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GENUS *MEGISTO* IN FLORIDA AND THE TAXONOMIC STATUS OF *MEGISTO VIOLA* (LEPIDOPTERA: NYMPHALIDAE: SATYRINAE)

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ABSTRACT.– *Megisto cymela* (Cramer) and *M. c. viola* (Maynard) were studied to evaluate variation and subspeciation, using 274 specimens from Florida (239 from the peninsula and 65 from the panhandle) and 163 from the northern range limits in Ontario and Quebec. The few specimens suggesting multiple broods in Florida were either misidentified or probably mislabelled. The study sample and additional observations suggest a single flight period from late February to late April in the peninsula, late February to mid-June in the panhandle, and late May and June at the northern range limit in Canada. There are no constant morphological characteristics within the subspecific blend zone in northern Florida to suggest more than one species, but recognition of *M. c. viola* as a subspecies in peninsular Florida appears valid. Habitats and flight periods are also discussed.

KEY WORDS: Arkansas, Canada, cline, development, distribution, evolution, flight period, Georgia, *Hermeuptychia*, Louisiana, Nearctic, North America, Ontario, Pennsylvania, Quebec, symmpatry, USA, voltinism.

C. J. Maynard (1891a,b) briefly described *Neonympha cymela viola* Maynard, now in the genus *Megisto*, from specimens collected along the east coast of Florida, at Enterprise, Volusia Co. Subsequent literature (e.g., Klots, 1951; Emmel, 1975) and the most recent monograph of *Megisto* (Miller, 1976), indicate *Megisto cymela* (Cramer) to have two subspecies, the northern nominate *M. c. cymela*, blending into the southern subspecies, *M. c. viola* of Florida, southern Georgia and the Gulf coastal plain, west to southern Louisiana. The difficulty of assigning specimens from the blend zone to a subspecies caused Miller (1976) to doubt the validity of the two subspecies. However, some recent literature has elevated *M. c. viola* to species rank (Opler and Krizek, 1984; Opler and Malikul, 1992), based on the following observations by Oliver (1982):

(1) *M. c. cymela* and *M. c. viola* are sympatric in Florida, as well as parts of Louisiana and Arkansas, without a blend zone.

(2) The two subspecies have different flight periods in regions of symmpatry, *M. c. cymela* being multiple brooded while *M. c. viola* has a single brood.

(3) *M. c. viola* is highly distinctive, differing in its larger size and rich coloration on the ventral hindwing. To these differences, Opler and Malikul (1992) have added that *M. viola* has larger eyespots and a more strongly bowed postmedian line on both wings below.

(4) Larvae of *M. c. cymela* are a darker brown and have a shorter development time (90-100 days instead of 300-360 days in the lab), correllating with the multiple broods. Oliver considered it unlikely that differences in development time were related to foodplant suitability.

Scott (1986), on the other hand, suggested that the species level distinction had not been proved, and he noted that the genitalia did not differ. He also noted that *M. c. cymela* generally has only one flight; this latter point in particular casting doubt on Oliver's (1982) contention. Recently, Calhoun (1996) noted the presence of *M. cymela* in four counties in the Florida panhandle and observed that these individuals appeared intermediate between *M. c. cymela* and *M. c. viola*, casting further doubt on the species status of the latter. These differences between recent authors have highlighted Oliver's earlier (1982) suggestion, that researchers in the Gulf Coast region should further assess the ecological differences between the two taxa. Here, we evaluate data relating to the recognition of *M. c. viola* as a possible separate species relative to Oliver's (1982) observations.

Although specimens attributed to *M. c. viola* have been recorded as far north and west as Arkansas, we have focused our study on Florida, where the type locality is located.

METHODS

Collection dates, locations, collectors, forewing lengths, band widths, eyespot widths and sexes were recorded from 274 specimens of *Megisto* from Florida. The sample included 239 from the peninsula and 65 from the panhandle (west of the Suwannee River) as well as 163 from the northern range limit in Ontario and Quebec. The Florida sample included 128 specimens in the Florida State Collection of Arthropods (FSCA), at Gainesville; 51 in the Allyn Museum of Entomology, Sarasota; 76 in the collection of J. Calhoun; 49 in the collection of P. Catling; and 23 in the collection of Marc C. Minno, Gainesville, Florida. Methods of measurement of eyespot width (lower spot on underside of forewing), forewing length and eyespot band width (distance between postmedial and submarginal brown lines on underside of forewing) are shown in Fig. 1. Each of the three

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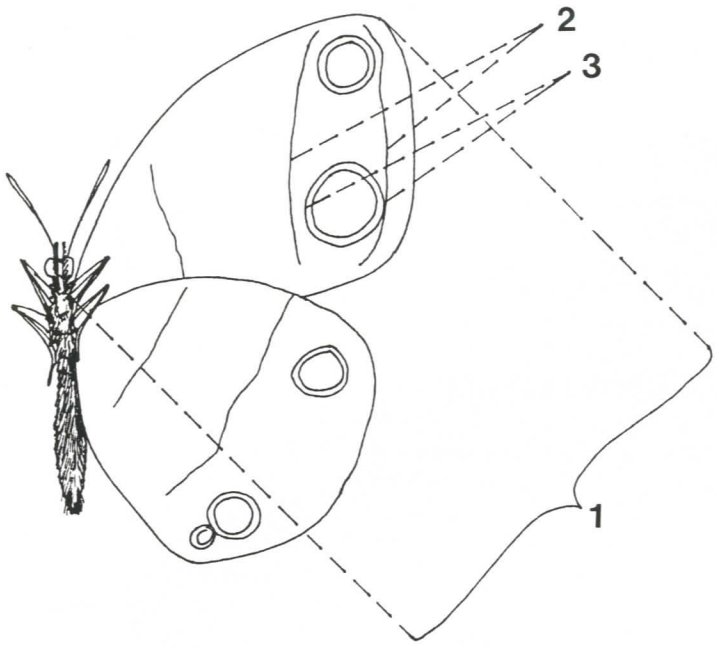

