



AN EVOLUTIONARY SUBSPECIFIC ASSESSMENT OF *DECIDUPHAGUS HENRICI* (LYCAENIDAE) BASED ON ITS UTILIZATION OF *ILEX* AND NON-*ILEX* HOSTS: DESCRIPTION OF A THIRD *ILEX* ASSOCIATED SUBSPECIES. DESIGNATION OF A NEOTYPE AND TYPE LOCALITY FOR *DECIDUPHAGUS IRUS*.

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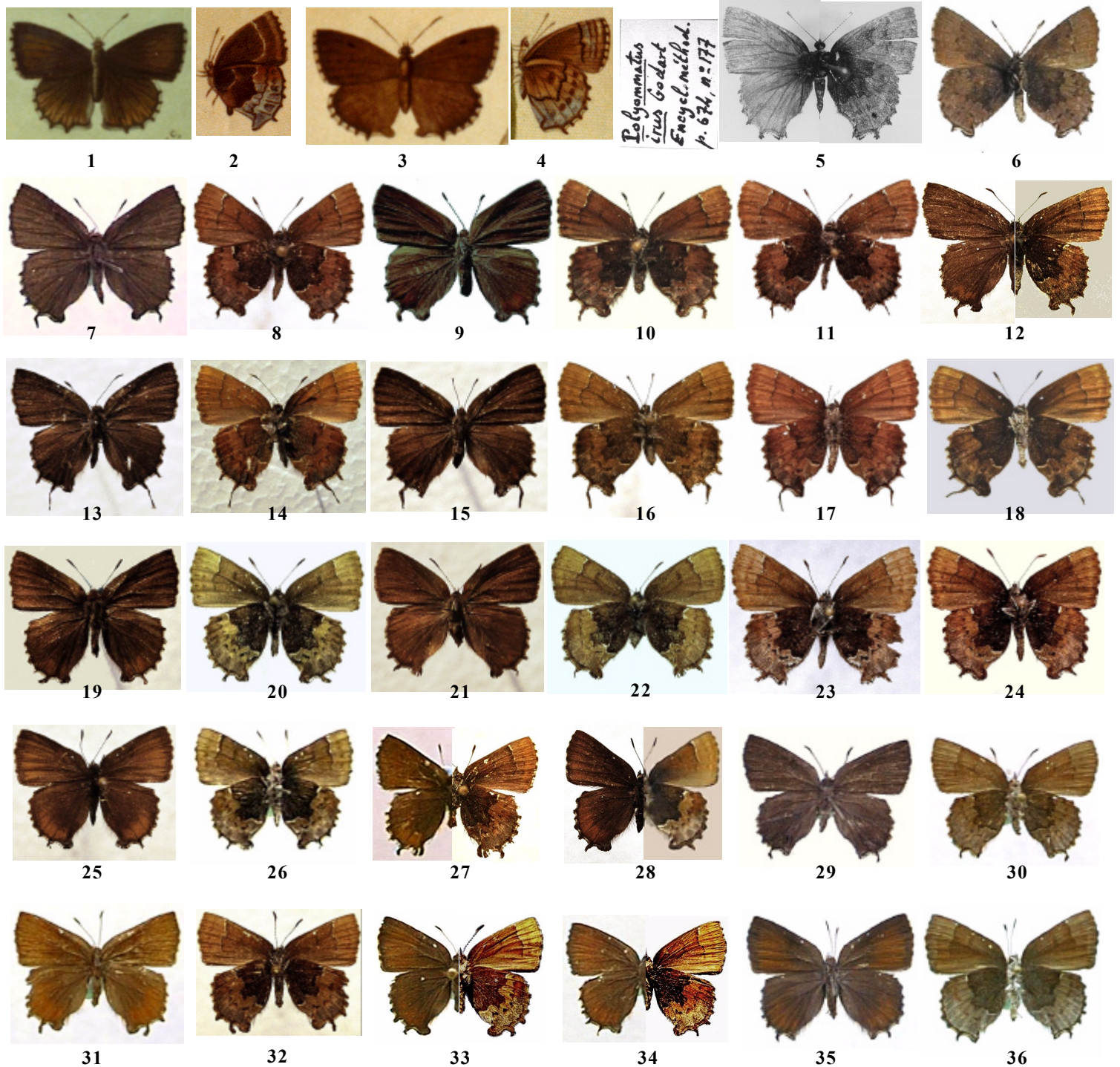
ABSTRACT. *Deciduphagus henrici* subsists as six subspecies which have evolved into two distinct larval host associated groups of three taxa each. **Group one** is composed of those taxa which utilize primarily *Ilex* (holly – various species) as their host. They inhabit the non-montane area of the southeastern United States and up the Atlantic coast to at least southern New Jersey. They are: *D. h. margaretae* (TL Deland, Volusia Co., FL) occupying east-coastal to south central Florida; *D. h. viridissima* (TL Nag’s Head, Dare Co., NC) occupying the upper Outer Banks area of NC north through the Chesapeake and Delaware Bays to perhaps Rhode Island; and a new subspecies herein described as *D. h. yahwehus* (TL Orangeburg Co., SC) occupying the area from south central North Carolina south through Georgia then westward to perhaps Mississippi and the upper west coast of Florida. This *Ilex* host association is believed to be peri-Pleistocene and Floridian in origin. **Group two** consists of two subspecies which use primarily non-*Ilex* plants, and one taxon which is oligophagous (including *Ilex*). The primarily non-*Ilex* subspecies are: *D. h. solatus* (TL Blanco Co., TX) occupying south central Texas westward; *D. h. turneri* (TL Cowley Co., KS) occupying the area from north Texas northeast to at least Indiana; and (the oligophagous) *D. h. henrici* (TL Philadelphia, PA) occupying southeastern Canada south through the Appalachians. Nominate *D. h. henrici* is the most recently evolved of the six *henrici* subspecies. In parts of the northeastern U.S. *D. h. henrici* is in tension with *D. h. viridissima*, both phenotypically and biologically. *D. henrici* and *D. irus* were often confused. To stabilize the taxonomy, the false holotype of *D. irus* is designated as neotype. Its type locality is restricted to southern NJ.

