MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 107

The Systematics of *Tetragoneuria*, Based on Ecological, Life History, and Morphological Evidence (Odonata: Corduliidae)

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ANN ARBOR
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
SEPTEMBER 28, 1959

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THE SYSTEMATICS OF *TETRAGONEURIA*, BASED ON ECOLOGICAL, LIFE HISTORY, AND MORPHOLOGICAL EVIDENCE

(Odonata: Corduliidae)*

INTRODUCTION

THE GENUS *Tetragoneuria* Hagen[1] comprises a group of North American dragonflies that is of wide occurrence in the temperate, deciduous-forest biome and the southern part of the taiga biome. Its members are of medium size, brown to olive with dull yellowish markings, and have an exceedingly hairy thorax. Short erect black hairs sparsely cover the face, the labrum and frons of which are suffused with yellow. Hair on the thorax is whitish and sufficiently dense to more or less obscure the color pattern of black markings on carinae and sutures. Wing markings vary both intra- and interspecifically as does the transparency of the membrane; however, venation is quite uniform. The predominantly black abdomen is scantily hairy and more or less constricted at the third segment. Anal appendages are black; the subgenital plate of the females is brownish and deeply bifurcate. The form of the anal appendages has been the chief character of distinction. Classification of the species presents many uncertainties, especially with regard to the females. Fourteen taxa have been described, five of which are reported from the Great Lakes region, four of them as species and one as a subspecies. Aside from descriptions of the last larval instar of most of the species, nothing has been known of the life history of these dragonflies; their ecology has been almost unstudied.

The present paper embodies the results of a four-year study (1953-1956), which was undertaken to learn as much as possible about the Tetragoneurias in Michigan and to establish, by means of field and laboratory methods, a procedure for investigating other members of the genus. In particular, it was sought to (1) evaluate the reliability of the taxonomic characters heretofore used to separate the species, (2) determine what valid taxonomic entities occur in the Great Lakes region and their separating characters as immatures and imagos in both sexes, (3) analyze the variation of these forms, and (4) describe their life history and ecology.

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Accepted for publication August 15, 1958.

[1] E. M. Walker has informed me that he will shortly publish his conclusion that *Tetragoneuria* Hagen and *Epicordulia* Selys are congeneric with the Palearctic *Epitheca* Burmeister, which has priority. I concur in this view but wait the appearance of Walker's paper before changing from the present usage.

Acknowledgments

The author recognizes the varied assistance that made this investigation possible. Special thanks are due to the Insect Division of the Museum of Zoology of the University of Michigan (UMMZ) for permission to use the Williamson-Kennedy library and collection of Odonata and to Professor Theodore H. Hubbell, Director of the Museum of Zoology, for supervising the investigation and for his suggestions and criticisms of the manuscript. The following institutions loaned specimens: Academy of Natural Sciences of Philadelphia (P. P. Calvert and J. A. G. Rehn), Boston University (A. G. Humes), Carnegie Museum (G. Wallace), Michigan State University (R. Fischer), Milwaukee Public Museum (K. W. MacArthur), Museum of Comparative Zoology (P. J. Darlington, Jr.), and U. S. National Museum (R. Kellogg). Valuable comments on various phases of the study or pertinent records came from Mrs. Leonora K. Gloyd and Drs. I. J. Cantrall, F. C. Gates, F. F. Hooper, H. B. Hungerford, M. E. Jacobs, J. W. Leonard, B. E. Montgomery, E. M. Walker, and M. J. Westfall, Jr. Mr. William L. Brudon prepared the plates; Miss Elsa Hertz typed the manuscript. My wife, Peggy Hedrick Kormondy, helped to collect, rear, and prepare specimens for study, in addition to assisting in the preparation of illustrations. To all these persons, and to others who aided in various ways, I wish to express my grateful appreciation and thanks.

MATERIALS AND METHODS

At the outset of this study the UMMZ collections contained the following specimens from Michigan: *Tetragoneuria cynosura* (Say) and *T. cynosura simulans* Muttkowski, 275; *T. spinigera* (Selys), 170; and *T. canis* MacLachlan, 13. The only examples of *Tetragoneuria morio* Muttkowski were the allotype female and a paratypic male, both from Maine. With the exception of moderate-sized samples from Washtenaw, Roscommon, and Otsego counties, the first three species were represented by only one or a few individuals and these were from scattered localities. Since the Museum material was obviously inadequate for the purposes of this investigation, survey and collecting trips were made to all parts of the state, except the southwestern quarter of the Lower Peninsula, during the field seasons of 1953 through 1956. In all, some 280 *cynosura*, 150 *spinigera*, and 75 *canis* adults were added to the collections. Observations on weather, vegetation, and ecology were recorded in the field.

Collecting Methods

Immature stages and eggs were taken by a dip net; a pan with a No. 30 mesh screen bottom facilitated their rapid examination. A triangle bottom dredge (Welch, 1948) and an Eckman dredge were used in quantitative sampling at Douglas Lake. Eggs and larvae were transported in widemouth jars half-filled with water and containing sufficient vegetation to give protection from injury and predation. On the longer field trips the bottles were placed in a portable ice chest to prevent oxygen depletion and to slow down metabolism and feeding.

Observational Methods

Marking-recapture studies on *Tetragoneuria cynosura* were conducted at Douglas Lake and at First Sister Lake. Individuals were identified with white oil paint. At Douglas Lake, the code of marking was according to the Borror method (1934), in which one to three dots of paint are placed at one or more of four transverse positions on the wing, the number of dots in each of the four positions making a four-digit number. The maximum number of individuals which can be marked in this fashion is 1020 when the four wings are used. A different coding system, suggested by I. J. Cantrall, was used successfully at First Sister Lake. By this system more than 50,000 individuals can be marked using only one wing. The right hindwing is considered divided into sixteen spaces as if by four longitudinal and four transverse parallel lines.[2] Four longitudinal rows of spaces result (wing terminology follows Borror, 1945): (1) the costal space between the costa and subcosta to the nodus and extending to the wing tip; (2) the median space between the fused radius and medius and the fused cubitus and analis to the arculus and extending to the wing tip; (3) the cubitoanal space between the fused cubitus and analis and the secondary analis to the triangle and extending to the wing tip; and (4) the middle third of the anal field and extending to the wing tip. Location of transverse lines are: (1) at the first antenodal of the first series; (2) at the nodus; (3) midway between the nodus and stigma; and (4) at the stigma. As in manual punch-card systems the successive spaces in a given row, proceeding distad from the wing base, are numbered 1, 2, 4, and 8 and are used in additive combination. Comparison of the Borror method and the Cantrall method demonstrates that the difference consists in the assigning of numbers to spaces rather than having each dot represent the integer one, thus the greatly enlarged potential involves no great increase in painted spots and in possible interference with wing action.

The technique of marking as a means of studying individuals and populations of dragonflies has been criticized by Mittelstaedt (1950), because large dragonflies frequently suffer damage to the wings or to the delicate orientation mechanism when captured. Jacobs (1951, 1955) and Moore (1952) avoided this difficulty by squirting oil paint on free individuals and recording the resulting pattern. Their method is not adapted to large numbers of individuals. My experience indicates that Mittelstaedt's criticisms have little validity when medium-sized dragonflies such as Tetragoneurias are studied. Inspection of a series of 130 individuals after capture for marking revealed no wing breakage and none of them showed any flight disorientation upon release; only two died from injury and that was due to decapitation.

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[2] In narrow-winged Odonata there is usually room for only three longitudinal rows.

Culture Methods

Eggs were cultured at a room temperature of about 70°F. in partly covered 5 x 5 x 3-inch containers filled and replenished with tap water which had been allowed to stand 24 hours. Two methods of raising the immatures were tried on successive years. The first year fifteen newly hatched larvae from each culture were placed each in a separate 1-inch covered Stender dish. Each was transferred, at the ninth stadium to a 2-inch covered Stender dish, and in the latter part of the last stadium, to 5 x 5 x 3-inch dishes; a pillow cage, open at the water end, was inserted in each dish to entrap the emerging individual. The second year, five hatchlings were placed in each of four 2-inch Stender dishes; survivors to the third instar were isolated and reared. During the early stadia of larval development only tap water that had stood exposed 24 hours was added as needed; in the later, fresh tap water was used or the water was completely exchanged, with no untoward effects. Although the two methods are equally effective, that used the second year is the more efficient in handling larger population samples.

The first year the young larvae were fed on plankton; the second, they were fed protozoans. In both years third and fourth instar larvae were fed various microcrustacea (including *Daphnia* and *Cyclops*) and amphipods. After reaching the fifth stadium all the larvae were fed exclusively on tubificid worms. These worms are easily reared by the method described by Krull (1924). In raising them, it was not necessary to use running water as Krull recommends; tap water served effectively. Potato slices buried in the mud concentrated the worms, and artificial heat increased the rate of development.

Larvae collected in the field were cultured in individual containers as described above for those reared from eggs. Exuviae of the instars of each individual were stored separately in 75 percent alcohol.

Measurements and Statistical Methods

Each adult was initially analyzed for thirty-eight mensurable and meristic characters. Preliminary inspection and testing eliminated approximately half as unsuitable for comparative purposes. Each larval stage was analyzed for thirty-five mensurable and meristic characters. Measurements on all individuals were made with an ocular micrometer calibrated at 18x and 27x for the adults, and at 30x and 45x for the larvae, which were temporarily mounted in alcohol. Analyses of bilateral structures were made on the right side of the body. Ocular-micrometer readings were converted into millimeters. In adults, a centimeter standard rule was used to obtain the lengths of the wings, body, and abdomen; since these characters vary by contraction and expansion of their nonsclerotized sutures, more precision would have been meaningless.

Adult characters analyzed (measurements as described):

Head width. — Maximum dorsal at eye level.

Tibia length (pro-, meso-, and metathoracic). — Maximum along lateral mid-line.

Femur length (metathoracic). — Maximum along lateral mid-line.

Substigmal to nodus distance (fore- and hindwing). — First cross vein in postnodal series to nodus.

Stigma length. — Along costa in forewing.

Stigma width. — Along proximal edge in forewing.

Forewing length (in cm.). — Maximum ventral from tip to base.

Hindwing length (in cm.). — Maximum ventral from tip to base.

Total length (in cm.). — Maximum middorsal from anterior aspect of head to distal end of anal appendages.

Abdomen length (in cm.). — Maximum middorsal from anterior transverse carina of segment 1 to tip of appendages.

Abdominal segment length (segments 3, 6, and 9). — That of supplementary lateral carina of tergum, from anterior to posterior transverse carina.

Abdominal segment width (segment 6). — Mid-transverse ventral from supplementary lateral to ventral carina.

Superior anal appendage length. — Maximum mid-lateral from base to tip (in *canis* measured as a straight line from base to tip of declined distal portion).

Inferior anal appendage length. — Maximum mid-lateral from base to tip.

Vulvar length. — Maximum mid-ventral of right process from base to tip.

Larval characters analyzed (head width, pro-, meso-, and metathoracic tibia length, and metathoracic femur length, characters that are the same as in the adult, are not included; measurements as described; terminology for the labium follows Corbet, 1953):

Antennal-segment length (segments 1 to 7). — Mid-lateral.

Palpal-setae count. — Number on outer border of labial palpus (= lateral lobe of labium, *auct.*) exclusive of movable hook.

Premental-setae count. — Setae on labial prementum (= mentum, *auct.*), in two series: (1) long lateral setae; (2) short medial setae.

Head length. — Maximum middorsal.

Eye width. — Maximum dorsal.

Dorsal head-knob height. — Mid-lateral above epicranium.

Forewing-sheath length. — Dorsal along medial carina.

Metathoracic tarsus length (tarsi 1 to 3). — Maximum mid-lateral, posterior aspect.

Abdomen length. — Mid-ventral from anterior transverse carina of abdominal segment 1 to posterior transverse carina of 9th or 10th sternite, whichever is longer.

Abdominal-segment width (segments 3, 6, and 9). — Ventral along posterior transverse carina from right to left.

Abdominal-segment length (segments 3, 6, and 9). — Mid-ventral from anterior to posterior transverse carina of sternite.

Total length. — Maximum middorsal from anterior tip of relaxed labium to line joining tips of lateral spines of 9th segment or to tips of anal appendages, whichever is longer.

Superior anal-appendage (epiproct) length. — Middorsal from base to tip.

Inferior anal-appendage (paraproct) length. — Mid-ventral from base to tip.

Lateral anal-appendage (cercus) length. — Mid-lateral from base to tip.

Lateral-spine length (abdominal segments 8 and 9). — Middorsal from base of tergite to tip.

Distance between lateral spines of 9th abdominal segment. — Dorsal between medial aspects of tips of spines.

Standard statistical procedures were used to derive the mean ($\bar{X}$), standard deviation (S.D.), coefficient of variability (C.V.), and standard error (S.E.). The significance of difference in the means of two populations is measured by the coefficient of significance (C.S.) and is the difference in the means divided by the square root of the sum of the squared standard errors of the means (Simpson and Roe, 1939). The coefficient of difference (C.D.) is the difference in the means divided by the sum of the standard deviations of the means (Mayr, *et al.*, 1953). The Brooks-Przibram method and theoretical ratio ($1/1.26^n$) were used in the analysis of growth rate. Chi Square was used to analyze frequency distribution of the sex ratio. Standard statistical tables were employed, and calculations were made with an electric calculating machine or, where permissible, with a slide rule.

DESCRIPTION OF REGION

The land surface of Michigan has been determined to a very great extent by the form and distribution of the deposits of the last glacial retreat. Typical of most of the Lower Peninsula and the eastern half of the Upper Peninsula are a gently undulating surface and incomplete drainage; the western highlands of the Upper Peninsula have a more rugged topography, but there also drainage is incomplete. Throughout the state, especially in the morainic districts, are many lakes, ponds and swamps, some of them extensive; their characteristics are discussed by Scott (1931). In the following discussions, the use of the terms "bog" and "bog lake" is in the sense of Dansereau (in Dansereau and Segadas-Vianna, 1952).

The mean annual temperature of the state is 45° F.; mean annual precipitation is 31 inches, with about half occurring from May to October (White, 1951). Climographs of the parts of Michigan with which this study is concerned are given in Figure 1. Data are from U. S. Weather Bureau records for the localities cited. According to Thornthwaite (1931, 1948) the Upper Peninsula and the northeast part of the Lower Peninsula are characterized by a humid microthermal climate with a high percentage of potential evapotranspiration during the summer months (climatic type $B_2 rC'_2 b_1$). The remainder of the state has a less humid mesothermal climate with a lower percentage of potential evapotranspiration (climatic type $B_1 rB'_1 b_2$).

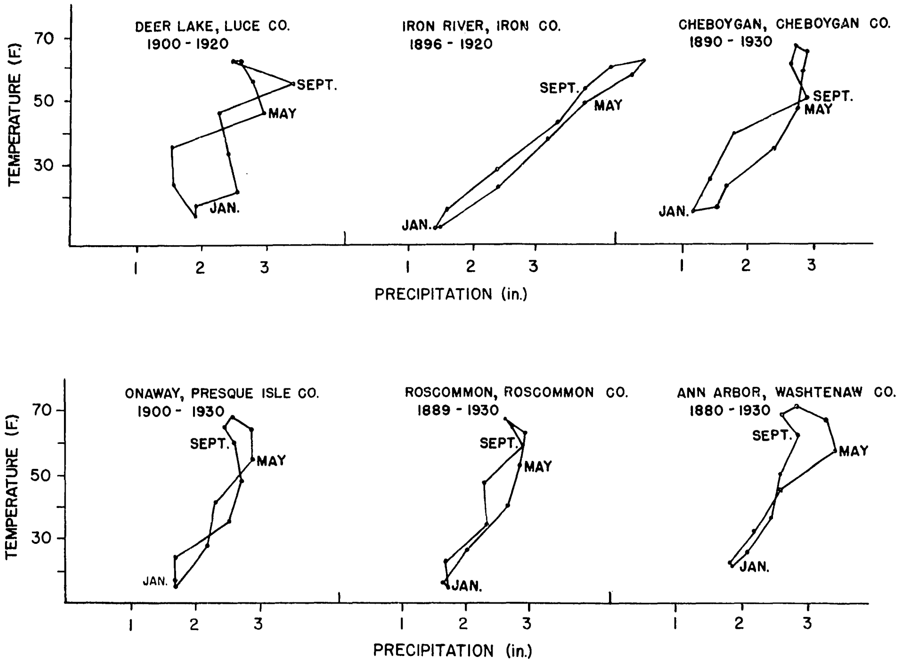
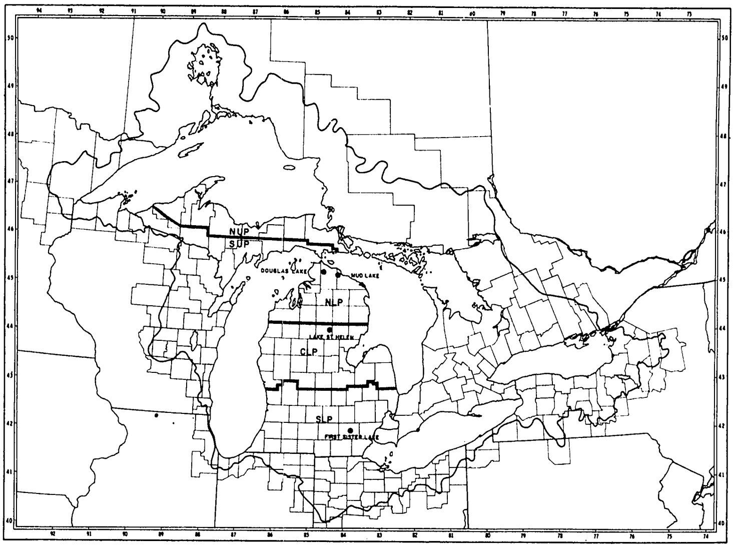


Fig. 1. Climographs of six regionally representative localities in Michigan. Data from U. S. Weather Bureau records.

Study Areas

Douglas Lake, Cheboygan County. — Douglas Lake (Map 1) is part of the Cheboygan River watershed. Morphometric data of the lake are as follows: area, 5.8 sq. mi.; maximum length, 3.8 mi.; maximum width, 2.3 mi.; maximum depth, 89 ft.; mean depth, 17.9 ft. (Welch, 1927). The lake is fish-shaped, oriented northwest-southeast, and receives the bulk of its water from Lancaster Lake to the north by way of Bessey Creek; additional water enters it by way of Beavertail Creek in North Fishtail Bay and by runoff. The study area (1953) was restricted to the shore and shoal of Maple Bay, which occupies the southwest part of the lake at the Maple River outlet to Burt Lake. The shoreline of the bay exceeds one mile and the shoal extends out more or less uniformly for one-half mile except for a small 10-foot depression a third of a mile from shore. Its substrate is a mixture of sand and marl, the marl being of considerable depth in many places.

The vegetation of the bay is essentially homogeneous. Rushes *(Scirpus validus, S. americanus,* and *S. acutus)*, sedges (*Carex* spp.), and spike rush (*Eleocharis* sp.) form a more or less continuous emergent zone varying in width from 5 to 30 feet. A small colony of cattail *(Typha latifolia)* is at the entrance to a beach pool at the eastern end and clumps of an alga (*Chara* sp.) are occasional throughout. Floating parts of bladderwort (*Utricularia* sp.), pondweeds (*Potamogeton* spp.), hornwort (*Ceratophyllum*



Map 1. Great Lakes drainage basin, showing regional divisions of Michigan and major study areas mentioned in the text. Chart symbols: NUP, Northern Upper Peninsula; SUP, Southern Upper Peninsula; NLP, Northern Lower Peninsula; CLP, Central Lower Peninsula; SLP, Southern Lower Peninsula.

sp.) and watermilfoil (*Myriophyllum* sp.) were often entrapped among the stems of the emergents. There is virtually no free beach, as the narrow shrub border of red osier *(Cornus stolonifera)*, alder *(Alnus rugosa)*, and willows (*Salix* spp.) abuts the usual waterline. Branches of these shrubs overhang the water in such a way as to provide numerous natural divisions along the shore. Maple *(Acer saccharum)*, aspens *(Populus grandidentata* and *P. tremuloides)*, and paper birch *(Betula papyrifera)* growing back of the shrub zone, form an almost unbroken canopy 40 feet overhead.

Climatic conditions affecting Douglas Lake are like those shown for Cheboygan (Fig. 1), which is 14 miles to the east. The summers differ only in being slightly drier (Gates, 1937); 1953 was a much wetter season than usual (Gates, MS). The lake lies in Thornthwaite's microthermal zone (C'_2). Several chemical analyses of the Maple Bay water were made; all samples were taken 1 inch below the surface. The data obtained on July 9, 1953 are typical: O_2, 10.08 ppm.; pH, 8.6; Phth.Alk., 6.4 ppm.; M.O.Alk., 121 ppm.; Conductivity, 220; Water Temp., 22.5°C.; Air Temp., 21°C.

Douglas Lake is essentially a eutrophic marl lake, as it has an abundance of nutrients and relatively high organic productivity. Gates (1942), when he pointed out the bog potentialities, referred particularly to a mat of *Carex lasiocarpa*, a bog incipient, in Maple Bay. No mat was present in the area which I studied. Bog potentials, boglike conditions, and true bogs are frequently encountered in the northern half to two-thirds of Michigan and result primarily from the poor drainage and cooler climates prevailing.

First Sister Lake, Washtenaw County. — This lake (Map 1) is at the west city limit of Ann Arbor, and is part of the Huron River watershed. Morphometric data available[3] are as follows: area, 3.5 acres (0.005 sq. mi.); length, 600 ft.; width, 300 ft.; maximum depth, 20 ft.; mean depth, 15 ft. The lake is oval and oriented northeast-southwest. It receives most of its water from subterranean springs near the center, additional water entering as seepage from Second Sister Lake, to the southwest, and by runoff. An intermittently connected outlet to Honey Creek and, thence, to the Huron River is in the southwest. In general, the bottom slopes uniformly to the 15-foot level, but toward the southwest end a small 20-foot depression is in the center. For some 60 feet from shore the substrate is fibrous peat; the rest is pulpy peat and marl, except that marl is lacking in the depression and in certain scattered areas in the southwest.

The area studied (1954) was along the shore of the southern portion and on the open water of the lake. Dense thickets surrounding the eastern and western shores, and the soft porous nature of the substrate in the northern parts, precluded effective work in those sections.

Vegetation of the lake is fairly well zoned and is essentially uniform on all sides. A narrow near-shore belt of sedge (*Carex* sp.), spike rush (*Eleocharis* sp.), and cattail *(Typha latifolia)* is followed lakeward by a belt of water lilies *(Nymphaea odorata* and *Nuphar advena)* about 20 feet wide; and that in turn is succeeded by a more or less open-water zone, in which various pondweeds (*Potamogeton* spp.) grow in the deeper water. On the northeast shore a dense, wet, shrub thicket abuts the near-shore zone, while to the south there is an extensive graminoid marsh ending in a narrow but dense growth of willow (*Salix* spp.) at the water's edge. Along the mid-part of the western shore a resilient floating mat of sedge, typha, and moss (*Sphagnum* sp.), about 25 feet wide, grades sharply into an extensive swamp forest.

Climatic conditions are presumably the same as at Ann Arbor (Fig. 1). The season of 1954 was much wetter than usual. First Sister Lake lies in Thornthwaite's mesothermal zone (B'_1). Results of a water analysis made on January 22, 1942, by the Institute for Fisheries Research, are as follows: O_2, 11.4 ppm.; pH, 7.4; Phth.Alk., 0.0 ppm.; M.O.Alk., 111.0 ppm. Not enough is known about this lake to assign it to a lake type, but the poor drainage, the presence of a vegetation mat, and a fibrous peat substrate are good indicators of bog conditions. Tentatively, the lake is considered to be moderately eutrophic with considerable bog potential.

Mud Lake, Presque Isle County. — This lake (Map 1) lies about one and one-half miles west of Hammond Bay, Lake Huron, and is part of the Ocqueoc River watershed. It is elliptical, about two-thirds of a mile long and a quarter of a mile wide, and oriented north-south. A false bottom of colloidal nature was observed 3 feet below the surface. Mud Lake receives the bulk of its water from bog-swamp areas to the northwest; the surrounding terrain is of such low relief and the sandy soil so porous that little runoff probably occurs; the outlet at the south end connects with Orchard Lake. The contour and surrounding topography strongly suggest

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[3] Institute for Fisheries Research, Michigan Department of Conservation.

that the lake originated as a shallow impoundment of the river. The substrate along the east border of the open water is fibrous peat.

The study area (1954, 1955) extended along the east and west sides of the lake, over open water, and along the east shoreline. The vegetation of the lake differs markedly on the two shores. The eastern shore is a graminoid sward, some 100 feet wide, which consists of hummock-forming sedge (*Carex* sp.), its homogeneity broken by a few scattered willows (*Salix* spp.) and cinquefoil (*Potentilla* sp.); substrate between the hummocks is cohesive and resilient. Shoreward from the sedge there is a jack pine *(Pinus Banksiana)* woods on a sandy soil. The western side is bordered by a floating, resilient mat, some 150 feet wide, in which leatherleaf *(Chaemedaphne calyculata)* is dominant and moss (*Sphagnum* spp.) prevalent, and beyond which black spruce *(Picea mariana)* and tamarack *(Larix laricina)* form the beginning of a bog forest. The open water has only occasional and small discontinuous clusters of pondweeds (*Potamogeton* spp.) and water lily *(Nuphar advena)*.

