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***Cercyonis pegala agawamensis* (Satyridae): A new butterfly subspecies from the coastal salt marshes of the northeastern United States of America**

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Abstract: A new subspecies of the Common Wood Nymph (*Cercyonis pegala*) from the New England coastline in the northeastern region of the United States is described on the basis of phenotype, behavior, habitat, seasonality, flight period, and phenology. *Agawamensis* is univoltine as in all *pegala*. The newly described subspecies occurs almost entirely in coastal salt marshes and estuarine meadows, quite atypical as understood for *Cercyonis pegala*. The newly described subspecies *agawamensis* predominately prefers and occurs within large open salt marshes but can also be found in similar habitat along smaller tidal rivers, coastal inlets and streams.

Additional key words: phenotype, behavior, habitat, seasonality, flight period, phenology, coastal salt marshes.

INTRODUCTION

A new subspecies of the Common Wood Nymph is described from the New England coastline in the northeastern region of the United States. The new subspecies is described on the basis of phenotype, behavior, habitat, and voltinism. As noted above, *agawamensis* is univoltine as in all *pegala*. Within the scope of this paper we have not as of yet examined the early stages or analyzed the DNA, in order to determine if further splitting of this subspecies from *Cercyonis pegala* is warranted. We point out, however, that there is precedence for such an assumption: Two rather restricted taxa occurring locally in similar salt marsh habitats in New Brunswick and adjacent coastal Gaspé, Quebec have been recently awarded specific status on the basis of similar criteria to those noted above. These taxa are the Maritime Ringlet (*Coenonympha nipisiquit* McDunnough) which has been split from the Common Ringlet (*Coenonympha tullia inornata* W. H. Edwards), and the Dos Passos Copper (*Lycaena dospassosi* McDunnough), which has been split from the Dorcas Copper (*Lycaena dorcas* W. Kirby) or more specifically from the Clayton's Copper (*L. dorcas claytoni* A. E. Brower) - known only from a few calcareous bog localities in northern Maine and in adjacent New Brunswick.

OVERVIEW OF NAMED TAXA OF “WOOD NYMPHS” OCCURRING IN EASTERN NORTH AMERICA:

This paper is not intended as an in-depth investigation of taxonomic issues involving the *Cercyonis pegala* group in the East, but is intended to only highlight the following discussion in deference to future anticipated publications on this subject. According to Klots (1951), there have been three recognized subspecies of *Cercyonis pegala* in New

England. These are *C. p. alope* (Fabricius), *C. p. maritima* (W. H. Edwards) and *C. p. nephele* (W. Kirby). In addition to the above three subspecies, a number of subspecies of *Cercyonis pegala* have been recognized and described from the Eastern United States. These include the nominate subspecies *C. p. pegala* (Fabricius), *C. p. abbotti* F. M. Brown, *C. p. carolina* (F. Chermock & R. Chermock) and *C. pegala texana* (W. H. Edwards).

The following subspecies (some in debatably infrasubspecific forms) were described from the eastern United States and southern Canada (in part from Klots 1951):

***pegala* (Fabricius, 1775):** TL “America”, defined as vicinity of Charleston, South Carolina (F. M. Brown, 1966). Klots (1951) listed this as occurring from “Florida and Gulf States n. to North Carolina and (blend zone with *alope*) New Jersey in coastal plain; northern limits in Mississippi Valley uncertain; large, brightly colored, with tendency to reduce or lose lower ocellus in orange FW eye patch [*in males*]; ocellus of HW above prominent”.

***abbotti* F. M. Brown, 1969:** TL Chipley, Washington Co., Florida. Like *pegala* but with a tendency to reduce or lose the lower ocellus in FW eye patch *in both males and females* (Mather, 1966; Sourakov, 1995). Florida, but apparently occurs along the Gulf Coast to at least Mississippi.

***alope* (Fabricius, 1793):** TL “India”, corrected to Burke-Screven-Bulloch counties, Georgia (F. M. Brown 1966). Klots listed this as occurring from “Virginia (mountains) and New Jersey n. to Maine and Quebec (coastal plain) and New York (inland); blends with *maritima* along its eastern limits, with *nephele* northward, with *carolina* and *pegala* southward; smaller and not so richly colored as nominate *pegala*, both ocelli in orange of FW well developed”. The HW ocellus is typically smaller. Harry Pavulaan (pers. comm.) describes *alope* as “...a population of mutts occurring between coastal *pegala* and *carolina* of the southern Appalachians...” that “...constitutes an essentially highly variable southern Piedmont group of populations...” The FW eye patch is more typically yellow in *alope*. What is further confusing about *alope*, which also warrants study and probable further revision is the fact that the TL of *alope* is located only two counties west of the TL of *pegala* in the State of Georgia.

***maritima* (W. H. Edwards, 1880):** TL Oak Bluffs, Martha’s Vineyard, MA. Like *alope*, but smaller, darker, and with FW eye patch deeper orange. Klots (1951) defined the range as: “Coastal edge, Maryland to Maine”, but this phenotype apparently extends west along the northern limits of the lighter (yellowish) eye-patched southeastern populations of *C. pegala* at least to western Pennsylvania (see description of *ochracea* below) also into Ohio and southern Michigan and perhaps as far west as Illinois.

***nephele* (W. Kirby, 1837):** TL “Canada”, defined as “the extreme western end of North Channel, Lake Huron...in Ontario, Canada” (F. M. Brown 1966). Klots (1951) describes *nephele* as: “FW dark, lacking yellow orange patch (but ocelli present); New York and New England (mountains) n. and w. through northern Mississippi Valley and Canada to Hudsonian Zone”.

***texana* (W. H. Edwards, 1880):** TL “Texas”, defined as Bastrop, Bastrop Co., Texas (F. M. Brown 1964). Klots (1951) provides the range description as: “Southwest, Texas n. to Kansas; like [nominate] *pegala* but markings beneath more clear cut and distinct; paler colored”.

***carolina* (F. Chermock and R. Chermock, 1942):** TL Conestee Falls, North Carolina. Southern Appalachian Mountains and inner Piedmont, north to about the Washington D. C. region. Klots (1951) described: “Paler brown than in *alope* and *pegala*, a minor form”. The FW eye patch is creamy white. Apparently intergrades with *alope* to the east (central North Carolina), *maritima* toward the northeast (central Maryland), *nephele* to the north (western Pennsylvania), and with *olympus* to the northwest.

