

ISSN 1061-3781

BULLETIN OF AMERICAN
ODONATOLOGY

Volume 2 Number 4
Feb 1995

THE SUBGENUS *TETRAGONEURIA* (ANISOPTERA: CORDULIIDAE: *EPITHECA*)
IN NEW JERSEY
Michael L. May p. 63-74

THE DRAGONFLY SOCIETY OF AMERICA

Business address: c/o T. Donnelly, 2091 Partridge Lane, Binghamton NY 13903

EXECUTIVE COUNCIL 1991-1993

President	G.L. Harp	Jonesboro AR
President Elect	K. Tennessen	Florence AL
Past President	T.W. Donnelly	Binghamton NY
Past President	C. Cook	Center KY
Vice President, SIO Affairs	M. Westfall, Jr.	Gainesville FL
Vice President, Canada	R. Cannings	Victoria, British Columbia
Vice President, Latin America	R. Novelo G.	Jalapa, Veracruz
Secretary	S. Dunkle	Plano TX
Treasurer	J. Daigle	Tallahassee FL
Regular member	R. Glotzhober	Columbus OH
Regular member	M.L. May	New Brunswick NJ
Regular member	T.E. Vogt	Cypress IL

JOURNALS PUBLISHED BY THE SOCIETY

ARGIA, the quarterly news journal of the **DSA**, is devoted to non-technical papers and news items relating to nearly every aspect of the study of Odonata and the people who are interested in them. The editor especially welcomes reports of studies in progress, news of forthcoming meetings, commentaries on species, habitat conservation, noteworthy occurrences, personal news items, accounts of meetings and collecting trips, and reviews of technical and non-technical publications. Articles for publication in **ARGIA** should preferably be submitted as hard copy and (if over 500 words) also on floppy disk (3.5" or 5.25"). The editor prefers MS DOS based files, preferably written in WORD, WORD for WINDOWS, WordPerfect, or WordStar. Macintosh WORD disks can be handled. All files should be submitted **unformatted and without paragraph indents**. Each submission should be accompanied by a text (=ASCII) file. Other languages should be submitted only as text (=ASCII) files. Line drawings are acceptable as illustrations.

T. Donnelly (address above) is the interim editor of **ARGIA**.

BULLETIN OF AMERICAN ODONATOLOGY is devoted to studies of Odonata of the New World. This journal considers a wide range of topics for publication, including faunal synopses, behavioral studies, ecological studies, etc. The **BAO** publishes taxonomic studies but will not consider the publication of new names at any taxonomic level. Enquiries and submission of manuscripts should be made to **BAO** editor T. Donnelly, 2091 Partridge Lane, Binghamton NY 13903. Final submissions (after review) should be made on floppy disk, as above, with illustrations in final form and preferably adjusted to final size.

MEMBERSHIP IN THE DRAGONFLY SOCIETY OF AMERICA

Membership in the **DSA** is open to any person in any country. Dues for individuals are \$10 for regular membership and \$15 for contributing membership, payable annually on or before 1 March of membership year. Institutional (e.g. libraries or universities) membership is \$15 per year. All members receive **ARGIA** via surface mail at no additional cost. For delivery by first class in the U.S. there is an additional charge of \$4, and for Air Mail delivery outside the U.S. a charge of \$10.

The **BULLETIN OF AMERICAN ODONATOLOGY** is available by a separate subscription at \$15 for members and \$18.75 for non-members and institutions.

THE SUBGENUS *TETRAGONEURIA* (ANISOPTERA: CORDULIIDAE: *EPITHECA*)
IN NEW JERSEY

Michael L. May
Department of Entomology, Cook College
New Jersey Agricultural Experiment Station
Rutgers University, New Brunswick, NJ 08903, U.S.A.

ABSTRACT

Three apparently distinct forms of *Epitheca* (*Tetragoneuria*) exist in Southern New Jersey, based on the extent of basal wing maculation and relative abdomen width. Multivariate analyses of morphometric characters largely substantiates the validity of these putative species. One is certainly *E. (T.) cynosura*, a second is closely related to and very likely conspecific with *E. (T.) costalis*, and a third related to and probably conspecific with *E. (T.) semiaquea*. The last may intergrade with *cynosura* in New England, however, and shows some distinctions from typical *semiaquea*, so its taxonomic status cannot be resolved with certainty at present.

INTRODUCTION

Few North American taxa of Odonata have generated more confusion than *Tetragoneuria* (here considered a subgenus of *Epitheca*; Walker, 1966; K. J. Tennessen, pers. comm., 1989). Some 20 names have been referred to it, only 9 or 10 of which are widely accepted today. Despite four revisions (Davis, 1933; Kormondy, 1959; Muttkowski, 1911, 1915; Tennessen, 1973), discriminating species remains problematic. Although I make no pretense of solving all these problems here, I can present new information on the morphology and distribution of species in New Jersey (NJ) and nearby areas that may shed some light on the situation.

Historically, four currently-recognized species have been reported from the state: *cynosura*, *semiaquea*, *spinigera*, and *spinosa* (Calvert, 1900; Davis, 1913, 1933; Smith, 1910). In addition to these, *T. canis* has been taken from two ponds in the Big Flat Brook watershed of Sussex County, in the northwestern corner (A. Barlow, F. L. Carle, J. Michalski, pers. comm.). Davis (1913, 1933) reported three specimens of *spinigera* from northern NJ, but the species has not, to my knowledge, been taken since; it is at the southern

limit of its range here, however, and probably occurs sporadically and/or in small numbers. Both these northern species are distinctive and only marginally a part of our fauna, and I will not treat them further.

Tetragoneuria spinosa was reported and figured by Davis (1933) based on specimens from Clementon and Old Bridge. No subsequent published records exist from the state, and I have not rediscovered this species despite a deliberate search; however, a male in the ANSP collection, from Gibbsboro in central Camden County, was taken in May, 1972. This is close to Clementon, near where several earlier specimens were taken, so this uncommon species may still exist in that vicinity. Males of *spinosa* are quite distinctive and the species' identity is in no doubt.

My primary aim here is to assess possible distinctions among 1) typical *cynosura*, 2) populations from the NJ Pine Barrens that possess extensive dark wing maculation and have commonly been called *semiaquea*, and 3) populations from southern and central NJ, apparently closely related to and probably identical with, *costalis* (Barber, 1994; Soltesz, 1991).

