied state for the genus, and the pattern itself suggests that *hyllus* probably was derived from a *Gaeides*-like progenitor. The ventral surface pattern of *H. hyllus* and *G. xanthoides dione* (Scudder) are almost identical, only the wing shape being markedly different. Clearly, then, *Hyllolycaena* is a truly American genus, notwithstanding its superficial resemblance to some Palearctic Coppers.

<center>**Chalceria** Scudder, 1876</center>

*Chalceria* Scudder, 1876: 125. Type-species by original designation *Chrysophanus rubidus* Behr, 1866: 208.

Included species: *Chrysophanus rubidus* Behr (1866: 208); *Lycaena ferrisi* Johnson and Balogh (1977:40); *Lycaena heteronea* Boisduval (1852: 298).

*Chalceria* is characterized as follows:

Antenna somewhat less than half length of forewing; comprised of 33-35 segments; club gradual and moderate, occupying terminal third of antenna. Palpi rather long and semi-porrect; third segment half length of second.

♂ foreleg (Fig. 39) rather miniaturized with moderate tarsal claw; tibia and tarsus
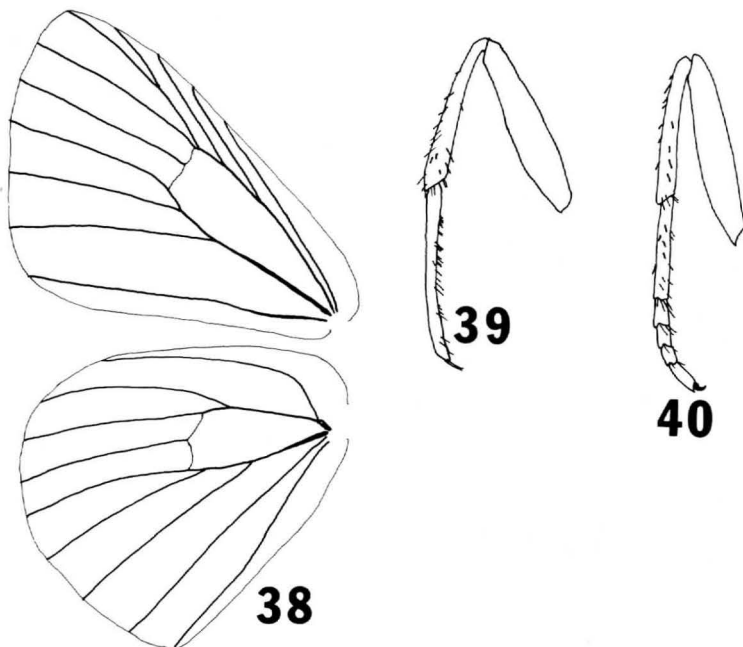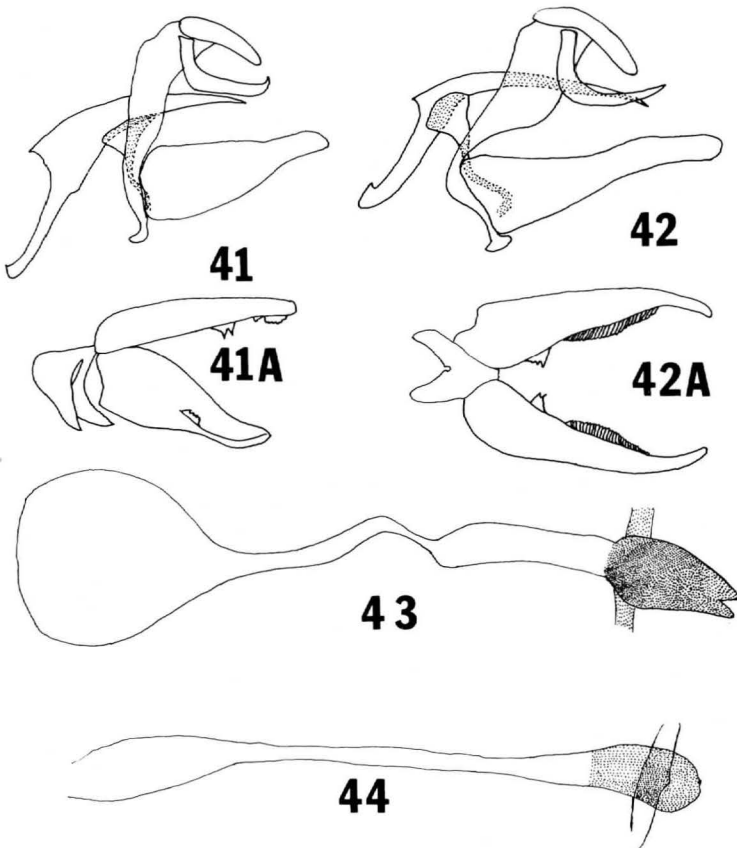


Figures 38-40: *Chalceria rubidus sirius* (W. H. Edwards). 38, ♂ venation; COLORADO: Teller Co.: SW of Florissant (Slide M-3080, Lee D. Miller). 39, ♂ forefemur + -tibia + -tarsus; same data as Fig. 38. 40, ♀ forefemur + -tibia + -tarsus; COLORADO: Teller Co.: SW of Florissant (Slide M-3106, Lee D. Miller). Magnifications as in Figs. 1-5.

lightly fringed and spined; femur longer than tibia, which in turn is equal in length to tarsus. ♀ foreleg (Fig. 40) with tibia and tarsus moderately heavily spined; femur longer than tibia, which in turn is shorter than tarsus. First midtarsal subsegment not inflated.