Fig. 1. Measurements recorded: 1) Maximum length of forewing along costal margin (mm). 2) Maximum width of eyespot band between postmedial and submarginal brown lines on underside of forewing (mm). 3) Maximum diameter of lower eyespot on underside of forewing (mm).

data sets were separated into males or females for comparisons, so that differences between sexes could be separated from geographically based differences and potential infrataxa differences. Plots and histograms illustrating eyespot widths, forewing lengths, and band widths, were examined for bimodal patterns suggesting more than one taxon. A plot of frequency by Julian date was prepared to evaluate flight periods in each of the three regions. The relationship between eyespot size and flight date was evaluated separately in 29 females and 48 males, all from the Gainesville area of Alachua Co., using linear regression. Distribution in Florida is illustrated using different symbols for private and institutional records.

RESULTS AND DISCUSSION

Possible Errors and the Number of Broods

Oliver's (1982) conclusion about symmpatry and multiple broods was based largely on 8 of 128 Florida specimens in the Florida State Collection of Arthropods (FSCA), in Gainesville. Most of these specimens corresponded to *M. c. cymela*, and all were collected by H. V. Weems, Jr. Six were from Alachua Co., one was from Highlands Co. and one was from Dade Co.

With respect to the Alachua Co. material, one of six specimens is labelled 10 July 1947, giving the impression of a second brood. However, a second brood in the peninsula, or anywhere in the east, is not supported by other material in the Gainesville collection, or by additional material examined in other collections (Allyn Museum, Calhoun, Catling, CNC, Minno: Fig. 2-3). Furthermore, it is not supported by the observations of Florida field biologists (Minno, Calhoun, etc.). Of particular importance regarding the concept of a second brood in Alachua Co. are the observations of Mr. Richard Worth, who kindly made notes on

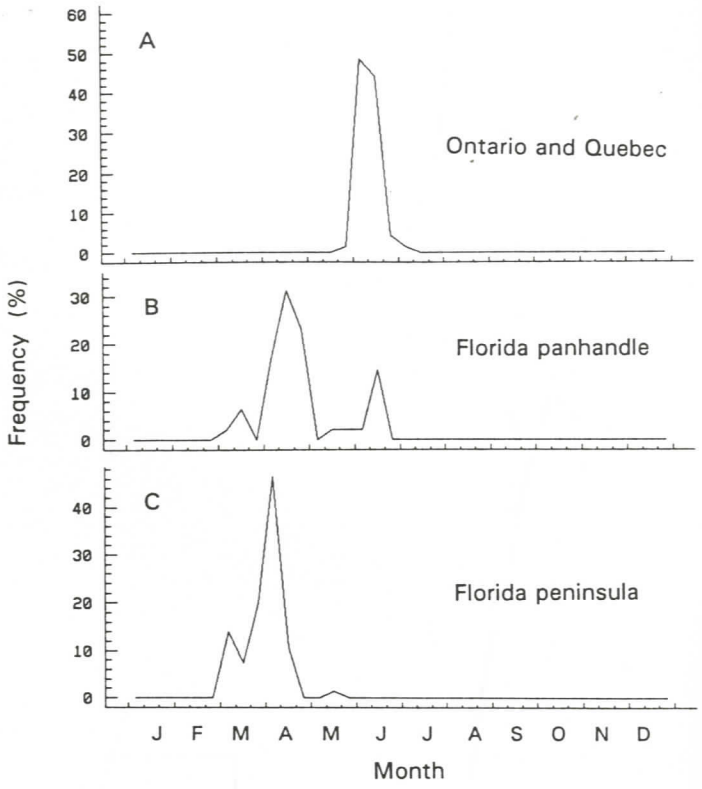

Fig. 2. Percentage frequency polygons for collection dates of males of *Megisto* based on 10 day intervals throughout the year: A) Canada (Ontario and Quebec, n=140). B) Florida panhandle (n=48).C) Florida peninsula (n=156).

the occurrence of *Megisto* in Gainesville (Williston Rd. and SW 34th street) during his continuous 1996 study of another satyrine, *Hermeuptychia sosybius* (Fabricius). He observed the first specimens of *Megisto* (males) on 25 March and the last (female) on 7 May (R. Worth, pers. comm.). Thus, in a single year, the flight period at a single location lasted 6 weeks. With variation in the weather from year the year, records from a single location could easily extend over a period of 8 or possibly even 10 weeks. Mr. Worth was at the site continuously (including July) and could recognize *Megisto* easily in flight. The fact that he did not encounter a second brood of *Megisto* at the large population within his study area is further evidence that one does not occur there. We suspect that the specimen collected by Weems allegedly from Gainesville in July 1947 is mislabelled.

