Volume 11 Number 5 **December 10, 2023**

The Taxonomic Report

OF THE INTERNATIONAL LEPIDOPTERA SURVEY

ISSN 2643-4776 (print) / ISSN 2643-4806 (online)

Reassessment of *Amblyscirtes hegon* (Hesperiidae) as a complex of four distinct species revealed by genomic analysis

Harry Pavulaan[1], Ricky Patterson[2], and Nick V. Grishin[3]

[1]606 Hunton Place NE, Leesburg, Virginia, USA, 20176
[2]400 Winona Road, Vicksburg, Mississippi, USA, 39180
[3]Departments of Biophysics and Biochemistry, University of Texas Southwestern, 5323 Harry Hines Blvd., Dallas, Texas, USA, 75390-9050, grishin@chop.swmed.edu

ABSTRACT. After the discovery of a unique phenotype in the southern United States with a different ventral ground color than nominotypical *Amblyscirtes hegon* (Scudder, 1863), which occurs in the northeastern United States, genomic analysis revealed that *A. hegon* is a species complex. Phenotypic, genitalic, and genomic differences of the complex are presented here. Four species are identified: *A. hegon*; *A. nemoris* (W. H. Edwards, 1864), **stat. rest.**; *A. matheri* Patterson, Pavulaan & Grishin, **sp. n.** (TL: USA, Mississippi, Warren Co.); and *A. gelidus* Grishin, Patterson & Pavulaan, **sp. n.** (TL: USA, Michigan, Van Buren Co.).

Additional keywords: biodiversity, cryptic species, genitalia, skipper butterflies, pepper-and-salt skipper.

ZooBank registration: urn:lsid:zoobank.org:pub:466F6B4C-6BD9-43C5-9181-3CADE6C5F7EB

INTRODUCTION

One of the authors (Patterson) first noted a unique ventrally tan-brown colored *Amblyscirtes* Scudder, 1872 in Warren County, Mississippi, in the early 1980's. Despite ventral coloration different from what was initially considered to be typical *Amblyscirtes hegon* (Scudder, 1863) in the same region, this unique color morph was identified by several knowledgeable lepidopterists as *A. hegon*. One exception was Dr. Andrew Warren, Senior Collections Manager, McGuire Center for Lepidoptera and Biodiversity, who felt there were differences from *A. hegon* but, through analysis of the genitalia, could not identify differences that were clearly definitive. He encouraged further work on this issue.

Early on in the present study, the undescribed ventrally tan-brown phenotype was further documented from several locations in the Loess Bluff Hills region of Mississippi and the only locality known for sympatry of the unique color morph with what was considered to be *hegon* is the J. C. 'Sonny' Gilbert WMA (formerly the Sicily Island Hills Wildlife Management Area, renamed in 2015), in Catahoula Parish, LA. This was discussed in *The Butterflies of Louisiana* (Marks, 2018 [ref. pages 159-160]), which has the only published account and photo known to us of the "*A. hegon* ventral (alternate coloring)" phenotype, having an underside colored differently than the strongly grayish color of *hegon*. What we initially considered *A. hegon* and the new species have been collected flying sympatrically and synchronously in the J. C. 'Sonny' Gilbert WMA, with no evidence of integration. Marks (2018) explained that "one out of five" *A. hegon* observed at Sicily Hills were of the tan-colored form. There are presently no other known localities where they are sympatric.

After the initial phenotypic analysis, genomic analysis was performed (the Grishin lab) on the nominotypical *hegon* including the neotype of its junior subjective synonym *nemoris*, as well as specimens of the newly discovered tan-brown phenotype, and a broad distribution of samples from across the eastern United States. Genomic analysis revealed a complex of four distinct species within what has historically been recognized as *A. hegon*.

ORIGINAL DESCRIPTIONS OF PREVIOUSLY KNOWN TAXA

Hesperia hegon and *H. samoset* (Scudder, 1863)

The familiar "Pepper and Salt Skipper" was originally described as *Hesperia hegon* (Scudder, 1863, sp. #77) (**Fig. 1**) from a female specimen. Scudder had also described *Hesperia samoset* in the same paper (sp. #78) (**Fig. 2**) from a male specimen. The name *hegon* thus takes precedence over *samoset* on the basis of line priority. Neither description was accompanied by illustrations. Scudder (1889) first illustrated *H. samoset* on plate 10, in Vol. 3 of The Butterflies of the Eastern United States and Canada with Special Reference to New England (**Figs. 3, 4**). In that work, Scudder gave priority of the name *samoset* over *hegon*, likely due to *samoset* being the male specimen (**Fig. 3**). The female is shown in **Fig. 4**, below. Scudder appears to have mistakenly reversed the sexes on his plate. Specimen No. 1 of plate 10 (**Fig. 4**) is indicated as a female, yet has the characteristic wing shape and thin abdomen of the male. Conversely, specimen No. 3 of plate 10 (**Fig. 3**) is indicated as a male, yet has the characteristic wing shape and thicker abdomen of the female. The *hegon* holotype is indicated in **Fig. 5**. A typical male from near the TL is indicated in **Fig. 6**.

77. HESPERIA HEGON nov. sp. Above and beneath uniform dull dark-brown, with faint white markings on both surfaces of primaries situated as in *H. Oneko;* on under surface of secondaries, a submarginal series of small indistinct whitish spots, a small white spot in the centre, and another between the costal and subcostal nervures, midway between the base and the submarginal band. Expanse of wings nearly 1 inch.

I have seen but a single specimen, a female taken by myself at the White Mountains in the latter part of July.

Fig. 1. Original description of *Hesperia hegon* (Scudder, 1863).

78. HESPERIA SAMOSET nov. sp. Above dark-brown with a few ochraceous scales especially at base of primaries and on disk of secondaries. *Primaries* with three small yellowish spots one above the other on costal border a little more than three-fourths the distance from the base; below these and a little further removed from the outer border than they, between the uppermost branches of the median, a small spot; in the space below, situated near the base, another small spot or slender oblique line, and sometimes another below it between median and submedian; a double spot at the end of the cell.

Beneath dark-brown with profusely scattered pale-yellowish scales most abundant toward the outer margin; a very delicate purplish reflection, especially on secondaries. *Primaries* with the markings of the upper surface repeated. *Secondaries* with a narrow transverse pale yellowish band, two-thirds the distance from the base, nearest the outer margin at the lowest band of subcostal, where it is bent at right angles, and whence towards the costal border it is interrupted; a small spot in centre and another between costal and subcostal midway between the base and transverse band; fringe of both wings pale yellowish interrupted with dark-brown, most distinct upon primaries. Expanse of wings fully 1 inch. Very rare; I have seen two specimens from Mass. and N.H.

Fig. 2. Original description of *Hesperia samoset* (Scudder, 1863).

Interestingly the original descriptions of both *hegon* and *samoset* indicate a dorsal and ventral ground color of "dark brown". The specimen illustrated in **Fig. 3** and imaged in **Fig. 5**, reflect this description. This was confirmed by examining a series of *hegon* in the topotypical

region of northern New England, from specimens in the NMNH collection and specimens in the collections of the present authors. Scudder (1889) gave a more detailed description of the adults, again stating: “Wings above rich dark brown” and “Beneath of the same brown as above”, while not mentioning any greyish or greenish scaling on the ventral hindwings which has been a popular description of *hegon*’s ventral appearance. While the other described wing characters (spots, fringes, etc.) can apply to most individuals of all populations comprising the *hegon* complex, ventral ground color stands as the most definitive character, though there is considerable variation with the grey “peppering”. Genomic analysis of specimens in the topotypical region of northern New Hampshire establishes a baseline against which to compare additional populations from across eastern North America.

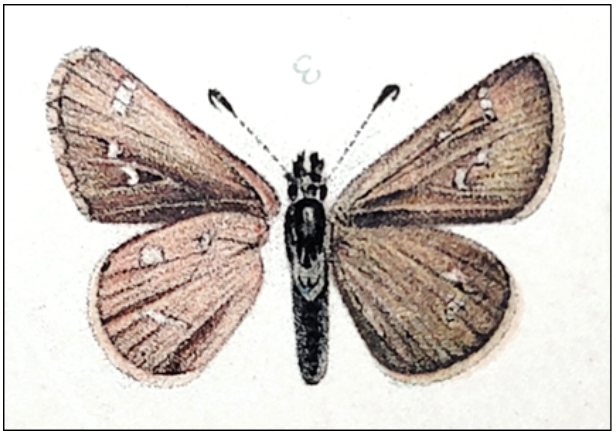


Fig. 3. *Hesperia samoset,* specimen #3 indicated as male in Plate 10 (Scudder, 1889).

Fig. 4. *Hesperia samoset,* specimen #1 indicated as the female in Plate 10 (Scudder, 1889).

Fig. 5. Holotype, *A. hegon*. Images courtesy Museum of Comparative Zoology, Harvard University. http://creativecommons.org/licences/by-nc-sa/3.0/legalcode

Fig. 6. Typical *A. hegon* near type locality. Male. June 18, 1966, Glencliff, Grafton Co., N.H., leg. Charles G. Oliver. Images courtesy Museum of Comparative Zoology, Harvard University. http://creativecommons.org/licences/by-nc-sa/3.0/legalcode

Hesperia nemoris (W. H. Edwards, 1864)

W. H. Edwards (1864) subsequently described *Hesperia nemoris* (**Fig. 7**):

HESPERIA NEMORIS, nov. sp.

Male. Expands one inch. Upper side glossy brown; secondaries covered with greenish hairs except a narrow space along the costal and inner margins; primaries have three yellow dots in line, on the costa, and two small spots on the disk; fringes long, whitish, dark brown at tips of nervules on primaries only.

Under side greenish grey, except on inner margin of primaries, which is brown; same spots as above on primaries, but enlarged; on secondaries a sub-marginal band of small spots, not reaching the inner margin; two minute spots on the costa and a third on the disk, scarcely paler than the ground color.

Taken at Portsmouth, Ohio, by Mr. John Bolton.

Fig. 7. Original description of *H. nemoris* (W. H. Edwards, 1864).

Fig. 8. Original illustrations of *H. nemoris* (W. H. Edwards, 1865).

In his description of *nemoris*, Edwards indicates a ventral ground color of "greenish grey". No life history notes were given. An illustration of *nemoris* was later published in Edwards (1865) (**Fig. 8**). The difference when compared to the original illustrations of *hegon* and *samoset* indicates a more complete ventral postmedian band of light spots in *nemoris*. However, the primary difference is that *nemoris* appears to have a denser covering of light scales on the ventral hindwing, giving specimens a grayer appearance (**Fig. 9**). As in the earlier descriptions of *hegon* and *samoset*, the other described wing characters (spots, fringes, etc.) can apply to most individuals of the *hegon* complex due to considerable variation. By comparison with the original descriptions of *hegon* and *samoset*, the ventral ground color of *nemoris*, as originally described by Edwards, provides a readily observable baseline character. Research with further access to larger series is suggested to better differentiate the two phenotypes.

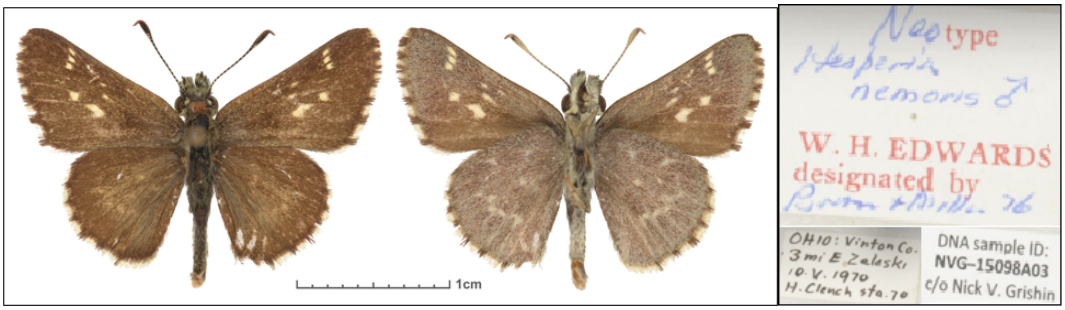
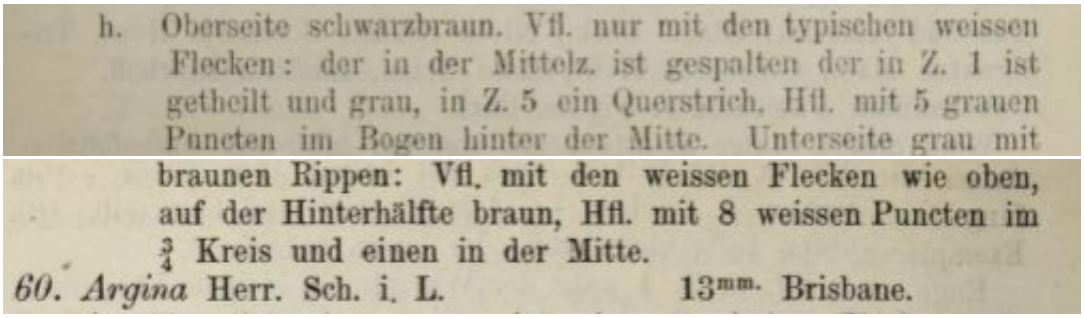


Fig. 9. Neotype of *A. nemoris*. Ohio: Vinton Co., nr. Zaleski (leg. Harry K. Clench), 10 May 1970

***Pyrgus argina* Plötz, 1884**

Plötz (1884) subsequently described *Pyrgus Argina* (**Fig. 10**):


h. Oberseite schwarzbraun. Vfl. nur mit den typischen weissen Flecken: der in der Mittelz. ist gespalten der in Z. 1 ist getheilt und grau, in Z. 5 ein Querstrich. Hfl. mit 5 grauen Puncten im Bogen hinter der Mitte. Unterseite grau mit braunen Rippen: Vfl. mit den weissen Flecken wie oben, auf der Hinterhälfte braun, Hfl. mit 8 weissen Puncten im ¾ Kreis und einen in der Mitte.

60. Argina Herr. Sch. i. L. 13mm. Brisbane.

Fig. 10. Original description of *P. argina* Plötz (1884). Plötz placed the descriptions before the names.

An approximate translation: "Upperside black-brown. Forewings only with the typical [for *Pyrgus*] white spots: the one in the discal cell is split, the one in Cell 1 is divided and grey, in Cell 5 a horizontal streak. Hindwings with five gray dots in the arc past the middle. Underside grey with brown veins: Forewings with the white spots as above, on the posterior half brown, hindwings with eight white dots in the ¾ circle and one in the middle." The description is rather general and could apply to any population of the *hegon* complex. TL is erroneously given as "Brisbane". Genomic analysis of a specimen collected in 1887, shortly after the description of *P. argina* and resembling a drawing of *P. argina* (see p. 21) revealed it to be *A. hegon* by the Z chromosome.