***olympus* (W. H. Edwards, 1880):** TL “...between New York and Illinois...” F. M. Brown limited the TL to Chicago, IL. This subspecies has been considered as occurring across the Upper Austral and Transition Zones of the upper Midwest, west to the eastern slopes of the Rocky Mountains. *Olympus* is suggestive of *nephele* except that the FW eye patch, typically lacking in *nephele*, is suffused by dark orange-red or reddish brown scales,

sometimes tending toward yellowish, with a definite reddish or purplish-red iridescence on the dorsal surfaces of the wings especially in fresher individuals. The dorsal FW ocelli as well as the ventral ocelli on both wings are well developed. The ground color is very dark. We have taken specimens that are probably best referred to as *olympus* in southwestern Ontario (Essex Co.) and adjacent southeastern Michigan, in old dry shrubby fields bordering deciduous woodlands. Populations further east into southern and eastern Ontario (i.e. Elgin Co. and eastward across the northern shores of Lake Erie) are perhaps also referable to *olympus*, while we have taken specimens in southwestern Maine (i.e. Streaked Mountain, Oxford Co., el. 900 feet) which could be referred to as either *olympus* or *maritima*. Specimens along the north shore of Lake Ontario feature a brown ground color with the FW eye patch yellow; these intergrade northward to *nephele*, southward and southeastward they appear to intergrade to *alope*.

***ochracea* (F. Chermock & R. Chermock, 1942):** TL Washington Park, Providence, Providence Co., R. I. This was originally described as a form of *alope*. Chermock and Chermock (1942) noted: "...on examination of Edwards' type material, the name *maritima* cannot be applied to this form". However, specimen series from both Rhode Island and coastal islands of Nantucket and Martha's Vineyard (TL of *maritima*) show a similar range of variation. Presently, it is probably best considered as a form (or synonym) of *maritima*. The relationship and comparative distributions of *ochracea* and *maritima* warrant review.

Howe (1975) retained the use of the name *abbotti* to describe the "large and beautiful subspecies" occurring from Florida and Georgia and along the Gulf Coast to Mississippi, but sunk, however, each of the various forms occurring north of the range of *abbotti* in the East into *pegala*, referring to them as "phenotypes of *pegala*". He stated that the typical form of *pegala* is restricted to the southeast coast, and stated that this form is "probably the same as *maritima*", pointing out that *pegala* "...tends to have only one ocellus whereas *maritima* has two and is usually smaller in size". He further stated that "these coastal forms with a dark orange-yellow postmedian eye patch on the forewings intergrade with the inland form with a bright yellow patch which is called '*alope*'; and that 'in turn in the north Atlantic states '*alope*' blends with a form that lacks the yellow patch and is called '*nephele*' (probably incorrectly!). Howe also referred to *olympus* as a synonym, presumably of *pegala*, and recognized *carolina* as a "...larger paler form from the southern Appalachians."

While there is probably some merit to Howe's conclusions, it is our opinion that the above is somewhat oversimplified. Certainly *maritima* is not the same thing as *pegala*, at least from the coastal Carolinas and Virginia, and that the name *nephele* probably does need to be retained as a valid taxon from the northern, Canadian Zone regions of the range of the species.

Perhaps, rather predictably, Scott (1986) condensed his treatment of eastern *C. pegala* even farther than Howe (1975). Scott recognized only TWO subspecific names: Those being *nephele*, consisting of patchless populations ranging from "Nova Scotia, c Penn., and Ill. north and west..." and *pegala* - which he ascribed to ALL yellow and/or orange patched eastern populations south of his stated range of *nephele*.

Most currently, the Butterflies of America website (<http://www.butterfliesofamerica.com>) offers a rather reasonable treatment of eastern *C. pegala* based upon the landmark 'Catalogue of the Butterflies of the United States and Canada' (Pelham, 2008), which is updated frequently on the website to reflect recent taxonomic changes. Pelham recognized the following subspecies: *pegala* (southeastern - presumably Florida to Massachusetts), *texana* (southwestern - Texas to Kansas), *alope* (regions north and west of *pegala*, including *carolina* and *maritima* as synonyms), *olympus* (Upper Midwest, including the synonym *borealis*) and *nephele* (north). While certainly more comprehensive than the rather scant treatments rendered by Howe and Scott, these treatments also appear to have apparent flaws but are based upon current literature. For example, *maritima* and *abbotti* are certainly not the same thing biologically and cannot both be synonyms of *pegala*; likewise *ochracea* probably can be listed as a synonym of *maritima*.

Klots (1951) also noted that "...the above forms [that Klots refers to] represent merely averages. Intermediates not only occur abundantly in blend zones but also may occur anywhere in an area. Sometimes, within blend zones, local colonies of one form or another seem to be segregated out..." Caution should be taken here not to

misinterpret and expand the concept of intermediates to distant ends of the various clines seen in *pegala*, as many authors have. Intermediates appear primarily in blend zones. For example, there are no known records of “nephele” forms in the southeastern U.S. and conversely no known records of “abbotti” forms in Canada. Many authors interpret the presence of intermediates in bland zones as applying species-wide, which we suggest is an incorrect application of the concept of intermediates. Klots also suggested “...a terrific amount of work is needed on the distributional problems of this clinal species...”

At this point, we would like to point out - in response to the treatment of some authors such as Cech & Tudor (2005) and Bouseman & Sternburg (2001) - the exact parallel between the relationship of *Cercyonis pegala/nephele* (and/or *maritima/nephele*) and *Limenitis arthemis/astyanax* in New England. In virtually all butterfly field guides since the time of Klots (1951), *astyanax* has been treated as a subspecies - and not a form - of *artemis*; while in at least the publications referred to above, *nephele* has been defined as merely a form of *pegala*. This, despite the fact that there exist in BOTH cases, within *artemis/astyanax* and *pegala/nephele*, extensive and broadly overlapping subspecies ranges or zones of hybridization of each of the two pairs. In New England, for example, the zone of hybridization between *artemis* and *astyanax* extends from almost the south coast of Connecticut, Massachusetts and Rhode Island - where traces of the white bands along with other subtle characters of *artemis* can be seen in specimens of *astyanax* - to at least the latitude of the Kancamagus Highway of northern New Hampshire (we have actually taken a partially white-banded hybrid specimen that otherwise resembles *astyanax* even further north of this at the Scott Bog region of extreme northern New Hampshire only a few miles from the Quebec border at an elevation of 2,000 feet, well into the Canadian Life Zone). In terms of the *Cercyonis*, we have similarly found specimens of *nephele* with partial to full development of the orange forewing eye patch at least as far north as the vicinity of Streaked Mountain near Buckfield, Oxford Co., Maine at elevation of 950 feet. At the same time we have also found totally dark specimens of *nephele* well southward into west central Massachusetts in the vicinity of Hawley in Franklin Co. at elevation of approximately 800 feet, and the *nephele* phenotype has been found in Rhode Island; while fine examples of *alope* with fully developed yellow forewing eye patches, in some cases with the lower eyespot reduced, have been taken substantially north of this in the hilly regions west of Brattleboro, Windham Co., Vermont.