Additional key words: sibling species, original descriptions.

EARLY HISTORICAL AND BIOLOGICAL INFORMATION

John Abbot found two species of *Deciduphagus* Johnson (1992) in coastal Georgia. Abbot sent his paintings and life history information regarding these taxa to Boisduval and Leconte who in 1833 published Abbot’s renditions and information. Today, we know these species as *Deciduphagus henrici* (Grote & Robinson, 1867) and *Deciduphagus irus* (Godart, 1824) (see appendix). However, at the time of Boisduval and Leconte’s publication, *henrici* had not yet been described, and Godart had only recently described *Polyommatus irus* from a single male specimen, of uncertain origin, which he had deposited in the Museum Nationale, Paris (see appendix). Thus, upon the receipt of Abbot’s paintings and information, Boisduval and Leconte had to determine which of Abbot’s depictions was Godart’s *P. irus* and which was an undescribed species. After examining Godart’s type (which they said was so “defected by dilapidation, it would not have been possible to recognize this type, if we had not seen it”), they determined one Abbot species to be Godart’s *irus* (Figs. 1-2) and described the other as a new species, *Thecla arsace* Boisduval and Leconte (Figs. 3-4). However, they associated the wrong Abbot species with Godart’s *irus*.

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Figs. 1-36. 1-2 (d/v), ♂ *Thecla irus* (=henrici) reproduced from Boisduval & Leconte 1833. 3-4 (d/v), ♂ *Thecla arsace* from Boisduval & Leconte 1833. 5 (d/v), false ♂ holotype *Polyommatus irus* herein designated as neotype. 6 (v), ♂ topotype *D. irus*, 15 May 1971, Lakehurst, Ocean Co., NJ, leg. Stanford. 7-8 (d/v), ♂ holotype *D. h. yahwehus*, 10 March 1994, Nr. Bull Swamp, Orangeburg Co., SC. 9-10 (d/v), ♀ allotype *D. h. yahwehus*, same data as 7. 11 (v), ♂ *D. h. yahwehus*, 29 March 1986, Edisto Is., Colleton Co., SC. 12 (d/v), red HW ♂ *D. h. yahwehus*, 19 March 1977, Ft. Stewart, Bryan Co., GA. 13-14 (d/v), ♂ topotype *D. h. margaretae*, 7 March 1976, Deland, Volusia Co., FL. 15-16 (d/v), ♀ topotype *D. h. margaretae*, same data as 13. 17 (v), topotype ♂ *D. h. margaretae*, 9 March 1975, Deland, Volusia Co., FL. 18 (v), dark topotype ♀ *D. h. margaretae*, same data as 17. 19-20 (d/v), ♂ holotype *D. h. viridissima*, 3 April 1991, Bodie Is. lighthouse, Dare Co., NC, leg. Pavulaan. 21-22 (d/v), ♀ allotype *D. h. viridissima*, same data as 19. 23 (v), ♂ int. morph *D. h. viridissima*, 15 April 1992, Sussex Co., DE, leg. Pavulaan. 24 (v), ♂ brown morph *D. h. viridissima*, same data as 23. 25-26 (d/v), ♂ *D. h. turneri*, 21 April 1979, Ernie Miller Pk., Johnson Co., KS, leg. unknown. 27 (d/v), ♂ *D. h. henrici*, 10 April 1977, Lee Co., VA, leg. Hyatt. 28 (d/v), ♂ *D. h. henrici*, 29 April 1988, Great Swamp, Washington Co., RI, leg. Pavulaan. 29-30 (d/v), ♂ topotype *D. h. solatus*, 24 February 1976, 8 Mi. E. of Blanco, Blanco Co., TX, leg. unknown. 31-32 (d/v), ♀ *D. h. turneri*, 18 March 1973, Tyler, Smith Co., TX, leg. unknown. 33 (d/v), ♀ *D. h. turneri*, 8 March 1987, Nr. Dow, Pittsburg Co., OK, leg. unknown. 34 (d/v), ♀ *D. h. turneri*, 6 May 1975, Zaleski St. For., Vinton Co., OH, leg. Parshall. 35-36 (d/v), ♀ topotype *D. h. solatus*, same data as 29. Specimens leg. R. Gatrelle unless otherwise noted; (d) = dorsal, (v) = ventral.

Abbot provided paintings and basic information to Boisduval and Leconte. Boisduval and Leconte made the determinations and wrote the descriptions. These authors saw no actual Abbot specimens. We know now that the Abbot painting to which Boisduval and Leconte assigned the name *irus* was in fact not Godart's *irus*, but the species Grote and Robinson would describe as *Thecla henrici* 34 years later. We know this because: 1) Abbot's adult figures depict *henrici* (no male scent patch), not *irus*; 2) his description of the larva fits *henrici*, not *irus*; 3) his larval hosts (*Ilex* L. and *Vaccinium* L.) are that of *henrici*, not *irus*; and 4) the verbal description (see appendix) is in all aspects, except one, *henrici* and not *irus*. Conversely, Boisduval and Leconte's *arsace* is an *irus* in these same four points (see appendix). Abbot's male figure of what Boisduval and Leconte called *arsace* has scent patches on the forewings.