AMBLYSCIRTES '*HEGON*' IN LITERATURE

Amblyscirtes hegon has historically been recognized as a single species. The current analysis views previously published life history accounts as broadly applying to a complex of four newly-identified species under the guise of "*hegon*". The following sampling of literature treatments provides us with a general guide to the life histories of various populations, but cannot be reliably attributed to any of the four species revealed in this study. The butterfly is generally described as uncommon, though occasionally being found in numbers. A review of morphological descriptions, as follows below, focuses on the ventral hindwing ground color, which is the most revealing (though variable) character that we have found, to differentiate the species. All populations of the *hegon* complex bear similar lightly colored markings set against a dark ground color, especially the highly variable arc of light marks across the ventral hindwing, as well as checkered wing margins. Interestingly, the ventral hindwing is often described as "greenish" or "greenish-gray", based primarily on the effect of the peppering of pale scales set against the darker ground color. This greenish look is more the result of human perception. The greenish appearance apparently fades in collections (Forbes, 1960), but color analysis reveals a different ventral color relationship, based on collected specimens of varying ages. Interestingly, not one of the published images in the literature, nor in 900 images on inaturalist.org, butterfliesandmoths.org, or butterfliesofamerica.com show the reported "greenish" appearance of the ventral hindwing; just varying degrees of gray peppering on a variable brown background. The reference to "green" in later works might simply be a repeat of earlier works subject to visual misinterpretation (Fernald, 1884; French, 1886; Scudder, 1889). [One of us (Pavulaan) previously worked at a printing company, where a cost-saving "green" print was made by combining yellow with gray. This combination might account for the apparent "green" look of the underside of the wings, where pale, yellowish scales overlay a grayish ground color.]

The *hegon* complex is generally reported to be univoltine throughout its range, flying from March (Gulf Coast region) to July (Canadian Maritimes), but there are curious reports of possible second-generation individuals in August in Connecticut (O'Donnell, et al., 2007), Massachusetts (Stichter, 2015), and North Carolina (Glassberg, 1999; LeGrand & Howard, 2023), and even into September in Missouri (Heitzman & Heitzman, 1987). This requires future investigation and may reveal either an extended univoltine flight of any of the four taxa in the *hegon* complex into August in some places, or a partial second brood. Essentially, little is known of the hostplant choices of the four species in the *hegon* complex. Several hosts have been identified for *'A. hegon'*, but most published works simply appear to repeat earlier lists, including some which are certainly in error. More fieldwork is needed here as well. The only images of the larvae we have found are those shown in Allen (1997), Allen, et al. (2005), and Venable (2014).

William F. Kirby (1871) applied line priority, treating *Hesperia hegon* as a species over *H. samoset*. No life history information was given.

Charles H. Fernald (1884) listed this butterfly as *A. samoset.* The underside is described as "lighter than above, and heavily overlaid with greenish scales."

George H. French (1886) listed this butterfly as *A. samoset.* The underside is described as "lighter than the upper, overlaid with greenish scales…"

Samuel H. Scudder (1889), in his discussion of *samoset* at species rank, gave a rather detailed description of the adults. He describes the ventral color as "uniformly and profusely flecked with very pale greenish yellow scales, giving the wing a greenish gray appearance." Life history information concerning the broods, immature stages and the host was based on the illustrations of John Abbot: "Nothing is known of the earlier stages but what may be gleaned from Abbot." However, Calhoun (2019 and pers. corr.) convincingly stated that Abbot's drawings depicted a well-marked *Amblyscirtes alternata,* as well as the immature stages and host of *alternata*: "Scudder…misidentified the butterflies in the DBC and HLHO drawings as the species now recognized as *Amblyscirtes hegon*." Calhoun also stated: "While Abbot illustrated *A. alternata* many times, I found no evidence that he encountered *A. hegon.*" Based on this misidentification, Scudder erroneously believed that *samoset* has two broods in the southern states.

Scudder identified the host grass in Abbot's illustration as *Sorghastrum avenaceum* (Indiangrass), now known as *Sorghastrum nutans* per the USDA PLANTS Database (https://plants.usda.gov/home/plantProfile?symbol=SONU2). [*S. nutans* should be stricken from the record as a host of *A. hegon*, since Abbot's image shows it associated with *A. alternata.*] Scudder stated: "In the Boisduval MS, it is given as *Sorghum secundum."*, now known as *Sorghastrum secundum* (Lopsided Indiangrass). However, Abbot's original drawing of *A. alternata* depicts this grass accurately, matching the image of *Sorghastrum secundum* in the USDA PLANTS Database (https://plants.usda.gov/home/plantProfile?symbol=SOSE5). [Thus, *S. secundum* should also be stricken from the record as a host of *A. hegon.*]

Charles J. Maynard (1891) listed this butterfly as *A. samoset.* He described the underside as "brown, overwashed with whitish…"

William J. Holland (1898, 1931 [Revised Edition]) listed this butterfly as *A. samoset.* He described the underside as "pale gray".

William F. Fiske (1901) listed this butterfly as *A. samoset.*

Harrison G. Dyar (1902) listed this butterfly as *A. samoset*, with *hegon*, *nemoris* and *alternata* listed as synonyms.

John H. Comstock & Anna B. Comstock (1912) listed this butterfly as *A. samoset.* The ventral surface of the wings is described as "being overlaid with greenish scales."

James H. McDunnough (1938) listed this butterfly as *A. hegon*, with *samoset* and *nemoris* listed as synonyms.

Alexander B. Klots (1951) described the ventral hindwing of *A. hegon* as "heavily and coarsely dusted with light, greenish gray on a dark background." He erroneously followed Scudder (1889) in description of the larvae and broods: "One brood in north, supposedly two southward". The hostplant is given as "grasses".

Harrison M. Tietz (1952, 1972) correctly assigned *hegon* to species rank, and listed *samoset* and *nemoris* as synonyms. *Sorghum bicolor* (as *S. vulgare*) (Grain Sorghum) is listed under food plants.

Douglas C. Ferguson (1954) listed *hegon* as occurring in Nova Scotia, occurring from May 31 to July 2, and being "scarce and local."

William H. Evans (1955), citing Scudder (1889) as "first reviser", treated *samoset* at species rank, and *hegon* as a synonym. Line priority of *hegon* over *samoset* in the original descriptions (Scudder, 1863) shows this to be an erroneous treatment.

Bryant Mather & Katherine Mather (1958) list only two records for *hegon*, both from Tishomingo County in extreme northeast Mississippi. These would most likely actually be *nemoris*. The specimens of *matheri* were collected in southwest Mississippi after publication of this work and it's three supplements.

William T. M. Forbes (1960) provided a rather enlightening taxonomic account under *A. samoset*: "The two names [referring to *hegon* and *samoset*] were published together, and Scudder later chose *samoset*, as he then (and now) had a right to do; the use of *hegon* is based on a blind following of "page priority". Forbes described the underside: "Below evenly dusted with pale yellow, giving a faint greenish effect when fresh (fading in a collection) …"

Cyril F. dos Passos (1964) listed *samoset* at species rank, with *hegon, nemoris* and *argina* as synonyms.

Lucien Harris, Jr. (1972) chose to refer to this as *Amblyscirtes samoset*. Flight dates in Georgia are April through May, but one July record is listed.

Roderick R. Irwin & John C. Downey (1973) listed *samoset* at species rank.

Auburn E. Brower (1974) correctly assigned *hegon* to species rank, and listed *samoset* as synonym.

Arthur M. Shapiro (1974) describes the flight of *hegon* as: "One brood, late vi-early vii, northward; partially double-brooded in Finger Lakes, vi.3-vi.20 and vii.22."

C. Don MacNeill *in* William H. Howe (1975) described the ventral hindwing of *A. hegon* as being "heavily dusted with greenish gray scaling. The listed hostplants *Sorghastrum nutans* (=*avenaceum*) and *S. secundum* are, no doubt, cited from Scudder and are in error.

Bryant Mather & Katherine Mather (1976) interestingly changed the Mississippi listing of *hegon* to *samoset*. This would most likely actually be *nemoris*.

Lee D. Miller & F. Martin Brown (1981) listed *hegon* at species rank, with *samoset, nemoris* and *argina* listed as synonyms.

Robert M. Pyle (1981) described the ventral side of *hegon* as "putty gray with understated light spots; greenish cast over HW."

Lee D. Miller & F. M. Brown *in* Ronald W. Hodges (1983) listed *hegon* at species rank, with *samoset, nemoris* and *argina* listed as synonyms.

Paul A. Opler & George O. Krizek (1984) described the ventral hindwing as: "dusted with light gray-green scales". The habitat is described as "glades or at the edges of mixed or coniferous forest as well as at the edges of bogs or boggy streams." The authors correctly state that "*hegon* is univoltine throughout its range, but rare, late-emerging adults are occasionally found in late July [northern New York]". The hostplants are given as *Poa pratensis* (Kentucky Bluegrass), *Sorghastrum nutans* and *Sorghastrum secundum* [both likely in error as host of *A. alternata*], and *Uniola latifolia* (Indian Woodoats) [now recognized as *Chasmanthium latifolium* (Indian Sea Oats)].

Bryant Mather & Katherine Mather (1985) interestingly changed the Mississippi listing of *samoset* back to *hegon*. This would most likely actually be *nemoris*.

James A. Scott (1986) described the ventral hindwing as "greenish-gray." The hostplants are given as *Poa pratensis*, *Sorghastrum nutans* and *S. secundum* [both likely in error as host of *A. alternata*], and *Uniola latifolia* [now recognized as *Chasmanthium latifolium*].

Ernest M. Shull (1987) described the ventral hindwing of *hegon* as "heavily dusted with greenish gray…"

J. Richard Heitzman & Joan E. Heitzman (1987) describe *hegon* as having "greenish-gray scaling of the wings beneath." They described the brood sequence in Missouri: "Most specimens have been found in April and May, but there are June, July and September records, indicating at least partial broods during the summer."

Paul Klassen, A. Richard Westwood, William B. Preston & W. Brian McKillop (1989) describe the underside of *hegon* as "dusted with pale gray…The veins on the underside of the hindwings are highlighted with whitish-gray…Most specimens have a greenish-gray hue on the underside of the wings."

Paul A. Opler & Vichai Malikul (1992) described the ventral hindwing of *hegon* as "light gray-green". The flight period is described as "April-July, rarely early Aug. (1 brood), earliest in the south."

Jeffrey Glassberg (1993) described the underside as "yellowish tinged gray-brown ground…"

Thomas J. Allen (1997) described the underside as "brownish gray". He describes the habitat preference as: "This skipper prefers wet areas and is found along streams, bogs, low-lying wet meadows, and glades at the edges of mixed or coniferous forests." He correctly stated that *hegon* is univoltine throughout its range. The larvae is described as "pale green with 3 dark green dorsal stripes and a pale lateral stripe" and the host is given as *Glyceria striata* (Fowl Mannagrass).

Ross A. Layberry, Peter W. Hall & J. Donald Lafontaine (1998) described *A. hegon* with the ventral hindwing as "grey, with a slightly greenish tinge that is most noticeable in fresh specimens…"

Paul A. Opler & Amy B. Wright (1999) described the ventral hindwing of *hegon* as "light gray-green".

Jeffrey Glassberg (1999) described the underside as "olive-tinged gray-brown…" The brood sequence is given as "1 brood + partial second north to Virginia and Missouri-mid April-May, rare partial July-Aug."

Mogens C. Nielsen (1999) described the underside of hegon as "grayish green."

Jim P. Brock & Kenn Kaufman (2003) describe the ventral hindwing of *hegon* as "frosted greenish gray". The brood sequence is described as "late spring (mainly) to summer in south (1-2 broods), early summer in north (1 brood).

Marc C. Minno, Jerry F. Butler & Donald W. Hall (2005) indicate a single *hegon* flight in Florida, and suggest the host as "probably" *Glyceria striata*. The larva is illustrated.

Jane O'Donnell, Lawrence Gall & David Wagner (2007) describe the underside in Connecticut specimens as "Wings below medium to dark brown with extensive gray frosting and fainter spots."

W. Mike Howell & Vitaly Charny (2010) repeat previous host lists, including *Poa pratensis* and *Chasmanthium latifolium*. The listed hostplants *Sorghastrum nutans* (=*avenaceum*)

and *S. secundum* originate from Scudder and are certainly in error. The authors indicate a single brood in Alabama, late March to late June.

John K. Bouseman, James G. Sternburg & James R. Wiker (2010) describe the venter of *hegon* as "…the anterior half of the forewing is dusted with gray-green scales. Similar scales extend over the entire hindwing." The authors add *Cinna arundinacea* (Stout Wood Reed) to the list of hosts.

Jim Patterson (2011) identified *hegon* as "A very small dark gray skipper with greenish overtones on the ventral side."

Peter W. Hall, Colin D. Jones, Antonia Guidotti & Brad Hubley (2014) described *A. hegon* with the underside as: "Both wings flecked with greyish-green when fresh, creating the "pepper and salt" effect. With age, the flecking wears away and the wings become more uniform dark brown."

Rita Venable (2014) noted, regarding the ventral color of *hegon*: "…they start out gray and end up dark brown! Their gray scales just wear off with time." This accurately describes the difficulty observers will have, differentiating the four species described in this work based solely on ventral ground color. The host listed for Tennessee is *Chasmanthium latifolium* (River Oats, or Indian Woodoats), discussed extensively. Several hosts are repeated from previous authors, one very likely in error: *Sorghastrum* sp. (Indiangrass), a host of *A. alternata*. The larva is illustrated. A single brood is noted, flying in April through June.

Lori Spencer (2014) describes the ventral side of *hegon* as having "grayish green shading". Two broods are suggested: April-July.

Jeffrey Glassberg (2017) described the ventral side as "green-gray, sometimes pink/purple-gray." Interestingly he notes: "females usually tan [below]". Here, he describes the broods as "two broods, second is partial, Apr-May, July-Aug."

James L. Monroe & David M. Wright (2017) described the ventral side with "extensive gray overscaling…slight greenish sheen when fresh." The habitat is described as "woodland openings and edges, streamsides" and the host is given as *Brachyelytrum erectum* (Bearded Shorthusk).

Craig Marks (2017) was first to publish a note of two ventral color forms: "I have found two "forms" … of the Pepper and Salt Roadside Skipper in LA." Marks described the habitat as "heavily wooded loess hills with deep ravines" and also noted "there was a great deal of cane growing, both in the ravines and along the road." Marks additionally noted: "These skippers were extremely abundant, both on the road basking and taking nectar at wild garlic." Lastly, it was noted that one out of five seen that day were of the tan variety. The tan variant was illustrated for the first time.

Craig Marks (2018) further noted the two ventral color forms: "At Sicily Island Hills WMA, I would estimate that one out of five seen were tan colored dorsally [correctly: ventrally] rather than the typical slate gray." A single brood is reported for Louisiana, in March and April.

Phillip G. deMaynadier, John Klymko, Ronald G. Butler, W. Herbert Wilson, Jr., and John V. Calhoun (2023) described the ventral side of *hegon* in Maine and the Canadian Maritime Provinces as: "brown with grayish-green scaling…becoming more dark brown with wear." They note one annual generation from late-May to mid-July with a flight peak in mid-June, and that the host in that region is unknown.

METHODOLOGY AND GENERAL RESULTS

A combination of genomic and wing color analyses was performed on a series of specimens across the historically recognized range of *hegon*. An additional sample of specimens was used to determine differences in genitalia. Dr. Andrew Warren assisted, prior to this study, in extracting the male genitalia of *matheri* and *nemoris*.