In conclusion of this discussion, we can state that in New England, among the previously recognized subspecies, only *nephele* in the more northern Canadian Zone regions appears to be more or less well distinguished, while *alope* and *maritima* have been widely subject to confusion and appear to be rather poorly differentiated within the more southern and central New England regions. We have, however, somewhat frequently noted individuals in southeastern (or even occasionally in northeastern) Massachusetts and in southeastern Vermont featuring an extensive yellow FW eye patch with the LOWER eyespot reduced in size in males, suggestive of the nominate southeastern *pegala*; or specimens in western Massachusetts which are essentially brown, lacking the FW eye patch entirely, but with the FW ocelli large and pupiled in bright blue scales.

***Cercyonis pegala agawamensis* Arey and Grkovich, new subspecies**

ETYMOLOGY. The type specimens (holotype and allotype) are designated from the former historical settlement and territory of the Native American Agawam Tribe in northeastern Essex County, Massachusetts (ca. 1638) that has historically encompassed the current towns of Ipswich, Rowley, Essex, Newbury, Byfield and Georgetown. We propose the subspecies scientific name as *agawamensis* and the common name as the **Salt Marsh Wood Nymph**.

DESCRIPTION. Male somewhat distinct from nearby coastal and inland populations of *alope* and *maritima*; female quite noticeably distinct. Both sexes demonstrate a general brighter “southern look” in comparison to their neighboring inland populations occurring outside of salt marsh habitats.

Male: FW length 25-26 mm. **Upperside:** Ground color brown. FW apex typically somewhat more pointed than other *pegala* subspecies. FW eye patch fairly broad (width of patch 10 mm along costal margin), yellow to slightly yellow-orange; eyespots well developed, somewhat small but without tendency in most specimens for lower

eyespot to be reduced; occasional specimens however do have lower eyespot reduced or even absent. Pupils sharply defined and centered in light blue. Upper eyespot sometimes reduced in size. HW eyespot well developed, small but with well-defined outer circle of lighter orange-brown; pupiled in light blue. HW submarginal dark line prominent and well defined. **Underside:** Ground color lighter brown, particularly on outer half of HW. FW yellow eye patch prominent and wide, lower border at inner margin of FW wide and straight. Eyespots well-defined and round in shape, smaller with sharp edges not diffuse as in nearby *alope* and *maritima* populations. Dark lines bordering inner and outer edges of FW eye patch prominent; eyespots well-defined and sharply pupiled in light blue. HW eyespots smaller than in typical southeastern *Cercyonis* but well-defined. Striations sharp and crisp; median and submarginal dark lines prominent.

Female: FW length 29-31 mm. **Upperside:** Ground color lighter brown than in male; a lighter shade along outer half of HW beyond cell area. FW apex slightly rounded but FW broad and squarish. FW eye patch broad (12-15 mm along costal margin), extending nearly to (and sometimes into) the cell area, color of patch yellow to slightly orange-yellow; yellow patch extends into marginal area in some specimens; margins of patch very sharply defined and not diffuse. FW eyespots as in male, sharply defined without diffuse edges, pupiled in blue; upper eyespot round, lower eyespot somewhat squarish and only somewhat larger. [In nearby *alope* and *maritima* both FW eyespots are larger, rounded with diffuse edges, lower eyespot is often significantly larger than upper.] HW eyespot generally smaller than in nominate *pegala* but with well-defined orange-brown outer circle; submarginal dark line prominent; occasional second smaller eyespot above the main HW eyespot sometimes present. **Underside:** Ground color lighter brown and somewhat brighter, striations heavy and well-defined; FW eye patch very broad and bright yellow, eyespots as on the above surface, widely pupiled in light blue. Small third eyespot on FW below the lower main eyespot is present. There is no apparent tendency for lower eyespot to be reduced. HW eyespots are typically prominent, but apparently not quite as well developed as in the male.

Phenotypical comparison between *C. p. agawamensis* and *C. p. maritima*: We examined a series of males and females of *agawamensis* from the coastal salt marshes of northeastern Massachusetts and southern New Hampshire, in order to compare these to males and females of *maritima* from nearby higher “dry old fields”. Males of *agawamensis* average somewhat distinct from males of *maritima*; while females of *agawamensis* are particularly distinct from females of *maritima*.

Males of *agawamensis* are somewhat larger and average somewhat lighter above than in *maritima*; *agawamensis* males are also somewhat two-toned on the hindwing with the postmedian dark hindwing line often present. Males of *maritima* have the ground color above darker and more uniformly colored. The orange-yellow forewing eye patch is typically wider and more rectangular in *agawamensis* males, with the borders of the patch tending to be more clear-cut. The two forewing eyespots are smaller and tend toward equal size in *agawamensis*. Beneath, the above described characters are essentially repeated: *agawamensis* males tending to be more two-toned on the hindwing making the hindwing eyespots slightly more prominent; the forewing eye patch tends to be more yellow with less orange tint than in *maritima*.

Females of *agawamensis* are, as noted above, particularly distinct in comparison to females of *maritima*, and are suggestive of smaller examples of females of *texana*. Females of *agawamensis* are significantly larger than those of *maritima*, have much broader wings and have the forewing eye patch very broad. The ground color above is lighter and brighter with the hindwing tending toward two-toned as in the males. The forewing eyespots are rather clear cut and distinct and tend toward being equal in size; while in *maritima* the eyespots are larger with indistinct edges especially in the lower eyespot. Females of *agawamensis* have the anal eyespot above small in comparison to females of *pegala* but always well-defined and circled in orange; *maritima* females typically lack this eyespot altogether. Beneath, *agawamensis* females are rather brightly and robustly colored, again suggestive of *texana*, and differ conspicuously from females of *maritima*. *Agawamensis* females below have the forewing eye patch very large, broad and clear cut. The patch typically extends from the postmedian to the submarginal dark line and often extends beyond the submarginal line almost to the outer margin. The eyespots tend to equal size and, as above, are clear-cut with well-defined blue-white pupils. The ventral hindwing is distinctly two-toned with clearly defined postmedian dark line; the eyespots are smaller but at least 4 or 5 are present and fairly well-defined. *Maritima* females are less noticeably two-toned on the hindwing, the postmedian line is less distinct and the hindwing

eyespot are typically absent except for the two near the anal angle, even these are inconspicuous. The forewing eye patch in *maritima* is narrower and does not extend beyond the submarginal dark line; the eyespots are larger and less clear-cut.