Forewing (Fig. 38) apex not so acute as that of *Gaeides;* veins Rs and $M_1$ well separated at their origins; $Cu_1$ slightly nearer $M_3$ than $Cu_2$ at origin. Hindwing (Fig. 38) without "tail" or tornal lobe; veins Rs and $M_1$ well separated at origin; $M_3$ arising approximate to, but separate from, $Cu_1$.

♂ genitalia (Figs. 41 and 42) with somewhat divergent uncus lobes that are not downturned; saccus very short, but definite; penis rather long and slightly diverted



Figures 41-44: genitalia of *Chalceria* species. 41, *C. rubidus sirius* (W. H. Edwards), ♂ genitalia (preparation M-3301-V, Lee D. Miller); same data as Fig. 38. 41A, dorsal view of furca and valvae of same preparation as Fig. 41. 42, *C. heteronea heteronea* (Boisduval), ♂ genitalia (preparation M-3302-V, Lee D. Miller); WYOMING: Teton Co.: Snow King Mtn. 42A, dorsal view of furca and valvae of same preparation as Fig. 42. 43, *C. r. sirius,* ♀ genitalia (preparation M-3319-V, Lee D. Miller); same data as Fig. 40. 44, *C. h. heteronea,* ♀ genitalia (preparation M-3320-V, Lee D. Miller); UTAH: Summit Co.: N Fork of Provo River. Magnifications as in Figs. 1-5.

ventrad; furca nearly as massive as that of *Gaeides* and of similar configuration; valvae more or less of same thickness throughout (narrowest in *heteronea*, Fig. 42); no terminal teeth, but internal teeth well developed (especially in *heteronea*, Fig. 42).

♀ genitalia (Figs. 43 and 44) similar to those of *Gaeides;* sterigma very similar to that of *Gaeides* in *rubidus* (Fig. 43), less so in *ferrisi* or *heteronea* (Fig. 44); ductus bursae expanded in sterigmal region and narrowed anteriad, grading from heavily (near ostium bursae) to lightly sclerotized near bursa copulatrix.

Larval foodplants various Polygonaceae.

Wing pattern especially polyommatine with no influx of thecline characters.

Johnson and Balogh (1977) monographed "*Lycaena rubidus*", describing a number of subspecies and the sibling species *ferrisi*. They illustrated schematic male and female genitalia which showed the obvious similarity of these structures between *rubidus* and *heteronea*. Still, no one seems to have placed *heteronea* with these other members of the genus — in fact, for many years *heteronea* stood as an aberrant Blue in the literature. The implication here is that the blue upper surface color in *heteronea* and the fiery red dorsal surface of *rubidus* and *ferrisi* somehow outweighed the obviously similar under surface pattern and genitalic affinities for these other workers. In fact, the scales that produce the blue color of *heteronea* are only slightly different in their ridge lines to the scales that produce the reddish color in *rubidus* and its allies. The male genitalia are far more similar between all of these species than are the female terminalia, but all three species appear to be one another's closest relatives.

## Epidemia Scudder, 1876

*Epidemia* Scudder, 1876: 127. Type-species by original designation *Polyommatus epixanthe* Boisduval and Leconte, [1833]: 127.

Included species: *Polyommatus epixanthe* Boisduval and Leconte ([1833]: 127); *Polyommatus helloides* Boisduval (1852: 291); *Lycaena dorcas* W. Kirby (1837:299); *Polyommatus nivalis* Boisduval (1869: 44); *Polyommatus mariposa* Reakirt (1866: 149).

*Epidemia* is characterized as follows:

Antenna somewhat less than length of forewing; comprised of 30-35 segments; club usually stout to fairly stout (but gradual and moderate in *helloides*) and occupies distal quarter to three-tenths of antenna. Palpi of moderate length and semi-erect; third segment usually half as long as second (five-eighths as long in *nivalis*, but less than half as long in *mariposa*).

♂ foreleg (Figs. 47 and 48) quite minaturized with very weak claw; tarsus and lower half of tibia usually weakly (but moderately in *dorcas*, Fig. 48) spined and fringed; femur usually longer than tibia, which in turn is usually longer than tarsus (all segments subequal in *helloides*). ♀ foreleg (Figs. 49 and 50) about as miniaturized as that of ♂ with moderate spinosity; femur longer than tibia, which in turn is longer than or equal to tarsus. Basal midtarsal subsegment not at all inflated.

Forewing (Figs. 45 and 46) with rounded apex (especially in *epixanthe*); veins Rs and $M_1$ connate at origins, frequently on a short stalk; $Cu_1$ arising somewhat nearer $M_3$ than $Cu_2$ (often nearly midway between them). Hindwing (Figs. 43 and 44) lacking "tail" or tornal lobe; veins Rs and $M_1$ well separated at their origins; $M_3$ and $Cu_1$ approximate, but separate, at their origins.