Genomic DNA extraction (from legs), sequencing, and computational analyses were carried out using the Grishin lab published protocols (Li et al. 2019; Cong et al. 2021; Robbins et al. 2022). In brief, a leg was detached from a specimen and non-destructively soaked in DNA extraction solution. Genomic libraries were constructed from DNA and sequenced at 150 bp or shorter. Every DNA sequence that made it into the libraries was sequenced, even very short ones (30 bp), thus allowing us to sequence old specimens with DNA degraded to short fragments. The resulting sequences were mapped on protein-coding genes of a reference genome of *Lerema accius* (J. E. Smith, 1797) (i.e., a well-assembled genome of a close relative made from recently collected specimens), and phylogenetic trees constructed from such alignments: for a random sample of positions from all nuclear genome genes in autosomes, those predicted to be in the Z chromosome and those in the mitochondrial genome. The Z chromosome tree is typically best correlated with speciation (Cong et al. 2019) and is shown in **Fig. 11**.

We used whole genome shotgun sequencing to learn about genetic differences between the tan-brown and what we assumed at the time was "regular" *A. hegon* and sequenced several specimens of each "form". To our initial surprise, the two "forms" separated into two groups in the Z chromosome. Genetic differentiation between them in the Z chromosome was strong and suggestive of distinct species with F_{st}/G_{min} values of 0.43/0.003 (Cong et al. 2019). Much intrigued by this initial assessment, we broadened sequencing efforts, and got even more surprising results (**Fig. 11**). What was considered a single species *A. hegon*, partitioned into four distinct and strongly supported clades in the Z chromosome tree. The most genetically differentiated from other clades is the tan-brown "hegon". Three other clades are closer to each other, but they are overlapping in distributions (**Fig. 12**), some quite significantly, over hundreds of miles and therefore are expected to be sympatric. For instance, representatives of all three clades have been recorded from West Virginia. Within each clade, specimens are close to each other regardless of the locality. This lack of genetic differentiation within each clade suggests ongoing gene flow throughout the range of the clade.

Conversely, the separation between the clades in the Z chromosome is prominent. Due to the sympatry of the clades, individuals from different clades have the opportunity to meet and exchange genes. If this exchange was frequent, it would have led to the equilibration of allele frequencies (as we see within clades), and there would be no prominent clades in the tree as a result. Therefore, a combination of this Z chromosome tree structure (distinct well-separated clades and the lack of statistically supported clustering within clades, **Fig. 11**) with the sympatry of the

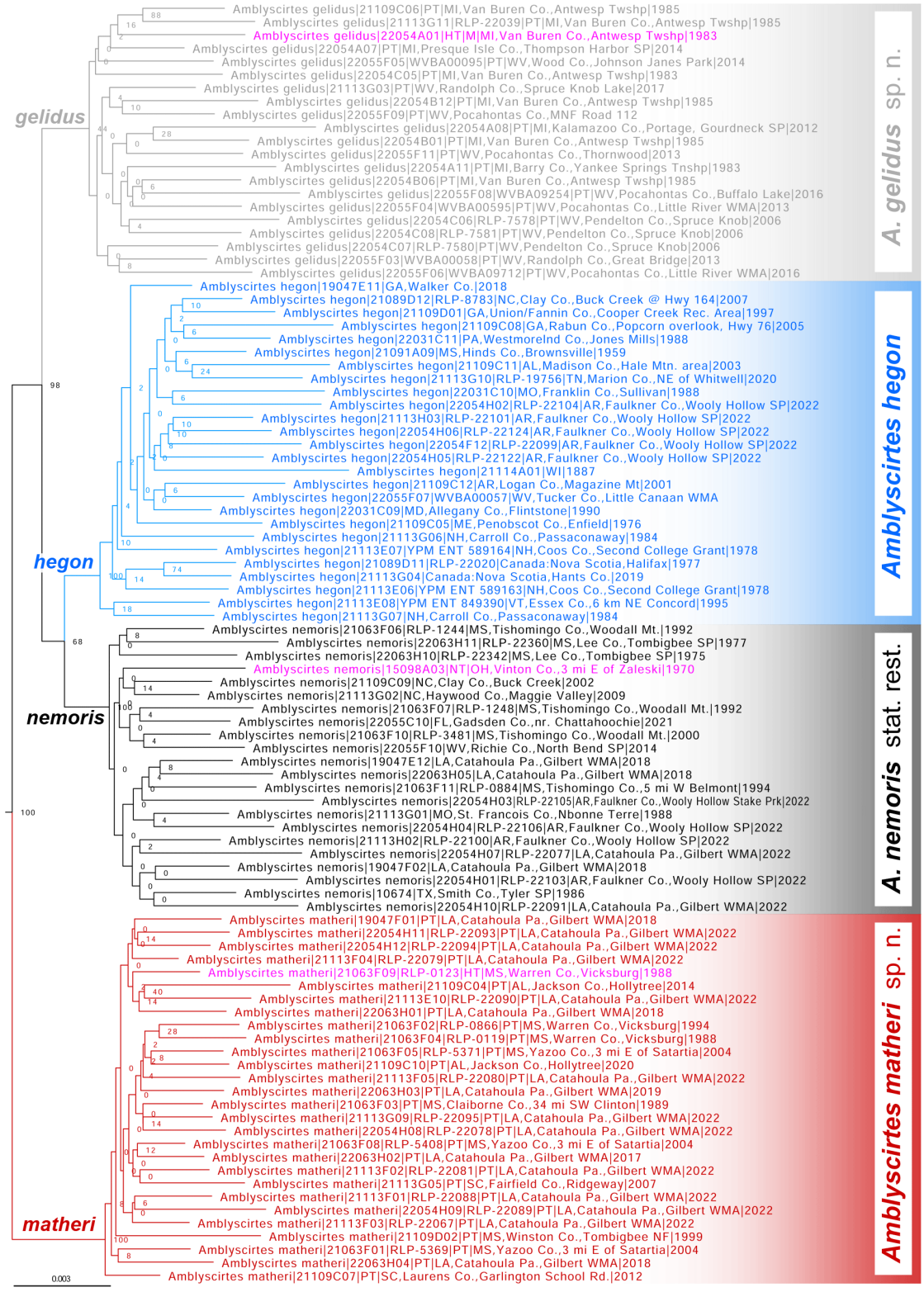


Fig. 11. The phylogenetic tree of the *Amblyscirtes hegon* complex inferred from protein-coding regions in the Z chromosome. Different species are colored in different colors: *A. gelidus* (gray), *A. hegon* (blue), *A nemoris* (black), and *A. matheri* (red). Primary type specimens are labeled in magenta. Values by nodes show statistical support values (in %) for corresponding bipartitions.

clades suggests that the four clades represent four distinct species. Indeed, restricted (or nearly absent) gene flow between the clades (meaning that they represent species) would explain the prominence of these four clades. Further details of the genomic analysis of these specimens will be presented elsewhere. This study focuses on the phenotypic analysis and description of the new species. We only note that the mitochondrial DNA reveals a number of haplotypes and introgression between these species but the most distinct tan-brown, which has a unique set of haplotypes among sequenced specimens. The COI barcodes between the tan-brown species and others differ by about 0.9%.

From the genomic analysis of the Z chromosome, we deduce that *A. hegon* is a complex of four distinct species. Only one species reaches the extreme northeast of the range, where the type locality of *A. hegon* was established. Therefore, we identify this species as *A. hegon*. Incidentally, this is the most widespread species out of four (blue in **Figs. 11, 12**). We continue treating *Pyrgus argina* Plötz, 1884 as conspecific with *A. hegon* (the blue clade) based on an old specimen in MFNB (sequenced as NVG-21114A01) resembling a drawing of *P. argina* (see p. 21). Genomic sequencing of the neotype of *Hesperia nemoris* W. H. Edwards, 1864, places it in the black clade. Therefore, the black clade is *A. nemoris*, **stat. rest**. The other two clades (red and gray) do not have available names associated with them and represent new species that are described below.

In summary, **genomic sequencing reveals that *A. hegon* is a complex of four species**. Combining this information with the type localities of available names and sequencing of primary type specimens assigns names to two species and implies that two others are new.

Employing genomic analysis, specimens that were identified to species, and additional specimens from several of these locations, were subjected to color analysis using the Color Grab™ cellphone application (www.loomatix.com), version 3.9.2, to establish exacting RGB and HSB color codes under "daylight" fluorescent lighting, in combination with the Colblindor™ application (www.color-blindness.com/color-name-hue/) to produce refined color swatches rather than giving generalized color descriptions as is traditional with taxon descriptions. Six different areas of the wings (**Fig. 13**) were measured for their red/green/blue (RGB) and hue/saturation/brightness (HSB) color codes. Color codes of individual specimens were then averaged to produce results for each species (**Fig. 14**). Color names in the description of each of the four species reference the color names given in the Color Grab and Colblindor applications. Of particular interest are the results of analyzing the ventral hindwings. While the human eye perceives a "greenish" look on the ventral hindwing, particularly in *nemoris*, and as is often described for "*hegon*" in the literature, primarily due to the over-peppering of pale scales, both of the color applications apparently view the base ground color and not the effect of peppering.

Additionally, wing measurements were made from the examined series. Measurements were made of wingspan, forewing length, and the angle of the apical spot row from the leading edge of the forewing (**Fig. 15**). These were then averaged and a range for each was determined (**Fig. 16**).

Specimens subjected to genomic analysis were then mapped to determine their geographic distribution (**Fig. 12**).

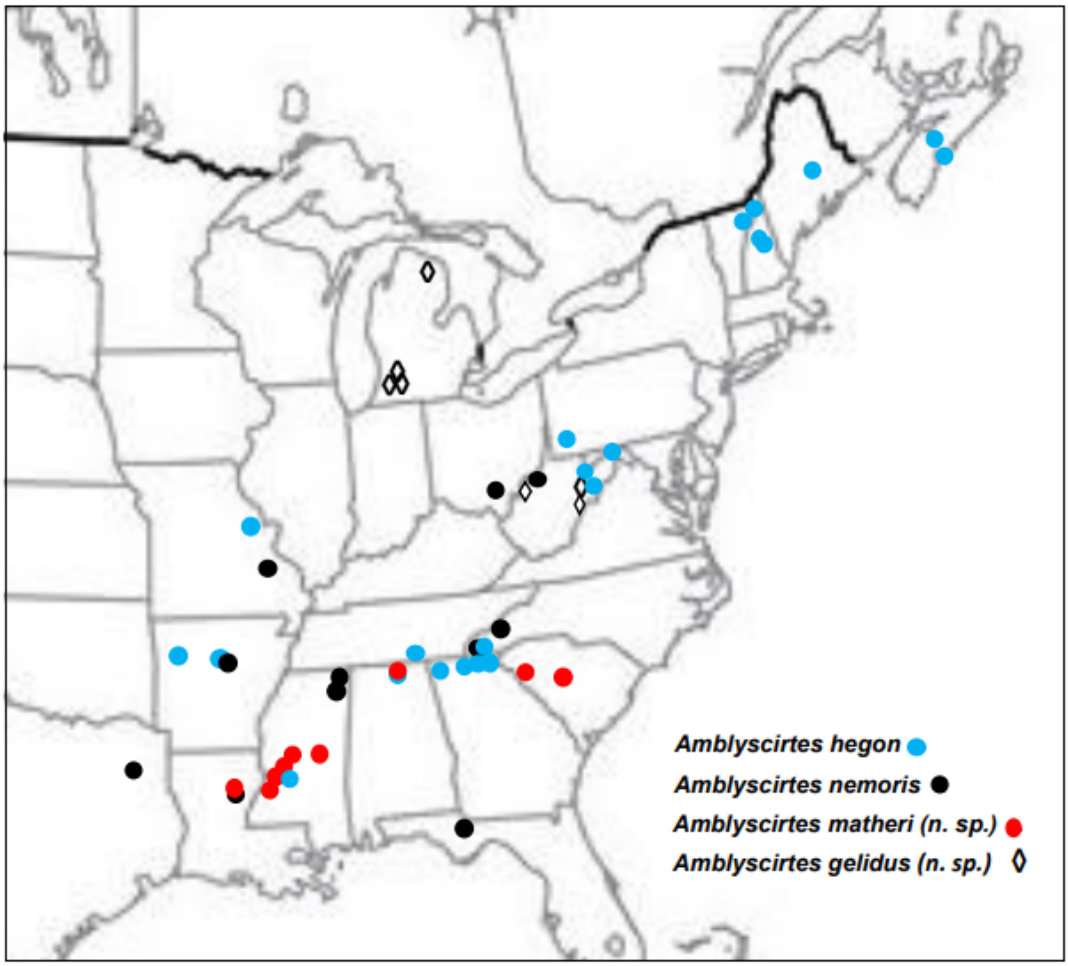
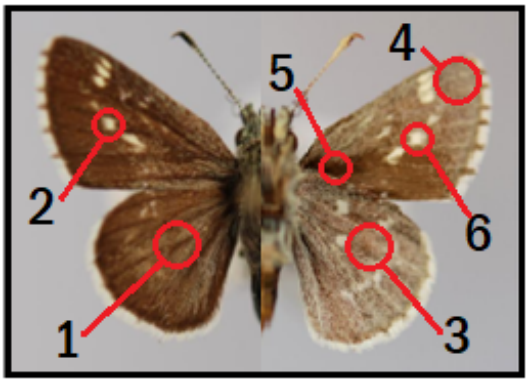


Fig. 12. Distribution of specimens of the four species determined by genomic analysis.



1 – Dorsal ground color.

2 – Dorsal spots color.

3 – Ventral hindwing ground color.

4 – Ventral forewing apex color.

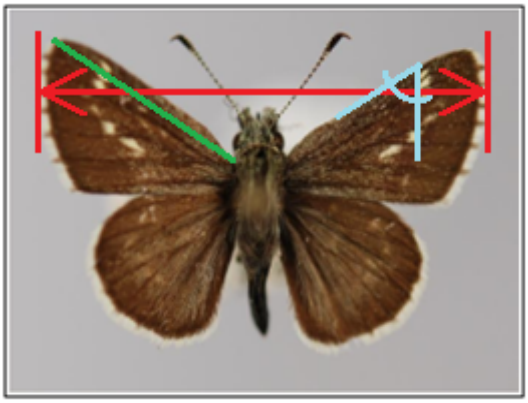
5 – Ventral forewing base color.

6 – Ventral spots color.

Fig. 13. Wing areas analyzed using color analysis.