VOLTINISM & PHENOLOGY. Single brooded, diapausal (hibernal) first or second instar larva. The flight period of *agawamensis* commences during the latter part of the flight period of sympatric *C. pegala alope* or *maritima*; and as currently understood extends from late July through mid September. The peak flight time for *agawamensis* as noted in surveyed colonies in northeastern Massachusetts and southern New Hampshire is from 28 July to 20 August. Extreme dates of *agawamensis* as we have observed are 17 July and 26 September. Comparative phenology for *C. pegala alope* or *maritima* are very late June through mid August, with peak flights occurring from 12 July to 30 July. Extreme dates for *C. pegala alope* or *maritima* are 25 June and 8 September. These phenology and voltinism differences have strong similarity to the recent taxa split of another Satyrid genus *Megisto* (Hübner) where a late spring flight of *Megisto eurytris* (Fabricius, *sensu* Gatrell) or formerly called *M. cymela viola* (Maynard) is split from the early summer flight of *M. cymela* Cramer) (Gatrell, 2005) and these flights often do overlap as does the *P. pegala alope* / *P. pegala agawamensis* complex.

HABITAT AND BEHAVIOR. Newly described subspecies *agawamensis* inhabits coastal salt marshes and estuarine meadows, which are quite atypical as understood for *Cercyonis pegala*. It predominately prefers and occurs within large open salt marshes but can also be found in similar habitat along smaller tidal rivers, coastal inlets and streams. Adults occasionally wander into adjacent habitats such as old fields, hayfields, wet meadows and open woodland margins and hammocks where they then mingle with nearby populations of *C. pegala alope*. Dominant halophilic salt marsh plant species in the northeastern U.S. are Cordgrasses (*Spartina alterniflora*, *S. patens*, *S. pectinata*), Common Reed (*Phragmites australis*), Spike Grass (*Distichlis spicata*), Black Grass (*Juncus gerardii*), Sea Lavender (*Limonium nashii*), High-Tide Bush (*Iva frutescens*), Salt Marsh Goldenrod (*Solidago sempervirens*), Siff-Leaved Quackgrass (*Agropyren pungens*), Sea Myrtle (*Baccharis halimifolia*), Seaside Gerardi (*Agalinus martima*), Glassworts (*Salicornia sp.*), Seaside Plantain (*Plantago maritima*), Salt Marsh Aster (*Aster tenuifolius*), Widgeon Grass (*Ruppia maritima*) and Switchgrass (*Panicum virgatum*). Larval host plant(s) is (are) likely one or more types of the salt marsh grass species.

However, if habitat - along with phenotype - serves to distinguish *agawamensis*, then we must also discuss behavior to further distinguish it and differentiate it from its closest relatives. Both sexes fly in open estuarine salt marsh or along tidal waterways. Unlike almost all other populations of *C. pegala*, *agawamensis* will often seek nectar from flowering plants, both within the habitat or in nearby adjacent habitat. The adults are more likely to stray from the salt marsh habitat in the latter part of their flight period. Most frequented nectar sources include Purple Loosestrife (*Lythrum salicaria*), Joe-Pye-Weed (*Eupatorium purpurea.*), Common Milkweed (*Asclepias syriaca*), Swamp Milkweed (*A. incarnata*), Red Clover (*Trifolium sp.*), Goldenrod (*Solidago sp.*), Asters (*Aster sp.*) and other composites in adjacent habitat. Nectar sources utilized within the estuarine biomes include Salt Marsh Goldenrod (*Solidago sempervirens*), Sea Lavender (*Limonium nashii*) and bordering thickets of Purple Loosestrife.

Agawamensis, unlike either *alope* or *maritima* which can and do occur in significant numbers in a relatively small area of their typically DRY old field and meadow habitats, is noticeably communal and is frequently observed perching communally on salt marsh Cordgrasses and associated vegetation in large numbers over a small area. When approached, one or more individuals will take flight, followed in rapid succession by nearly all individuals making up the group. We believe that this behavior serves to confuse a potential predator by making it difficult for the predator concentrate on any one particular individual as prey. As it is perceived that the danger has passed, they will once again perch in similar fashion. While we have never observed this communal behavior in North American *Cercyonis*, we have observed similar behavior of Neotropical Satyrids (i.e. *Taygetis*, *Cissia*, *Hermeuptychia* etc.), especially toward dusk when their typically brown ground colors effectively conceal them and render this evasive and confusing behavior even more effective. The flight characteristic itself of *agawamensis* appears to differ from eastern (if not all) *Cercyonis*, in that its flight as we have observed in the salt marshes is not as “bouncy” or as “jerky” as typical *Cercyonis*, but is quicker and more straight-ahead 12 to 18 inches above the substrate, suggestive of a typical *Erebia* or *Oeneis* rather than of a typical *Cercyonis*.

As noted elsewhere, *agawamensis* also differs from all eastern *Cercyonis* - except for unusual populations of *C. pegala* “*nephele*” occurring in northern Coos Co., New Hampshire - in that it nectars freely in its salt marsh habitat. These “*nephele*” which we suspect should be further studied, also differ from typical *nephele* in that they also occur in rather boggy wet meadows and roadsides, nectar freely and frequently on Joe Pye Weed, Everlastings, etc. and also have a fast and rather straight-ahead “unbouncy” flight. We have observed these very blackish populations with very conspicuous ocelli in early to late August at such elevated locations as Pinkham Notch (Mount Washington, 2100 ft.) and at the Scott Bog, East Inlet Road, etc. (above 1900 ft.) near the New Hampshire/Quebec border.