The specimen from Highlands Co., collected at Sebring on 24 Dec 1947, is also problematic. It is entirely alone among the peninsular specimens with regard to its collection date (Fig. 2-3). Specimens from the nearest sites in Hardee and Polk counties were collected from mid to late March.

Oliver (1982) did not mention a specimen in the FSCA collection from Ross-Costello Hammock collected by Weems on 27 May 1967. Ross Hammock and Costello Hammock were once more or less connected hardwood hammocks in the pinelands of Dade Co. between Miami and Homestead. Not surprisingly, for someone who collected many thousands of insects and was not a lepidoptera specialist, Weems did not recall this or his other records of *Megisto* (pers. comm.). The Ross-Costello record is potentially of great importance, being the southernmost record of

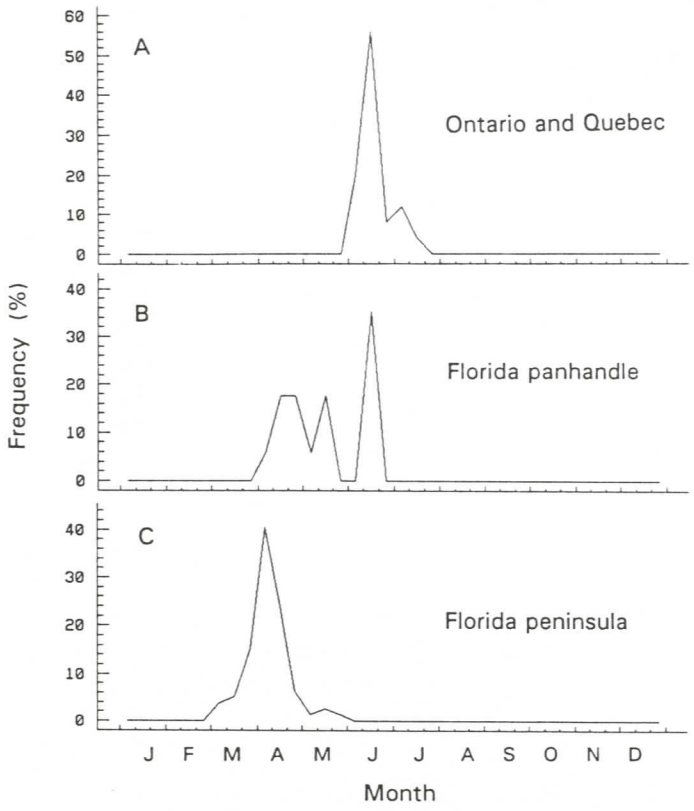

Fig. 3. Percentage frequency polygons for collection dates of females of *Megisto* based on 10 day intervals throuhout the year: A) Canada (Ontario and Quebec, n=55). B) Florida panhandle (n=17). C) Florida peninsula (n=83).

Megisto, and referable to *M. c. cymela* rather than *M. c. viola*. Ross-Costello Hammock is a park that had an active interpretive center and continues to be much visited and used by biologists. Neither *M. c. cymela* nor *M. c. viola* was listed among the butterflies recorded from the park and it was never seen there by active biologists in the area (R. Hammer, W. P. Gould, pers. comm.). In fact, the species has not been found in the Miami area despite over a century of extensive field studies. Thus, the Ross-Costello record is likely the result of mislabelling.

The only other reference to *Megisto* in Florida that would suggest multiple broods is that of Grossbeck (1917), based on records of William T. Davis and Charles E. Sleight at Ortega (Volusia Co.) on 6 Sep 1911 and La Grange (Brevard Co.) on 9 and 11 Sep 1911. The voucher specimens for these reports, in the collection of the Staten Island Institute of Arts and Sciences, New York, were kindly examined by curator Ed Johnson who reported that they were referable to *Hermeuptichia sosybius* and classified in the collection with that species.

With the Weems records under suspicion and the Grossbeck reference discounted, the available data, including more than 70 locations and 300 records (Fig. 2-3), suggests that *Megisto* does not "have up to four broods" in Florida as suggested by Oliver (1982), and is in fact univoltine with a single flight beginning in March and ending in June depending on latitude.

The mid-June specimens from the panhandle in Fig. 1-2 are from the inland Appalachicola River area (Chattahoochee and Torreya State Park), where the earliest specimens were collected in mid-April. Consequently, they fall within the 6-10 week flight

