VARIABILITY, DISTRIBUTION AND TAXONOMY OF
CALOPTERYX DIMIDIATA
(ZYGOPTERA: CALOPTERYGIDAE)

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ABSTRACT

This study reviews the taxonomic instability of the names Calopteryx apicalis Burmeister and C. dimidiata Burmeister. The data support Hagen's early revision where he recognized only one species with the name C. dimidiata. A complete synonymy appears followed by criteria for distinguishing the species from other Western Hemisphere congeners, an interpretation of the unstable nomenclatural usage, and summary of distribution by county for each state. An analysis of variability through the species range finds spring adults to be typically larger in wing, leg, and body characters than summer and fall specimens from the same regions. A possible explanation is advanced based on larval growth periods. Wing color patterns, female stigma size, and female morphs have little to no seasonal variation and occur in geographical clines.

This study reviews the taxonomic validity of Calopteryx dimidiata Burmeister and its seasonal and geographical variability. Damselflies of the genus Calopteryx are large, colorful forms occurring only in the Northern Hemisphere and having stream to riverine habitat preferences. Three species occur in portions of both Canada and the United States, and 2 additional species (including C. dimidiata) exist in the eastern U.S.

Differences in body proportions and wing patterns lead Burmeister (1839) to describe 2 taxa, C. apicalis and C. dimidiata. Subsequent writers varied in recognizing one or both of these species, and some authors following the conspecific interpretation used both names at different times. This situation contrasts with a rather stable taxonomy for North American Zygoptera and is particularly undesirable as calopterygids appear increasingly in ecological and ethological studies.

Small samples having limited geographic representation handicapped earlier efforts to resolve the problem. Material for this study (634 specimens) came from several sources acknowledged below, and represents most of the geographic range.

DIAGNOSIS AND TAXONOMIC BACKGROUND

Data given here support Hagen's (1889) conclusion that C. apicalis and C. dimidiata are conspecific. The following synonymy adopts this interpretation. Citations in the synonymy appear with complete title and source under Literature Cited.

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Calopteryx dimidiata Burmeister


*Calopteryx cognata* Rambur, 1842, p. 222 (type female: "l'Amerique septentrionale"; loc. type ?); Selys, 1853 (syn.).

*Calopteryx syriaca* Rambur, 1842, p. 223 (type male: "Liban"; loc. type ?); Selys, 1854 (syn.).

*Calopteryx dimidiata apicalis* Burmeister; Hagen, 1889 (revis.); Calvert, 1890 (distr.); Calvert, 1893 (descr., distr.); Kellicott, 1894 (distr., in error); Calvert, 1895 (distr.); Williamson, 1900 (distr.); Calvert, 1906 (distr.); Byers, 1927 (quotes erroneous distr.); Kormondy, 1958 (corrects distr.).

*Agrion apicalis* (Burmeister); Kirby, 1890 (cat., distr.); all following authors spelled the specific name *apicalis*; Needham and Heywood, 1929 (key, descr., distr.); Montgomery, 1933 (distr.); Brimley, 1938 (distr.); Beatty, 1946 (distr.).

*Agrion dimidiata* (Burmeister); Kirby, 1890 (cat., distr.); all following authors spelled the specific name *dimidiatum*; Muttkowski, 1910 (cat., distr.); H. Garman, 1924 (quotes Burmeister's 1839 local.); Needham and Heywood, 1929 (key, descr., distr.); Byers, 1930 (key, descr., distr.); Byers, 1931a, b (distr.); Brimley, 1938 (distr.); Davis and Fluno, 1938 (distr.); Ferguson, 1942 (distr.); Wright, 1943 (distr.); Wright, 1946 (larva descr.); Needham, 1946 (distr.); Bick, 1957 (distr.); Trogdon, 1961 (distr.).

*Agrion dimidiatum apicalis* (Burmeister); Muttkowski, 1910 (cat., distr.); Howe, 1917-1921 (distr.); P. Garman, 1927 (descr.).

*Calopteryx dimidiata* Burmeister; Kormondy, 1958 (distr., notes, author's name erroneously presented).

The following diagnosis, distinguishing *C. dimidiata* from its 4 nearctic congeneres, rests largely on color pattern and wing shape. Mate recognition in *Calopteryx* derives largely from behavior while structural differences in male abdominal appendages and genitalia are slight.

