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ABSTRACT. The purpose of this paper is to firmly identify subspecific authorship of the name *floridensis* for the Floridian population of *Eurytides marcellus* (Cramer, 1779), which I recognize as a distinct, though slightly differentiated, subspecies ranging north and west along the Atlantic and Gulf of Mexico coastal regions. Though the name has been in historical use by multiple authors since description by William J. Holland (1898), it has not been readily evident which, if any, published work to date clearly and validly elevated the name to subspecific rank. The name "floridensis" is not preoccupied by any other members of the butterfly family *Papilionidae*. I determine the authorship to be *floridensis* Klots (1951).

Additional key words: Infrasubspecific, International Code of Zoological Nomenclature.

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INTRODUCTION

Pieter Cramer (1779) was the first to illustrate the familiar Zebra Swallowtail (as '*Papilio marcellus*') of the eastern United States (Fig. 1). Other than a brief etymology, there was essentially no descriptive text, nor reference to a type locality other than an elusive reference under '*Maja*' [*Hemileuca maia*] that all the specimens illustrated in plate XCVIII were taken in Virginia. The painted illustration is clearly of a specimen originating north of Florida by the primary distinguishing character of the forewing (see below) and appears to match Virginia spring form specimens very closely.

Fig. 1. *Papilio marcellus* (Cramer, [1779]), in "De Uitlandsche Kapellen…" Plate XCVIII, Fig. F.

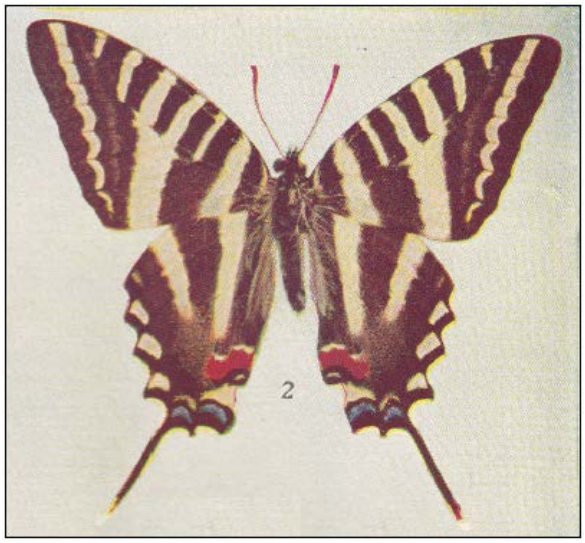

Fig. 2. *Papilio ajax*, Linnaeus, var. *floridensis*, Holland (1898), in "The Butterfly Book", Plate XLIV, Fig. 2.

Chainey (2005, page 305) provides an account of the possible disposition of Cramer's original specimen: "There is one specimen ex Felder collection but no other data (BMNH(E)#665081) …As this species was described from van Lennep's collection it is possible that this specimen is a syntype." Note in Fig. 4 that the label is correctly numbered: 665381. The purported syntype is the only specimen in the Natural History Museum, London, bearing any data label in relation to any "types" of *marcellus*. There is no collection data label or information associated with the specimen. Also, while the specimen represents the northern population of *marcellus*, it is a SUMMER phenotype by its elongated tails (Fig. 3). Cramer's image (Fig. 1) depicts a SPRING phenotype by its short tails, only tipped with white, and an enlarged red hindwing anal mark. Thus, the purported syntype is clearly not the specimen illustrated in Cramer (1779), though representative of the summer form of nominotypical *marcellus*. [Photos courtesy of Blanca Huertas, Natural History Museum, London].