Boisduval and Leconte's error of associating Godart's name *irus* with the as yet undescribed *henrici*, resulted in their describing the true coastal Georgian *irus* under the name *T. arsace*. Thus, *Thecla irus* Boisduval and Leconte 1833, should be listed under the synonymy of *Deciduphagus henrici* and noted as preoccupied by *Polyommatus irus* Godart, 1824.

To preclude the possibility that anyone might ever suggest that Godart's *irus* was a *henrici*, I wrote the Museum Nationale in 1975 and asked if Godart's *P. irus* type was extant. Dr. P. Viette not only confirmed that the holotype was there, but also sent me the specimen for taxonomic verification (Fig. 5). It is a *D. irus*. (See the appendix under *Polyommatus irus* for additional information.)

Boisduval and Leconte are not the only ones to have confused *D. henrici* with *D. irus*. Scudder (1889) lists both *T. henrici* and *T. arsace* in his synonymy of *D. irus*. He devotes seven pages of narrative to what is actually an *irus/henrici* composite. There is a wealth of information, but it is untrustworthy because he unknowingly goes back and forth between data relating to *henrici* and *irus*. However, for the reader who knows that Scudder was actually dealing with two species, this information is enlightening.

Scudder's comments under the heading "variations" manifests this confusion. He muses as to why some male *irus* nearly lack DFW scent spots (being *henrici*, they actually had none) and how these same males had noticeable HW tails "twice as long as usual [for *irus*]." He also notes that some of these same tailed (*irus = henrici*) specimens from Albany, NY were "decidedly olivaceous" in hue. This reference to **decidedly** olivaceous (greenish) specimens in upstate New York in 1889 is significant now that the often greenish *D. h. viridissima* Pavulaan has been described (1998).

Scudder quotes Abbot as stating that *irus* (actually *henrici* not *irus*) is often found in swampy areas. I too have found southeastern *henrici* in very wet areas. I have also found it curious that *henrici* in this area have the trait of firmly attaching their pupa to holly leaves or bark. I have wondered if this wetland habitat association might have caused these *henrici* to develop this trait – because the ground is often inundated with water. Or, is this characteristic of other populations in dryer environs also?

Holly (*Ilex*) and Lupine (*Lupinus perennis* L.) are the only plants Scudder confirmed as definite hosts for his "*irus*." We know now that the former only applies to *D. henrici* and the latter to *D. irus*. Scudder mentioned other plants, but stated he could not confirm any of them as being oviposited on by wild females. Scudder noted that larvae (of which species?) accepted wild plum fruit in captivity. He also documented that females (of which species?) refused to lay eggs when confined with *Vaccinium* (blueberry), *Quercus* L. (oak), or *Cyrilla racemifolia* L.

His comments on *Cercis canadensis* L. (redbud) are noteworthy. He records that Abbot only noted *C. canadensis* as an adult nectar source and not a larval aliment. I have often found local *henrici* adults around redbud (never *irus*). But I have never succeeded in getting *henrici* larvae from this area to eat, or females to oviposit on, *C. canadensis*. This plant is documented (in lit.) as a primary host of *D. h. henrici* and *D. h. turneri* Clench, in the Appalachian, northeastern, and western areas of the United States.

This confusing of *D. henrici* and *D. irus* adults, coupled with the unclear references to plants as either larval hosts or adult nectar sources by the early workers, should make the long list of *henrici* larval hosts as recorded in much of the modern literature suspect (i.e. Scott 1986). A lot of field work needs to be carried out throughout the range of *D. henrici* to accurately reassess and document its actual hosts.

BIOGEOGRAPHICAL EVOLUTION AND SUBSPECIATION

The six subspecies of *Deciduphagus henrici* can be divided into two groups of three subspecies each according to their known larval host associations. Three subspecies appear to be nearly monophagous toward *Ilex*. I call this group the *Ilex* group. The other group of subspecies is composed of two taxa which are primarily non-*Ilex* feeders and one which is oligophagous (including *Ilex*). I call this the non-*Ilex* group.

The *Ilex* group is found in the non-montane areas of the southern and eastern United States. The three taxa which comprise the *Ilex* group are: *D. h. margaretae* dos Passos, type locality Deland, Volusia County, Florida occupying east-coastal to south central Florida; *D. h. viridissima*, type locality Nag's Head, Dare County, North Carolina occupying the upper Outer Banks area of NC north through the Chesapeake and Delaware Bays and in scattered coastal colonies to perhaps Rhode Island; and a new subspecies herein described as *D. h. yahwehus* Gatrell (TL Orangeburg County, South Carolina) occupying the area from south central North Carolina south to north Florida then westward through Georgia to perhaps Mississippi and the upper west coast of Florida.

The non-*Ilex* subspecies are: *D. h. solatus* Cook & Watson, type locality Blanco County, Texas occupying south central Texas westward; *D. h. turneri* Clench, type locality Cowley County, Kansas occupying the area from north Texas northeast to at least Indiana; and the oligophagous (including holly) *D. h. henrici*, type locality Philadelphia, Pennsylvania and occupying the southeastern area of Canada south through the Appalachians.