Males: Apical black bands on all wings terminating in essentially straight borders across wing distal to nodus, rarely differing more than 2 mm in length between fore and hindwings (measured on wing's longitudinal axis). Poorly-defined bands in northern teneral specimens. Sternum abdominal segment 10 black, not white or cream-colored.
Females: Hyaline wings lacking dark apical bands, or bands, if present, like male or on hindwings only. Wings wide about mid-length, rounded in outline, length equals width X 4 or less. Labrum and labium dark (metallic black, blue or green, not pale-cream color). Stigma absent or exceeds 2 mm in length.

The only taxa possibly confused with *C. dimidiata* are *C. aequibilis* and *C. amata*, and their full descriptions appear in Walker (1953).

Difficulties in separating the 2 taxa, *C. apicalis* and *C. dimidiata* may have occurred only 3 years after Burmeister’s 1839 descriptions. Rambur (1842) completely omitted, without explanation, *C. apicalis* from his treatment of neuropterous insects. Possibly, *C. apicalis* specimens were not available; however, he did describe 2 new taxa, *C. cognata* and *C. syrica*, synonymized 12 years later with *C. dimidiata* by Selys. Selys (1853, 1854) recognized both *C. apicalis* and *C. dimidiata*; however, he found no distinct differences and remarked of *C. dimidiata*, “Cet eespecie est tres-voisine de *l’apicalis* ...”

Hagen (1889) revised the North American *Calopteryx*, concluding *C. apicalis* and *C. dimidiata* were conspecific and treated *C. apicalis* as “... *dimidiata* race *apicalis*.” Later writers interpreted the revision as recognizing a subspecies, *C. d. apicalis*; however, the nominal subspecies name, *C. d. dimidiata* appeared only once (Kormondy, 1958). Hagen (1889, 1889) gave shorter body and abdominal lengths and wing expanse in *C. dimidiata apicalis* and allocated the name to northern colonies (Pennsylvania and Massachusetts). P. P. Calvert noted on his personal copy of Hagen’s paper that Philip Laurent contributed part of the *C. dimidiata* sample from material collected during March in Florida, and also noted the published measurements as larger than the actual specimens.

Universal acceptance of Hagen’s revision extended 11 years (Calvert 1890, 1893; Kellicott, 1894; Calvert 1890; Williamson 1900). Odonatologists in the subsequent era encountered several questions; namely, why Hagen chose *dimidiata* in deference to *apicalis* having page precedence, was Hagen’s conclusion of conspecificity correct, and what response was preferable to the generic change from *Calopteryx* to *Agrion* proposed in 1890 by Kirby. Hagen’s (1889) paper was the first revision affecting the species name, thereby giving him first-reviser prerogative of choice. Hagen gave no reason for using *dimidiata* and 3 possible explanations exist. He possibly interpreted Rambur’s work of 1842 as a revision where only *C. dimidiata* appeared. In 1861, Hagen’s Synopsis of North American Neuroptera misquoted Burmeister’s page number from 829 to 826, thus giving *dimidiata* page precedence. The same mistake reappeared in his 1889 paper. Calvert’s (1893) study of Burmeister’s types revealed the mistake was also on the type label. The attention Hagen paid to page precedence is unknown. Hagen was surely aware of changes proposed for Kirby’s 1890 catalog when writing his 1889 revision, and his choice of *dimidiata* was possibly to avoid later problems of homonymy (L. K. Gloyd, per. com. 1972). Thomas Say (1840) described, among many species, a coenagrionid damselfly as *Agrion apicalis*, now known as *Argia apicalis* (Say). Using the name *dimidiata* avoided homonyms when applying the genus *Agrion* to calopterygid-type Zygoptera. Odonatologists, including Hagen, used 1839 for Say’s publication, the same year as Burmeister’s descriptions: however, Say’s official publication date for taxonomic priorities is 5 May 1840 (Nolan 1913). In any event, Hagen’s revision leaves the name *dimidiata* for writers following the conspecific interpretation.

