A Reevaluation of Papilio pegala F. and Papilio alope F., with a Lectotype Designation and a Review of Cercyonis pegala (Nymphalidae: Satyrinae) in Eastern North America

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Source: The Journal of the Lepidopterists' Society, 70(1) : 20-46

Published By: The Lepidopterists' Society

URL: https://doi.org/10.18473/lepi.70i1.a5

Journal of the Lepidopterists' Society
70(1), 2016, 20–46

A REEVALUATION OF *PAPILIO PEGALA* F. AND *PAPILIO ALOPE* F., WITH A LECTOTYPE DESIGNATION AND A REVIEW OF *CERCYONIS PEGALA* (NYMPHALIDAE: SATYRINAE) IN EASTERN NORTH AMERICA

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ABSTRACT. A review of the available evidence related to the descriptions of *Papilio pegala* F. and *Papilio alope* F. (now generally recognized as *Cercyonis p. pegala* and *C. pegala alope*, respectively) reveals that the suggested type localities of these nominal taxa are untenable for the reasons originally given. The vicinity of Charleston, South Carolina, is retained for *P. pegala*, but for different reasons than those first proposed. Based on an eighteenth century illustration in "Jones' Icones," the Georgia type locality for *P. alope* is revised to the vicinity of New York, New York, and a lectotype is designated. Additional nominal taxa are discussed, including *Satyrus alope* var. *maritima* W. H. Edwards, *Satyrus nephele* var. *olympus* W. H. Edwards, *Cercyonis pegala* race *borealis* F. Chermock, *Cercyonis alope carolina* F. Chermock & R. Chermock, *Cercyonis alope ochracea* F. Chermock & R. Chermock, *Cercyonis pegala abbottii* F. Brown, and *Cercyonis pegala agawamensis* Arey & Grkovich. The holotypes of *C. p. borealis*, *C. a. carolina*, and *C. a. ochracea* are figured for the first time. Perceived morphological trends within *C. pegala* in eastern North America are mapped, revealing a broad clinal blend zone in the southeast and an extensive contact zone northward, which partly exhibits characteristics of a mosaic hybrid zone. Evidence suggests that temperature may influence phenotypic expression in *C. pegala*. Based strictly on wing pattern, an arrangement is proposed that recognizes four subspecies of *C. pegala* in eastern North America.

Additional key words: John Abbot, distribution, Alexander Garden, William Jones, "Jones' Icones," subspecies

The recent description of a new subspecies of the butterfly *Cercyonis pegala* (F.) by Arey and Grkovich (2014) emphasizes the need to reconsider the proposed type localities of *Papilio pegala* F. and *Papilio alope* F., which are commonly recognized as the subspecies *C. p. pegala* and *C. pegala alope*, respectively. These taxa were described during the eighteenth century and both lacked definitive type localities. Attempting to rectify this deficiency, Brown ([1966a]) proposed a type locality for each, but based his conclusions on meagre evidence. As a result, the type locality of *P. alope* shifted the traditional concept of this taxon from the northeastern United States to the southeastern coastal plain, in proximity to the proposed type locality of *P. pegala*. My own examination of the available evidence, much of which was not previously considered, refutes the conclusions of Brown ([1966a]). *Papilio alope* serves as the type-species of the genus *Cercyonis* Scudder, increasing the importance of stabilizing its nomenclature.

Cercyonis pegala exhibits a dizzying array of phenotypes across its broad North American range, fostering an ongoing debate about the validity of various described forms and subspecies. Klots (1951) mentioned five eastern subspecies of *C. pegala*, but thought it was perhaps best to "lump" them into a single clinal subspecies. Emmel (1969, 1975) recognized four eastern subspecies and four forms. Like Klots (1951), Miller and Brown (1981, 1983) listed five eastern subspecies. Sourakov (1995) conducted a more comprehensive investigation and concluded that *C. pegala* is highly clinal. He suggested that only the nominotypical subspecies be recognized in the east, with two major wing-pattern forms ("*alope*" and "*nephele*") defining most populations. Despite this recommendation, up to seven subspecies are currently recognized in eastern North America, though interpretations vary (Pelham 2008, 2014, Arey & Grkovich 2014). The treatment of western populations is even more complicated (Austin 1992). Based on my own investigation involving thousands of specimens, including recently rediscovered type material, I propose an alternative treatment that recognizes four subspecies in eastern North America.

METHODS

The original descriptions of *Papilio pegala* and *P. alope* were translated from Latin and compared. The conclusions of Brown ([1966a]) were studied. The following museums were searched for relevant historical specimens, many of which were photographed by me or staff of those institutions: Alabama Museum of Natural History, Univ. of Alabama (Tuscaloosa; UANH), Carnegie Museum of Natural History (Pittsburgh, Pennsylvania; CMNH), Hope Entomological Collections, Oxford University Museum of Natural History (Oxford, UK; OUMNH), Hunterian Museum, University of Glasgow (Glasgow, UK; HMUG); L. C. Bates Museum (Hinckley, Maine; LCBM), Linnean Society of London (London, UK; LSL); Macleay Museum, University of Sydney (Sydney, Australia; MAMU); Museum of Comparative Zoology, Harvard

University (Cambridge, Massachusetts; MCZ); Natural History Museum, London (London, UK; BMNH); National Museum of Natural History, Smithsonian Institution (Washington, D.C.; USNM); and Übersee-Museum Bremen (Bremen, Germany; UMB). In addition to the numerous *C. pegala* in some of the collections above, several thousand additional specimens were examined in the collection of the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History (Gainesville, Florida; MGCL) and my personal collection. Hundreds of photographs of living and preserved *C. pegala* were reviewed, including those available in the online databases of The Academy of Natural Sciences of Philadelphia (Philadelphia, Pennsylvania; ANSP), Peabody Museum of Natural History, Yale University (New Haven, Connecticut; PMNH), and MCZ. Many regional publications on butterflies were consulted, as well as various unpublished manuscripts, including the personal journals and correspondence of William H. Edwards (Charles C. Wise, Jr. Library, West Virginia State Archives, West Virginia University, Morgantown; WVSA) (photocopies in the MGCL archives).

Results

Original descriptions. In 1775, the Danish zoologist Johan (Johann) C. Fabricius (1745–1808) described a number of new North American insects in his treatise entitled *Systema Entomologiae* (Fabricius 1775). Among them was a new butterfly named *Papilio pegala*, which he vaguely attributed to "America." Fabricius (1781, 1787) subsequently published abbreviated versions of this description, followed by the entire description with slight alterations in Fabricius (1793). The original Latin description of *P. pegala* and English translation are as follows. The last line indicates that Fabricius based his description on more than one specimen.

Pegala. 223. P. N. G. *alis dentatis, fuscis: anticus fascia rufa ocelloque unico, posticis supra ocello, subtus sex.*

Habitat in America. Mus. D. Hunter.

Magnitudo P. Semele. Corpus fuscum. Alae anticae fuscae, fascia lata rufa, quae tamen margines haud attingit. Ocellus utrinque unicus, pupilla alba. Posticae supra fuscae ocello atro, iride fulva pupillaque alba, subtus variegatae, ocellis sex atris, iride ferruginea pupillaque albida, Tres e his ocellis ad margenem tenuiorem connati, quintus maximus.

Variat interdum ocello primo et quarto obsoletis

English translation:

Pegala. 223. Genus *Papilio* [butterflies], division *Nymphales* [with scalloped wings], subdivision *Gemmati* [with eyespots]. Wings scalloped, brown: forewing with ruddy band with one eyespot, hindwing with eyespot above, six below.

Inhabits America. [From the] Museum of Dr. Hunter.

Size of *Papilio semele.* Body brown. Forewings brown with wide ruddy band that does not reach the margin. Both sides [above and below] have one eyespot with a white pupil. Hindwing above brown with dark eyespot, ringed in reddish-yellow with white pupil. Variegated below with six dark eyespots ringed by rust with white pupil. Three of these eyespots are joined near the margin, the fifth is the largest.

The first and fourth eyespots are sometimes absent.

Nearly twenty years after naming *P. pegala*, Fabricius described *Papilio alope* within the third volume of another important systematic work, *Entomologia Systematica* (Fabricius 1793), and stated that the butterfly inhabited "India." The original Latin description of *P. alope* and English translation are as follows. There is no indication from this description that Fabricius consulted multiple specimens.

Alope 715. *P. S. alis dentatis fuscis: anticis utrinque fascia flava; ocellis duobus, posticis ocello supra unico subtus sex.*

Papilio Alope. Jon. fig. pict. 4 tab. 12 fig. I.

Habitat in India Dom. Francillon.

Corpus medium, fuscum. Alae anticae concolores, fuscae fascia lata, abbreviata, flava & in hac ocelli duo atri pupilla alba strigaque postica atra. Subtus obscurae, fusco irroratae ocellis sex pupilla alba.

English translation:

Alope 715. Genus *Papilio* [butterflies], division *Satyri* [hindwing inner margin grooved to accommodate the abdomen]. Wings dark brown and scalloped: both sides [above and below] of forewings with yellow band; two eyespots. One eyespot on the hindwing above, six below.

Given as *Papilio alope* in Jones' drawings, volume 4, plate 12, figure 1.

Inhabits India. Owned by Francillon.

Body brown and of average size. Forewings the same brown color with wide, narrowed, yellow band containing two dark eyespots with white pupils, dark streak at bottom [of hindwings]. Obscure pattern below, marked with six darkened eyespots with white pupils.

After its description, *P. pegala* was largely misunderstood and mostly treated as a form of *P. alope*. The majority of known specimens that matched the description of *P. pegala* were in European collections and unseen by American lepidopterists. The concept of this taxon was essentially lost until the mid-nineteenth century (Edwards 1865). Meanwhile, the identity of *P. alope* was variously interpreted in the literature.

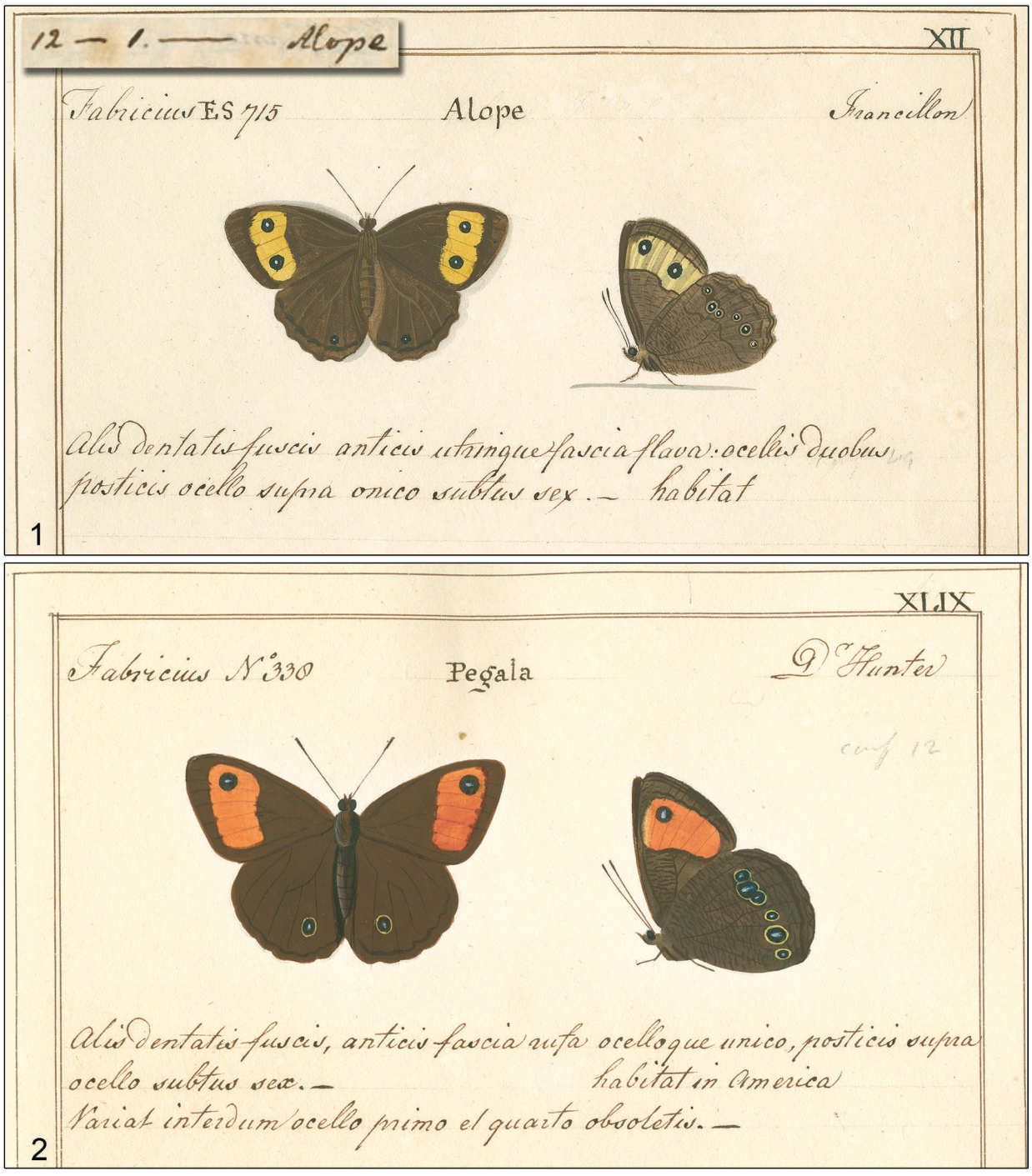
"Jones' Icones." As part of his description of *Papilio alope*, Fabricius (1793) cited an illustration of this butterfly by William Jones (1745–1818), a wine merchant and naturalist from Chelsea, now an affluent area of central London. During the early1780s, Jones began rendering life-sized watercolor drawings of Lepidoptera specimens that were contained in notable collections around London. He continued to work on his illustrations for over a decade, adding new drawings and inserting handwritten identifications for those he had previously rendered. When Jones illustrated an undescribed species, he left enough space around the figures to add its name and other details at a later date. Once the description of that species appeared in print, Jones inserted its name and cited a publication for reference. He also copied a portion of the species' Latin diagnosis as it appeared in the works of Linnaeus or Fabricius, regardless if these authors were responsible for the original description. Many of the species that Jones depicted were described decades after his death, demonstrating the great amount of material that remained unrecognized in British collections during his lifetime. Jones ultimately filled seven volumes with about 1500 figures. These drawings, long ago nicknamed "Jones' Icones," are currently bound into six volumes and are preserved at the Hope Library of Entomology (OUMNH) (see Calhoun 2009, Vane-Wright 2010). Images of all these drawings were recently made available online (OUMNH 2014). Surprisingly, Brown ([1966a]) did not consult Jones' drawings as part of his research concerning *P. alope*.