The nearest place for which climatic data are available is Onaway (Fig. 1), some 12 miles southwest. The climate at Mud Lake is doubtless somewhat different, for it is not only nearer to Lake Huron but lies in an extensively forested area. If one accepts the Onaway data, spring precipitation in the Mud Lake area is greater than at Cheboygan and Douglas Lake. The lake lies in Thornthwaite's more humid (B_2) microthermal zone (C'_2). No chemical analyses are available for Mud Lake, but the ericaceous floating mat, the fibrous peat substrate, the false bottom of accumulated colloids, and the brownish water are characteristic of a dystrophic or bog lake.

Lake St. Helen, Roscommon County. — Although this lake (Map 1) was not intensively studied, interesting observations on *Tetragoneuria* were made there and in the surroundings throughout the period of investigation. Near Lakeview, on the northeast section of the lake, there is a shrub border of willow (*Salix* spp.) in direct contact with the water. The emergent rush *(Scirpus)* and sedge *(Carex)* zones are narrow and the water-lily zone extensive; the substrate is noncohesive, porous, and of peatlike texture and appearance. A bog of leatherleaf, tamarack, and black spruce lies to the north at the Cedar Creek inlet. No morphometric or chemical data are available for this lake. Climatically, it is comparable to but probably cooler than Roscommon (Fig. 1) to the northwest; it lies in Thornthwaite's microthermal zone (C'_2). The part of the lake where collecting was done is more boglike than the others, which appear closer to the eutrophic type.

ECOLOGY OF MICHIGAN *TETRAGONEURIA*

In what follows, equal and parallel treatment could not be accorded every aspect of each species. Material available and observations were, for the most part, more adequate for *cynosura*. Hence, the fuller account there and, in some instances, anticipation of matter properly belonging under *spinigera* or *canis*. Occasionally, the reverse is true.

Tetragoneuria cynosura (Say)

The Adult

Season

Although earliest and latest records for *Tetragoneuria cynosura* in Michigan (May 6 and July 28) point to a length of season of approximately 10 weeks, when data were treated by regions, it became evident that the flight period is shorter, in certain parts of the state much shorter, than this (see dates of capture, tabulated below; also, Map 1 for regional divisions of the state).

Region	Earliest Date	Latest Date	Interval in Weeks
Northern Upper Peninsula	June 8	July 28	7.0
Southern Upper Peninsula	June 14	July 9	3.5
Northern Lower Peninsula.	June 13	July 13	4.3
Central Lower Peninsula.	June 3	July 8	5.0
Southern Lower Peninsula	May 6	July 1	8.0

While capture data suggest that the flight period in a given region is 4 to 8 weeks, since the records are not for a single season or for single localities, the inclusive dates do not necessarily represent the flight period at any time or particular place. For example, the interval between capture of first and last adults in the 1954 season at First Sister Lake was 4½ weeks, but there is a lapse of a week between the time of initial emergence and the appearance of the first mature adult flying over the lake. Hence, the actual season at First Sister Lake, therefore, must have extended from May 25 (date of initial emergence) to July 1 (date last adult observed) for a total of 5½ weeks.

Arranged by regions, as above, capture data indicate a northward trend in progression of season for the species. Observations made during four seasons corroborate the inference that a seasonal progression correlated with increase in latitude does exist. In 1954, to cite an example, the season began the last few days in May in the southern Lower Peninsula, about a week later in the central Lower Peninsula, two weeks later in the northern Lower Peninsula and southern Upper Peninsula, and three weeks later in the northern Upper Peninsula.

Sex Ratio and Emergence Rate

Sex ratio. — With few exceptions, in collections of Odonata, male specimens of a species outnumber the female by a ratio of 4:1 or even higher. This disparity is not due to a preponderance of males in nature but to a difference in behavior between the sexes which results in the males being more frequently captured. Since reliable information on the actual sex ratio can be obtained by a count of exuviae during the emergence period, three stations at First Sister Lake were systematically and periodically searched. Those exuviae present on a given day represented the *cynosura* adults which had emerged since the last count, and from them the sex ratio could be determined. Some exuviae were undoubtedly overlooked or had been destroyed; this source of possible error in dealing with the small sample obtained should be remembered in considering the results.

Of the 212 exuviae collected at First Sister Lake 82 were male and 130 female. Such a sex ratio departs significantly from a 1:1 ratio ($X^2 = 10.868$, P is less than 0.01) but is not significantly different from a ratio of 1:2 ($X^2 = 0.2404$, P about 0.60). But the total number of exuviae collected during the study was 110 males and 159 females; this does not depart significantly from a ratio of 2:3 ($X^2 = .0892$, P is greater than 0.70), but does differ significantly from both a 1:1 and a 1:2 ratio (P for both is less than 0.01). As a result of an analysis, in the manner described here, Tiensuu (1935) suggested that there is an excess of females greater than 5 percent in *Cordulegaster boltonii* (Donovan). His conclusion, however, was based on limited sampling (two collections, three days apart). Corbet (1951*a*), on the other hand, using a month's sampling of over 2000 exuviae, found a 1:1 ratio in *Anax imperator* Leach.

Emergence rate. — The data on exuviae collected on successive dates at First Sister Lake also provide evidence that the period of emergence in *cynosura* is about 3 weeks, that nearly half the imagos emerge within the first week, and that an initial "explosive" peak is followed by another smaller peak some 2 weeks later (Fig. 2). Corbet's data are comparable. He demonstrated for *Anax imperator* a similar 3-week period, with half the imagos emerging within the first week. In that species, however, the curve for daily rate of emergence is more nearly symmetrical, there being but one peak and that on the third day. Tillyard (1917) held that females emerge before males, but my figures show that in *cynosura*, at least, males and females emerge at about the same rate for the first few days; therefore, should the 1:2 sex ratio prove to be a true index of this species, males initially emerge significantly before the females. Corbet found that males of *Anax imperator* emerged significantly before the females in the first 2 weeks of the emergence period.

Duration of Life

Only by marking specimens and recapturing them, can the length of life of individual dragonflies be reliably ascertained. Two studies of this nature have been made on Odonata. In one, Borror (1934) reported a 3- to 4-week life span for the damselfly, *Argia moesta*, and in the other Moore (1951), a 3- to 5-week life for *Libellula quadrimaculata*, *L. depressa*, *Orthetrum cancellatum*, and *Sympetrum striolatum*. I had very little success with this technique. Although 138 *cynosura* were marked, only eight were recaptured; of these only one (at First Sister Lake) had been marked for as long as 5 days. Many more marked individuals were observed but could not be captured, because of the wariness this species exhibits after once having been caught.

Since conclusive data on individual life span were not obtained from marking studies, I employed two indirect methods. In the first the lapse

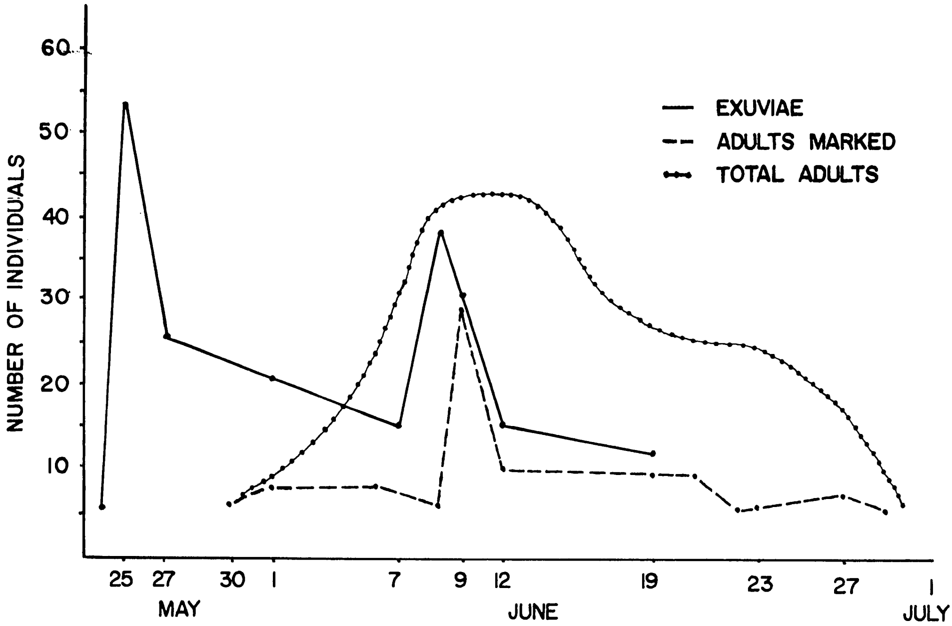


Fig. 2. Relation of emergence to population density of *Tetragoneuria cynosura*, First Sister Lake, 1954. Note absence of adults for the first week following emergence, continued presence of adults for two weeks after cessation of emergence, and adult-population peaks that follow two weeks after the emergence peaks.

of time between the date on which the last exuviae were found and the date on which the last adult was observed was taken as giving the minimal duration of life. This presumes that there has been no immigration or emigration. At First Sister Lake, the last exuviae were found on June 19 and the last adult was observed on July 1, 10 days later. Since no exuvial collections were made here between June 12 and June 19 there is a strong probability that the last exuviae were actually shed at some time prior to the 19th, and that a minimum life of about 2 weeks may be safely postulated for *cynosura* at this locality.

In the second method, the length of individual life was estimated by comparing the dates of maximum emergence with those of the highest adult-population density. This species exhibits an explosive emergence, the maximum of which occurred at First Sister Lake May 25-27, with the peak adult population attained about June 10-12, approximately 2 weeks later. Relationship of the rate and duration of emergence to the abundance of the adult population is shown in Figure 2, from which it can be seen that major variations in the emergence rate are reflected about 2 weeks later in the size of the adult population. The results obtained by both indirect methods suggested that the individual life span in *cynosura* was slightly over two weeks, an estimate which is near the lower limit of Kennedy's (1950) of 2 to 4 weeks for adults of Odonata.

Precopulatory Habits of Male

Even though it has often been suggested that dragonflies exhibit territoriality, only three critical studies have been made on this aspect of odonate behavior — with conflicting results. Using a fly-casting rod and line Saint Quentin (1934) introduced males or females of the same or other species into an occupied "Jagdrevier," which he concluded to be of a transitory nature. Moore (1952) modified the fish-line technique and combined it with marking studies on six species, and came to the conclusion that "dragonflies do not possess territories in any accepted sense of the term." Jacobs (1951, 1955) presented convincing evidence that *Plathemis lydia* and *Perithemis tenera* do exhibit territoriality.

Notice of spacing activities of *cynosura* males, described below, first led me to suspect that this behavior was territorial. Marking studies yielded some information on this matter, but the greater part accrued through field observation on localized populations. I believe that the fish-line technique yields no result that cannot be duplicated by careful observation, for by its use one merely tabulates the frequencies of reactions, which can be equally well seen as responses to natural instead of artificial incursions of other individuals.

At the height of the adult season at Douglas Lake, males were dispersed and flying at intervals of 10 to 30 feet along the shoreline, 1 to 3 feet from shore and 3 feet above the water. Spacings coincided closely with microtopographic areas (micro-areas) that were delimited by the overhanging shrubs along the shore. As the season waned and the population size decreased, the intervals between males correspondingly increased, until one or more adjacent micro-areas were incorporated with the original area. Along any shore where the distribution of the vegetation is such as to set apart natural areas, the spacing of these dragonflies reflects the distribution of these divisions quite clearly; but the absence of overhanging vegetation at First Sister Lake did not prevent manifestation of the spacing phenomenon.

Observation that a male tended to be in a spaced relationship with other males satisfies one of the prime requisites for postulation of territorial behavior. It then becomes necessary to ascertain the duration of occupancy, and to study the interaction of males occupying adjacent micro-areas and the reaction of one such male to other dragonflies coming near his micro-area.

Duration of occupancy is relative, dependent on time of day, population phase, and immediate prevailing ecological conditions. In the early afternoon each male tended to remain in his micro-area for an hour or more, but as the mid-afternoon peak of mating activity neared, the period of stay was considerably shortened. During the early afternoon, also, a vacated micro-area might remain unoccupied for as long as 20 minutes, while at the peak of mating activity as many as five or six males may successively occupy a single micro-area within 15 minutes. At the height of the season clashes between males in adjoining micro-areas were fairly frequent. They usually resulted in each male returning to his own, but occasionally one of the males was ejected and his area added to that of the victor. The successful male maintained the enlarged area until or unless subsequent interactions occurred; as a result of such the enlarged area was usually again subdivided into its former parts. Interactions with either a male or female *cynosura* are the only normal stimuli which result in a male abandoning his micro-area during the period of the day when micro-areas are used. There is no conclusive evidence as to whether a male seeks to regain a micro-area which he formerly occupied. Five of eight recaptured males were taken within 100 feet of the site where they were marked, either on the same day or at a later time, but it seems improbable that this was other than fortuitous.

The first reaction of a male to another dragonfly coming into his micro-area is to sally forth as though to chase the intruder; the same response, within certain size limits, is elicited regardless of the sex or species of the stranger. For instance, reaction to the larger Libellulas, to *Basiaeschna janata*, and to *Hagenius brevistylus* is the same as to either a male or female *cynosura*; the only forms which are tolerated are the smaller ones, like the Leucorrhinias, Sympetrums, and Enallagmas. The chase response appears to be exploratory or inquisitive rather than aggressive, since an actual clash follows only when the intruding form is a *cynosura*. It would seem then that the releaser mechanism for the aggressive behavior, or clash, is the visual perception of another *cynosura*. Observation showed that the clash was sexual in nature, since a male occupying a micro-area attempts to achieve the tandem or precopulatory position with the invading *cynosura* regardless of sex. These facts indicate an ability to recognize kind but an inability to distinguish sex, which is consistent with the lack of strong sexual dimorphism in *cynosura*; the sexual differences which exist appear to be beyond the immediate perception of the male.

In his studies of ten other species of Odonata, Moore (1952) found no essential difference between the way a male behaved toward females and males of his own species; he also found that clashes were most frequent between members of the same species and were followed by attempts to achieve the copulatory position. According to Moore, the intermale clashes, resulting from a lack of sex recognition, effect a temporary dispersal throughout the breeding area, the dispersal simulating territorialism.

The most generally accepted concept of territory is that of a "defended area" (Noble, 1939; Nice, 1941), a spatial unit, the extent and mode of use of which differ markedly with various groups of organisms. Defense usually implies active aggressive behavior; mere occupancy may also prove an effective, though passive, defense. The *cynosura* male does not exhibit territorialism involving active aggression, but it does express territorialism passively by micro-area occupancy. The function or effect of territorialism in *cynosura* is to promote dispersal in the breeding area and thereby provide optimal opportunity for a coursing female to be taken by a male.

Flight Styles

Four flight styles have been distinguished in *cynosura* males, two of which also involve females and one other species as well. In addition, there is the preoviposition flight of the female which is treated under "Reproductive Behavior," below.

Patrol flight: A type of flight exhibited in territorial behavior of the male over the water and characterized by extended periods of hovering, considerable maneuvering, and no alighting. In hovering, the male is suspended and stationary in the air, although the wings are beating so fast as to be nearly invisible. Individuals may remain in exactly the same hovering position for 15 minutes or longer, but more often, after some minutes in one place, the male moves a few feet to one side and hovers again. When disturbed by a collector's net, some individuals fly upward and return to the original position after completing a circle some 30 feet in diameter, but the majority merely move 10 to 20 feet away, usually in the direction of the air wash caused by the swing of the net. Movement from one hovering position to another is of the darting type common to many Odonata and, as in the Libellulidae, lacks the jerkiness characteristic of the aeshnines. During the several seasons of observation no male has ever been seen to alight during patrol flight. The features of this flight type are diagrammatically shown in Figure 3.

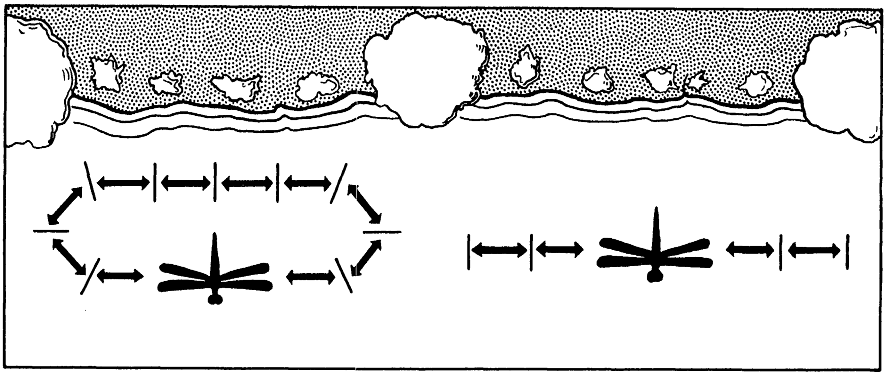


Fig. 3. Pattern of patrol flight of *Tetragoneuria cynosura*, Douglas Lake, 1953. The two males, in adjacent micro-areas, are oriented lakeward. Arrows indicate direction during short flights between hovering positions, which are represented by lines.

Feeding flight: A flight style exhibited away from water and characterized by very little or no hovering, moderately fast speed, and both vertical and considerable horizontal displacement. It usually occurs six or more feet above the ground, is less fixed in pattern than patrol flight, and invariably occurs in mid-morning to early afternoon. Use of the term "feeding flight" should not be taken to imply that feeding never occurs during patrol flight; it does sometimes but appears to be of secondary importance. In feeding flight, activity is primarily directed towards food procurement and, while there is usually area localization, no territorialism is exhibited. In this flight type the pattern consists of a series of larger and smaller loops, followed in no fixed order or direction, as shown in Figure 4.

Copulatory flight: This style involves both sexes and occurs about 3 feet above the surface of the water. There is no hovering, and flight speed is about half that of the male in feeding flight. The direction of flight is more or less linear for considerable distances, a quarter of a mile or more being not unusual. Unlike both patrol and feeding flights, copulatory flight is quite noisy, probably because the air currents produced by the beating of the male wings strike the wings of the female. Some authors (Asahina, 1950, among others) have used the term "mating flight" to include both patrol and copulatory flight, whereas others have applied the term to either one or the other. Confusion can best be eliminated by the use of separate designations.

Swarming flight: A type of flight that involves both sexes and one or more species. In *Tetragoneuria* no swarmings were observed that did not also involve other species, either of *Tetragoneuria* or other genera. In *cynosura*, swarming occurs at a height of ten or more feet and may be near or at some distance from the water's edge. It involves no hovering, but a continual gentle swooping and gliding, with little wing activity and considerable horizontal and vertical displacement. It is most similar to feeding flight, and of the four flight types is the most graceful.

Precopulatory Behavior of Female

Almost nothing was learned of the precopulatory behavior of the female, for the reason that shortly after emergence the females disappeared. Observations were confined to two newly emerged females, and to females, presumably considerably older, which were encountered in swarms. Extensive and repeated searches along and back of the shores of many lakes where the species occurs were of no avail. This vanishing of the females is the more perplexing in view of the fact that they emerge in numbers apparently exceeding those of the males. About all that can be said with certainty is that the females disappear from the immediate vicinity of the lake shores shortly after they emerge and reappear when, immediately prior to copulation, they fly into the micro-areas of the males.

Reproductive Behavior

The first step in copulation is the transfer of sperm by the male from the gonopophyses on his ninth abdominal segment to the seminal vesicle on his second abdominal segment. This is followed by the clash of a male and female *cynosura*, which invariably results in effecting the tandem position within a matter of seconds. In this position the anal appendages of the male take a viselike grip on the female head. The two superior appendages lie against the rear of the head of the female and are separated by her prothorax; the inferior appendage lies on the vertex-occiput area of the head with the tiny terminal dorsolateral hooks of the appendage

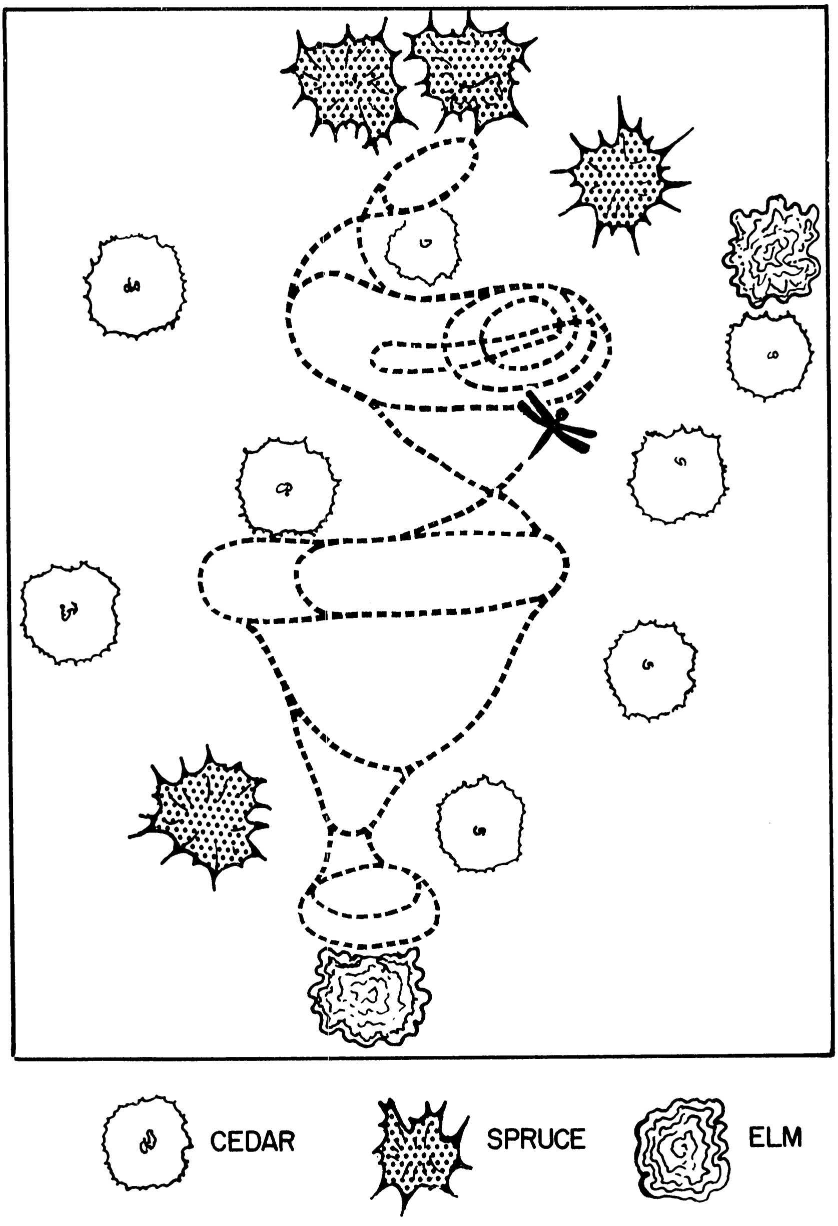


Fig. 4. Pattern of feeding flight of *Tetragoneuria cynosura*, First Sister Lake, 1954. Note extent of area covered and the absence of hovering as compared to patrol flight (Fig. 3).

caught at the junction of the eyes and vertex. With this grip secure, the male appears to pull the female behind him as they continue in flight. Transfer of the sperm from the seminal vesicle by way of the penis to the female genital orifice between the eighth and ninth abdominal sternites is the final step. These actions, as they occur in *cynosura*, are similar to those of other anisopterous dragonflies (see May, 1933, for an excellent account of this process) but show several peculiarities. In *cynosura*, the entire copulatory process occurs in flight, whereas many other forms make the final sperm transfer while in a resting position. In *cynosura*, because of a peculiar arching of the male abdomen, the two sexes are in nearly parallel horizontal flight planes so that the female contributes to copulatory flight, whereas in many other forms which copulate in flight the female may be nearly at right angles to the male and thereby deter forward flight. As far as could be learned, the entire copulatory flight in *cynosura* does not last for much more than 5 minutes. Other males very frequently attempt to separate a copulating pair and are often successful in doing so. In that event one of the two males then mated with the female, but whether it was the original mate or the interloper was not ascertained. Upon completion of copulation the sexes separate and the male invariably left the lake, but the female continued coursing over it.

Amount of mating activity appears to be directly related to the intensity of light. Copulation is rarely observed before 1 P.M. and reaches a peak in mid- to late afternoon, so long as the lake is in full sunshine; no activity of any kind is observed at dusk, and rarely on heavily overcast days.