The latter interpretation was slipping by 1903. Needham (1903) and Cal
Calvert (1903, 1909a, 1909b) were again using *apicalis* as the species name for northern specimens; however, Calvert (1905) also used *C. d. apicalis* in this interval. Calvert apparently had reservations on the correct interpretation but never explained his doubts in print. Needham's position is unclear as he never used trinominals for any species. Specific recognition for northern populations continued, including Needham and Heywood (1929), Montgomery (1933), Donnelly (1961), and Beatty, et al. (1969). Paulson (1968) used *apicalis* for Florida material but favored Burmeister's original page precedence. The biological basis for these interpretations never accompanied published data. Only Williamson (1934) and Montgomery (1940) commented that one species probably existed but did not have sufficient material to resolve the question. Montgomery (1940) allocated the name *apicalis* to colonies north of the Chesapeake Bay area.

The first American writer following Kirby's generic change was Muttkowski (1910) in his Catalogue of the Odonata of North America where he also accepted Hagen's revision. The use of *Agrion* dominated North American papers following 1910 and received impetus when Needham and Heywood (1929) adopted the genus for the "Handbook of North American Dragonflies." The review of the *Agrion-Calopteryx* problem by Montgomery (1954) reversed opinions, and only 2 titles used *Agrion* for *dimidiata* subsequently.

**Geographical Distribution**

The distribution for *C. dimidiata* appears below by county for each state, and Fig. 1 graphically illustrates the pattern using one symbol per county. Where data permit, symbols are on collection sites, and otherwise appear in the center of the county. Literature, personal communications and collection(s) documenting distributions accompany each county in the following list. Collections cited carry the following abbreviations: CJ Coll.—author's coll., G.H.B. Coll.—G.H. Bick's Coll., J.A.L. Coll.—J.A. Louton's Coll., R.McM. Coll.—R. McManaway's Coll., Will. Coll.—Williamson's Coll. (University of Michigan), FSCA—Florida State Coll. of Arthropods, PASC—Philadelphia Academy of Science Coll. All acceptable distribution records appear from the above synonymy.

- **Alabama**: Baldwin and Covington counties. Wright (1943); FSCA.

- **Delaware**: Sussex County. L.P. Kelsey (per. com. 1972); PASC. Calvert (1890) initially reported the species from Delaware without specific locality data.

- **Florida**: Alachua, Bradford, Calhoun, Clay, Duval, Escambia, Franklin, Gadsden, Highlands, Hillsboro, Jefferson, Lake, Levy, Liberty, Leon, Madison, Okaloosa, Orange, Putnam, Santa Rosa, Seminole, Wakulla, and Walton counties. Hagen (1861, 1875, 1889); Byers (1930, 1931a); Davis and Fluinu (1938); Wright (1946); Needham (1940); Roback and Westfall (1967); Johnson and Westfall (1970); CJ Coll.; FSCA.

- **Georgia**: Bartow, Bibb, Brantley, Burke, Coffee, Colquitt, Decatur, Gwinnett, Jefferson, Lee, Lowndes, Pierce, Ware, and Wayne counties. Williamson (1934); CJ Coll.; FSCA. Hagen (1861) initially reported the species from Georgia without specific locality data.

- **Kentucky**: Burmeister (1839) described the species from a female specimen listed for "Kentucki." All subsequent writers listing Kentucky in the species'
distribution trace back to Burmeister; however, other specimens are unknown from the state. At least one other species listed for Kentucky by Burmeister has never again appeared in collections from the state (Gloyd, 1968). Locality data available to Burmeister was meager and his C. dimidiata type was possibly not from present-day Kentucky.


Massachusetts: Middlesex, Norfolk, and Plymouth counties. Howe (1917); Hagen (1889); PASC. Hagen (1861) initially listed the species from Massachusetts without specific locality data.

Michigan: Kellicott (1894) reported C. dimidiata from Michigan. Byers (1927) and Needham and Heywood (1929) followed Kellicott’s report. Kormondy (1958), although unable to locate Kellicott’s specimens, concluded the
record was a misidentification for *C. aequabilis*. He based his conclusion largely on the known geographic range of *C. dimidiata*. I agree with Kormondy's interpretation.


New Jersey: Atlantic, Burlington, Gloucester, Mercer, Ocean, Salem, and Warren counties. Calvert (1903, 1909a); Montgomery (1933); Roback and Westfall (1967); H. B. White (per. com. 1972); PASC; Will. Coll.