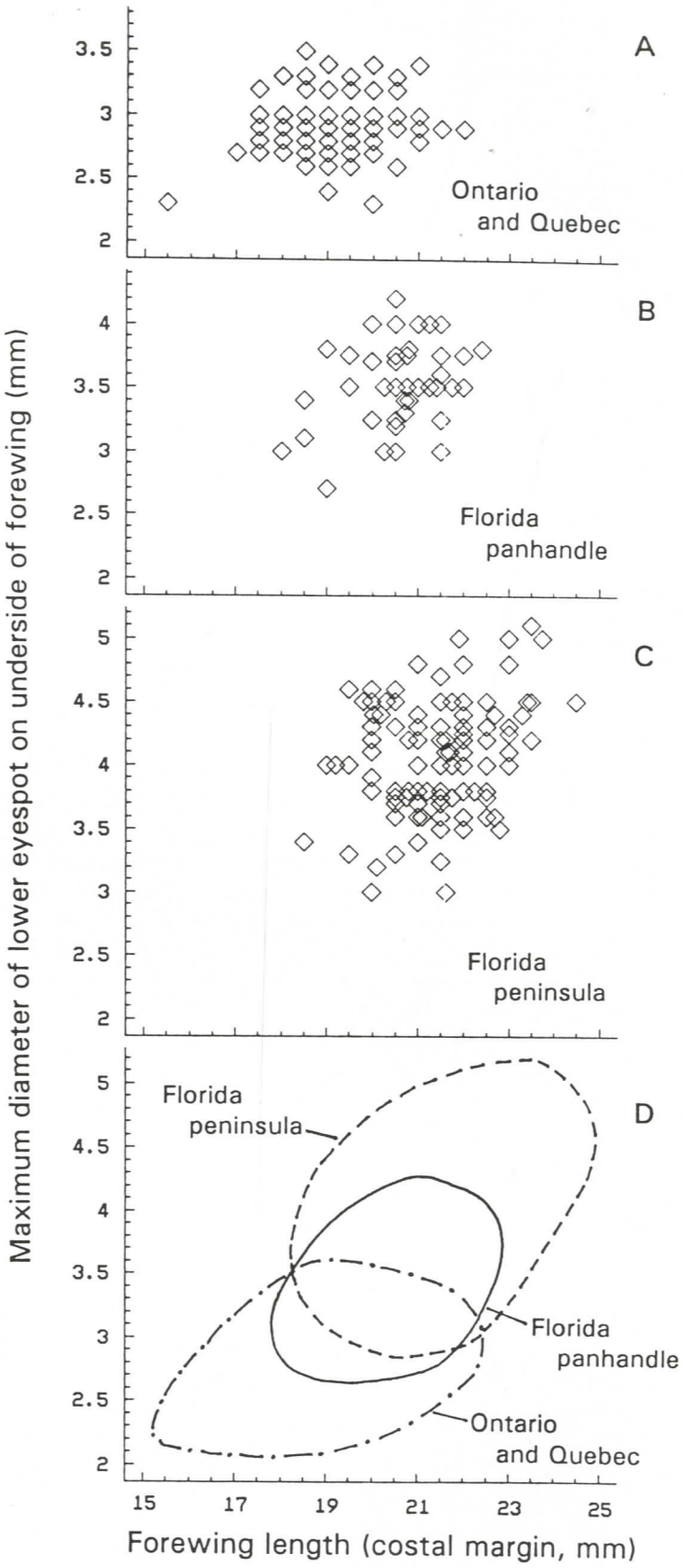

Fig. 4. Scatterplots for width of the lower eyespot on the underside of the forewing versus forewing length in *Megisto* males for: A) Canada (n=140). B) Florida panhandle (n=48). C) Florida peninsula (n=156). D) delineated areas on the graph for all three demonstrating amounts of overlap.

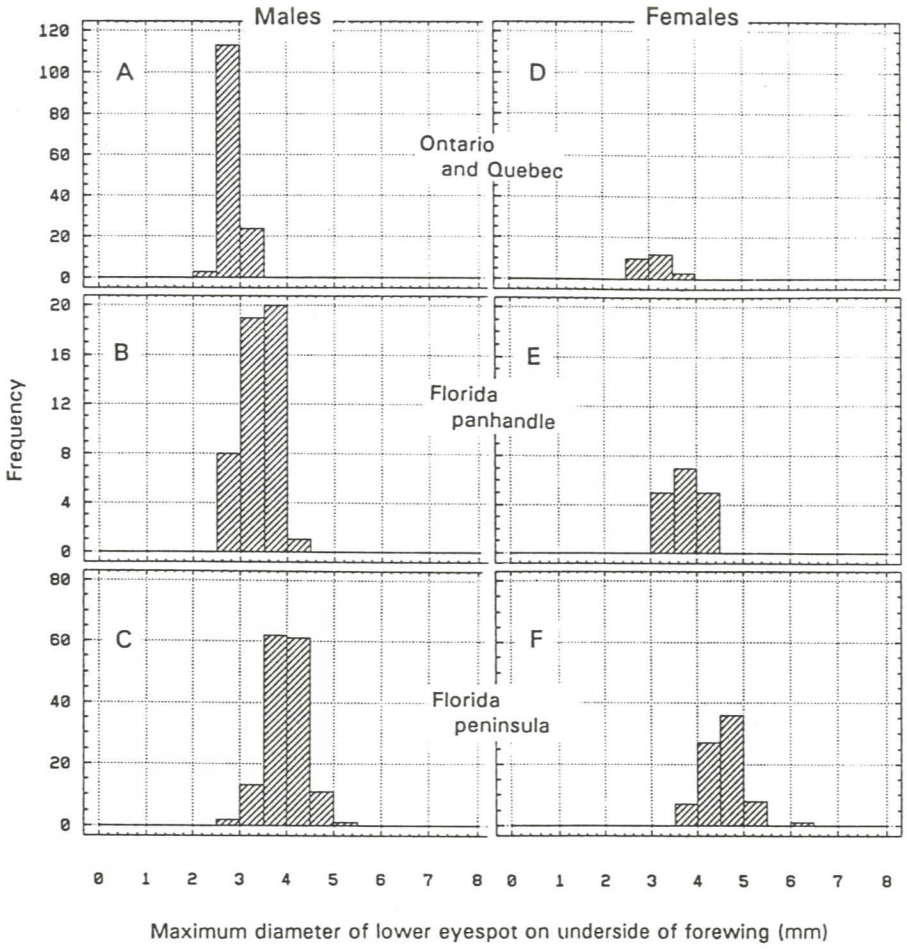

Fig. 5. Frequency histograms for width of the lower eyespot on the underside of the forewing in *Megisto* males from: A) Canada (Ontario and Quebec, n=140) B) Florida panhandle (n=48). C) Florida peninsula (n=156). *Megisto* females: D) Canada (Ontario and Quebec, n=55). E) Florida panhandle (n=17). F) Florida peninsula (n=83).
NOTE: frequency grids vary in verticle measure.