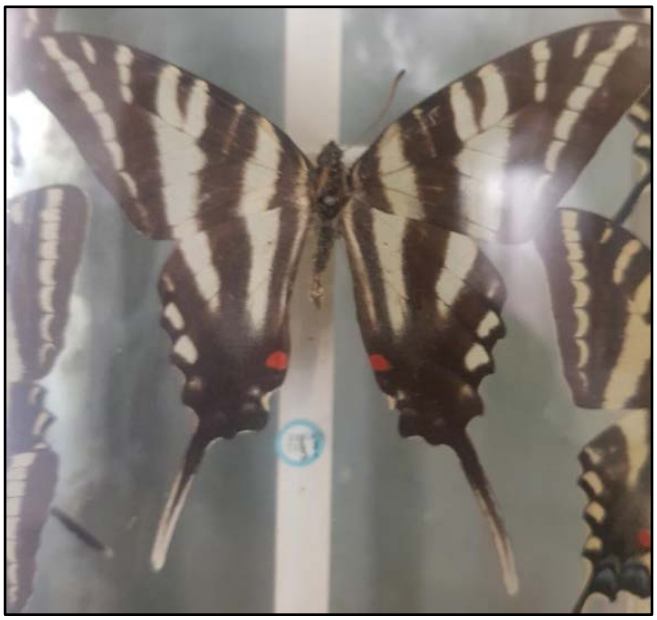

Fig. 3. Purported "syntype" of *Papilio marcellus* in the Natural History Museum, London. Photo © by permission of the Natural History Museum, London.

Fig. 4. View of same specimen showing data labels. Photo © by permission of the Natural History Museum, London.

"FLORIDENSIS" HOLLAND (1898)

William J. Holland (1848-1932), born on the island of Jamaica, received a theological education during his childhood in Salem, N.C. through several prestigious colleges, then continuing his education at Princeton Theological Seminary, graduating in 1874. Holland then became a Presbyterian pastor in Pittsburgh, PA., later assuming chancellorship of Western University, also in Pittsburgh, and simultaneously served as chair of Zoology and Comparative Anatomy. Holland's studies found him travelling extensively throughout the U.S. and worldwide. He is known to have traveled to Florida several times and certainly collected butterflies there. In 1885, he was a founder and first president of the Academy of Science and Art of Pittsburgh, then in 1901 became director of the Carnegie Museum, until 1922, while maintaining membership in several entomological societies (Johnson & Brown, 1904). Holland was known to be an ambitious, even obsessive collector, and considered butterfly collecting as a means to high social rank among peers (Leach, 2013), thus amassing a sizeable personal collection. Holland is best known for his landmark "Butterfly Book", in which he described winter form "floridensis", first published in 1898, then reprinted several times until 1951.

W.J. Holland (1898) described the taxon "floridensis" as an infrasubspecific form of *Papilio ajax* Linnaeus, as follows:

> "Another winter form, for which I propose the name floridensis, is represented in Plate XLIV, Fig. 2, by a male specimen. It is characterized by the great breath and intensity of the black bands on the upper side of the wings, which are quite as broad as in the summer form *marcellus*. I find this form prevalent in the spring of the year on the St. Johns River, in Florida. Expanse, 2.50-2.75 inches."

The caption for Plate XLIV, Fig. 2 in Holland describes the illustrated specimen (Fig. 2) as follows:

> "*Papilio ajax*, Linnaeus, var. *floridensis*, Holland, ♂. (This is the dark form found in Florida in the early spring.)"

Literature treatment of "floridensis" since its original description as either a seasonal (infrasubspecific) form or as a subspecies, remained inconsistent by various authors for over a century. Evaluating literature and internet-sourced imagery, specimens in institutional collections, and from personal field experience, it is evident that the Floridian population of *Eurytides marcellus* is represented by a weakly-differentiated subspecies, with either an inland contact zone or cline with nominotypical *marcellus* (Fig. 12). [The dynamics of clines are a result of a long period of evolution with many factors at work, and are frequently more complex than simply zones where one phenotype gradually grades into another. This is not the focus of the present paper and will not be addressed here.] The question remains over which author rightfully first assumed authorship of the name in a subspecific capacity. In an attempt to apply the principles of priority as established by the International Commission on Zoological Nomenclature it is necessary to review the historic literature. The name *floridensis* was first assigned subspecific rank by Klots (1951), as discussed below, though more recent works incorrectly attribute subspecific rank to Holland (1898).

HISTORICAL SYSTEMATIC TREATMENT FOLLOWING ORIGINAL DESCIPTION (including major synonymic treatments)

Rothschild & Jordan (1906), in their authoritative 'A Revision of the American Papilios', described, under a summary of "spring forms" (page 689): "*P. marcellus* f. loc. hib. *floridensis* Holl. (1899)" indicating that they also considered "floridensis" to be an infrasubspecific local spring form ("hib." = from hibernation [of pupae]). They describe "the black bands broader than in f. hib. *marcellus*."

Grossbeck (1917), lists "Form floridensis" as an infrasubspecific form of *Papilio marcellus* with only flight dates and locations.