♂ genitalia (Figs. 51, 52, 53 and 54) with divergent uncus lobes (less so in *mariposa*); saccus almost absent (very slightly developed in *mariposa*); penis slightly downturned and not extremely long; furca well developed, but not so well as in *Gaeides*, etc.; valvae narrowed throughout, usually knobbed distally (except in *epixanthe*), without terminal or internal teeth.

♀ genitalia (Figs. 55 and 56) less heavily sclerotized than in other Coppers; sterigma usually simple (most complicated in *epixanthe*, Fig. 55; ductus bursae not heavily sclerotized (heaviest in *mariposa*) and more or less straight and uncomplicated.

Larval foodplants vary with the species; most on Polygonaceae, but Rosaceae (dor-

*cas)* and Ericaceae *(epixanthe)* also frequently utilized.

Pattern and wingshape distinctly polyommatine.

They have been perhaps the most "successful" American lycaenines, having ex-
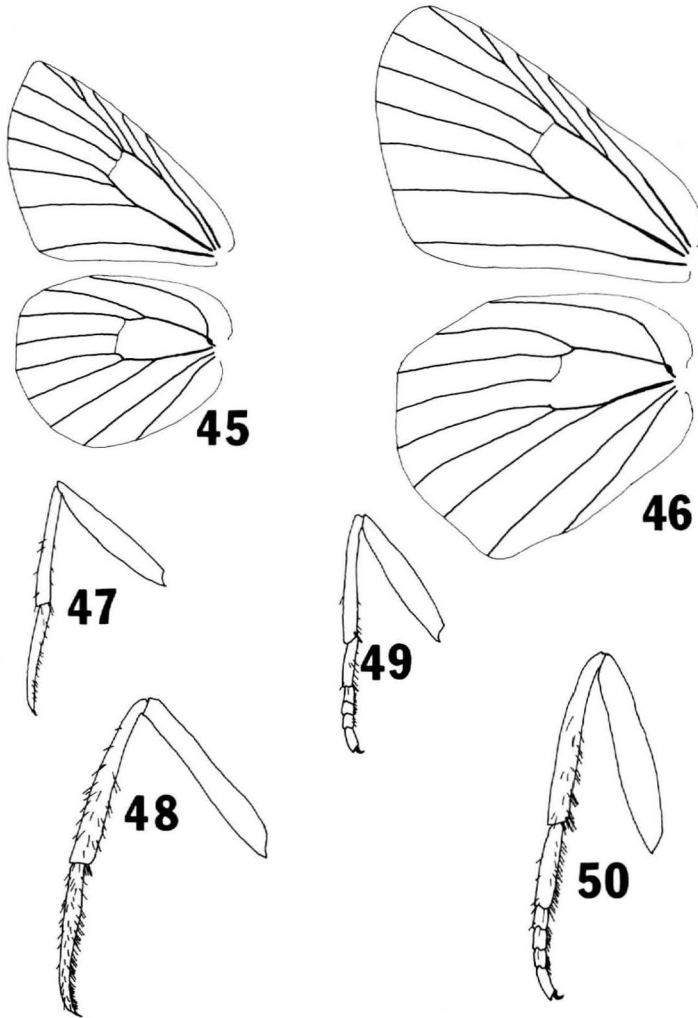


Figures 45-50: venation and forelegs of *Epidemia* species. 45, *E. epixanthe phaedra* (Hall), ♂ venation; NOVA SCOTIA: vic. Big Indian Lake, Halifax (Slide M-3087, Lee D. Miller). 46, *E. helloides* (Boisduval), ♂ venation; CALIFORNIA: Sacramento Co.: N of Sacramento (Slide M-3089, Lee D. Miller). 47, *E. e. phaedra*, ♂ forefemur + -tibia + -tarsus; same data as Fig. 45. 48, *E. dorcas dospassosi* (McDunnough), ♂ forefemur + -tibia + -tarsus; NEW BRUNSWICK: Bathurst (Slide M-3088, Lee D. Miller). 49, *E. e. phaedra*, ♀ forefemur + -tibia + -tarsus; NEW BRUNSWICK: Grande Anse (Slide M-3113, Lee D. Miller). 50, *E. d. dospassosi*, ♀ forefemur + -tibia + -tarsus; NEW BRUNSWICK: Bathurst (Slide M-3114, Lee D. Miller). Magnifications as in Figs. 1-5.