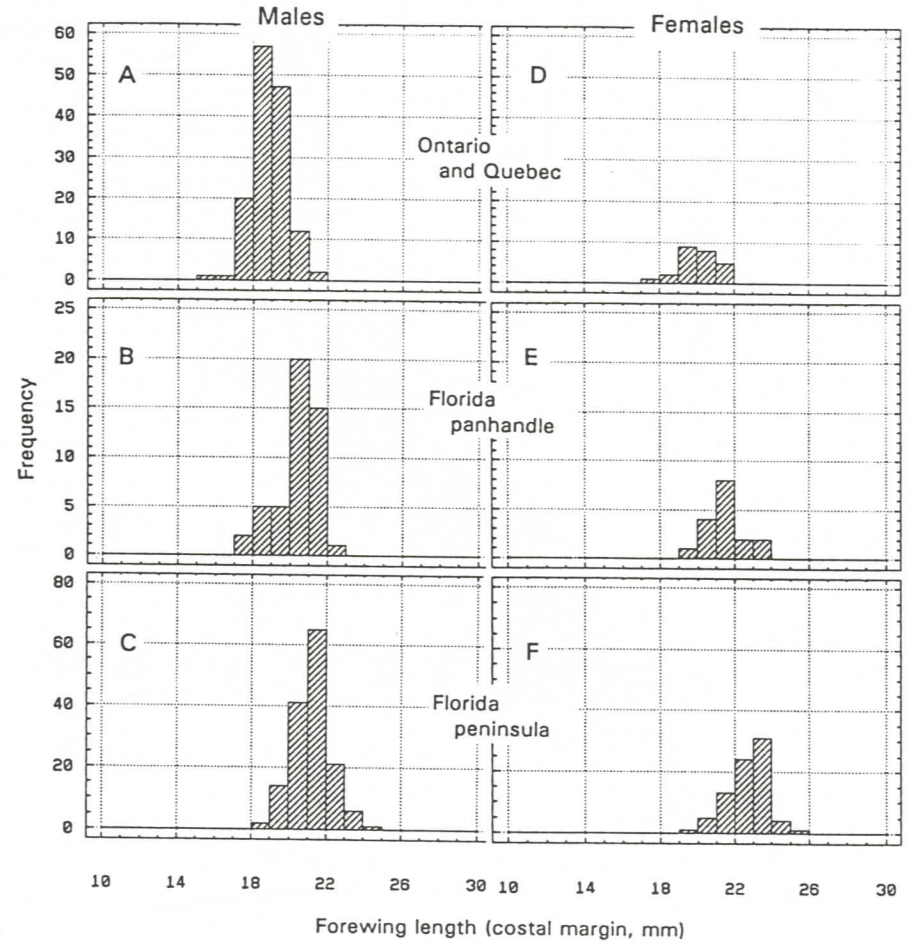

Fig. 6. Frequency histograms for forewing length in *Megisto* males from: A) Canada (Ontario and Quebec, n=140). B) Florida panhandle (n=48). C) Florida peninsula (n=156). *Megisto* females: D) Canada (Ontario and Quebec, n=55). E) Florida panhandle (n=17). F) Florida peninsula (n=83).
NOTE: frequency grids vary in verticle measure.

TABLE 1. Mean, maximum, minimum and standard deviation (all mm) for eyespot width (lower spot on underside of forewing), forewing length and eyespot band width (distance between postmedial and submarginal brown lines on underside of forewing) in groups of *Megisto cymela* from the Florida peninsula, Florida panhandle, and Ontario-Quebec.

Location	Eyespot width	Forewing length	Band width
Florida peninsula			
Males (150)[1]	4.04	21.46	5.99
	3-5.1	18.5-24.5	4.8-7.8
	0.405	1.009	0.558
Females (79)	4.62	22.90	6.93
	3.8-5.4	20-25.2	5.5-9
	0.378	1.047	0.664
Florida panhandle			
Males (48)	3.51	20.54	5.42
	2.7-4.2	18-22.4	4.3-6.6
	0.357	1.042	0.518
Females (17)	3.81	21.83	6.17
	3.25-4.25	20-23.8	5.1-7.6
	0.305	0.977	0.600
Ontario - Quebec			
Males (140)	2.91	19.10	5.17
	2.3-3.5	15.5-22	3.9-6.1
	0.208	0.953	0.398
Females (25)	3.20	20.20	5.70
	2.7-3.9	18-21.5	5-6.5
	0.322	0.968	0.423

[1]Sample size.

period to be expected at any site, and do not necessaily represent a second brood. Moreover, most of these specimens are worn, aluding to the end of a single spring brood.