Barnes & McDunnough (1917), in their synonymic 'Check List of the Lepidoptera of Boreal America', the authors list "floridensis" as an infrasubspecific form of *Papilio marcellus*.

Seitz (1924) lists, under *Papilio marcellus*: "forma hib. loc. floridensis *Holl.* is the spring form from Florida", indicating that he considered "floridensis" to be an infrasubspecific local spring form ("hib." = from hibernation [of pupae]).

McDunnough (1938), in 'Check List of the Lepidoptera of Canada and the United States of America', the author again lists "floridensis" as an infrasubspecific form of *Papilio marcellus*.

Clark & Clark (1951), under *Graphium marcellus*, give a detailed description indicative of an intergrade zone into eastern North Carolina: "On the outer Coastal Plain of Virginia the size of the early-spring form increases considerably, the fore wings being up to 40 mm. in length, though the color remains the same. Farther southward the dark bands become broader, and finally as broad as in the summer form, but the tails have only the tips white, and the red anal spot on the hind wings is large and undivided. This early-spring form with the broad dark bands (*floridensis* Holland) ranges northward…to eastern North Carolina, where it intergrades with the normally colored but large early-spring form found along the coast farther north." The authors imply infrasubspecific treatment by use of the term "early-spring form". They continue: "Early in September 1940 we were surprised to find occasional individuals in the Dismal Swamp and elsewhere on the Coastal Plain…They resembled closely the southeastern spring form "floridensis" and, were the origin and date of capture unknown, would certainly be referred to it."

W. J. Holland (1951): In the revised edition of 'The Butterfly Book', the author briefly describes form "floridensis" in slightly different wording than the earlier editions but still implies it is infrasubspecific: "The spring form in Florida is very dark..."

Klots (1951), under *Papilio marcellus*, treats *floridensis* as follows, though he does not make a clear differentiation from nominotypical *marcellus*: "In central Florida is the weakly distinguished *P. m. floridensis* Holland (similar to *lecontei*) with heavy, dark markings in even the early brood; the southernmost population of a cline." This is the first reference I can find, that treats *floridensis* at subspecific rank.

Forbes (1960), under *Papilio marcellus*, states: "*Floridensis* Holland represents the southern (chiefly Florida) race." thus indicating subspecific rank. However, no description of the phenotype is provided.

dos Passos (1964) lists *Graphium marcellus* form "floridensis" (Holland), 1898, at infrasubspecific rank.

Kimball (1965), under *Graphium marcellus*, merely cites notes by George D. Morgan (unpublished?): "Of the three subspecies described as differing slightly in size, hairiness, color, pattern, and length of tails, and supposed to be restricted to certain seasons or regions, all may be matched by Hillsborough County specimens throughout the year. While it is convenient to follow the line of least resistance and call all our Florida specimens *floridensis* (Holland), it is perhaps more accurate to separate them by color pattern into three series corresponding to *marcellus*, *telamonides* (Felder), and *floridensis.* The rest will be found to vary in all sorts of ways between these." Kimball stated also: "…the whole subject of subspeciation in *marcellus* needs to be worked out." Thus, Kimball (1965), following the reasoning of Morgan, recognizes "floridensis" at infrasubspecific rank.

Mather (1970) gives extensive discussion of seasonal variation in *marcellus* in Mississippi. Citing Holland (1931), Mather states: "the form represented as # 2 "floridensis" by Holland…is matched by a few Mississippi specimens but is not differentiable as a seasonal form in the present sample." Mather goes on to conclude that two primary seasonal forms occur in Mississippi: spring (*gen. vern.* "marcellus") and summer (*gen. aest.* "lecontei"). This implies infrasubspecific treatment.

Maudsley (1973), in his thesis, studied the influence of temperature, photoperiod and diapause on producing seasonal polymorphism in *marcellus*. Maudsley recognized "three distinct forms": *marcellus* (Cramer, 1777), *telamonides* (C. Felder & R. Felder, 1864) and *lecontei* (Rothschild & Jordan, 1906), stating: "All three forms occur throughout the butterfly's range…Populations in peninsular Florida and adjacent areas of southern Georgia represent the subspecies *G. m. floridensis* Holland. *G. m. floridensis* differs from the nominate subspecies, which would now be *G. m. marcellus*, in the extent of black banding, *G. m. floridensis* having comparatively wider bands in each form than *G. m. marcellus*. The subspeciation is clinal with odd occurrences of *floridensis*-like specimens in northern *G. m. marcellus* populations and vice versa." Maudsley compares respective "early spring", "late spring" and "summer" forms in both subspecies and gives detailed character analyses. He also goes on to note that only two forms occur in southern Florida: the "late spring" and "summer" forms. Thus, he considers *floridensis* to be subspecific.