ploited a variety of niches (old fields, salt marshes, cranberry bogs, forests, *etc.*) and evolved into an array of closely related organisms. *E. dorcas* and *helloides* are especially closely allied, and more than one worker has suggested their conspecificity. These two insects are more clearly separated ecologically than morphologically, but the idea of conspecificity is denied by the morphology of the micropylar region of the eggs (Fig. 57,
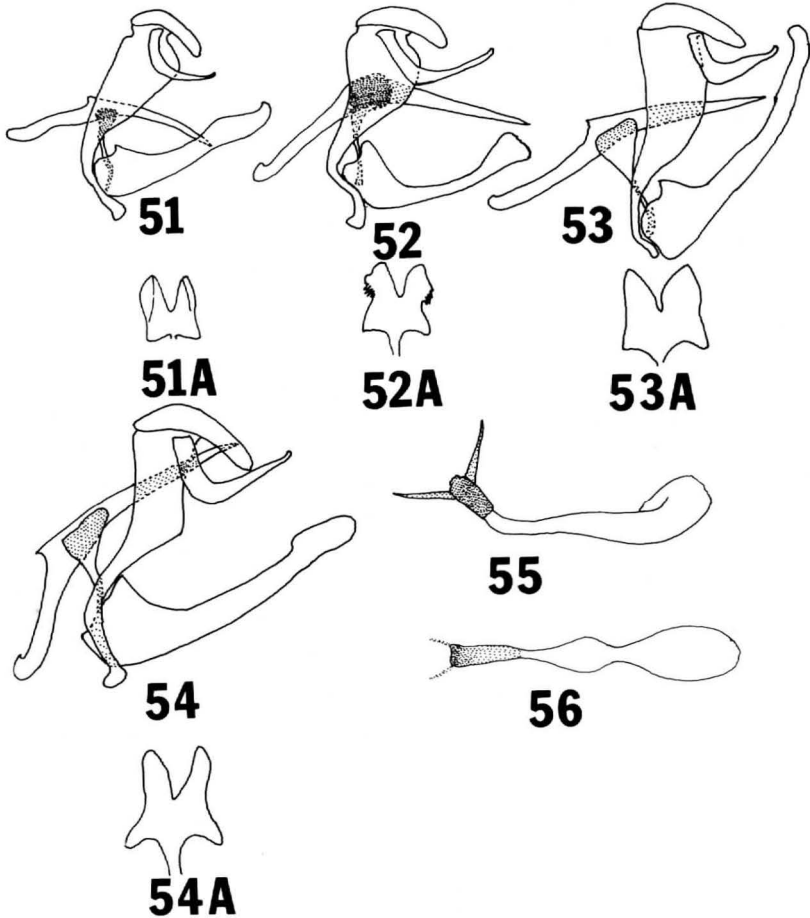


Figures 51-56: genitalia of *Epidemia* species. 51, *E. epixanthe phaedra* (Hall), ♂ genitalia (preparation M-3307-V, Lee D. Miller); same data as Fig. 45. 51A, spread out furca of same preparation as Fig. 51. 52, *E. n. nivalis* (Boisduval), ♂ genitalia (preparation M-3310-V, Lee D. Miller); CALIFORNIA: Mono Co.: Saddlebag Lake. 52A, spread out furca of same preparation as Fig. 52. *E. helloides* (Boisduval), ♂ genitalia (Preparation M-3308-V, Lee D. Miller); same data as Fig. 46. 53A, spread out furca of same preparation as Fig. 53. 54, *E. mariposa mariposa* (Reakirt), ♂ genitalia (preparation M-3309-V, Lee D. Miller); CALIFORNIA: Siskiyou Co.: vic. Toad Lake. 54A, *E. e. phaedra*, ♀ genitalia (Preparation M-3613-V, Jacqueline Y. Miller); same data as Fig. 49. 56, *E. m. mariposa*, ♀ genitalia (preparation M-3616-V, Jacqueline Y. Miller); CALIFORNIA: Shasta Co.: Castle Lake. Magnifications as in Figs. 1-5.

*helloides,* **58,** *dorcas).* The two insects are undeniably one another's closest relatives, but separable (Ferris, 1977).

Probably the most aberrant *Epidemia* is the type-species, *epixanthe,* but the relationships shown by many other characteristics far out weigh the comparative shapes of the valvae of the various species. On balance, *Epidemia* is a tightly knit assemblage of Coppers, one of the most easily seen natural groups within the subfamily.

<div align="center">

**Hermelycaena,** new genus

</div>

*Tharsalea* Scudder, 1876: 125, in part.

Type-species and only species included *Chrysophanus hermes* W. H. Edwards, 1870: 21.

Antenna somewhat less than half length of forewing; comprised of 31 segments; club moderate and gradual, occupying terminal three-tenths of antenna. Palpi of moderate length and semi-erect; third segment four-sevenths length of second.

♂ foreleg (Fig. **60**) quite miniaturized with a moderate claw; tarsus well fringed, lower half of tibia moderately fringed and spined; femur longer than tibia, which in turn is considerably longer than tarsus. ♀ foreleg (Fig. **61**) about as miniaturized as that of ♂ and only lightly spined; femur longer than tibia, which in turn is longer than tarsus. Basal midtarsal subsegment not inflated.

Forewing (Fig. **59**) apex rather acute; veins Rs and $M_1$ arising approximately, but separate; $Cu_1$ arising much nearer $M_3$ than $Cu_2$. Hindwing (Fig. **59**) tailed at end of $Cu_2$, but tornal lobe absent to faintly indicated; veins Rs and $M_1$ well separated at their
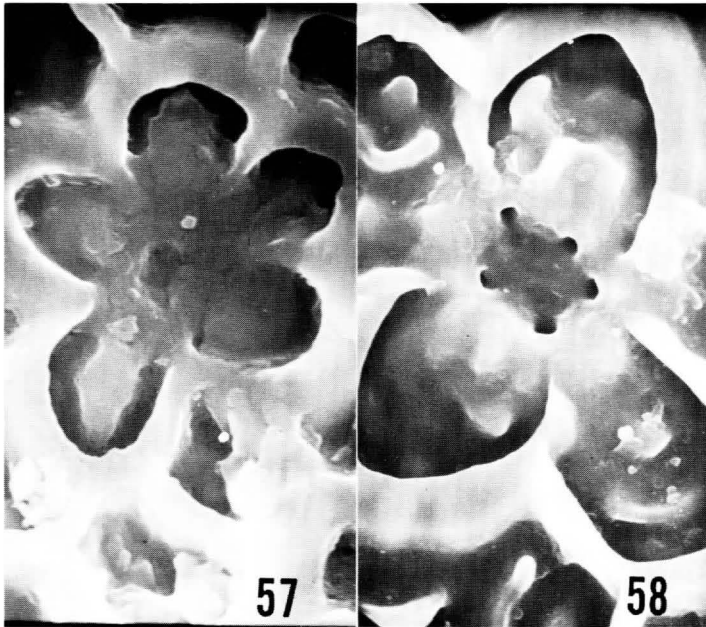