Quantitative Characters

Maximum diameter of lower eyespot on underside of forewing (mm), maximum length of forewing along costal margin (mm), and maximum width of submarginal band on underside of forewing (mm), all decrease in value northwards (Table 1, Fig. 4-6). Females are consistently larger in these characteristics than males. There was no bimodal pattern in characters within a region to suggest more than one taxon (Fig. 4-6). The dispersion of variation is approximately the same for Canada, the Florida panhandle, and the Florida peninsula (Fig. 4), and in each of these plots of forewing length *versus* eyespot width, only one descrete cluster is evident. Band width was correllated with eyespot width, but demonstrated a little less geographic variability. Although the pattern of increasing forewing size, band width and eyespot size southward is very clear, the broad overlap of Florida peninsula and Florida panhandle records with records from the northern range limit in Canada (Fig. 4-9) strongly suggests that the recognition of *M. c. viola* as a separate species is unwarranted.

Eyespot width had the most significant relationship to both latitude and Julian day (increasing with decrease in either). Forewing lengths and band widths demonstrate a similar pattern but were less significant and were not always significant for both sexes (Table 2). The association of eyespot width with flight period is probably related to climate, the relatively greater significance of Julian day being a consequence of the fact that latitude does not allow compensation for inland effects. Some inland peninsula locations are cooler and subject to more frequent frosts than coastal areas on the same latitude.

TABLE 2. F-ratios and associated probability levels from analysis of variance in eyespot width (lower spot on underside of forewing), forewing length and eyespot band width (distance between postmedial and submarginal brown lines on underside of forewing) against latitude and Julian day for Florida records of *Megisto* including 196 males and 93 females.

Character	Latitude		Julian day	
	males	females	males	females
Eyespot width	21.590 (0.0000)	24.345 (0.0000)	26.600 (0.0000)	36.436 (0.0000)
Forewing length	11.782 (0.0007)	2.680 (0.1050)	4.221 (0.0412)	3.197 (0.0770)
Band width	8.584 (0.0038)	2.937 (0.0898)	3.187 (0.0757)	9.333 (0.0029)

The female with the largest eyespots (Fig. 7) was found at Kelly Park, Orange Co., on 25 March 1996 and was worn at a time when males were prominant and fresh, suggesting that eyespots of exceptional size may be correllated with abnormally early emergence. However, we were unable to detect significant differences within a sex in the samples from Alachua Co. (P=0.18 for males, P=0.28 for females). The possibility of a significant relationship between eyespot diameter and flight time at a single location within the relatively long flight period needs to be assessed with more data from single sites, and could perhaps be achieved as part of mark-recapture studies so as to limit impact. Nevertheless the variation in eyespot diameter within a site on a single day also makes the formal taxonomic recognition of a species with large eyespots inappropriate. For example, on 2 April 1996, in San Felasco Hammock, Alachua Co., a male with unf lower eyespot 4.6mm in diameter (corresponding to some from Kelly Park, Orange Co., near the southern range limit), was flying with another that had an eyespot diameter of 3.2mm, which is consistent with some from the northern range limit in Ontario (Fig. 8-9).

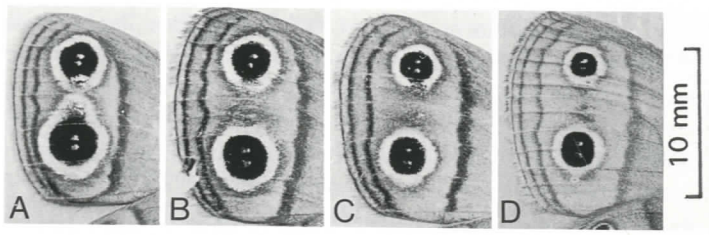

Fig. 7. Outer portion of unf of female *Megisto* from eastern North America: A) Florida, Orange Co., Kelly Park, 28°45' N, 81°29' W, 25 Mar 1996. B-C) Florida, Alachua Co., San Felasco Hammock, 29°43' N, 82°24' W, 2 Apr 1996. D) Ontario, Norfolk Co., St. Williams, 42°40' N, 80°25' W, 28 Jun 1969. All collected by P. M. Catling.