Emmel (in Howe, 1975) states under *Graphium marcellus*: "The subspecies *G. marcellus floridensis* (Holland) is similar to "lecontei" and weakly distinguished; it is found in central Florida." The statement clearly applies subspecific rank.

Tyler (1975) lists, under *Eurytides marcellus*: "A fourth form, "floridensis"…was described as a subsp. by Holland; its status and relationship to the other forms should be studied." Tyler thus appears to imply that he considers "floridensis" to be infrasubspecific.

Miller & Brown (1981), under *Eurytides marcellus*, list = f. "floridensis", implying infrasubspecific rank.

Hodges (1983) lists "*floridensis* (Holl., 1898)" in the synonymy under *Eurytides marcellus*, implying infrasubspecific rank.

Gillmore (1988), editor of the Southern Lepidopterists News, for the Zone V report, states: "Ron Gatrelle commented that…the SC coastal *marcellus* are identical phenotypically with peninsular Floridian *marcellus*! Unknown to many researchers is the University of Georgia PhD dissertation of member Jim Maudsley of Athens, GA completed in 1970…The most significant aspect of Jim's research was his recognition of the validity of *Eurytides (Graphium) marcellus floridensis* (Holland) as our SE subspecies, whereas most authorities have considered *floridensis* as a form name…the major difference between nominate *marcellus* and *floridensis* is the consistent enlargement of the dark bands on the upper surface of the wings as demonstrated by the SE population in all broods. The material from other areas to the north and west appear almost white by comparison…Clinal gradients between subspecific populations are commonplace among lepidoptera in the SE Coastal Plain region." Gillmore's assessment clearly implies subspecific recognition.

Gerberg & Arnett (1989) list *Eurytides marcellus floridensis* at full subspecific rank: "The only…subspecies in Florida." The authors give a complete description but fail to differentiate it from nominotypical *marcellus.*

Minno & Emmel (1993) list *Eurytides marcellus floridensis* (Holland) at full subspecific rank but did not differentiate it from nominotypical *marcellus.*

Tyler, Brown & Wilson (1994) simply list "floridensis" as a "spring form" under *Protographium marcellus*, implying infrasubspecific rank.

Smith, Miller & Miller (1994) provide the following brief assessment under *Protesilaus marcellus*: "Populations in Florida were separated as subspecies *floridensis* Holland, heavily marked and resembling form 'lecontei' even in the earliest adults to emerge…", thus implying subspecific rank.

Möhn (2002) treats "*Neographium* (*Neographium*) *marcellus floridensis* (Holland, 1898)" as follows (specimens are illustrated from Ocala National Forest, Marion Co. and West Palm Beach, Dade County): "Often viewed as a synonym of *m. marcellus*. Specimens of the spring generation however, are markedly darker than those of *m. marcellus*. Specimens which fly later are darker too. Flight period substantially longer, from March – December. Distribution: USA, Florida (central Florida, Dade County, Marion County; southern Florida, West Palm Beach)." The author gives clear, descriptive status of the taxon as the Floridian subspecies and differentiates it from nominotypical *marcellus*.

Heppner (2003) lists, under *Eurytides marcellus* - "f. *floridensis* (Holland, 1898)", clearly indicating he considers this an infrasubspecific form.

Lamas (2004) lists "f. *floridensis*" in the synonymy of *Protographium marcellus*.

Pelham (2008) lists the name "= *floridensis* (W. Holland, 1898)" as a synonym of *Eurytides marcellus* (Cramer, 1777), thus implying availability as a subspecific name.