Preoviposition flight: A type of flight that involves the female only. Its duration is not known, but it is doubtful that it persists more than 5 or 10 minutes. In this flight style the orientation is more or less haphazard, but tends toward a line parallel to the shore and some 10 or more feet from it; the flight has about the speed of copulatory flight and occurs 2 or 3 feet above the water. The seventh to tenth segments of the abdomen are arched in the form of an inverted U, with the apex at the ninth segment, the venter in this region is considerably dilated and the yellowish extruding eggs are contained by the long vulvar lamina which act as a flexible lower member of a vise. Gradually the flight orientation becomes less haphazard as the female more or less systematically searches the area for a proper site to oviposit. Having selected the site she then circles away, returns at lower speed, hovers momentarily, and flies away again. On her return flight (the third) the path is a descending arc and, without interrupting her flight or reducing its speed, the abdomen is deflected at a 75-degree angle into the water as the forepart of the body maintains a position parallel to the water and barely an inch above the surface. While the abdomen is pulled through the water in this position, the eggs are released in a gelatinous string or strand until the abdomen touches some more or less solid object; the distance between the initial point of entry and the object is usually 2 to 3 inches. When the abdomen touches the object the end of the string adheres to it, the rest of the string floating on or just below the surface. As soon as oviposition is completed the female flies lakeward 30 feet or more, deflects the abdomen and dips most of it in the water, rises perpendicularly some 6 feet and descends on the same path to repeat the dipping. She then flies rapidly almost perpendicularly about 100 feet, and finally soars away from the lake. This peculiar cleansing behavior after oviposition has been observed repeatedly, but it does not always occur.

Williamson (1905), who first described oviposition in a *Tetragoneuria* female, does not record the cleansing behavior nor the deliberate approach to the oviposition site. He speaks of the eggs being contained in a coiled pellet held by the vulvars and released as a unit. My observations on numerous females indicate that the string is released gradually but rapidly as the abdomen is pulled through the water. No success was achieved in inducing oviposition in females which were captured just as the abdomen deflected for its initial entry. When they were held, either by the wings or by the body with the wings free, eggs were not released as the abdomen was pulled through the water at about the same speed as in free oviposition.

Males often attempt to copulate with females about to oviposit as the latter fly near a micro-area. It is not unusual to see a freely roaming male attempt unsuccessfully to capture a female as she oviposits; this invariably causes the disturbed female to leave the area. One female, so disturbed, flew away with an egg string about 4 inches long hanging from the vulvars; she approached an emerged *Scirpus* and when very near it veered sharply, causing the dangling string to become attached to the reed. Then, with the posterior end of the abdomen pointing toward the reed, she flew sideways in a clockwise direction, wrapping the egg string around the stem several times. When the space between the tip of the abdomen and the reed was shortened to about 1 inch the string was released; the female flew off and performed the cleansing act. Cordulines are said to be unusual in being able to fly backward and sideways; I have found no previous record of any dragonfly flying sideways in a circle.

The factor apparently responsible for choice of an oviposition site seems to be the presence of some object in the water to which the gelatinous egg string may be attached. Strings have been found fixed to a wide variety of floating or emergent objects, including live plants, fallen logs, floating parts of plants, and exposed roots of shrubs; none have been found unattached. The presence of a single egg string apparently provides some stimulus to other ovipositing females, eliciting the deposition of their egg strings at the same place and attaching them either to the first string or nearby on the anchoring object. On one occasion ten females, seven of which were captured after they had laid eggs, oviposited on the same object within 15 minutes, producing an egg-string aggregation; on the following day some twenty additional strings were evident on this mass, but no others were added later. Numerous observations on egg-string aggregations in other localities indicate that the additive oviposition which results in their formation takes place only during a single day; egg strings are not added to strings or aggregations laid on previous days. Less than 10 percent of all the egg strings observed in this species were found singly. The vast majority represent the combined depositions of numerous females, with the usual volume ranging from a half pint to a pint and the dimensions varying from 6 to 12 inches in length and width. An egg-string aggregation of this species is illustrated in Plate I.

Needham (1901) described egg-string aggregations of *Tetragoneuria* (which he assigned to this genus by supposition), but the mode of their formation has not previously been described. Oviposition in strands as well as aggregational deposition is peculiar to two genera, both Cordulines; other than the North American *Tetragoneuria* and *Epicordulia,* the only form known to exhibit this behavior is the Palearctic *Epitheca* (Heymons, 1896). See Footnote 1 regarding the congeneric status of these groups.

The Larva

Unlike the aerial and active adult, the larva is aquatic and more or less lethargic. In contrast to the 2-week period of adult life, the larval stage endures for two years in the Lower Peninsula of Michigan and may last as long as three years in the colder parts of the Upper Peninsula. Diet of the carnivorous larva alters with increased growth of the mouth parts. Protozoa and protozoan-sized Metazoa form the initial items, but as growth proceeds these are gradually replaced by various microcrustacea. By the later stadia the food is quite varied and consists of anything of suitable size which moves and can be grasped by the prehensile labium.

The larvae live in shallow water within a few feet of shore in all stages of their development. Their distribution tends to be clumped and discontinuous. Needham and Heywood (1929) stated that, "The nymphs [of dragonflies] move shoreward and climb higher as the time of transformation approaches..," but, according to my observations, this does not happen in *cynosura* nor in many other groups. During the early stadia many larvae will occur in confined areas, but as competition for the available food supply increases the numbers decrease so that in the final stages usually only five or six larvae can be found in a space of roughly 4 by 4 feet. The clumped distribution possibly results directly from the aggregational egg-laying habits of the adults; hatching of the eggs of such a mass would produce heavy concentrations of the larvae in the immediate vicinity. The extremely light weight of the hatchlings, however, makes them much like zooplankters and permits them to be carried about by turbulence and currents. Even allowing for dispersal by this factor, the concentration of early-stage larvae should be greatest close to the site of the egg masses from which they emerged. It has not been possible to test this, but it does not seem untenable.

Very young larvae are true sprawlers; their disproportionately long legs afford little support but serve as effective paddles in locomotion. They are very active, almost constantly moving about and only occasionally "resting" by folding their legs under their bodies and lying half on their sides. Regardless of the amount of detritus on the bottom, the young larvae make no attempt to burrow. Half-grown larvae bury themselves to the lateral abdominal line, with the head at a slightly higher level; occasionally, the head will be completely buried and the abdomen just as completely exposed. They are much less active than the younger stages;

movement is infrequent and occurs mostly by jet propulsion, which is effected by forcing water out of the rectal respiratory chamber. In the last stadia the larvae more or less completely bury themselves under about a sixteenth of an inch of detritus; they are extremely lethargic and very rarely move about. In crawling, the movement of the legs is very slow and labored, suggesting the creaky joints of an arthritic; movement by jet propulsion on the other hand, is extremely fast but rarely employed. During the lattermost portions of the last stadium, feeding becomes highly irregular, and finally ceases altogether 1 to 3 weeks before emergence. Last-instar larvae collected in the spring stopped feeding 7 to 10 days prior to emergence, whereas those collected in the fall ceased feeding 11 to 21 days prior to emergence. The reason for such a difference between fall- and spring-collected larvae is not clear.

Metamorphosis

Final transformation from larva to adult usually occurs, both in field and in laboratory, during the early morning, that is, after sunrise and before 8 A.M. Emergence, however, has been noted in both sexes at 11 A.M. and as late as 3:30 P.M. The transformation site is usually within a foot or so of the water, on plant stems or on the ground, but cast skins were found 15 feet above the water on the trunk of a tree whose roots were exposed in the water and thereby served as a pathway.

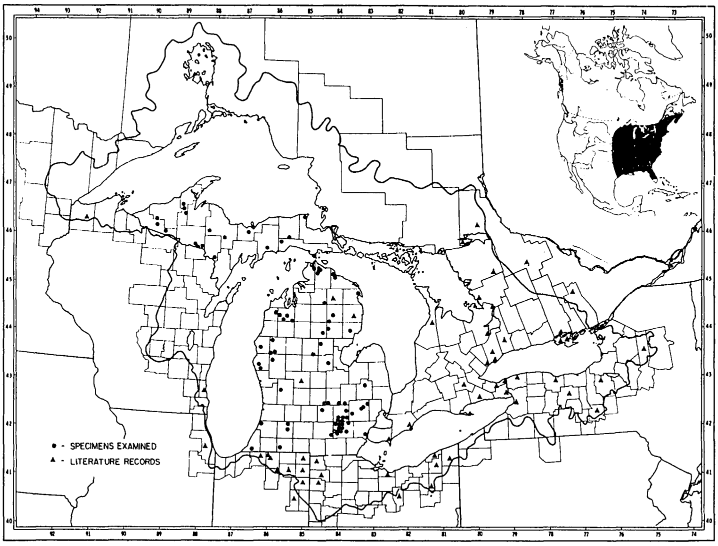
Final ecdysis and preflight changes in *cynosura* do not differ from those in *spinigera,* as detailed below. Adults of *cynosura* which emerged in the laboratory invariably died within two days, an indication that they retain little food reserve from the larval stage. Mittlestaedt (1950) kept *Anax imperator* alive 14 days by hand feeding. No attempt was made to repeat this on *cynosura.*

Habitat

Tetragoneuria cynosura is essentially an inhabitant of marl lakes with eutrophic tendencies but is tolerant of less eutrophic conditions. Some 80 percent of the lakes where I found *cynosura* imagos and larvae are similar to or intermediate between Douglas Lake and First Sister Lake in respect to physical and biotic characteristics. For the most part these are marl-producing lakes trending toward a eutrophic condition. They possess similar vegetation, varying principally in the extent to which this occupies the various zones. The remaining 20 percent of the lakes showed varying degrees of approach to, but no true development of bog conditions.

Distribution

Tetragoneuria cynosura is the most common species of the genus in the northeastern United States and is generally distributed from Nova Scotia to Ontario and Wisconsin and south to Florida and Texas (Map 2, inset). It has been reported from all the intervening states except the



Map 2. Distribution of *Tetragoneuria cynosura*. Main map: known distribution in the Great Lakes region; dark line indicates Great Lakes drainage basin. Inset: known distribution in North America.

Dakotas and West Virginia, and reaches a recorded northern limit in Canada at Timagami in Nipissing County, Ontario (Walker, 1941), at the same latitude as the known northern limit in Michigan. The geographical distribution of this species coincides closely with the Eastern Faunal Group recognized by Hays (1956) in his study on Michigan Tabanidae.

The distribution of *cynosura* in Michigan, based on 793 specimens examined in this study, is shown in Map 2. The species evidently occurs throughout the state except for the Keweenaw Peninsula and Isle Royale; lack of records from the south-central counties doubtless is the result of inadequate collecting. Of the three Michigan species, *cynosura* is the one most frequently encountered, but its abundance lessens northward from the Douglas Lake area. If Walker's Canadian records are also indicative, the northern limit of this species probably lies not far beyond the known northernmost Michigan occurrences.

Tetragoneuria spinigera (Selys)

The Adult

Season

As in *Tetragoneuria cynosura*, the earliest and latest records for *T. spinigera* in Michigan (May 8 and July 26) indicate a season of approximately 10 weeks, but like that species, when arranged on a regional basis, the data show a much shorter flight period and also a gradual northward progression. Dates of capture for *spinigera* are given below.

Region	Earliest Date	Latest Date	Interval in Weeks
Northern Upper Peninsula	June 15	July 23	5.4
Southern Upper Peninsula	June 1	July 9	5.4
Northern Lower Peninsula	May 16	July 26	10.1
Central Lower Peninsula	May 21	July 4	6.3
Southern Lower Peninsula	May 8	June 27	7.1

The tabulated records represent no single season nor locality and, hence, do not necessarily give the length of the flight period at a particular place. At Lake St. Helen in 1954 the flight season for *spinigera* lasted at least 5 weeks (from May 30, first emergence, to July 4, last adult observed). At Mud Lake that same year the season was slightly shorter, since no adults had emerged May 30 and no surviving individuals were seen on July 3. It appears that the length of season in this species is not less than 4 and not much longer than 5 weeks.

Observations over several years corroborate the inference that the flight season is progressively later northward. In 1954, the southernmost populations observed were in Roscommon County, where the season began on May 30; farther north in the northern Lower Peninsula and in the southern Upper Peninsula the season began a few days later; and in the northern Upper Peninsula it was two weeks later.

Sex Ratio and Emergence Rate

The sex ratio in *spinigera*, based on the total number of exuviae collected in various parts of the range (43 males, 36 females), does not differ significantly from a 1:1 ratio ($X^2 = .6202$, P is greater than 0.30). I have no data on the length of the emergence period. Such information on rate of emergence as has been obtained from experimental rearing studies and from field observations indicates that emergence is explosive and that the sexes emerge at about the same rate.

Duration of Life

By comparing data on emergence and population density, as explained for *cynosura*, the average life span of individuals of *spinigera* at Lake St. Helen and Mud Lake in 1954 was estimated at slightly over 2 weeks. No attempt to obtain direct evidence on this matter by marking studies was made.

Behavior

Tetragoneuria spinigera exhibits the same type of territorial behavior as does *cynosura*. Its flight styles are similar; it differs principally in being a somewhat faster flier. As in *cynosura*, females disappear after emergence and no amount of search has furnished clues as to what they do at this time. They reappear for mating and oviposition.

In reproductive behavior *spinigera* differs only slightly from *cynosura.* Reproductive activity does not seem so dependent upon sunlight as in *cynosura* and reaches its peak later in the afternoon. An occasional mating may occur as early as 2 P.M., but copulations usually begin about 4 P.M., reach a peak between 6 and 7 P.M., and persist well beyond dusk; a few copulating pairs have been seen as late as 8:30 P.M.

In premating flight, females of *spinigera* frequently deflect the distal end of the abdomen beyond the sixth segment at an angle of about 45 degrees, especially while they are in the vicinity of the micro-areas occupied by the males. This peculiarity of posture may help the male to identify the female in the waning light; it is most frequently observed toward dusk and when mating activity is at a peak.

Oviposition in *spinigera* is as described for *cynosura*, except that it usually occurs in reduced or indirect light, at dusk and even as late as 9 P.M. As in *cynosura*, no activity of any kind is observed on heavily overcast days. Odonata are predominantly heliophilic, and dusk-flying dragonflies are not at all common. This is the first time *Tetragoneuria* has been reported to fly under such conditions.

The egg strings are aggregated in the same manner as is described for *cynosura*. The sizes of the individual strings and of the aggregations are comparable in the two species. The largest aggregation was found at Munro Lake, Cheboygan County, on July 4, 1953; it was 3 feet long and 1 foot in maximum width, with an average thickness of about 2 inches. Its volume was estimated at over half a gallon. This tremendously large mass was floating partly submerged and was attached by the ends of only three strings to an emergent branch of a submerged rotting cedar.

The Larva

The larvae of *spinigera* resemble those of *cynosura* in ecology, diet, local distribution within a lake, and duration of life history.

Metamorphosis

One to two weeks before emergence the larvae of *spinigera* cease feeding, and adults die within two days after emergence if not fed. The changes in morphology and coloration that occur at metamorphosis have not been described for *Tetragoneuria*, but they do not differ from those reported for other genera of dragonflies (Tillyard, 1917, and others). The following notations on the sequence were made on a male collected as a last-instar larva at Mud Lake, on August 23, 1953. It emerged in the laboratory on the morning of March 2, 1954.

A.M.

8:00. Head and thorax thrust out of water, indicating direct air breathing through thoracic stigmata; rectal chamber not functioning.

10:00. Emerged from water, climbed 1 foot up cage.

10:15. Shifted position from full sunlight to partial shade; partly dried off.

10:30. Completely dried off.

10:40. Ecdysis beginning, skin splitting along middorsal line of thorax and quickly extended to fore part of epicranium.

10:45. Head freed first, followed by thorax and legs; pro- and mesothoracic legs free to mid-tibia, metathoracic legs free to distal end of femur.
10:47. Abdomen free to fourth segment, body deflected dorsally and downward, bringing head to mid-wing sheath level; mouth parts moving; both anterior pairs of legs completely free; metathoracic legs free to mid-tibia; all parts pale, slight pattern indicated on thorax and abdomen.
10:50. Legs completely free, insect motionless.
11:00. Slight jerking motion, increasing in intensity; eyes, thorax, and venter darkening slightly.
11:02. Strong jerking and rocking motions raised body upright, so that legs grasped cage.
11:03. Strong flexions withdrew the telescoped abdomen; all appendages without pigment, membranous in appearance; wings crumpled.
11:06. Wings and abdomen expanding, vertex hair darkening; generalized darkening of body except appendages; anal appendages nearly full size.
11:11. Wings three-quarters full size; wing membrane foggy without spotting, veins medium brown; abdomen fully expanded.
11:16. Wings fully expanded, folded together overhead; darkening continues except in appendages.
11:30. Wing membrane clearing; legs medium brown, anal appendages pale.
11:40. Slight darkening of anal area of hind wing; wing membrane hyaline; anal appendages pale brown; legs brown-black.
11:50. Wings still folded overhead, final body color nearly complete; spotting in anal area of hind wing brown-black.
11:55. Wings open.

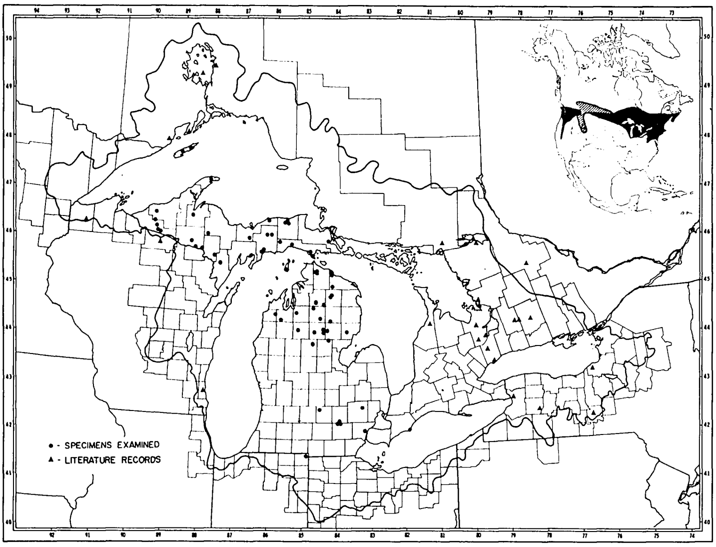
P.M.
12:05. Imago moved slowly 4 inches from exuvia; no changes apparent after this time.

Habitat

Tetragoneuria spinigera is essentially an inhabitant of transitional lakes of dystrophic tendencies, but is tolerant of extreme deviations toward the dystrophic or eutrophic. Most of the lakes where it was studied are similar to or intermediate between Mud Lake and Lake St. Helen in physical and biotic conditions. They contain little or no marl, and show various degrees of bog potential or bog development, with a trend toward the dystrophic condition. Few of them, however, so nearly approximate a true bog condition as does Mud Lake.

Distribution

Tetragoneuria spinigera ranges in North America from Nova Scotia to Vancouver Island; the northernmost point from which it has been recorded is Kenora County, Ontario (Walker, 1941), about 250 miles north of Isle Royale, Michigan (Map 3, inset). The southern distribution is irregular; it extends south in the east as far as West Virginia, in the midwest to southern Michigan, and in the far west to northeastern California. In the plains and Rocky Mountain regions it is unknown south of the Canadian border. The California material reported by Kennedy (1917), now in the Williamson-Kennedy UMMZ collections, has been examined and verified in the course of this study. The only Indiana record is from Clear Lake in the extreme northeast corner of Steuben County, a few miles from the Michigan state line. To list *spinigera* as an Indiana species suggests it to



Map 3. Distribution of *Tetragoneuria spinigera.* Main map: known distribution in the Great Lakes region; dark line indicates Great Lakes drainage basin. Inset: solid area represents known distribution in North America; cross-hatched area, predicted range.

have a more southern range than is actually true. I have not seen the West Virginia material, but do not doubt that the species may occur there in suitable upland areas. Needham and Westfall (1955) include Louisiana in the range of *spinigera.* They did this apparently on the authority of Wright (1937). Wright, however, stated only that there are specimens of *spinigera* without data in the Louisiana State Museum. The presence of unlabeled specimens in a regional-museum collection is no proof that the material actually came from that particular region. I believe it unjustifiable, in view of authenticated records which indicate otherwise, to include Louisiana in the range of *spinigera.*

The distribution of *spinigera* in Michigan, based on the 441 specimens examined in this study, is shown on Map 3. The species is rather generally distributed throughout the state, but is more often encountered in the northern two-thirds. In 1954 I found no individuals south of Roscommon County; however, in 1955 a large series was collected in Washtenaw County.

Tetragoneuria canis MacLachlan

Since *Tetragoneuria canis* is both scarce and infrequent in the southern part of Michigan, where most of my studies were made, little knowledge of its bionomics was obtained. The earliest record for the species in the state is May 30; the latest, July 23. Arranged by regions, the earliest and latest dates of capture are given below.

Region	Earliest Date	Latest Date	Interval in Weeks
Northern Upper Peninsula	June 8	July 23	6.4
Southern Upper Peninsula	June 3	July 7	4.9
Northern Lower Peninsula.......	May 30	July 10	5.9

Here again, as in *cynosura* and *spinigera*, a northward progression of season with increase of latitude may be noted. Minimal length of season in a small population a mile northeast of Mud Lake was $5\frac{1}{2}$ weeks.

The sex ratio among the specimens of *canis* available for study is about 2:1 in favor of the males; but, as discussed under *cynosura*, this indicates nothing as to the actual sex ratio in the live population.

No differences in territorial behavior and flight style were noted between this species and either *cynosura* or *spinigera*. Speed of flight is intermediate but closer to that of *spinigera*. The precopulatory attitude of the female is like that in *spinigera*, that is, the distal part of the abdomen is deflected at a 45-degree angle. Mating activity reaches a peak in late afternoon or early evening; in this respect *canis* is intermediate between *spinigera* and *cynosura*. No copulation was noted before 3 P.M., the peak of mating seemed to be attained between 5 and 7 P.M., and no pairs *in copulo* were observed after 8 P.M. Several females in different localities were in preoviposition flight as late as 8:30 P.M., which may indicate that the mating period lasts until then.

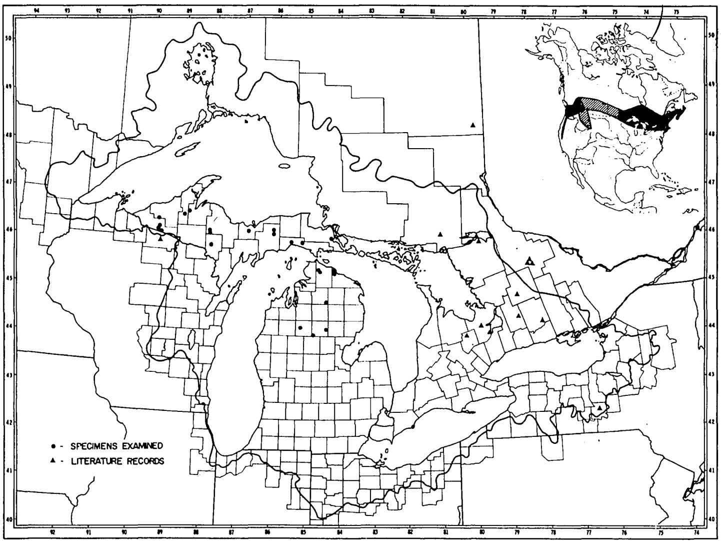
Not only is the female of *canis*, during the period just prior to oviposition, the most elusive of the three forms studied, but its flight is the most erratic and least predictable. Oviposition has not been observed, but from the nature and disposition of the egg strings associated with *canis* populations it may be assumed to follow the same pattern as in the other two species. Most of the egg strings seen were single; a few two-stringed clumps were found and one five-string aggregation. The preponderance of single strings and the absence of large egg masses appear to differentiate *canis* from the other two species, but this distinction is probably a direct result of small population size. A more significant difference is that *canis* eggs are deposited along the edges of fairly slow streams and in pondlike impoundments of streams, as well as in lakes.

The larvae of *canis* resemble those of *cynosura* and *spinigera* in behavior, ecology, diet, and local distribution within a lake. The evidence points to a 3-year larval period for this species in regions where *spinigera* and *cynosura* have a 2-year cycle. Although several larvae transformed in the laboratory, I was unable to observe the pattern of metamorphosis.

If one accepts the dictum that the true habitat of an insect with aquatic larvae is that of its larvae (Wright, 1943), the only reliably determined habitat for *Tetragoneuria canis* in Michigan is a sluggish impoundment of Fontinalis Run in Cheboygan County, southeast of Douglas Lake. Here adults, egg strings, and larvae were collected, proving the species to be fully at home. The narrow stream has its source some 300 feet north of the impoundment in a bog forest of the swamp type. The ponding is caused by a dirt road which blocks the outflow (except for a culvert) by which the stream reaches Burt Lake some 200 feet to the south. Sedge and cattail border the pond, and the water surface is about 70 percent covered by water lilies *(Nymphaea odorata* and *Nuphar advena)*. Brownish water overlies a substrate of fibrous peat that is in many places nonresilient and noncohesive. No chemical data were taken on this pond.

Other situations, in which *canis* adults were observed, show a gradation from ponds with marked bog tendencies to typical bog lakes and streams draining from bog areas. On the basis of present information, therefore, *Tetragoneuria canis* may be regarded as an inhabitant of more or less typically dystrophic bog lakes and streams.