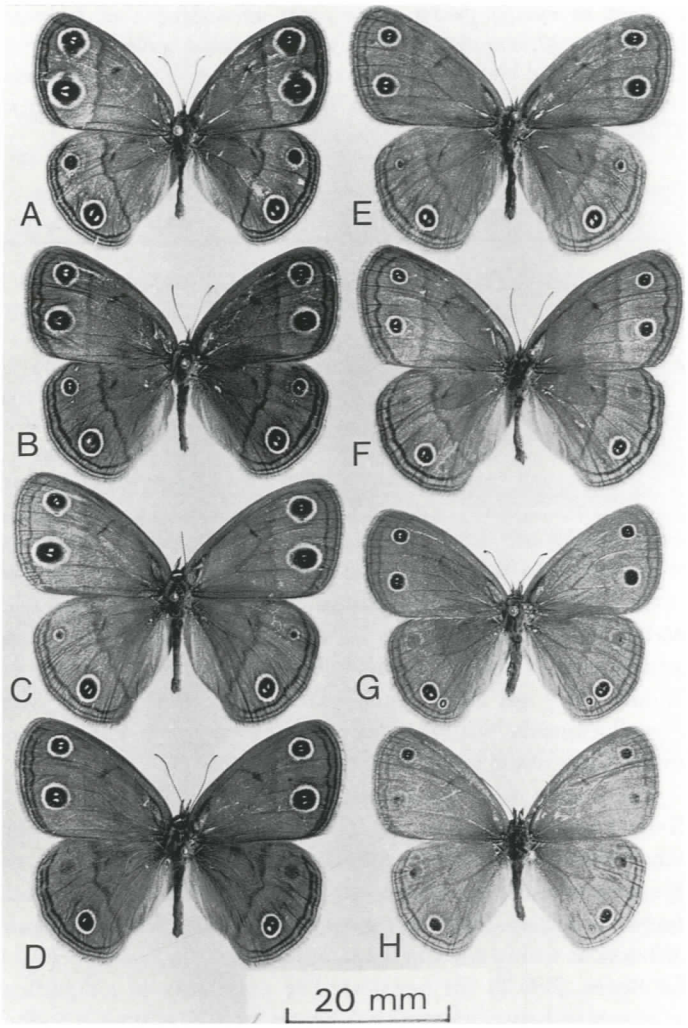

Fig. 8. Upperside of male *Megisto* from eastern North America showing variation from south (A) to north (H): A-B) Florida, Orange Co., Kelly Park, 28°45' N, 81° 29' W, 25 Mar 1996. C) Florida, Alachua Co., Gainesville, 29°39' N, 82°22' W, 2 Apr 1996 D-F) Florida, Alachua Co., San Felasco Hammock, 29°43' N, 82°24' W, 2 Apr 1996. G) Ontario, Ottawa-Carleton, Carlsbad Springs, 45°22' N, 75°28' W, 5 Jun 1996. H) Ontario, Ottawa-Carleton, Dwyer Hill Siding, 45°07' N, 75°56' W, 15 Jun 1996. All collected by P. M. Catling.

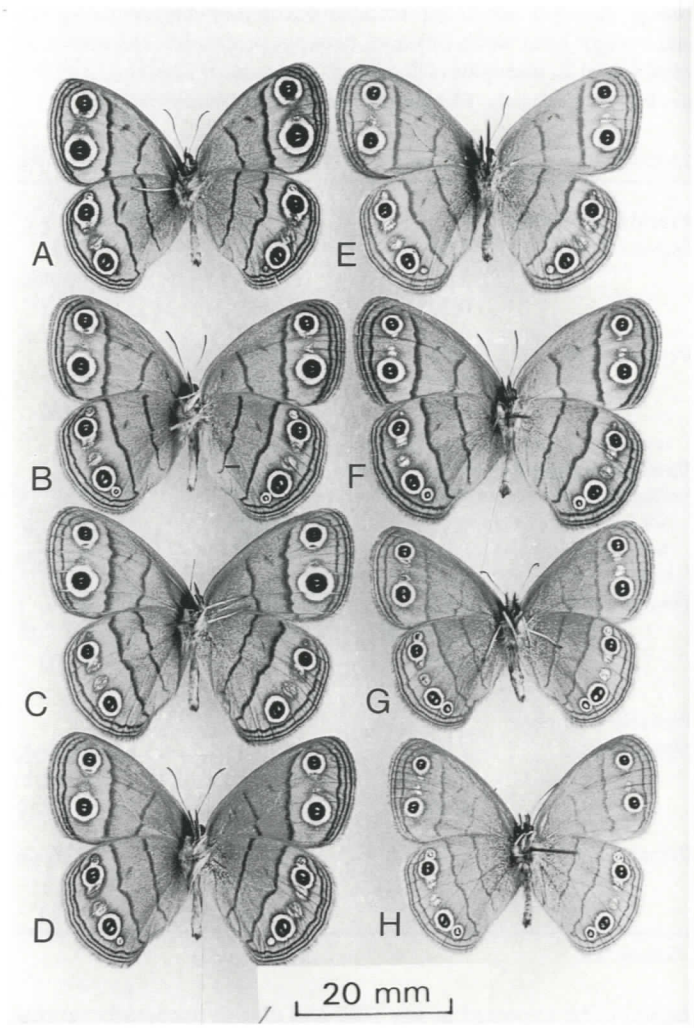

Fig. 9. Underside of male *Megisto* from eastern North America showing variation from south (A) to north (H) (same sites as in Fig. 8): A-B) Florida, Orange Co., Kelly Park, 25 Mar 1996. C) Florida, Alachua Co., Gainesville, 2 Apr 1996. D-F) Florida, Alachua Co., San Felasco Hammock, 2 Apr 1996. G) Ontario, Ottawa-Carleton, Carlsbad Springs, 5 Jun 1996. H) Ontario, Ottawa-Carleton, Dwyer Hill Siding, 15 Jun 1996. All collected by P. M. Catling.

Development Times

Oliver (1982) believed that the 90-100 day development time of *M. cymela* from Pennsylvania correllated with the alleged 3-4 months between flights in Florida, but it also correllates approximately with the length of frost-free period or growing season in Pennsylvania after June and before June the following year. The development times of *M. cymela* from Pennsylvania (Flowertown, Montgomery Co.) noted by Mr. Richard W. Boscoe were variable extending from 108-162 days (R. W. Boscoe, pers. comm.). Oliver (1982) recorded development times of approximately twice as long for *Megisto* from Gainesville, and Boscoe (pers. comm.) recorded development times of 192-291 days in eggs from a population in Withlacoochee State Forest, in Hernando Co., Florida. The longer development time of the Florida individuals correllates with the longer growing season there. Through either a shorter development time in the north or a longer one in the south, young larvae are able to take advantage of the relatively moist early spring period of fresh graminoid growth in deciduous forests. Adaptation of races to different lengths of growing season does not, however, require that the races be recognized as distinct species.