GEOGRAPHIC RANGE AND DISTRIBUTION. Range confirmation for this subspecies is so far restricted to coastal estuarine habitat from southern Essex County, Massachusetts (vicinity of Salem) extending northward to southern York County, Maine (near Ogunquit). The greatest and most continuous concentration of this insect occurs in the more extensive coastal salt marshes north of Cape Ann in Massachusetts (Ipswich River, Parker River and Merrimack River drainages) to the New Hampshire seacoast approximately 12 to 15 Km. south of the Piscataqua River. This encompasses the coastal towns/cities of Essex, Ipswich, Rowley, Newbury, Newburyport and Salisbury in Massachusetts (Essex Co.), and the salt marshes in Seabrook and Hampton (Rockingham Co.) of the southernmost coastline in New Hampshire. This subspecies has also been confirmed in less extensive habitat south of Cape Ann in the Danvers River / North River drainage in the vicinity of Pope’s Landing (Danvers) and the tidal flats within the Forest River drainage system in Salem. Another population occurs in a more extensive estuarine meadow located in Ogunquit, Maine (Piscataqua and Kennebunk River coastal watersheds), which is speculated to be the northernmost range of *agawamensis*. Habitats south of Essex County, MA, especially in Plymouth, Barnstable and Bristol Counties, and even coastal Rhode Island have yet to be explored. However, there is a strong likelihood that they do occur in the more extensive estuaries and tidal river basins in much of this region. *Agawamensis* should also be compared to the geographically restricted island populations of subspecies *maritima* that occur specifically on the islands of Nantucket, Martha’s Vineyard, Block Island (R.I.) and Naushon Island (MA.) located in Buzzards Bay. *Maritima* is also very common in dry weedy open field habitats on mainland Rhode Island, on Long Island, and also near Gettysburg, PA.

TYPE LOCALITY AND TYPE SERIES. TL: Estuarine salt marsh (open), Boston Road, Newbury (Parker River watershed), Essex Co., Massachusetts. The holotype specimen will be deposited in the McGuire Centre for Lepidoptera and Biodiversity, Gainesville, Florida. Holotype (female), allotype paratype (male) and all paratypes are identified as follows:

MASSACHUSETTS:

ESSEX CO., Newbury (Parker River watershed):

- NB001 (female): Boston Road, estuarine salt marsh (open), 7/21/2007 (**HOLOTYPE**).
- NB002 (male): Boston Road, estuarine salt marsh (open), 7/21/2007 (**ALLOTYPE**).
- NB003-NB004 (2 males): Boston Road, estuarine salt marsh (open), 7/21/2007.
- NB005-NB006 (2 females): Boston Road, estuarine salt marsh (open), 7/21/2007.
- NB010 (female): U.S. Route 1, wet meadow/salt marsh (open), 7/17/2007.
- NB011-NB012 (2 males): Boston Road, estuarine salt marsh (open), 7/20/2008.
- NB013-NB014 (2 males): Boston Road, estuarine salt marsh (open), 8/2/2008.
- NB015 (female): Boston Road, estuarine salt marsh (open), 7/20/2008.
- NB016-NB018 (3 females): Boston Road, estuarine salt marsh (open), 7/28/2013.
- NB019-NB020 (2 females): Boston Road, estuarine salt marsh (open), 8/2/2008.
- NB021 (1 male): Plum Island, salt marsh, 8/14/1999.
- NB022-NB023 (2 females): Plum Island, salt marsh, 8/14/1999.
- NB024-NB029 (6 males): Boston Road, estuarine salt marsh (open), 7/28/2010.
- NB030-NB033 (4 females): Boston Road, estuarine salt marsh (open), 7/28/2010.
- NB034-NB038 (5 males): Boston Road, estuarine salt marsh (open), 7/24/2011.
- NB039-NB042 (4 females): Boston Road, estuarine salt marsh (open), 7/24/2011.
- NB043-NB045 (3 females): U.S. Route 1, salt marsh, 8/12/2011.
- NB046-NB050 (5 males): U.S. Route 1, salt marsh, 8/8/2013.
- NB051-NB053 (3 females): U.S. Route 1, salt marsh, 8/8/2013.

NB054-NB055 (2 females): Plum Island, salt marsh, 7/24/2003.

ESSEX CO., Essex (Essex River watershed):

EX001-EX004 (4 males): Route 133, salt marsh, 7/26/2008.

EX005-EX007 (3 females): Route 133, salt marsh, 7/26/2008.

ESSEX CO., Ipswich (Ipswich River watershed):

IW003-IW004 (2 males): Argilla Road, estuarine salt marsh (open), 7/22/2007.

IW005 (female): Argilla Road, estuarine salt marsh (open), 7/22/2007.

IW006 (female): Argilla Road, old field (coastal), 7/22/2007.

IW007 (male): Argilla Road, estuarine salt marsh (open), 7/9/2013.

IW008 (female): Argilla Road, estuarine salt marsh (open), 7/9/2013.

IW009-IW011 (3 males): Argilla Road, estuarine salt marsh (open), 8/5/2013.

IW012 (female): Argilla Road, estuarine salt marsh (open), 8/5/2013.

ESSEX CO., Newburyport (Merrimack River watershed):

NP001 (female): Plum Island Turnpike, coastal salt marsh (open), 7/31/1983.

ESSEX CO., Rowley (Rowley River watershed):

RW001 (male): Route 1A, estuarine salt marsh (open), 7/27/2007.

RW002-RW005 (4 males): Route 1A, estuarine salt marsh (open), 7/19/2013.

ESSEX CO., Salem (Forest River watershed):

SA001-SA002 (2 males): Forest River Park, estuarine salt marsh – tidal river basin, 7/22/2007.

ESSEX CO., Salisbury (Merrimack River watershed):

SB001-SB002 (2 males): U.S. Route 1A, estuarine salt marsh (open), 7/24/2007.

SB003 (female): U.S. Route 1A, estuarine salt marsh (open), 7/20/2008.

SB004 (female): U.S. Route 1A, estuarine salt marsh (open), 7/31/2008.

SB005-SB007 (3 males): U.S. Route 1A, estuarine salt marsh (open), 7/30/2009.

SB008-SB011 (4 females): U.S. Route 1A, estuarine salt marsh (open), 7/30/2009.

SB012-SB013 (2 females): U.S. Route 1A, estuarine salt marsh (open), 8/3/2009.

MAINE:

YORK CO.: Ogunquit (Stevens Brook watershed):

OQ001 (1 male): Furbish Road, estuarine salt marsh (open), 8/1/2007.