Ilex Group

Ilex is the primary, perhaps exclusive, larval substrate of this group. After nearly 30 years of experience with *D. henrici* in Florida, coastal Georgia, and South Carolina I have only found it in association with *Ilex*. *Ilex opaca* Aiton, *I. cassine* L., and *I. vomitoria* Aiton are known larval aliments of *margaretae*, *yahwehus* and *viridissima*. Where more than one of these hollies grow in the same location, they are all utilized by the local *henrici* population. *I. opaca* and *I. vomitoria* are found from Virginia south to Florida and west to Mississippi, with *vomitoria* primarily along the coast. *I. cassine* is found from south coastal North Carolina south to Florida and west to Mississippi (includes var. *myrigloia* Aiton). This mutual host association and shared morphological characters of prominent tails and limited red scaling dorsally is consistent with a common ancestry of these three subspecies. This *Ilex* host association is therefore evidently peri-Pleistocene and Floridian in origin. Thus, they have arisen from a Floridian Pleistocene relict.

I. cassine prefers mesic, even paludal, habitats more than the other known hosts of this group. Thus, *I. cassine*'s range is restricted to the wet areas of the lower coastal plain. *I. cassine* is the primary host of *margaretae* in east coastal Florida. *I. opaca* is tolerant of both mesic and xeric habitats. Thus, *I. opaca* is by far the most upland of the known larval hosts. *I. opaca* is the primary host of the inland populations of *yahwehus*. *I. vomitoria* is the primary host of *yahwehus* on the coastal islands of South Carolina. *D. h. viridissima* utilizes *I. opaca* and *I. vomitoria* in the same fashion as *yahwehus* does.

In my evolutionary model, this group of subspecies arose from an ancestor adapted to lowland *Ilex* during the Pleistocene in island Florida with *margaretae* being the oldest most direct descendent. By this model, the species then followed the host(s) and invaded low wetlands northeastward and westward from Florida adapting to other hollies in the process. Those which followed *I. opaca*'s adaptation to xeric and upland environs moved inland with it and gave rise to *yahwehus*.

D. h. yahwehus is both phenotypically and geographically closest to *D. h. margaretae*. *D. h. viridissima* is equally distinct in phenotype from both of these. It is not possible to determine, without an involved study, if *viridissima* arose from *margaretae* or *yahwehus*. However, it is likely that *yahwehus*, based on its upland host adaptation, is the most recently evolved; and *viridissima*, by its continued lowland

coastal acclimation, is older than *yahwehus* and younger than *margaretae* having simply moved northward from Florida along the coast.

However, regardless of *viridissima*'s evolutionary ancestry, I disagree with Pavulaan's idea that *viridissima*'s green morph may have stemmed from environmental factors. If this were true, it would only be an ecotype (form) and not a subspecies. Further, if this were the case, why are not all coastal North and South Carolina populations predominantly greenish? All North and South Carolina maritime populations feed mostly on *I. vomitoria* and are subject to the same basic ecological conditions. It is far more likely that the great frequency of the green morph arose over thousands of years as the direct result of green gene selection and its eventual genetic dominance within the isolated population on the upper Outer Banks of North Carolina. I see *viridissima* as a genetically distinct *Ilex* group subspecies, with green, brown, and intermediate morphs, which now extends along the northeast coast from the upper Outer Banks of North Carolina to perhaps the Great Swamp of Rhode Island.

Regardless of what evolutionary models are eventually demonstrated to be the most likely, these three biologically similar *Ilex* associated *henrici* subspecies 1) form a group most probably evolved from a Floridian ancestor, and as such are 2) separated by thousands of years from the non-*Ilex* associated taxa.

Non-*Ilex* Group

I am by no means as familiar with this group as I am with the *Ilex* group. However, it seems fairly probable that the non-*Ilex* group is 1) from a common ancestor, and 2) from a different refugium than the *Ilex* group. The range of the three subspecies in this group, their host associations, and phenotypic similarities indicate that their ancestor is from a Texan or Mexican population.

Cercis canadensis seems to be the primary larval host of *D. h. turneri* and *D. h. henrici* (Pavulaan, 1998) from Texas northeastward to southeastern Canada and eastward to the southern Appalachians. This includes the northern glaciated and southern non-glaciated areas within this range. This dictates that *C. canadensis* became the primary host of this group before it came to occupy the formerly glaciated regions. Hypothetically then, there should be two biological situations in place in the Midwest, eastern US, and in southeast Canada which need to be investigated through careful field observations.

Bio-situation A. The older (more biologically conformed) populations in the **non-glaciated** areas would be expected to be monoalimentary in larval host selection. One plant genus, or species, would be the dominant larval aliment (i.e. *Cercis*). However, occasional colonies within this large geographic primary host area might utilize plants of one or two other genera (including *Ilex*) as secondary hosts; or even as a primary host in certain micro populations within the non-*Ilex* group's total range. *D. h. turneri* is the expected taxon of bio-situation A (Figs. 25-26, 31-34).

Bio-situation B. The newer (more biologically unstable) populations in formerly **glaciated** areas would be expected to be largely polyalimentary in larval host selection. They would equally utilize plants of multiple genera as larval hosts. *D. henrici*'s recent adaptation to *Rhamnus frangula* (Layberry et al., 1998), is indicative of this type of ongoing host adaptation by populations still in ecological and geographic advance. Situation B populations should be endemic to Remington's (1968) suture zone one. *D. h. henrici* is the expected taxon of bio-situation B (Figs. 27-28). *D. h. henrici* was the first taxon of *henrici* to be named; however, by my model, it is the most recently evolved and is the eastern extension of *turneri*.