Figures 57-58: micropylar regions of ova of *Epidemia helloides* (Boisduval) (57, Allyn Museum SEM 0898) and *dorcas* (W. Kirby) (58, Allyn Museum SEM 0888). Both pictures are 2000x magnification and demonstrate the micropylar differences between these two very similar species.

origins; $M_3$ and $Cu_1$ approximate at origins, but separate.

$\male$ genitalia (Fig. 62) with somewhat divergent uncus lobes that are not downturned; saccus almost non-existent; penis moderately long and downturned; furca rather weakly developed; valvae elongate and bent ventrad at tips; no terminal valval teeth; internal teeth of valvae well developed and asymmetrical, more or less fitting together.

$\female$ genitalia (Fig. 63) with rather bipartite sterigmal region; ductus bursae slender, straight and rather lightly sclerotized.

Foodplant *Rhamnus* (Rhamnaceae) (T. & J. Emmel, 1973: 62-63).

Wing shape rather "*Thecla*-like", but the pattern is highly modified, neither polyommatine or eumaeine.

It is difficult to relate *H. hermes* with any other Copper, American or Old World. It is certainly our most aberrant species and seems to embody characteristics from virtually all other lycaenine genera. The female genitalia are reminiscent of those of *Lycaena*, the male genitalia of *Epidemia;* but the pattern and venation resemble no other genus closely. Perhaps this species is our most highly evolved Copper.
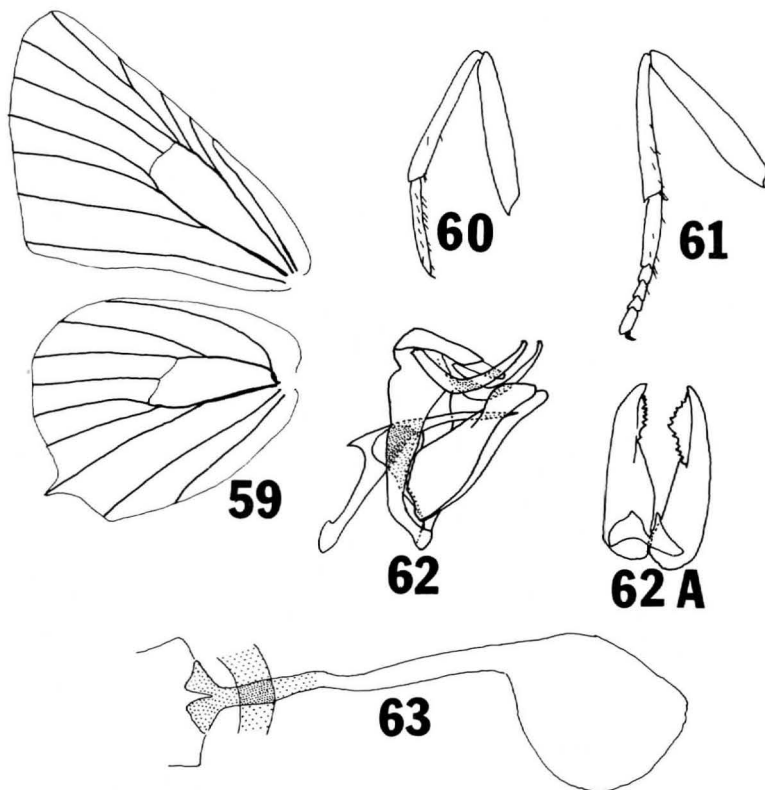


Figures 59-63: *Hermelycaena hermes* (W. H. Edwards). 59, $\male$ venation; CALIFORNIA: San Diego Co.: Suncrest (Slide M-3094, Lee D. Miller). 60, $\male$ forefemur + -tibia + -tarsus; same data as Fig. 59. 61, $\female$ forefemur + -tibia + -tarsus; CALIFORNIA: San Diego Co.: Mission Gorge (Slide M-3120, Lee D. Miller). 62, $\male$ genitalia (preparation M-3312-V, Lee D. Miller); same data as Fig. 59. 62A, dorsal view of furca and valvae of same preparation as Fig. 62. 63, $\female$ genitalia (preparation M-3621-V, Jacqueline Y. Miller); same data as Fig. 61. Magnifications as in Figs. 1-5.