Species	Ventral HW ground color	Ventral HW ground color RGB color code HSB color code	Ventral FW apex color	Ventral FW apex color RGB color code HSB color code	Ventral FW base color	Ventral FW base color RGB color code HSB color code	Ventral spots color	Ventral spots color RGB color code HSB color code	Dorsal ground color	Dorsal ground color RGB color code HSB color code	Dorsal spots color	Dorsal spots color RGB color code HSB color code
A. hegon		121, 87, 90 355, 28, 47		87, 73, 54 34, 37, 34		62, 44, 33 22, 46, 24		204, 192, 159 43, 22, 80		59, 42, 30 24, 49, 23		208, 190, 154 40, 25, 81
A. nemoris		112, 100, 86 32, 23, 43		91, 77, 61 31, 32, 35		64, 46, 30 28, 53, 25		204, 192, 160 43, 21, 80		69, 56, 37 35, 46, 27		211, 195, 153 43, 27, 82
A. matheri		149, 124, 96 31, 35, 58		144, 116, 86 31, 40, 56		76, 50, 28 27, 63, 29		202, 184, 153 37, 24, 79		107, 77, 44 31, 58, 41		200, 179, 134 40, 32, 78
A. gelidus		144, 136, 123 37, 14, 56		105, 93, 79 32, 24, 41		79, 59, 52 15, 34, 30		207, 196, 167 43, 19, 81		84, 58, 48 16, 42, 32		215, 199, 159 42, 26, 84

Fig. 14. Color analysis results (average colors) of four species in the study. Note ventral HW ground colors.



Wing measurements:

Red line – Wingspan.

Green line – Forewing Length.

Blue angle – Angle of subapical spots from leading edge of forewing.

Fig. 15. Wing measurement areas.

Species	Wingspan average (mm)	Wingspan range (mm)	FW length average (mm)	FW length range (mm)	Angle of apical spots average (degrees)	Angle of apical spots range (degrees)
A. hegon	23.4	20-26	11.9	10-13	78.0	65-90
A. nemoris	22.8	22-24	11.8	11-13	79.8	65-90
A. matheri	24.0	22-25	12.4	11-14	72.0	54-85
A. gelidus	24.1	23-25	12.3	11-13	75.3	68-80

Fig. 16. Wing measurements.

Lastly, the genitalia of males of each of the four identified species was microscopically examined for differences (**Figs. 16 & 17**).

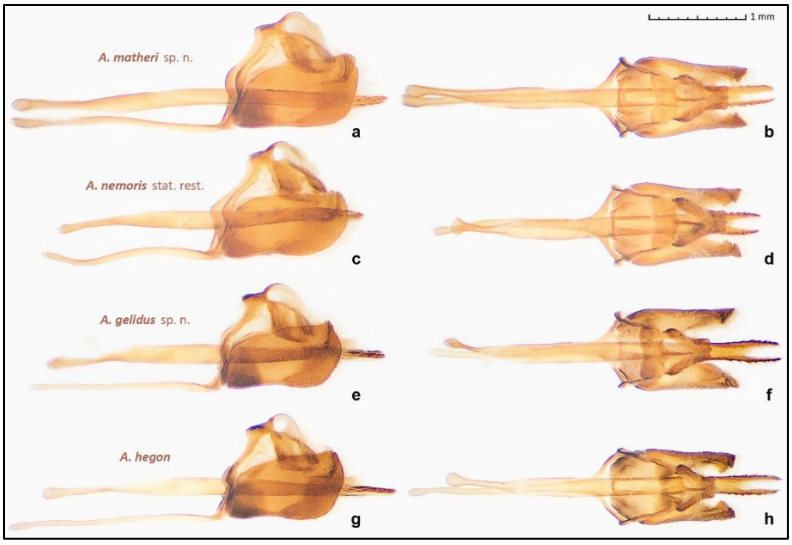


Fig. 16. Male genitalia of *Amblyscirtes hegon* complex from USA. **a–b.** *A. matheri* **sp. n.** paratype, Mississippi, Warren Co., Vicksburg, 27-Mar-2000, R. Patterson leg., genitalia vial #01-02 Andrew D. Warren. **c–d.** *A. nemoris* **stat. rest.**, Mississippi, Tishomingo Co., Woodall Mt., 4-Apr-2000, R. Patterson leg., DNA sample NVG-21063F10, genitalia vial #01-03 Andrew D. Warren. **e–f.** *A. gelidus* **sp. n.**, holotype, DNA sample NVG-22054A01, genitalia NVG230128-01. **g–h.** *A. hegon*, Arkansas, Faulkner Co., Wooly Hollow State Park, 26-Apr-2022, R. Patterson leg., RLP#22101, DNA sample NVG-21113H03, genitalia NVG230130-01. **a. c. e. g.** left lateral and **b. d. f. h.** dorsal views.

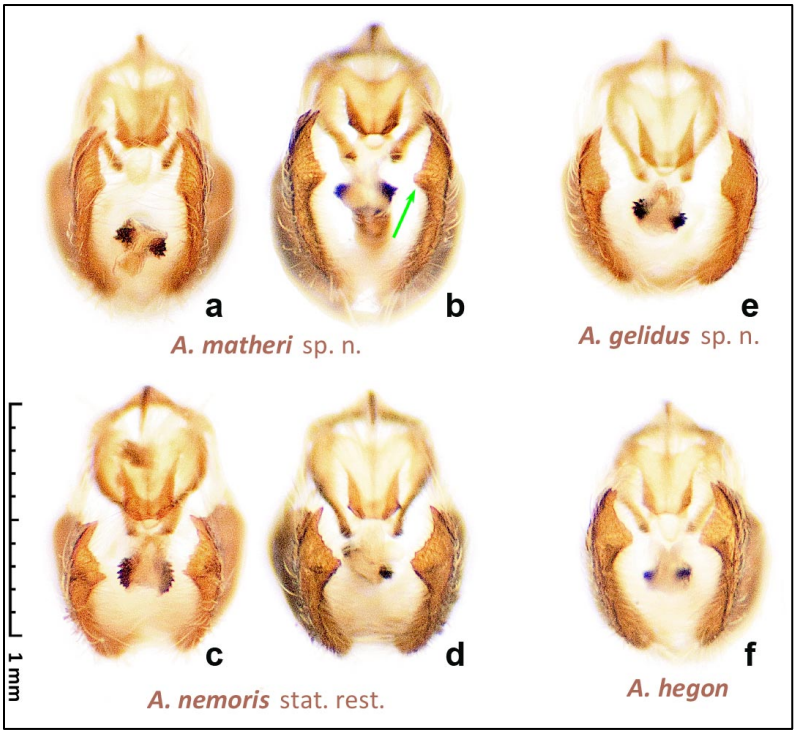


Fig. 17. Male genitalia of *Amblyscirtes hegon* complex in posterior view. Green arrow points to broad tooth on the inner surface of harpe, expanded differently in these species. **a-b:** *A. matheri* **sp. n.** [**a:** ADW#01-02. **b:** NVG-21113F02, NVG230130-03], **c-d:** *A. nemoris* **stat. rest.** [**c:** NVG-21063F10. **d:** NVG-21113H02, NVG230130-02], **e:** *A. gelidus* **sp. n.**, holotype [NVG-22054A01, NVG230128-01], **f:** *A. hegon* [NVG-21113H03, NVG230130-01].

DESCRIPTIONS: THE *AMBLYSCIRTES HEGON* COMPLEX

Amblyscirtes hegon **(Scudder, 1863)**

syn: *samoset* (Scudder, 1863)
syn: *argina* (Plötz, 1884)

DESCRIPTION AND PHENOTYPIC COMPARISON OF ADULTS

Color names are given per Color Grab™ and Colblindor™ applications used in the analysis for sake of easy reference. Per Scudder (1863, 1889), this species is recognized primarily by the dark brown color of the ventral hindwings, identified as "Buccaneer" (brown) in the present analysis. The color swatches (**Fig. 14**) show *hegon* to have a very slight violet pigment, compared to *nemoris, matheri* and *gelidus.* Some individuals vary to gray brown, with a perceived "peppery" look, making differentiation from *nemoris* and *gelidus* problematic. The ventral forewing apex is similarly colored to the hindwing, being slightly darker ("Brown Derby"). The last area of the forewing that was analyzed was the darkest portion of the base of the forewing ("Bistre" brown). There was no appreciable difference in color here, between the four species.

The dorsal brown ground color ("Bistre") differs little from either *nemoris* ("Mikado") or *gelidus* ("Very Dark Brown"), but is considerably darker than *matheri* ("Horses Neck") *(***Fig. 14**). Scudder (1889) gives detailed description of the dorsal and ventral spot pattern, which are individually variable in extent across all four species in the *hegon* complex. The colors of the light dorsal spots ("Double Spanish White") and ventral spots ("Soft Amber") differ very little from either *nemoris, matheri* or *gelidus* (**Fig. 14**) and are essentially unreliable for differentiating the species. In *hegon* the ventral hindwing spot pattern tends to be reduced in extent, frequently being absent altogether. Specimens confirmed as *hegon* from northern New England, the Canadian Maritimes and southern Appalachian Mountains have a high percentage of individuals with unmarked ventral hindwings. Other features in the descriptions of *hegon* and *samoset* (Scudder, 1863, 1889) similarly apply to *nemoris, matheri* and *gelidus* and pose identification challenges to observers.

Scudder (1889) provided measurements of the forewings in millimeters. Males (n=3) ranged 11.6–12.2 mm and averaged 12.2 mm. The present analysis of forewing length measured males (n=17) ranging 10.0-13.0 mm, and averaging 11.6 mm. Scudder measured female (n=3) forewings, ranging 11.5-12.5 mm, and averaging 12.1 mm. The present analysis measured females (n=7) ranging 12.0-13.0 mm, and averaging 12.4 mm. All sexes averaged together (**Fig. 16**) shows *hegon* adults having forewing length ranging 10-13 mm, and averaging 11.9 mm. Wingspan of males was measured at 20-25 mm (n=17), averaging 22.8 mm, and females (n=7) measured at 24-26 mm, averaging 24.9 mm. All sexes averaged together (**Fig. 16**) show *hegon* adults having a wingspan of 20-26 mm, averaging 23.4 mm; showing *hegon* to have the largest and smallest individuals of the four species. Specimens from the northeastern portion of the species' range

averaged slightly smaller, whereas specimens from the southern Appalachian Mountains averaged slightly larger. The measurements show that *hegon* and *nemoris* have similar forewing length and wingspan, whereas *matheri* and *gelidus* were both larger (**Fig. 16**). A larger sample would be necessary to better define size differences between the two regions.

Of interest to us was the difference in the angle of the subapical spot row from the leading edge of the forewing (**Fig. 16**), showing little difference between *hegon* and *nemoris*. Both *matheri* and *gelidus* showed the alignment of the apical spots to have a sharper average angle. While the measured angle varied greatly, *hegon, nemoris* and to a lesser degree, *gelidus* ranged closer to a 90° angle than *matheri*, which showed the apical spot row to sit at a sharper angle from the leading edge of the forewing.

Differences in male genitalia between species are slight and difficult to assess due to individual variation. Typically, a combination of two characters would distinguish the species. First is the extent of development of the broad tooth on the inner surface of harpe, best seen in posterior view (**Fig. 17**, note green arrow on panel **b**) and dorsal view (**Fig. 16b, d, f, h**). Second is the shape of valva and harpe in lateral view (**Fig. 16**). In *A. hegon*, the tooth is larger and more robust (**Fig. 17d**), similar to *A. nemoris* **stat. rest.**, but different from both of the two new species, in which the tooth is shallower and does not protrude much between the valvae. In *A. hegon*, the valva tends to broaden somewhat from the base to harpe, with its dorsal and ventral margins at an angle (in lateral view). This broadening is not only due to expansion of the ampulla region on costa, but also because harpe ventral margin is more convex near the base and somewhat expanded ventrad (**Fig. 16g**). This valva shape is quite similar in *A. gelidus*, from which it can be distinguished by a more robust tooth on the inner surface of valva.

IMMATURE STAGES

Scudder (1889) gave a rather detailed description of the caterpillar, chrysalis and host of what he believed to be *samoset*, based on the illustrations of John Abbot. The host in Abbot's illustration is determined to be *Sorghastrum nutans* (=*avenaceum*) (Indiangrass). However, Calhoun (2019 and pers. corr.) believes that Abbot's drawings depicted the immature stages and host of *Amblyscirtes alternata*.

SPECIMENS OF *A. HEGON* EXAMINED IN PRESENT STUDY:

Alabama: Madison Co., Hale Mtn. area (leg. Howard Grisham), 4 May 2003.

Arkansas: Faulkner Co., Wooly Hollow State Park (leg. Ricky Patterson), 26 April 2022 (2 ♂ RLP #22101/NVG-21113H03, RLP #22099/NVG-22054F12, 1 ♀ RLP #22104/NVG-22054H02), 8 May 2022 (2 ♂).

Arkansas: Logan Co., Magazine Mountain (collection of Howard Grisham), 25 May 2001.

Georgia: Rabun Co., Hwy 76 @ Popcorn Overlook (leg. Ron Gatrelle), 25 May 2005.

Georgia: Union/Fannin Co., Cooper Creek Recreation Area (collection of Howard Grisham), 5 July 1997.

Georgia: Walker Co. (leg. Jeff Slotten), late April 2018.

Maine: Penobscot Co., Enfield (leg. L. Paul Grey), 5 June 1976 (collection of Howard Grisham).
Maryland: Allegany Co., Flintstone (Harry Pavulaan), 20 May 1990.
Mississippi: Hinds Co., Brownsville (leg. Bryant Mather), 24 March 1959 (1 ♂), NVG-21091A09.
Missouri: Franklin Co., Sullivan (leg. Harry Pavulaan), 28 May 1988.
New Hampshire: Carroll Co., Passaconaway (leg. Harry Pavulaan), 13 July 1984.
New Hampshire: Coos Co., Second College Grant (leg. Richard E. Grey), 11 June 1978 (2 specimens via PMNH collection).
North Carolina: Clay Co., Buck Creek @ Hwy. 164 (leg. Ricky Patterson), 17 May 2007 (2 ♂).
Nova Scotia (Canada): Halifax Regional Municipality, Fairview (leg. Chris T. Maier), 5 June 1995 (via PMNH collection).
Nova Scotia (Canada): Fairview, Halifax Regional Municipality (leg. Ken Neil), 26 June 1977 (1 specimen).
Nova Scotia (Canada): Hants Co., Mt. Uniacke (leg. Derek Bridgehouse), 18 June 2019 (1 specimen).
Pennsylvania: Westmoreland Co., Jones Mills (leg. Harry Pavulaan), 22 May 1988.
Tennessee: Marion Co., NE of Whitwell (leg. Ricky Patterson), 23 May 2020 (1 ♀).
Vermont: Essex Co., 6 km NE of Concord, (leg. Chris T. Maier) 5 June 1995 (via PMNH collection).
West Virginia: Tucker Co., Little Canaan W.M.A. (leg. Susan Olcott), 31 May 2013 (♂), WVBA00057, NVG-22055F07.
"Wisconsin", 1887, NVG-21114A01 in MFNB (Berlin, Germany) (**Fig. 18b**).

HABITAT AND DISTRIBUTION

The habitat is described as "open places in woods" (Scudder, 1889) but is primarily associated with forest habitats, and mostly found along forest roads. Specimens confirmed as *hegon* were taken along dirt roads through shale barren forest habitat near Flintstone, MD. At Markham, VA., a single specimen was collected along a forest edge adjacent to a lake. Many varied habitats are given for "*hegon*", but extensive fieldwork and verification to species will be required to determine the exact habitat requirements of the four species in this complex.