MATERIALS AND METHODS

I examined specimens from throughout NJ and selected sites elsewhere in the eastern U.S. in the collections of the Academy of Natural Science of Philadelphia (ANSP), American Museum of Natural History (AMNH), Florida State Collection of Arthropods (FSCA), National Museum of Natural History (NMNH), Rutgers University (RU), and my personal collection (MLM). Additional specimens were supplied by A. Barlow (PA and Bergen and Ocean Co.'s, NJ), R. Barber (Cumberland Co., NJ), J. Michalski (Morris, Ocean, and Sussex Co.'s, NJ), K. Soltesz (NY and Cape May and Cumberland Co.'s, NJ), M. Westfall (FL, NC, SC), and H. White (DE and Burlington

MAY - *EPITHECA* (*TETRAGONEURIA*) IN NEW JERSEY

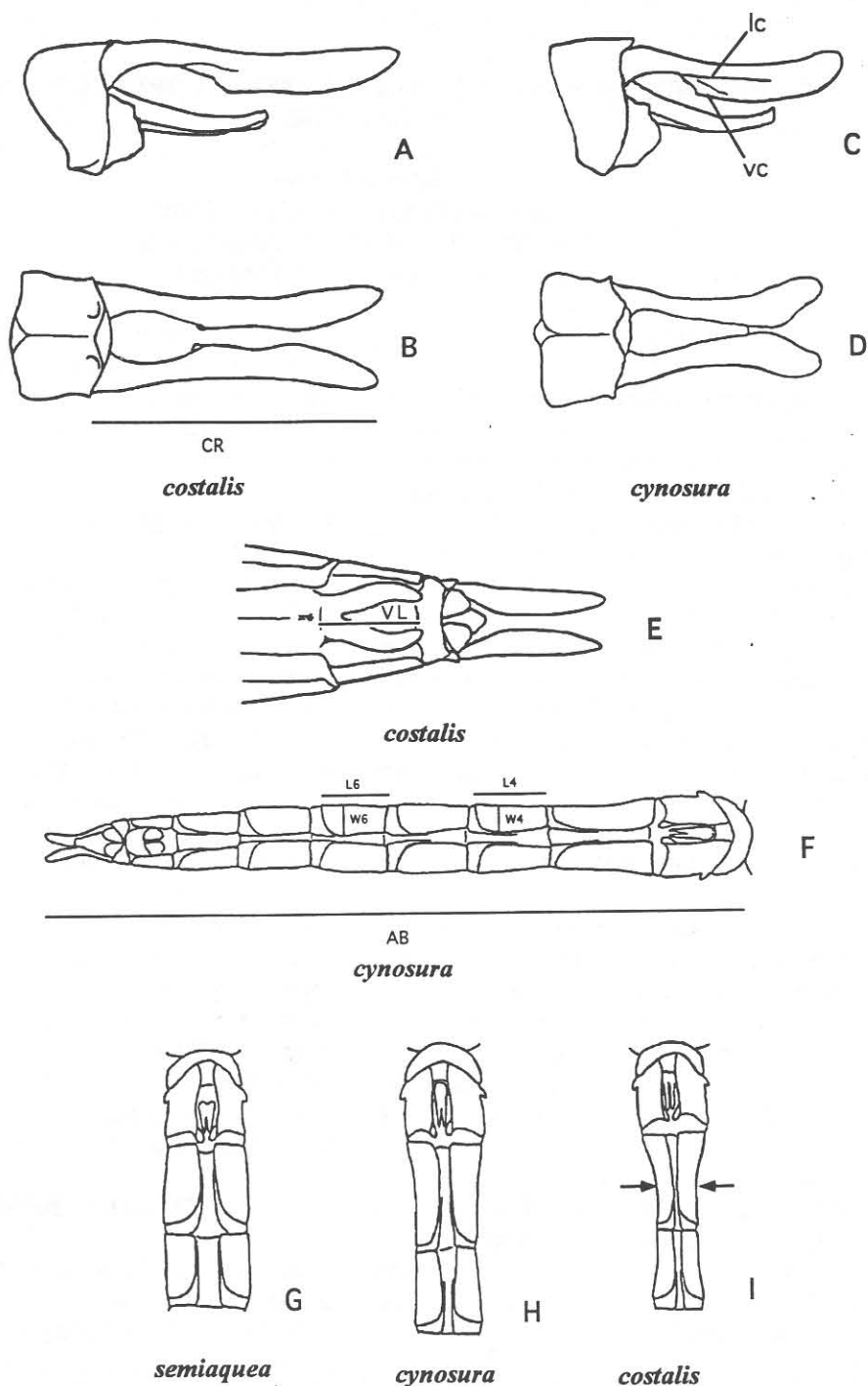


Figure 1: Morphological characteristics of *Epithecina* (*Tetragoneuria*) of southern NJ; labeled bars indicate characters used in multivariate analyses.

A., B. Lateral and dorsal views of terminalia of male *costalis* (modified from Tennessen, 1977).

C., D. Lateral and dorsal views of terminalia of male *cynosura* (modified from Tennessen, 1973); lc - lateral carina, vc - ventral carina; the terminalia of NJ *semiaquea* do not differ consistently from this morphology, although in many specimens vc is distinctly less developed.

E. Ventral view of apex of abdomen of female *costalis* (modified from Tennessen, 1977).

F. Ventral view of abdomen of male *cynosura* (modified from Donnelly, 1992).

G., H., I. ventral views of base of abdomen of male *semiaquea*, *cynosura*, and *costalis* respectively (modified from Donnelly, 1992); arrows indicate constriction of third segment.

and Ocean Co.'s, NJ). I also made special collections for this study during 1987 in Middlesex, Monmouth, and Burlington Counties and 1992 in southern Monmouth and northern Ocean Counties, NJ. Most specimens were preserved dry in cellophane envelopes, a few in ethanol.

New Jersey specimens were first placed into one of three *a priori* categories: Pine Barrens populations with extensive hindwing maculation (brown area typically extending to nodus), stout abdomens and relatively divergent cerci, as in Fig. 1A (hereafter called *semiaquea* for convenience, but see Discussion); clear-winged individuals (brown not extending beyond first antenodal crossvein) with conspicuously slender abdomens and more nearly parallel cerci, as in Fig. 1B (hereafter *costalis*, but see Discussion); and clear-winged individuals of medium stature with divergent cerci (*cynosura*). Individuals that could not be assigned unambiguously to one of these phenotypes were omitted from the preliminary analysis.

Both males and females were measured to 0.5 mm using a ruler or to 0.01 mm using a Wild dissecting microscope fitted with a filar micrometer; care was taken to insure that the line of sight was normal to the distance measured. The characters analyzed are illustrated in Fig. 1. Five characters were useful for both sexes: abdomen length (**AB**), cercus length (**CR**), ratio of wing to abdomen length (**RWA**; value was not transformed because it varied on either side of 1.0), ratio of length to width of ventral tergite of abdominal segment 4 ($R4 = W4/L4$, Fig. 1E; the transformed value, $\arcsin R4$, designated **TR4**, was used in statistical analysis to normalize the distribution), and the corresponding ratio for abdominal segment 6 ($R6 = W6/L6$; transformed as above, designated **TR6**); a sixth character, vulvar lamina length (**VL**; Fig. 1F) was also used in analysis of females.

In addition I visually scored each specimen for extent of hindwing maculation and the degree of constriction of abdominal segment 3, and I noted the characteristics of the male cerci. Penes were extruded from a few selected males, using ethanol preserved specimens when available to minimize distortion, and examined using light and scanning electron microscopy (see May, 1992, for details).

Discriminant analysis (**SAS PROC DISCRIM**;

SAS, 1985) and canonical discriminant analysis (**SAS PROC CANDISC**) using the selected characters was performed by sex for these specimens to derive discriminant functions against which to test additional specimens and to assess the correspondence between my *a priori* categories and groupings based on morphometric characters. **PROC DISCRIM** derives best fit lines (or multidimensional equivalents) for preselected classes of data, then evaluates each data point based on its least squared distance from the reference lines. **PROC CANDISC** generates linear combinations of measured variables to form new, canonical variables that maximize separation of group means, subject to the limitation that each successive canonical variable is uncorrelated with those derived previously (equivalent to an axis rotation, and similar to principal components analysis).