## PHYLOGENETIC AND ZOOGEOGRAPHIC CONSIDERATIONS

To develop a phylogeny solely from the structures of modern species is dangerous and possibly foolhardy. Yet, it is done by many conservative students of both plants and animals. Our speculations are based upon a broad knowledge of the structures of Lycaeninae on a worldwide basis, a considerable knowledge of present-day distribution, knowledge of the paleontology of butterflies in general and an understanding of current concepts of crustal plate mechanics.

It appears to us that the American lycaenine fauna is rooted in three ancient ancestral lines, plus one very modern one. It is our belief that *Lycaena phlaeas* was added to our fauna during the Pleistocene by migration across the Bering Sea land bridge. Its congenor, *cupreus*, has been here long enough to evolve structural features sufficiently distinct from Old World *Lycaena* for Sibatani (1974) to ponder the usefulness of a separate genus or subgenus for it. We see these differences, but hesitate to name the genus, and actually have some questions about the advisability of separating *cupreus* from *Lycaena*.

The three ancient roots are those that lead to *Iophanus*, *Hermelycaena* and the *Tharsalea*-related genera. Of these, *Iophanus* seems to represent the least progressive development from the initial American root. *Hermelycaena* is puzzling with its mixture of features that seem to be drawn from many genera and may represent the modern derivation of the ancient Old World root of the Lycaeninae. The *Tharsalea*-related genera appear to us to have been derived from a common stem with *Iophanus* and to have evolved in the New World. We would place the origin of the *Tharsalea-Iophanus* split from the *Hermelycaena* stem in the Old World.

How did these American genera reach our hemisphere and when? Our guesses
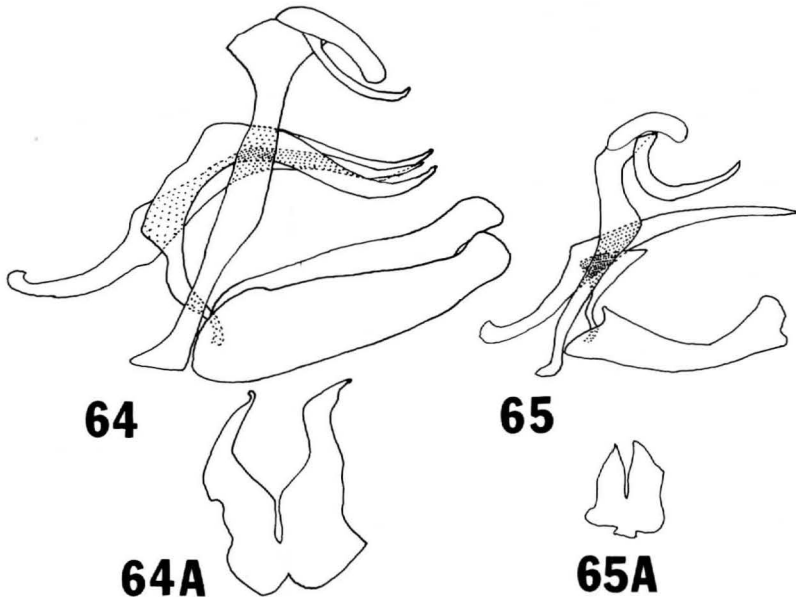


Figures 64-65: ♂ genitalia of Palearctic Lycaeninae. 64, *Thersamonia thersamon* (Esper); no locality data (preparation M-3200-V, Lee D. Miller). 64A, spread out furca of same preparation as Fig. 64. 65, *Phoenicurusia phoenicurus* (Lederer); RUSSIA: Aschenabad (preparation M-3195, Lee D. Miller). 65A, spread out furca of same preparation as Fig. 65. Magnifications as in Figs. 1-5.

about this are based on the very limited number of butterfly fossils known and upon the current concepts of the migration of the American crustal plates. Recent work by Durden (1978) has shown that the Lycaenoidea pre-date Eocene time. He found valid Riodinidae among fossils collected from the Eocene Green River shales of Colorado. Thus we must assume that Lycaenidae also was extant at that time. The split between the lycaenoid families probably dates from late Cretaceous. That was a stirring time for the holarctic landmass. North America drifted away from Europe and northwestern Africa. Thus, it appears to us that the root taxa for most American Lycaeninae were denizens of the portion of drifting crust that we now call North America. They did *not* migrate to the New World. The New World did the migrating!

Once isolation took place, evolution led to our modern fauna. Through those 100 million years many genera and species evolved, flourished and died. The lycaenids we know today are remnants of that long history of the American fauna. As yet we have found no lycaenid fossils, and it would be most helpful to have some from the mid-Tertiary. Perhaps when excavation is resumed at the Florissant Fossil Beds National Monument a future reviewer of butterflies will have fossil evidence from the middle of the evolutionary "tree".

Figure 67 explains our current ideas. We believe that both the *Hermelycaena* and *Iophanus* stems lost all branches but one during the Tertiary Period. On the other hand, the *Tharsalea* branch proliferated and its offspring found the developing continent emminently suited to its survival. Early in the development of this root there was a branching. One ramus led to *Tharsalea*, losing any branches that may have occurred before today. The other we believe led directly to *Chalceria* and retains some of the branches developed during the Tertiary Period. First *Gaeides-Hyllolycaena* broke away and later gave rise to the modern genera *Gaeides* and *Hyllolycaena*. Probably earlier the branching that developed that pair of genera, *Epidemia* split from the *Chalceria* ramus. Of course, all of this is guesswork, but it is educated guesswork. It is what we currently think.