Plate 12 of volume 3 (cited by Fabricius as vol. 4) of "Jones' Icones" portrays dorsal and ventral aspects of a male specimen of *Cercyonis*, identified as "*Alope*," which Jones credited to "Francillon" (Fig. 1). John Francillon (1744–1816) was a prominent jeweler and natural history dealer who owned a shop on Norfolk Street, along the Strand in central London (Cowan 1986). As the authority for the name *alope*, Jones cited "Fabricius ES 715," meaning species no. 715 in *Entomologia Systematica* (Fabricius 1793), the publication in which it was originally described. Below the figures, Jones transcribed a portion of Fabricius' description. The figures portray a medium-sized, dark brown male butterfly. On the forewing is an ochre-yellow postdiscal patch (band), slightly narrowed at vein M_2, containing two nearly equal-sized eyespots. The ventral hindwing bears a row of six small postdiscal eyespots. The length of the forewing (base to apex) measures 26 mm. The figures portray a North American butterfly that is now generally recognized as the subspecies *Cercyonis pegala alope*. Possibly as an oversight, or because he disagreed with Fabricius' reference to India, Jones did not indicate the published "habitat" (purported region of occurrence) on his drawing.

Within the same volume of illustrations, on Plate 49, Jones figured a larger *Cercyonis* under the name "*Pegala*" (Fig. 2). As the authority for this name, he cited "Fabricius N^{o} 338," a reference to species no. 338 in *Species Insectorum* (Fabricius 1781), though *P. pegala* was actually described in Fabricius (1775). As in Fabricius' original description, Jones attributed the origin of his figured specimen to "Dr. Hunter." The figures portray a large, cocoa-brown male butterfly with pointed forewings that possess broad reddish-orange forewing patches containing single eyespots. The ventral hindwing displays a row of six prominent postdiscal eyespots. The length of the forewing (base to apex) measures 31 mm. The figures portray a butterfly from southeastern North America, which is now generally recognized as the subspecies *Cercyonis pegala pegala*. Written faintly in pencil on the right side of the drawing, probably by a later researcher, is "Conf [*confer* in Latin] 12," a suggestion to compare these figures with those of *P. alope* on Plate 12. Based on a reassessment of its origin (see below), and the completion date of Fabricius (1775), the figured specimen of *"Pegala"* was most likely collected between 1755 and 1773.

In a letter to the English physician and botanist Sir James E. Smith (1759–1828), dated August 1787, William Jones remarked, "Fabricius is in London...he is going thro' my drawings to correct amend and add to a Mantissa that he has now in hand, yet I have more than he will be able to accomplish in the time he has limited to stay" (Linnean Society of London; Smith 1832). This visit preceded the publication of Fabricius' *Mantissa Insectorum*, published in December of that year (Fabricius 1787). By the time Fabricius visited Jones, however, the *Mantissa* was already in press and he was working towards the publication of the multi-volume systematic work, *Entomologia Systematica*, in which *P. alope* would appear in the first part of the third volume (Fabricius 1793).

Fabricius (1792) listed Jones ("Jones Londoni") among the naturalists that he visited during his travels. On the other hand, Fabricius (1781, 1792) did not name Francillon among those that he called upon in England.



FIGS. 1, 2. Figures from "Jones' Icones." **1**, "*Alope*," consulted by J. C. Fabricius to describe *Papilio alope*. Inset is Fabricius' handwritten identification of the figures (enhanced). **2**, "*Pegala*," possibly depicting the lectotype of *Papilio pegala*. (images © Oxford University Museum of Natural History).

This suggests that Fabricius' description of *Papilio alope* was derived entirely from Jones' figures, not a physical specimen in Francillon's collection. James E. Smith, a friend of Jones, confirmed that many of Jones' drawings were "themselves the original authority for many of Professor Fabricius's recently published *Papiliones,* which were actually described from thence alone" (Smith & Abbot 1797). Smith was alluding to the publication of *Entomologia Systematica*, which had appeared four years earlier and included the description of *P. alope*. In a separate handwritten list, preserved with the third volume of "Jones' Icones," Fabricius identified the figures on Plate 12 as "*Alope*" (Fig. 1, inset), thus confirming that he personally consulted this illustration. Because there is no clear indication that Fabricius visited Jones more than once, he presumably conceived the name *alope* in 1787, six years before publishing its description. Fabricius did not include the name *pegala* on his list because Jones had already identified that illustration based on Fabricius (1781). This implies that Fabricius agreed with Jones' determination, reinforcing the concept of nominotypical *pegala* as we recognize it today.

Brown's analysis. In his original description, Fabricius (1775) attributed the type material of *P. pegala* to "Dr. Hunter." While studying nomenclatural aspects of *Cercyonis*, the American lepidopterist F. Martin Brown wrote to Ella Zimsen, the former Conservator of Insects at the Zoologisk Museum in Copenhagen, who had just published a treatise on Fabrician types. In early 1965, Zimsen informed Brown about the existence of two specimens identified as *Papilio pegala* at the University of Glasgow, which were from the collection of "Mr. Hunter." Brown was unaware that Kerr (1910) had previously listed these specimens as the types of *P. pegala.* Brown obtained photographs of the specimens and designated one of them as the lectotype of *P. pegala* (Brown [1966a]) (Fig. 5). Deposited at HMUG, these specimens are accompanied by a large cabinet label which identifies them as "*Pap. Pegala*" (Fig. 5, inset). This label includes the citation "Fabr. pag 76 N^{o} 338," referring to the entry for *pegala* in Fabricius (1781), rather than the original description in Fabricius (1775). This is not unusual, as the cabinet labels for all the butterflies in Hunter's collection cite entries in Fabricius (1781), regardless if they were described previously. They were prepared between 1783 and 1785 by Hunter's nephew, Matthew H. Baillie (Hancock et al. 2015).

Brown ([1966a]) associated "Dr. Hunter" with the celebrated Scottish surgeon and comparative anatomist John Hunter (1728–1793). Brown also claimed that Hunter had visited America during the 1750s while serving in the British Navy. Because Charleston, South Carolina, served as an important British port during the mid-eighteenth century, and the lectotype of *P. pegala* resembles butterflies from that area, Brown ([1966a]) concluded that the appropriate type locality of *P. pegala* is "the vicinity of Charleston, South Carolina."

Unfortunately, Brown's ([1966a]) investigation of *P. pegala* is flawed for several reasons. Not only was John Hunter not in the British Navy (he served as a surgeon in the British Army), the "Dr. Hunter" cited by Fabricius (1775) was actually John's older brother, William Hunter (1718–1783). William was a prominent obstetrician and "Physician Extraordinary" to Queen Charlotte, the wife of King George III (Liston 2013, Hancock et al. 2015). He assembled large and diverse natural history collections, including over 7,600 insects, which were bequeathed to the University of Glasgow, where they were received in 1807 (Keppie 2010, Brown et al. 2011). Fabricius spent entire days curating William's insects during several visits to London between the years 1767 and 1787 (Armitage 1958, Hancock 2004, Hancock et al. 2015). Fabricius (1775) based many descriptions on William's specimens (Kerr 1910, Zimsen 1964, Brock 1980, Douglas & Hancock 2007). Fabricius last visited William's collection in 1782, just months before William's death. *Species Insectorum* (Fabricius 1781) was then the standard of reference, explaining why Matthew Baillie subsequently cited only this publication on William's labels, presumably following Fabricius' suggested identifications.

In addition to his misidentification of "Dr. Hunter," Brown was also mistaken about Hunter's presence in America. In truth, neither of the Hunter brothers ever visited America (Simmins 1783, Bynum & Porter 1985, Keppie 2010). The central premise for Brown's suggested type locality of *P. pegala* is therefore invalid.

Brown's ([1966a]) study of *P. alope* is equally problematic. He reviewed the original description and concluded that it was consistent with "the characteristic form [of *C. pegala*] from the North Atlantic states." Ignoring this observation, he ultimately argued that the description of *P. alope* was likely based upon specimens collected by the English naturalist John Abbot (1751–c.1840), who lived in Georgia from 1776 until his death. It is widely known that John Francillon, who owned the specimen of *alope* portrayed by Jones, received many butterflies from Abbot. Brown therefore suggested a type locality for *P. alope* of "Burke-Screven-Bulloch counties region of Georgia," where Abbot is known to have lived. Miller and Brown (1981) later restricted this to "Screven County, Georgia," presumably at the insistence of Brown, who was primarily responsible for the arrangement of *Cercyonis*

in that publication (see Sourakov 1995). The Georgia type localities for *P. alope* are all the more surprising given that they are situated within the southeastern coastal plain, relatively near Brown's ([1966a]) proposed type locality for *P. pegala.* This action was perhaps Brown's way of reinforcing his opinion about the status of these taxa. In a 1963 letter, Brown wrote, "I tend to think of *pegala* as a species distinct from *alope*" (Knudson & Post 1963). His placement of these type localities in such close proximity was possibly intended to encourage this treatment. Brown apparently changed his mind, however, as Miller and Brown (1981, 1983) listed *alope* as a subspecies of *pegala*, just as dos Passos (1964) had done. The connection of *P. alope* to John Abbot is often cited as an example of the scientific significance of Abbot's work (e.g. Rogers-Price 1983). Regrettably, this correlation is unfounded, as Abbot's involvement is not supported by available evidence.

John Abbot's illustrations and specimens. Based on my previous studies of John Abbot's contributions, I realized that his illustrations and specimens of *C. pegala* did not agree with *P. alope* as portrayed in "Jones' Icones." An accomplished artist, Abbot illustrated *C. pegala* at least eleven times, even incorporating a female into an ornithological watercolor (Fig. 3, inset). I have examined all these renderings, including two duplicate compositions preserved at the Alexander Turnbull Library, Wellington, New Zealand (Calhoun 2007a) (Fig. 3) and the Hargrett Rare Book and Manuscript Library, University of Georgia (Calhoun 2007b). A portion of yet another duplicate of this composition was used to portray the hostplant and early stages of "*Satyrus Alope*" on Plate 59 in Boisduval and Le Conte (1829–[1837]) (Fig. 4). To accommodate the smaller size of that published plate, the engraver rearranged Abbot's figures of the larva and pupa, and also modified the leaves of the hostplant. Although Abbot's original drawing for this plate is missing, his accompanying notes are deposited at the Houghton Library, Harvard University. The entry for this drawing reads, "Great Meadow brown Butterfly. Feeds on the grass figured, and other grasses. Tyed up 19th June changed 20th bred 5th July. Frequents the pine woods etc. is not common" (Calhoun 2004). This is nearly identical to the notes that Abbot wrote to accompany his two other duplicate drawings (Calhoun 2007a, 2007b). These three drawings were completed between 1816 and 1825.

The specimens figured by Boisduval and Le Conte (1829–[1837]), as well as those portrayed in Abbot's two duplicate compositions, represent the southeastern coastal plain phenotype of *C. pegala.* Strecker (1878) was the first to correctly associate these figures with Fabricius' concept of *pegala*, followed by Edwards (1880). All the males of *C. pegala* in Abbot's drawings lack the lower eyespot on the forewing (Fig. 3). Although this is a variable trait, a large percentage of southeastern males lack this eyespot, including the lectotype and paralectotype of *Papilio pegala* at HMUG (Fig. 5).

None of Abbot's addtional illustrations of *C. pegala* include early stages or hostplants, and only one other is accompanied by written notes. Abbot's earliest known illustration of this species is included in a series of drawings that were completed c. 1790–1805 for John Francillon. These and many other natural history illustrations by Abbot are preserved at the Natural History Museum, London (BMNH). Accompanying a rendering of a large female *C. pegala* is the caption "Female, the Male has one spot or Eye in the upper wing. Taken in Oak Woods and the Pine Woods near Savannah River, the Male was taken 25th June, the Female which don't come out till after the Males, was taken 12th July, not common." These observations were transcribed by Francillon from Abbot's handwritten notes, which were apparently discarded. Abbot collected insects in Georgia along the Savannah River from Burke County (where he lived when this particular drawing was rendered), southeastward to Chatham County. Due to his lack of familiarity with southeastern *C. pegala*, Brown (1969) associated these coastal populations with sedge marsh habitats. Abbot actually collected these butterflies in upland oak and pine woods, which is the typical habitat of this butterfly in the region.