New York: Monroe and Westchester counties. Calvert (1899b). Needham (1928) listed a single specimen from Rochester in the northeastern sector of the state. Needham's specimen cannot be located. Other records for the species lie east of the Appalachian Mountains, excepting the single Tennessee record. I suggest that the Rochester record is an error of the same nature or an unlikely accident. Calvert (1893) initially reported the species for New York without locality data.

North Carolina: Madison, McDowell, Moore, Transylvania, and Robeson counties. Byers (1931b); Brimley (1938); FSCA; Will. Coll.

Pennsylvania: Montgomery and Lancaster counties. Selys (1854); Hagen (1861, 1875, 1889); Calvert (1893, 1909b); Beatty etc. (1969); PASC.


South Carolina: Aiken, Allendale, Calhoun, Chesterfield, Florence, Greenville, Oconee, Orangeburg, and Pickens counties. Montgomery (1940); Roback and Westfall (1967); Will. Coll.; FSCA.


Texas: Hardin and San Jacinto counties. Ferguson (1942); Johnson (1972); T. Donnelly (per. com. 1969).


Wisconsin: Muttkowski (1908) reported *C. dimidiata* from Wisconsin; however, he omitted reference to the state 2 years later (Muttkowski 1910), and other authors ignored the report. I assume the 1908 reference was in error.

The adult flight season through this range progressively shortens to the north. Dates for New Jersey are 28 May to 25 August. All northeastern records fall into this interval. Dates for south Florida are 7 March to 24 October, although sight records extend this range from 26 February to 5 November, and the flight season probably extends year-around for mild winters. A 3-month interval in the northern habitats compares typically with approximately 8 months in south Florida. The data suggest intervening sites have intermediate intervals.

The distributional pattern in Fig. 1 reveals essentially a coastal plain species. Inland colonies north of the Chesapeake Bay area are apparently rare. The Pennsylvania specimens constitute Burmeister's 1839 types of *C. apicalis* and a few additional specimens taken prior to 1900. Beatty etc. (1969) referred to a Pennsylvania specimen as a "... one time occurrence." Needham (1903) stated that it is only found at "... lower altitudes in the southern parts..." referring to New York. Howe (1917-1921) described the species as "rare" in Massachusetts; however, other coastal colonies are more abundant. Calvert (1909a) found it "not rare" in New Jersey, and Waage (per. com. 1972) collected 70 individuals on 10 August 1972, in Rhode Island without making "... a dent in the population..."

Southern colonies have a wider distribution correlating with more exten-
sive coastal plain conditions. The apparent distributional hiatus seen in Fig. 1 about Virginia and northern parts of North Carolina is possibly real as discussed below. The geographical comparison of variability recognizes a north and south Florida. For this study, Levy and Lake counties are the southernmost north Florida and northernmost south Florida counties respectively.

Calvert (1890) reported a single male specimen determined as *C. dimidiata apicalis* from Honduras. He received the specimen from R. Uhler who in turn received it from J. L. Le Conte. Calvert (1901-1908) included the species in the Central American Fauna on the basis of the same specimen, this time naming it *C. dimidiata*. No other *Calopteryx* specimens have appeared south of Texas, and *C. dimidiata*’s westernmost records are in east Texas where it is apparently uncommon. The questionable specimen is currently not in the Philadelphia Academy Series for the species, although other specimens collected in that era remain. I suggest an accidental mislabeling accounts for the Honduras record.

**Variability**

Analyzed characters are apical wing band length/wing length ratios and forewing, abdominal segment 7, left third tibia, and wing stigma length measured parallel to the anterior wing margin. Inaccurate measurements of whole abdomens result from contraction and expansion of nonsclerotized parts and folded, twisted segments. Forewing, abdominal, and tibial characters appear below only as wing, abdominal, and tibial lengths. Stigmas occur only in females. Comparisons appear also for male abdominal appendages and female morphs. Vernier caliper measurements provided linear dimensions to the nearest tenth of a millimeter. Abdominal appendage lengths utilized ocular-micrometer conversions into millimeters.