Nevertheless, this does not mean that *D. h. turneri* is not also present in some situation B areas. I agree with Pavulaan (1998) that *D. h. turneri* extends from Texas well into the eastern United States and is probably the best name for *henrici* in much of Ontario, Canada. *D. h. turneri* was determined as the subspecies in Missouri by Heitzman (1987), and in Indiana by Shull (1987). Specimens I have from Vinton, Co., Ohio (Fig. 34) also fit best with *turneri*. It is the frequently extensive amount of red scaling on the dorsal surface of *turneri* that differentiates it from *henrici henrici*. Ventrally, they are very similar. The name *henrici* should be limited to the oligophagous, dorsally dark (compared to *turneri*) populations of the northeast and Appalachians. Nominate *henrici* has more red dorsally than any of the *Ilex* group subspecies.

Diospyros texana (persimmon) is apparently the exclusive foodplant of *D. h. solatus* in Texas. This host association and *solatus*' distinct phenotype (Figs. 29-30, 35-36), indicates that it is either from a third ancestor (further to the west), or is an early subspecific split from the Texan ancestor of it and the other two taxa in the non-*Ilex* group. A breeding experiment between *solatus* and *viridissima* would be of interest to test if these two, by evolutionary distance, act as sibling species.

The *Ilex* and non-*Ilex* groups already act as sibling species in some aspects stemming from their host association. For example, Pavulaan was not able to get females of *viridissima* to oviposit on *Cercis*. And his *viridissima* larvae also exhibited difficulty in accepting *Cercis*. The *viridissima* larvae he was able to rear through to pupae on *Cercis* had extremely high pupal mortality. I have found this same condition to exist in nature here in South Carolina. The possibility exists that the taxa in these groups do not just act in some ways as sibling species, but are in fact such.

Subspecies In Tension

Mr. Harry Pavulaan and Dr. Dale Schweitzer have provided me with a great deal of information and offered their personal opinions and interpretations regarding *henrici/viridissima* in the northeastern United States. Dr. Schweitzer's input was specifically offered relative to his review of this paper. These two workers agree on the relevant biological and ecological data. However, they differ, sometimes dramatically, in their interpretation of these data. The facts and advice provided by Schweitzer and Pavulaan constitutes virtually all of the specific information in this section. Accordingly, they deserve special acknowledgment here. The subspecific theory is mine.

Cryptic species look exactly alike, but the factors of reproductive isolation and biological diversity distinguish them. Subspecifically, because there is no reproductive isolation, many butterfly taxonomists have come to rely almost entirely on morphological wing differences to determine subspeciation. I believe this is incorrect. As with species, **major** biological differences are of greater subspecific importance than wing coloration.

Pavulaan, in his description of *viridissima*, documented many populations which contained various percentages of green morph *viridissima* and/or intermediate *viridissima* like individuals meshed with predominately brown populations (which he called *henrici*) ranging through the entire Chesapeake Bay area and reaching as far west as West Virginia and northeast to New Jersey. According to both Schweitzer and Pavulaan, all Chesapeake Bay populations are *Ilex* feeders be they green, brown, or intermediate. They also agree that virtually all populations along the east coast from the Outer Banks through southern New Jersey and then in scattered colonies north to the Great Swamp of Rhode Island, are holly feeders.

However, Pavulaan limited the range of his *viridissima* to only that area of the upper Outer Banks of North Carolina containing the highest frequency of green individuals. I understand why he did this; however, I feel his approach is too narrow and simplistic. In actuality, his delineation of *viridissima* nearly renders *viridissima* as little more than a form. The situation in the northeast is about much more than green verses non-green specimens or even populations.

According to Pavulaan's original description, *viridissima* specimens vary in the degree to which the subspecies' three ventral green scaling characters are manifest – including brown topotypical individuals with **no** green scaling. While the green characters are the most **visible** *viridissima* attribute, subspeciation is primarily about evolutionary factors and not just how something appears to the human eye. Thus, Pavulaan errs throughout his article by using the subspecific **name** *viridissima* in relation to reported “greenish” individual specimens (**forms**) in the Midwestern populations of *turneri* and other areas. The term *viridissima* is a subspecific name, not a tag for a variation or form.

He misuses the subspecific **name** *henrici* in the same way for the “brownish” **form** within the topotypical *viridissima* population. The all-brown individuals at the type locality of *viridissima* are just as much *viridissima* as the green ones. I embrace *viridissima* as being subspecifically distinct from *henrici*

because of their different evolutionary ancestry, larval host associations, and morphological characters. *Viridissima* also differs phenotypically from its nearest relatives – *margaretae* and *yahwehus*.

Mr. Pavulaan did not figure or describe the brown *viridissima* morph. The following is a brief comparison of brown *viridissima* (Figs. 23-24) with *yahwehus* and *henrici*, and *yahwehus* and *margaretae*.

Dorsally, all *viridissima* (males and females) are typical of the *Ilex* group in that they have **very little**, if any, red on their forewings; on their hindwings, they frequently have red patches along the outer margin at the tails (especially females). Thus, in the dorsal aspect, *viridissima* is marked much like *yahwehus*. *Henrici* often have **much more** dorsal red scaling than *viridissima*, especially on the forewings of males (Fig. 27). Ventrally, the apical area of the forewing in *viridissima* is usually a much lighter brown than, and in strong **contrast** with, the dark brown of the basal two thirds of the wing inward of the postmedian line. On the hindwings, the area between the dark basal area and the marginal gray scaling is **also light** brown.

Viridissima's overall ventral appearance is light brown in the limbal areas **contrasted** against dark warm brown basally (sometimes washed or peppered with green). The brown morph of *viridissima* differs from the green morph only in its lack of green scaling. *Viridissima*'s tails are true tails – they are narrow, have length, and a pointed terminus.

Yahwehus' overall ventral forewing appearance is medium rust brown in the limbal area with the area basad of the postmedian line **only slightly** darker rust brown; on the hindwing *yahwehus* is dark brown to black brown basally with dark rust brown in the limbal area and sometimes glazed (in fresh specimens) over the entire ventral surface with a wine color.