Using the discriminant functions, additional specimens were evaluated for similarity with one of the initial three morphometric groups. This second group of specimens included reliably identified *costalis* (FL) and *semiaquea* (NC, SC), specimens identified as *cynosura* from DE, FL, PA, ME, and NY that had extensive hindwing maculation (brown area extending more than half the distance from wing base to nodus), and specimens from CT, ME, MA and southern NJ not readily assigned to *a priori* groups.

Finally, as a third independent estimate of morphometric similarity among phenotypes I performed separately by sex a cluster analysis (**SAS PROC CLUSTER**; **SAS**, 1985) using an average linkage algorithm (**UPGMA**) on all the measured specimens. The same characters and transformations were used as described for the discriminant analyses.

RESULTS

The known distributions of all the NJ species are shown in Figure 2. It is noteworthy that, while the typical *cynosura* phenotype is syntopic with all other taxa, its overlap with *costalis* and especially with *semiaquea* is slight. Apparently *cynosura* is largely replaced by the latter in most of the Pine Barrens and by the former elsewhere south of northern Burlington and Ocean Counties. Literature records (Smith, 1910) exist for Camden County, in and near Clementon, but all specimens

MAY - EPITHECA (TETRAGONEURIA) IN NEW JERSEY

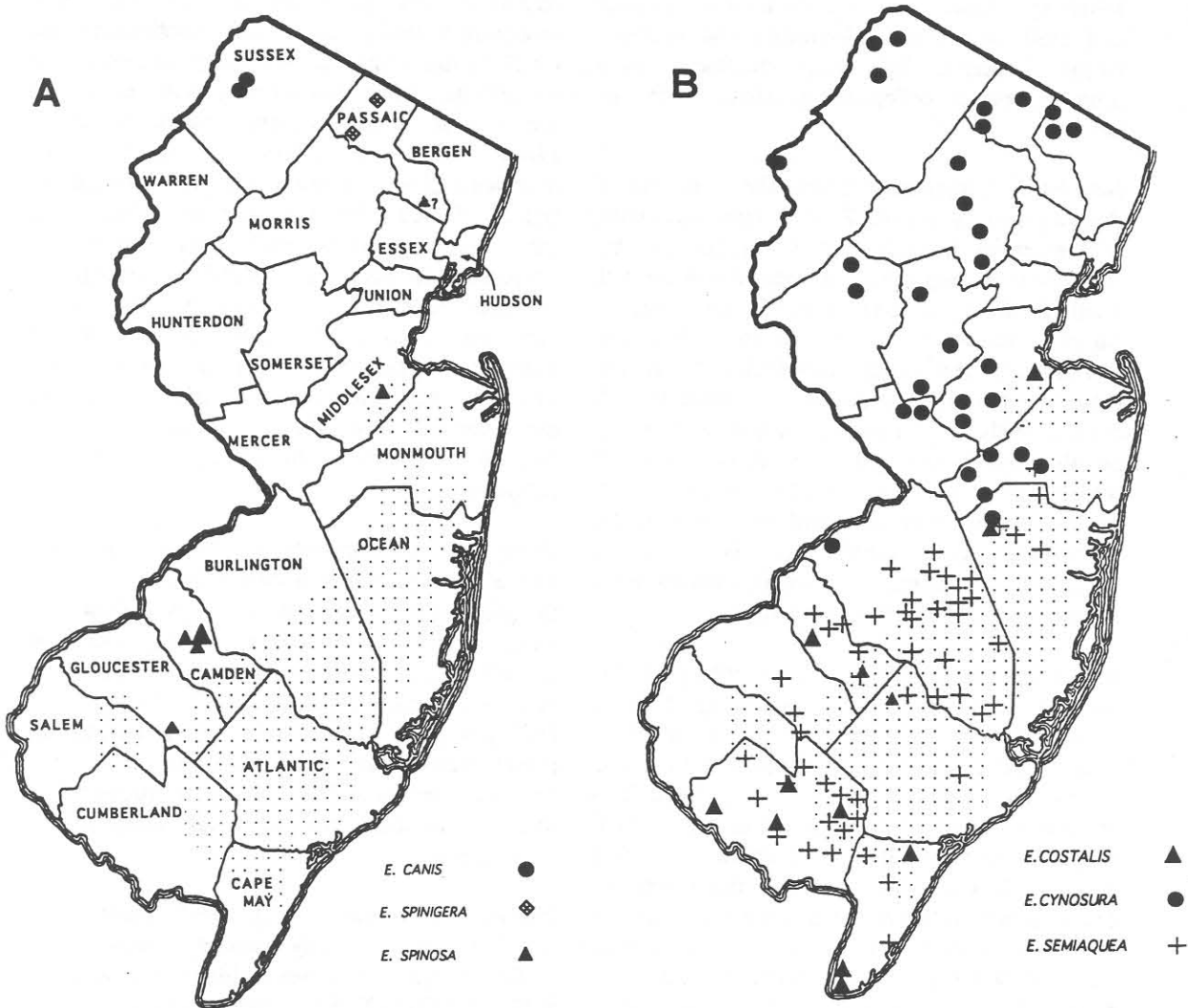


Figure 2: Known distributions of *E. (Tetragoneuria)* spp. in NJ; stippled area indicates approximate extent of the Pine Barrens. Large triangle in A marks location of most recent (1972) record of *spinosa*, stippled triangle with "?" indicates a doubtful record of that species. County names are omitted from B for clarity.

I have seen from there are *semiaquea*, including two misidentified by Calvert as *cynosura simulans*. Because of past confusion by Calvert and others, Fig. 2 includes only records of those two species for which I have examined specimens.

Few genuine *cynosura* from NJ have dark maculation extending even as far as the second antenodal crossvein. In particular, extensive collecting from Middlesex and Mercer Counties southward has revealed no dark-winged individuals that are not referable to *semiaquea*, although maculate specimens do occur in Bergen Co. and possibly in other northern areas of the state. Throughout most of its range, dark-winged (*simulans*-type) *cynosura* are fairly common, although of variable frequency (Kormondy, 1959). I have seen numerous examples from southern DE, northeastern PA, and southeastern NY; on the other hand, most or all specimens from northern DE and southeastern PA apparently are nearly clear-winged, resulting in an area of about 100 km radius, centered on the Pine Barrens, in which only *semiaquea* normally has extensive dark maculation.

Table 1 lists descriptive statistics for morphometric variables describing NJ *Tetragoneuria*. Multivariate analyses of data summarized there reveal substantial concordance with *a priori* categories; this is illustrated in Fig. 3 for the outcome of canonical discriminant analysis. For both males and females a rather clear distinction exists among *cynosura*, *costalis*, and *semiaquea* groups along the axes defined by the first (CNV1) and second (CNV2) canonical variables; the squared distances between group centroids are highly significant ($p < 0.001$) for all pairwise comparisons within each sex. For males, as indicated by standardized canonical coefficients, CNV1 is most strongly influenced by CR (positive loading) and R4 and R6 (negative loading), while for females, CNV1 primarily reflects AB and CR (+) and R4 (-). In both sexes CNV2 is mainly determined by AB (-) and CR (+).