It may be interesting to point out that *Iophanus*, at least America's most
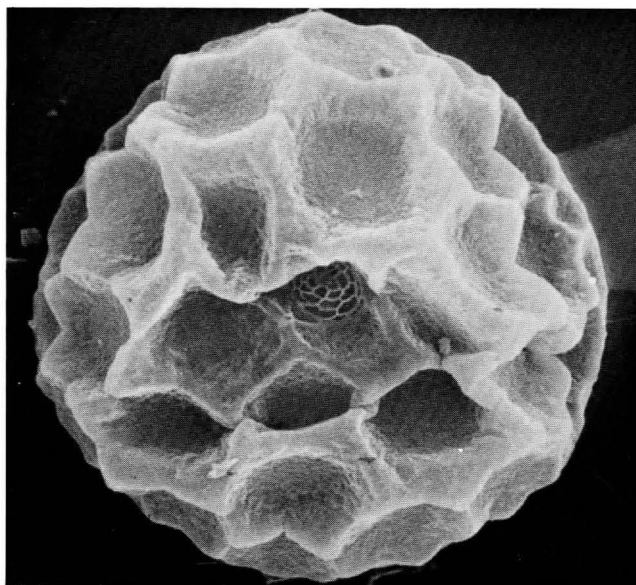


Figure 66: scanning electron micrograph of the egg of *Lycaena phlaeas americana* (Harris) taken at 130x (Allyn Museum SEM 1028).

"primitive" Copper, *Anetia*, the most "primitive" danaid and *Baronia*, the most primitive papilionid, are found in the state of Chiapas, Mexico. A *Baronia*-like genus dates from the Eocene of Colorado and has suggested to us the initial time for our "roots".

## A REVISED CHECK-LIST OF THE AMERICAN LYCAENINAE

### LYCAENINAE

**Iophanus** Draudt, 1920. Type: *pyrrhias* (Godman & Salvin, [1887])
1. **pyrrhias** (Godman & Salvin, [1887])
**Tharsalea** Scudder, 1876. Type: *arota* (Boisduval, 1852)
2. **arota** (Boisduval, 1852)
  a. **a. arota** (Boisduval, 1852).
  b. **a. nubila** (J. A. Comstock, 1926)
  c. **a. virginiensis** (W. H. Edwards, 1870)
  d. **a. schellbachi** (Tilden, 1955)
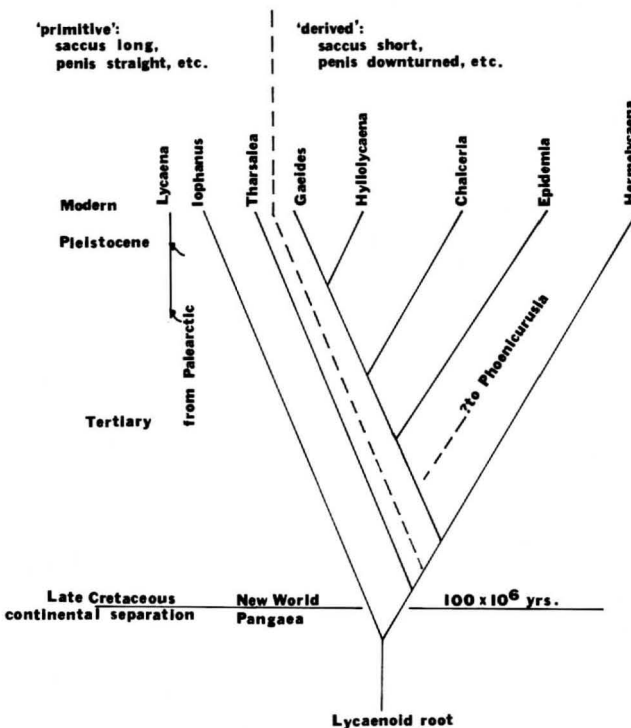**Lycaena** Fabricius, 1807. Type: *phlaeas* (Linnaeus, 1761)[2]



Figure 67: a possible phylogenetic chart for the New World Lycaeninae. Various points referring to this figure may be found in the text. The time schemes are approximate.

[2]dos Passos (1964: 60) gives *Heodes* Dalman, 1816, and *Chrysoptera* Zincken, 1817, as synonyms of *Lycaena*. Actually, *Heodes* is a valid Palearctic generic name and *Chrysoptera* its synonym. Accordingly, both names are deleted from American lists.