Henrici's overall ventral hindwing appearance is typically **black** basally with the limbal areas either (northeastern US westward to *turneri*) a very contrasting light brown, or (in Appalachians) a contrasting medium brown. The forewing contrasts in the same manner except that the area basad of the postmedian line is brown not black. *Henrici* does not have true tails – they have broad extended lobes with a rounded terminus.

Margaretae, *yahwehus*, and *viridissima* all have restricted red dorsally. *Henrici* and *turneri* may have a great deal of red dorsally. All individuals of the three *Ilex* group subspecies have true tails. Most non-*Ilex* group specimens do not (there are individual exceptions). *Henrici* and *turneri* are usually noticeably smaller than the three *Ilex* group subspecies. Ventrally, *margaretae* usually appears concolorous light to medium brown, *yahwehus* appears more contrasting but in dark dirty brown shades, while *viridissima* usually appears brighter and more contrasting in pleasing shades of brown and green.

The relationship of the populations in the northeastern area of the United States is very complex because two very distinct and evolutionarily distant subspecies are now in direct contact. One is *D. h. viridissima* of the Floridian parented *Ilex* group, and the other is *D. h. henrici* of the western parented non-*Ilex* only group. These two subspecies while in contact geographically, are separated evolutionally by thousands of years. The morphological and biological characteristics of each of these subspecies, which have taken tens of thousands of years to evolve, have doubtlessly been clashing in this tension zone² for a long time. A great deal of detailed field work needs to be done in this tension zone area.

The correct understanding of *viridissima*, based on the information supplied to me by Schweitzer and Pavulaan, seems to be that all of the monophagous *Ilex* populations along the east coast from about New York City south to the upper coastal area of North Carolina should be considered *viridissima*. These populations vary greatly in the percentage of green and brown morphs. However, this is the only *henrici* subspecies to have any significant amount of green specimens. Thus, the green morph remains as the most distinctive phenotypic character of this subspecies.

The limit of *viridissima*'s inland range, and where it meets and is in tension with *henrici*, is beyond my knowledge and remains for others to work out. Dos Passos' lectotype of *henrici* is from Philadelphia, PA. According to Schweitzer, the shift to holly is east of the type locality in New Jersey. The fact that *D. h. henrici* includes *Ilex* as a host in some of its oligophagous populations (i.e. in Rhode Island) complicates this situation. In the tension zone, non-*Ilex* associated green *henrici* specimens may occur on occasion due to the interbreeding of these two subspecies.

² A "blend zone" is where two subspecies, one having arisen from the other, blend (a phenomena of divergent evolution). A "tension zone" is where two subspecies, of different refugia ancestors, meet and clash (a phenomena of convergent evolution).

DESCRIPTION OF A THIRD *ILEX* ASSOCIATED SUBSPECIES.

I have been collecting butterflies extensively throughout the southeastern United States for 31 years. Occasionally, I have come in contact with colonies of *D. henrici* in this region. It became apparent to me about 1973 that two *henrici* subspecies were present in this area. In 1975 I submitted an article to the *Bulletin of the Allyn Museum* describing the South Carolina population as a new subspecies. This paper was accepted and an initial time frame was set for publication. However, several factors unrelated to the research itself, resulted in that and several other projects, being put on hold – until now.

D. h. margaretae

Dos Passos described *Incisalia henrici margaretae* in 1943 from only four Florida specimens: two males taken at Deland, Volusia County, in the central coastal region, and two females collected near Auburndale, Polk County, in the south central part of the state. The holotype was a male from Deland, so that has become the type locality, though dos Passos did not specify it as such. His subspecies was based on four characters as contrasted against nominate *D. henrici*. His description is as follows. I have highlighted these characters in **bold**. In his comments section, dos Passos stated that the AMNH had no specimens from Georgia or South Carolina. The AMNH did have two specimens from Southern Pines, North Carolina, which he considered intermediate in dorsal color (more HW red) and length of tails.

“In Florida a very distinct race occurs, which, while having certain characters of *henrici*, is easily differentiated by the **length** of its tails. These are more than twice as long as in typical *henrici*. It is also somewhat **larger**, especially the females, and is **uniformly** dark grayish brown on the upperside. The underside is a more **uniform** color because the basal area is lighter and the limbal area darker than in *henrici*.”

From 1973 to 1988 I made several excursions to the type locality of *D. h. margaretae* on Hwy. 44 just east of Deland. The habitat is usually very wet, almost marshy, in the spring. Depending on the arrival of warmer weather, topotypical *margaretae* could be on the wing as early as the end of January or be found as late as the first of April. The topotypical population is very homogeneous in appearance.

During this time, I accumulated a large number of specimens of topotypical *margaretae* which was usually abundant about its larval host, *I. cassine*. *I. cassine* grows profusely in this forested area of Florida. *D. h. margaretae* fly high in the trees and only occasionally drop to within 10 feet of the ground, which is usually to nectar at low *I. cassine* or *Salix* L. (willow) flowers. I employed a series of pole extensions that enabled me to net specimens up to 30 feet high. Even with this method, the majority of observed individuals were too high and could not be caught. Specimens could often be seen about the tops of the highest pines. In this respect, collecting *margaretae* is very similar to collecting *Mitoura hesseli*. A good idea of its abundance is illustrated by the fact that even with this general unobtainability, 50 specimens could be captured in just 3 - 4 hours. This abundance was normal and did not represent a “population explosion” as hairstreaks are occasionally known to have.