ESTABLISHING SUBSPECIES AUTHORSHIP

Holland distinctly described "floridensis" as "another winter form", implying infrasubspecific rank. All subsequent authors until 1951, maintained "floridensis" as a seasonal form. Klots (1951) was the first author to apply subspecific rank to *floridensis*. The pertinent ICZN articles to apply are:

Article 10.2. Availability of infrasubspecific names

> An infrasubspecific name is not available [Art. 45.5] from its original publication, unless it was published before 1961 for a "variety" or "form" and is deemed to be available under Art. 45.6.4.1. If an author uses a name, previously published at infrasubspecific rank, in a way which makes it available for a species or subspecies, that author thereby establishes it as a new name and it takes his or her authorship [Art. 45.5.1] (see also Articles 23.3.4 and 50.3.1).

Article 45.6. Determination of subspecific or infrasubspecific rank of names following a binomen

> The rank denoted by a species-group name following a binomen is subspecific, except that 45.6.1. it is infrasubspecific if its author expressly gave it infrasubspecific rank, or if the content of the work unambiguously reveals that the name was proposed for an infrasubspecific entity (see also Article 45.6.4);
>
> **Article 45.6.4.** It is subspecific if first published before 1961 and its author expressly used one of the terms "variety" or "form" (including use of the terms "var.", "forma", "v." and "f."), 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, in which case it is infrasubspecific [see also Art. 45.6.1]; except that
>
> **Article 45.6.4.1.** a name that is infrasubspecific under Article 45.6.4 is nevertheless deemed to be subspecific from its original publication if, before 1985, it was either adopted as the valid name of a species or subspecies or was treated as a senior homonym

Article 50.3. Authorship unaffected by changes in rank or combination

> **50.3.1.** The authorship of the name of a nominal taxon within the family group, genus group or species group is not affected by the rank at which it is used. But if an infrasubspecific name that otherwise satisfies the criteria of availability is used in a manner that makes it available for a species or subspecies, its author is the one who first so uses it [Arts. 10.2, 45.5.1].

The code clearly states that an infrasubspecific name described prior to 1961, which is elevated by a subsequent author to subspecific rank, the subsequent author is responsible for that usage and takes authorship of the name. Klots (1951) thus takes authorship of the name *floridensis* at subspecies rank.

DESCRIPTION OF THE PHENOTYPE

The original description of *Papilio ajax* f. *floridensis* was published in Holland (1898). In the original description, Holland simply indicates: "It is characterized by the great breadth and intensity of the black bands on the upper side of the wings, which are quite as broad as in the summer form *marcellus*". Klots (1951) describes it as similar to [summer form] *lecontei* "with heavy, dark markings in even the early brood." Maudsley (1973) describes *floridensis* in similar terms: "*G. m. floridensis* differs from the nominate subspecies…in the extent of black banding…having comparatively wider bands in each form than *G. m. marcellus*."

The original "type" (now lectotype) of *Papilio ajax* f. "floridensis" (Holland, 1898) is located in the collection of the Carnegie Museum of Natural History [photo courtesy of Vanessa Verdecia, Carnegie Museum of Natural History, Pittsburgh]. The specimen's right forewing had been detached and pinned beneath the specimen (Fig. 5).