OQ002 (1 female): Furbish Road, estuarine salt marsh (open), 8/1/2007.

OQ003 (1 male): Furbish Road, estuarine salt marsh (open), 8/1/2007.

NEW HAMPSHIRE:

ROCKINGHAM CO.: Seabrook (Blackwater River watershed):

SK001-SK004 (4 males, dark type): Route 286, estuarine salt marsh (open), 7/24/2007.

SK005-SK007 (3 males): Route 286, estuarine salt marsh (open), 8/6/2007.

SK008-SK0010 (3 females): Route 286, estuarine salt marsh (open), 8/6/2007.

SK011 (male): Route 286, estuarine salt marsh (open), 8/6/2007.

SK012 (female): Route 286, estuarine salt marsh (open), 8/6/2007.

SK013-SK015 (3 males): Route 286, estuarine salt marsh (open), 8/6/2007.

SK016-SK017 (2 females): Route 286, estuarine salt marsh (open), 8/6/2007.

Additional locations where *C. p. agawamensis* have been vouchered:

MASSACHUSETTS: ESSEX CO.: Danvers. MAINE: WASHINGTON CO.: Addison (possible intermediate with *C. p. nephele*). NEW HAMPSHIRE: ROCKINGHAM CO.: Hampton.

Locations where *C. p. alope* have been vouchered for comparison to *C. p. agawamensis*:

MASSACHUSETTS: ESSEX CO.: Boxford, Georgetown, Groveland, Ipswich, Newbury, Rowley, Topsfield. NORFOLK CO.: Norfolk. BERKSHIRE CO.: Sheffield, Ashley Falls. MAINE: CUMBERLAND CO.: Gorham. YORK CO.: Buxton, Hollis, Saco, York. VERMONT: WINDHAM CO.: Mount Snow, Green River, Guilford.

Locations where *C. p. maritima* have been vouchered for comparison to *C. p. agawamensis*:

MASSACHUSETTS: WORCESTER CO.: Wachusett Mountain. ESSEX CO.: Danvers, Peabody, North Andover, Boston Hill. MIDDLESEX CO.: Melrose (Middlesex Fells), Woburn (Horn Pond Mountain). DUKES CO. (MARTHA'S VINEYARD): Oak Bluffs (TL of *maritima*), Edgartown. PLYMOUTH CO.: Plymouth, Carver, Middleboro. RHODE ISLAND: PROVIDENCE CO.: Central Falls. WASHINGTON CO.: Westerly, West Kingston. MAINE: ANDROSCOGGIN CO.: Lewiston, Auburn. OXFORD CO.: Oxford.

Locations where *C. p. nephele* have been vouchered for comparison to *C. p. agawamensis*:

MASSACHUSETTS: HAMPSHIRE CO.: West Hawley. MAINE: AROOSTOOK CO.: Sherman Mills Twp. KENNEBEC CO.: Augusta, Vassalboro. OXFORD CO.: Streaked Mountain. PENOBSCOT CO.: Dixmont. WALDO CO.: Belfast, Troy, Unity. WASHINGTON CO.: Addison, Cherryfield, Columbia, Columbia Falls, Harrington. NEW HAMPSHIRE: COOS CO.: Pinkham Notch, Pittsburg, Scott Brook Road, East Inlet Road, Clarkston. GRAFTON CO.: Franconia Notch. VERMONT: RUTLAND CO.: Pittsford. GRANDE ISLE CO.: Grande isle.

DISCUSSION OF THE EVOLUTIONARY ORIGINS OF SUBSPECIES AGAWAMENSIS

We hypothesize that the “*agawamensis*” subspecies developed and evolved due to the result of ecological isolation within the estuarine biomes following the last glaciation of the Pleistocene approximately 12,000 to 15,000 years ago: A post-Pleistocene ‘coastal refugium’.

As has been discussed above, *Cercyonis pegala* subspecies *alope* and *maritima* occur along the New England coastal areas in proximity to, if not in actual association with, *agawamensis*. While we have observed *maritima* and/or *alope* in drier meadows near the *agawamensis* habitats, we have never observed either of the two subspecies WITHIN the typical *agawamensis* salt marsh habitat. *Alope* is described as having a yellow FW eye patch and a somewhat lighter ground color, while *maritima* is generally understood as having a deeper orange-yellow or orange-red FW eye patch, and a somewhat darker ground color. Intergrades between *agawamensis* at, and along, the “tension zone” between the salt marshes and the adjacent wet meadow habitats appear to be chiefly if not entirely with the *alope* phenotype; while *maritima* appears to occur in the drier meadows somewhat more inland. These observations could be the result, however, of the expression of the more yellow FW eye patch of *agawamensis* into the intergrades, rather than the expression of more frequent contact between *agawamensis* and *alope*. Outside of the salt marshes and in adjacent and nearby open meadows along the coast, however, the *alope* phenotype with the yellow FW eye patch does appear from our observations to be the dominant form.

Further inland and upland in the Transition Zone (i.e. at Streaked Mountain, Oxford Co., Maine), it is possible that the darker, more reddish forms of *C. pegala* (*maritima*?) that occur there can be referred to as *olympus*, which may range across the Upper Midwest and through the Transition Zone of central New England.

As the glaciers retreated northward, the tundra, and then temperate grasslands followed, and the typical associated insect fauna soon followed as the Northern Hemisphere gradually warmed. At this latitude, forests rapidly took hold shortly thereafter, and therefore ‘open habitat’ species such as *C. pegala* were confined to the few vestiges of scattered prairies, margins along inland waterways, open hilltops and coastal estuaries. As the forests matured further, most of the *C. pegala* populations were pushed into more and more isolation at the immediate but relatively more expansive coastline, as other favorable habitats along riverbanks, on hilltops and other features became closed in by encroaching woodland. The bulk of the *C. pegala* population likely collapsed and retreated west of the densely wooded Appalachians - except for those still existing in the coastal marshes. These populations were both ecologically and geographically isolated and became adapted to the coastal marine environment and likewise probable host-plant shifts from inland prairie grasses to more coarse halophilic estuarine grass species. This further led to changes in phenology, flight behavior and adult food preferences and other ecological requirements. They also began to differ morphologically. These populations were hypothetically in the process of becoming a distinct species...but this process was then interrupted by another abrupt change.

The first Native American peoples arrived in the Northeast approximately 8,000 years ago as predominately nomadic hunter-gatherers. Agricultural practices and techniques adopted from tribes of the Southwest and Central America arrived soon thereafter. The dense forests were beginning to be cleared for crops, and thinned in order to attract large game animals such as deer, elk and wood bison.