I examined eight museum specimens of *C. pegala* that were collected during the twentieth century in and around Screven County, Georgia: five males and one female from Screven County (MGCL and UANH) (Fig. 14); one female from Bullock County (also included within the type locality suggested by Brown [1966a]) (UANH); and a male from nearby Emanuel County (MGCL). A female from Screven County was also figured by Ehrlich and Ehrlich (1961, fig. 160). Like Abbot's illustrations, all of these specimens represent the large southeastern coastal phenotype. None resemble the figures in "Jones' Icones," which were consulted by Fabricius for his description of *P. alope* (Fig. 1). This agrees with previous authors (e.g. Richards 1931), who ascribed specimens from that portion of Georgia to the coastal phenotype. Although this evidence is extremely persuasive, it is also important to consider specimens that were likely collected by Abbot.

A close examination of the figures of "*Alope*" on Plate 59 in Boisduval and Le Conte (1829–[1837]) reveals that the wing veins are more accurate than those in Abbot's duplicate compositions, and the eyespot configurations

Figs. 3–8. Illustrations and specimens of C. *P. pegala*. **3**, J. Abbot drawing, ca. 1816–1818 (Alexander Turnbull Library). Inset is drawing of "Blue Warbler" by Abbot, including a female *C. pegala*, ca. 1825 (private collection). **4**, Plate 59 of "*Satyrus alope*" in Boisduval & Le Conte (1829–[1837]). **5**, male lecotype of *Papilio pegala* (dorsal/ventral) (HMUG), with Baillie's cabinet label. **6**, ventral figure of "*Pegala*" from Pl. 49 of "Jones' Icones," possibly depicting the lectotype, with the name as written by Jones. **7**, ventral figure in Boisduval & Le Conte (1829–[1837]), with the name as published. **8**, male, probably ex J. Abbot, used as the model for the ventral figure in Boisduval & Le Conte (1829–[1837]) (USNM), with Boisduval's cabinet label.

differ. Many of Boisduval's specimens are now deposited at USNM (Calhoun 2004, 2006b). Among them are three specimens of *C. pegala*, two males and one female. The female (Fig. 9), and a male with a greatly reduced lower eyespot on the forewing (Fig. 8), doubtless served as models for the adult figures on the published plate. The dark striations on the ventral wings of the male, like a fingerprint in this species, are equivalent (Figs. 7, 8). The ventral pattern is unlike that of Abbot's illustrations, which include fewer eyespots on the hindwing and a larger lower eyespot on the forewing (Fig. 3). Labels associated with these two specimens of *C. pegala* at USNM indicate that they were identified in Boisduval's collection as "*Alope*" (Fig. 8, inset). The remaining male from Boisduval's collection, with a single eyespot on the forewing (Fig. 10), was identified as "*Pegala*," reflecting his opinion that *pegala* represents a form of *alope* with a single forewing eyespot (Boisduval & Le Conte 1829–[1837]). All three of these specimens were almost certainly collected by Abbot. In preparation for their book, J. E. Le Conte visited Boisduval in Paris in 1825, bringing with him a large number of Abbot's butterfly specimens and drawings (Calhoun 2006a).

The American entomologist Thaddeus W. Harris (1795–1856) received many insects from Abbot. Harris' collection, which is deposited at MCZ, contains six specimens of *C. pegala.* His accompanying handwritten collection catalog (also at MCZ) records that he received four "*Hipparchia Alope*" from Georgia: two from Abbot and two from Abbot's friend, Augustus G. Oemler (1770–1854). One large male *C. pegala* in Harris' collection, without lower eyespots on the forewings, is labeled "Georg^{a}" in Harris' hand (Fig. 11). A female is labeled "Geo" in Harris' hand. These specimens, representing southeastern coastal *C. pegala*, were possibly received from Abbot. Harris' letters (MCZ) imply that he received Abbot's specimens between 1834 and 1836, when Abbot was residing in Bulloch County, Georgia. Another large, unlabeled southeastern male *C. pegala* in the collection, surely from Georgia, bears very small lower eyespots on the forewings. The fourth specimen from Georgia is missing. The three remaining specimens of *C. pegala* in Harris' collection (two females and one male) were apparently collected in Massachusetts and are consistent with phenotypes from that area. Beyond the four Georgia specimens, Harris' collection catalogue lists several from Massachusetts, but none from any other localities. Among Harris' other documents at MCZ is a handwritten manuscript entitled "North American Diurnal Lepidoptera in the Cabinet of T.W.H. 1837." Like his collection catalog, it also lists "*Alope*" only from Massachusetts and Georgia. At no time did Harris refer to any specimens by the name *pegala*, which is consistent with the usage of that era.

In the collection of the Linnean Society of London (LSL) are two old specimens of *C. pegala*, male and female. They were received by the Society in 1829 from James E. Smith, who in 1784 purchased the prized collection of Carl Linnaeus (Carl von Linné) (Gage & Stearn 1988, Fitton & Harman 2007). Smith published a series of Abbot's watercolors in the magnificent work *The Natural History of the Rarer Lepidopterous Insects of Georgia* (Smith & Abbot 1797). Based on their labels, the two *C. pegala* at LSL are from Smith's personal collection. The male, labeled "Georgia" (Fig. 12), was received from another English botanist, Sir William J. Hooker (1785–1865), from whom Smith obtained a large number of insects, including over 20 butterflies labeled "Georgia" (Fig. 12, inset). Several of these butterflies are dated 1806, which is probably when Smith acquired them. The female *C. pegala* from Smith's collection lacks locality data and was received from the amateur horticulturalist Mary Watson-Wentworth, Marchioness of Rockingham (1735–1804), who met Smith during the 1780s and remained his good friend until her death (Smith 1832). Both specimens of *C. pegala* at LSL are consistent with the southeastern coastal phenotype and were likely collected by Abbot, whose insects circulated widely among English naturalists of the period. Other specimens of Lepidoptera at LSL are labeled "Georgia - Abbot" in Smith's handwriting. All such specimens were probably acquired via John Francillon.

John Francillon served as Abbot's agent by selling his drawings and specimens to other naturalists in Europe. After his death, Francillon's collection was auctioned in two segments. The catalogs for these auctions (King 1817, 1818) list at least seven specimens of "*Alope*," but only one entry includes a locality: "Georgia." Numerous other unidentified Lepidoptera specimens were listed from "America" without specific localities. About 1200 of Francillon's specimens were purchased by the English naturalist Alexander Macleay (1767–1848), who moved to Australia in 1825 (Holland 1988, Stacey & Hay 2007). Macleay's collection serves as the core of the Macleay Museum (MAMU). A number of North American insects at MAMU are labeled "Georgia," and all were probably collected by Abbot. Within this collection are seven specimens of *C. pegala* from eastern North America: five males and two females. One male bears a dubious label reading "Boston New Engl." All represent the large phenotype found in coastal Georgia. One male lacks a lower eyespot on the forewing like those in Abbot's illustrations (Fig. 13), whereas others have reduced lower eyespots. It is

conceivable that all of these specimens were collected by Abbot, including the male labeled "Boston New Engl."

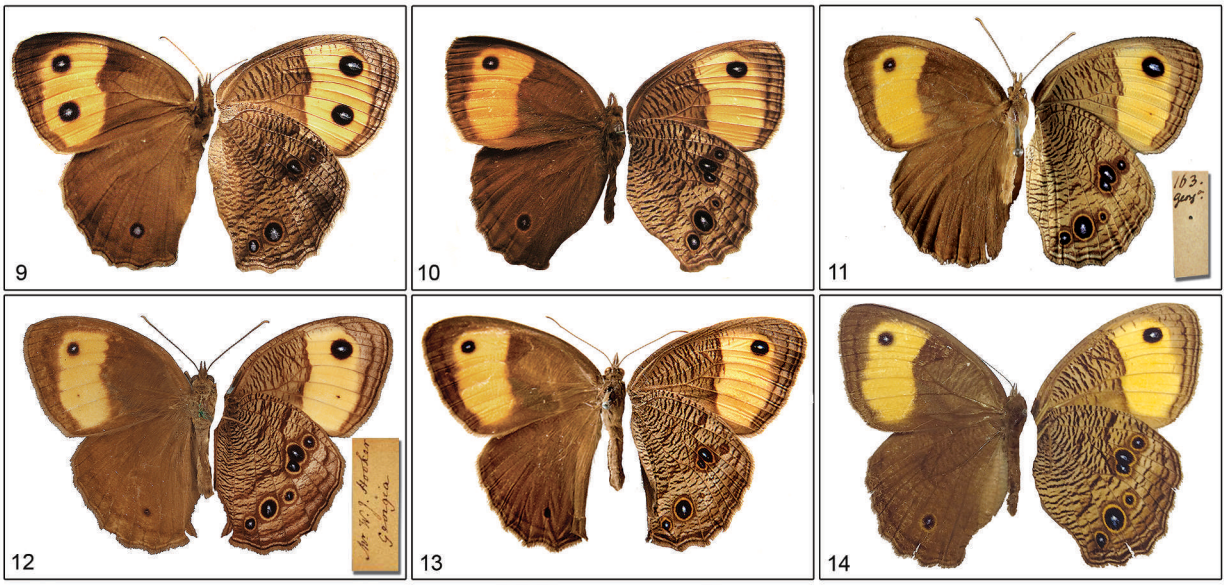
Alexander Macleay's son, William S. Macleay (1792–1865), also collected insects. On his return to London from Cuba in early 1836, William visited Philadelphia and arranged to acquire quantities of American specimens via exchange (Holland 1988, Horning 1988). While in Philadelphia he met the esteemed naturalists Titian R. Peale (1799–1885) and Charles Pickering (1805–1878) (Macleay 1838). Pickering was a close friend of the Massachusetts entomologist T. W. Harris. Probably at the urging of Pickering, Macleay wrote to Harris on 4 June 1836 asking if he was interested in exchanging insects. Harris responded on 16 June that he was pleased to offer Macleay whatever interesting insects he considered "most singular" or "least common or unknown in Europe" (Harris correspondence, MCZ). With this letter Harris sent 156 specimens of various insect orders, but no Lepidoptera. Although this shipment did not include butterflies, it demonstrates that Harris was acquainted with Macleay and they exchanged specimens. The specimen labeled "Boston N. Engl." may be the missing Georgia specimen of *C. pegala* from Harris' collection. Because Harris' specimens typically lack data, Macleay possibly assumed it was collected in the Boston area, or simply cited the city from which it was received. William immigrated to Australia in 1839, taking with him "what he may have collected or obtained by exchange or gift in Cuba, or at Philadelphia and the other ports of call on the outward and homeward voyages; and what he may have acquired in England, after his return, by exchange or otherwise" (Fletcher 1920). In 1848, William inherited his father's insect collection. Upon William's own death, the joint collection of 480 cabinet drawers was bequeathed to his cousin, Sir William J. Macleay (1820–1891), who added additional material. Sir William donated the entire collection, contained in 936 drawers, to the University of Sydney, where it was transferred into the newly constructed Macleay Museum in 1888.

Abbot also sent insects to the English artist and natural history dealer Thomas Martyn (fl.1760–1816), who was one of Abbot's benefactors when he emigrated to America. From 1797 until about 1802, Martyn issued parts of a book of illustrations under the title *Psyche, Figures of Non descript Lepidopterous Insects* (Martyn 1797–[c. 1802]). Included among the life-sized figures in this book are specimens from "New Georgia," which were undoubtedly collected by Abbot. Portrayed on Plate 23 is a female identified as "*Papilio Macularia*" from "Brazils" (Fig. 15). The origin of this specimen was apparently forgotten and Martyn believed it was from tropical America. Again, Abbot is the most likely source of this specimen, which represents the same phenotype found in coastal Georgia.

From 1776 to 1840, John Abbot lived in Bulloch, Burke, Chatham, and Screven Counties of Georgia. For nearly 50 years he collected butterflies extensively throughout the region, but there is no evidence that he ever encountered any *C. pegala* like that figured as "*Alope*" by Jones. The Georgia type localities suggested by Brown ([1966a]) and Miller and Brown (1981) are therefore untenable. When the Georgia type localities are rejected, and Jones' figures are considered, it becomes obvious that the concept of *Papilio alope* applies to a phenotype of *C. pegala* that occurs in the northeastern United States.