The only other Florida *henrici* I have personal experience with is an *I. cassine* associated population I came across in March of 1988 near the Jct. of roads 337 and 326 in Levy County. I collected 17 specimens which all have the ventral basal area markedly darker than topotypical *margaretae*.

In addition to my own specimens, I have seen Florida *henrici* in the collections of Rick Gillmore, Jeff Sloten, Dave Baggett, and the Florida State Collection of Arthropods, Gainesville.

There is one striking observation to be made about these Florida *henrici* – only specimens from the central east coast to the south central area of Florida seem to possess all four of dos Passos characters and are thus true *D. h. margaretae*. I consider the range of *margaretae* to be limited to this basic area. Exactly how far inland this subspecies may be found is not known by me. I do know that specimens from Nassau and

Duval counties (Jacksonville) are atypical of *margaretae* and are probably best considered a blend zone population near the new subspecies, or the new subspecies described herein.

A New Subspecies

To lepidopterists who are only familiar with *henrici* from outside the deep south, the first thing noticed about specimens from central North Carolina south are their very long tails. (These tails may often be six mm long on some Floridian males.) This striking character is undoubtedly why some popular butterfly book authors have extended the range of *margaretae* well north of central Florida into southern Georgia (Harris, 1972 & Scott, 1986), and South Carolina (Howe, 1975). However, there are three other characters which typify *margaretae*, and these seem to have been largely ignored by those observing southern specimens. Even many Florida lepidopterists are apparently only assessing *margaretae* by the length of their tails.

A comparison of Southern and Floridian specimens against the four characters dos Passos listed as being definitive of *margaretae*, reveals that two phenotypes are present in this region. One is *margaretae*, from within the previously restricted range. The other extends from central North Carolina south through Georgia to Jacksonville and apparently down the west coast of Florida to Levy County and (evidently) west to Mississippi. Specimens from throughout this broad area are quite similar, are very different from *margaretae* in two characters, and moderately different in one. The moderately different character is that specimens from this area are noticeably larger (character noted by Pavulaan, 1998). They differ markedly in that they have more red at the margin of the dorsal HW (as noted by dos Passos), and most noticeably, have very contrasting ventral basal and limbal areas which are often partially delineated by a white line (as pictured by Abbot). The tails are about the same, reducing as one goes northward.

I first encountered this undescribed subspecies in Givhans Ferry State Park, Dorchester County, South Carolina in 1971. Since then I have collected it from the following locations. GEORGIA: Bryan County, about 30 specimens nr. Fort Steward, 1976 (mid March); SOUTH CAROLINA: Aiken, Barnwell, Berkeley, Charleston, Colleton, Dorchester, and Orangeburg counties, about 90 specimens accumulated from 1971 to 1998 (mid February - late April); NORTH CAROLINA: Hoke County, 1 worn specimen near Raeford, 1974 (early April).

I have also seen additional specimens from Bryan County, Georgia in the collection of R. T. Arbogast, and a long series collected by the late R. B. Dominick at the Wedge Plantation, Charleston County, South Carolina (now at the University of South Carolina).

Biologically, this new subspecies differs from *margaretae* in that it is the result of larval host adaptation to *Ilex opaca* which, in turn, allowed the species to expand its range, both environmentally and geographically, into dryer and upland environs. It is distinct morphologically, as noted above and in its description as follows. It should be remembered that this new subspecies, as a part of the *Ilex*-group, has never been directly related to the nominotypical *D. henrici*, and as such, can have no clinal or blend zone relation with *henrici*. At any place where these two may be found to be in contact (and thus producing phenotypically intermediate offspring), these populations should technically be referred to as tension zone populations, not blend zone populations.

Deciduphagus henrici yahwehus Gatrell, new subspecies

Diagnosis. There is very little variation in *margaretae* (Figs. 13-18). The overall general appearance of both sexes of *margaretae* is about the same. They are a warm gray brown dorsally. Females occasionally have a few red scales on the DHW margin at the tails, males **rarely** do. The ventral HW basal and limbal **browns** of *margaretae* are much **less contrasting** than in the other subspecies (especially in males). Specimens of *margaretae* are often encountered with a good bit of rusty red-brown suffusion over the ventral forewings. The anterior portion of the submarginal line of basally pointed chevrons that borders the gray marginal area on *margaretae*'s ventral HW may also contain patches of rusty red. The tails are quite long, as can be seen from the figures. *Yahwehus* differs in that the ventral HW basal and limbal areas are **much darker** and **more contrasting**. The basal area in *yahwehus* is **blackish** and the limbal area brown. As pointed out by

Pavulaan, fresh specimens of *yahwehus* sometimes have a purplish **wine** tint to the ventral surface. Dorsally, *yahwehus* is a darker brown than *margaretae* and have browner, less checkered margins. Specimens of *yahwehus* **often** have a small patch of red along the outer margin of the hindwings at the tails (both sexes). The tails are not as long as in *margaretae*, varying from 2 to 4 mm throughout its range. Generally, these tails are always twice as long as in *henrici*. The average forewing radius (from base of wing to apex, right FW) of the 49 specimens comprising the type series is 14 mm (same for both sexes) – nearly all specimens are 13 to 15 mm.