The distribution of *Tetragoneuria canis* (Map 4, inset) is quitè similar to that of *spinigera*, although the species appears to be somewhat more boreal. It ranges from Nova Scotia to British Columbia, and its northern limits, which in Ontario are about the same as for *spinigera* (Walker, 1941) but in British Columbia are reached north of latitude 54° (Whitehouse, 1941), are some 200 miles north of the limits of *spinigera*. Along the southern margin its distribution, like that of *spinigera*, is irregular; it extends south in the east to central New York, in the midwest to central Michigan, and in the far west to central California. Specimens reported by Kennedy (1917) from California are in the UMMZ collection; they have been re-examined and the determination verified. Bird's (1932) record of *canis* from Latimer County, Oklahoma was based on a male which I have redetermined as *T. spinosa* Hagen.



Map 4. Distribution of *Tetragoneuria canis*. Main map: known distribution in the Great Lakes region; dark line indicates Great Lakes drainage basin. Inset: solid area represents known distribution in North America (note record from Saskatchewan); cross-hatched area, predicted range.

The distribution of *Tetragoneuria canis* in Michigan, based on the 97 specimens examined, is shown in Map 4. So far as is known the species is confined to the northern half of the state; it is scarce and infrequent in the Lower Peninsula, but rather abundant and frequent in the Upper Peninsula.

Interspecific Relations

Progression and Sequence of Season

Northward progression of flight season with time occurs in all three species. The phenomenon was inferred to be a direct result of temperature differences, but in order to test this directly it would have been necessary to determine lake and air temperatures at localities in which the three species occur during the critical months, that is, from the time of the spring turnover through that of emergence and the establishment of the adult population. Since I could not obtain such information, I approached this problem indirectly by a study of available air-temperature records. From these data the general temperature trend in the lakes of the various regions may be assumed. Although the relation between the air temperature and the water temperature of a given lake follows no exact rule, the approximation is sufficient for the purposes at hand.

The mean monthly temperatures for April-June, 1954 (Fig. 5), show definite regional differences at a given time, as well as a northward progression, during the three-month period. The northward progression of the seasons for each of the three species of *Tetragoneuria* follows the same general pattern. Adult populations in the Northern Upper Peninsula appeared about 2 weeks later than in the Northern and Central Lower Peninsula, and some 3 weeks later than in the Southern Lower Peninsula. Furthermore, in any area there is a sequence of flight seasons, which starts with that of *canis*, is followed by that of *spinigera* in less than a week, then by that of *cynosura* about two weeks after the latter. The season of *spinigera* comes to an end first; then, within a few days, that of *canis*; and finally, about 2 weeks later, that of *cynosura*. E. M. Walker (*in litt.*, May 21, 1954) confirmed these conclusions from his observations, which were made over a 30-year period.

The earlier seasonal appearance of *canis* and *spinigera* and their more boreal distribution indicate that these two species emerge and establish their populations at lower temperatures than does *cynosura*.

Mutual Occurrence

In view of the overlap in season and distribution of *cynosura*, *spinigera*, and *canis*, it was not surprising that during the 1954 season two or all three of these species were found together in eleven instances. Five additional examples of joint occurrence were discovered on examining the locality data of specimens in the collections studied. Such coexistence is of interest, for it strongly suggests reproductive isolation between the populations. If such isolation exists, it could either result from physio-

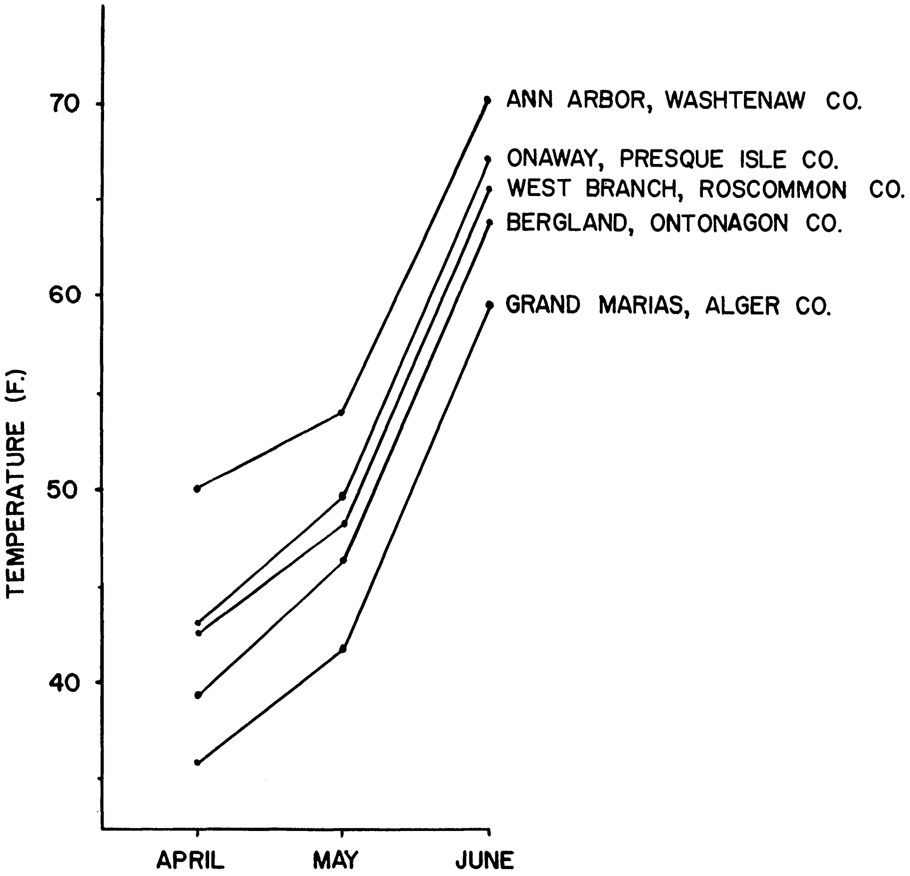


Fig. 5. Mean temperature distribution in five regionally representative localities in Michigan. Data from U. S. Weather Bureau records for 1954.

logical or genetic incompatibility, or from differences in behavior or morphology. No tests of the first two possibilities were made. No sharp differences in behavior among the three species were observed; such differences as exist show much variation and overlap. The daily mating periods of the three species differ in the time of their peaks, but coincide during much of their extent. The deflected abdomens of female *spinigera* and *canis* in the premating flight may set these species apart from *cynosura*, but certainly not from each other. Nothing that might serve as a recognition mark was seen in the flight pattern. Furthermore, the similar behavior of the males, while patrolling their micro-areas and dashing toward every approaching dragonfly about their own size, is convincing evidence that there is no recognition of *Tetragoneuria* species or sex at a distance, but only upon contact.

Barring physiological or genetic factors or differences in behavior, it would seem, therefore, that morphological incongruities between the conformation of the female head and the terminal abdominal appendages of the male effect isolation by preventing the male of one species from grasping the female of another. The copulatory mechanism peculiar to Odonata involves an unusually diverse group of structures for effecting the transfer of sperm. Necessary congruities between parts of the two sexes which are opposed in the copulatory position include the following: (1) the length of the male superior anal appendage in relation to the posterior length of the female head; (2) the form and size of the male inferior anal appendage in relation to the distance it must span across the top of the female head (from the posterior margin of the occiput to the junction of the eyes and vertex); (3) the position of the basal modification of the male superior anal appendage relative to that of a groove on the posterior aspect of the female occiput; (4) the relative lengths of the male and female abdomens, since the middle of the ninth sternite of the female must reach the male genitalia on the second sternite. Presumably, discrepancies in any or all of the first three of these sets of correlated characters would cause the prompt breakup of an attempt at copulation by a male and female of different species; incongruity in the fourth would likely prevent its successful completion. The four sets of characters were studied in samples in which more than one of the species were simultaneously present. The interspecies combinations and the likelihood of their success are tabulated below (each measurement given is the mean of the sample).

SOUTHERN MICHIGAN (based on 25♂, 11♀ of *cynosura* and 6♂, 11♀ of *spinigera* collected by L. K. Gloyd at Joslin Lake, Washtenaw County, 1934):
(1) *cynosura* ♂ x *spinigera* ♀, not very probable:
a) Inferior appendage shorter than occiput-to-eye length (1.8 and 1.9 mm., respectively)
b) Basal modification position shorter than occipital groove position (0.8 and 1.0 mm.)
(2) *spinigera* ♂ x *cynosura* ♀, possible, grip not firm:
a) Inferior appendage too much longer than occiput-to-eye length (2.0 and 1.7 mm.)
b) Basal modification position considerably longer than position of occipital groove (1.1 and 0.7 mm.)
c) Abdomen considerably longer than female abdomen (32.2 and 26.9 mm.)

NORTHERN MICHIGAN (based on 4♂, 3♀ of *cynosura,* 10♂, 11♀ of *spinigera,* and 2♂, 2♀ of *canis* collected by the author at Gogebic Lake, Ontonagon County, 1954):
(3) *cynosura* ♂ x *spinigera* ♀, not very probable:
a) Inferior appendage shorter than occiput-to-eye length (2.1 and 2.2 mm., respectively)
b) Basal modification position shorter than occipital groove position (0.9 and 1.1 mm.)
(4) *cynosura* ♂ x *canis* ♀, possible, grip not firm:
a) Inferior appendage too much longer than occiput-to-eye length (2.1 and 1.7 mm.)
(5) *spinigera* ♂ x *cynosura* ♀, possible, grip not firm:
a) Inferior appendage too much longer than occiput-to-eye length (2.3 and 2.0 mm.)
b) Basal modification position considerably longer than position of occipital groove (1.2 and 0.8 mm.)
c) Abdomen considerably longer than female abdomen (33.4 and 28.0 mm.)
(6) *spinigera* ♂ x *canis* ♀, possible, grip not firm:
a) Inferior appendage too much longer than occiput-to-eye length (2.3 and 1.7 mm.)
b) Basal modification position considerably longer than position of occipital groove (1.2 and 0.9 mm.)
c) Abdomen considerably longer than female abdomen (33.4 and 32.0 mm.)

(7) *canis* ♂ x *cynosura* ♀, not very probable:
  - *a)* Inferior appendage shorter than the occiput-to-eye length (1.8 and 2.0 mm.)
  - *b)* Basal modification position longer than position of occipital groove (1.0 and 0.8 mm.)
  - *c)* Abdomen considerably longer than female abdomen (33.1 and 28.0 mm.)

(8) *canis* ♂ x *spinigera* ♀, not very probable:
  - *a)* Inferior appendage shorter than occiput-to-eye length (1.8 and 2.2 mm.)
  - *b)* Basal modification position shorter than occipital groove position (1.0 and 1.1 .mm.)

Mating was in progress in only one of the eleven instances in which two or more of the species were in flight together, and no mixed pairs were seen. The only instance known to me of possible miscegenation between any of these species is that reported in a letter from L. K. Gloyd (April 5, 1954). At Joslin Lake, while making the collections analyzed above, she took a male *spinigera* that was clasping a female *cynosura*, but could not determine whether copulation had been successful. Whatever possibility that such a pairing may occur is indicated in the above tabulation.

As a result of this analysis, admittedly limited, I believe that the primary factor isolating these species is morphological and that it results from a physical incompatibility in copulation. Such a factor may, it is true, be reinforced by subtle differences in behavior or habitat. No specimens which I have examined in any way resembled hybrids, and in numerous samplings of aquatic habitats no two of the species have occurred together as larvae.

Extraspecific Relations

Although field observations were primarily concerned with the three species of *Tetragoneuria* under study, there was ample opportunity to investigate the relations of the three to their associated animal and plant assemblages.

Associations with Other Odonata

In comparing the niche of the dragonfly in the insect world to that occupied by hawks and owls in the bird world, Kennedy (1950) stated that "they are at the peak of the pyramid of numbers." However, when dragonflies are compared to the totality of life, they are considerably removed from this peak, since they are, in turn, preyed upon by other animals. Even within their own level in the pyramid, different kinds of dragonflies occupy different or successive sublevels. These sublevels are primarily the effect of relative size, since the larger and more swift prey upon the smaller and less fleet. Maintenance of a niche by each of some twenty carnivorous species occurring as imagos with *cynosura* at First Sister Lake appeared to result primarily from differences in spatial arrangement, both horizontal and vertical.

At the beginning of the *cynosura* season at First Sister Lake competition for space is at a minimum: *cynosura* occupies a position at the junction of the water-lily zone and the open water, with no interference from individuals of *Leucorrhinia intacta* Hagen (which fly over and just above the reeds and water lilies) nor from those of *Enallagma ebrium* Hagen and *E. signatum* (Hagen) (whose movements are barely perceptible as they fly among the reeds and water lilies several inches above the water surface). *Ladona julia* Uhler was never seen over the open water or near the juncture of the water-lily and open-water zones, but preferred the near-shore zone a foot or more above the Leucorrhinias; it often rested on the ground. This community structure did not alter significantly until the *cynosura* population began to decrease in mid-June. At this time only *Epicordulia princeps* Selys, and then rarely and only momentarily, would occupy the *cynosura* space. The Leucorrhinias maintained their position, as did the Enallagmas mentioned above, with the addition of *Enallagma traviatum* Selys and *Ischnura verticalis* (Say), which appeared at this time. *Libellula cyanea* Fabr. and *Pachydiplax longipennis* (Burm.) competed for a horizontal level comparable to that of *cynosura* but situated at the near-shore zone. *Libellula pulchella* Drury and *L. luctuosa* Burm. were found in the space formerly occupied by *Ladona julia*. *Erythemis simplicicollis* Say, *Sympetrum obtrusum* (Hagen), *S. rubicundulum* (Say), and *Celithemis monomelaena* Williamson began emerging during late June but did not affect the established structural relationship. At the close of the *cynosura* season the relationships were still very much as described but with two major exceptions: *Libellula cyanea* and *Pachydiplax longipennis* had moved lakeward from their original near-shore position to vie for and occupy the *cynosura* space, and the tiny amber-winged *Perithemis tenera* (Say) was present virtually everywhere on the lake flying barely an inch or so above the water. The vertical stratifications and horizontal displacements described here presumably account for the paucity of actual conflicts observed.

The spatial distribution of *Tetragoneuria* species and other dragonflies was also observed at other localities. In general, the description of what was seen to occur at First Sister Lake applies to the observations made elsewhere; such differences as existed were caused in part by differences in vegetation and in part, but to a lesser degree, by the presence of some other species of dragonflies. For instance, at Douglas Lake *Libellula pulchella* competed for the *cynosura* space as the season waned, and at Mud Lake *Dorocordulia libera* competed for and eventually took over the *spinigera* position at the juncture of the sedges and open water.

Swarming in dragonflies is not very common; its occurrence therefore evokes interest. During the 1954 season, four swarms involving *Tetragoneuria* were observed. Flight characteristics in swarming are described under Flight Styles above (p. 22). The occurrence and constitution of the swarms seen was as follows:

1. Luce County, east shore Muskallonge Lake, June 15, 1954, 1-1:30 P.M. Over sandy shore in jack pine clearing about 10 feet above ground; about ten individuals each of *Tetragoneuria spinigera*, *Somatochlora franklini*, *S. kennedyi*, *Cordulia shurtleffi*, and *Libellula quadrimaculata*.

2. Alger County, Grand Sable Lake, June 15, 1954, 3-3:30 P.M. Over dirt road and open field one-half mile east of lake, 10 feet above ground, five to ten individuals of each of the species mentioned in (1).

3. Ontonagon County, Gogebic Lake, 200 feet from Gogebic County line, June 16, 1954, 5:30-6 P.M. Over dirt road adjacent to lake, 10 to 20 feet over ground; about a hundred individuals altogether, of *Tetragoneuria spinigera* (the majority), *T. canis*, *T. cynosura*, *Cordulia shurtleffi*, *Somatochlora kennedyi*, and *Basiaeschna janata*.

4. Grand Traverse County, Boardman River Bridge, on County Road 611, June 27, 1954, 1-2 P.M. Over a grassy, shrub-lined, morainic knob separating two parts of the river, 10 feet above ground; about fifty individuals, chiefly *Tetragoneuria spinigera* and *Epicordulia princeps*, with a few *T. cynosura*. *Epicordulia princeps* was also in haphazard patrol flight along the river.

Associations with Other Organisms

Although not much direct evidence is available, Tetragoneurias are vulnerable to predation, especially in the larval stage. The egg strings are attached to various emerged objects, among which are the floating parts of plants. When the plant chosen is a bladderwort (*Utricularia* sp.), as often happens, an interesting biological association is set up. The capillary dissected leaves of bladderworts bear tiny bladders, each furnished with a valvular lid and a few flagellae at the orifice. The bladders entrap small creatures and are reported to have the ability to digest soft animal tissues. Upon hatching the *Tetragoneuria* prolarvae and early-instar larvae become entangled in the bladderwort leaves and, although I have not seen them caught in the bladders, it seems probable that many of them are eliminated in this way.

Shortly after the initial hatchings at Douglas Lake several schools of the bullhead, *Ameiurus m. melas* (Rafinesque), consisting of about a hundred young individuals each, were observed in the shoal waters and they often passed near or underneath hatching egg strings. I suspect that the bullheads were feeding upon the prolarvae and young larvae, since some of them, when placed in aquaria, consumed all early-instar larvae put in with them. Other probable predators upon the larval stages in the shoal waters include the northern pike, the bluegill, and the painted turtle.

First Sister Lake supports a sizable population of marsh-inhabiting birds. Many birds were seen to descend close to the water surface, presumably to catch flying insects including dragonflies. However, I saw only one instance of a bird preying on *Tetragoneuria*. On June 28, 1954, a red-winged blackbird (*Agelaius p. phoeniceus* [Linn.]) flew very rapidly toward the lake and captured a male *T. cynosura* that was patrolling its micro-area.

LIFE HISTORY OF MICHIGAN TETRAGONEURIA

In dragonflies, the larva is as well suited, physiologically and morphologically, to aquatic life as the adult is to aerial life. The result of adaptation to such different habitats is the striking dissimilarity that exists between the two stages. Students of the group have used the term "nymph" to designate the immature stage, primarily because the wing pads develop externally, as in orthopteroids; the Odonata, however, differ markedly from the orthopteroid groups in having a greater contrast between the form of the young insect and the adult. The dissimilarities between young and adult Odonata are most pronounced in the morphology of the head (particularly the mouth parts), and in the abdominal proportions, abdominal processes and appendages, and the method of external respiration; indeed, only the thorax and its wing pads bear any resemblance to each other in the two stages. Because of this and to stress the distinctions, Snodgrass (1954*a*, 1954*b*) preferred to apply the term "larva" to the immature dragonfly, and I have followed his usage. Although Snodgrass (1954*a*) classified Odonata among the hemimetabolous insects, he suggested that they "might almost be said to be holometabolous insects without a pupal stage." His interpretation is based on the facts that (1) the last stadium is considerably longer than the others and (2) a greater amount of structural change occurs during the latter part of this stadium owing to a reorganization essentially comparable to that which takes place during the pupal stage in holometabolous insects.

Four stages may be distinguished in the life history of species of *Tetragoneuria*: egg; prolarva (= pronymph, *auct.*); larva; and adult. This section deals with the first three; the adult is treated under Comparative Morphology of Adult Michigan *Tetragoneuria* (below). Life-history data were obtained on 377 different stadia: *cynosura*, 162 (including 5 prolarvae and 56 ultimate larvae); *spinigera*, 162 (5 prolarvae and 55 ultimate larvae); *canis*, 53 (5 prolarvae and 13 ultimate larvae). Exclusive of the prolarval and ultimate larval stages, the average number of individual skins analyzed for each instar was 9 in *cynosura* and *spinigera* and 4 in *canis*. Most of the *cynosura* material was collected at Douglas Lake and First Sister Lake; most of the *spinigera* material at Mud Lake and Lake St. Helen; all the *canis* material came from Fontinalis Run, Cheboygan County.[4]

Egg

Egg strings of the three species are identical in length, width, and make-up (Fig. 6*a*). The eggs are alike in all respects except size; hence, the description of those of *cynosura* (which follows) applies equally well to those of *spinigera* and *canis*. A freshly laid egg string is 1 mm. wide and 5 cm. long, but as the result of rapid endosmosis its width increases within five minutes to 3.5 mm. and its length to 11 cm.; after this time no change in volume is apparent. The string is open at both ends to a depth of about 5 mm. and consists of a uniform gelatinous matrix. The eggs have no common orientation, but are more or less equally spaced from each other. They are light yellowish brown at oviposition, darken to a medium brown within a day and subsequently exhibit no further color change. They are oval, somewhat blunt on one end with a conspicuous

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[4] The complete list of localities and the tables of statistical parameters for the characters measured are too lengthy to be included here. They may be examined in the doctoral thesis which is available on microfilm from the Library of Congress.

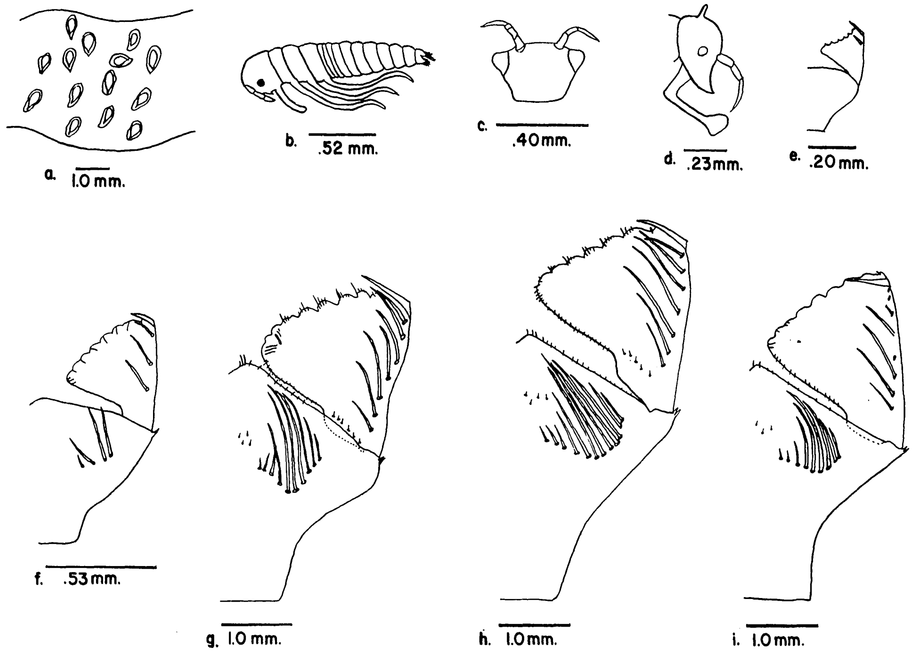

Fig. 6. Immature stages of Michigan species of *Tetragoneuria*: *a*. Egg string of *T. canis*. *b*. Prolarva of *T. spinigera*; *c-d*. Head of first-instar larva of *T. canis*: *c*. dorsal view, *d*. lateral view; *e*. right half of labium of 1st instar larva of *T. canis*; *f*. right half of labium of 6th instar larva of *T. cynosura*; *g-i*. right half of labium of last-instar larvae: *g*. *T. cynosura*, *h*. *T. spinigera*, *i*. *T. canis*.

peduncle (micropyle?) at the opposite end; they range (in *cynosura*) from 0.55 to 0.60 mm. in length and from 0.29 to 0.31 mm. in width. Each egg is enclosed in a membranous sac, which separates it from the gelatinous matrix of the string, and is bathed by a clear nongelatinous, nonviscid fluid. The sac is most evident for about a week, after which it appears to shrink and become adherent to the egg. This apparent shrinkage is in reality caused chiefly by a swelling of the egg, with little actual shrinkage of the sac. The egg increases in size to a maximum at the time of the appearance of the embryonic eye spots. No change in size of the egg occurs after the eye spots develop, and comparative dimensions in the three species at this stage are: eggs of *cynosura* (those from southern and northern Michigan are alike) 0.67 to 0.70 mm. in length by 0.35 to 0.40 mm. in width; of *spinigera*, 0.73 to 0.76 mm. by 0.40 to 0.42 mm.; of *canis* (which are the largest), 0.80 to 0.86 mm. by 0.45 to 0.46 mm.

Four days after oviposition the peduncle is reduced; by the seventh or eighth day it is no longer visible and indefinite opacities have appeared in the egg. The opaque areas become organized as the eye spots by the ninth day. Hatching (eclosion) begins 6 days after the appearance of the eye spots (14 days postoviposition). Duration of embryonic development in freshly deposited eggs reared concurrently in the field and in the laboratory agreed closely; the field-reared culture showed hatchings on the fourteenth day; the laboratory culture one day later. But in many individuals the embryonic development required considerably more than the usual 14 to 15 days.[5] Why this is so is not known. Once the eye spot stage is reached, however, the remaining development requires only 6 to 7 days.

The rate of hatching was observed concurrently on (1) a single egg string of *cynosura*, (2) a sample from an egg-string aggregation of *cynosura*, and (3) part of a string from an aggregation of *spinigera*. The cultures were examined daily at about the same time, and all larvae (representing the hatchings of the preceding 24-hour period) were removed and counted. Hatching continued in the single egg string of *cynosura* for 40 days; in the aggregate egg string of *cynosura* for 48 days (after which observation was discontinued); and in the part of the single egg string of *spinigera* for 34 days. The *spinigera* culture began hatching 6 days after the *cynosura* culture, but the eggs were of later deposition. In two cultures of *canis* only fifteen hatchings occurred, and I was unable to study the hatching rate in this species.