DISCUSSION

The type locality of *Papilio pegala*. The type localities of *Papilio pegala* as suggested by Brown ([1966a]) and Miller and Brown (1981) cannot be accepted on the principle that the type specimens were personally collected by John Hunter in the vicinity of Charleston, South Carolina. However, this type locality can be retained if we consider a more likely source: Alexander Garden (1730–1791). Garden was a Scottish physician and naturalist who lived in Charleston from 1752 to 1783, when the city was known as Charles Town. Although he was most interested in botany, Garden was a prominent naturalist who collected a wide variety of natural history specimens, many of which he sent back to Europe (Berkeley & Berkeley 1969). A proponent of the Linnaean classification system, Garden provided numerous specimens, including insects, to Linnaeus for description (Finger 2010). He maintained an active correspondence with the London merchant and naturalist John Ellis (c.1710–1776), who, as a Fellow of the Royal Society of London, was among the natural history elite of that city and received many of Garden's shipments (Sanders & Anderson 1999). Linnaeus referred to Ellis as "the main support of natural history in England" (Stearn 1981). Among the shipments to Ellis were butterflies, as Garden indicated in a letter dated 25 March 1755: "I have sent you some butterflies. . . If these will be agreeable, I can send you any number of them . . ." (Smith 1821). Zoological specimens from Garden are preserved at LSL (Jackson 1913), including some Lepidoptera labeled "Carolina." Garden's insects were also introduced to London collections through other contacts, such as Henry Baker (1698–1774), another Fellow of the Royal Society who received natural history specimens from Garden from the 1750s to the 1770s (Berkeley & Berkeley 1969). From these



Figs. 9–14. *Cercyonis p. pegala* (dorsal/ventral) likely ex. John Abbot, with a more recent specimen from Georgia. **9**, female, [pre-1825], used as the model for the dorsal figure in Boisduval & Le Conte (1829–[1837]) (USNM). **10**, male, [pre-1825] (USNM). **11**, male, [c. 1834–1836], "Georga" (MCZ-ENT213251), with original label. **12**, male, [c. 1806], "Georgia" (LSL), with original label (cropped). **13**, male, [pre-1817], (MAMU). **14**, male, 9.vii.1946, Screven Co., GA, Leg. A. K. Wyatt (UANH).

primary recipients, Garden's specimens were evidently dispersed to additional naturalists. A worn female *Antheraea polyphemus* (Cramer) at LSL bears J. E. Smith's label attributing it to "South Carolina, Dr. Garden." Like Baker and the Hunter brothers, Garden was a Fellow of the Royal Society. John Hunter examined an electric eel and other specimens that Garden sent to London (Finger 2010). In a letter to Ellis, written in 1768, Garden referred to John Hunter: "If you could introduce my brother to Mr. Hunter, it would be a great favour done him, and it might give rise to an acquaintance between them" (Smith 1821). Garden was clearly familiar with the Hunters and was undoubtedly aware of William's collections. Garden returned to England in 1783, when he was expelled from South Carolina for being a British sympathizer during the American Revolution.

During the mid-eighteenth century there were very few collectors in southeastern North America who sent butterflies to England. John Abbot arrived in America in 1773, but he first lived in eastern Virginia, where *C. pegala* somewhat differs from the types of *P. pegala* (see below). Although the types of *P. pegala* agree with populations of this species in coastal Georgia, Abbot did not move there until 1776, the year after this taxon was described. Although William Hunter received numerous American insects from some of his former medical students who visited there (Keppie 2010, Hancock et al. 2015), Alexander Garden is a plausible source of the *P. pegala* types, which are consistent with the phenotype of *C. pegala* found in the Charleston area (see below).

The shifting concept of *Papilio alope*. Holland (1915) defined the range of *Satyrus alope* as "Atlantic seaboard from New Jersey to New Hampshire, and westward to the Mississippi." Macy and Shepard (1941) gave the northern limits of *Minois alope* as "southern New England westward to the Middle West." Klots (1951) stated that the subspecies *C. p. alope* is found from "Virginia (mountains) and New Jersey n. to Maine and Quebec (coastal plain) and New York (inland)." These authors identified populations within the southeastern coastal plain and Piedmont as a separate form or subspecies named *pegala*. Due to a poor understanding of eastern *C. pegala*, and the omission of Jones' figures from evidence, Brown ([1966a]) and Miller and Brown (1981) proposed Georgia type localities for *P. alope* based exclusively on the relationship between John Abbot and John Francillon. Screven County, Georgia, is located only about 137 km (85 mi) west of the proposed type locality of *P. pegala* and within the same physiographic region (southeastern coastal plain). The proposed Georgia type localities for *P. alope* encouraged a shift in the long-held concept of

this taxon, from populations in the northeastern United States to those in the southeastern coastal plain, where nominotypical *pegala* also occurs.

Based on Brown's ([1966a]) conclusions, Harris (1972) identified populations within the upper coastal plain and Piedmont of Georgia as the subspecies *C. p. alope*. Gatrelle (1985, 1992) also accepted the Georgia type locality and considered typical *alope* to represent populations that are intermediate between the southeastern coastal phenotype (i.e. *C. p. pegala*) and those of the southern Appalachians, which he identified as the subspecies *C. p. carolina* F. Chermock & R. Chermock. The name *carolina* is often used to identify pale-patched phenotypes that occur sporadically within the southern Appalachian Mountains and Piedmont. Although Klots (1951) popularized the notion of *carolina* as a weak subspecies of *C. pegala*, all subsequent North American checklists and catalogs (e.g. dos Passos 1964, Miller & Brown 1981, 1983, Pelham 2008, 2014) listed *carolina* as a form or synonym of the subspecies *C. p. alope* (for more on the status of *carolina* see Distributional Analysis, below).

Because of its Georgia type locality, Gatrelle (1985) believed that the name *alope* would have to be "dropped into the synonymy of *pegala*" and that the name *carolina* would then be used to represent the "eastern 'yellow' subspecies of *pegala*." Gatrelle (2004) later wrote, "*Alope* does not exist as a taxon—it is described from the edge of the range of nominate *pegala* . . . So, *alope* is not a valid 'subspecies' and thus does not occur anywhere as such." This opinion persuaded Scott (2008a) to identify all patched populations in the northeastern United States as the subspecies *C. p. maritima* (W. H. Edwards), explaining, "R. Gartrelle found that topotypical *alope* is a syn. of ssp. *pegala* (in the blend zone *pegala*×*carolina*), thus *maritima* replaces the usual usage of *alope*." Scott (2008b) omitted the subspecies *C. p. alope* and instead listed only *C. p. maritima*, maintaining that the name *alope* applies to "a form in blend zone of *pegala-carolina*, according to Ronald Gatrelle." Following this scheme, *alope* was recently defined as "an essentially highly variable southern Piedmont group of populations" (Arey & Grkovich 2014). In spite of this approach—instigated by Brown ([1966a])—most authors associated the name *alope* with patched populations in the northeast, as either a form or a subspecies (e.g. Fales 1974, Shapiro 1974, Shull 1987, Iftner et al. 1992, Nielsen 1999, Webster & DeMaynadier 2005, Belth 2013).

The type locality of *Papilio alope*. During the eighteenth century, European naturalists sustained a network of contacts in foreign lands from which they received countless specimens. As expected, most insects from America were obtained from collectors who visited or resided in states located immediately along the Atlantic seaboard. To determine a more appropriate type locality for *Papilio alope*, I compared Jones' figures with thousands of specimens of *C. pegala*, mostly at MGCL. Concentrating on coastal material from central Florida northward to southern Maine, it was immediately apparent that these populations are extremely clinal in nature, with size and pattern complexity decreasing northward. Individual butterflies within any given area also vary in size, coloration, and pattern. Regardless of this variability, populations exhibit morphological trends that are helpful in determining the most likely geographical origin of the male figured by Jones. As observed by Remington (1985), females of *C. pegala* are extremely variable across the species' range, while males are more geographically diagnostic. The measurements below denote approximate male forewing lengths, base to apex.

In Florida, adults are medium brown and large (32 mm) (Fig. 36, bottom center). The forewing of the male is rather pointed. Both sexes have a broad postdiscal forewing patch, which varies in color from cream (rarely) to reddish-orange (usually paler in females). Males have one eyespot on the forewing, though the presence of two full eyespots or a diminished lower spot is not uncommon. Females usually possess two eyespots, though many bear only one. The ventral wings are pale brownish-gray with a complex pattern of bold, dark transverse striations. The ventral hindwing ground color is often paler beyond the median, imparting a two-toned effect. The eyespots on the ventral hindwing are large and usually five or six in number; the three located towards the apex are typically oval and often conjoined. Populations in extreme northeastern Florida, southeastern Georgia, and southeastern South Carolina (including the type locality of *P. pegala*) are like those found farther south, but adults average slightly smaller in size (29 mm) (Figs. 5, 8, 9–15).

From northeastern South Carolina into coastal North Carolina and extreme southeastern Virginia, individuals are duskier brown and the ventral striations are less defined (Fig. 36, center, second from bottom). Males average somewhat smaller (27 mm) and the forewing is more rounded. Northward in this region, males more often possess two forewing eyespots. The eyespots on the ventral hindwing are smaller on average and usually more rounded. Klots (1951, Pl. 7, fig. 6) figured a male from Currituck Co., North Carolina, to represent the nominotypical subspecies.

Populations in the vicinity of Baltimore, Maryland, eastward to Delaware and southern New Jersey, express

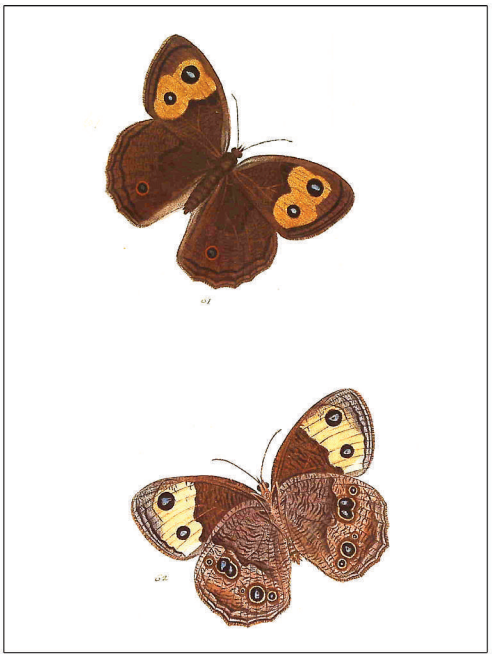


Fig. 15. Illustration of "*Papilio Macularia*" from Martyn (1797–[c.1802]), portraying a female *C. p. pegala*, probably ex J. Abbot.

a wide range of variation in overall size and eyespot development. Although most males have two forewing eyespots, occasional individuals possess a single forewing eyespot or a greatly reduced lower eyespot (Fig. 36, middle center). The color of the forewing patch varies from ochre-yellow to orange. This geographical area lies at the narrow eastern edge of a significant blend zone, where populations transition to smaller, less well-marked phenotypes. These populations are the basis of reports of southeastern phenotypes (i.e. *C. p. pegala*) occurring as far north as Maryland and New Jersey (e.g. Edwards 1880, Smith 1884, 1890, Muller 1968, Simmons & Andersen 1971). Figures of a specimen from southern New Jersey in Edwards (1890, Pl. *Satyrus* I, figs. 6, 7) mislead Brown (1969) into believing (erroneously) that these populations represent the same phenotype of *C. pegala* that occurs at the type locality of Charleston, South Carolina, prompting him to describe the subspecies *C. p. abbottii* to differentiate populations in southern Georgia and northern Florida.

From southeastern Pennsylvania and northern New Jersey, northward into southeastern Maine, occur variable populations of smaller (25 mm), darker adults (Fig. 36, center, second from top). The eyespots on the ventral hindwing are reduced and they are often entirely lacking in females. The forewing patch varies from yellow to dark orange. Males typically have two eyespots on the forewing, but they sometimes possess a reduced lower eyespot, especially southward. Towards the north/northwest, populations show the effects of introgression from patchless phenotypes, resulting in individuals with absent or greatly diminished forewing patches (e.g. Figs. 20; 36, top center). Patchless northeastern phenotypes are often identified as the subspecies *C. p. nephele* (W. Kirby).

Although butterflies associated with the name *alope* are nearly always described in the literature as having a "yellow" forewing patch, this diagnosis overlooks a wide range of variation. Harris (1862) described the patch as "ochre-yellow." Scudder (1888–1889) characterized the patches of males as "pale dull orange" and Weed (1917) referred to the patch as "yellowish brown." Klots (1951) called the patch "orange" and "yellow orange," while Allen (1997) said it ranged from "yellow to orange." Color illustrations of butterflies identified as *alope* in popular books portray decidedly orange-hued patches (Maynard 1886, Scudder 1888–1889, Holland 1898, 1915, 1931, Comstock & Comstock 1904, Klots 1951, Howe 1975). My analysis revealed that the majority of patched males in eastern North America exhibit some degree of orange coloration, ranging from ochre-yellow to dark pumpkin. The patches of females can be considerably paler, sometimes nearly white, even within populations that produce richly-hued males.

Originally intended to distinguish dark, diminutive butterflies with "reddish-yellow" forewing patches, *Satyrus alope* var. *maritima* W. H. Edwards was described from specimens collected on the islands of Martha's Vineyard (Dukes Co.) and Nantucket (Nantucket Co.), Massachusetts (Edwards 1880). However, *maritima* has since become a confusing and nebulous concept that lacks a consistent definition. Some authors (e.g. Maynard 1891, Forbes 1960, Shapiro 1966, 1974) claimed that the forewing patch of *maritima* is more poorly defined than in *alope*. Conversely, Holland (1931), who was familiar with the type series of *maritima* from the collection of W. H. Edwards, described the forewing patch of these populations as "bright and sharply defined." While Klots (1951) considered lowland coastal populations from Maryland to Maine to represent the subspecies *C. p. maritima*, some authors (e.g. Brimley 1938) applied the name to montane Appalachian butterflies. Clark and Clark (1951) observed that the first adults of *C. pegala* to emerge in the Piedmont of Virginia resembled *maritima*, while later adults resembled *alope*. Contrary to most accounts, Arey and Grkovich (2014) assigned coastal populations to *C. P. alope* and more inland populations to *C. p. maritima*, which they believed to range "west along the northern limits of the lighter

(yellowish) eye-patched southeastern populations of *C. pegala* at least to western Pennsylvania . . . also into Ohio and southern Michigan and perhaps as far west as Illinois." Arey and Grkovich (2014) also remarked that populations of *C. P. alope* and *C. p. maritima* appear to be "rather poorly differentiated" in southern and central New England. Like Edwards (1880), most authors considered *maritima* to be a form of *alope*, including Jones and Kimball (1943), who collected specimens on Martha's Vineyard and Nantucket. Klots (1951) was the first to treat *maritima* as a subspecies, but most subsequent authors (e.g. dos Passos 1964, Emmel 1969, Miller & Brown 1981, Pelham 2008, 2014) listed it as a synonym of either *C. p. pegala* or *C. p. alope*. Although *maritima* is supposedly distinguished from *alope* by a more richly colored forewing patch, the interpretation of this trait is extremely subjective and inconsistently applied. Even Edwards' (1880) interpretation of the patch color in the original description of *maritima* was somewhat exaggerated.