Not surprisingly, inclusion of NJ specimens not readily assignable *a priori*, as well as specimens from other geographic areas, complicates the picture (shown for males in Fig. 4). The use of additional categories of specimens (defined in figure legend) makes it possible to calculate five canonical variables, of which the first three are

significant ($p < 0.001$). In this case the main determinants of CNV1 are CR (+) and R4 (-) in both sexes; of CNV2 AB (-) and CR (+) in both sexes and also R4 (+) in males; of CNV3 R4 (+) in both sexes plus AB (+) in males or VL (+) in females. To calculate values of the canonical variables for comparative purposes, the following unstandardized equations may be applied to the raw variables (note, however, that for calculation of intergroup distances or significance levels the coefficients must be recalculated when additional data are added):

for males,

$$\begin{aligned} \text{CNV1} &= -0.18 \text{ AB} + 4.99 \text{ CR} - 3.82 \text{ RWA} - 18.20 \\ &\quad \text{TR4} - 13.36 \text{ TR6} + 15.05, \\ \text{CNV2} &= -0.68 \text{ AB} + 6.21 \text{ CR} - 13.08 \text{ RWA} + 20.31 \\ &\quad \text{TR4} - 14.36 \text{ TR6} + 8.92, \\ \text{CNV3} &= 0.90 \text{ AB} + 0.060 \text{ CR} + 3.43 \text{ RWA} + 22.08 \\ &\quad \text{TR4} - 7.16 \text{ TR6} - 37.79; \end{aligned}$$

for females,

$$\begin{aligned} \text{CNV1} &= 0.32 \text{ AB} + 4.26 \text{ CR} + 2.43 \text{ RWA} - 27.49 \\ &\quad \text{TR4} - 9.83 \text{ TR6} + 2.32 \text{ VL} + 2.33, \\ \text{CNV2} &= -0.84 \text{ AB} + 7.90 \text{ CR} - 10.68 \text{ RWA} + 7.70 \\ &\quad \text{TR4} + 10.26 \text{ TR6} - 3.26 \text{ VL} + 13.34, \\ \text{CNV3} &= -0.074 \text{ AB} + 1.27 \text{ CR} + 9.64 \text{ RWA} - 6.95 \\ &\quad \text{TR4} + 20.26 \text{ TR6} + 7.88 \text{ VL} - 36.00. \end{aligned}$$

As suggested by Fig. 4, the squared distances between group centroids of clear-winged *cynosura* are significantly different (pairwise comparisons) from all other groups of corresponding sex except dark-winged "*simulans*-type" specimens and a single Colliers Mills male specimen (hereafter "*CM*") that appeared intermediate between *cynosura* and *costalis*. A group of specimens from northeast and east-central MA and northeastern CT, although significantly different as a group from *cynosura* as well as *semiaquea*, overlaps both, but especially *semiaquea*.

The NJ *semiaquea* group differs significantly from all groups of corresponding sex except for *semiaquea* from NC and SC, specimens from Cape Cod and southeastern ME, and 3 female NJ specimens from the Pine Barrens, not assigned to *semiaquea* because, despite their small size and stocky stature, their wings were clear or of intermediate maculation.

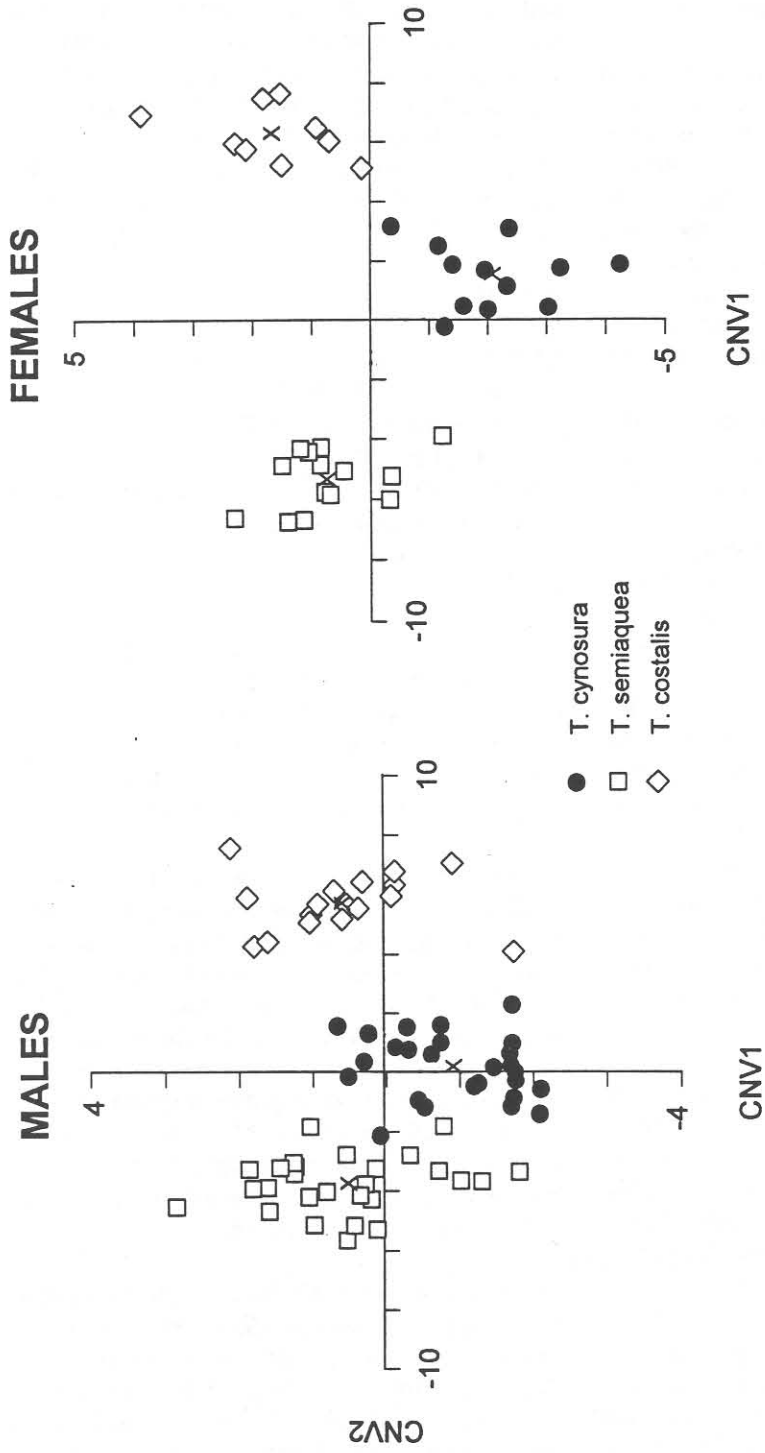


Figure 3: Plot of first (CNV1) vs. second (CNV2) canonical variables for each sex of *E. (Tetragoneuria)* found in southern NJ; X's indicate position of centroid of each group.