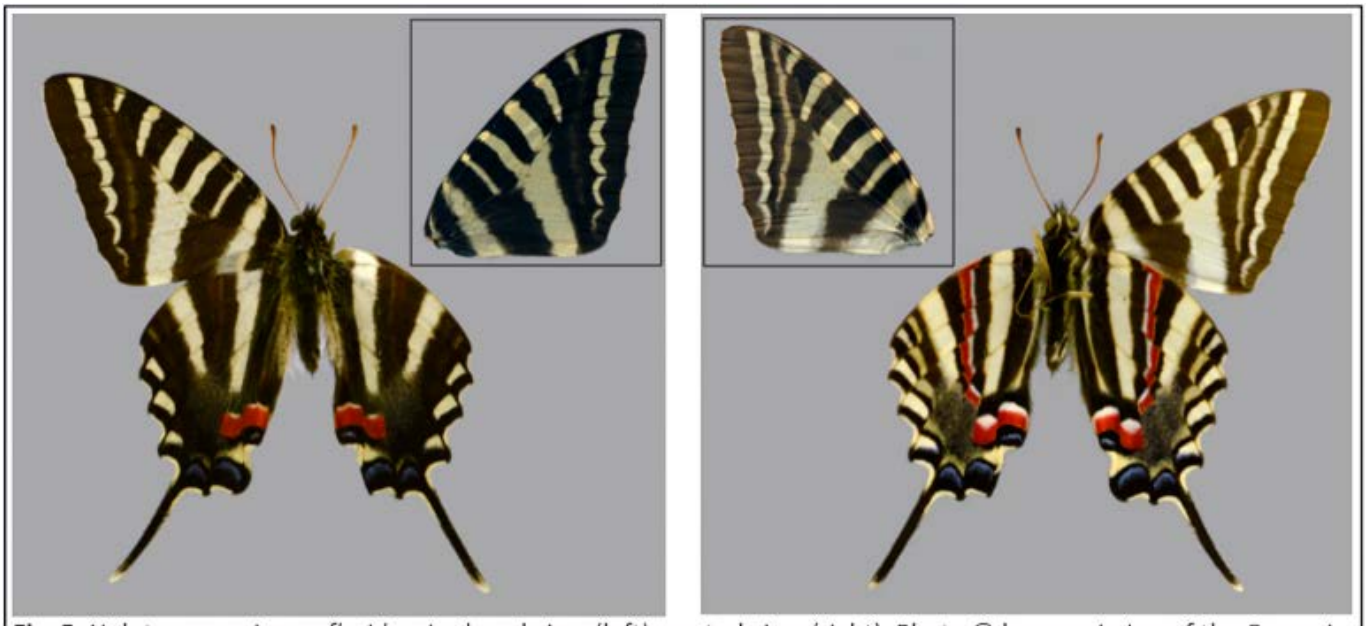

Fig. 5. Holotype specimen, *floridensis*, dorsal view (left), ventral view (right). Photo © by permission of the Carnegie Museum of Natural History. [Right forewing (insets) is detached from the pinned specimen.]

Three diagnostic characters of the forewing primarily differentiate subspecies *floridensis* from nominotypical *marcellus* (Fig. 6) and are based on the earliest Floridian spring form in comparison to the earliest Virginia spring form. These characters apply to all seasonal phenotypes. Differences in hindwing morphology between the two subspecies are not evident between respective seasonal phenotypes.

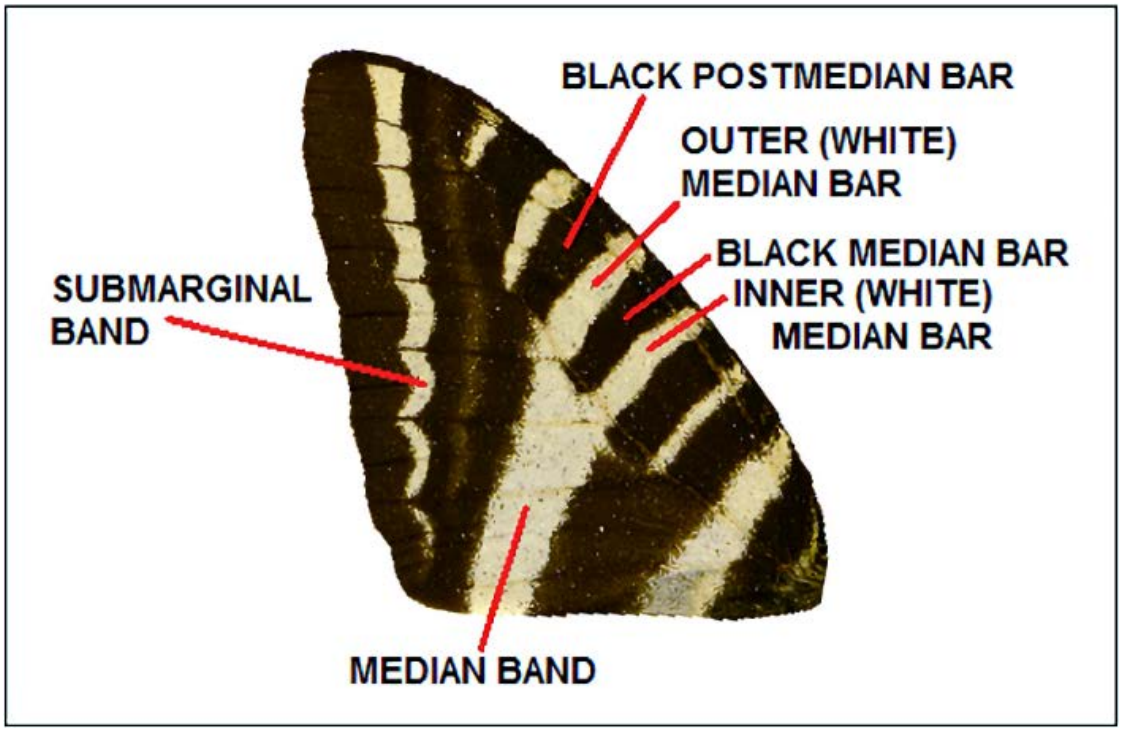

Fig. 6. Diagnostic characters of the forewing used to compare subspecies (the illustrated wing shows subspecies *floridensis*).