I examined ten male specimens of *C. pegala* from Martha's Vineyard, Massachusetts, including images of the lectotype (Figs. 18, 35a) and four paralectotypes of *S. a.* var. *maritima* from Edwards' collection at CMNH. One of the paralectotypes likely served as the model for the specimen figured by Edwards (1882, Pl. *Satyrus* II, figs. 6) (Fig. 17). Although Edwards (1880) described the forewing patches of *maritima* as "reddish-yellow," the patches of all the specimens examined from the type locality are yellow-orange, without any reddish hue. Holland (1898) fittingly described the patch of *maritima* as "orange-yellow." The patch color of more recent specimens of *maritima* from Martha's Vineyard figured by Arey and Grkovich (2014) are similarly colored.

It is fairly easy to understand why Edwards (1880) described *S. a.* var. *maritima.* Soon after publishing his description of *maritima*, Edwards (1882, Pl. *Satyrus* II, fig. 6) illustrated his concept of this taxon alongside a pair (male and female) with yellow patches (Pl. *Satyrus* II, figs. 1–4), which he identified as "*alope*" (Figs. 16, 17). In a letter to the Massachusetts entomologist Samuel H. Scudder, Edwards referred to his figures of *alope* as "typical" (5.iii.1881, Museum of Science, Boston, Massachusetts). He noted that the patches of *alope* were originally described as "*flava*" (yellow), thus he defined the forewing patch of *alope* as "pale yellow in both sexes" (Edwards 1880, 1882). Specimens of *C. pegala* from Edwards' collection at CMNH infer that his figured male *alope* (Fig. 16) most likely originated from the foothills around his home in Coalburgh, Kanawha County, West Virginia, where he rarely encountered this species (Edwards' Journal H, WVSA). The figured female *alope* is from Hunter, New York (Edwards 1882). Edwards' experience with yellow-patched butterflies encouraged him to describe the orange-tinted (as "reddish-yellow") *maritima* as an island variety, not realizing that such phenotypes are frequent throughout the northeast. Shortly after the description of *maritima* was published, the Chicago lepidopterist Charles E. Worthington (1851–1926) informed Edwards that he had an example of *maritima* from Connecticut (Edwards' Journal I, WVSA). Afterward, Edwards supposed that *maritima* "must be fd [found] about the coast for a ways inland" (24.iii.1880, Scudder corresp., MCZ). The Massachusetts entomologist Samuel H. Scudder, who was more familiar with *C. pegala* in New England, never mentioned *maritima* in his own publications. Edwards was unaware that specimens from as far west as Indiana can closely agree with the type series of *maritima*.

Chermock and Chermock (1942) examined 32 specimens from Rhode Island and western Pennsylvania, which they described as having an "ochraceous replacement of the yellow in the patch of the limbal area of the primaries." They concluded that these specimens did not agree with the types of *maritima* at CMNH (Fig. 18), nor other specimens identified as *maritima* by W. H. Edwards. The Chermocks therefore described these specimens as "*Cercyonis alope ochracea* New Form," which they also called a subspecies in the same publication. The Code (ICZN 1999) dictates that the use of the term "form" prior to 1961 refers to a subspecific name unless "its author also expressly gave it infrasubspecific rank, or the content of the work unambiguously reveals that the name was proposed for an infrasubspecific entity." Pelham (2008, 2014) considered *ochracea* to be infrasubspecific, stating "The text clearly indicates that this taxon was described as an individual variant."

The butterfly collection of Franklin (Frank) H. Chermock (1906–1967) is deposited at MGCL (ex. Allyn Museum of Entomology 1980; see Miller 1983). The collection of his brother, Ralph L. Chermock (1917–1977) is deposited at UANH (Calhoun 2015). Within these two collections I located all but one of the 32 specimens from the type series of *C. a. ochracea.* Missing for decades, I found the holotype within R. H. Chermock's collection at UANH and it is herein figured for the first time (Fig. 19). It is a male from Washington Park, Rhode Island, dated 18 July 1935, with a red holotype label signed "F. H. & R. L. Chermock" (Fig. 35b). A paratype male at MGCL bears the same data, revealing that the collection year of 1933 reported by Chermock and Chermock (1942) is in error. Both of these specimens exhibit a full yellow-orange forewing patch, which agrees with the original description of

ochracea ("ochraceous replacement of the yellow in the patch of the limbal area of the primaries"). Despite the claim by Chermock and Chermock (1942) that specimens of *ochracea* do not agree with the types of *maritima*, the primary types of these taxa represent analogous phenotypes (Figs. 18, 19). The remaining paratypes of *ochracea* (23 males and six females) possess patches ranging from yellow to orange in color, which are suffused to varying degrees; in some cases the forewing patch is lacking and the eyespots are merely surrounded by yellow scales (Fig. 20). The original description mentioned such variants: "As in the normal *alope*, the amount of ochraceous varies from a large patch to a fairly small one" (Chermock & Chermock 1942). Only twenty of these darker paratypes bear locality labels and all are from counties in western Pennsylvania (Fig. 35c).

The great variation in the type series makes it extremely difficult to understand the Chermock's concept of *ochracea*. The Chermock's confusing taxonomic notions sometimes resulted in friction with other lepidopterists. The prominent writer and lepidopterist Vladimir Nabokov charged F. H. Chermock with creating subspecific names for "chance series and morphological intergrades," arguing that Chermock was merely interested in "giving names to things" (Boyd & Pyle 2000). Some of F. H. Chermock's concepts and descriptions are certainly debatable (Masters 1968). His brother, Ralph, had a special interest in Satyridae. As early as 1947, while still a graduate student at Cornell University, Ralph planned to publish an extensive study of the genus *Cercyonis* (Chermock 1947, Brown 1954). Although this project was never realized, Ralph was regarded as an "expert" on this group of butterflies (Mather 1952).

Although I do not agree with Pelham (2008, 2014) that the original description of *ochracea* unambiguously reveals infrasubspecific rank, the Chermock's use of the term "form" for *ochracea*, as opposed to "race" for *C. a. carolina* (which they described in the same publication), certainly suggests this intention. Unfortunately, the Chermocks seemingly employed the terms "form," "race," and "subspecies" interchangeably, thus it is probably best to defer to the Code and treat *ochracea* as a subspecific name. Scott (2008a) curiously characterized *ochracea* as "an infrasubspecific *pegala*×*carolina* intergrade." Emmel (1975) mistakenly cited the type locality of *ochracea* as "Ohio," which was reiterated by other authors (e.g. Hess 1977).

The subspecies *C. p. agawamensis* was recently described by Arey and Grkovich (2014) from a few coastal salt marshes and estuarine habitats in Massachusetts, New Hampshire, and Maine (TL Newbury, Massachusetts). In late 2014, Alex Grkovich generously donated to MGCL five males and two females identified as *agawamensis*, as well as one comparative female from Massachusetts identified as *C. p. maritima*. All seven of these *agawamensis* were collected on 5 August 2007 in Rockingham County, New Hampshire, where 17 paratypes of *agawamensis* originated (Arey & Grkovich 2014). Also, I had the opportunity on 23 July 2015 to visit the type locality of *C. p. agawamensis* in Essex Co., Massachusetts, where I observed numerous adults and vouchered specimens from the salt marshes and nearby upland habitats. On 31 July 2015, I located a previously undocumented population of *C. pegala* in a salt marsh in York Co., Maine, within the range of *agawamensis* as defined by Arey and Grkovich (2015).

In common with other northeastern populations of *C. pegala*, individuals from salt marsh habitats exhibit a great deal of variation in size, ground color, forewing patch coloration, patch size, and eyespot configuration (Figs. 21, 22). One New Hampshire male received from Grkovich has a greatly restricted orange forewing patch, similar to the male from Sagadahoc Co., Maine in Figure 36 (top center). Most males (Fig. 21) closely resemble the lectotype of *maritima* from Massachusetts (Fig. 18) and the holotype of *ochracea* from Rhode Island (Fig. 19).

The seven specimens identified as agawamensis from Grkovich, as well as the specimens that I collected in salt marshes in 2015, reveal inconsistencies in the published definition of *C. p. agawamensis*. Although the original description indicated that male *agawamensis* are "somewhat larger" and females are "significantly larger" than individuals identified as *C. p. maritima* (Arey & Grkovich 2014), the forewing lengths of the specimens that I examined are consistent with other northeastern *C. pegala*. For example, the two female *agawamensis* at MGCL measure 29 and 30 mm, while Grokovich's female "*maritima*" measures 29 mm. These dimensions agree with the specimens that I collected in Massachusetts and Maine. Arey and Grkovich (2014) also stated that the anal eyespot on the dorsal hindwing of female *agawamensis* is "always well-defined and circled in orange," whereas "*maritima* females typically lack this eyespot altogether." This eyespot, however, is absent on one of the two female *agawamensis* from Grkovich (Fig. 23), and is very poorly developed and not ringed with orange on the other. This spot is likewise very small and not ringed with orange on two females that I collected in salt marshes in Massachusetts and Maine. Conversely, the "*maritima*" female received from Grokovich, and a number of females that I collected in upland habitats in Massachusetts and

FIGS. 16–35. *Cercyonis pegala* phenotypes (dorsal/ventral unless otherwise indicated). **16**, male (dorsal), fig. 1 from Pl. *Satyrus* II of Edwards (1882). **17**, male (dorsal), *Satyrus alope* var. *maritima*, fig. 6 from Pl. *Satyrus* II of Edwards (1882). **18**, male, lectotype of *S. alope* var. *maritima*, [July 1877], [Oak Bluffs], Martha's Vineyard [Dukes Co.], MA (CMNH). **19**, male, holotype of *Cercyonis alope ochracea*, 18.vii.1935, Washington Park [Providence Co.], RI (UANH). **20**, male (partial dorsal), paratype of *C. a. ochracea*, Big Run Base, Foltz Hill, Butler Co., PA (UANH). **21**, male, identified as *C. pegala agawamensis*, 5.viii.2007, Rt. 286, Hampton, Rockingham Co., NH (images reversed) (MGCL). **22**, male, identified as *C. p. agawamensis*, same data (MGCL). **23**, female, identified as *C. p. agawamensis*, same data (MGCL). **24**, female (dorsal), 13.vii.1985, Hwy 27, Southampton Twp., Suffolk Co., Long Island, NY (MGCL). **25**, female (ventral), same data (MGCL). **26**, male, from Pl. 12 of "Jones' Icones;" specimen herein designated the lectotype of *Papilio alope*. **27**, male, 28.viii.1941, Bedford [Westchester Co.], NY (MGCL). **28**, male, 16.vii.1924, Trenton [Mercer Co.], NJ (MGCL). **29**, male (ventral), Mt. Kisco [Westchester Co.], NY (MGCL). **30**, male (dorsal), no data (HMUG); specimen that R. Gatrelle intended to designate as the lectotype of *P. alope*. **31**, male forewings, both 14.vii.1974, Kingston [Bartow Co.], GA. **32**, male, holotype of *C. alope carolina*, Conestee [sic Connestee] Falls near Brevard [Transylvania Co.], NC (UANH). **33**, female, holotype of *C. pegala* race *borealis*, 10.vii.1920, Trumbull Co., OH (MGCL). **34**, male (ventral), lectotype of S. *alope* var. *texana,* Bastrop [Bastrop Co.], TX (CMNH) (side mounted specimen). **35**, original labels from type specimens (enlarged): **a**, lectotype of *S. a.* var. *maritima*; **b**, holotype of *C. a. ochracea*; **c**, paratype of *C. a. ochracea* (see Fig. 20); **d**, holotype of *C. a. carolina*; **e**, holotype of *C. pegala* race *borealis*; **f**, lectotype of S. *alope* var. *texana.*

Maine, bear a small anal eyespot. Some female *C. pegala* at MGCL are very similar in appearance to those identified as *agawamensis* by Grokovich, but they were collected in more upland habitats, including mixed forest openings (Figs. 24, 25).

Behavioral traits associated with *C. p. agawamensis* are also shared with other populations of *C. pegala.* Although Arey and Grkovich (2014) claimed that nectaring behavior in *agawamensis* was "unlike almost all other populations of *C. pegala*," it is well-documented in other populations across North America, including coastal Massachusetts (Scudder 1888–1889, Saunders 1932, Allen 1987, Iftner et al. 1992, Bouseman & Sternburg 2001, Pyle 2002, Mellow & Hansen 2004, Leahy 2006, Patterson 2006, Scott 2014). I have personally observed patched *C. pegala* nectaring in upland habitats in Maine. I agree with Tveten and Tveten (1996), who remarked that nectar habits in *C. pegala* "undoubtedly vary with individual populations and with the resources available."