Daily rates of hatching from the single egg strings are presented in Figure 7. The results showed: (1) An initial explosive hatching rate in *cynosura* and *spinigera*, but more abrupt in *spinigera*; a hatching within 2 days of 29.2 percent of *cynosura* and 4.0 percent of *spinigera*; within 4 days, of 34.5 percent of *cynosura* and 51.0 percent of *spinigera*; within 7 days, 51.7 percent of *cynosura* and 83.3 percent of *spinigera*; within 2 weeks, 77.1 percent of *cynosura* and 93.0 percent of *spinigera*. (2) Considerable daily fluctuation in hatchings of *cynosura*; relatively less in those of *spinigera*. (3) A slowly decreasing trend in *cynosura* (after the peak), as compared with the rate in *spinigera* that at first decreases rapidly and then levels after about 8 days.

Hatching rates from the egg-string aggregation of *cynosura*, which were based on a greater number of individuals, showed a curve comparable to the single strand. The *cynosura* string, which yielded 1060 individuals, was about 11 cm. long and had a volume of 2 cc.; the *spinigera* string, which yielded 524, measured about 5.5 cm. long and had a volume slightly under 1 cc. On this basis there are about 525 eggs per cubic centimeter or 95 eggs per centimeter, approximations which can be used to estimate the number of eggs in large aggregations of both species. By this method of calculation there are over 250,000 eggs in the usual-sized aggregations produced by *cynosura* and *spinigera* and over one million eggs in the extremely large *spinigera* egg group found at Munro Lake.

Few dragonflies deposit their eggs so conveniently for the observer as do species of *Tetragoneuria*. It is impossible, however, to compare the number of eggs they produce with the number produced by dragonflies of other genera, because egg counts for the latter are not available. The high count of eggs in an individual *Tetragoneuria* string stimulates one's interest in the question of whether the female oviposits more than once;

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[5] Bick (1941) reported the average hatching time for *Erythemis simplicicollis* as 11.6 days.

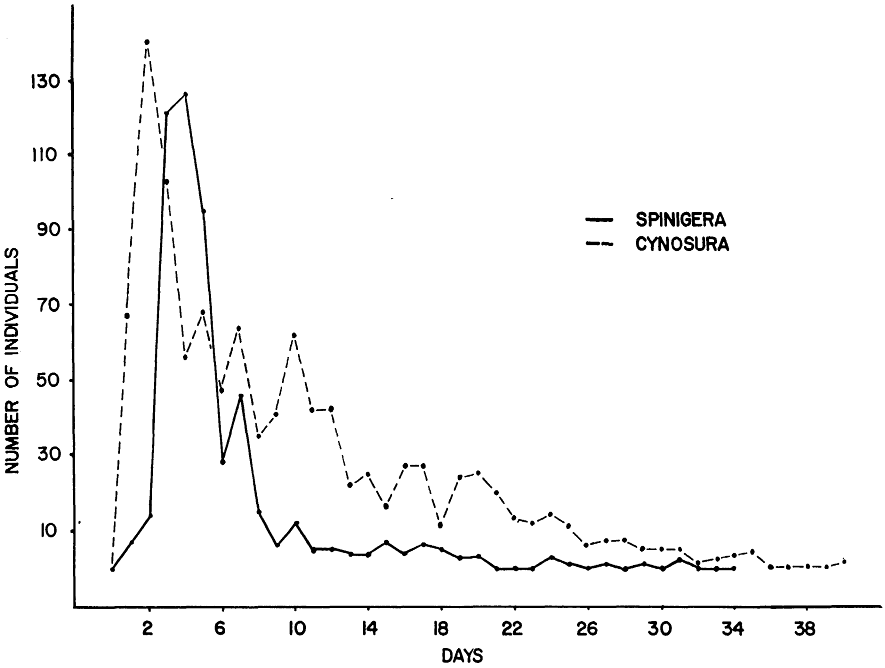

Fig. 7. Daily hatching rate of *Tetragoneuria cynosura* and *T. spinigera*, based on laboratory rearings, Douglas Lake, 1953.

this problem has not yet been investigated. Another interesting aspect of the situation regarding egg aggregations is the effect of their mass on the innermost eggs. When some of the large ones were pulled apart and examined in the field, the innermost eggs were totally undeveloped and appeared to be freshly deposited. The same condition was observed repeatedly in the laboratory in that portion of larger egg masses which rested on the bottom of the container. When some of these were turned over, the development which had been in progress in the upper eggs ceased and, after a two-week interval or more, eye spots appeared in some of the eggs which had previously been underneath. Very few of these retarded eggs hatched. Such undeveloped eggs can be observed even late in the fall, in the interior of eggs masses that have survived from the early summer deposition. In a single large egg mass the number of eggs thus prevented from developing is enormous; it approaches tens of thousands. In consequence of their aggregational egg-laying habits, therefore, these species pay a tremendous price in this peculiar type of mortality.

Prolarva

Immediately prior to hatching, rhythmic peristaltic pulsations occur in the head region of the embryo. These are followed by a swelling of this region, which Grieve (1937) attributed to the swallowing of the water in the amniotic cavity by the unhatched individual. The swelling of the head region increases the pressure on the amnion and serosa, which in a few minutes rupture and free the prolarva. Tillyard (1917) and others recognized that this first stage deserves special designation because of the considerable differences between it (the prolarva) and the remaining larval stages. The prolarval stage persists for so very few minutes (2, 2.5, and 3 minutes in three *cynosura* individuals) that it has been questioned whether it is merely an embryonic condition or a true postembryonic stage. I believe that the evidence for the latter interpretation is the more convincing, for the embryonic membranes (amnion and serosa) split and remain in the egg as the prolarva frees itself and at the first ecdysis, the cast skin is chitinous, complete and well formed, and shows every feature of the prolarval stage. This is a condition homologous to that which characterizes all subsequent ecdyses.

Some *Tetragoneuria* prolarvae remain attached to the egg at their posterior end, but the vast majority rise to the water surface and float there with no evident autonomous locomotion. Morphologically, the prolarva of each of the three species resembles a small amphipod (Fig. 6*b*); it is laterally compressed, gently convex dorsally, and the legs and labium project ventroposteriorly. Maximum measurements of a few features are: dorsal mid-line length, 1.55 mm.; head length, 0.24 mm.; width of the right half of the dorsum of the first abdominal segment, 0.3 mm. At the end of 2 to 4 minutes after hatching the first ecdysis occurs; it follows the pattern of odonate molting described by others for the later stages.

Although the prolarval stage differs from the later stages in morphology and in duration, it truly represents the first larval stage. Reckoning of odonate larval instars, however, as in most other insects, has always begun with the succeeding stage, known as the first-instar larva; hence, it seems preferable to conform to established usage. In the following discussions, however, it should be kept in mind that any given larval stage mentioned in reality represents one stage beyond its arbitrarily assigned number.

Larva

In discussing larval development, Snodgrass (1935) suggested that, from a physiological standpoint, the duration of a stadium should be reckoned from the time the old cuticula is loosened from the epidermis until the loosening occurs in the next stage. Although theoretically this is sound, determination of the time of loosening is scarcely practicable. Molting is the final physical manifestation of the underlying physiological change, and this change, in turn, is under hormonal control (Wigglesworth, 1954). Molting occurs at some time after the old cuticula has loosened, but the resulting larval stage persists until the next molting. The physiologic and morphologic durations are thus comparable in length, and molting may be taken as an easily observed and probably quite reliable index to the duration of a given stage. The number of any given molt does not, however, necessarily indicate the age of an individual, because under certain conditions a molt between two normally separate stadia may be skipped, while under others additional molts may be interpolated into the life history. By combining criteria of molts, exuvial characteristics, and size classes, I have been able to determine that, in addition to the prolarval stage, there are normally twelve larval stadia in both *cynosura* and *spinigera* and thirteen in *canis*. All three species exhibit some consolidation of stadia, but only in the range from the fifth to the seventh stages in *spinigera* and *cynosura* and from the eighth to tenth in *canis*. These consolidations have been dealt with by including the resulting stages in the best-fitting size class and by omitting them in determining the duration of stadia.

Duration of Larval Stadia

There is considerable variation in the duration of the larval stages of the three species, as well as in the length of a given stadium in each species. In *cynosura* and *spinigera* a trend of increase in average interval exists in the first four stadia, followed by a decrease to the seventh *(spinigera)* or eighth stage *(cynosura)*, after which there is again a marked increase. Larval development in *spinigera* proceeded faster through the middle stages and much more slowly through the last stages than it did in *cynosura*. The average length of the larval period was 320 days for *cynosura* and 375 days for *spinigera*; the last stadium occupied 32.8 percent of the total interval in *cynosura* and 48.5 percent in *spinigera* (see Table I). Although the data on *canis* are incomplete, a comparable trend of increasing duration of the later stages is evident. The single observation for this species on the length of the last stadium suggests that the final stadium constitutes a much higher percentage of the total life history in *canis* than it does in either *cynosura* or *spinigera*.

Records on individual specimens showed little or no correlation in extent between successive stadia in one individual, or between corresponding stadia in different individuals. The third stage averages long; it clearly is a period of very high mortality, as is evident from the small number of survivors from the third to the fourth stage in laboratory rearings. Both the length of this stadium and the low survival rate may be attributed to a change which occurs at this time in larval food habits, a shift from the capture of protozoan-sized prey to the larger microcrustacea and small tubificid worms. The relatively longer duration of the last stadium is undoubtedly related to the great amount of internal reorganization which takes place in the latter part of this stage in preparation for metamorphosis. The percentage of time spent in the final stadium by the larva of *cynosura* (32.8 percent) is closely comparable to that (35 percent) spent in this stage by the larva of *Erythemis simplicicollis* (Bick, 1941).

In sampling for larvae of *cynosura* and *spinigera* throughout the Lower Peninsula of Michigan, I found two "size classes" simultaneously present. In the early summer one class consisted of very early-instar larvae and the other of larvae in the eighth to tenth stadia; in late fall only eighth- to tenth-instar larvae and last-instar larvae were collected. Mutual occurrence of two size classes suggests that in their natural environment both

TABLE I

DURATION (IN DAYS) OF LARVAL STADIA IN MICHIGAN SPECIES OF *TETRAGONEURIA*

N represents number of individuals; $\bar{X}$ average number of days spent in stadium.

Instar	*cynosura*			*spinigera*			*canis*		
	N	$\bar{X}$	Range	N	$\bar{X}$	Range	N	$\bar{X}$	Range
1	96	10.8	5 - 21	39	14.8	8 - 24	3	6.3	5 - 7
2	56	15.6	8 - 30	21	15.4	9 - 26	1	8	.....
3	39	17.7	9 - 31	4	21.0	15 - 26	1	5	.....
4	1	31.0	.....	1	16	.....	..	.....	.....
5	1	23	.....	3	15.3	7 - 25	..	.....	.....
6	6	14.8	3 - 29	4	6.8	5 - 10	..	.....	.....
7	9	11.6	5 - 22	11	5.6	3 - 9	..	.....	.....
8	10	7.9	5 - 15	11	6.8	4 - 10	3	7+*	5+ - 8+*
9	10	10.8	9 - 14	11	9.4	5 - 14	3	12	12 - 12
10	11	20.1	10 - 42	11	18.2	14 - 21	3	28.7	18 - 39
11	5	51.8	35 - 69	7	64.0	40 - 89	5	55.8	36 - 82
12	1	105	......	1	182	......	1	74	118+ †
13 *(canis)*	..	.....	......	...	.....	......	..	317+ ‡	......
Average Total Time	..	320.1	......	..	375.3	......	..	.....	......
Range	..	.....	248 - 432	..	.....	308 - 452	..	.....	......

* Interval between collection and molting.

† Maximum duration for six individuals which died before molting.

‡ Maximum duration for ten individuals which died before transforming.

spinigera and *cynosura* spend two years in the immature state. Both species matured in about a year under laboratory conditions. Such an artificial environment, however, permits continuous and fairly constant growth, a situation that is not comparable in nature. In natural bodies of water, larval development is probably very slow or even absent during the period of low temperatures between the fall and spring turnovers. In Figure 8 length of larval stages (as determined in the laboratory) is related to field conditions. In plotting the occurrence of the fall and spring turnovers and then the average length of the stadia, virtually no adjustment had to be made to accommodate the field data. The high degree of correlation between the field and laboratory data when graphed in this manner verifies the existence of a 2-year larval life cycle in both species.

Field and laboratory data on *canis* larvae indicate, although they do not prove, a 3-year cycle for this species, in regions in which the other two persist only 2 years.

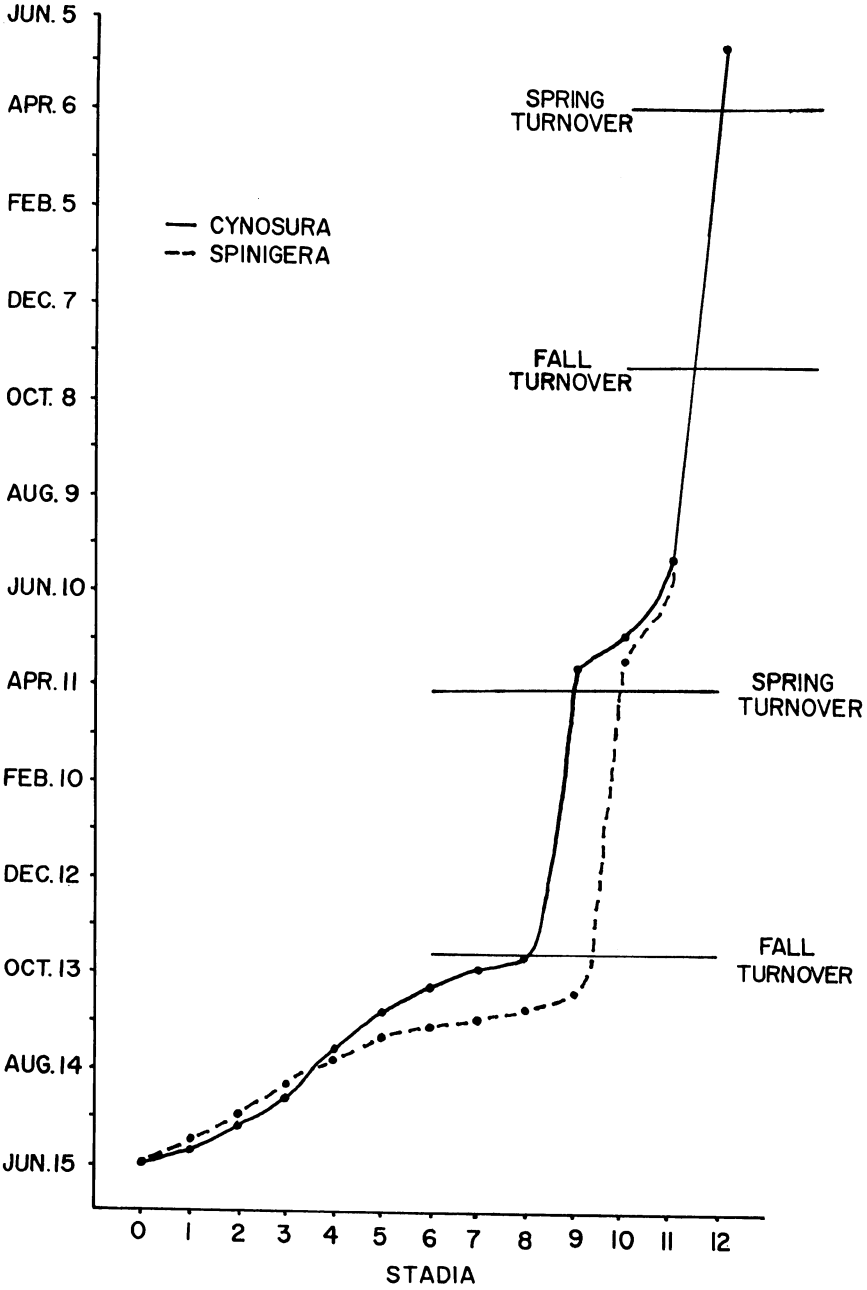

Fig. 8. Cumulative duration (in days) of larval stadia of *Tetragoneuria cynosura* and *T. spinigera*. An extrapolation of laboratory data to field conditions in Michigan. Note the nearly complete retardation of development between fall and spring turnovers.

Morphology of Larval Stadia

During their growth some features of the larvae of *cynosura, spinigera,* and *canis* remain the same from the time of initial appearance, whether in the first or a later instar, throughout the larval period. Many features, however, exhibit change in size, proportion, and number of parts; they may also develop structures not originally present.

The more salient of the constant larval features are those listed below, under the body part involved.

Head: (1) Slightly convex at the anterior margin; (2) almost straight or slightly concave at the posterior margin (Fig. 6*c*-*d*).

Labium: (1) Inner and outer margins of labial palpus entire; (2) movable hook as long as or 1/3 to 1/2 longer than the nearest palpal seta; (3) premental setae of the middle group 1/2 to much less than 1/2 the length of the nearest lateral premental seta (Fig. 6*e*-*i*).

Thorax: Legs disproportionately longer than body; larva has a "gangly" appearance, especially in the early stages.

Abdomen: (1) Widest at the posterior margin of the sixth segment, tapering gently anteriorly and posteriorly to the end of segment 8, posterior margin of segment 9 much narrower than posterior margin of segment 8; (2) first three segments viewed dorsally occupying about 1/5 the length of the abdomen; (3) superior, inferior, and lateral anal appendages gently tapering to a point, not curved.

Of the features which exhibit change, thirty-five that more or less demonstrate major ontogenetic alterations in the larvae of the three species were studied. Growth trends in all three may be appreciated by examining Figure 9. In that figure the development of a small-dimension and a large-dimension character for each species is displayed.

The principal data on the thirty-five variable features are summarized below (except for coloration) under the part involved.

Coloration: Pale to translucent through the 3d instar; darkening is gradual to the 5th instar, after which it does not intensify significantly. Final larval color is medium to dark brown with diffuse pale yellowish green areas on the abdomen.

Head: (1) Antennal segments increase from three to seven: three segments in the 1st and 2d instars of *cynosura, canis*, and *spinigera*; four in the 3d instar of *canis* and occasionally in that of the other two, which usually have five in the 3d, 4th, and 5th instars; six occasionally in the 5th and invariably in the 6th and 7th of *cynosura* and *spinigera*; seven in the remaining instars. As shown in Figure 10 for *cynosura*, segment 3 gives rise (by division) to segments 3, 4, and 5, when the increase is from three to five, and to segment 6 (by interpolation between the 3d and 4th segments), when the increase is from five to six. The same origins for corresponding segments are exhibited in *spinigera* (except that the source of segment 6 is not evident); that is, segment 3 retains its individuality and gives rise, (by division) to the next three segments. Segment 7 in both *cynosura* and *spinigera* presumably arises by division of segment 6, but my measurements do not demonstrate it. The data on *canis* did not cover this critical period (the 4th to 7th instars). (2) Head width/eye width increases from the first to the last instar: in *cynosura*, from 7.0 to 7.75; in *spinigera*, from 6.0 to 7.95; and in *canis*, from 6.0 to 6.45. Average head width in last-instar larvae in *cynosura* is 5.3 mm.; in *spinigera*, 5.8 mm.; and in *canis*, 5.5 mm. (3) Head width/head length increases from the first to the last instar: in *cynosura*, from 1.02 to 1.55; in *spinigera*, from 1.11 to 1.63; and in *canis*, from 1.05 to 1.70. (4) Cone-shaped knobs dorsally located at the junction of the epicranium and occiput, are present in the 1st instar (Fig. 6*d*). They increase in size until the 5th to 7th instar, rapidly decrease in the 8th and 9th instars, and are not evident in the 10th. The function of these processes is unknown; they are probably sensory and possibly tactile. Average

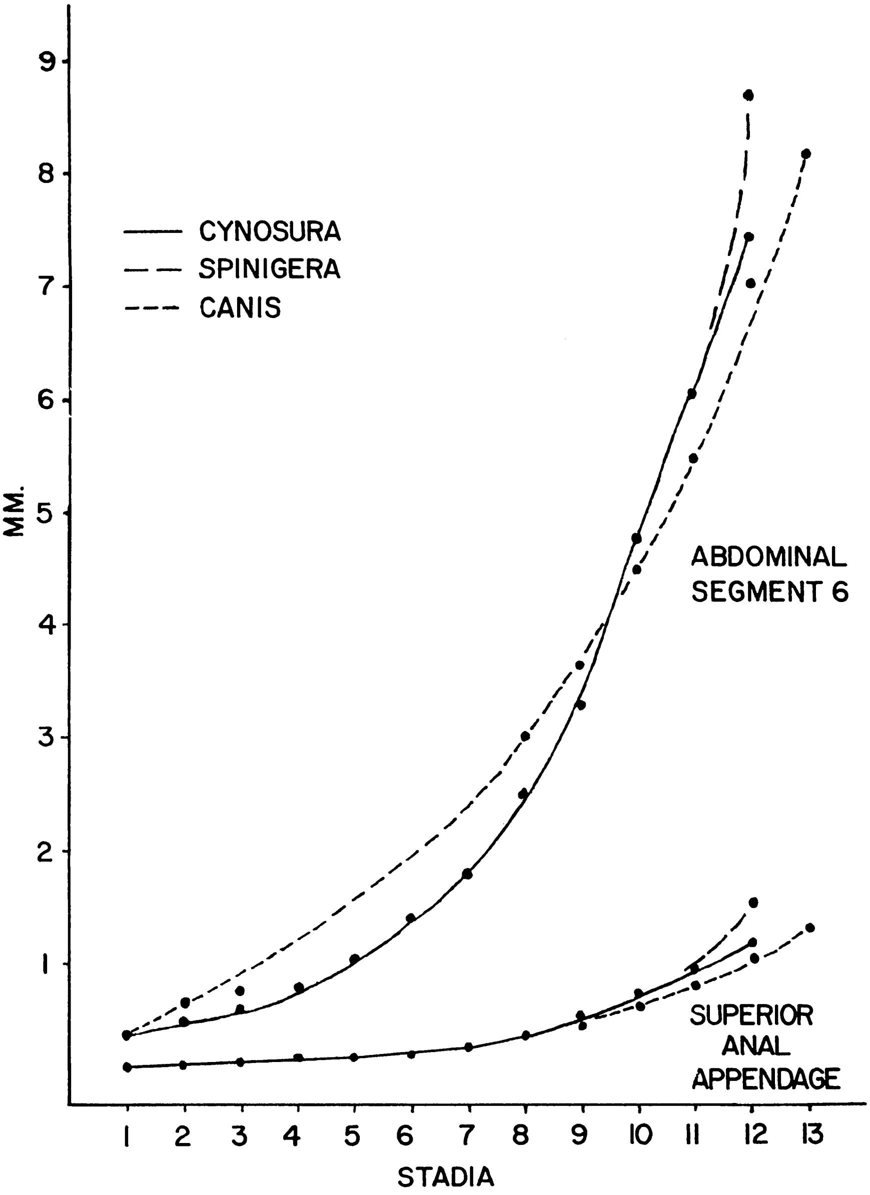

Fig. 9. Cumulative growth of small- and of large-dimension characters in *Tetragoneuria* larvae. Coincidence of growth curves of both characters in *spinigera* and *cynosura* is interrupted by a positive heterogony in *spinigera* from the 11th to 12th instars.

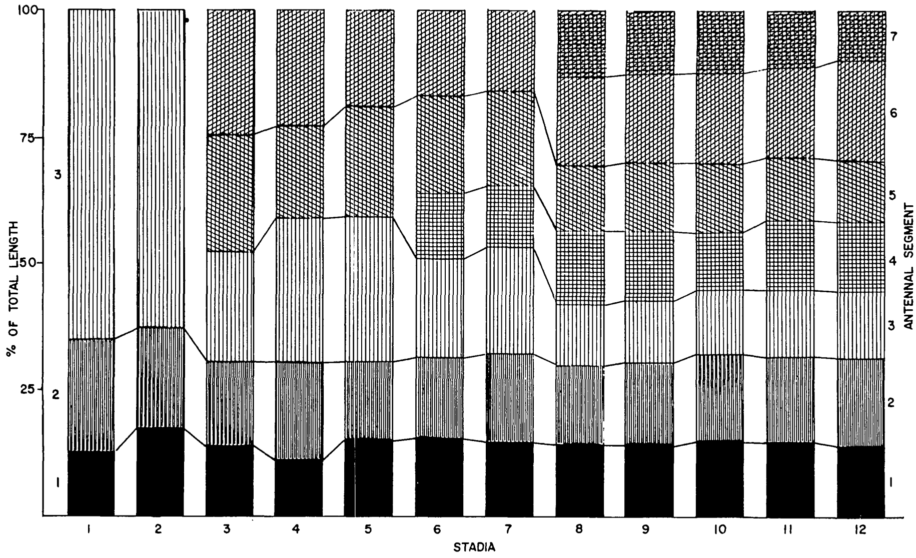

Fig. 10. Antennal development in *Tetragoneuria cynosura*. Note the percentage of total antennal length occupied by each segment in each of the twelve instars and the origin of segments by division of existing segments.

maximum height of the knobs in the 7th instar in *cynosura* is 0.20 mm.; in *spinigera*, 0.20 mm.; and in *canis*, 0.14 mm.