Finally, NJ *costalis* differ significantly from all other groups except two MD males previously identified as "*williamsoni*" (a taxon probably synonymous with *costalis*; K. J. Tennessen, pers. comm., 1994) and from the *CM* male noted above. Both sexes differed from *costalis* from FL, although it should be noted that the latter differ from all other groups in approximately the same direction as, but to a greater degree than, NJ *costalis*.

Cluster analysis and discriminant (i.e., SAS PROC DISCRIM) analysis give similar results. For both sexes, NJ and FL *costalis* and MD "*williamsoni*" cluster together and are most different from all other specimens. All clear-winged and *simulans*-type *cynosura* cluster together, with the *CM* male also in that cluster. All NJ and NC/SC *semiaquea* form one cluster, along with the southeastern ME (only males measured) and Cape Cod specimens. The northern MA and CT males are divided about equally between the *cynosura* and *semiaquea* clusters, although the females all cluster with *semiaquea*, despite considerable variation in wing maculation. Two of the Pine Barrens females with reduced maculation cluster with *semiaquea* and one with *cynosura* (the last is the individual in that cluster least clearly separated from *semiaquea*).

Discriminant analysis, in the sense used here, can determine the probability of association of individuals with *a priori* groups in addition to discriminating the groups as a whole. The overall outcome of these calculations is quite similar to the results of the cluster analysis. One male NJ clear-winged *cynosura* and one male NJ *semiaquea* were misclassified, i.e., the analysis based on morphometric properties suggests a closer relationship of the former with the *semiaquea* group and of the latter with the *cynosura* group. I re-examined these two specimens in an effort to determine why they were misclassified. The *cynosura* specimen is unusually small (possibly a developmental accident) and hence resembled *semiaquea* in AB and CR measurements, but not in body proportions. The presumed *semiaquea* was taken with other males and females that were readily classified as *semiaquea*, but it shows no outstanding features that explained its classification as *cynosura*. On the other hand, both in the cluster analysis and the canonical discriminant analysis, it is grouped unambiguously with other *semiaquea*.

Discriminant classification of the specimens not categorized *a priori* also produces outcomes very like those of the previous analyses, except that the *CM* male is classified with *costalis* rather than *cynosura*, and all the Pine Barrens females with reduced maculation are classified with *semiaquea*. As in the cluster analysis, all the Cape Cod and ME specimens, as well as NC/SC *semiaquea*, are closest to *semiaquea* and *simulans*-type specimens to *cynosura*; the other New England specimens are divided between those two categories. The "*williamsoni*" and FL *costalis* specimens are classified with NJ *costalis*. In all these analyses, the discriminant functions on which classification was based are derived only from the NJ specimens classified *a priori*.

Penis morphology apparently does not differ consistently among the populations under study. In particular, I did not find either the whole penis or the first segment in NJ *costalis* to be obviously larger than that of other groups (Tennessen, 1973). It is possible, of course, that careful measurements of a larger sample would reveal useful penile characters.

Likewise the morphology of the cerci does not correspond entirely to groupings based on wing maculation or morphometrics. *Costalis* males differ from those of other groups as described by Tennessen (1977). However, no clear distinction is evident between *cynosura* and *semiaquea*. Tennessen (1973) found the ventral keels on specimens of *semiaquea* from the Carolinas to be much shorter than in typical *cynosura*, and the lateral surface between ventral and lateral keels to be more convex. In NJ, however, this distinction does not hold. Although some NJ *semiaquea* have cerci resembling those described by Tennessen, many appear indistinguishable from those of *cynosura*. Among females, the cerci differ in average length, with *semiaquea* shortest, *cynosura* intermediate, and *costalis* longest (Table 1). The mean lengths of the first two are similar to lengths reported by Tennessen (1973, 1977), but the cerci of *costalis* are much shorter than southern specimens. They are similar to NC specimens considered by Tennessen to be probable *costalis*.

On the other hand, my subjective assessment of the degree of constriction of abdominal segment 3 in males was well correlated with both morphometric analyses and *a priori* assessments of NJ and most

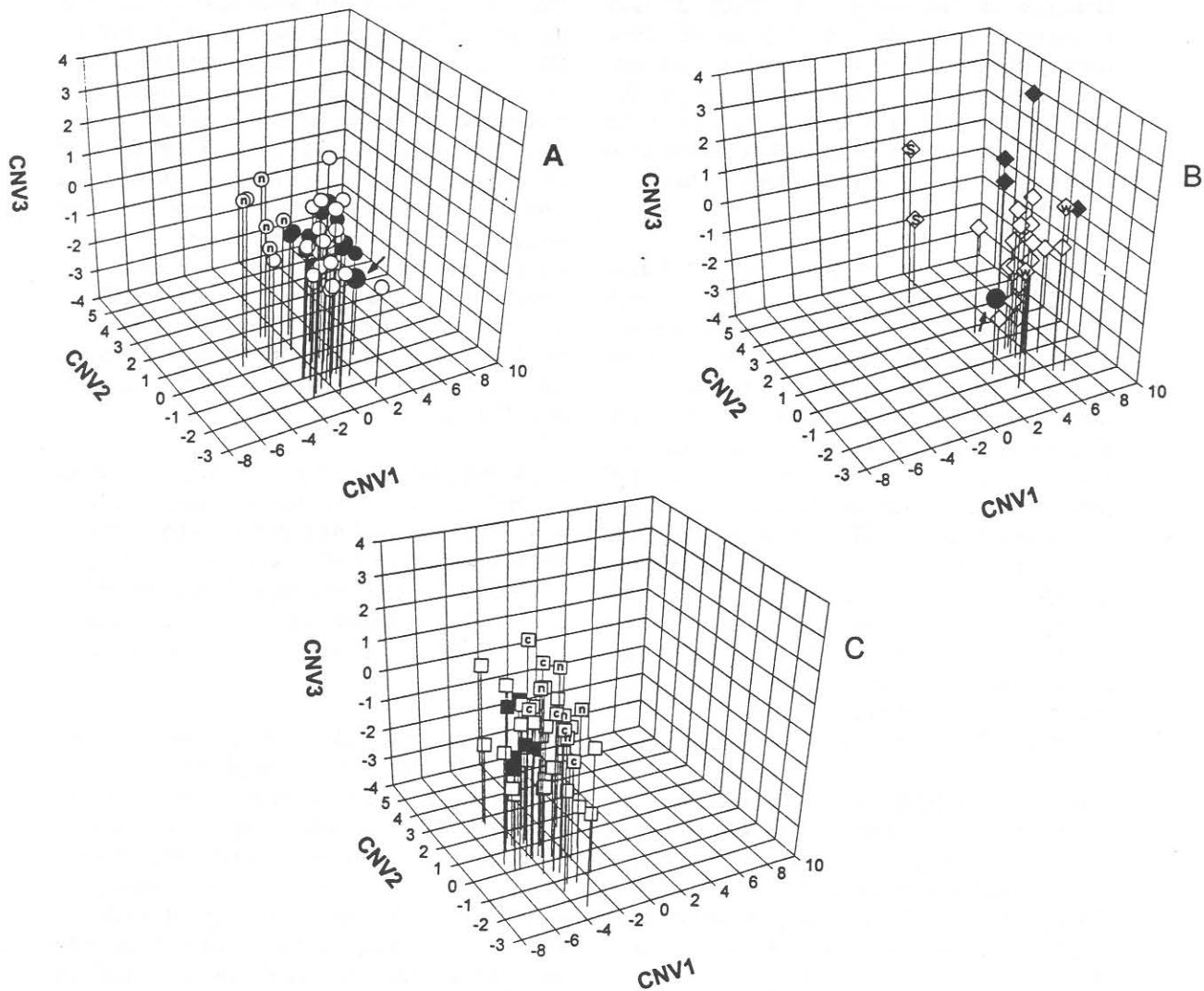


Figure 4: Three dimensional plots of first (CNV1) vs. second (CNV2) vs. third (CNV3) canonical variables for males only of *E. (Tetragoneuria)* spp. from the eastern United States.