Thousands of years later in the early 17th Century, came the arrival of the first Europeans. With the European settlers came the sawmill, the plow and herds of livestock. The ecological impact brought forth by the Europeans was unprecedented, and over a period of several decades, the forests in Eastern North America were cleared for

agriculture, grazing and valuable timber. The decimation of the forests allowed for prime open habitat consisting of grasses, wildflowers and other herbaceous plants. *C. pegala alope* and/or *maritima* soon re-colonized the vast new tracts of required grassland habitat. The “inland” type *C. pegala alope* and/or *maritima* then began to mingle with the coastal populations of *C. p. agawamensis*, and so began intergrading. This genetic introgression combined with coastal development and alteration of habitat has led this subspecies to now exist in the few large tracts of open salt marsh that are still present today and now protected. Introgression is however suspected to be still ongoing in areas where both grassland ecotones meet and the flight of *C. p. agawamensis* overlaps with the “inland” populations of *C. pegala*.

Evidence of this introgression has turned up in a number of vouchered specimens, especially in areas where both types of habitat are in close proximity to one another. One intriguing example of this is evident in a few examples collected along the far northeast coastline in Maine (Washington Co.) in salt marsh habitat along a tidal river. At this latitude, the typical southern *C. pegala (maritima?)* featuring the orange FW eye patches, are replaced by a northern dark phenotype suggestive of *nephele* totally lacking the eye patch. A few male specimens were vouchered having a residual amount of the FW patch, and wing shape similar to male specimens of *C. p. agawamensis* occurring further south of the Canadian Zone. It can be suggested, based upon the occurrence of these dark male *agawamensis*-like populations, that *agawamensis* may have historically occurred at these latitudes but may have been eliminated by periods of much colder atmospheric conditions, and/or that these northern *agawamensis* populations may have been almost completely genetically “washed out” by the strong influx of *C. p. nephele* at the periphery of these coastal habitats. Another hypothesis is that these northern populations do indeed represent non-patched *C. p. agawamensis* and are in fact exhibiting a type of convergent evolution or non-aposematic mimicry in coexistence with the dark *C. p. nephele*, and are therefore a “dark phase” *agawamensis*, in which the deep orange-red or reddish scales have invaded the FW yellow patch. Intensive future exploration of the Maine coastline is needed to determine the status of these mysterious northern Canadian Zone coastal populations, with observations of behavior required along with voucher specimens of both sexes.

ACKNOWLEDGMENTS

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Figure 1. Holotype of *Cercyonis pegala agawamensis*. Female, wingspan 54 mm.

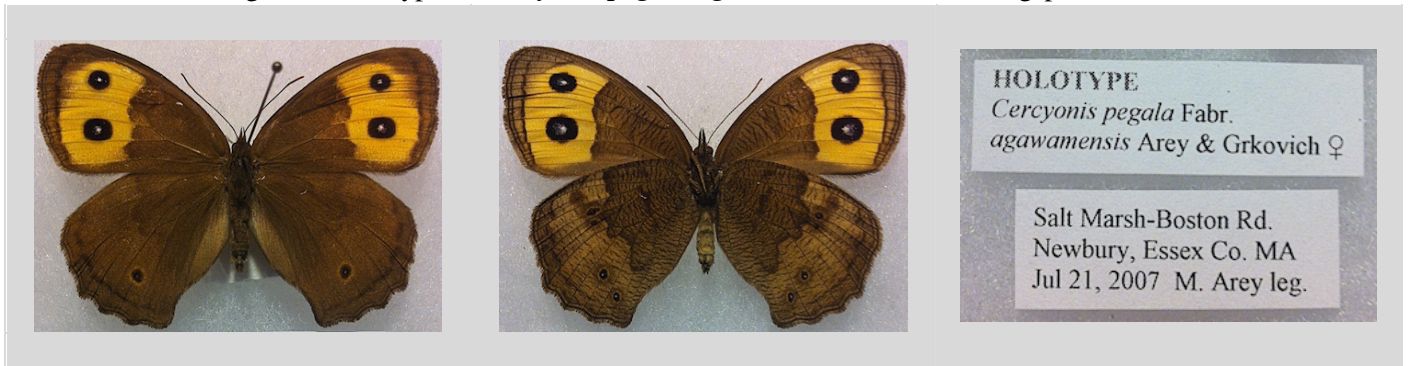


Figure 2. Allotype of *Cercyonis pegala agawamensis*. Male, wingspan 51 mm.

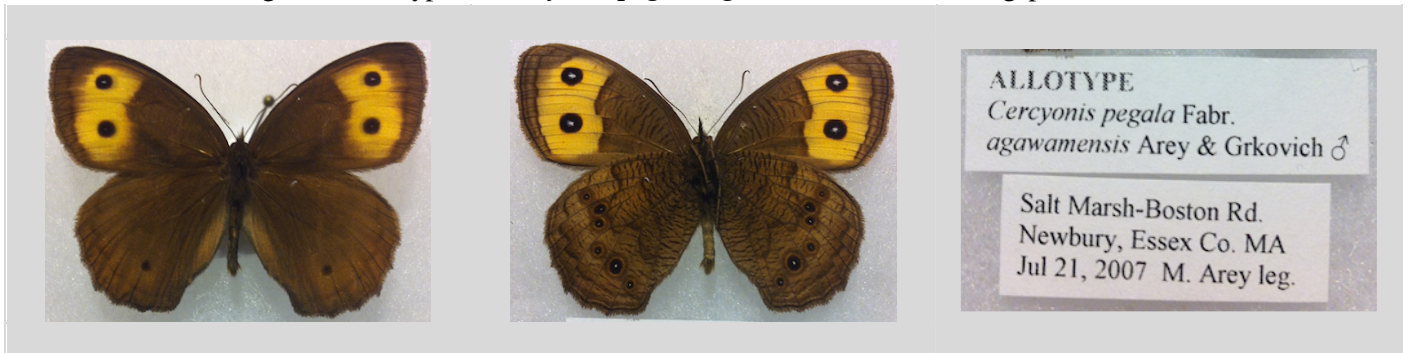


Figure 3. Male topotype of *C. pegala maritima*, wingspan 49 mm.
Manuel Correllus S.F., Oak Bluffs, Dukes Co. MA, (Martha's Vineyard Is.), July 24, 2010 M. Arey leg.