Labium: (1) Palpal setae increase from one to (usually) six in *cynosura*, and from one to seven or eight in *spinigera* and *canis*; they are not added in equal increments at each molt, but by the 10th instar in *cynosura* and *spinigera* and the 11th in *canis* the usual complement is reached. A few large last-instar larvae of *cynosura* had eight setae; none of the *spinigera* had as few as six and only the larger individuals had eight. Although association of more setae with larger size suggests a correlation between available basal area and number of setae,[6] the amount of variation in the final setal count makes this character unreliable for taxonomic purposes. (2) Premental setae increase from none to (usually) nine or ten in *cynosura* and to eleven or twelve in *spinigera* and *canis*; they are added somewhat more regularly than the lateral setae, usually one, occasionally two, at each molt; a full complement is usually attained by the 11th instar in *cynosura* and *spinigera* and by the 12th in *canis*. The long premental setae first appear in the 2d instar, the short in the 3d or 4th instar. (3) Spiniform setae on the inner and distal margins of the palpus and on the anterior (or distal) margin of the prementum do not appear until the 5th or 6th instar; thereafter they increase in number and differentiate in size; full complement is not attained until the last instar. (4) Distal margin of the palpus is coarsely serrate in the 1st and 2d instars; the serrations become coarsely crenulate in the 3d and 4th instars and then remain essentially unmodified. (5) Anterior (distal) margin of the prementum is very slightly convex in the 1st instar but gradually assumes the form of an obtuse angle with its apex at the mid-point.

Thorax: (1) Mesothoracic and metathoracic wing sheaths are first mere traces in the 7th instar in *cynosura* and *spinigera* (8th in *canis*). They become obvious in the 8th instar (9th in *canis*), increase in size rapidly through the remaining stages, and by the last instar reach the middle of the posterior margin of the sixth abdominal segment. Average

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[6] In his study of the development of the labium in *Sympetrum striolatum*, Corbet (1951*b*) made no allusion to a possible relationship of this kind.

wing-sheath length in last-instar larvae in *cynosura* is 6.06 mm.; in *spinigera*, 6.77 mm.; and in *canis*, 6.85 mm. (2) Tarsal segments increase from one to three; the second usually appears in the 3d instar, occasionally in the 2d; the third develops in the 5th or 6th. Individual segments increase in length more or less regularly; the first segment gives rise to the second segment by division and the second to the third.

Abdomen: (1) Length/maximum width decreases from the 1st to the last instar in *cynosura*, from 1.87 to 1.52; in *spinigera*, from 2.08 to 1.56; and in *canis*, from 1.92 to 1.66; that is, the larva tends to become relatively broader and shorter from the first to the last stage. Average abdominal length in last-instar larvae in *cynosura* is 11.3 mm.; in *spinigera*, 13.6 mm.; and in *canis*, 13.7 mm. (2) Lateral spines of the 9th abdominal segment, one on each side, appear in the 4th instar; they increase in length rather regularly throughout the remaining stages to an average of 1.67 mm. (max. 2.23 mm.) in *cynosura*, 2.18 mm. (max. 3.06 mm.) in *spinigera*, but only 0.82 (max. 0.93 mm.) in *canis*. In *cynosura* and *spinigera* the two spines reach the tips of the anal appendages in the 8th instar and show all gradations from parallel to moderately divaricate alignment. (3) Lateral spines of the 8th abdominal segment, one on each side, are not usually present until the 6th instar; they increase in length throughout the remaining stages, but the increment at each molt is small. Final average and maximum lengths in *cynosura* are 0.22 and 0.30 mm.; in *spinigera*, 0.27 and 0.30 mm.; and in *canis*, 0.33 and 0.40 mm. (4) Dorsal processes first appear in the 6th or 7th instar as small protuberances on segments 6 through 9; by the next stadium (8th or 9th) they are indicated on segments 2 through 9, the posterior ones the more prominent. In last-instar larvae the processes on segments 2 through 5 are spinelike and very gently curving posteriorly; those on segments 6 through 8 become progressively flattened to a cultriform appearance; the process on segment 9 is about half the height of that on segment 8, is much broader, and is low and cultriform. (5) Rudimentary lateral anal appendages appear in the 8th instar, increase more or less regularly thereafter, and attain average lengths of 0.85 mm. in *cynosura*; 1.17 mm. in *spinigera*; and 0.97 mm. in *canis*. They are occasionally, but not invariably, shorter in female larvae. (6) Sexual characters, as indicated by rudimentary gonopophyses on the 9th sternite, appear in male larvae as early as the 9th instar. Males are always identifiable in the 10th instar by this character and in the 11th gonopophyses are also present on the third sternite. Females may be reliably determined in the last instar by a rudimentary vulvar lamina between the 8th and 9th sternites, but are identifiable in the 10th and 11th by the lack of the male gonopophyses. In females, the superior anal appendage tapers uniformly to the tip; in males, it only tapers uniformly for one-half to two-thirds its length, then abruptly to the tip.

Although features of *canis* are included in the above account, some aspects of its life history merit further comment. I did not succeed in rearing this species and, hence, was unable to obtain exuviae of the 4th to 7th instars, but the morphology of the other stages gives every indication that its development is similar to that in *cynosura* and *spinigera* except for (1) the character of the development of the lateral spines of the 8th and 9th abdominal segments, (2) the presence of thirteen rather than twelve instars, and (3) the longer duration of the last instar and the probability, in consequence, of a longer life cycle in nature. In *canis* the spines of the 8th abdominal segment develop more rapidly and to a greater length and those of the 9th less rapidly and not so extensively as do both in *cynosura* and *spinigera*. Although the egg is somewhat larger in *canis*, the prolarva and first-instar larva are no larger than these stages in the other two species; the final larval stage is, on the average, intermediate in size between those of the other two species.

Needham (1901) described the last-instar larva (which he identified as

T. spinosa Hagen) in a key to *Tetragoneuria* "immatures," using the key character, "spines of the ninth segment distinctly shorter than that segment, and slightly incurved at tips." By repetition in keys Needham's identification has been tacitly accepted. The larva of *canis* is not mentioned in lists of "undescribed larvae," and it has never to my knowledge been unquestionably identified and acceptably described.

The general characters of *canis* larvae are like those of other forms of *Tetragoneuria* described by Needham (1901). I found *canis* intermediate in size between *cynosura* and *spinigera* but closer to *spinigera*. Its setal counts are similar to those of *spinigera*; that is, seven or eight palpal setae, and eight long plus four short (or seven plus five) setae on each half of the prementum. The lateral spines of the 8th abdominal segment are relatively longer and those of the 9th segment are considerably shorter than in the other two species. As Needham supposed, the lateral spines of the 9th segment barely reach the tips of the anal appendages, a condition attained in the 8th or 9th instar in both *cynosura* and *spinigera*. The dorsal abdominal processes are as he described them for the other species, but are barely one-half as high.

Comparative Morphology of Last Instar

In most insects the reliable stages for larval identification are the very late ones, and in closely related species only the ultimate larva or nymph can be determined to species with any degree of certainty. This is also true for *cynosura* and *spinigera* (see also the previous section). The two are very similar throughout their development, a fact which precludes separation of their larvae by linear measurements, proportions, or morphology in the first eleven instars; even in the last instar they can be distinguished from each other only with considerable reservation and doubt. On the other hand, *canis*, with its characteristically shorter spines of the 9th segment, offers no such problem; its larvae, at least in the ultimate and penultimate instars, are readily recognized.

Results of statistical analysis of seventeen characters (the parameters of four are illustrated in Figure 11) of the three species showed that: (1) Male exuviae do not differ significantly from female exuviae with respect to any of the characters involved; they are distinguished by their gonopophyses and the difference in tapering of the superior anal appendage. (2) The average coefficient of variation is 9.40 (5.24 - 18.00) for *cynosura*; 5.86 (2.60 - 13.05) for *spinigera*; and 5.77 (2.06 - 15.10) for *canis*. The higher degree of variability which appears to exist in *cynosura* is probably a result of the weighting of the *cynosura* sample (the majority of the individuals of *cynosura* are from the southern part of the state, where they are relatively smaller). (3) The most variable and, therefore, taxonomically the least reliable characters in the three species are the lengths of the 3d and 4th antennal segments and the length of, and distance between, the lateral spines of the 9th segment in *cynosura* and *spinigera*. (4) *Cynosura* and *spinigera* differ significantly in the means of all characters except the length of the 4th antennal segment; they therefore represent two different species or at least two populations with different means.

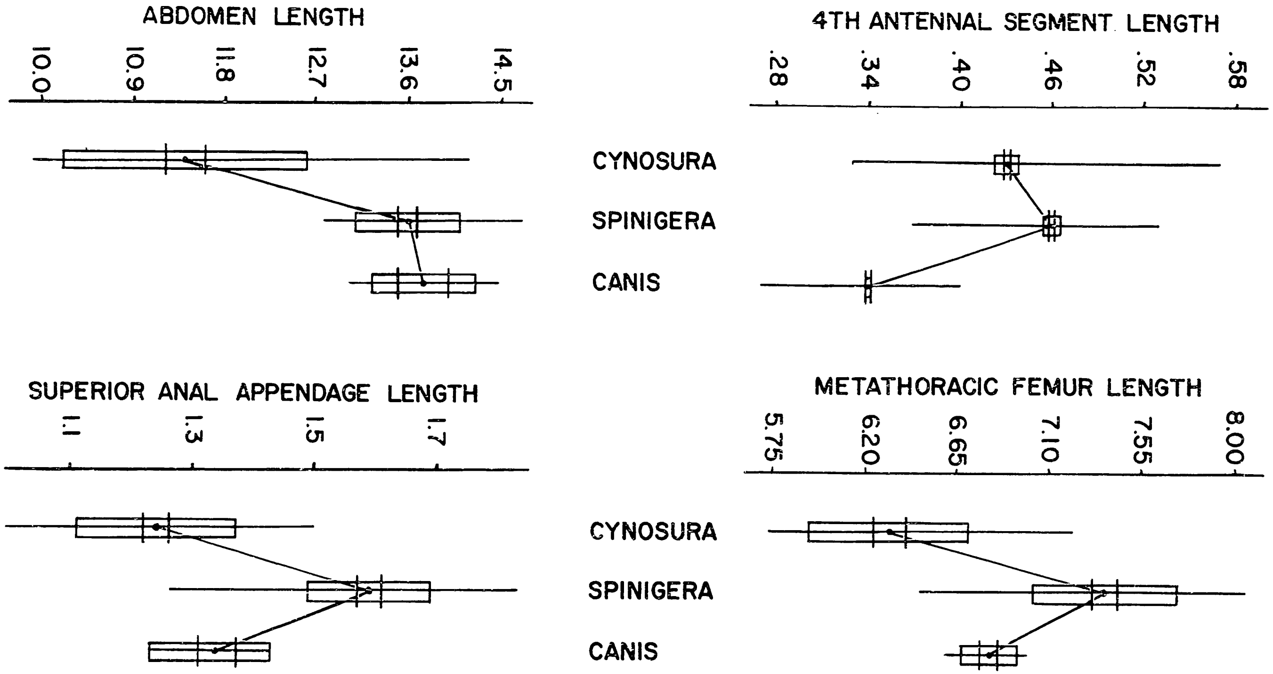

Fig. 11. Comparison of statistical parameters in four characters of male last-instar larvae of Michigan species of *Tetragoneuria*. Measurements (mm.) of length of 4th antennal segment, metathoracic femur, abdomen, and superior anal appendages. Chart symbols: mean (dot), standard error of mean (cross bars), standard deviation (rectangle), and range (vertical line).

(5) Exuviae of *cynosura* and *spinigera* have a joint nonoverlap in excess of 90 percent in the distribution curves of only three characters; namely, those of the length of the metathoracic femur, abdomen, and superior anal appendage.

Since their morphological development is virtually identical, it is not surprising to find no reliable way of separating these species by linear measurements. It was at first thought that differentiating characters might be found in setal number or in some aspect of the lateral spines of the 9th segment, but the high degree of variability in both precludes their use as reliable taxonomic features.

In a key to the larval stages of *Tetragoneuria*, Needham and Westfall (1955) stated that the lateral spines of the 9th abdominal segment of *spinigera* are divergent; those of *cynosura* and *canis* parallel. For *canis* this apparently holds, but in the other two species these spines vary from parallel to divergent. When a graded series of *spinigera* and *cynosura* is examined the amount of such divergence appears to be a function of the width of segment 9. These authors also stated that in *spinigera* the side margin of segment 8 is distinctly concave before the base of the spine, and the dorsal hooks large. Actually, very few *spinigera* larvae have such a concavity and the side margin is essentially uniform to the base of the spine, which may be somewhat swollen; any apparent concavity is caused by the basal swelling of the spine. This is also true for *cynosura.* In addition, Needham and Westfall reported that *cynosura* averages 22 mm. in length, the lateral spines of the 9th segment are as long as the width of that segment, and the dorsal hooks are large, rough-clad and scurfy. The size given is larger (by 1.5 mm.) than my results for the Michigan material and is closer to the average found in northernmost populations of the species. Total length, however, is always an unreliable characteristic, owing to expansions and contractions of the nonsclerotized sutures. I found the dorsal processes of *cynosura* indistinguishable from those of *spinigera.* The relation of the lateral spines of the 9th segment to the length of segment 9 varied from specimen to specimen in my series and was subjected to regressional analysis. The value of the correlation coefficient was found to be extremely low *(i.e., r* is .25 in *cynosura* and .12 in *spinigera)* and the regression lines overlapped considerably.

Search for proportional differences between the last-instar larvae of *cynosura* and *spinigera* revealed that: (1) The only characters which have a fairly high and consistent correlation are the lengths of the 3d and 4th antennal segments. The magnitude and slope of the regression lines, however, are such as to render untenable the use of this set of characters. (2) Correlation in the other sets of characters is too low to give any reliability to their use, even though the *spinigera* and *cynosura* regression lines are considerably separated. (3) In all instances difficulty would be encountered among the larger *cynosura* larvae, since minor errors of measurement of either member of a set of characters might throw the specimen onto the line of *spinigera.*

In summary, separation of the larger *cynosura* larvae from the smaller *spinigera* ones as individuals is extremely difficult if not impossible (see Pl. II). All the analytic results indicate that the relationship between *cynosura* and *spinigera* is extremely close, whereas that between these two species and *canis* is much more distant.

Growth Rates

Of 5000 species of Odonata the complete life histories of some twenty-five are known. Thirteen of these had been described, when Calvert (1929) reviewed the subject of growth rates in Odonata. Interest in life history and growth rate has been revived in recent years by G. H. Bick in the United States; P. S. Corbet and A. E. Gardner, in England; and S. Asahina, in Japan. My study adds two life histories that are complete and one that is nearly complete (the first among the cordulines).

Growth rates in Odonata have generally been determined by the Brooks-Przibram method. This method, here briefly described, is based on the numerical relationship in growth which Brooks (1886) found in the stomatopod crustacean *Coronis*. It was formalized as "Brooks' Law" by Fowler (1909) in his work on Ostracoda: "During early growth each stage increases at each moult by a fixed percentage of its length, which is approximately constant for the species and sex." This ratio of increase is known as the "growth factor" and was suggested by Brooks to be 1.25. Apparently independently of Brooks' findings and Fowler's application of this growth factor, Przibram and Megusar (1912), from their studies on the Egyptian mantid *Sphodromantis bioculata*, reached essentially the same conclusion, for they proposed very nearly the same growth factor, namely, 1.26. The relationship described by Brooks and by Przibram and Megusar is now known as the Brooks-Przibram growth factor. This is numerically equivalent to $1/1.26^n$, where n is one less than the number of intervening instars. Although the proposed growth factor was based on a limited number of observations, it has been substantiated in subsequent studies by Calvert (1929, 1934) and Bick (1941) on Odonata, and by Kesling (1953) and Kesling and Soronen (1957) on Ostracoda, among others.

In this study the growth factor in each instar for six characters, representative of the three body regions, of the three species was calculated. The average of these individual growth factors is tabulated below.

Character	*cynosura*	*spinigera*	*canis*
Total Length	1.27	1.28	1.23
Head Width	1.27	1.27	1.26
Abdomen Length	1.28	1.31	1.30
6th Abdominal Segment Width	1.30	1.34	1.29
Prothoracic Tibia Length	1.21	1.24	1.22
Inferior Anal Appendage Length	1.26	1.31	1.26

These results indicate that the mean of the average growth factors for these six characters is close to the ideal of 1.26 in *cynosura* (1.27) and *canis* (1.26), but is somewhat higher (1.29) in *spinigera*. None of these differences is significant, however. Further, my findings agree with Calvert's (1934) for *Anax junius* and those of Bick (1941) for *Erythemis* *simplicicollis* and they corroborate Calvert's conclusions that the rate of growth "*(a)* varies from instar to instar, *(b)* is different for different parts in the same instar, *(c)* is higher on the whole in those parts... which are to be functional in the adult than in those the significance of which is larval rather than imaginal." Calvert's third conclusion is supported by my data on wing-sheath length, which are not presented here.

The ratio of initial to maximum larval measurements was calculated for seventeen characters which are present throughout development and which are not (as are the antennae and tarsi) subject to multiplication of parts. Results obtained by this analysis showed that: (1) there was considerable variation in the growth ratio of the various characters; (2) thoracic characters exhibited a trend toward a higher rate of development posteriorly, while the abdominal characters did not; (3) in *cynosura*, head width, length of metathoracic tibia, and length of inferior anal appendage agreed closely with the results predicted by the Brooks-Przibram formula, but in *spinigera* only the length of the mesothoracic tibia and in *canis* only the length of the 9th abdominal segment showed such agreement; the remaining characters of the three species differ more or less markedly in growth rate from that predicted; (4) the average of the ratios of initial to maximum size of the seventeen characters in each species is slightly below expectation in *canis* (expected 1:16.0; obtained 1:15.3), but considerably above it in *cynosura* (expected 1:12.7; obtained 1:14.3) and *spinigera* (expected 1:12.7; obtained 1:16.7). A closer approximation to the average growth-factor ratio is: for *cynosura*, $1/1.275^{11} = 1/14.47$; for *spinigera*, $1/1.29^{11} = 1/16.42$.

Growth rates of *cynosura* and *spinigera*, when compared for all stages, are, with a few exceptions, essentially the same through the first to eleventh instars but are markedly different in the last instar. Figure 9 illustrates this difference with respect to the growth of a large- and of a small-dimension character in the two species. The trend is essentially isogonic in both through the eleventh instar, but is positively heterogonic in *spinigera* from the eleventh to the twelfth. The average growth factor in this ecdysis, based on thirty-two characters, is 1.31 for *cynosura* and 1.47 for *spinigera*. In all but six essentially isogonic characters *spinigera* exhibits a considerably higher growth rate in the next to the last ecdysis than does *cynosura*.

COMPARATIVE MORPHOLOGY OF ADULT MICHIGAN TETRAGONEURIA

Comparison of specimens of *cynosura* and *spinigera* from northern and southern Michigan showed that the northern individuals were larger and had a darker body coloration, and those of *cynosura* also had a darker and more extensive hindwing marking. Comparable regional color and size differences were lacking in specimens of *canis*, the result undoubtedly of its more limited distribution in the state. Earlier, Muttkowski (1915) said of the color phenomenon: "color development is from south to north; that is, the farther north, the more color on the wings of a given species of *Tetragoneuria*," and Walker (1941) stated: "in the region immediately north of Lake Superior this species [*spinigera*] appears of uniformly larger size than elsewhere. In general northern specimens are somewhat larger than southern, but the Lake Superior form appears to be a local race." Since the observations strongly suggested the presence of clines in *cynosura* and *spinigera* rather than well-defined geographic races (subspecies), I sought (1) to decide which of these two situations exists in each species and (2) to discover what characters are taxonomically reliable for distinguishing the three species from one another. The results are given in the following sections. Failure of regional differentiation in color and/or size in *canis* and the collection of only five individuals that approximate *spinigera suffusa* made it impossible to carry out an analysis comparable to that given the *cynosura* complex.

The *cynosura* Complex

Individuals of *Tetragoneuria cynosura* may be separated into groups according to the color types established for the species by Muttkowski (1911). Because of this and because my material for *cynosura* was more adequate than for the other two, as an initial step, I determined by statistical analysis the relationship between northern and southern populations of this species. These populations were proved to be in fact different. The significant differences between the means and distribution curves are discussed below.

Localized populations of *cynosura*, comprising 152 males and 62 females, were sorted into three types on the basis of the extent of the hindwing color pattern. These types I designated as: (1) *cynosura "cynosura,"* those in which the hindwing marking reached the base of the triangle or less (20 males and 8 females from the Southern Lower Peninsula); (2) *cynosura* "intermediate *simulans*," those in which the marking extended beyond the base but not to the tip of the triangle (40 males and no females from the Southern Lower Peninsula); (3) *cynosura "simulans,"* those in which the marking extended to the tip of the triangle and beyond (47 males and 34 females from the Southern Lower Peninsula, 30 males and 14 females from the Northern Lower Peninsula, and 15 males and 6 females from the Southern Upper Peninsula.) The mensurable morphology of each sex in the three groups was determined for nineteen characters. An analysis was made of the difference in the distribution curves of the measured characters employing the conventional level of subspecific difference which, according to Mayr, *et al.* (1953), is a C. D. value at or above 1.28. At this level, "75 percent of population A [is] different from 97 percent of population B. Then about 90 percent of the individuals of A are different from about 90 percent of the individuals of B." In making this analysis I assumed that the distribution curves are normal and that the sample mean is the population mean.

The first step was to compare the three groups of *cynosura* from the Southern Lower Peninsula, sorted as described above on the extent of the hindwing marking, these results showed: (1) there is no actual difference in the means or ranges of linear measurements between the males and females; (2) the maximum difference in the means of any of the measured characters is 0.1 mm. in the males, 0.2 mm. in the females; (3) very pronounced statistical "subspecific" identity is indicated in all characters of the males and females, the maximum amount of nonoverlap is 12 percent for males in the length of the superior anal appendage and about 80 percent for females in the length of the forewing; (4) no "intermediate *simulans*" are recognizable among the females, although they are among the males.

The second step was to compare southern and northern populations of cynosura *"simulans."* Here the findings indicated that: (1) in populations from the two areas there are apparent differences in the means and ranges of linear measurements for both sexes; (2) Northern Lower Peninsula males are statistically "subspecifically" different from Southern Lower Peninsula males in ten characters and Northern Lower Peninsula females from Southern Lower Peninsula females in ten characters, nine of which are the same as in the males; (3) Southern Upper Peninsula males and females are statistically "subspecifically" identical with Southern Lower Peninsula males and females in all characters except the width of abdominal segment 6; (4) Northern Lower Peninsula males are statistically "subspecifically" identical with Southern Upper Peninsula males except in head width, and the females from the two regions are statistically "subspecifically" identical in fourteen of the nineteen characters but show strong differences in the remaining five.

Results of the foregoing may be summarized as follows. First, there is no mensurable divergence within the arbitrarily distinguished samples (based on extent of hindwing marking) into which the southern Michigan collections were broken down. Second, in *cynosura "simulans"* there is no mensurable divergence between Southern Upper Peninsula and Southern Lower Peninsula populations; (2) there is slight mensurable divergence between Southern Upper Peninsula and Northern Lower Peninsula populations; and (3) there is considerable mensurable divergence between Northern and Southern Lower Peninsula populations. Although the disparities between the Southern Upper Peninsula and Northern Lower Peninsula populations of *cynosura "simulans"* and Southern Lower Peninsula populations of it indicate that the alleged subspecies *"simulans"* is not a geographic race, they strongly suggest the existence of a size gradient from south to north (see Regional Differentiation, below).

Morphologically, aside from variation in hindwing marking and in degree of darkness of body color, there is no characteristic that is exclusively restricted to either the "typical" or the *"simulans"* "subspecies." In any localized population, individual variability is extremely high in such characters as the frontal "T"-spot, which may be completely absent to fully formed, and the color of the thoracic pile, which varies from grayish white to medium brown. Davis (1933) stated that *simulans* lacks a transparent area between the radius and cubitus; however, I found this feature is too inconstant to be taxonomically reliable. In any localized population some individuals will have the space transparent for a considerable length but others lack it altogether.

In conclusion, the analysis of mensurable and morphological characters in population samples of the *cynosura* complex, sorted to "typical" *cynosura*, "intermediates," and *cynosura "simulans,"* reveals no reliable characteristics to support the view that the typical and *simulans* forms are subspecifically different. Because of the high probability that there is clinal variation in color in both *cynosura* and *spinigera* (see below), it seems most unlikely that two subspecies, differing only in color, exist.

Regional Differentiation

The regional differences in size and color that can be observed in *cynosura* and *spinigera* are so great that many of them are obvious to the eye, and with a little experience one can easily distinguish northern from southern specimens by size alone. These differences have possible taxonomic implications, the significance of which is here assessed.