Evolutionary Considerations

For both male and female *Megisto* in both the Florida peninsula and panhandle there was a significant decrease in eyespot size in relation to increasing latitude and later collection dates, but a significant relationship was not found within the Canadian sample. This and the dispersion in Fig. 4 suggests that the cline exists mostly at the southern limit of the range of *Megisto* in eastern North America, and particularly within the Florida panhandle. Florida populations occupy more or less isolated southern hardwood forests, but interestingly the most extreme variants do not occur in the the most well established area of relict flora and fauna in the Appalachicola drainage, but much further south in the peninsula. This suggests the possibility that the larger size and eyespots in the Florida populations may be a selected trait conferring advantage in predator evasion in a

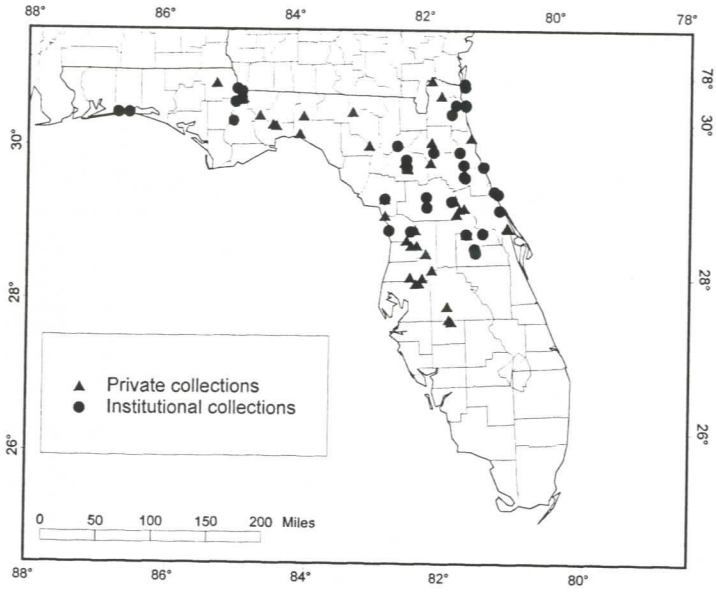

Fig. 10. Geographic distribution of *Megisto* in Florida based on specimens in institutional (dots) and private (triangles) collections.

situation where the insects are more vulnerable to predators due to lack of leaves on most woody vegetation during the relatively early flight period. There is much more leaf cover available during the later flight periods northward, even in the Florida panhandle. The development time may also play a role.

Distribution in Florida

Within Florida, *Megisto* occurs in areas of more or less isolated hardwood forests south to near the middle of the peninsula in northern Hardee Co., near the west coast, and to Orange Co., near the east coast (Fig. 10). It was not found in the region around Archbold Biological Station, Highlands Co., despite extensive field surveys in that area (M. C. Minno, pers. comm.).

CONCLUSIONS

The Florida specimens referred to *M. c. viola* are extremes of clinal variation and Florida populations overlap in variation in eyespot size, forewing band width and forewing length with similar amounts of variation further north, and even to the northern range limit in Canada. There is no evidence for two separate species in scatter plots of putatively distinctive characters in Florida and there is only one brood, although this brood may peak at different times over short distances in the Florida panhandle. Shorter development times in more northern populations may be explained in terms of adaptation to to spring flush of growth in woodland graminoids and latitudinal differences in length of growing season. A significant decrease in eyespot size in relation to increasing latitude and later collection dates within both the Florida peninsula and the panhandle suggests that the cline exists mostly at the southern limit of the range of *Megisto* in eastern North America.

The pattern of geographic variation is of great interest in terms of evolution, and although taxonomic recognition of *M. c. viola* as a separate species appears inappropriate, subspecies rank seems valid. With a narrow cline in the Florida panhandle, it appears that *M. c. viola* may be limited to the northern half of the Florida peninsula. Additional research is needed on the relationships of Florida populations of *M. cymela* and those elsewhere along the Gulf Coast and lower Mississippi Valley.

ACKNOWLEDGEMENTS

We would not have been able to complete this work without the substantial help of several entomologists. Lee D. Miller and Jacqueline Y. Miller kindly provided data and measurements from specimens in the Allyn Museum of Entomology, Sarasota, Florida. Marc C. Minno (Gainesville, Florida) provided data from his personal collection, as well as a very useful review of the manuscript. Richard W. Boscoe (Lafayette Hill, Pennsylvania) provided data on reared specimens. Richard Worth (formerly Gainesville, Florida; now Belmont, California) made continuous observations over a period of several months in the Gainesville area and also collected specimens. Ed Johnson (Staten Island, New York) provided information concerning specimens in the Staten Island Institute of Arts and Sciences. Information on butterfly occurrences at Ross-Costello Hammock was supplied by Roger Hammer and Walter P. Gould (Miami, Florida). John B. Heppner (FSCA, Gainesville, Florida) and Thomas C. Emmel (University of Florida, Gainesville) provided useful advice.

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