A. Specimens of clear-winged *cynosura* from NJ (open circles) and *simulans*-type *cynosura* from FL-ME (closed circles); also includes data for inland New England specimens ("n") and a male, designated "CM" in text, apparently intermediate between *cynosura* and *costalis* (large closed circle and arrow).

B. Specimens of *costalis* from NJ (open diamonds) and FL (closed diamonds); also includes datum for male "CM" (large closed circle and arrow; see A. above) and data for MD *williamsoni* specimens ("w") and for two males of *E. spinigera* ("S"), included to indicate the difference of this well marked species from the taxa studied here.

C. Specimens of *semiaquea* from NJ (open squares) and NC-SC (closed squares); also includes data for coastal ("c") and inland ("n") New England specimens (the last also shown in A).

other specimens. In all of the male *costalis* (including "*williamsoni*") a constriction is very strongly developed (Fig. 1G-I). Males grouped with *semiaquea* have segment 3 nearly parallel-sided, with some appearing actually to have slightly convex sides. *T. cynosura* has a distinct constriction but less pronounced than in *costalis*. These subjective data are reinforced by the related quantity, the ratio of R4 to R6; a low value indicates that the abdomen is relatively more slender toward the anterior end, and this quantity is significantly lower in *costalis* than in *cynosura*, which in turn is significantly lower than *semiaquea* (Table 1).

Females typically follow the same pattern as males, but they are considerably more variable and typically less constricted on segment 3 than the corresponding males; female *costalis*, in particular, often show little narrowing of that segment, although their abdomens are more slender overall than those of other females, as reflected by the higher values of R4 and R6 and the ratio of these quantities (Table 1).

The specimens examined from southeastern New England mostly have relatively short, stocky abdomens and in general, except for their variable hindwing maculation, resemble NJ *semiaquea* at first glance. About half of both sexes showed slight to moderate constriction of abdominal segment 3, however. A number of the specimens were slightly teneral and a little dorso-ventrally compressed, which contributed to the impression of a short, wide abdomen.

DISCUSSION

There have been very few previous attempts, with the exception of Garrison's (1976, 1992) work on *Libellula* and *Tramea*, to use multivariate statistical techniques to resolve taxonomic problems among Odonata, but such approaches offer great promise when qualitative characters are insufficient. In the present case both qualitative and quantitative avenues of analysis point to the distinctness of three taxa of *Tetragoneuria* in southern NJ. Of 136 NJ specimens, only 6 (3 males and 3 females) were ambiguously classified. This suggests that, although a small amount of genetic interchange may occur, the three populations designated here as *costalis*, *cynosura*, and *semiaquea* are effectively isolated reproductively.

No doubt some variation in measured characteristics within each population is developmental rather than genetic in origin, but this should simply add to the unexplained variance in the data.

Two questions remained unresolved, however. First, although *costalis* and *cynosura* apparently differ throughout their range, the distinction between *cynosura* and *semiaquea* in New England may be less constant than in NJ. The question of whether or not these phenotypic groups can be reliably discriminated in that area will require more data, perhaps using different characters, than is available here. Thus their taxonomic status remains uncertain.

If the NJ populations do represent separate taxa, as I think will prove to be the case, then the question of their true identity remains. Are the names applied in the paper heretofore the appropriate ones? The specimens here called *cynosura* apparently are indistinguishable except by wing color from *simulans*-type specimens from ME to FL, supporting their identity as *cynosura*; these data also support those of Tennessen (1973) in identifying "*simulans*" as no more than a color form of *cynosura*, not a geographically distinct subspecies.

New Jersey *costalis* appear very similar to *costalis* from the southeastern US except in their slightly smaller overall size and, especially in females, their markedly shorter cerci (Tennessen, 1973, 1977). The latter nevertheless average significantly longer than those of NJ *cynosura*, and, in fact, the lengths of female cerci do not overlap with those of NJ *cynosura*. Cerci of both sexes are similar to those of NC and SC specimens thought by Tennessen (1977) to be *costalis*; in the same study he presented evidence that cercus length changes clinally, decreasing from south to north at least to NC and TN. Thus the relatively short cerci of the NJ populations, as well as of the MD "*williamsoni*" is not inconsistent with their identification as *costalis*.

The NJ populations identified heretofore as *semiaquea* are the most problematical group. They are not distinguishable from true *semiaquea* from NC and SC on the basis of the morphometric characters analyzed here. On the other hand, the morphology of the male cerci often is more similar to that typical of *cynosura* than that of *semiaquea*

(Tennesen, 1973; personal observation), and the pattern of wing maculation differs consistently from southern populations. In the latter the dark area of the wing normally is distinctly convex postero-distally and extends to the posterior wing margin (occasional specimens may have greatly reduced wing maculation; K. J. Tennesen, pers. comm., 1994). In NJ specimens the spot is essentially triangular and extends only slightly beyond the anal triangle; the midbasal space is usually almost transparent centrally, unlike most southern *semiaquea*, but this character is somewhat variable in both areas. Since no similar populations are known between NJ and southern VA, it is difficult to evaluate the significance of these color differences. If northeastern populations, including those in NJ, that resemble *semiaquea* are eventually shown to be distinct throughout their range from *cynosura*, then they may deserve to be distinguished at least subspecifically from typical *semiaquea*, as suggested by Carle (1982). Pending a resolution of questions raised by possible intergradation in southeastern New England, however, it seems preferable not to name these populations now, but to continue provisionally to refer to them as *semiaquea*.

The biological function of the dark basal wing spot of some *E. (Tetragoneuria)* is unknown. The distribution in southern NJ, of population(s) with very extensive dark maculation (*semiaquea*) geographically surrounded for a considerable distance by populations comprising only individuals with minimal maculation, is striking. Also noteworthy is the observation that in this region morphometric evidence suggests effective reproductive isolation between dark- and clear-winged taxa. It certainly would be worth investigating whether the difference in wing pattern is involved in maintaining reproductive isolation. This might, in fact, be a rare example of character displacement in response to selection against interspecific mate choice (Waage, 1975). One possible explanation of the apparently reduced isolation between *cynosura*-like and *semiaquea*-like populations in New England could be the lack of a sharp distinction between dark-winged and clear-winged forms. Arguing against this, at least as a general phenomenon, is the apparent lack of isolation between clear-winged and *simulans*-type *cynosura*. It is possible, of course, that both morphometric intergradation and occurrence of intermediate wing color types is the consequence rather than the cause of interbreeding. Only careful

behavioral observation, possibly in concert with correlation of molecular-genetic and color characteristics of populations, can elucidate definitively the role of wing color in the biology of these dragonflies.