‡*Lycia* Sodovskii (not Hübner, [1825]), 1837
‡*Migonitis* Sodovskii (not Rafinesque, 1815), 1837
*Rumicia Tutt, 1906*
*Chrysophanus* of authors, not Hübner, 1818
*Heodes* of authors, not Dalman, 1816
*3. phlaeas (Linnaeus, 1761)
    many Palearctic synonyms not included here
    a. p. americana Harris, 1862
       *bacchus* (Scudder, 1889)
       *hypophlaeas* of authors, not (Boisduval, 1852)
         ab. "fasciata" (Strecker, 1878)
         ab. "fulliolus" (Hulst, 1886)
           *neui* (Rummel, 1928)
         ab. "obliterata" (Scudder, 1889)
           *caeca* (Reiff, 1913)
           *obsoleta* (Barnes & McDunnough, 1917), *lapsus*
           *adrienne* (Baynard, 1891)
         ab. "octomaculata" (Dean, 1918)
         ab. "banksi" (Watson & W. P. Comstock, 1920)
           *fulvus* (Rummel, 1928)
    b. p. feildeni (M'Lachlan, 1878)
       *fieldeni* Dyar, 1902, *lapsus*
    c. p. arethusa (Wolley-Dod, 1907)
    d. p. arctodon Ferris, 1974
    e. p. hypophlaeas (Boisduval, 1852)
4. cupreus (W. H. Edwards, 1870)
    a. c. cupreus (W. H. Edwards, 1870)
         ab. "maculinita" (Gunder, 1926)
    b. c. snowi (W. H. Edwards, 1881)
         ab. "mcdunnoughi" (Gunder, 1927)
           *macdunnoughi* dos Passos, 1964, emendation
    c. c. henryae (Cadbury, 1937)
**Gaeides** Scudder, 1876. Type: *dione* (Scudder, 1868), ssp. of *xanthoides* (Boisduval, 1852)
5. xanthoides (Boisduval, 1852)
    a. x. xanthoides (Boisduval, 1852)
         f. "luctuosa" (Watson & W. P. Comstock, 1920)
    b. x. dione (Scudder, (1868)
         ab. "gibboni" (Gunder, 1927)
6. editha (Mead, 1878)
    a. e. editha (Mead, 1878)
         ab. "vanduzeei" (Gunder, 1927)
    b. e. montana (Field, 1936)
7. gorgon ((Boisduval, 1852)
**Hyllolycaena** L. Miller & F. M. Brown, 1979. Type: *hyllus* (Cramer, 1775)
    *Chrysophanus* Scudder (not Hübner, 1818), 1876
8. hyllus(Cramer, 1775)
    *thoe* (Guérin-Ménéville, [1831])
         ab. "wyatti" (Gunder, 1927)
         ab. "wormsbacheri" (Gunder, 1927)
**Chalceria** Scudder, 1876. Type: *rubidus* (Behr, 1866)
9. rubidus (Behr, 1866)
    a. r. rubidus (Behr, 1866)
    b. r. duofacies (K. Johnson & Balogh, 1977)
    c. r. perkinsorum (K. Johnson & Balogh, 1977)
    d. r. longi (K. Johnson & Balogh, 1977)

e. **r. sirius** (W. H. Edwards, 1871)
f. **r. monachensis** (K. Johnson & Balogh, 1977)
10. **ferrisi** (K. Johnson & Balogh, 1977)
11. **heteronea** (Boisduval, 1852)
   a. **h. heteronea** (Boisduval, 1852)
   *gravenotata* (Klots, 1930)
   *klotsi* (Field, 1936)
      ab. "coloradensis" (Gunder, 1925)
   b. **h. clara** (Hy. Edwards, 1877)
**Epidemia** Scudder, 1876. Type: *epixanthe* (Boisduval & Leconte, [1833])
12. **epixanthe** (Boisduval & Leconte, [1833])
   a. **e. epixanthe** (Boisduval & Leconte, [1833])
   *hypoxanthe* (W. F. Kirby, 1862)
   b. **e. amicetus** Scudder, 1876
   c. **e. phaedra** (Hall, 1924)
   d. **e. michiganensis** (Rawson, 1948)
13. **dorcas** (W. Kirby, 1837)
   a. **d. dorcas** (W. Kirby, 1837)
   *anthelle* (Westwood, 1847)
   b. **d. castro** (Reakirt, 1866)
   c. **d. florus** (W. H. Edwards, 1873)
      ♀ f. "hulbirti" (Field, 1936)
      ♀ f. "sternitzkyi" (Field [not Gunder, 1927], 1936)
   d. **d. dospassosi** (McDunnough, 1940)
   e. **d. claytoni** (Brower, 1940)
   f. **d. megaloceras** Ferris, 1977
   g. **d. arcticus** Ferris, 1977
14. **helloides** (Boisduval, 1852)
   *halloides* (McDunnough, 1914), *lapsus*
      ab. "williamsi" (Gunder, 1927)
      ab. "sternitzkyi" (Gunder, 1927)
      ab. "gunderi" (Rudkin, 1932)
15. **nivalis** (Boisduval, 1869)
   a. **n. nivalis** (Boisduval, 1869)
   *ianthe* (W. H. Edwards, 1871)
   b. **n. browni** (dos Passos, 1938)
16. **mariposa** (Reakirt, 1866)
   a. **m. mariposa** (Reakirt, 1866)
   *zeroe* (Boisduval, 1869)
   b. **m. charlottensis** (Holland, 1930)
   c. **m. penroseae** (Field, 1938)
   *penrosae* (F. M. Brown, Eff & Rotger, 1955), *lapsus*
**Hermelycaena** L. Miller & F. M. Brown, 1979. Type: *hermes* (W. H. Edwards, 1870)
   *Tharsalea* Scudder, 1876, in part
17. **hermes** (W. H. Edwards, 1870)
   *delsud* (W. G. Wright, 1905)


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