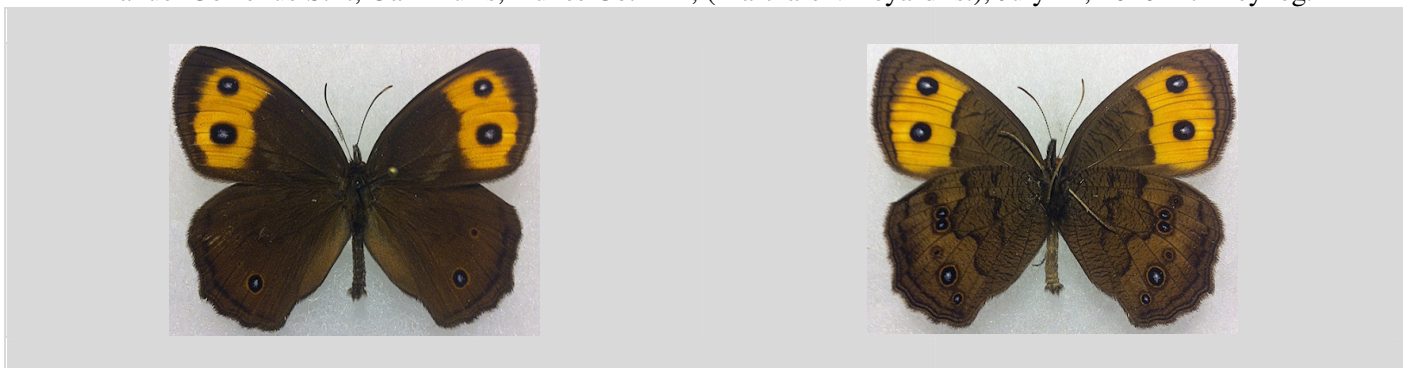


Figure 4. Female topotype of *C. pegala maritima*, wingspan 55 mm.
Manuel Correllus S.F., Oak Bluffs, Dukes Co. MA, (Martha's Vineyard Is.), July 24, 2010 M. Arey leg.

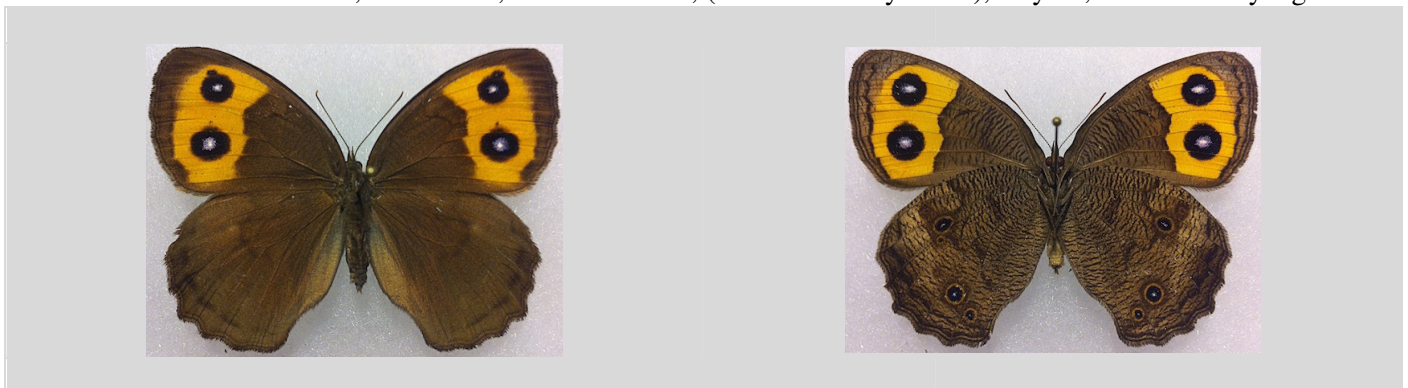


Figure 5. Male *C. pegala nephele*, wingspan 47 mm
Dry meadow – Rt. 220 E Troy, Waldo Co. Maine, August 11, 2007 M. Arey leg.



Figure 6. Male *C. pegala alope*, wingspan 49 mm
Witch Hollow Farm, Boxford, Essex Co. MA, July 4, 1998 M. Arey leg.



Figure 7. Female *C. pegala alope*, wingspan 53 mm
Powerline cut – Rt 97 S Georgetown, Essex Co. MA, July 23, 2002 M. Arey leg



Figure 8. A large female *C. pegala agawamensis*, wingspan 60 mm
Salt Marsh – Salisbury Beach S.P., Salisbury, Essex Co. MA July 30, 2008 M. Arey leg.



Figure 9. Possible female intergrade between *nephele* and *agawamensis*, wingspan 54 mm
Along tidal river – Columbia Rd. W Addison, Washington Co. ME, August 6, 2006 M. Arey leg.



Figure 10. Male *C. pegala agawamensis*, wingspan 51 mm
Salt marsh – Rt. 286 E Seabrook, Rockingham Co. NH, August 6, 2007 M. Arey leg.

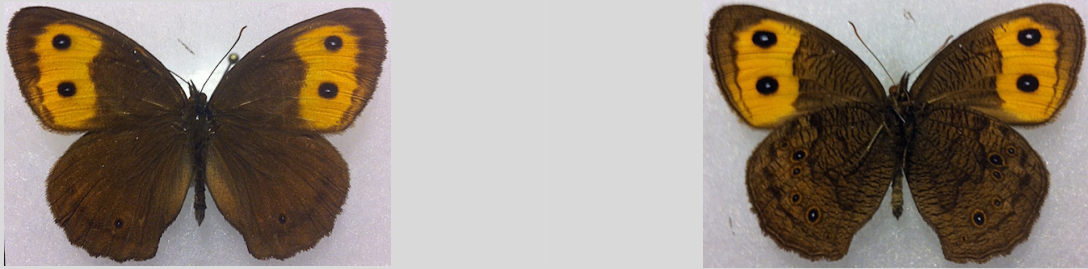


Figure 11. Female *C. pegala agawamensis*, wingspan 57 mm
Salt marsh – Rt. 286 E Seabrook, Rockingham Co. NH, August 6, 2007 M. Arey leg.



Figure 12. Habitat at type locality - Boston Rd. Newbury, Essex Co. MA; June 6, 2014



Figure 13. Habitat at type locality - Boston Rd. Newbury, Essex Co. MA; June 6, 2014



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