The width of the median band is narrower in *floridensis*. The outer edge of the band generally aligns with the outer edge of the outer (white) median bar. In nominotypical *marcellus* the outer edge of the median band extends outward beyond the outer (white) median bar, reaching to about a halfway point up on the inner edge of the black postmedian bar. Similarly, the inner edge of the median band in *floridensis* generally aligns with the inner edge of the inner (white) median bar, while in nominotypical *marcellus*, it extends inward.

In *floridensis*, the black median bar is well-developed, sharply defined and often noticeably rectangular. In nominotypical *marcellus*, the bar is variably less well-developed, often forming a slight "v" shape in the inward side of the discal cell. In many northern individuals, the bar may be faded.

In nominotypical *marcellus* the submarginal band is essentially straight, with only a slight concavity in the lowest two wing cells. In *floridensis* the cells that comprise the band each tend to show well-developed concavity except in the apical area.

In general, the white areas of nominotypical *marcellus* are more expansive than in *floridensis* in all of the comparative seasonal variants (early spring, late spring, summer). To better visualize and compare these diagnostic characters, composite images are shown below, with Fig. 7 showing the lectotype (Floridian spring form) and Fig. 8 showing a typical northern spring form of *marcellus*. Fig. 9 shows a typical Floridian summer form and Fig. 10 shows a typical northern summer form.

Fig. 7. Composite image of lectotype. Dorsal (left), ventral (right). February 28 flight date is indicative of earliest annual Floridian brood. Photo © by permission of the Carnegie Museum of Natural History. Leg. W. J. Holland.

Fig. 8. Composite image of early spring form *marcellus* in Virginia. Dorsal (left), ventral (right). Leesburg, VA. June 17, 2006. Leg. H. Pavulaan.

Fig. 9. Composite image of *floridensis* summer form. Dorsal (left), ventral (right). Marineland, FL. August 7, 2000. Leg. M. DeGrove.

Fig. 10. Composite image of Virginia summer form. Dorsal (left), ventral (right). Ex-ova, Leesburg, VA. Em: July 11, 2015. Leg. H. Pavulaan.

TYPE LOCALITY DATA

The exact locality where the type specimen was collected remains generally unknown. The specimen data label (Fig. 11) simply reads "Florida" with a collection date of February 28, 1884. Calhoun (pers. corr.) pointed out that the type label is, in fact, in Holland's handwriting. Holland (1898) states: "I find this form prevalent in the spring of the year on the St. Johns River, in Florida." While the description of the location "St. Johns River" applies in a general sense to an approximate type locality, it will have to suffice. As the River winds over 300 miles from its headwaters in Indian River County, to the mouth at Jacksonville (Duval County), Holland's exact travel routes and collecting site(s) in the area remain unknown. In 1898, most of the west shore of the river was accessible between Jacksonville and Palatka (along what is now Route 17). South of Palatka, there were few access points along the east side (off today's Route 17) until one travelled down as far south as the Deland and Sanford area. Early rail transportation to the region was a primary means for travelers, but with limited stops along this route. However, the entire river lies well within the range of subspecies *floridensis*. It would essentially be pointless to assign an arbitrary type locality without more detailed information.