Conditions for differential growth rates clearly exist within the elongate, coastal plain distribution of Fig. 1. The north-south arrangement of states provides units, where specimens permit, for subdividing the sample geographically and recognizing a north and south Florida as given above. Seasonal subdivision of each state’s sample consists of specimens taken during (1) May and earlier, (2) June and July, and (3) August and later. Seasonal trend comparisons utilized within-state samples having an N > 9; however, this approach requires lumping data from the states of North and South Carolina.

The total sample consists of 387 males and 247 females, with the values for states being: Rhode Island, 45 males, 30 females; New Jersey, 27 males, 29 females; the Carolinas, 35 males, 32 females; Georgia, 69 males, 29 females; north Florida, 186 males, 115 females; south Florida, 18 males, 6 females. Seven females and 6 males do not appear in the statistical analysis due to incomplete seasonal data or single state records (Alabama, Delaware, Louisiana, Massachusetts, Mississippi, and Pennsylvania), and every specimen did not contribute data for every structure due to occasional breakage. Standard deviations and standard errors appear for samples with N > 10. Fig. 2 follows the example in Hubbs and Hubbs (1953).

Examination of Table 1 and Fig. 2 reveals generally smaller wing characters in New Jersey and Rhode Island samples compared with southern material. Statistical significance exists between some extreme means; however, means from geographically intervening samples have intermediate
TABLE 1. A NORTH-SOUTH ARRANGEMENT OF STATISTICS FOR FOREWING LENGTH IN *Calopteryx dimidiata*. Seasonal subdivision of samples show material taken in May and earlier, . . . May; in June and July as such; and in August and later, August . . ; O R, observed range; X, mean; SE, standard error of the mean; N, sample size.

<table>
<thead>
<tr>
<th>Locality</th>
<th>Males</th>
<th></th>
<th>Females</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>O R</td>
<td>X±2SE</td>
<td>SD N</td>
<td>O R</td>
</tr>
<tr>
<td>Rhode Island</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10 August</td>
<td>24.5–27.4</td>
<td>25.9±3</td>
<td>.89</td>
<td>45</td>
</tr>
<tr>
<td>New Jersey</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>. . . May</td>
<td>27.3–27.4</td>
<td>27.3</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>June, July</td>
<td>25.4–28.2</td>
<td>26.5±5</td>
<td>.93</td>
<td>16</td>
</tr>
<tr>
<td>August . .</td>
<td>23.8–26.9</td>
<td>25.2</td>
<td>9</td>
<td>23.6–27.8</td>
</tr>
<tr>
<td>South-North Carolina</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>. . . May</td>
<td>27.3–30.3</td>
<td>28.7±4</td>
<td>.84</td>
<td>14</td>
</tr>
<tr>
<td>June, July</td>
<td>24.9–31.9</td>
<td>28.1±7</td>
<td>2.63</td>
<td>10</td>
</tr>
<tr>
<td>August . .</td>
<td>25.9–30.5</td>
<td>27.9±9</td>
<td>1.53</td>
<td>11</td>
</tr>
<tr>
<td>Georgia</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>. . . May</td>
<td>29.1–31.3</td>
<td>30.1±3</td>
<td>.75</td>
<td>18</td>
</tr>
<tr>
<td>June, July</td>
<td>28.0–31.1</td>
<td>29.4±6</td>
<td>1.04</td>
<td>12</td>
</tr>
<tr>
<td>August . .</td>
<td>26.4–27.4</td>
<td>27.0±3</td>
<td>.50</td>
<td>39</td>
</tr>
<tr>
<td>North Florida</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>. . . May</td>
<td>26.3–31.9</td>
<td>29.9±4</td>
<td>1.44</td>
<td>44</td>
</tr>
<tr>
<td>June, July</td>
<td>26.4–32.3</td>
<td>28.5±9</td>
<td>1.73</td>
<td>14</td>
</tr>
<tr>
<td>August . .</td>
<td>25.6–30.0</td>
<td>27.4±5</td>
<td>1.14</td>
<td>128</td>
</tr>
<tr>
<td>South Florida</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>. . . May</td>
<td>25.8–30.1</td>
<td>28.3±7</td>
<td>1.23</td>
<td>12</td>
</tr>
<tr>
<td>June, July</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>August . .</td>
<td>24.0–25.7</td>
<td>24.9</td>
<td>6</td>
<td>25.9–27.4</td>
</tr>
</tbody>
</table>

values reducing taxonomic meaning. Seasonal variation likewise reveals considerable character overlap from north to south. The trend and pattern of variation for wing characters correlated very closely with abdominal and tibial lengths.