Size gradient: The most obvious environmental correlation of the south-to-north size increase is with temperature. According to studies on various holometabolous insects reviewed by Uvarov (1931), a decrease in temperature results in a corresponding increase in adult size. He stated: "This increase in size at low temperature lengthens the larval life and [increases the] total amount of food taken by the larva, while the percentage of food absorbed and utilized for building up the tissues is greater than at high temperature." Apparently, such a relationship of size to temperature also exists in the hemimetabolous Odonata, since in *cynosura* and *spinigera* a northward size increase accompanies diminution of annual mean temperature (Figs. 1 and 12). In Figure 12 characters representative of different parts of the body are plotted regionally to show their correlation with mean annual temperatures. Minor deviations on the size-gradient line may represent the action of microclimatic conditions modulating the effects of the mean annual temperatures. Even if one assumes that the temperature-size relationship has a causal basis, it must be affected by other factors and can scarcely exhibit an exact correspondence. In *spinigera* adults the following relations appear to exist between mean annual temperatures and measurements: for each one-degree decrease in temperature (F.), the length of the prothoracic tibia increases about 0.08 mm.; head width about 0.06 mm.; length of segment 6 about 0.05 mm.; and length of forewing about 0.05 mm. Decreased temperature appears to favor the growth of the legs, because their growth rate increases faster than that of other body parts.

Although a size cline from south to north undoubtedly occurs in *cynosura*, as well as in *spinigera*, the relationship to temperature (Fig. 12) is not so apparent. Study of additional populations of *cynosura* between Douglas Lake (Northern Lower Peninsula) and southeastern Michigan will probably reveal a situation quite similar to that which exists in *spinigera*. The disparity between the Douglas Lake and the Lake Mary (Upper Lower Peninsula) populations is very likely the result of microclimatic influences. Presence of a size cline from south to north in *cynosura* would explain the significant statistical differences that exist between its southern and northern populations.

Color gradient: Regional variation in coloration is almost as striking

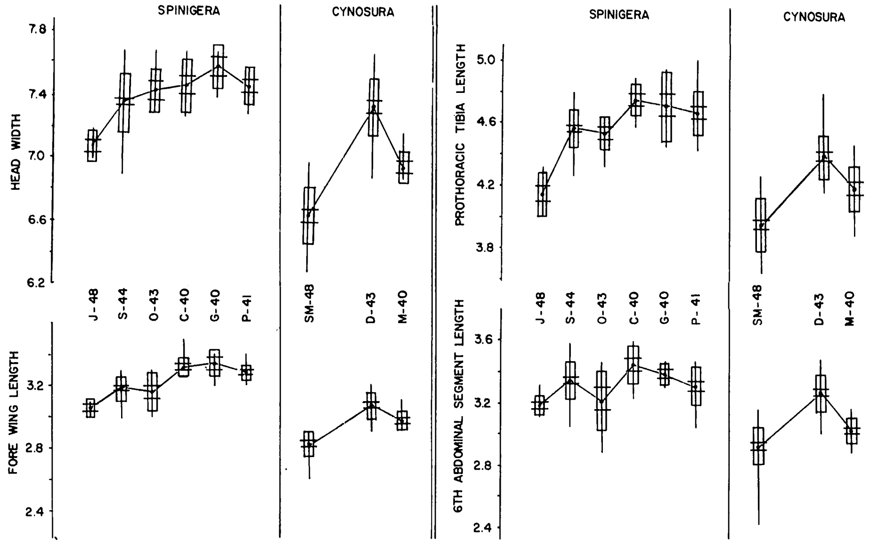

Fig. 12. Clinal variation in size in four characters in adult males of *Tetragoneuria cynosura* and *T. spinigera*. All measurements in mm. except length of forewing which is in cm. Abbreviations: J=Joslin Lake, S=Lake St. Helen, O=Otsego Lake, C=Cisco Lake, G=Gogebic Lake, P=Perch Lake, SM=Southern Michigan lakes, D=Douglas Lake, M=Lake Mary; the number following an abbreviation is the mean annual Farenheit temperature. Chart symbols same as for Figure 11.

a phenomenon as is that in size. Specimens of *cynosura* from the southern United States differ so strongly from those taken in Michigan in color as well as size that they appear to be different taxa. Even within the 400-mile length of Michigan the progressive darkening from medium to dark brown approaching black in *cynosura* and *spinigera* is clearly evident as one proceeds north.

In addition to the northward darkening trend in general body color, the basal hindwing marking of *cynosura* becomes darker and extends farther out on the wing membrane. The typical *"cynosura"* wing marking is found in populations from the Gulf Coast to the central states, where the marking reaches the extent characteristic of *"simulans."* According to B. E. Montgomery (*in lit.*, April 11, 1953), both the *"cynosura"* and *"simulans"* patterns occur at least as far south as Clark County in southeastern Indiana. Both these coloration types range northward as far as the Southern Lower Peninsula of Michigan, with the relative numbers of *"simulans"* increasing as one proceeds north. Northward from southern Michigan the *"simulans"* markings become more extensive and darker, eventually becoming black (Pl. III).

Undoubtedly, the south-to-north color change in body and wings is a temperature-related phenomenon. Only on such an hypothesis am I able to explain the presence of the *"cynosura"* form as far north as Oceana County on the Lake Michigan shoreline. Isotherms of annual temperature are bent strongly northward along the Lake Michigan shore and the prevailingly higher temperatures in the counties bordering the lake should tend to produce the "*cynosura*" coloration rather than the "*simulans*," which occurs inland at the same latitude. An analogy can be drawn with the experimental results obtained by Knight (1922) on the pentatomid *Perillus bioculatus* and by Parker (1930) on the orthopterans *Melanoplus m. mexicanus* and *Camnula pellucida*; in all of these forms progressive darkening accompanied the decrease in temperature at which they were reared.

In order to test the effects of temperature on color in *Tetragoneuria*, forty last-instar larvae of *spinigera* and forty of *cynosura* were collected in mid-April, 1954, for rearing under controlled conditions. Fourteen of each group (controls) were kept at room temperature (about 70^{0} F.) without prior chilling. The rest were first subjected to refrigeration at 2^{0}C., half of them for 5 weeks the other half for 10 weeks, and then reared at the same room temperature as the controls. Results were: (1) In the nonchilled group, body color and hindwing marking were less dark than in field-caught samples of the populations from the same locality where the larvae were obtained; this group emerged in the laboratory about 4 weeks earlier than those in the field. (2) In the group chilled for 5 weeks, body color and hindwing marking color were about as dark as in the normal population; this group emerged in the laboratory at about the time emergence was occurring in the field. (3) In the group chilled for 10 weeks, body coloration and hindwing marking were considerably darker than in the normal populations. While the color varied from less dark to dark in both species, the extent of the hindwing marking showed no change in *spinigera* with either period of chilling. However, in the laboratory-reared *cynosura*, as compared with field-caught samples from the locality where the larvae were obtained, the extent of the hindwing marking averaged less than normal in the nonchilled group; normal in the group chilled for 5 weeks; considerably above normal in the group chilled 10 weeks.

The conclusions to be drawn from laboratory results are that the same factor(s) operates in *cynosura* and *spinigera* to determine body coloration and hindwing marking color, but that extension of the hindwing marking in *cynosura* is caused by some other factor(s). Both (sets of) factors appear to be directly related to temperature. Under field conditions, as well as in the laboratory, the hindwing marking in *spinigera*, although not always typical, shows only individual variation, without any geographic trend such as occurs in *cynosura*. Of the five specimens of "*T. spinigera suffusa*" Davis (the dark form reported here for the first time from Michigan), four are from Roscommon County, near the presently known southern limits of *spinigera*, and one is from Luce County, not far from the northern limits of the species.

Interspecific Differentiation

In order to ascertain, if possible, what the reliable taxonomic characters for separating the three species are, 319 males and 153 females representing localized populations of *cynosura*, *spinigera*, and *canis* were examined and comparatively analyzed for nineteen characters. The individuals of *cynosura* used are those listed in the section on the *cynosura* complex. Of *spinigera*, 126 males and 64 females, were analyzed: Northern Upper Peninsula (22♂, 16♀); Southern Upper Peninsula (10♂, 4♀); Northern Lower Peninsula (7♂, 9♀); Central Lower Peninsula (81♂, 24♀); Southern Lower Peninsula (6♂, 11♀). The analysis of *canis* was based on 41 males and 27 females: Northern Upper Peninsula (20♂, 6♀); Southern Upper Peninsula (9♂, 13♀); Northern Lower Peninsula (5♂, 5♀); Central Lower Peninsula (7♂, 3♀).

Size relations of the males of the three species are demonstrated graphically in Figure 13. Females exhibit almost the same relationships. In the males, the linear measurements of the nineteen characters of *cynosura*, *spinigera*, and *canis* overlap in virtually every character. Although most often used to distinguish subspecies, the coefficient of difference seems applicable on the interspecific level, because it measures the degree of overlap of the distribution curves of homologous characters. Data on the males show that: (1) the means of most characters are significantly different; all characters overlap except the length of the superior anal appendage in *spinigera* and *canis*; limited variability is exhibited by all characters except the width of the 6th abdominal segment in *cynosura*. Hence, all these characters are taxonomically reliable. (2) Statistically significant differences in the means of the nineteen characters occur as follows: *(a)* in all characters between *cynosura* and *canis*; *(b)* in all characters between *cynosura* and *spinigera*; *(c)* in all characters, except stigma length, total length, abdomen length, and width of the 6th abdominal segment, between *canis* and *spinigera*. (3) Within the assumptions of the coefficient of difference: *(a) cynosura* is separable from *canis* by the lengths of abdominal segment 6 and the superior anal appendage in at least 96 percent of the individuals of each species; *(b) cynosura* is separable from *spinigera* by the lengths of the metathoracic femur and superior anal appendage in at least 95 percent and by the lengths of the mesothoracic and metathoracic tibiae and abdominal segment 9 in at least 90 percent; *(c) canis* is separable from *spinigera* by the length of the superior anal appendage in more than 99 percent and by the length of the inferior anal appendage in at least 94 percent.

Morphologically, the males of the three species are distinct from each other in the form of the superior anal appendage. These appendages have been described by Muttkowski (1911), but for purposes of clarity, the following notations are presented to accompany Plate IV *(a-c')*. The superior anal appendage in *cynosura* has an inferior angle at the basal third and usually a lateral ridge about two-thirds the length of the appendage; the tip is subacute to rounded. In *spinigera*, there is a ventromedially directed spine at the basal third, and no lateral ridge; the tip is subacute to rounded. In *canis*, it has a ventral tubercle at the basal third, and occasionally a slight lateral ridge; the tip is more or less truncate and is declinate beyond a superior anteapical tubercle.

Aside from the superior anal appendage, no other morphological characters were found to be diagnostic of the males of any of the three species. The "T"-spot on the frons that is supposed to be always present in *spinigera* is sometimes absent; supposed to be never present in *canis*, it is

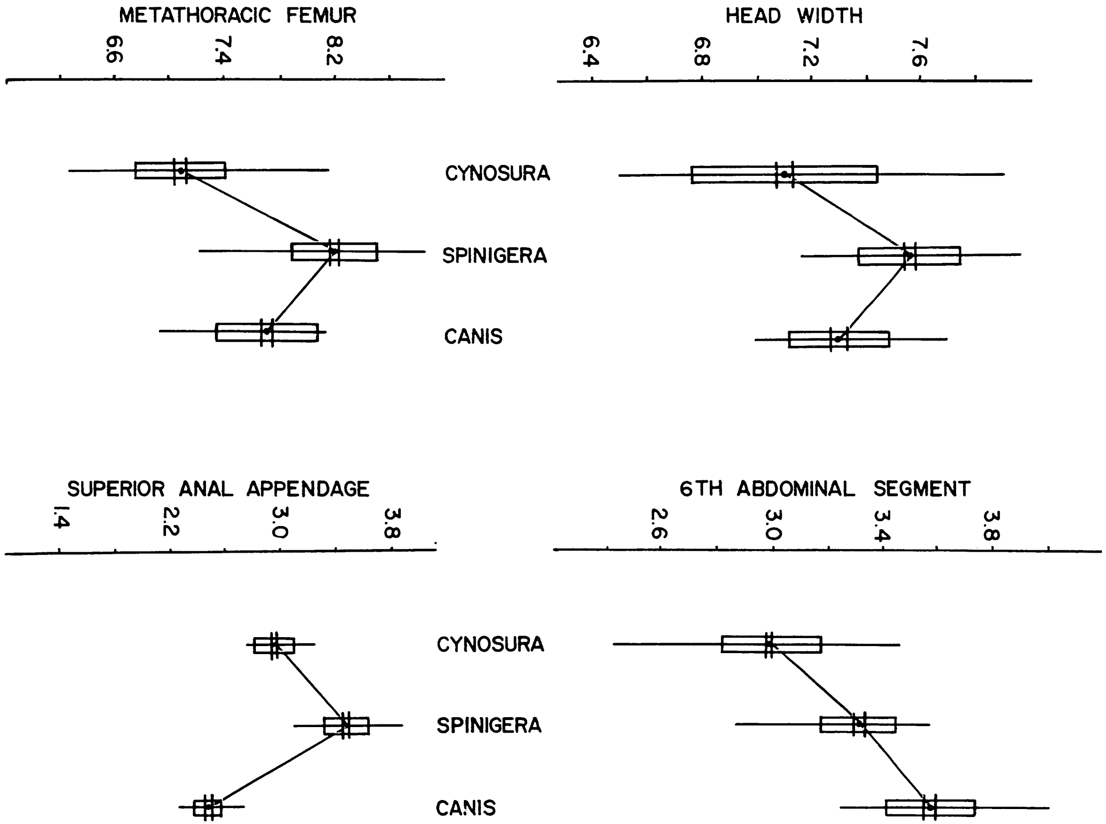

Fig. 13. Comparison of statistical parameters in four characters of adult males of the three species of Michigan *Tetragoneuria*. All measurements in mm. Chart symbols same as for Figure 11.

often represented by a substantial stem; supposed to be sometimes present in *cynosura*, it may show all gradations from complete absence to a fully formed "T." With respect to wing coloration, both pairs are often flavescent throughout the greater part of their length in *canis*; frequently so in *spinigera*; never in *cynosura*. Nevertheless, analyses of the males give statistical support for the distinctness of the three species.

Similar data on the size relations of females were obtained; they conformed closely with those of the males, except as follows: (1) The ranges of all characters except the length of segment 6 in *cynosura* and *canis* and the length of the superior anal appendage in *cynosura* and *spinigera* overlap. (2) There are statistically significant differences in the means of *(a)* all characters between *cynosura* and *spinigera*; *(b)* all characters between *cynosura* and *canis*; *(c)* twelve characters between *spinigera* and *canis*, with the exception of the lengths of the mesothoracic and metathoracic tibiae, stigma, abdomen, abdominal segments 3 and 9, and total length. (3) Within the assumptions of the coefficient of difference: *(a) cynosura* is separable from *canis* by the lengths of the stigma, abdomen, and total length in at least 95 percent of the individuals of both species, and by the lengths of the mesothoracic tibia and 9th abdominal segment in at least 90 percent; *(b) cynosura* is separable from *spinigera* by the lengths of the abdomen and the 6th abdominal segment in at least 95 percent of the individuals of both species, and by the lengths of the metathoracic femur, stigma, abdominal segment 3, and total length in at least 90 percent; *(c) canis* is separable from *spinigera* by the width of the stigma and length of the vulvar lamina in at least 91 percent of the individuals of both species.

Females as well as males lack unique species characters other than those of the genital structures. The morphology of the distinctive vulvar laminae has been cursorily described by Muttkowski (1911); those of *cynosura* and *spinigera* he figured. A more complete description of the vulvar lamina than has hitherto been published for each species is given below and the laminae are also illustrated (Pl. IV *d-f*). In *cynosura*, outer faces of processes divaricate two-thirds their length, then gently recurving; inner faces slightly divaricate one-third their length, strongly divaricate for the next one-sixth, then more or less parallel to the tips; processes moderately inflated throughout, their tips subacute and parallel; space between processes distinctly U-shaped with an abruptly narrowed proximal stem. Length (mm.), 2.09 ± .13 (1.79-2.37). In *spinigera*, outer faces of processes divaricate one-half their length, then strongly recurving; inner faces moderately divaricate one-third their length, strongly divaricate the next one-third, then equally strongly recurving toward one another distad; processes moderately inflated throughout, their tips truncate to rounded and convergent; space between processes distinctly ovoid or goblet-shaped with an abruptly narrowed proximal stem. Length (mm.), 2.47 ± .18 (2.10-2.84). In *canis*, outer faces of processes divaricate three-fourths their length, then very slightly recurving mesad; inner faces uniformly and moderately divaricate their entire length; processes strongly inflated giving a robust appearance, their tips subacute and divergent; space between processes distinctly V-shaped and without an abruptly narrowed proximal stem. Length (mm.), 2.05 ± .08 (1.89-2.16).

Evidence furnished by analyses of the females provides further statistical support for the distinctness of the three species. The significant linear features and especially the differences in length of the superior anal appendage, offer additional means of separating the females.

TAXONOMY OF TETRAGONEURIA

Some of the difficulties inherent in evaluating the taxonomy of the genus *Tetragoneuria* may be inferred from the prior treatment accorded it. Muttkowski (1911, 1915) recognized ten species, two subspecies; Needham and Heywood (1929) four species, one subspecies indirectly in key; Davis (1933) nine species, three subspecies; and Needham and Westfall (1955) admitted ten species but no subspecies. Subsequent to the revisionary studies by Muttkowski and by Davis, only one species has been described, *T. sepia* Gloyd (1933), based upon a male from Greenville, Florida. The validity of *sepia* has been established by Westfall, who obtained additional males (1941) and described the female and larva (1951).

Up to the present time taxonomic separation has been based largely on the morphology of the superior anal appendage of the male. The similarity between these appendages in several species caused difficulty in identification and added to the uncertainty of determining systematic status. Since there was no sure way of distinguishing females of the different species from one another, identification had to be based primarily upon their association with the male.

Of the eleven nominal species and three nominal subspecies of *Tetragoneuria* described, the six reported from Michigan are: *T. cynosura cynosura* (Say), *T. c. simulans* Muttkowski, *T. spinigera spinigera* (Selys), *T. s. suffusa* Davis (in this paper), *T. canis* MacLachlan, and *T. morio* Muttkowski. Of them, I recognize only *cynosura*, *spinigera* and *canis* as valid (see below). These three species are similar in the following features: (1) Ecology of adult: late spring to early summer season; northward progression of season; territorial and reproductive behavior of the male; patrol, feeding, copulatory, and swarming flight styles. (2) Life history: ovoid egg shape; morphology of prolarvae and of 1st through 10th instar larvae; carnivorous diet; discontinuous and clumped distribution in a lake (or pond). (3) Adult morphology: general (nonmorphometric) morphology; accessory genitalia of the males; physical incompatibility in interspecific copulation. The data pertaining to comparisons among the three species are presented in Table II (pp. 72-73).

Tetragoneuria cynosura (Say)

Libellula cynosura Say, 1839. Jour. Acad. Nat. Sci. Phila., 8: 30-31. Not figured.

Tetragoneuria cynosura simulans Muttkowski, 1911. Bull. Wisconsin Nat. Hist. Soc., 9(3): 95, 106. Wings figured. [New synonymy.]

Tetragoneuria morio Muttkowski, 1911. Bull. Wisconsin Nat. Hist. Soc., 9(3): 96, 125-27. Appendages ♂(?), ♀, figured. [New synonymy.]

Tetragoneuria cynosura (Say) is a distinct taxonomic entity, worthy of the species recognition initially accorded it. The larva is morphologically separable from *canis* but not from *spinigera*. It is, however, physiologically distinguishable from *spinigera* in hatching rate, duration of stadia, and in lacking a final heterogonic spurt in growth rate (which in *spinigera* produces a marked terminal rise in the growth curve). As imagos, both sexes of *cynosura* are morphologically distinct from *spinigera* and *canis*, especially in their reproductive structures, that is, the superior anal appendages of the male and the vulvar lamina and superior anal appendages of the female. The nature of the structures constitute the chief effective factor in establishing reproductive isolation between the three species, as a result of physical incompatibility in copulation. Ecological differences among them are not so striking, but, nevertheless, have been found; these relate to seasonal occurrence, diurnal behavior, precopulatory behavior of the female, habitat, and distribution.

Muttkowski's forma *"simulans"* was raised to subspecific rank by Davis (1933), who designated Bluffton, Indiana, the type locality (the type locality of *T. c. cynosura* (Say) is Massachusetts). On the basis of the studies reported here I conclude that the *cynosura* complex consists of a one-species population, showing clinal variations in size, general body color, and basal hindwing marking from south to north. Of *cynosura* and *simulans* forms it may be said that: (1) their life histories are identical; (2) they cannot be distinguished on the basis of mensurable characters, since such differences as do obtain are the result of a temperature-related size cline extending from south to north; (3) they cannot be distinguished morphologically except by the basal hindwing marking, which exhibits a temperature-related cline in its extent and coloration from south to north; (4) in certain areas of southern Michigan, as well as south of this region, the two forms occur together.

In treating clinal variation, Hubbell (1954) has pointed out that it is characters and not populations that show clinal change, and that clines cannot be considered taxonomic units. He expresses a widely accepted view in stating that where clinal change is gradual or where two or more noncoincident clines exist in a population it is inadvisable to attempt to distinguish parts of the population as subspecies. Treatment of clinal variation as variation and not as grounds for subspecific recognition is the least arbitrary and most objective manner of dealing with this type of situation, and the evidence seems cónclusive that *T. cynosura simulans* Muttkowski should be synonymized with *T. cynosura* (Say). If the extremes of the cline need to be designated, the phrases "light wing" and "dark wing" may be appended to the specific name.

Tetragoneuria morio Muttkowski is placed in synonymy because I regard it as an invalid species. It was described from the holotypic male (Milwaukee Public Museum), the allotypic female (UMMZ), a paratypic male (U. S. National Museum), and a paratypic female from Detroit (UMMZ), all of which I have examined. Since its description, the species has been reported only once from New Hampshire and Massachusetts (Howe, 1919). Through the kindness of A. G. Humes, I examined one of the three Massachusetts specimens in Howe's collection; this female from Concord, Massachusetts, May 26, 1918, is *T. cynosura* (Say). According to Muttkowski, the "male appendages in dorsal view [are] like those of *spinigera*, that is twice recurved and with tips approximated. In lateral view [they are] somewhat like *cynosura*, but with a longer, slightly produced angle, and no lateral ridge." The figures of the superior appendages on the lower left of Muttkowski's plate are said to have been drawn from the holotype and are like those of the type and paratype males which I have examined. Neither the figure nor the type specimens agree with the description, especially as regards the claimed similarities to *spinigera*. The lower right-hand figure of the superior appendages does agree with the description given but, as Davis wrote in reply to a query from E. B. Williamson, "We do not know the source of the lower right hand figure."

I believe that the type and paratypic male of *T. morio* Muttkowski are actually *cynosura* males; the species *morio* is, therefore, synonymized with *T. cynosura* (Say). The appendages of the male types of *morio* that I examined are unlike those of *spinigera* dorsally; in fact, many specimens of *spinigera* do not have the "twice recurved, tips approximated" feature. They lack distinct lateral ridges, although there is a slight indication of a ridge on the right member in the paratypic male. In *cynosura* males it is not uncommon to find the lateral ridge more or less indistinct on one or both appendages; in most cases, however, the ridge is present and distinct on both. The superior appendages of *cynosura* males are not uniform in either the pronounced nature of the basal angle or the degree of divarication of the tips; they conform to a definite pattern, but there is considerable variation within that pattern. My measurements of the types agree with Muttkowski's and both sets lie well within the range found in *cynosura*. The remainder of the original description applies equally to *cynosura* and *morio*.

The females of *T. morio* are characterized by Muttkowski as follows, "The vulvars like those of *spinigera*. Appendages somewhat stouter and longer. The wings with fuscous in the anal field, usually only along the veins out to the level of the triangle." In the allotypic and paratypic females the vulvar lamina in *morio* is indistinguishable from that in *spinigera*, varying slightly from the "typical" but being well within the range of variability of this character. The allotype appendages are "somewhat longer and stouter" than those of the paratypic female, but again both are well within the range of variation shown by *spinigera* in this regard. The fuscous color marking of the hindwing is of the same type as that in specimens which I initially treated as "intermediate" *spinigera*. In no respect are these two females in the type series of *morio* distinct from the *spinigera* population; they are, therefore, assigned to *T. spinigera* (Selys).

Tetragoneuria spinigera (Selys)

Cordulia spinigera Selys, 1861. Bull. Acad. Belg., (2)31: 269-70. Not figured.
Tetragoneuria spinigera suffusa Davis, 1933. Bull. Brooklyn Ent. Soc., 28: 100-01. Body, ♂, ♀, figured. [New synonymy.]

Tetragoneuria spinigera (Selys) is a distinct taxonomic entity, worthy of the species recognition initially accorded it. In its adult morphology, physiological life history, and aspects of its ecology it is distinct from *cynosura*; in its morphological life history and adult morphology it is distinct from *canis*, but it is similar to that species in ecology and distribution.