ACKNOWLEDGMENTS

I am grateful to Nancy Adams (NMNH), Don Azuma (ANSP), Allen Barlow, Bob Barber, Oliver Flint (NMNH), John Michalski, Ken Soltesz, Minter Westfall (FSCA), and Hal White for the loan of specimens and to Ken Tennesen for assistance with identifications. New Jersey Agricultural Experiment Station Publication D-08002-19-94, supported by State funds.

REFERENCES

- Barber, R. D. 1994. Dragonflies and Damselflies of Cumberland County, New Jersey. Cape May Bird Observatory, Cape May, NJ. 38 pp.
- Calvert, P. P. 1900. Order Odonata. In Insects of New Jersey, J. B. Smith (ed.), 27th Annual Report of the State Board of Agriculture (Suppl.). Pp. 66-75.
- Carle, F. L. 1982. A contribution to the knowledge of the Odonata. Ph.D. Dissertation, VPI&SU.
- Davis, W. T. 1913. Dragonflies of the vicinity of New York with a description of a new species. Journal of the New York Entomological Society 21:11-29.
- Davis, W. T. 1933. Dragonflies of the genus *Tetragoneuria*. Bulletin of the Brooklyn Entomological Society 28:87-104.
- Donnelly, T. W. 1992. Taxonomic problems (?) with *Tetragoneuria*. Argia 4(1):11-14.
- Garrison, R. W. 1976. Multivariate analysis of geographic variation in *Libellula luctuosa* Burmeister (Odonata: Libellulidae). Pan-Pacific Entomologist 52:181-203.
- Garrison, R. W. 1992. Using ordination methods with geographic information: species resolution in a partially sympatric complex of neotropical *Tramea* dragonflies (Odonata: Libellulidae). In Ordination in the Study of Morphology, Evolution and Systematics, J. T. Sorenson and R. L. Footitt, (eds.). Elsevier, Amsterdam. Pp. 223-240.
- Kormondy, E. J. 1959. The systematics of *Tetragoneuria*, based on ecological, life history, and morphological evidence. Miscellaneous Publications of the Museum of Zoology, University of Michigan 107:1-79.
- Muttkowski, R. A. 1911. Studies in *Tetragoneuria*. Bulletin of the Wisconsin Natural History Society 9:91-134.
- Muttkowski, R. A. 1915. Studies in *Tetragoneuria*, II. Bulletin of the Wisconsin Natural History Society 13:49-61.
- SAS Institute. 1985. SAS Users Guide: Statistics, Version 5 Edition. SAS Institute, Inc., Cary, NC. 956 pp.
- Smith, J. B. 1910. Order Odonata. In Report of the Insects of New Jersey, J. B. Smith (ed.), Annual Report of the New Jersey State Museum, 1909. Pp. 73-82.
- Soltész, K. 1991. A Survey of the Damselflies and Dragonflies of Cape May County, New Jersey. Cape May Bird Observatory, Cape May, NJ. 54 pp.
- Tennessen, K. J. 1973. A preliminary report on the systematics of *Tetragoneuria* (Odonata: Corduliidae) in the southeastern United States. M.S. Thesis, University of Florida.
- Tennessen, K. J. 1977. Rediscovery of *Epitheca costalis* (Odonata: Corduliidae). Annals of the Entomological Society of America 70:267-273.
- Waage, J. K. 1975. Reproductive isolation and the potential for character displacement in the damselflies, *Calopteryx maculata* and *C. aequabilis* (Odonata: Calopterygidae). Systematic Zoology 24:24-36.
- Walker, E. M. 1966. On the generic status of *Tetragoneuria* and *Epicordulia* (Odonata: Corduliidae). Canadian Entomologist 98:897-902.

Table 1: Descriptive statistics for morphometric characters of populations of *Epithea* (*Tetragoneuria*). Characters are defined in text; data are given as mean \pm S.E. (range).