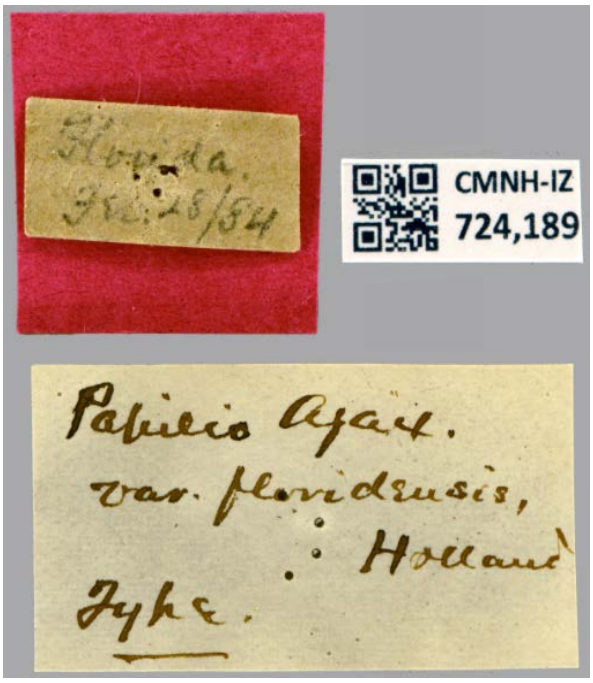

Fig. 11. Original data labels (CMNH).

DISTRIBUTION, FLIGHT PERIOD AND HOSTS

Distribution: Primarily Florida and adjacent areas of Georgia; then northward along coastal South Carolina, where the *floridensis* phenotype is dominant (Fig. 12). The *floridensis* phenotype occurs abundantly throughout southern Alabama during the summer months, while nominotypical *marcellus* and intermediates dominate the spring brood statewide and northern half of the state in summer. The *floridensis* phenotype also ranges west in rapidly diminishing numbers along the Gulf Coast at least to southern Mississippi (Mather, 1970), but there are surprisingly few records of the *floridensis* phenotype in Lousiana and Texas, among greater numbers of nominotypical *marcellus*.

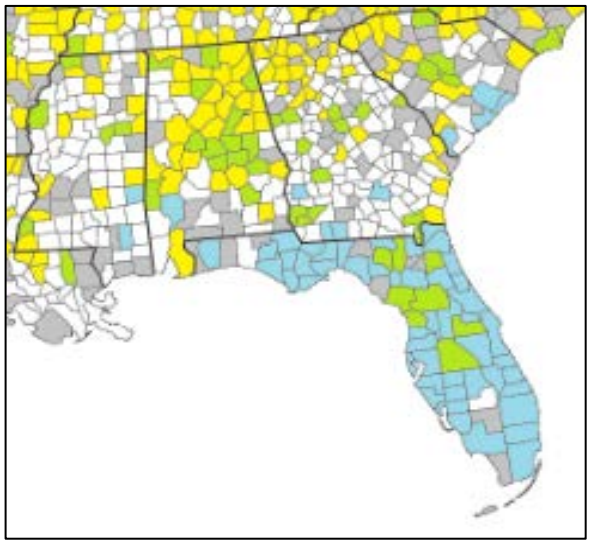

Fig. 12. Blue counties indicate only *floridensis* present. Green indicates intermediate forms present. Yellow indicates only nominotypical *marcellus* present. Grey county records indicate no images available.

Review of 6000+ images from many sources reveals a small percentage of *floridensis* intermediates and variants throughout the inland range of *marcellus*, almost exclusively as an extreme variant of the summer form, thus consistent with the observations of Maudsley (1973).

These intermediates occur more frequently north along the Atlantic Coastal Plain, as far north as Maryland, where it appears primarily as a late summer variant form among greater numbers of nominotypical *marcellus*. I have taken a single wild specimen (out of hundreds) as far north as Loudoun Co., VA. on 7/27/2015 that perfectly matches the Floridian phenotype. Reared specimens of *marcellus* from Loudoun Co. are normally of the nominotypical phenotype, but a very small percentage (<4%) of summer specimens appear nearly indistinguishable from Floridian specimens, thus representing a minor variant form in the nominotypical population. Conversely, a very small number of intermediates occur in northern Florida, primarily in the spring brood.

Flight period: Multiple broods in Florida. Flight dates span February-December.

Hosts: All known hosts are members of the Annonaceae, mainly *Asimina*. On the Florida peninsula, found on *Asimina angustifolia* (=*longifolia*), *A. incana* (=*speciosa*), *A. obovata, A. parviflora, A. pygmaea, A. reticulata, A. tetramera, Deeringothamnus pulchellus and D. rugelii*. On the Florida panhandle and in areas northward reported to use *A. triloba*, the sole host of nominotypical *marcellus*. Other non-Annonaceae hosts are suggested in Heppner (2003) but require confirmation.

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