Amblyscirtes hegon flies in early to mid-spring (mid-March in Mississippi through mid-June in Nova Scotia) which due to the wide distribution of this species will vary along with spring from south to north following the distribution. We have confirmed specimens of *Amblyscirtes hegon* from the northeast (Nova Scotia, New Hampshire, Pennsylvania, Maryland, Maine, and Vermont), the Appalachian Mountains in southwest North Carolina, northern Georgia, northeast Alabama, and southeast Tennessee, as well as the Ozark and Ouachita mountains of Arkansas and Missouri, and near Brownsville in Hinds County, Mississippi. This last specimen is the odd one, it is not from a mountain area, but a hardwood forested area in central Mississippi. Based on this, it seems possible that *Amblyscirtes hegon* could appear in many places in the eastern and central United States.

As with its sister species, the habitat of *Amblyscirtes hegon* is openings in or near shaded wooded areas, often nectaring on flowers such as blackberry, clover, and other early spring

flowers. It also is often found at damp soil, or resting on bare areas on gravel roads and forested foot trails. This species has been found flying sympatrically with *Amblyscirtes nemoris* in North Carolina and Arkansas.

Amblyscirtes hegon seems to be a generally more northeastern species, but specimens have been identified from as far west as Arkansas and Missouri, and as far southeast as northern Georgia, and as far southwest as Hinds County, Mississippi.

Based on specimens examined by us, Mississippi and West Virginia are the only states that have three of these species resident (*Amblyscirtes hegon, A. matheri,* and *A. nemoris* in Mississippi, and *A. hegon, A. matheri,* and *A. gelidus* in West Virginia), but none were found flying sympatrically with each other in these two states.

Analysis of *Pyrgus* (*Syrichthus* [sic]) *argina* Plötz, 1884

The name *Pyrgus* (*Syrichthus* [*sic*]) *argina* was published by Plötz (1884), who attributed it to Herrich-Schäffer, from an unstated number of specimens with the locality given as "Brisbane." Plötz assigned this species to the genus *Pyrgus* Hübner, [1819] but placed it near the end of his identification key (the description was in the form of a key), next to a couple of species that are currently not in *Pyrgus*. We regard that *P. argina* is differentiated from other species by the following characters, as translated from Plötz (1884): "Black-brown upper side. Forewing only with the typical white spots: that in the discal cell is split, that in cell 1 is divided and gray, in cell 5 a dash. Hindwing with 5 gray dots in the arch past the middle. Underside gray with brown veins: FW with the white spots as above, brown on the posterior half, hindwings with 8 white dots in the ¾ [of a] circle and one [dot] in the middle." By "typical white spots" for *Pyrgus*, Plötz meant the postdiscal row and the discal forewing spot, not including the submarginal rows of spots or dots characteristic of many *Pyrgus* and *Burnsius* Grishin, 2019 species.

In addition to the description, Plötz prepared drawings of many species included in his keys, but the whereabouts of the original drawings remain unknown (Nakahara et al., 2022). Godman studied these originals and recruited Horace Knight (and possibly other artists) to make copies for the species he could not immediately recognize (Godman, 1907). A compilation of these copies is in the library of the Natural History Museum, London (Zhang et al., 2022a; Zhang et al., 2022b), and it contains *P. argina* under the number 903, reproduced here as **Fig. 18a**. Inspecting these Godman's copies of Plötz's drawings, Evans (1949) concluded that *P. argina* was not the Old World, but American species conspecific with *A. hegon*, which at that time was treated as a junior subjective synonym of *Hesperia samoset* Scudder, 1864 (Evans, 1955). Evans' opinion has not been challenged since, and *P. argina* was included as a junior subjective synonym of *A. hegon* in all subsequent literature (Evans, 1955; Mielke, 2005; Pelham, 2023).

With our discovery that *A. hegon* is a complex of four cryptic species, confidently identifiable only by DNA, it became desirable to study the taxonomic identity of *P. argina*. Because we were not aware of *P. argina* type specimens, we undertook a brief search for them in

the MFNB collection. We found an old specimen somewhat resembling the illustration of *P. argina*, but nevertheless differing from it in several aspects, such as ventral hindwing postdiscal row of pale spots being mostly connected into a band (instead of separated round spots as illustrated in **Fig. 18a**) and the lack of a pale spot in the forewing cell M_1-M_2. This specimen (**Fig. 18b**), a female unidentified in the MFNB collection that we placed in the *A. hegon* complex by visual inspection, came from the Möschler collection. Möschler was sending specimens to Plötz for identification (Möschler, 1876), and Plötz used some of them in his drawings and descriptions. However, this female was collected in 1887 according to its label, and therefore after the description of *P. argina*, hence cannot be a syntype. The only locality information about this female is "Wiscons." There was also a second specimen, a male, with the same locality and collection label, but identified as "samoset." A leg of the female was sampled for genomic sequencing (NVG-21114A01), and the Z chromosome tree implied that out of the four species, it was conspecific with *A. hegon* (**Fig. 11**) that is treated as a senior synonym of *P. argina* in nearly all publications. Therefore, we concur with the previous assessment of *P. argina* being a junior subjective synonym of *A. hegon*. We will conduct a more detailed search for *P. argina* syntypes prior to proceeding with the neotype designation.

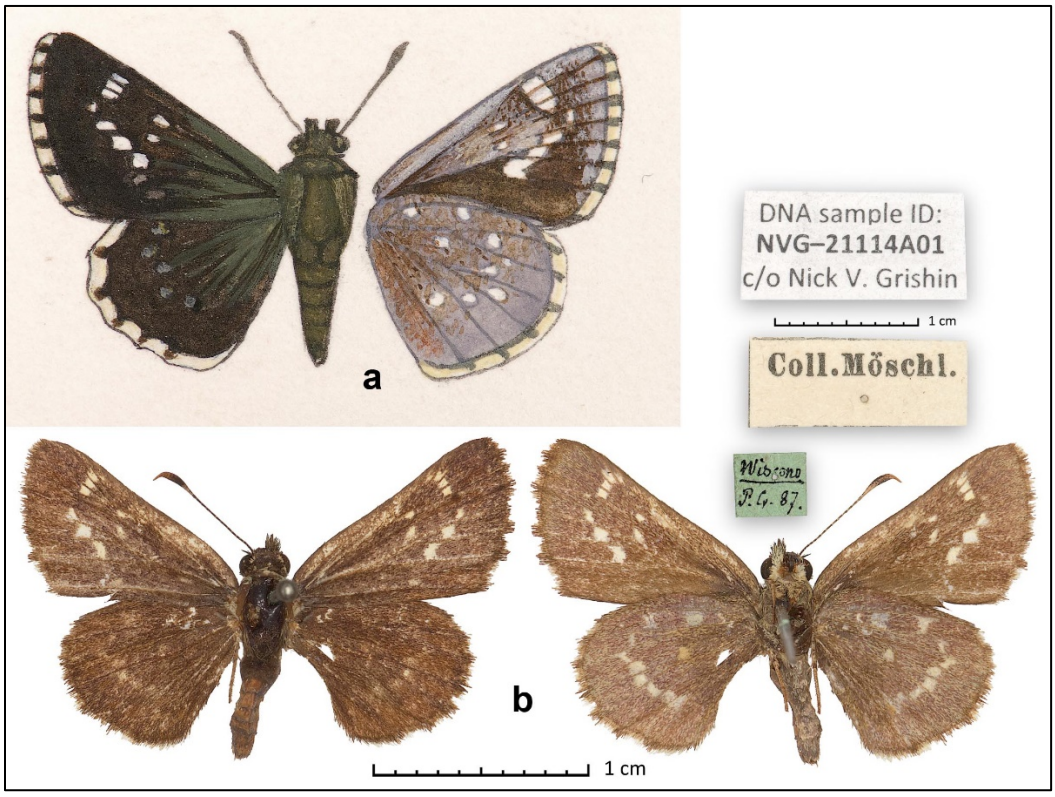


Fig. 18. Specimens and illustrations of *Amblyscirtes hegon*. **a.** Godman's copy of an unpublished Plötz's illustration of *Pyrgus* (*Syrichthus* [sic]) *argina* Plötz, 1884, © of the Trustees of the Natural History Museum London and are made available under Creative Commons License 4.0 (https://creativecommons.org/licenses/by/4.0/); **b.** an old specimen of *A. hegon* from Wisconsin and its labels (above the ventral image) that resembles the illustration of *P. argina* [MFNB]. Dorsal (left side of the panel letter) and ventral (right side of the panel letter) views are shown.

Amblyscirtes nemoris (W. H. Edwards, 1864) - reinstated status

DESCRIPTION AND PHENOTYPIC COMPARISON OF ADULTS

Genomic analysis of the holotype of *Hesperia nemoris* revealed that *nemoris*, long considered a synonym of *hegon*, is, in fact, a species distinct from *hegon*.

Per W. H. Edwards (1864), this species is characterized by a "greenish gray" venter. Color analysis shows no green background pigment, rather a brown color ("Pine Cone") that differs only slightly from *hegon*, but differs appreciably from both the tan-brown venter of *matheri* and grayish venter of *gelidus* (**Fig. 14**). The "greenish" appearance is certainly due to the visual effect of light scales "peppered" over the brown ground color. Though there is considerable character overlap with *hegon*, making identification to species challenging, *nemoris* generally has more of the light ventral peppering of light scales (**Fig. 9**), whereas *hegon* is primarily brown-ventered with less of the light peppering of *nemoris*. The ventral forewing apex is similarly colored to the hindwing, being slightly darker ("Metallic Bronze"). The last area of the forewing that was analyzed was the darkest portion of the base of the forewing ("Morocco Brown"). There was no appreciable difference in color here, between the four species.

The dorsal brown ground color ("Bistre") differs little from either *hegon* (also "Bistre") or *gelidus* ("Very Dark Brown"), but is considerably darker than *matheri* ("Horses Neck") *(***Fig. 13**). W. H. Edwards (1864) gives a detailed description of the dorsal and ventral spot pattern, which are individually variable in extent across all four species in the *hegon* complex. The colors of the light dorsal spots ("Tahuna Sands") and ventral spots ("Soft Amber") differ very little from either *hegon, matheri* or *gelidus* (**Fig. 14**) and are essentially unreliable for differentiating the species. In *nemoris* the ventral hindwing spot pattern tends to be well-developed, similar to both *matheri* and *gelidus*, but dissimilar to *hegon* which has a tendency for a reduced or absent spot pattern. Other features in the description of *nemoris* (W. H. Edwards, 1864) similarly apply to *hegon, matheri* and *gelidus* and pose identification challenges to observers.

The present analysis measured the length of the forewing of the males (n=13), ranging 11.0-13.0 mm, and averaging 11.6 mm. The measurement of females (n=4) was consistently 12.0 mm, averaging 12.0 mm. All sexes averaged together (n=17) show *nemoris* adults having forewings measuring 11.8 mm and ranging 11-13 mm (**Fig. 16**). W. H. Edwards (1864) provided a single measurement for the male wingspan, expanding 1" (25.5 cm). In the present study, wingspan of the males was measured at 22-24 mm (n=13), averaging 22.6 mm, with females (n=4) measuring 23-24 mm and averaging 23.5 mm. All sexes averaged together (n=17) show *nemoris* adults having a wingspan measuring 22.8 mm and ranging 22-24 mm (**Fig. 16**). The measurements show that *nemoris* and *hegon* have similar forewing length and wingspan, whereas *matheri* and *gelidus* were both larger (**Fig. 16**).

The difference in the angle of the subapical spot row from the leading edge of the forewing (**Figs. 15 & 16**), shows little difference between *nemoris* and *hegon*. Both *matheri* and *gelidus* showed the alignment of the apical spots to have a sharper average angle. While the measured angle varied greatly, *nemoris, hegon* and to a lesser degree *gelidus* ranged closer to a 90° angle than *matheri*, which showed the apical spot row to sit at a sharper angle from the leading edge of the forewing.

In male genitalia of *A. nemoris*, the tooth on the inner surface of harpe is larger and more robust (**Figs. 17c, d, 16d**), similar to *A. hegon* (**Figs. 17f, 16h**), but different from both of the two new species, in which the tooth is shallower and does not protrude much between the valvae. *Amblyscirtes nemoris* differs from *A. hegon* by the valva with more or less parallel dorsal and ventral margins in lateral view and the base of harpe along ventral margin is straighter and less convex (or curved) (**Fig. 16g**).

SPECIMENS OF *A. NEMORIS* EXAMINED IN PRESENT STUDY:

Neotype: Ohio: Vinton Co., 3 miles east of Zaleski (leg. Harry K. Clench), 10 May 1970 (**Fig. 9**).
Arkansas: Faulkner Co., Wooly Hollow State Park (leg. Ricky Patterson), 26 April 2022 (1 ♂ RLP #22100/NVG-21113H02, 3 ♀ RLP #22103/NVG-22054H01, RLP #22105/NVG-22054H03, RLP #22106/NVG-22054H04), 8 May 2022.
Louisiana: Catahoula Parish, J. C. 'Sonny' Gilbert WMA (leg. Ricky Patterson), 21 March 2022 (1♀), 25 March 2022 (1 ♂), (leg. Jeff Slotten), 23-Mar-2018 (2 ♀ NVG-19047E12 & 19047F02)
Mississippi: Tishomingo Co., 5 miles west of Belmont (leg. Ricky Patterson),16 April 1994 (2 ♀)
Mississippi: Tishomingo Co., Mt. Woodall (leg. Ricky Patterson), 4 April 1992 (2 ♂), 18 April 1993 (3 ♂, 1 ♀), 16 April 1994 (1 ♂, 2 ♀), 4 April 2000 (1 ♂, 1 ♀)
Missouri: St. Francois Co., Bonne Terre (leg. Harry Pavulaan), 24 April 1988
North Carolina: Clay Co., Buck Creek @ Hwy. 164 (leg. Ricky Patterson), 17 May 2007 (1 Specimen - genetic analysis NVG-21109C09 per tree).
North Carolina: Haywood Co., Maggie Valley (leg. Harry Pavulaan), 10 May 2009
Texas: Smith Co., Tyler State Park (leg. June and Floyd Preston), 15 March 1986 (via Texas A & M collection)

HABITAT AND DISTRIBUTION

A. nemoris flies in early spring (mid-March through mid-May). Early and late dates are 21 March to 10 May. In Louisiana and Mississippi, it is found in late-March to late-April; in Arkansas it flies from late-April to mid-May based on confirmed specimens.

The confirmed range of this species is from east Texas to Ohio (the Type Locality), Louisiana, Arkansas and Mississippi to North Carolina. This species like the others is also found in wooded areas, along gravel roads and small openings in wooded areas (hardwoods primarily),

nectaring on blackberry blooms, wild garlic, clover, and various spring flowers. In Louisiana at the J. C. 'Sonny' Gilbert WMA this species flies sympatrically with *Amblyscirtes matheri*, and in Arkansas at Woolly Hollow State Park and in North Carolina at Buck Creek/Hwy 164 in Macon County, *Amblyscirtes nemoris* flies sympatrically with *Amblyscirtes hegon*. *Amblyscirtes nemoris* seems to have a more east central United States distribution, but extremes range from east Texas, thence east through Louisiana and Mississippi, and on to southwest North Carolina. It goes north to Ohio (the Type Locality), the northern most record we have.