Davis established the subspecies *suffusa* upon the basis of a difference from typical *spinigera* in hindwing marking. The type locality for *suffusa* is Hudson Highlands, New York; that for *T. spinigera* (Selys) is simply "Canada." As the name implies, in *suffusa* the dark mark on the hindwing is spread out in a smoky suffusion over a larger part of the wing than is usual for *spinigera*; by contrast this spot in *cynosura* forma *"simulans"* is deeply colored and sharply bounded. To my knowledge, *T. s. suffusa* has not been recorded since its description, even in regions where its occurrence might be anticipated (cf. Whitehouse, 1941, 1948; Walker, 1941); the only individuals, other than the types, known to me are five that I collected in the course of the present study.

The dark *"suffusa"* form and the "intermediates" are indistinguishable from the typical form except in hindwing coloration, in which they show no regular geographic gradient. This does not suggest a cline in wing coloration; instead, the data are compatible with the concept that the variation is genetically determined in a manner unrelated to climate. The situation in *spinigera* seems essentially unlike that in *cynosura*, as indicated both by the geographic pattern and by the results of rearing experiments designed to test the effect of temperature upon the size and intensity of the markings. In *cynosura*, there is a cline in which the extent and intensity of the dark marking of the hindwing increase to the north, with lowering of temperature; also, the larvae reared at lower temperatures produce adults in which the spots are larger and darker than in field-collected counterparts. In *spinigera*, by contrast, an increase in infumation of the hindwing shows no geographic regularity, and larvae reared at the lower temperatures show only an intensification of the coloration of the hindwing spot but no increase in its size and no spreading of a smoky suffusion over the wing. In *spinigera*, then, the genetic factor(s) responsible for the infumation seems to be independent of those affecting the size and intensity of the spot; and of the genetic factor(s) affecting the spot, only those related to its intensity and not to its size show a relation to temperature. Considering that the small amount of variation in the spot marking is well within the limits of variability to be expected in a species population, and that *"suffusa"* is only the extreme of a condition encountered in about half the individuals examined, it seems evident that *suffusa* Davis should be synonymized under *spinigera* (Selys). If the *"suffusa"* coloration needs designation for purposes of discussion, it may be spoken of as the suffused or "suffusa" phase of *T. spinigera* (Selys).

Tetragoneuria canis MacLachlan

Tetragoneuria canis MacLachlan, 1886, Ent. Mon. Mag., 23: 104-05. Not figured.

Tetragoneuria canis MacLachlan is a distinct taxonomic entity, worthy of the species recognition initially accorded it. No subspecies have been recognized and none are suggested as a result of my study. The last-instar larva is morphologically distinguishable from both *cynosura* and *spinigera*, as well as physiologically, by having a growth factor lower than those of the two other species and by having thirteen rather than twelve larval stages. The imagos of both sexes of *canis* are morphologically distinct from those of *cynosura* and *spinigera*, especially as regards their reproductive structures. Ecological differences between *canis* and the other two species are not striking, but have been shown with respect to seasonal occurrence, diurnal behavior, precopulatory behavior of the female, habitat, and distribution. *T. canis* is ecologically most like *spinigera* and most unlike *cynosura*.

KEYS TO MICHIGAN SPECIES OF TETRAGONEURIA

Adults and last-instar larvae may be identified as members of the genus *Tetragoneuria* by the generic keys of Wright and Peterson (1944) and Needham and Westfall (1955), but the keys to species given by the last-named authors are unreliable, especially the one for the immatures. The keys below are intended only to separate the species found in the Great Lakes region.

Adult Males

1. Superior anal appendage with apical third sharply declinate beyond a superior anteapical tubercle; tip more or less truncate. . . . . *canis*
   Superior anal appendage not declinate and with no anteapical tubercle; tip subacute to rounded *2*
2. Superior anal appendage with a lateroventral angle at the basal third . . . . . *cynosura*
   Superior anal appendage without a lateroventral angle but with a ventromedially directed spine at the basal third . . . . *spinigera*

Adult Females

1. Vulvar lamina strongly inflated, robust in appearance, inner faces of processes uniformly but narrowly divaricate to tip, outer faces divaricate three-fourths their length and then very slightly recurving, space between processes V-shaped; length of lamina (mm.), 2.05 (1.89-2.16); length of superior anal appendages (mm.), 2.29 (2.10-2.63) . . . . *canis*
   Vulvar lamina not or only moderately inflated, inner and outer faces not uniformly nor narrowly divaricate to tip, space between processes not V-shaped. *2*
2. Superior anal appendages barely as long as or shorter than vulvar lamina, tips pointed, length (mm.), 1.76 (1.42-2.26); vulvar lamina with tips subacute and parallel, space between processes U-shaped; length of lamina (mm.), 2.09 (1.79-2.37). . *cynosura*
   Superior anal appendages more than one-third longer than vulvar lamina, tips rounded, length (mm.), 3.18 (2.84-3.63); vulvar lamina with tips truncate to rounded and convergent, space between processes ovoid or goblet-shaped; length of lamina (mm.), 2.47 (2.10-2.84) . . . . *spinigera*

TABLE II

SUMMARY OF COMPARISONS AMONG MICHIGAN SPECIES OF *TETRAGONEURIA*

CHARACTERISTIC	*T. cynosura* (Say)	*T. spinigera* (Selys)	*T. canis* MacLachlan
ECOLOGY OF ADULT			
Length of Flight Season	5 1/2 weeks	5 1/2 weeks	6 weeks ±
Seasonal Occurence in a given Region	Latest, but overlaps	Intermediate, but overlaps	Earliest, but overlaps
Emergence Temperature	Warmest	Intermediate	Coldest
Emergence Rate	Explosive	Explosive	?
Emergence Rate/Sex	Same	Same	?
Emergence Period	3 weeks	?	?
Sex Ratio	1:1 to 2 ♂: 3 ♀	1:1	(1:1)?
Life Span	2 weeks ±	2 weeks ±	?
Flight Speed	Slowest	Fastest	Intermediate
Mating Peak	Late afternoon	Early evening	Early evening
Precopulatory Behavior of ♀	Straight abdomen	Deflected abdomen	Deflected abdomen
Oviposition	Direct sunlight	Sunlight and dusk	Sunlight and dusk
Egg Strings	Large clusters	Large clusters	(Large clusters)?
HABITAT	Eutrophic marl-forming lakes	Eutrophic-dystrophic lakes, usually nonmarl-forming	Dystrophic bog lakes, ponds, and slow streams
DISTRIBUTION			
North America	Temperate	More boreal than temperate	More boreal than temperate
Michigan	Throughout	Northern half, rare in southern half	Northern half only
LIFE HISTORY			
Egg Size at Eye Spot	0.69 mm. x 0.38 mm.	0.75 mm. x 0.40 mm.	0.80 mm. x 0.45 mm.
Eclosion Rate	Explosive, 50% in one week	Explosive, 83% in one week	?
Number of Larval Instars	12	12	13

11th and 12th Instar Larvae	Like *spinigera*	Like *cynosura*	Distinguishable from *cynosura* and *spinigera*
Development Rate	Initially slower than *spinigera*	Initially faster than *cynosura*	Initially faster than both *cynosura* and *spinigera*
Life Span, laboratory	One year	One year	1 1/2 - 2 years
Life Span, in field	Two years	Two years	Three years?
Percentage of Days in Last Stadium	33%	48%	(above 50%)?
Average Growth Factor	1.275	1.29	1.26
Growth Factor, 11th to 12th Instar	1.31	1.47	1.27
Metamorphic Changes	Same	Same	?
MORPHOLOGY OF ADULT			
Body Size	Smallest	Largest	Intermediate, close to *spinigera*
Difference in Means and Distribution Ranges of Characters in ♂ and ♀	Significantly different from *spinigera* and *canis*	Significantly different from *cynosura* and *canis*	Significantly different from *cynosura* and *spinigera*
Superior Anal Appendages of ♂	Distinct from *spinigera* and *canis*	Distinct from *cynosura* and *canis*	Distinct from *cynosura* and *spinigera*
Superior Anal Appendages of ♀	Distinct from *spinigera*	Distinct from *cynosura*	Intermediate between *cynosura* and *spinigera*
Vulvar Lamina ♀	Distinct from *spinigera* and *canis*	Distinct from *cynosura* and *canis*	Distinct from *cynosura* and *spinigera*
REGIONAL DIFFERENTIATION			
Size Cline	Yes	Yes	(Yes)?
Body Color Cline	Yes	Yes	(Yes)?
Wing Marking Cline			
Increase in Intensity	Yes	Yes	(Yes)?
Increase in Extent	Yes	No	(No)?

Last-instar Larvae

1. Lateral spine of the 9th abdominal segment short, barely attaining the level of the tips of the anal appendages. . . . .*canis*
Lateral spine of the 9th abdominal segment long, usually extending twice its length beyond the tips of the anal appendage . . . . *spinigera* and *cynosura*

The last-instar larvae of *spinigera* and *cynosura* are indistinguishable as individuals, except by association with adults or from known mutually exclusive habitats, or (in early season in nonexclusive habitats) by the earlier seasonal appearance of *spinigera*. The two may also be distinguished by a difference in the growth rate from the 11th to 12th instars, since that of *spinigera* is much higher. As populations they are significantly different in a number of characters: *spinigera* averages larger; small individuals are most likely to be *cynosura*.

Eggs

The method of oviposition by members of *Tetragoneuria* is unlike that of other Odonata of Michigan. Eggs are deposited in gelatinous strings, typically about 11 cm. long and 3-4 mm. wide, and the strings are usually found in aggregations. The eggs of the three species may be distinguished, at the eye-spot stage of embryonic development, by having the following dimensions:

1. Length 0.8 mm., width 0.45 mm. . . . .*canis*
2. Length 0.69 mm., width 0.38 mm. . . . . *cynosura*
3. Length 0.75 mm., width 0.40 mm. . . . . *spinigera*

SUMMARY

The population-species concept was applied to the ecology, life history, and morphology of the six taxa of the genus *Tetragoneuria* that occur in Michigan and in the Great Lakes region. On the basis of my four-year study, the evidence from these disciplines shows that (1) *Tetragoneuria cynosura* (Say), *T. spinigera* (Selys), and *T. canis* MacLachlan are valid species; (2) *T. morio* Muttkowski is a synonym of *T. cynosura* (Say); and (3) the subspecies *T. cynosura simulans* Muttkowski and *T. spinigera suffusa* Davis are clinal variants without taxonomic status.

Adult males and females of *Tetragoneuria cynosura*, *T. spinigera*, and *T. canis* can be distinguished by the morphology of the superior anal appendage in the male and the vulvar lamina in the female. The species are characterized by statistically significant differences in a number of mensurable features.

Last-instar larvae of *Tetragoneuria canis* can be separated from *T. cynosura* and *T. spinigera* by the length of the lateral spine on each side of the 9th abdominal segment. But no dependable morphological characters serve to separate individual last-instar larvae of *cynosura* and *spinigera*; populations of last-instar larvae of these two species can be distinguished by virtue of a statistically significant larger size in *spinigera.*

Temperature-related clinal variation of a nonstepped nature from south to north exists in size and general body color in *Tetragoneuria cynosura* and *T. spinigera* and in extent and nature of the basal hindwing marking of *cynosura.* Variation in the hindwing marking in *spinigera* is unrelated to variation in temperature.

Life histories, complete for *Tetragoneuria cynosura* and *T. spinigera* and nearly complete for *T. canis*, are described. The first two species have a two-year larval period of twelve stadia; that of *canis* is three years with thirteen stadia. Eggs of the three species are distinguishable only by size; the prolarva and first through tenth-instar larvae are inseparable morphologically, as are the last two instars of *cynosura* and *spinigera.* Physiological differences exist in the average growth factor in the three species and between *cynosura* and *spinigera* in eclosion rates, duration of stadia, and in the manifestation by *spinigera* of a positive heterogony in growth rate from the eleventh to twelfth instar.

Ecological data on *Tetragoneuria cynosura*, *T. spinigera*, and (though less complete) on *T. canis* are discussed. The three species are similar in length and northward progression of season, duration of adult life, explosive emergence, maturation period, territorial behavior of the male, flight styles, oviposition, diet, larval distribution in a lake, and metamorphosis. They differ in geographic distribution, habitat, adaptation to lower temperature, flight speed, seasonal occurrence, diurnal peaks of activity, and precopulatory behavior of the female.

Taxonomic relationships of the three species are discussed and keys are included for adult males, adult females, last-instar larvae, and eggs.

CONCLUSIONS

Application of the principles of population analysis to the genus *Tetragoneuria* Hagen has shown the value of this approach, not only for determining taxonomic entities and testing the validity of their distinguishing characters, but also for obtaining evidence on the degree of relationship among taxa. In replacing the older type-species concept, the population-species concept of the new systematics presents numerous opportunities for objective re-evaluation of the classification of groups in which, as is true in many Odonata, minor morphological differences have been virtually the sole basis for separating supposed entities. *Tetragoneuria* is such a group: the taxonomic characters which had been used were not only few but rather minor; several of its recognized forms, in consequence, have dubious status. In the study reported here, two subspecies and one species, previously thought distinct when studied by Muttkowski and others under the then prevailing typological concept, are synonymized. From the population viewpoint it is evident that these forms are merely variants, parts of species populations which exhibit clinal variation in size and coloration. Considered as populations, the three species *Tetragoneuria cynosura*, *T. spinigera*, and *T. canis* were found to be distinct as immatures and adults on the basis of linear measurements; the measurements not only differ significantly in their means but also have significant degrees of nonoverlap of distribution curves for many characters. In addition, the various lines of evidence derived from the study of these species (as populations) have revealed degrees of relationships not previously evident. Of these relationships, those of primary interest are the closeness of that between *cynosura* and *spinigera* and the rather distant one that exists between those two and *canis*.

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PLATES

PLATE I

Egg-string aggregation of *Tetragoneuria cynosura*. Cedar Hedge Lake, Grand Traverse Co., 1954. The mass (indicated by arrow) is attached to the stick; several loose ends of egg strings are evident.

PLATE I

PLATE II

Last-instar exuviae of Michigan species of *Tetragoneuria*. Left, *T. cynosura* (Say), First Sister Lake, Washtenaw Co., 1954; center, *T. spinigera* (Selys), Lake St. Helen, Roscommon Co., 1954 (note extreme similarity of these two exuviae); right, *T. canis* MacLachlan, Lake Simcoe, Ontario (E. M. Walker Collection). The *canis* specimen is one of the largest examined.

PLATE II

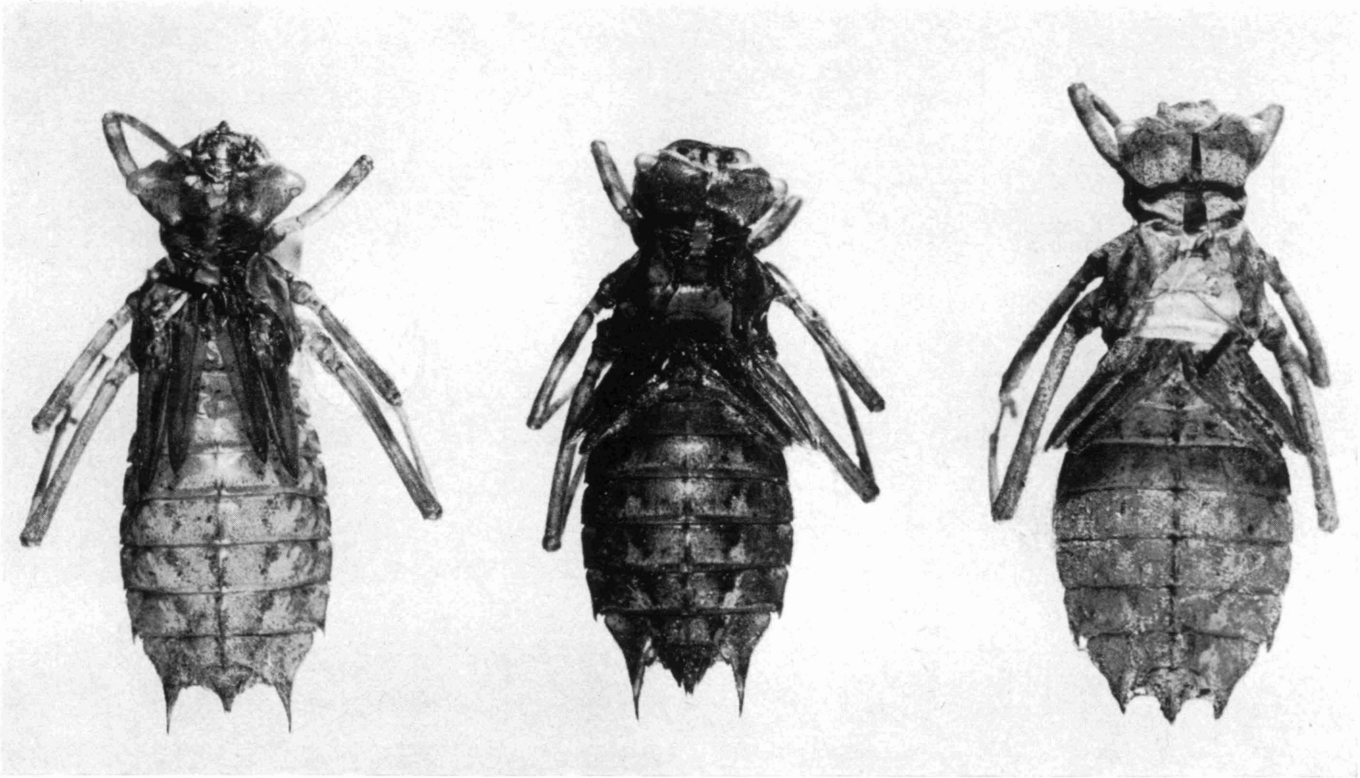


PLATE III

Clinal variation in hindwing marking of *Tetragoneuria cynosura*. The males (top and center) are from Joslin Lake, Washtenaw Co., 1954, and illustrate the variation in localized populations in southern Michigan; the male (bottom) is from Douglas Lake, Cheboygan Co., 1953, and illustrates the maximum extent of basal marking.

PLATE III

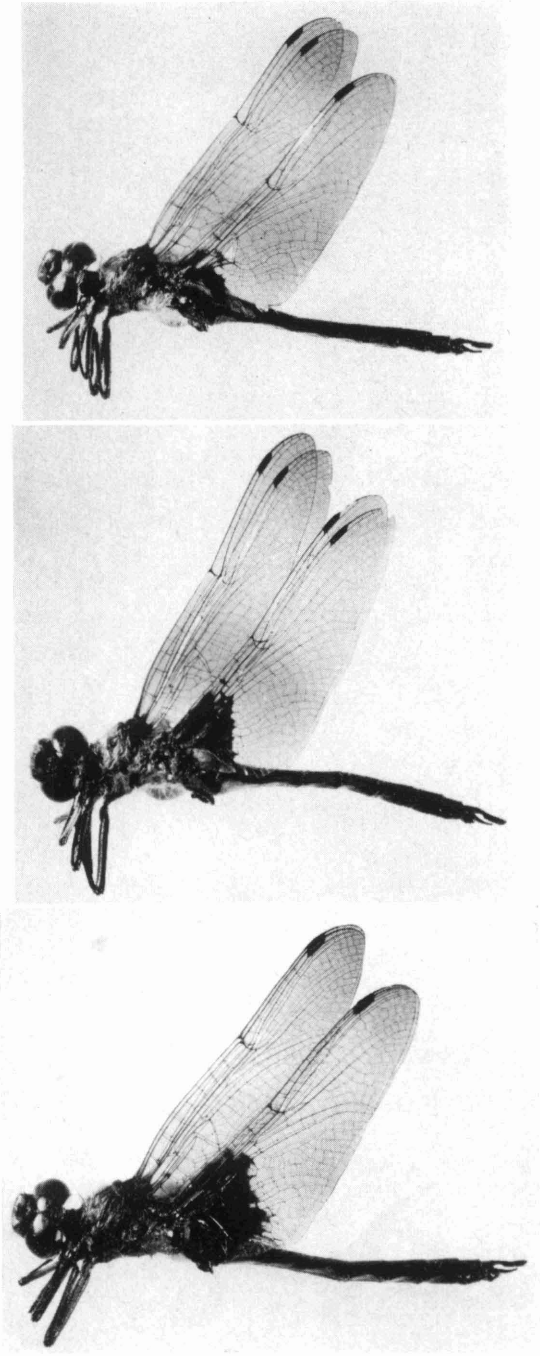
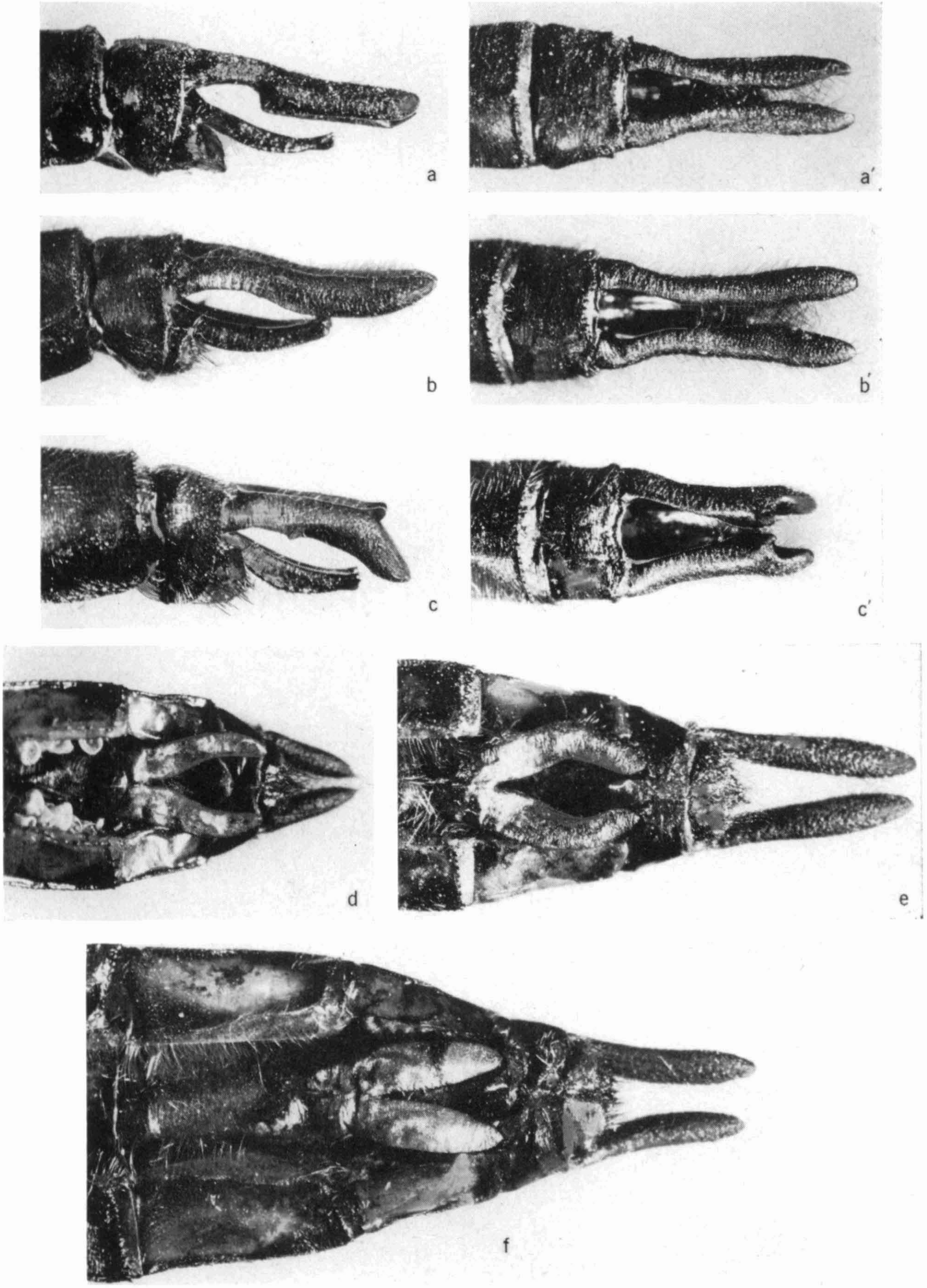


PLATE IV

Anal appendages and vulvar laminae of adults of Michigan species of *Tetragoneuria*. *a, a'*: Lateral and dorsal views of anal appendages of male *T. cynosura* (Say), Third Sister Lake, Washtenaw Co., 1935. *b, b'*: Lateral and dorsal views of anal appendages of male *T. spinigera* (Selys), Gogebic Lake, Ontonagon County, 1954. *c, c'*: Lateral and dorsal views of male anal appendages of *T. canis* MacLachlan, Prickett Dam Backwater, Houghton County, 1954. *d–f*: Ventral views of vulvar laminae and anal appendanges of females: *d*—*T. cynosura* (Say), near Joslin Lake, Washtenaw Co., 1934; *e*—*T. spinigera* (Selys), near Joslin Lake, Washtenaw Co., 1934; *f*—*T. canis* MacLachlan, bog drainage along U.S. Highway 2, Gogebic Co., 1954.

PLATE IV



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