These characters are larger in spring specimens for a given state and appear to decrease in size through the remaining season. The magnitude of seasonal variation within a state approaches or exceeds geographical difference. For example, means of north Florida wing length differ seasonally by 2.5 mm, and the August means of north Florida and New Jersey differ by only 2.2 mm (Table 1). Both season and geography appear correlated to wing, abdominal, and tibial lengths. The apical band/wing ratios (males, Fig. 2) show less seasonal effect; however, the differences are geographically discordant. For example, the coefficient of difference (C. D. of Mayr 1969) for Fig. 2 data between New Jersey (June, July) material and Rhode Island (August) is 1.60 and the C. D.'s between the New Jersey (June, July) sample and similar
APICAL BAND/FOREWING LENGTH RATIO DATA IN *CALOPTERYX DIMIDIATA*

RHODE ISLAND; AUG. (45)

NEW JERSEY; --- MAY (2)

NEW JERSEY; JUNE & JULY (16)

NEW JERSEY; AUG. --- (9)

N. & S. CAROLINA; --- MAY (14)

N. & S. CAROLINA; JUNE & JULY (10)

N. & S. CAROLINA; AUG. --- (11)

GEORGIA; --- MAY (18)

GEORGIA; JUNE & JULY (12)

GEORGIA; AUG. --- (39)

N. FLORIDA; --- MAY (44)

N. FLORIDA; JUNE & JULY (14)

N. FLORIDA; AUG. --- (128)

S. FLORIDA; --- MAY (12)

S. FLORIDA; AUG. --- (6)

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Fig. 2. Geographical variation in apical band/forewing length ratios in mm of *Calopteryx dimidiata* males. Black triangles give means. In each sample, horizontal line, clear bar and black bar indicate the range and 1 standard deviation and 2 standard errors of the mean on each side of the mean, respectively.
samples of the Carolinas, Georgia, and north Florida are 0.30, 1.23, and 1.80 respectively. The Rhode Island colony, geographically close, differs more from New Jersey than the more distant Georgia sample. Stigma length (females) revealed no seasonal trend. A geographical cline exists with small northern and large southern stigmas. The FW stigma mean lengths in mm ± 2 standard errors per state were Rhode Island, 1.1 ± 0.2; Carolinas, 1.3 ± 0.2; Georgia, 1.8 ± 0.2; north Florida, 1.9 ± 0.1; south Florida, 2.2. Sample sizes per state appear above. The HW stigmas follow a similar pattern, being slightly smaller than their companion FW stigmas.

Females may have clear wings devoid of apical bands, heteromorphs, or resemble males with similar, fully-developed apical bands, andromorphs. An intermediate phase exists in some females having apical bands only on hindwings with forewings clear or with only a faint deposition of pigment. Johnson and Westfall (1970) and Johnson (1972) illustrated these patterns. Fig. 5C of the former paper shows a nonbanded forewing photo erroneously placed as a hindwing. The frequency of heteromorphs drops consistently from approximately 93 to less than 1.0% moving from Rhode Island south to north Florida (Table 2). Frequency of the intermediate phase peaks in Georgia at 44.8%; southward, north Florida has only 20.0, and the Carolinas and New Jersey to the north have 18.4 and 10.3%, respectively (Table 2).

Fig. 3 shows dorsal and lateral views of appendages from a Delaware male in A and B, and similar views of a Florida male, C and D. Differences between appendages have not been quantified; however, note the downward-curved apical end of the superior appendage in lateral view, B, as compared to the stockier appendage in D having a straighter dorsal margin. In dorsal views, note the medial, angulate shoulders on bases of inferior appendages of C and their absence in A. The apically curved superiors typify all males I have seen.