***Amblyscirtes matheri* Patterson, Pavulaan and Grishin - new species**

ZooBank registration: urn:lsid:zoobank.org:act:7809EA3B-C188-428A-91BE-9778BAE52327

DESCRIPTION AND PHENOTYPIC COMPARISON OF ADULTS

New species *A. matheri* differs from *hegon*, *nemoris* and *gelidus* primarily by the distinct tan-brown ("Sorrell Brown") ground color of the ventral hindwing surfaces. Wing marks differ little between the four species.

Fig. 19. Holotype (♂) of *Amblyscirtes matheri.* Warren Co., MS. 3 April 1988, RLP #0123/NVG-21063F09.

Size. Adults of *A. matheri* are generally of similar size to nominotypical *hegon* and *nemoris*, though very slightly larger (**Fig. 16**). The length of the male forewings of the examined *matheri* (n=28) series ranges 11-14 mm, averaging 12.4 mm. Male wingspan of *A. matheri* [maximum wing spread] is measured at 22-25 mm, averaging 24 mm. Female *A. matheri* have more rounded wings than males, with forewing length ranging 12-14 mm (n=31), averaging 12.4 mm. Female *A. matheri* have a wingspan ranging 23-28 mm, averaging 25.7 mm. All adults analyzed in the study had a forewing length of 11-14 mm, averaging 12.4 mm (n=59) with a wingspan of 22-25 mm, averaging 24 mm.

Dorsal ground color. The dorsal ground color of *A. matheri* males and females is a uniform ("Horses Neck") brown. Applying the Color Grab™ and Colblindor™ applications, males and females of *A. matheri* averaged a red/green/blue (RGB) color code of **107, 77, 44**, with a hue/saturation/brightness (HSB) color code of **31, 58, 41** (**Fig. 14**). The dorsal ground color is a lighter brown than in *hegon, nemoris* and *gelidus*.

Dorsal pattern and color of markings. The dorsal wing marking pattern of *A. matheri* is similar to *hegon, nemoris* and *gelidus*. The markings are a light tan ("Yuma") and do not differ appreciably from *hegon, nemoris* and *gelidus*. The three apical spots near the FW apex of *matheri* are at a sharper angle from the leading edge of the forewing than in *hegon, nemoris* and *gelidus*, though there is considerable variation and overlap between the four species in this complex (**Fig. 16**).

Ventral ground colors. New species *A. matheri* differs from *A. hegon*, *nemoris* and *gelidus* primarily by the distinct tan-brown ("Sorrell Brown") ground color of the ventral hindwing surfaces, as opposed to the ventral brown ("Buccaneer") of *hegon*, the dark brown ("Pine Cone") of *nemoris*, and the brown/gray ("Schooner") of *gelidus*. Color analysis revealed an averaged red/green/blue (RGB) color code of **149, 124, 96**, with a hue/saturation/brightness (HSB) color code of **31, 35, 58** (**Fig. 14**). In *matheri* the "peppering" of light scales on the ventral side of the wings is absent. This peppering is present in *nemoris* and *gelidus*, and variably present in *hegon*, and causes the perception of the "greenish" color of the ventral hindwings.

The apical area of the ventral forewings of *matheri* approximated the color of the ventral hindwings closely, averaging red/green/blue (RGB) color code of **144, 116, 86**, with a hue/saturation/brightness (HSB) color code of **31, 40, 56** (**Fig. 14**). Additional color measurements were made for the ventral postbasal area of the forewings, primarily within cell CuA_2 which is the darkest portion of the ventral side of the wings. In *matheri*, this area averaged a red/green/blue RGB color code of **76, 50, 28** and a hue/saturation/brightness (HSB) color code of **27, 63, 29** (**Fig. 14**) and did not differ appreciably from *hegon, nemoris* and *gelidus*.

Ventral pattern and color of markings. Ventrally, the spot pattern of *matheri* is well-developed and is similar to *hegon, nemoris* and *gelidus*, though the ventral pattern of *hegon* is variable and frequently absent altogether. The markings are a light tan ("Yuma") and do not differ appreciably from *hegon, nemoris* and *gelidus* (**Fig. 14**).

Male genitalia. The tooth on the inner surface of harpe is shallower and does not protrude as strongly between the valvae (**Figs. 17a, b, 16b**), in contrast to larger and more robust tooth in both *A. hegon* (**Figs. 17f, 16h**) and *A. nemoris* (**Figs. 17c, d, 16d**). Valva with somewhat expanded ampulla that overlays the harpe, and a result, broadening somewhat from the base to harpe along its costa, but not along the ventral margin (**Fig. 16a**), where harpe is not more expanded at the base as in *A. hegon* (**Fig. 16g**) and *A. gelidus* (**Fig. 16e**). Harpe is usually straighter at the distal margin.

TYPES

Holotype:
USA: Mississippi: Warren Co., Vicksburg, (leg. Ricky Patterson), 3 April 1988 (**Fig. 19**), (♂).
Deposited in the Carnegie Museum of Natural History, Pittsburgh, PA, USA.

Allotype:
Mississippi: Warren Co., Vicksburg, (leg. Ricky Patterson), 3 April 1988 (♀).

Paratypes:

Alabama: Jackson Co., Hollytree (leg. Howard Grisham), 3 May 2014 (1 ♂), 28 April 2020 (1 ♂).

Louisiana: Catahoula Parish, J. C. 'Sonny' Gilbert WMA (leg. Craig Marks), 10 March 2012 (3 ♂ - none of these are on genomic analysis chart). 1 ♂ NVG-19047F01 (leg. Jeff Slotten), 3 March 2018

Louisiana: Catahoula Parish, J. C. 'Sonny' Gilbert WMA (leg. Ricky Patterson), 21 March 2022 (4 ♂, including NVG-21113F02, 1 ♀), 25 March 2022 (5 ♂ 1 ♀), 7 March 2023 (8 ♂ 2 ♀).

Mississippi: Claiborne Co., Rocky Springs Campground 34 mi. SW of Clinton (leg. Drew Hildebrandt and Maria Plonczynski), 7 April 1991 (1 ♂), 22 April 1989 (1 ♂).

Mississippi: Grenada Co., T12N, R3E, Section 7 SW (leg. Terry Schiefer), 9 April 1987 (1♂) (via MEM collection)

Mississippi: Holmes Co., Holmes County State Park (leg. Drew Hildebrandt and Maria Plonczynski), 9 April 1988 (3 ♂)

Mississippi: Leflore Co., CR 518 north of Greenwood (leg. Leroy Koehn), 2-24 April, 1994 (4 ♂ 3 ♀).

Mississippi: Warren Co., Vicksburg, (leg. Ricky Patterson), 3 April 1988 (7 ♂ 9 ♀), 4 April 1988 (1 ♂ 1 ♀), 9 April 1988 (1 ♀), 24 March 1992 (6 ♂ 1 ♀), 28 March 1993 (4 ♂ 3 ♀), 18 April 1993 (1 ♂), 9 May 1993 (1 ♂), 25 March 1994 (1 ♀), 2 April 1995 (1 ♂ 2 ♀), 27 March 1998 (5 ♂), 27 March 2000 (2 ♂), 17 March 2002 (1♀)

Mississippi: Warren Co., Vicksburg, (leg. Ricky Patterson), 27 March 1988 (1 ♂), 19/20 April 1993 (1 ♂ 1 ♀) (via C. H. Grisham collection)

Mississippi: Winston Co., Tombigbee NF (leg. David Pollock and Terry Schiefer), 22-29 March 1999 (1 ♂) (via MEM collection)

Mississippi: Yazoo Co., 3 miles E of Satartia (leg. Ricky Patterson), 2 April 2004 (5 ♂ 13 ♀), 9 April 2004 (2 ♂ 5 ♀)

South Carolina: Fairfield Co., Ridgeway (leg. Harry Pavulaan), 6 May 2007 (1 ♂)

South Carolina: Laurens Co., Garlington School Road (leg. R. G. Simpson), 20 April 2012 (1 ♂)

In addition to the known type series, there appear to be recent photographic images of *A. matheri* (as "*A. hegon*") on iNaturalist from Catahoula Parish, LA dated March 29, 2020; March 21, 2021; April 3 and 8, 2022.

Etymology: The species is named in honor of Bryant Mather, lifelong lepidopterist devoted to the study of Mississippi Lepidoptera.

HABITAT AND DISTRIBUTION

Amblyscirtes matheri flies in early spring (mid-March through mid-April) in Mississippi and Louisiana, early April in NE Alabama, and early April in South Carolina. Early/late dates are: 3 March (Louisiana) to 9 May (Mississippi).

The butterfly is found in openings in hardwood forest habitats in hilly areas, particularly in the Loess Bluff Hills that border the Mississippi River alluvial plain. The loess deposits found

their origin in the Pleistocene ice age glaciers far to the north in Canada and the northern United States. As the glaciers ground the bedrock into a fine flour-like deposit, the deposit was washed down the Mississippi River and deposited onto the adjacent flood plains. The Loess deposits were then blown by winds onto the bluffs on either side of the river. The loess bluffs trend north-south throughout the state of Mississippi along the Mississippi River delta. This region is dominated by deciduous hardwood and pine forest consisting primarily of various species of Oaks (*Quercus* sp.), Loblolly Pine (*Pinus taeda*) and Shortleaf Pine (*Pinus echinada*), which comprise approximately two-fifths of the Loess Bluff Hills in Mississippi. The remainder of the area is under cash crops and pasture or hay farms.

Amblyscirtes matheri seems to be associated with this particular biogeographic region in Mississippi and Louisiana. In northeast Alabama it has been confirmed in wooded, hilly areas that are foothills of the Appalachians, where other more normally mountain species such as *Erora laeta* have been found. A single South Carolina specimen was collected in the Sandhills region of the eastern part of the state; a habitat in which Loblolly Pines predominate along with an understory of Switch Cane (*Arundinaria tecta*). While presently recorded in seven counties in Mississippi, in Louisiana the skipper has only been found in the J. C. "Sonny" Gilbert Wildlife Management Area (formerly the Sicily Island Hills Wildlife Management Area until renamed in 2015), in northeast Catahoula parish, which is in east central Louisiana. The complete range of *A. matheri* has yet to be determined, but as stated above it is known to range from Louisiana to South Carolina. In Mississippi and Louisiana, only one specimen has been found outside the Loess Bluffs region in Mississippi/Louisiana. Whether this geographical tie to the Loess Bluffs is an artifact of the collected specimens or due to a specialized habitat is not known. The specimens from northeast Alabama are not in Loess Bluff hills, and this terrain is not found in South Carolina either. A review of various collections, websites, and publications have not found any confirmed specimens or photographs of adequate clarity to be determined as *A. matheri* outside of these four states. The only specimens from the Mississippi River delta flatlands examined were collected just north of Greenwood, very near the Loess Bluff Hills. It remains to be determined whether *A. matheri* ranges north through the Loess Bluffs region along the Mississippi River alluvial plain, potentially as far as southern Illinois. It would be expected that gaps in distribution between Louisiana and South Carolina will be filled as this species becomes known to collectors and watchers.

Adults can be found nectaring on flowers, especially white clover, wild garlic (as noted by Craig Marks), fleabane, and occasionally at mud. They are not normally found in the middle of fields or in thickly wooded areas, but along woodland edges and roadsides (especially gravel roads) going through hardwood areas, similar to the habitat of *A. hegon* and *A.nemoris*. Craig Marks (2018) describes the hostplants of related '*Amblyscirtes hegon*' (actually *nemoris*) in Louisiana as: "various types of grasses, including river oats, fowl manna-grass, and Indian grasses." These grasses should be investigated as potential hosts of *A. matheri* as well. One author (Patterson) has obtained eggs from a female but was unable to get the emerged larva to feed on any of the grasses offered.

Amblyscirtes gelidus **Grishin, Patterson, Pavulaan - new species**

ZooBank registration: urn:lsid:zoobank.org:act:24DEA1D8-3831-4D9F-9389-6FE3BAE642AA

DESCRIPTION AND PHENOTYPIC COMPARISON OF ADULTS

New species *A. gelidus* differs from *hegon, nemoris* and *matheri* primarily by the distinct brownish-gray ("Schooner") ventral hindwing. Freshly-emerged individuals display a "frosted" appearance. Wing marks differ little between the four species.

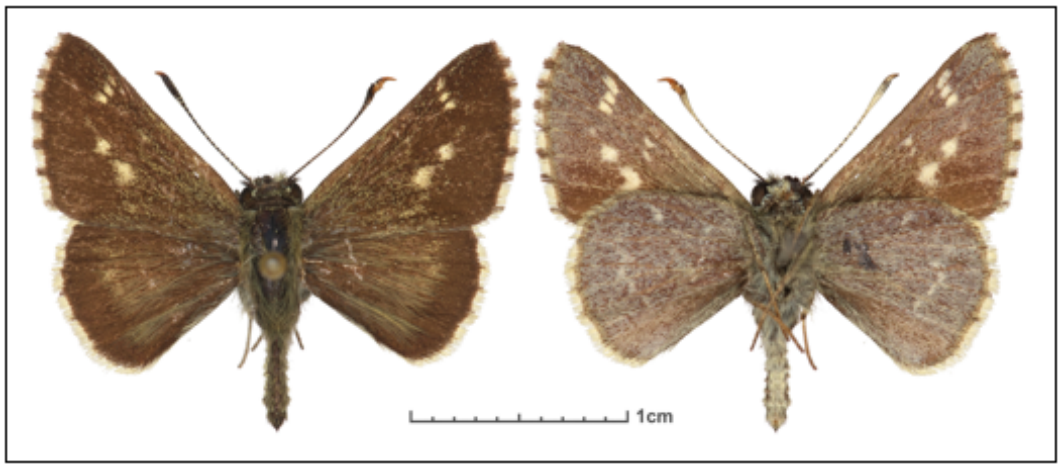


Fig. 20. Holotype (♂) of *Amblyscirtes gelidus.* Van Buren Co., MI. 5 June 1983, NVG-22054A01

Size. Adults of *A. gelidus* are generally of similar size to nominotypical *hegon* and *nemoris*, though very slightly larger, and are approximately the same size as *matheri* (**Fig. 16**). The length of the adult forewings of the physically examined series (n=6) ranges 11-13 mm, averaging 12.3 mm. Unfortunately, since only a single female specimen was available for examination, measurements are for all adults combined. The wingspan of *gelidus* is measured at 22-25 mm, averaging 24.1 mm.

Dorsal ground color. The dorsal ground color of *A. gelidus* is a uniform ("Very Dark Brown") with a slight overlay of light scales in many individuals. Applying the Color Grab™ and Colblindor™ applications, males and females of *A. gelidus* averaged a red/green/blue (RGB) color code of **84, 58, 48**, with a hue/saturation/brightness (HSB) color code of **16, 42, 32** (**Fig. 14**). The dorsal ground color is similar to *hegon, nemoris* and *matheri*.