Description. *Male* (Figs. 7-8): *Head*: face, eyes, palpi, and antennae slightly darker than *margaretae*. *Thorax and abdomen*: dark blackish brown dorsally, dark gray ventrally, with legs and ventral thoracic hairs dark charcoal gray (in *margaretae*, the ventral thoracic hairs are light gray and the legs are a markedly lighter gray.) *Forewings*: dorsally, uniform, dark brown, slightly grayish, with restricted white checkering along the fringe of wing and usually limited to the apical margin; ventrally, rusty brown with some specimens very lightly dusted with green scales, postmedian line prominent often black inwardly and highlighted with white outwardly, with the fringe more checkered looking on this surface. *Hindwings*: dorsally, same color as forewing, with about 30% of specimens having a small amount of red scaling along the outer margin in cells Cu₁ and Cu₂ in the area of the tail, average tail length 2.8 mm; ventrally, basal area dark blackish brown to black, often edged with white except at the middle of wing, fringe not checkered, marginal bluish gray area outlined by a row of occasionally prominent basally pointing black chevrons. *Female* (Figs. 9-10): *Head*: as male. *Thorax and abdomen*: ventral slightly lighter gray than male. *Forewings*: dorsally, ground color as in male, may have a very small amount of red scaling in postmedian area; ventrally, as in male. *Hindwings*: dorsally, color as in male except that about 75% of specimens have red scaling along the outer margin in cells Cu₁ and Cu₂ in the area of the tail, average tail length 2.5 mm; ventrally, as in male.

Types. *Holotype* ♂ (Figs. 7-8): vicinity of Bull Swamp, Orangeburg County, South Carolina, 10 March 1994, coll. Ronald R. Gatrell. *Allotype* ♀ (Figs. 9-10): vicinity of Bull Swamp, Orangeburg County, South Carolina, 10 March 1994, coll. Ronald R. Gatrell. *Paratypes*: 33 ♂♂, 14 ♀♀, all coll. R. R. Gatrell unless otherwise noted: SOUTH CAROLINA: AIKEN COUNTY: White Cedar bog north of Aiken State Park, 1 ♀ (worn), 21 April 1984; CHARLESTON COUNTY: Wedge Plantation, 1 ♂, 1 April 1971; 1 ♀, 30 March 1968 (both leg. R. B. Dominick); COLLETON COUNTY: Edisto Island on *I. vomitoria*, 1 ♂, 1 ♀ (worn), 4 April 1980; 4 ♂♂, 29 March 1986; DORCHESTER COUNTY: Givhans Ferry State Park, 1 ♂, ex pupa 10 February, 1 ♀, ex pupa 1 March, 3 ♀♀, 21 March 1976; on Hwy. 61 3 mi. east of Givhans, 1 ♂, 27 March 1986; ORANGEBURG COUNTY: Hwy. 172 1 mi. east of Hwy. 672, 1 ♂, 5 March, 1 ♂, 27 March 1992; Bull Swamp 2 mi. north of North off Hwy. 178, 3 ♂♂, 2 ♀♀, 10 March 1994, 1 ♂, 4 March 1997; GEORGIA: BRYAN COUNTY: Hwy. 204 nr Ogeechee River, 1 ♂, 1 ♀, 20 March 1976, 8 ♂♂, 19 March 1977; Hwy. 204 3 mi. north of Morgans Bridge, 1 ♂, 17 March 1980 (leg. R. T. Arbogast); 3.3 miles south of Ellabelle, 3 ♂♂, 17 March 1982 (leg. R. T. Arbogast); Pine Barrens Rd. 1 ♂, 2 ♀♀, 29 February 1992 (leg. R. T. Arbogast); 5 ♂♂, 2 ♀♀, 2 March 1992 (leg. R.T. Arbogast). The holotype, allotype, and 2 paratypes are deposited in the American Museum of Natural History (AMNH), New York, where the type series of *D. h. margaretae* is located. 2 ♂ and 2 ♀ paratypes are deposited in the Carnegie Museum (CMNH), Pittsburgh, where the bulk of the paratypes of *D. h. viridissima* are located. The remaining type specimens are in the Museum Of The Hemispheres (MOTH), Goose Creek, South Carolina.

Geocological type locality. *I. opaca* groves in 50 mile radius of Bull Swamp, Orangeburg County, South Carolina.

Etymology. YHWH (translated as Jehovah in English) is an ancient Hebrew name for God as Creator. This is the mono-Deity of the world's Jews, Moslems, and Christians. From this perspective, *yahwehus* is named for The Architect of the natural world. Its common name can be "The Architect," or "Architect's Elfin." Johnson established *Deciduphagus* as masculine. The *us* ending is correspondingly masculine in *yahwehus*.

Remarks. The parameters of *D. h. yahwehus*' range are not known. According to Pavulaan, it evidentially extends westward to Mississippi. The populations in the panhandle of Florida are *yahwehus*. In 1969, while living in Pensacola, Florida, I observed (but did not net) what was probably *yahwehus* flying about some *Ilex opaca* trees near Cantonment in Escambia County. When I moved a year later, the area was being considered for development as a park and zoo. That same year, I also observed (but was unable to net) two tailed elfins flying about a large planted *I. opaca* in a cemetery just east of Foley, Baldwin County, Alabama. How far down the west coast of Florida *yahwehus* extends is unknown. My specimens from Levy County (except for tail length) are certainly closer to topotypes of *yahwehus* than topotypes of *margaretae*. Likewise, specimens I have seen from Jacksonville, Florida seem to be closer to *yahwehus* than *margaretae*. Florida lepidopterists need to correctly define the range of *margaretae* subject to dos Passos characters, specifically the lightly contrasting ventral HW. Too much emphasis has been placed on tail length. The northern limit of *yahwehus*' range is probably north central North Carolina. However, too much attention can be placed upon the length of tails of *yahwehus* also. All biological and morphological characters must be considered together in accessing populations at the outskirts of its range. *Yahwehus* will undoubtedly prove to be the primary subspecies throughout the non-montane southern and southeastern US.