Sex and Taxon / Location	N ^a	Characters						
		AB	R4	CR	RWA	R6	R4/R6	VL
Males								
<i>cynosura</i> ^b / NJ	29	27.8 \pm 0.23 (25.5-30.0)	2.91 \pm 0.027 (2.65-3.26)	0.97 \pm 0.007 (0.90-1.08)	0.36 \pm 0.005 (0.28-0.44)	0.39 \pm 0.005 (0.33-0.44)	0.95 \pm 0.025 (0.84-1.06)	
<i>cynosura</i> ^c / ME-FL	12	27.9 \pm 0.24 (26.5-29.0)	3.01 \pm 0.014 (2.93-3.12)	0.97 \pm 0.007 (0.95-1.02)	0.37 \pm 0.007 (0.32-0.40)	0.40 \pm 0.011 (0.34-0.46)	0.92 \pm 0.016 (0.85-1.03)	
"CM" ^d / NJ	1	27.5	3.03	0.95	0.30	0.34	0.87	
<i>costalis</i> / NJ	19	29.1 \pm 0.27 (26.5-31.0)	3.34 \pm 0.032 (3.15-3.68)	0.93 \pm 0.006 (0.88-0.98)	0.26 \pm 0.005 (0.22-0.31)	0.30 \pm 0.005 (0.26-0.35)	0.84 \pm 0.024 (0.78-0.93)	
<i>costalis</i> / FL	4	31.6 \pm 0.83 (30.0-33.5)	3.80 \pm 0.14 (3.49-4.13)	0.91 \pm 0.006 (0.89-0.92)	0.26 \pm 0.013 (0.22-0.27)	0.30 \pm 0.006 (0.29-0.32)	0.86 \pm 0.041 (0.75-0.95)	
"williamsoni" / MD	2	28.8 (28.5-29.0)	3.27 (3.08-3.46)	0.92 (0.91-0.93)	0.28 (0.26-0.30)	0.30 (0.28-0.31)	0.95 (0.94-0.95)	
<i>semiaquea</i> / NJ	30	24.7 \pm 0.26 (21.5-27.0)	2.72 \pm 0.026 (2.39-2.97)	1.02 \pm 0.008 (0.94-1.12)	0.48 \pm 0.007 (0.41-0.56)	0.47 \pm 0.005 (0.42-0.53)	1.03 \pm 0.013 (0.94-1.21)	
<i>semiaquea</i> / NC-SC	6	24.2 \pm 0.25 (23.0-24.5)	2.73 \pm 0.30 (2.52-2.94)	1.03 \pm 0.012 (0.98-1.06)	0.51 \pm 0.006 (0.49-0.53)	0.48 \pm 0.010 (0.44-0.51)	1.06 \pm 0.028 (0.96-1.16)	
?? ^e / New England, coastal	6	26.0 \pm 0.45 (24.0-27.0)	2.86 \pm 0.054 (2.76-3.13)	1.01 \pm 0.010 (0.98-1.04)	0.48 \pm 0.012 (0.45-0.51)	0.45 \pm 0.011 (0.41-0.48)	1.06 \pm 0.034 (0.94-1.20)	
?? ^e / New England, inland	9	27.1 \pm 0.38 (25.5-29.0)	2.89 \pm 0.041 (2.66-3.10)	0.97 \pm 0.006 (0.95-1.00)	0.42 \pm 0.015 (0.34-0.48)	0.40 \pm 0.011 (0.34-0.45)	1.04 \pm 0.022 (0.91-1.11)	
Females								
<i>cynosura</i> ^b / NJ	14	27.2 \pm 0.24 (26.0-29.0)	1.80 \pm 0.041 (1.51-2.03)	1.07 \pm 0.007 (1.03-1.12)	0.38 \pm 0.008 (0.32-0.43)	0.36 \pm 0.006 (0.32-0.40)	1.05 \pm 0.025 (0.90-1.19)	2.21 \pm 0.030 (2.09-2.39)
<i>cynosura</i> ^c / ME-FL	3	27.5 \pm 0.50 (26.5-28.0)	1.74 \pm 0.010 (1.72-1.75)	1.06 \pm 0.013 (1.04-1.08)	0.42 \pm 0.023 (0.37-0.45)	0.39 \pm 0.010 (0.37-0.41)	1.06 \pm 0.077 (0.94-1.20)	2.25 \pm 0.083 (2.17-2.42)
<i>costalis</i> / NJ	9	28.8 \pm 0.36 (2.75-31.0)	2.34 \pm 0.054 (2.12-2.55)	1.10 \pm 0.012 (0.97-1.05)	0.30 \pm 0.006 (0.28-0.33)	0.31 \pm 0.007 (0.29-0.34)	1.00 \pm 0.024 (0.83-1.06)	2.10 \pm 0.039 (1.90-2.23)
<i>costalis</i> / FL	1	30.0	3.60	1.00	0.28	0.30	0.92	2.36
<i>semiaquea</i> / NJ	22	24.1 \pm 0.24 (22.0-26.0)	1.59 \pm 0.20 (1.39-1.76)	1.11 \pm 0.006 (1.06-1.15)	0.48 \pm 0.008 (0.43-0.54)	0.45 \pm 0.007 (0.40-0.50)	1.09 \pm 0.022 (0.92-1.20)	1.91 \pm 0.024 (1.67-2.06)
<i>semiaquea</i> / NC-SC	1	22.0	1.31	1.09	0.48	0.48	1.00	1.82
?? ^e / NJ	3	2.45 \pm 0.76 (23.5-26.5)	1.56 \pm 0.058 (1.50-1.68)	1.07 \pm 0.019 (1.04-1.10)	0.44 \pm 0.013 (0.42-0.47)	0.41 \pm 0.002 (0.41-0.41)	1.09 \pm 0.033 (1.03-1.14)	1.94 \pm 0.021 (1.91-1.98)
?? ^f / New England, coastal	3	24.5 \pm 0.29 (24.5-25.0)	1.75 \pm 0.012 (1.73-1.77)	1.09 \pm 0.019 (1.06-1.12)	0.48 \pm 0.013 (0.46-0.51)	0.48 \pm 0.026 (0.44-0.53)	1.01 \pm 0.031 (0.96-1.06)	2.13 \pm 0.015 (2.11-2.16)
?? ^f / New England, inland	4	25.1 \pm 0.31 (24.5-26.0)	1.76 \pm 0.026 (1.68-1.79)	1.10 \pm 0.019 (1.07-1.16)	0.45 \pm 0.015 (0.42-0.47)	0.42 \pm 0.007 (0.41-0.44)	1.05 \pm 0.044 (0.96-1.10)	2.10 \pm 0.020 (2.06-2.14)

^a Number of specimens examined; owing to distortion or breakage, sample size for some characters may be 1 or 2 less.

^b Clear-winged *cynosura* from NJ; see text.

^c Specimens of *cynosura* from the eastern U.S. outside NJ, with extensive dark wing maculation ("*simulans*- type"); females were from FL (2) and central ME (1).

^d Specimen apparently intermediate between *cynosura* and *costalis*, collected at Collier's Mills, NJ; see text.

^e Specimens from NJ Pine Barrens with strikingly reduced wing maculation.

^f Specimens from southeastern New England with broad abdomens and variable wing maculation; "coastal" specimens were from southeastern coastal ME (Lincoln Co.; males only) and Cape Cod; "inland" specimens from Tolland Co., CT, and Norfolk and Middlesex Co.'s, MA.

BULLETIN OF AMERICAN ODONATOLOGY

VOLUME 1

THE ODONATA OF NEW YORK, Thomas W. Donnelly 1(1): 1-27

DISTRIBUTION OF DRAGONFLIES AND DAMSELFLIES (ODONATA) IN FLORIDA, Sidney W. Dunkle 1(2): 29-50

MORPHOLOGICAL AND ECOLOGICAL DIFFERENCES AMONG SPECIES OF *LADONA* (ANISOPTERA: LIBELLULIDAE), Michael L. May 1(3): 51-56

COMPORTAMIENTO REPRODUCTIVO Y POLICROMATISMO EN *ISCHNURA DENTICOLLIS* Burmeister (Zygoptera: Coenagrionidae), [Reproductive behavior and polychromatism in *Ischnura denticollis*], with English summary
Alejandro Córdoba Aguilar. 1(3): 57-64

A CHECKLIST OF THE ODONATA OF THE DOMINICAN REPUBLIC BY PROVINCE, Jerrell James Daigle 1(4):65-69

ODONATA DE LA SIERRA DE HUAUCHINANGO, PUEBLA, MEXICO [Odonata of the Sierra de Huachinango, Puebla, Mexico], José A. Gómez Anaya y Rodolfo Novelo Gutiérrez 1(4):71-73

VOLUME 2

LA NAYADE DE *ARCHILESTES LATIALATUS* DONNELLY, 1981 (ZYGOPTERA: LESTIDAE) [The naiad of *Archilestes latialatus* Donnelly, 1981], R. Novelo-Gutiérrez 2(1): 1-7

DESCRIPCIÓN E HISTORIA NATURAL DE LAS LARVAS DE ODONATOS DE COSTA RICA. III: *GYNACANTHA TIBIATA* (KARSCH 1891) (ANISOPTERA, AESHNIDAE) [Description and Natural History of the Odonata Larvae of Costa Rica. III: *Gynacantha tibiata* (Karsch 1891)(Anisoptera: Aeshnidae)], Alonso Ramírez 2(1): 9-14

DESCRIPTION OF THE NYMPH OF *EPITHECA (TETRAGONEURIA) SPINOSA* (HAGEN) (ODONATA:CORDULIIDAE), K. J. Tennessen 2(2): 15-19

THE LARVA AND ADULT MALE OF *SOMATOCHLORA GEORGIANA* WALKER (ODONATA: CORDULIIDAE), Jerrell J. Daigle 2(2): 21-26

***MACROMIA ILLINOIENSIS* AND *GEORGINA*: A STUDY OF THEIR VARIATION AND APPARENT SUBSPECIFIC RELATIONSHIP (ODONATA: CORDULIIDAE)**, Thomas W. Donnelly and Kenneth J. Tennessen 2(3): 27-61

THE SUBGENUS *TETRAGONEURIA* (ANISOPTERA: CORDULIIDAE: *EPITHECA*) IN NEW JERSEY, Michael L. May 2(4): 63-74