Dorsal pattern and color of markings. The dorsal wing marking pattern of *A. gelidus* is similar to *hegon, nemoris* and *matheri*. The markings are a light tan ("Tahuna Sands") and do not differ appreciably from *hegon* and *nemoris*, but are lighter than *matheri.* The three apical spots near the FW apex of *gelidus* are at a slightly sharper angle from the leading edge of the forewing than in *hegon* and *nemoris* but greater than *matheri*, though there is considerable variation and overlap between the four species in this complex (**Fig. 16**).

Ventral ground colors. New species *A. gelidus* differs from *A. hegon*, *nemoris* and *matheri* primarily by the distinct brownish-gray ("Schooner") ventral hindwing which also displays a peppering of light scales; as opposed to the ventral brown ("Buccaneer") of *hegon*, the dark brown ("Pine Cone") of *nemoris*, and the tan-brown ("Sorrell Brown") ground color of *matheri*. Color analysis revealed an averaged red/green/blue (RGB) color code of **144, 136, 123**, with a hue/saturation/brightness (HSB) color code of **37, 14, 56** (**Fig. 14**). *A. gelidus* has the ventral "peppering" of light scales as seen in *nemoris* and variably in *hegon*. This peppering causes the perception of the "greenish" color of the ventral hindwings. Many individuals of this species display a distinct overlay of light wing scales on the inner half of the dorsal forewing surface, and elongated scales on the inner two-thirds of the dorsal hindwing that take on a more distinct appearance of hair.

The apical area of the ventral forewings of *gelidus* approximated the brownish-gray color of the ventral hindwings, but is slightly darker, averaging red/green/blue (RGB) color code of **105, 93, 79**, with a hue/saturation/brightness (HSB) color code of **32, 24, 41** (**Fig. 14**). Additional color measurements were made for the ventral postbasal area of the forewings, primarily within cell CuA_2 which is the darkest portion of the ventral side of the wings. In *gelidus*, this area averaged a red/green/blue RGB color code of **79, 59, 52** and a hue/saturation/brightness (HSB) color code of **15, 34, 30** (**Fig. 14**) and did not differ appreciably from *hegon, nemoris* and *matheri*.

Ventral pattern and color of markings. Ventrally, the spot pattern of *gelidus* is variably developed and is similar to *hegon, nemoris* and *matheri*, though the ventral pattern of *hegon* is variable and frequently absent altogether. The markings are a light tan ("Soft Amber") and do not differ appreciably from *hegon, nemoris* and *matheri* (**Fig. 14**).

Male genitalia. The tooth on the inner surface of harpe is shallower and does not protrude as strongly between the valvae (**Figs. 17e, 16f**), in contrast to larger and more robust tooth in both *A. hegon* (**Figs. 17f, 16h**) and *A. nemoris* (**Figs. 17c, d, 16d**), but is somewhat more prominent than in *A. matheri* (**Figs. 17a, b, 16b**). Valva tends to broaden from the base to harpe, with its dorsal and ventral margins at an angle (in lateral view). This broadening is not only due to expansion of the ampulla region on costa, but also because harpe ventral margin is more convex near the base and somewhat expanded ventrad (**Fig. 16e**). This valva shape is quite similar in *A. hegon*, from which it can be distinguished by less robust tooth on the inner surface of valva.

TYPES

Holotype:
USA: Michigan: Van Buren Co., Antwerp Township Section 14, (leg. W. A. Miller), 5 June 1983 (♂). deposited in the Carnegie Museum of Natural History, Pittsburgh, PA, USA.

Allotype:
West Virginia: Pendleton Co., Spruce Knob, Monongahela National Forest (leg. Ricky Patterson), 7 June 2006, (coll. of Ricky Patterson) (♀).

Paratypes:

Michigan: Barry Co., Yankee Springs Township, Section 31, (leg. W. A. Miller), 10 June 1983 (1♀).

Michigan: Kalamazoo Co., Portage, Gourdneck State Game Area, (leg. W. A. Miller), 17 May 2012 (2♂, 1♀).

Michigan: Presque Isle Co., Thompson Harbor State Park, (leg. W. A. Miller), 15 June 2014 (1♀).

Michigan: Van Buren Co., Antwerp Township Section 13, (leg. W. A. Miller), 17 May 1982 (1♂), 5 June 1983 (11♂, 4♀).

Michigan: Van Buren Co., Antwerp Township Section 14, (leg. W. A. Miller), 5 June 1983 (1♂).

Michigan: Van Buren Co., Antwerp Township Section 25, (leg. W. A. Miller), 29 May 1983 (1♂), 13 May 1985 (1♂, 1♀, 1 undet.), 14 May 1985 (5♂, 1♀), 22 May 1985 (1♂, 2♀).

West Virginia: Pendleton Co., Spruce Knob, Monongahela National Forest, (leg. Ricky Patterson), 7 June 2006 (2♂).

West Virginia: Pocahontas Co., Lake Buffalo Recreation Area, Monongahela National Forest, (leg. Susan Olcott), 8 June 2016 (1♂, dep. W.V. Butterfly Atlas Project).

West Virginia: Pocahontas Co., Little River WMA, Monongahela National Forest, (leg. Jane Whitaker), 3 June 2013 (1♂, dep. W.V. Butterfly Atlas Project).

West Virginia: Pocahontas Co., Little River WMA, Monongahela National Forest, (leg. Randall Casto), 19 June 2016 (1♀, dep. W.V. Butterfly Atlas Project).

West Virginia: Pocahontas Co., Thornwood, Monongahela National Forest, (leg. Susan Olcott), 4 June 2013 (1♂, dep. W.V. Butterfly Atlas Project).

West Virginia: Randolph Co., Durbin, Cheat Bridge, (leg. Susan Olcott), 4 June 2013 (1♂, dep. W.V. Butterfly Atlas Project).

West Virginia: Randolph Co., Spruce Knob Lake, Monongahela National Forest, (leg. Harry Pavulaan), 30 May 2013 (1♂, dep. W.V. Butterfly Atlas Project), 2 June 2017 (1♂, H. Pavulaan collection).

West Virginia: Wood Co., Parkersburg, Johnson T. Janes Park (leg. Susan Olcott), 5 June 2014 (1♂, dep. W.V. Butterfly Atlas Project).

Etymology: The species name reflects the frosted appearance of freshly emerged individuals.

HABITAT AND DISTRIBUTION

A. gelidus flies in late spring (mid-May through mid-June in Michigan, early June in West Virginia). Early/late dates of confirmed specimens are: 13 May to 15 June in Michigan and 30 May to 19 June in West Virginia.

While we have had little experience with this species, it does not seem to be much different in habitat or habits from *A. hegon, A. matheri*, or *A. nemoris*, though possibly more adapted to the cold climates of Michigan and highlands of West Virginia. Several West Virginia specimens were captured on and near Spruce Knob, the highest point in West Virginia. They were found on lightly traveled gravel roads in Transition Zone hardwood forested areas. The area is known as the Allegheny Plateau, on which the climate is considerably colder than surrounding lowlands, and likely similar in climate and habitats to Michigan. Nothing is known about the precise habitat of the evaluated Michigan specimens. Nielsen (1999) describes the habitat of *A. hegon* in Michigan

as "small, sunny forest openings, swamp edges and other partially shaded moist areas." This is similar to the habitat for the other species discussed in this work, and seems reasonable it would apply to this new species.

The ones from the Spruce Knob area of West Virginia were resting at wet areas on a shaded gravel road, and it can be assumed they nectar at flowers like the other *Amblyscirtes* discussed in this work.

The confirmed range of this species consists of Michigan, primarily southwest Michigan, plus one locality in NE Michigan, and in West Virginia, primarily the Spruce Knob area of West Virginia. The photo of *A. hegon* in 'Michigan Butterflies and Skippers' (Nielsen, 1999) appears to be this new species and states the distribution to be "throughout the Upper Peninsula and scattered counties in the Lower Peninsula." Since we have not examined any of these specimens that he based these records on, we cannot confirm the distribution of *gelidus* in Michigan based on Nielsen (1999). We expect that additional states will be added to this disjunct distribution as more specimens are evaluated.

IMMATURE STAGES

Nielsen (1999) described Michigan '*hegon'* larvae as "pale greenish white with dark green dorsal and white lateral stripes; the head is dark brown with pale brown bands." This might apply to *gelidus* but needs to be confirmed. He also listed the host of Michigan '*hegon*' as Kentucky Bluegrass, Indian Grass, and possibly other grasses.

DESIDERATA

Based on the current study and historical literature, considerable fieldwork is required to: (1) better determine reliable wing markings needed to differentiate *A. hegon, A. nemoris*, and *A. gelidus* (whereas *A. matheri* is more readily distinguished by its unique ventral coloration); (2) confirm hostplants of each of the four species within the '*hegon*' complex; and (3) determine the complete range of all four species.

Genomic analysis found that a specimen from Tombigbee State Park, Lee County, MS collected in June, 1979 was in the *Amblyscirtes gelidus* clade but appeared to potentially be a different, albeit closely related, taxon. At this time this is the only specimen available, and before any further conclusions can be made additional specimens need to be collected or located and further analyses performed. As such, this potential new species or subspecies is not addressed here but in a future study if deemed appropriate based on additional study.

CONCLUSIONS

Amblyscirtes hegon is a complex of four species: *A. matheri* **sp. n.**, *A. gelidus* **sp. n.**, *A. nemoris* **stat. rest.**, and *A. hegon*. These species can be definitively identified using DNA of the Z chromosome and display subtle differences in male genitalia. In facies, the species mostly differ by their colors, *A. matheri* being the most distinct. To facilitate direct color comparison, four specimens were photographed in a single frame instead of being combined in an image processing

Fig. 21. Four species of *Amblyscirtes hegon* complex photographed together in one frame on 20 November 2023. **a, e:** *A. matheri* **sp. n.** paratype [RLP#22081, DNA NVG-21113F02, genitalia NVG230130-03], **b, f:** *A. gelidus* **sp. n.**, holotype [DNA NVG-22054A01, genitalia NVG230128-01], **c, g:** *A. nemoris* **stat. rest.** [RLP#22100, DNA NVG-21113H02, genitalia NVG230130-02], **d, h:** *A. hegon* [RLP#22101, DNA NVG-21113H03, genitalia NVG230130-01] in dorsal (**a-d**) and ventral (**e-h**) views. Specimens of *A. nemoris* (RLP#22100) and *A. hegon* (RLP#22101) were collected on 26 April 2022 in Wooly Hollow State Park, Faulkner Co., Arkansas.

software, and we illustrate the color differences discussed above (**Fig. 21**). Except for the older *A. gelidus* holotype, others were collected in 2022 and have a similar degree of color fading.

ACKNOWLEDGEMENTS

Thanks go to David M. Wright for manuscript review; Dr. Andrew Warren (McGuire Center for Lepidoptera and Biodiversity) for preparation and initial examination of genitalia; Howard Grisham for access to specimens in his collection; Jeff R. Slotten for kindly sharing information, specimens, and leg samples that were crucial for the studies of sympatric *A. hegon* group species; and Craig Marks for additional paratype specimens. Thanks also to those who provided specimens and access to their collections, including Jason Weintraub (ANSP: The Academy of Natural Sciences of Drexel University, Philadelphia, PA, USA), Jim Fetzner, Bob Androw, Vanessa Verdecia, Cat Giles, and the late John Rawlins (CMNH: Carnegie Museum of Natural History, Pittsburgh, PA, USA), Richard L. Brown, Drew Hildebrandt, and personnel at the Mississippi Entomological Museum (MEM: Mississippi Entomological Museum, Starkville, MS, USA), Théo Léger, Wolfram Mey, and Viola Richter (MFNB: Museum für Naturkunde, Berlin, Germany), Lawrence F. Gall (PMNH: Peabody Museum of Natural History, Yale University, New Haven, CT, USA), Peter Michalik and Lara Lopardo (ZIMG: Zoological Institute and Museum Greifswald, Germany), Axel Hausmann, Andreas Segerer, and Ulf Buchsbaum (ZSMC: Zoologische Staatssammlung München, Germany), and Maria Plonczynski. We acknowledge Qian Cong, Jing Zhang, Jinhui Shen, Leina Song, Ping Chen, and Ming Tang for their help with DNA studies, computer scripts, and excellent technical assistance without which the genomics part of this project would have been impossible. Thanks also go to the Louisiana Department of Wildlife and Fisheries for permits to collect on Wildlife Management Areas (permits #WL-Research-2022-13, WDP-22-062, and WDP-23-004), to the Arkansas Department of Parks, Heritage, and Tourism (Division of State Parks, permit # 098-2022 and 098-2023), and Texas Parks and Wildlife Department (Natural Resources Program Director David H. Riskind, research permit 08-02Rev) for permits to carry out research projects and collect specimens on State Park lands. We acknowledge the Texas Advanced Computing Center (TACC) at The University of Texas at Austin for providing HPC resources. This study was supported in part by the HHMI Investigator funds and by grants from the National Institutes of Health GM127390 and the Welch Foundation I-1505 (all to NVG).

LITERATURE CITED

Allen, T. J. 1997. The Butterflies of West Virginia and Their Caterpillars. University of Pittsburgh Press, Pittsburgh, PA.: xii + 388 pp.

Allen, T. J. 2005. Caterpillars in the Field and Garden. A Field Guide to the Butterfly Caterpillars of North America. Oxford University Press, New York, N.Y.: viii + 232 pp.

Bouseman, J. K, J. G. Sternburg & J. R. Wiker. 2010. Field Guide to the Skipper Butterflies of Illinois. Second edition. Illinois Natural History Survey, Champaign, IL. Manual 11.: viii + 200 pp.

Brock, J. P. & K. Kaufman. 2003. Field Guide to Butterflies of North America. Kaufman Field Guides. Houghton Mifflin Company, New York, N. Y.: 392 pp.

Brower, A. E. 1974. A List of the Lepidoptera of Maine – Part 1, the Macrolepidoptera. Life Sciences and Agriculture Experiment Station, University of Maine, Orono, ME. Technical Bulletin No. 66: 136 pp.

Calhoun, J. V. 2019. From oak woods and swamps: the butterflies recorded in Georgia by John Abbot (1751-C.1840) based on his drawings and specimens. Journal of the Lepidopterists' Society 73(4): 211-256 [esp. page 242].

Comstock, J. H. & A. B. Comstock. 1912. How to Know the Butterflies. A Manual of the Butterflies of the Eastern United States. D. Appleton and Company, New York, N.Y.: xii + 311 pp. + 45 pl.

Cong, Q., J. Shen, J. Zhang, W. Li, L. N. Kinch, J. V. Calhoun, A. D. Warren, and N. V. Grishin. 2021. Genomics reveals the origins of historical specimens. Molecular Biology and Evolution 38(5): 2166–2176.

Cong, Q., J. Zhang, and N. V. Grishin. 2019. Genomic determinants of speciation. bioRxiv BIORXIV/2019/837666.

De Maynadier, P. G., Klymko, J., Butler, R. G., Wilson, Jr., W. K, and J. V. Calhoun. 2023. Butterflies of Maine and the Canadian Maritime Provinces. Cornell University Press, Ithaca, NY. 438 pp.

dos Passos, C. F. 1964. A Synonymic List of the Nearctic Rhopalocera. The Lepidopterists' Society. Memoir No. 1: v + 145 pp.