Arey and Grkovich (2014) mentioned supposed "intergrades" between what they identified as *C. p. agawamensis* and *C. p. alope*, suggesting that salt marsh and upland populations interact. Indeed, I observed adults of *C. pegala* freely moving between the salt marshes and adjacent upland habitats, and some were seen resting in trees at the edges of the marshes during the day. At the type locality, I watched a number of butterflies purposefully flying from the salt marshes into adjacent trees in the late afternoon, presumably to roost for the night. Although I detected no obvious differences in the condition of the adults that I found in salt marshes versus those of upland habitats, Arey and Grkovich (2014) reported a slight disparity in the phenology of these populations. If present, this may be the result of microclimatic differences of the cooler, more humid lowland marshes. More research is clearly needed to confirm the status of *C. p. agawamensis*.

Based on this review of Atlantic coast *C. pegala*, the specimen of "*Alope*" illustrated by Jones most closely agrees with a patched northeastern phenotype (Figs. 26–29). I therefore propose the vicinity of New York, New York, as the revised type locality for *Papilio alope.* This conclusion is supported by the following: 1) the City of New York was occupied by the British until 1783 and served as an important military and political base of operations; 2) many insect specimens were received from New York by British naturalists during the second half of the eighteen century; 3) this area is located roughly midway between Pennsylvania and Maine where these phenotypes occur; 4) populations of *C. pegala* in this area have been associated with the name *alope* for over a century (e.g. Beutenmüller 1893); 5) the popular concept of the subspecies *C. p. alope* was forged when Klots (1951, Pl. 7, fig. 5) figured a male by that name from Bedford, Westchester Co., New York; 6) individuals of *C. pegala* from this area agree with the specimen portrayed by Jones (Figs. 26, 27, 29).

Lectotype of *Papilio alope*. A few weeks before his untimely death, R. R. Gatrelle announced that he had rediscovered "the types of *Cercyonis pegala alope*" and believed that this taxon was not described from Georgia, but rather from "up north" (Gatrelle 2005). Gatrelle posted images of one of these specimens on the webpage of the International Lepidoptera Survey (TILS) with the caption, "This is the lectotype [in press] of *Cercyonis pegala alope.* Type locality: northeastern US [in press], USA." Although Gatrelle was unable to complete his planned publication, the images he posted on the TILS webpage (TILS 2013) could still be viewed at the time of this writing.

In 2009, I was asked by E. G. Hancock of HMUG to identify images of North American butterflies in William Hunter's collection. During the course of this project, I recognized Gatrelle's intended lectotype as one of two unlabeled males of *C. pegala* at HMUG. The intended lectotype is the larger of the two (28 mm) with poorly developed yellow-orange forewing patches (Fig. 30). The second specimen is small (25 mm) and worn, with a well-developed forewing patch of faded ochre-yellow, typical of an old individual. Both are identified on the Hunterian Museum webpage (HMAG 2006) as candidates for lectotype designation on the assumption that Fabricius, having worked with Hunter's collection, was familiar with these specimens when he described *Papilio alope.* These specimens are not identified like other butterflies in Hunter's collection, as Fabricius did not publish the description of *P. alope* until 1793, a decade or more after M. H. Baillie created the cabinet labels. Images of these specimens on the HMUG webpage are captioned as "probably collected in Pennsylvania" on the authority of "Ron Gatrelle, pers. comm., July 2005" (HMAG 2006). This locality was possibly based on information from the museum that a former student of Hunter's named William Wood (fl. 1770s–1780s) collected insects around Philadelphia during the late 1770s when he was serving as a surgeon in the British Army (Hunter correspondence, Univ. of Glasgow; Brown et al. 2011). Regardless of its origin, the specimen that Gatrelle intended to designate as the lectotype is inconsistent with the concept of *Papilio alope* as described by Fabricius (1793) and illustrated by Jones (Fig. 26). Contrary to the original description, it lacks a wide yellow forewing patch and bears only five spots on the ventral hindwing, not six. Although the second specimen at HMUG has a more defined yellow

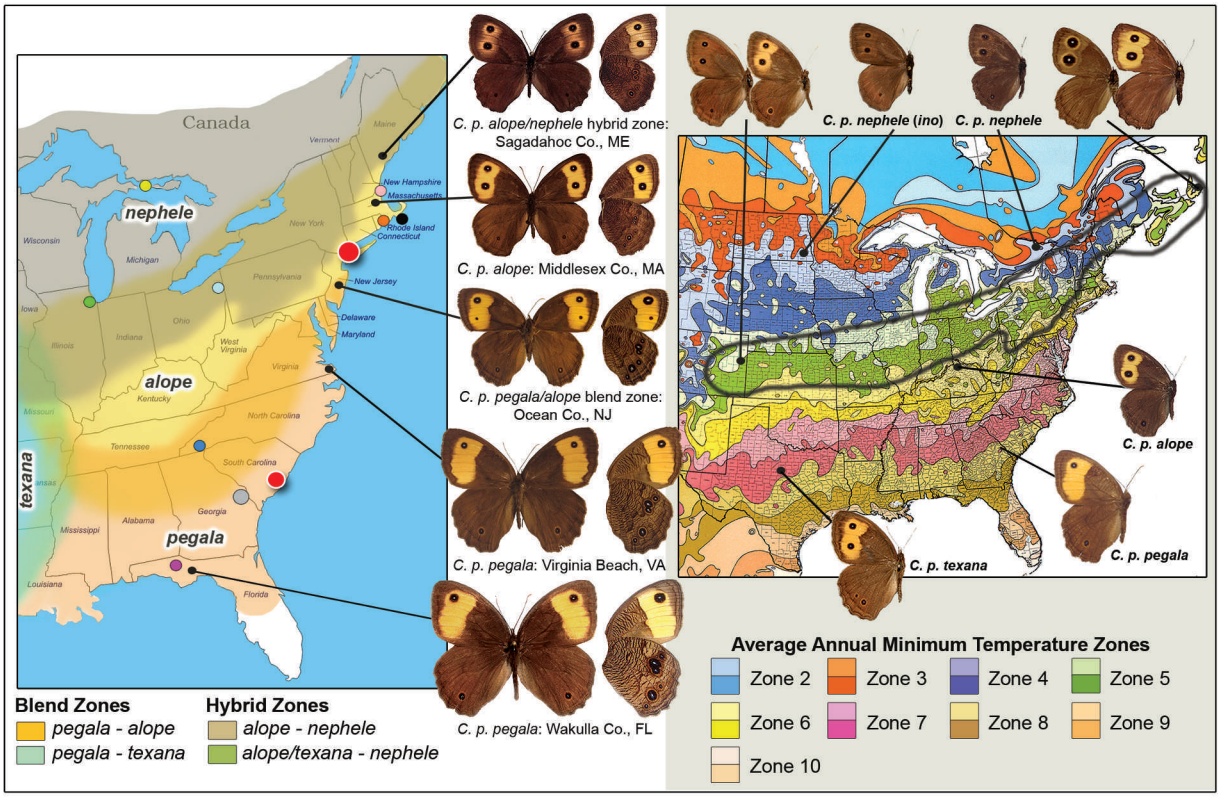


FIG. 36. Maps and phenotypes of *C. pegala*. Left map: eastern North America showing perceived blend zones and hybrid zones, with examples of patched butterflies that occur along the Atlantic coast (center). Type localities: *Papilio pegala* (vicinity of Charleston, SC), small red dot; *Papilio alope* (previously proposed; Screven Co., GA), gray dot; *Papilio alope* (newly proposed; vic. New York, NY), large red dot; *Cercyonis p. abbottii* (Chipley FL), purple dot; *Cercyonis alope carolina* (Connestee Falls, NC), dark blue dot; *Satyrus nephele* var. *olympus* (Chicago, IL), green dot; *Hipparchia nephele* (possibly Little Manitou Island, Ontario, Canada), yellow dot; *Cercyonis pegala* race *borealis* (Trumbull Co., OH), pale blue dot; *Satyrus alope* var. *maritima* (Oak Bluffs, Martha's Vineyard, MA), black dot; *Cercyonis p. agawamensis* (Newbury, MA), pink dot; *Cercyonis alope ochracea* (Providence, Rhode Island) orange dot. Right map: average annual minimum temperatures across much of North America (USDA 1990). Dark gray outline is the approximate boundary of the hybrid zone between patched and patchless *C. pegala.* Also shown are examples of *C. pegala* found at different points across the region.

forewing patch, it too has only five spots on the ventral hindwing. Despite these discrepancies, it could be argued that Fabricius examined these specimens and they contributed to his concept of *P. alope*, even though he did not publish the description of *alope* until many years after he may have seen them, nor did he refer to any such specimens in Hunter's collection (ICZN 1999, Art. 72.4.1.1). This underscores the need for a more suitable lectotype of *Papilio alope*.

Jones' illustration (Fig. 26) likely served as the basis of the description of *Papilio alope* Fabricius, 1793, thus the specimen it portrays is hereby designated as the **lectotype** of this nominal taxon in accordance with Article 74 of the Code (ICZN 1999). Although the fate of this specimen is a mystery, the designation of such "lost" specimens is permissible under the Code (Article 74.4). Jones' figures are accurate enough to represent the objective standard of reference whereby the application of the name *Papilio alope* can be determined.

Distributional analysis. Now that a type locality has been suggested for *P. alope*, and a lectotype designated, this nominal taxon must be considered within the concept of *C. pegala*. In other words, we must ask the question, "Where does *alope* occur within the range of *C. pegala* in relation to other nominal taxa?" Although variation is considerable, local populations of *C. pegala* tend to engender a principal phenotype. The interpretation of these phenotypes across eastern North America has led to the description of ten subspecies, whose recognition is as erratic and confusing as the phenotypes themselves. In addition, there are

aberrations and other pattern variants which occur throughout the species' range. Such variants sometimes possess characteristics that are evocative of distant populations, but they may have no direct genetic connection. The distributions of the various phenotypes of *C. pegala* in eastern North America are the result of postglacial expansion and more recent human influences. A detailed review of these processes is far beyond the scope of the present study, which focuses on perceived present-day ranges and their connection to described nominal taxa.

From the midst of this seeming chaos, I have attempted to map morphological trends within *C. pegala* across much of the eastern United States and Canada using established subspecies nomenclature. Based on a review of thousands of specimens, photographs, and other information, this map (Fig. 36, left) illustrates the approximate boundaries of these trends (or perceived "morphological averages"). It is not known how the distributions of the various phenotypes have changed over time, particularly in response to human alterations to the landscape. The map is based primarily on specimens and photographs dating from 1930 to the present. This analysis may help to locate appropriate areas from which to obtain DNA samples for future comparative studies.

As mentioned by other authors, transitional areas are extensive and serve as the basis of ongoing disagreements over the number of subspecies of *C. pegala* in eastern North America. However, equally extensive regions occur where phenotypes essentially stabilize into variable, yet distinguishable entities (i.e. subspecies). Nominotypical *pegala* is distributed entirely within the Lower Austral life zone, southeast of the fall line (boundary between the coastal plain and Piedmont), from Louisiana to southeastern Virginia (Fig. 36, left map). Although adults of *C. p. pegala* become somewhat smaller and darker northward along the southeastern coastal plain, they remain consistent with the concept of this taxon as originally described and defined by its lectotype. Larger adults found in northern Florida and southern Georgia were described by Brown (1969) as the subspecies *C. p. abbottii*, but the cline is so smooth between Florida and southeastern Virginia that any boundary used to segregate these populations would be arbitrary. Populations in Virginia and Florida represent the northern and southern extremes of *C. p. pegala*, whose type specimens from Charleston, South Carolina, convey the "average" expression of this taxon.

Phenotypes consistent with the concept of the subspecies *C. p. alope* are distributed from western Kentucky and northern Tennessee, eastward in a narrow belt to the coast, then northward into extreme southern Maine (Fig. 36, left map). This includes populations sometimes considered to represent the subspecies *C. p. maritima*. Pending additional research, the miniscule northeastern range of *C. p. agawamensis* is also included within *C. p. alope*.

A broad swath of populations that are intermediate between *C. p. pegala* and *C. p. alope* extends from the lower Mississippi Valley (within the Gulf Coastal Plain region of western Tennessee and southeastern Missouri), across the southern Appalachians and Piedmont, into southern New Jersey (Fig. 36, left map). This area represents a blend zone wherein populations cline northward from larger *C. p. pegala* to smaller *C. p. alope*. Such populations in and around Georgia were considered by Gatrelle (1985) and Scott (2008b) to represent typical *alope*, intermediate between *C. p. pegala* and the putative subspecies *C. p. carolina*.