**TABLE 2.** A north-south arrangement of morph frequencies in female *Calopteryx dimidiata.*

<table>
<thead>
<tr>
<th>LOCALITY</th>
<th>FW–HW BANDS</th>
<th>ONLY HW BANDS</th>
<th>Percent heteromorphic**</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhode Island</td>
<td>2*</td>
<td>28</td>
<td>93.3</td>
</tr>
<tr>
<td>New Jersey</td>
<td>3*</td>
<td>26</td>
<td>89.6</td>
</tr>
<tr>
<td>Delaware</td>
<td></td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>North–South Carolina</td>
<td>3</td>
<td>6</td>
<td>23</td>
</tr>
<tr>
<td>Georgia</td>
<td>15</td>
<td>13</td>
<td>1</td>
</tr>
<tr>
<td>Louisiana</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mississippi</td>
<td></td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>North Florida</td>
<td>88</td>
<td>23</td>
<td>4</td>
</tr>
<tr>
<td>South Florida</td>
<td>6</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Very pale pigment development.
** Sample > 6
Fig. 3. Dorsal (A,C) and lateral (B,D) views of abdominal appendages of a Delaware (Sussex Co.) male (A,B) and a Florida (Bradford Co.) male (C,D).

from north of the Carolinas. The slender, concave inferiors characterize northern males; however, occasional southern males from scattered localities tend toward this condition. The medial shoulder of the inferiors, seen from dorsal view, varies in contour; yet, the shoulder occurs in all southern males. Northern males may have equally-developed shoulders or they appear smaller or absent as in Fig. 3A.

DISCUSSION

Variability of body proportions reveals geographical clines largely modified by seasonal effects, or discordant patterns. The female morphs, perhaps considered most distinct by Burmeister in delineating C. apicalis and C. dimidiata, occur in a geographical cline. Differences in male appendages are minor or inconsistent without significant taxonomic meaning. These observations allow recognition of only one species by morphological criteria and extent of character overlap gives no objective basis for subspecies by the 75% concept (Mayr 1969).
The seasonal trend to smaller size parallels data reported for stoneflies (Khoo 1964), and may have a similar explanation. Large spring specimens presumably reflect a longer growth period in the larval instars. As the season progresses and temperatures rise, shorter growth intervals between instars occur, culminating in smaller late summer and fall adults. Life cycles of C. dimidiata are probably similar to other Calopteryx, having at least a 1-year period (Buchholtz 1951). The single C. dimidiata larval sample available (March, Alachua Co., Florida) is distinctly heterogeneous in body lengths, indicating a lack of synchronization by the initial emergence in April. Presumably the larger instars emerge as spring adults having completed larval growth through the past fall and winter, and the smaller instars emerge into late summer and fall adults following a relatively shorter interval of growth. Smaller sizes seen in south Florida specimens (Table 1) may result from the area's longer growth period. Suspension of growth by low temperature is probably infrequent, and late-season effects of northern colonies may occur most of the year in south Florida. A different form of seasonal variation appears in the apical band/WL length ratios of samples from the Carolinas and Georgia (Fig. 1). These differences disrupt the north to south increase of the ratio, and this character involves extent of pigment deposition rather than morphological structure.

The distribution in Fig. 1 suggests a hiatus in northern North Carolina and southern Virginia. Efforts to locate specimens from collections in this region failed, and sites immediately to the north in Virginia represent only one male each. Coastal Plain species in other groups frequently extend northward only to this area; for example, note distribution maps for amphibians, water snakes, turtles etc. in Conant (1956). C. Gilbert and F. Thompson (per. com. 1972) state that similar patterns occur in fish and freshwater gastropods respectively. The lack of specimens may represent a real hiatus in the species distribution. Calopteryx adults have a strong tendency to remain close to parental streams (Zahner 1960; Klotzli 1971; Heymer 1972; Waage 1972). A distributional hiatus or intervening area of low density as in Fig. 1 could reduce gene exchange between northern and southern components to near zero. This apparent allopatry may offer an opportunity for studying initial stages of speciation in damselflies.

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LITERATURE CITED


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ADDENDA

The following data, received subsequent to writing the above paper, significantly enhances the distribution of Calopteryx dimidiatum in Mississippi and North Carolina. Mississippi: Amite, Forrest, George, Hancock, Jackson, Jefferson Davis, Lamar, Pearl River, Perry, and Pike counties. W. Mauftrey Collection.


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