Dyar, H. G. 1902. A List of North American Lepidoptera and Key to the Literature of this Order of Insects. Bulletin of the United States National Museum, No. 52: xix + 723 pp.

Edwards, W. H. 1864. Description of certain species of diurnal lepidoptera found within the limits of the United States and British North America. No. 3. Proceedings of the Entomological Society of Philadelphia, 2(4): 501-507.

Edwards, W. H. 1865. Description of certain species of diurnal Lepidoptera found within the limits of the United States and British America, No. 4. Proceedings of the Entomological Society of Philadelphia, 4(1): 201-204; 4(3): Plate I (Fig. I).

Evans, W. H. 1949. A catalogue of the Hesperiidae from Europe, Asia, and Australia in the British Museum (Natural History). The Trustees of the British Museum (Natural History); London. xix + 502 pp., 53 pls.

Evans, W. H. 1955. A Catalogue of the American Hesperiidae Indicating the Classification and Nomenclature Adopted in the British Museum (Natural History). Part IV (Groups H to P) Hesperiinae and Megathyminae. British Museum, London, England: vi + 499 pp. + 34 pl.

Ferguson, D. C. 1954. The Lepidoptera of Nova Scotia. Proceedings of the Nova Scotian Institute of Science 23(3): 162-375.

Fernald, C. H. 1884. The Butterflies of Maine. Sprague & Son, Augusta, ME.: 104 pp.

Fiske, W. F. 1901. An Annotated Catalogue of the Butterflies of New Hampshire. New Hampshire College Agricultural Experiment Station, Durham, N.H. Technical Bulletin No. 1: 80 pp.

Forbes, W. T. M. 1960. Lepidoptera of New York and Neighboring States. Agaristidae Through Nymphalidae Including Butterflies. Part IV. Cornell University Agricultural Experiment Station, New York State College of Agriculture, Ithaca, N.Y.: 188 pp.

French, G. H. 1886. The Butterflies of the Eastern United States. J. B. Lippincott Company,

Philadelphia, PA.: 402 pp.
Glassberg, J. 1993. Butterflies Through Binoculars. A Field Guide to Butterflies in the Boston-New York-Washington Region. Oxford University Press, New York, N.Y.: 160 pp. + 40 pl.
Glassberg, J. 1999. Butterflies Through Binoculars, the East. A Field Guide to the Butterflies of Eastern North America. Oxford University Press, New York, N.Y.: x + 242 pp. + 71 pl.
Glassberg, J. 2017. A Swift Guide to Butterflies of North America. Second Edition. Princeton University Press, Princeton, N.J.: 420 pp.
Godman, F. D. 1907. Notes on the American species of Hesperiidae described by Plötz. Annals and Magazine of Natural History (7)20(16): 132–155.
Hall, P. W., C. D. Jones, A. Guidotti & B. Hubley. 2014. The ROM Field Guide to Butterflies of Ontario. Royal Ontario Museum, Toronto, Ontario: 488 pp.
Harris, L., Jr. 1972. Butterflies of Georgia. University of Oklahoma Press, Norman, OK.: xvi + 325 pp.
Heitzman, J. R. & J. E. Heitzman. 1987. Butterflies and Moths of Missouri. Missouri Department of Conservation, Jefferson City, MO.: viii + 385 pp.
Holland, W. J. 1898. The Butterfly Book. Hutchinson & Co., London, England: xx + 382 pp. + 48 pl.
Holland, W. J. 1931. The Butterfly Book. Revised Edition. Doubleday & Company, Inc., Garden City, N.Y.: xii + 424 pp. + 77 pl.
Howell, W. M. & V. Charny. 2010. Butterflies of Alabama. Learning Solutions, New York, N.Y.: vii + 509 pp.
International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature, 4th Edition. The International Trust for Zoological Nomenclature, The Natural History Museum: xxix + 306 pp.
Irwin, R. R. & J. C. Downey. 1973. Annotated Checklist of the Butterflies of Illinois. Illinois Natural History Survey, Urbana, IL. Biological Notes No. 81: 60 pp.
Kirby, W. F. 1871. A Synonymic Catalogue of Diurnal Lepidoptera. John Van Voorst, London, England: 690 pp.
Klassen, P., A. R. Westwood, W. B. Preston & W. B. McKillop. 1989. The Butterflies of Manitoba. Manitoba Museum of Man and Nature, Winnipeg, Manitoba: vi + 290 pp.
Klots, A. B. 1951. A Field Guide to the Butterflies of Eastern North America. Peterson Field Guide Series. Houghton Miffin Company, Boston, MA.: xvi + 349 pp.
Layberry, R. A., P. W. Hall & J. D. Lafontaine. 1998. The Butterflies of Canada. University of Toronto Press, Inc., Toronto, Ontario: vii + 280 pp. + 32 pl.
LeGrand, H. E., Jr. & T. E. Howard, Jr. 2023. Butterflies of North Carolina: their Distribution and Abundance. 30th Approximation [internet]. North Carolina Biodiversity Project and North Carolina State Parks.
Available online: https://auth1.dpr.ncparks.gov/nbnc/a/accounts.php
Li, W., Q. Cong, J. Shen, J. Zhang, W. Hallwachs, D. H. Janzen, and N. V. Grishin. 2019. Genomes of skipper butterflies reveal extensive convergence of wing patterns. Proceedings of the National Academy of Sciences of the United States of America 116(13): 6232–6237.
MacNeill, C. D. 1975. Family Hesperiidae, the Skippers. *In*: Howe, W. H. The Butterflies of

North America. Doubleday & Company, Inc. Garden City, N.Y.: 423-578.
Marks, C. 2017. A Clear Case of Mistaken Identity. Southern Lepidopterists News 39(4): 271-273.
Marks, C. 2018. Butterflies of Louisiana – A Guide to Identification and Location. Louisiana State University Press, Baton Rouge: viii + 462 pp.
Mather, B. & K, Mather. 1958. The butterflies of Mississippi. Tulane Studies in Zoology 6(2): 63-109.
Mather, B. & K, Mather. 1976. The butterflies of Mississippi – Supplement No. 2. Journal of the Lepidopterists' Society 30(3): 197-200.
Mather, B. & K, Mather. 1985. The butterflies of Mississippi – Supplement No. 3. Journal of the Lepidopterists' Society 39(2): 134-138.
Maynard, C. J. 1891. Manual of North American Butterflies. De Wolfe, Fiske & Co., Boston, MA.: iv + 226 pp. + 10 pl.
McDunnough, J. H. 1938. Check List of the Lepidoptera of Canada and the United States of America. Part 1: Macrolepidoptera. Memoirs of the Southern California Academy of Sciences, Vol. 1: 275 pp.
Mielke, O. H. H. 2005. Catalogue of the American Hesperioidea: Hesperiidae (Lepidoptera). Sociedade Brasileira de Zoologia; Curitiba, Paraná, Brazil. xiii + 1536 pp.
Miller, L. D. & F. M. Brown. 1981. A Catalogue/Checklist of the Butterflies of America North of Mexico. The Lepidopterists' Society. Memoir No. 2: vii + 280 pp.
Miller, L. D. & F. M. Brown. 1983. Hesperiidae *in* Hodges, R. W. Check List of the Lepidoptera of America North of Mexico. E. W. Classey Ltd. and The Wedge Entomological Research Foundation, Washington, D. C.: xxiv + 284 pp.
Minno, M. C., J. F. Butler & D. W. Hall. 2005. Florida Butterfly Caterpillars and Their Host Plants. University Press of Florida, Gainesville, FL.: xi + 341 pp.
Monroe, J. L. & D. M. Wright. 2017. Butterflies of Pennsylvania. A Field Guide. University of Pittsburgh Press, Pittsburgh, PA.: xiii + 304 pp.
Möschler, H. B. 1876. Beiträge zur Schmetterlings-fauna von Surinam. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botananischen Gesellschaft in Wien 26: 293-352.
Nakahara, S., A. Zilli, J. V. Calhoun, M. Espeland, P. S. Padrón, and N. V. Grishin. 2022. Resolving two centuries of mistaken identity: Reinterpretation of Papilio marcus Fabricius, 1787 (Lepidoptera: Nymphalidae, Hesperiidae). Zootaxa 5195((3)): 241–255.
Nielsen, M. 1999. Michigan Butterflies & Skippers, A Field Guide and Reference. Michigan State University Extension, Michigan State University, East Lansing, MI.: 248 pp.
O'Donnell, J. E., L. F. Gall & D. L. Wagner. 2007. The Connecticut Butterfly Atlas. State Geological and Natural History Survey, Hartford, CT. No. 118: 376 pp.
Opler, P. A. & G. O. Krizek. 1984. Butterflies East of the Great Plains, an Illustrated Natural History. The Johns Hopkins University Press, Baltimore, MD. xvii + 294 pp. + 54 pl.
Opler, P. A. & V. Malikul. 1992. A Field Guide to Western Butterflies. Peterson Field Guide Series. Houghton Mifflin Company, Boston, MA.: xvii + 396 pp. + 48 pl.
Opler, P. A. & A. B. Wright. 1999. A Field Guide to Eastern Butterflies. Peterson Field Guide Series. Houghton Mifflin Company, Boston, MA.: xiv + 540 pp. + 48 pl.
Patterson, J. 2011. The Butterflies of Minnesota (A 'flier's manual). Trafford Publishing, U.S.A.:

x + 410 pp.
Pelham, J. P. 2023. A Catalogue of the Butterflies of the United States and Canada., Revised 23 February 2023. Originally published (2008) by The Journal of Research on the Lepidoptera 40: xiv + 658 pp. Available online: https://butterfliesofamerica.com/US-Can-Cat.htm
Plötz, C. 1884. Analytische Tabellen der Hesperiinen-Gattungen *Pyrgus* und *Carcharodus.* Mittheilungen aus dem Naturwissenschaftlichen Vereine von Neu-Vorpommern un Rügen in Greifswald, 15: 1-24.
Pyle, R. M. 1981. National Audubon Society Field Guide to North American Butterflies. Alfred A. Knopf, Inc., New York, N.Y.: 924 pp.
Robbins, R. K., Q. Cong, J. Zhang, J. Shen, R. C. Busby, C. Faynel, M. Duarte, A. R. P. Martins, C. Prieto, G. Lamas, and N. V. Grishin. 2022. Genomics-based higher classification of the species-rich hairstreaks (Lepidoptera: Lycaenidae: Eumaeini). Systematic Entomology 47(3): 445–469.
Scott, J. A. 1986. The Butterflies of North America. A Natural History and Field Guide. Stanford University Press, Stanford, CA.: xiii + 583 pp. + 64 pl.
Scudder, S. H. 1863. A list of the butterflies of New England. Proceedings of the Essex Institute, Vol. III (1860-1863), Salem, MA.: 161-179.
Scudder, S. H. 1889. The Butterflies of the Eastern United States and Canada with Special Reference to New England. Vol. II. Published by the author. Cambridge, MA: xi, 768-1774.
Shapiro, A. M. 1974. Butterflies and Skippers of New York State. Search 4(3): 60 pp.
Shull, E. M. 1987. The Butterflies of Indiana. Indiana Academy of Science, Indianapolis, IN.: viii + 262 pp.
Spencer, L. 2006. Arkansas Butterflies and Moths, Second Edition. Ozark Society Foundation: xiv + 314 pp.
Stichter, S. 2015. The Butterflies of Massachusetts. Published by author: 488 pp.
Tietz, H. M. 1952. The Lepidoptera of Pennsylvania. A Manual. The Pennsylvania State College, School of Agriculture, Agricultural Experiment Station, State College, PA.: xii + 194 pp.
Tietz, H. M. 1972. An Index to the Described Life Histories, Early Stages and Hosts of the Macrolepidoptera of the Continental United States and Canada. Vol. I. The Allyn Museum of Entomology, Sarasota, FL.: 536 pp.
Venable, R. 2014. Butterflies of Tennessee. Maywood Publishing, Franklin, TN.: 391 pp.
Zhang, J., Q. Cong, J. M. Burns, and N. V. Grishin. 2022a. Checking the checkered taxonomy of Plötz's checkered skippers (Hesperiidae: Pyrgini). The Taxonomic Report of the International Lepidoptera Survey 10(5): 1–31.
Zhang, J., Q. Cong, J. Shen & N. V. Grishin. 2022b. Taxonomic changes suggested by the genomic analysis of Hesperiidae (Lepidoptera). Insecta Mundi 0921: 1–135.

ADDITIONAL INFORMATION SOURCES

United Stated Department of Agriculture. PLANTS Database. https://plants.usda.gov/home (accessed 17 February 2023).
www.butterfliesandmoths.org (accessed 20 February 2023).
https://butterfliesofamerica.com (accessed 20 February 2023).
www.inaturalist.org (accessed 20 February 2023).

The Taxonomic Report

is a platinum open access peer-reviewed publication of

The International Lepidoptera Survey (TILS)

The International Lepidoptera Survey is registered as a non-profit Limited Liability Company (LLC) in the state of Virginia, U.S.A. The Taxonomic Report (TTR), ISSN 2643-4776 (print) / ISSN 2643-4806 (online) is published for the purpose of providing a public and permanent scientific record. Articles are peer-reviewed but not necessarily through the anonymous editor-mediated review process. Typically, the authors are encouraged to solicit reviews of their manuscripts from knowledgeable lepidopterists before submission. TTR appears in digital, open-access form, is disseminated as a hardcopy to select institutional repositories, and is available as printed copy upon request at the discretion of authors and/or the editor. Printing and postage charges may apply. An initial run of 25 copies is printed on paper to meet ICZN Code recommendation 8B. All published TTR articles are freely available at the archival TTR website (http://lepsurvey.carolinanature.com/report.html) and via the following digital repositories:

Internet Archive (https://archive.org/)
Biodiversity Heritage Library (https://www.biodiversitylibrary.org)
Zobodat (https://www.zobodat.at/)
Zenodo (https://zenodo.org)
Digital Commons (https://digitalcommons.unl.edu)

TILS Purpose

TILS is devoted to the worldwide collection of Lepidoptera for the purpose of scientific discovery, determination, and documentation, without which there can be no preservation.

TILS Motto

"As a world community, we cannot protect that which we do not know"

Articles for publication are sought

Manuscripts may deal with any area of research on Lepidoptera, including faunal surveys, conservation topics, life histories and foodplant records, matters of nomenclature, descriptions of new taxa, methods, etc. Taxonomic papers are particularly welcome. There are no publication charges for authors. Before submitting a manuscript, email **TTR editor, Harry Pavulaan, 606 Hunton Place NE, Leesburg, VA, 20176, USA** at intlepsurvey@gmail.com (cc: to harrypav@hotmail.com if you do not receive a reply within one week) to initiate discussion on how to best handle your material for publication, and to discuss peer review options.

Visit *The International Lepidoptera Survey* on the World Wide Web at:
http://lepsurvey.carolinanature.com
&
Join the discussion at our list serve on Groups.io at:
https://groups.io/g/TILS
You can subscribe by sending an email to: TILS+subscribe@groups.io
&
Join The International Lepidoptera Survey on Facebook at:
https://www.facebook.com/groups/1072292259768446