The name *carolina* is often used to identify butterflies with white to pale yellow forewing patches that are found within the blend zone of the southern Appalachians and Piedmont. Usually uncommon, such pale-patched butterflies are often found in the company of darker-patched individuals (Harris [1950], 1972, Clark & Clark 1951). The original description defined *carolina* as a lighter brown butterfly with a white forewing patch. The description also indicated that the lower eyespot on the forewing of the male is reduced, and the eyespots on the ventral hindwing "suggest an approach toward *pegala*" (Chermock & Chermock 1942). Because patch scales in living *C. pegala* are easily lost, older individuals from any patched population can resemble the pale *carolina* phenotype. Among the thousands of *C. pegala* specimens at MGCL and UANH, I found relatively few fresh individuals with pale patches, and most are females. Most of these pale-patched butterflies originated from the mountains and Piedmont of North Carolina and Georgia, while others were collected in the mountains of eastern Tennessee, West Virginia, and the upper Piedmont of North Carolina. Two cream-patched males were collected in Alachua County, Florida. A few specimens from elsewhere in the southeastern coastal plain possess equally pale patches. In nearly all instances where multiple specimens were collected at a given locality, pale-patched individuals are accompanied by those with conspicuously yellow or orange-yellow patches (Fig. 31).

I recently located the "lost" holotype of *Cercyonis alope carolina* in the R. L. Chermock collection at UANH (Calhoun 2015) and it is herein figured for the first time (Fig. 32). Although the right wings are detached and the antennae are missing, it is otherwise in good condition. From Connestee Falls, Transylvania County, North Carolina, it is a relatively small male

bearing a red holotype label signed "F. H. & R. L. Chermock" (Fig. 35d). Reminiscent of *C. p. pegala*, the lower eyespot on the forewing is greatly reduced, the eyespots on the ventral hindwing are large, and the dark ventral striations are distinct. Although the original description indicated that *carolina* is "lighter brown in color than typical *alope*" (Chermock & Chermock 1942), the ground color of the holotype is quite dark (Fig. 32). The damaged female "allotype," also from the mountains of North Carolina, is deposited at UANH. Like the male, it is evocative of *C. p. pegala*, with contrasting ventral wings and larger ventral eyespots. Although lighter brown in color, it is a worn individual that was collected very late in the season (22.ix.1937). Miller and Brown (1981) and Pelham (2008, 2014) cited the existence of paratypes of *carolina* at MGCL (ex Allyn Museum), but I was unable to locate any of the remaining seven paratypes mentioned by Chermock and Chermock (1942). However, two specimens at MGCL, labeled in F. H. Chermock's hand, are from "Monteagle Tenn," which is a paratype locality (reported as "Mt. Eagle, Tennessee"). In addition, R. L. Chermock identified as *C. a. carolina* eight specimens in his collection from Madras, Coweta County, Georgia, which is located within the Piedmont.

I was surprised to learn that very few Chermock specimens identified as *carolina* possess white forewing patches as defined in the original description; those with the palest patches are worn females that lack patch scales. Even the patch of the holotype is slightly cream-colored (Fig. 32). Two males and a female from the F. H. Chermock collection at MGCL, collected in 1939 near the type locality, possess cream-colored patches. The patches of the remaining specimens of "*carolina*" in R. L. Chermock's collection vary from cream to yellow-orange. Like the Chermock's description of *C. a. ochracea*, it is extremely difficult to comprehend their concept of *C. a. carolina*. Because their specimens from Monteagle, Tennessee (a location within the type series) possess yellow patches, the Chermocks were undoubtedly aware that individuals with colored patches occurred alongside their white-patched concept of *C. a. carolina*. Moreover, R. L. Chermock identified specimens with yellow and yellow-orange patches as *carolina*.

I found no evidence of the alleged blend zone that Gatrelle (1985) recognized between pale-patched montane phenotypes and orange-patched butterflies of the coastal plain. Rather, pale-patched individuals occur in small numbers within the coastal plain (even rarely in Florida), northward into the southern Appalachian Mountains, where they are more frequent, but not exclusive. In overall appearance, pale-patched adults from North Carolina southward most closely resemble nominotypical *pegala* (often larger size, larger ventral hindwing spots, and the lower eyespot on the male forewing is often greatly reduced or wanting) (Figs. 31, 32). Individuals at higher elevations tend to be smaller and sometimes have reduced forewing patches, but they generally resemble *C. p. pegala*. Although cream-colored and pale yellow patched phenotypes also occur sporadically from West Virginia northward into Maryland and southern New Jersey, they more closely resemble *C. p. alope* (Fig. 16). The putative subspecies *Cercyonis alope carolina*, as originally described, is better recognized as an extreme form (i.e. "form *carolina*") that occurs with variable frequency in southeastern populations, particularly at higher elevations within the blend zone between *C. p. pegala* and *C. p. alope*.

Butterflies that are essentially recognizable as *C. p. alope* arise from the northern fringe of the blend zone within the Appalachian Plateau, and along the northern edge of the Piedmont in Maryland, Pennsylvania and New Jersey (Fig. 36, left map). Northward, *C. p. alope* shares a broad contact zone with patchless phenotypes commonly recognized as the subspecies *C. p. nephele* and/or *C. p. olympus* (W. H. Edwards) (Fig. 36, left map). A portion of this region corresponds to the area recognized by Remington (1968) as the "Northeastern—Central Suture-Zone," where multiple groups of otherwise allopatric taxa, including subspecies, meet and hybridize in northeastern North America. In fact, Remington (1968) included the pair "*Cercyonis pegala nephele* group"and "*C. p. alope* group" within this suture zone and considered the amount of crossing to be "Intense." Populations of *C. pegala* within this region do not gradually cline from south to north as they do in the southeast, but broadly overlap and intermingle. Phenotypes resembling either parental subspecies, along with presumed "intermediates," seem to haphazardly occur across the region. Edwards (1880) termed this region the "belt of dimorphism," where both patched and patchless *C. pegala* are found. Adults exhibit a wide range of variation across this region, even within the same populations. A series of 42 specimens at LCBM, collected during the 1890s in the vicinity of Manchester, Kennebec County, Maine, vary from near-*alope* to mostly *nephele*-like, with a wide range of intermediates. Fifty-four specimens at MCGL, collected in 1985 from a single locality in western Oxford County, Maine, vary from distinctly *alope*-like to distinctly *nephele*-like, with many intermediates. A single female collected near the northern limits of this region in Fulton County, Ohio, produced an assortment of phenotypes, from *alope*-like

to *nephele*-like (Sourakov 1995, 2008). Museum specimens from this region strongly suggest that *nephele*-like and intermediate phenotypes are more frequent than fully patched, *alope*-like butterflies, even southward. Nonetheless, some populations mostly produce *alope*-like butterflies. This is well documented in parts of Illinois (Irwin & Downey 1973, Sedman & Hess 1985) and I have personally observed this in northeastern Indiana. Such "islands" of opposite phenotypes were noted by Klots (1951). Patched or patchless phenotypes can also be limited to certain habitats. In central Ohio, *nephele*-like butterflies are found in wetlands with more northern affinities (e.g. bogs and fens), while *alope*-like butterflies occur in adjacent upland habitats (Iftner et al. 1992).

The transitional region between patched and patchless phenotypes of *C. pegala* is remarkably wide and exhibits characteristics of a mosaic hybrid zone, at least in part. A fairly recent concept proposed by Harrison (1986), a mosaic hybrid zone was defined by Howard (1993) as having "a patch quality" in which one taxon occurs in one patch and the other taxon occurs in another patch, while some patches contain a mix of the two taxa. Mosaic hybrid zones may be frequent where subspecies make contact along interdigitating environmental gradients (Jones & Collins 1992). This certainly describes the contact zone of *C. pegala*, which incorporates numerous biotic communities and elevations, from sea level coastal marshes to montane forest clearings. Larson et al. (2013) observed that hybrid zones across heterogeneous landscapes may exhibit a combination of different dynamics. *Cercyonis pegala* also seems to exhibit a high degree of genetic plasticity at the local level. Shifts at the same locality from one primary phenotype to the other during different years have been observed in western Illinois (Sedman & Hess 1985) and in parts of New York (M. B. Prondzinski pers. comm.). While the complex hybrid zone between patched and patchless *C. pegala* is very poorly understood, it is most likely of secondary origin, resulting from recolonization following the Wisconsin Glacial Episode (roughly 85,000–11,000 YBP). Another extensive hybrid zone in northeastern North America, likely also of secondary origin, involves the distinctive butterfly subspecies *Limenitis a. arthemis* (Drury) and *L. a. astyanax* (F.) (Mullen et al. 2008). A scenario of genetic differentiation, isolation, and reintegration of taxa along a portion of this shared contact zone was proposed by Remington (1968).

The southern boundary of the hybrid zone between patched and patchless *C. pegala* undulates with the occurrence of *nephele*-like and intermediate phenotypes at higher elevations, especially from Pennsylvania north through Massachusetts. Localized populations of these phenotypes also occur in the mountains of western Maryland and northern West Virginia (Simmons & Anderson 1971, Allen 1997). Although *nephele*-like phenotypes within the hybrid zone may closely resemble typical *C. p. nephele*, they are best regarded as transitional (i.e. "form *nephele*"). Brightly patched *alope*-like adults, mostly females, occasionally occur within hybrid zone populations as far northeast as New Brunswick and Nova Scotia, Canada. The northern limit of the hybrid zone between Lake Ontario and New Brunswick is difficult to determine, as relatively few specimens of *C. pegala* are known from that area. It should be noted that intermediate-like phenotypes with reduced forewing patches can occur anywhere within the eastern range of *C. pegala*, even in the extreme south (where they are rare). Such individuals are more frequently encountered at higher elevations in the Appalachians and Piedmont, where they appear to represent extreme variants or aberrations.

Edwards (1880) described *Satyrus nephele* var. *olympus* as a "slightly changed form of *Nephele*" found "somewhere between New York and Illinois . . . to and on the eastern slopes of the Rocky Mountains." Edwards (1882) subsequently restricted this to "Indiana and westward to the Rocky Mountains." Brown (1964) later proposed "Chicago, Illinois" as the type locality of *olympus* based on eggs that W. H. Edwards received in 1878 from Charles E. Worthington, who lived in that city. A male specimen that resulted from one of those eggs was designated by Brown (1964, fig. 19) as the lectotype of *S. nephele* var *olympus*. According to the specimen's label, as well as Edwards' journal "H" (WVSA), the butterfly emerged during the first week of June 1879. The proposed type locality of *olympus* ("Chicago, Illinois") lies 580 km (360 mi) almost due south of the type locality of *Hipparchia nephele* (=*C. p. nephele*), yet the ranges of these taxa are typically segregated in the literature from east (*nephele*) to west (*olympus*). Although Brown ([1966b]) suggested a vague type locality for *nephele* of "extreme western end of North Channel, Lake Huron [Ontario, Canada]," he simultaneously defined it as "vicinity of St. Josephs Island, Ontario, Canada" (Brown [1966a]). Ultimately, Miller and Brown (1981) suggested "possibly Little Manitou I., Ontario," referring to what is now known as Cockburn Island in northeastern Lake Huron, within the Manitoulin District of Ontario. Today, *olympus* is often treated as a synonym of *C. p. nephele* (Layberry et al. 1998, Scott 2006, 2008).

There are two significant problems with W. H. Edwards' description and subsequent recognition of *olympus*. Firstly, Edwards (1880) based his concept of

olympus on butterflies from within the hybrid zone between patched and patchless phenotypes of *C. pegala* (Fig. 36, right map). This explains the presence of faint to fairly evident forewing patches in some adults from so-called *olympus* populations, a condition also mentioned by Edwards (1882). As expected, patched *alope*-like adults have been recorded (albeit rarely) around the type locality of Chicago (Irwin & Downey 1973), which is located at the extreme northern fringe of the hybrid zone. Secondly, Edwards (1882) claimed that the larva and chrysalis of *olympus* are "readily differentiated" from those of *nephele* and *alope*, which he reported were analogous to one another. However, his early stages of "*nephele*" were all reared from ova obtained at Hunter, New York, which is located in the Catskill Mountains within the extreme southern portion of the hybrid zone. Edwards (1882) reported that one reared adult from the Catskills was "a typical female *alope*" and another was a female "intergrade." The former was figured by Edwards (1882, Pl. *Satyrus* II, figs. 3, 4). Edwards himself considered the Catskills to be located within the "belt of dimorphism," where both patched and patchless adults occur. He remarked, "In the Catskills, I have taken *Alope* as conspicuously banded as any in Virginia, but such examples are rare, forming, perhaps, two or three per cent of the flight" (Edwards 1882). Shapiro (1974) recorded "intermediate" populations from the Catskills and specimens at MGCL from that area are quite variable. In addition, some of the "*alope*" that Edwards reared for his comparison were received from Albany, New York. Like Hunter, Albany is also located at the southern edge of the hybrid zone. Edwards (1882) reported that one of the ova from Albany resulted in an "intermediate" adult without a forewing patch. Edwards therefore unwittingly compared early stages from three hybrid zone populations, thereby nullifying this key piece of evidence for differentiating *olympus*.

Although the early stages of *C. pegala* are extremely variable (Sourakov 1995), the differences that Edwards perceived can possibly be explained by the origin of the material. The "*olympus*" ova were from the far northern edge of the hybrid zone, where introgression from true *nephele* undoubtedly is greater. Conversely, populations in Hunter and Albany presumably experience a greater degree of introgression from *alope*. The similarity that Edwards observed between the early stages of "*alope*" and "*nephele*" can at least partially be attributed to his inclusion of "*alope*" ova from a locality less than 80.5 km (50 mi) from that of his purported "*nephele*" ova. Because his ova of "*nephele*" originated so far south of populations of "true" *nephele*, Edwards' (1877) description of the early stages of "*Satryus nephele*" is not applicable to the subspecies *C. p. nephele* as recognized today.

Patchless specimens that were described as *C. pegala* race *borealis* F. Chermock (TL Trumbull County, Ohio) are also from the hybrid zone. The holotype of *borealis*, a female with a red label signed "F. H. Chermock," is preserved at MGCL and is herein figured for the first time (Fig. 33). Although this taxon was described as "*Cercyonis* (*Satyrus*) *pegala* race *borealis*," its label identifies it as "*Satyrus pegalia* [sic]. race. *borealis*" (Fig. 35e).

West of Indiana and Kentucky, distinctive patched phenotypes identified as the subspecies *C. p. texana* (W. H. Edwards) blend with those of *C. p. pegala* and *C. p. alope* (Fig. 36, left map). Northward, *texana/alope* phenotypes hybridize with *C. p. nephele*. In western Illinois, especially southward, some individuals express traits associated with *C. p. texana*, such as paler ventral ground color with more distinct dark striations. These characters are evident on the large male lectotype of *S. alope* var. *texana* from Bastrop, Texas (Figs. 34, 35f). Northward, adults of *C. p. texana* are somewhat smaller and darker than those found farther south. A fairly narrow blend zone between *C. p. texana* and *C. p. pegala* occurs along the Gulf Coast, mostly within Louisiana.

The curious patched phenotype known at the "Salem Uplift form" of the Salem Plateau of the Missouri Ozarks (see Heitzman & Heitzman 1987) occurs where principal phenotypes intersect at higher elevations. These butterflies, whose males often have a greatly reduced or absent lower forewing eyespot, resemble those from the Appalachians. This is not surprising given that they occur under similar elevated conditions at the northern edge of a blend zone involving *C. p. pegala*. A series of Ozark *C. pegala* at MGCL, from the collection of the Missouri lepidopterist John "Richard" Heitzman (1931-2013), are accompanied by a typescript cabinet label that identifies them as "*Cercyonis pegala meinersii* Bouseman & Hess," implying a planned descriptive publication by the Illinois geologist David F. Hess and the late entomologist John K. Bouseman (1936-2006) of the Illinois Natural History Survey. According to D. F. Hess (pers. comm.), the description of *meinersii* was actually to be published by Hess and Heitzman during the 1980s to define a "color morph" of *C. pegala* that occurs in the Salem Plateau of southern Missouri and north-central Arkansas. The name honors Edwin P. Meiners (1893-1960), who collected the proposed holotype in Carter County, Missouri, in 1926 (deposited at the Univ. of Missouri, Columbia). Meiners was a physician and amateur entomologist from St. Louis, Missouri (Remington 1962). Hess and

Heitzman were ultimately dissuaded from publishing the description of *meinersii* to mitigate the proliferation of names ascribed to *C. pegala* (D. F. Hess pers. comm.).

Butterflies with forewing patches become less prevalent westward until they disappear just east of the Rocky Mountains in central Colorado. There, populations often attributed to the subspecies *C. p. olympus* occur within the western extension of the hybrid zone between patched and patchless phenotypes; in this case *C. p. texana* and C. p. *nephele* (Fig. 36, right map). Some authors identify at least some of the darker phenotypes in eastern Colorado as the subspecies *C. p. boopis* (Behr) (TL Contra Costa Co., California), but the application of this name to those populations is questionable (Fisher 2005). Northward, butterflies have been attributed to the subspecies *C. p. ino* G. Hall (TL Calgary, Alberta, Canada), but this is also controversial and some authors (e.g. Layberry et al. 1998, Scott 2008b) treated *ino* as a synonym of *nephele*. The characters used to separate *ino* (e.g. lack of ventral eyespots in the female) are not uncommon farther east. Westward in the hybrid zone, patched *texana*-like butterflies become less common and spottier in occurrence, possibly due to more pronounced differences in elevation. Many patchless butterflies from the hybrid zone west of Illinois possess more contrasting ventral patterns and larger ventral hindwing eyespots reminiscent of *C. p. texana*. This further supports the notion that *olympus* is comprised of an assemblage of hybrid populations within the contact zone between patched and patchless phenotypes, involving multiple parent taxa, extending from eastern Canada to the Rocky Mountains (Fig. 36, right map). Because of their apparent hybrid status, populations attributed to *olympus* should not be recognized as a discrete subspecies.

The selective forces acting upon patched and patchless phenotypes of *C. pegala* are unknown. Unlike the divergence between the subspecies *L. a. arthemis* and *L. a. astyanax*, hostplant specificity and mimetic factors are not known to play a role in *C. pegala*. It is possible that smaller, darker phenotypes have an advantage in colder climates by promoting heat absorption (Sourakov 1995). Butterflies without colorful patches may also rely on cryptic coloration to avoid predation, while brightly colored forewing patches may help to draw the attention of predators to the eyespots as part of a startle and/or deflection mechanism. Bowers and Wiernasz (1979) established the palatability of *C. pegala* to avian predators, but there is disagreement about the effectiveness of marginal eyespots as anti-predation devices (Lyytinen et al. 2003). More recent studies suggest that invertebrate predators are attracted to such patterns (Prudic et al. 2014).

The distribution of *C. pegala* phenotypes in eastern North America was compared against various ecological and climatological maps to reveal any potential correlation. A remarkably strong parallel was found with average annual minimum temperature (Fig. 36, right map). The boundaries of some of these temperature zones correspond to changes in elevation. Within the southeastern coastal plain, *C. p. pegala* is found within temperature Zones 8 and 9 (-12° to -1°C) (this subspecies is replaced westward by *C. p. texana*). The blend zone between *C. p. pegala* and *C. p. alope*, primarily within the Appalachians and Piedmont, corresponds to Zone 7 (-18° to -12°C). The range of *C. p. alope* is analogous to Zone 6 in the east (-23° to -18°C) (this subspecies is replaced westward by a somewhat smaller, darker phenotype of *C. p. texana*). The southern boundary of the hybrid zone between *C. p. alope* and *C. p. nephele* roughly follows the southern limits of Zone 5 (-29° to -23°C). Populations of *C. p.nephele* are mostly found within Zones 3 and 4 (-40° to -29°C).

The actual influence of temperature on phenotypic expression in *C. pegala* is uncertain. The temperature map in Figure 36 is based on data recorded 1974–1986 (USDA 1990) and more recent data are less acutely correlated. Nonetheless, significant long-term trends minimize the importance of such deviations. It is conceivable that the apparent ability of some hybrid populations to shift primary phenotypes from year to year is also temperature-related. The young larvae of *C. pegala* diapause during the winter, thus it is possible that a greater percentage of *nephele*-like adults are produced in response to colder temperatures, or more prolonged cool temperatures, during their development. This may help to explain the patchy, habitat-specific and elevational distribution patterns of phenotypes within some areas of the hybrid zone. Occasional southeastern butterflies with reduced patches may result from similar influences. How these and other potential factors combine to maintain the polymorphisms in *C. pegala* deserves investigation.

Proposed taxonomic arrangement. Despite over two centuries of study, a great deal more research is needed to understand the relationships between the various phenotypes of *C. pegala*. The extensive blend and hybrid zones that exist across eastern North America encourage a conservative arrangement as proposed by Sourakov (1995), in which all populations are considered to represent one polymorphic subspecies, *C. p. pegala*. The treatment of patched populations as *pegala* and all patchless populations as

nephele (as forms or subspecies), has long been employed in popular literature (e.g. Opler & Krizek 1984, Scott 1986, Layberry et al. 1998, Cech & Tudor 2005). However, this usage overlooks the obvious differences between regional phenotypes.

Pelham (2008, 2014) presented an arrangement of five eastern subspecies. Pending a more thorough revision of the group, I advocate a slightly more modest approach that recognizes four subspecies in eastern North America. The most obvious difference is that *C. p. olympus*, which consists of an assemblage of hybrid populations, is not recognized as a subspecies. The recently described *C. p. agawamensis* is regarded as a synonym of *C. p. alope*, not of *C. p. pegala* as indicated by Pelham (2014). Due to its closer resemblance to the nominotypical subspecies, *C. a. carolina* is listed as a synonym of *C. p. pegala*, rather than of *C. p. alope* as suggested by previous authors. For the purposes of this arrangement, the dark hybrid phenotypes denoted by the names *olympus* and *borealis* are aligned with *C. p. nephele*, though the primary types of these taxa do not represent "true" *C. p. nephele*.

Due to the previous misapplication of the name *P. alope*, Scott (2008b) considered *C. p. maritima* to be the valid name for all northeastern populations that had historically been associated with the subspecies *C. p. alope*. Because the names *S. a.* var. *maritima* and *S. a.* var. *texana* were proposed in the same publication (i.e. Edwards 1880), Scott (2008a) invoked the Principal of the First Reviser (ICZN 1999, Art. 24.2) to "make *maritima* the correct name [i.e. senior subjective synonym] for those who think they are synonymous," adding that the butterflies associated with these names "look similar." Not only are these taxa markedly dissimilar (Figs. 19, 34), such an action only applies when it is accepted that the entities involved are synonymous. Virtually all those who recognize multiple subspecies of *C. pegala* (e.g. Emmel 1969, Ferris 1981, Miller & Brown 1981, Neck 1996, Tveten & Tveten 1996, Fisher 2005, Pelham 2008, 2014) consider the name *texana* to apply to patched populations west of the Mississippi River. My own research endorses this view.

The following synonymy is proposed for *C. pegala* in eastern North America. Admittedly subjective, this arrangement acknowledges the undeniable trends that exist in wing pattern morphology. Current nomenclature is given for each subspecies, followed by its name as originally published (only original name combinations are given for subjective synonyms). Type localities (TL) and locations of primary types are also indicated.

Cercyonis pegala (Fabricius, 1775).

a. *Cercyonis pegala pegala* (Fabricius, 1775). *P*[*apilio*]. *N*[*ymphalis*]. *G*[*emmata*] *Pegala*. TL: vic. Charleston, Charleston Co., South Carolina. Lectotype ♂ at HMUG.
   =*Cercyonis alope carolina* New Race F. Chermock & R. Chermock, 1942. TL: Connestee Falls, Transylvania Co., North Carolina. Holotype ♂ at UANH.
   =*Cercyonis pegala abbottii* F. Brown, 1969. TL: Chipley, Washington Co., Florida. Holotype ♂ at CMNH.

b. *Cercyonis pegala alope* (Fabricius, 1793). *P*[*apilio*]. *S*[*atyri*]. *Alope*. TL: vic. New York, New York. Described from an illustration by William Jones at OUMNH. The specimen that served as the model for Jones' figures, probably lost, is herein selected as the lectotype.
   =[*Satyrus alope*] var. *Maritima* W. H. Edwards, 1880. TL: Oak Bluffs, Martha's Vineyard, Dukes Co., Massachusetts. Lectotype ♂ at CMNH.
   =*Cercyonis alope ochracea* New Form F. Chermock & R. Chermock, 1942. TL: Washington Park, Providence, Providence Co., Rhode Island. Holotype ♂ at UANH.
   =*Cercyonis pegala agawamensis* Arey & Grkovich, 2014. TL: Boston Road, Newbury, Essex Co., Massachusetts. Holotype ♂ to be deposited at MGCL.

c. *Cercyonis pegala texana* (W. H. Edwards, 1880). [*Satyrus alope*] var. *Texana*. TL: Bastrop, Bastrop Co., Texas. Lectotype ♂ at CMNH.

d. *Cercyonis pegala nephele* (W. Kirby, 1837). *Hipparchia Nephele*. TL: possibly Little Manitou Island, Manitoulin District, Ontario, Canada. Loc. of type(s) (probably a holotype ♀) unknown; possibly lost.
   =[*Satyrus Nephele*] var. *Olympus* W. H. Edwards, 1880. TL: Chicago, Cook Co., Illinois. Lectotype ♂ at CMNH.
   =*Cercyonis* (*Satyrus*) *pegala* race *borealis* F. Chermock, 1929. TL: Trumbull Co., Ohio. Holotype ♀ at MGCL.

ACKNOWLEDGEMENTS

For kindly providing images, information and other support, I wish to thank the following: Robert Blackburn (MAMU); Margaret Calder (Alexander Turnbull Library); Molly A. L. Carter, James Hogan, and Kathleen Santry (OUMNH); Elaine Charwat (LSL); Stanley Finger (Washington Univ., St. Louis, Missouri); E. Geoffrey Hancock and Jeanne Robinson (HMUG); Brian Harris (USNM); Rachel Hawkins (MCZ);

Blanca Huertas (BMNH); Volker Lohrmann (UMB); James L. Monroe; John E. Rawlins and Jane Hyland (CMNH). David F. Hess, who studied *Cercyonis* for many years, provided detailed observations and interpretations. Robert Young (Ernst Mayr Library, Harvard Univ.) sent photocopies of manuscripts. Lydia Ellington and Mary Beth Prondzinski (UANH), Philip D. Perkins (MCZ), and Deborah Staber (LCBM) permitted access to historical collections. Beverly Pope (Div. Plant Industry, Gainesville, Florida) helped with literature. Andrew D. Warren (MGCL) greatly assisted in locating specimens in the collection under his care. Andrew F. E. Neild reviewed my Latin translations. Accompanied by a sympathetic "good luck," Andrei Sourakov (MGCL) offered some helpful thoughts about his own studies of *Cercyonis*. Harry Pavulaan kindly shared his personal observations of *C. pegala* and reviewed an early draft of the manuscript. Michael E. Toliver reviewed the final draft and provided helpful suggestions.

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Submitted for publication 25 February 2015; revised and accepted 21 April 2015.