A STUDY OF THE *TIPULA FRATERNA*
COMPLEX IN THE SOUTHEASTERN
UNITED STATES (TIPULIDAE: DIPTERA)

By

C. DENNIS HYNES

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TABLE OF CONTENTS

ACKNOWLEDGMENTS	11
LIST OF TABLES	v
LIST OF ILLUSTRATIONS	vi
INTRODUCTION	1
METHODS AND MATERIALS	11
GEOGRAPHIC DISTRIBUTION OF THE COMPLEXES	17
SEASONAL DISTRIBUTION	28
HABITAT RELATIONSHIPS	32
LIFE HISTORY	39
MORPHOLOGICAL FEATURES OF THE ADULT	47
TAXONOMY	57
<u>T. fraterna</u>	57
<u>T. confraterna</u>	73
Intergradation of <u>T. fraterna</u> and <u>T. strepens</u>	85
Description of Neotype of <u>T. fraterna</u>	89
Description of <u>Tipula confraterna</u> sp. n.	92
REPRODUCTIVE BEHAVIOR	96
IMMATURE STAGES	107
Egg	107
First instar larva	107
Fourth instar larva	111
Pupa	121
Pupa of <u>T. confraterna</u>	126
STATUS OF THE FRATERNA COMPLEX IN RELATION TO THE OTHER COMPLEXES OF THE <u>TRICOLOR</u> GROUP	129

TABLE OF CONTENTS--continued

SUMMARY AND CONCLUSIONS	133
LITERATURE CITED	137

LIST OF TABLES

Table		Page
1.	Species of the Genus <u>Tipula</u> in North America with which this paper is concerned	2
2.	Lengths in mm. of all Stages of <u>T. fraterna</u> and Larval Head Capsule Lengths	44
3.	Percentage of Individuals from the Gadsden County Series Showing <u>fraterna</u> , <u>floridensis</u> , and intermediate Types of Setae Distribution on outer Dististyles	62
4.	Percentage of Individuals from Several Southeastern Samples Grouped Together Showing <u>fraterna</u> , <u>floridensis</u> , and Intermediate Types of Setal Distribution on outer Dististyles	63
5.	Results and Analysis of Wing and Body Measurements	68
6.	The Percentage of Individuals in Gadsden County Series Showing White or Light Areas in Wing Cells . .	73

LIST OF ILLUSTRATIONS

Figure

1.	Genital structure of <u>Tipula ludoviciana</u> as representative of <u>sayi</u> complex	7
2.	Genital structure of <u>Tipula furca</u> as representative of <u>furca</u> complex	7
3.	Map showing areas collected in southeastern states	19
4.	Distribution of <u>sayi</u> complex	19
5.	Distribution of <u>furca</u> complex	19
6.	Distribution of <u>caloptera</u> complex	19
7.	Distribution of <u>tricolor</u> complex	21
8.	Distribution of <u>concava</u> complex	21
9.	Distribution of <u>Tipula strepens</u>	26
10.	Distribution of <u>Tipula fraterna</u>	26
11.	Map showing soil groups, fall-line, and 60°, 65°, and 70° isotherms	31
12.	Distribution of <u>Tipula conffraterna</u>	31
13.	Graphic representation of lengths of all stages of <u>Tipula fraterna</u> , larval head-capsule, and longevity of all stages	46
14.	Structures of head and thorax of <u>Tipula fraterna</u>	50
15.	Wing venation of <u>Tipula fraterna</u>	50
16.	Male Hypopygial structures of <u>Tipula fraterna</u>	53
17.	Female Hypopygial structures	56
18.	Setal distribution of <u>fraterna</u> type outer dististyle . . .	66

LIST OF ILLUSTRATIONS--continued

Figure

19.	Setal distribution of <u>floridensis</u> type outer dististyle. .	66
20.	Strap-shaped stem of outer dististyle	66
21.	Irregular shaped stem of outer dististyle	66
22.	Nearly straight outer dististyle	66
23.	Curved outer dististyle	66
24.	Variation in distal tips of dististyle of specimens of Gadsden County Series	72
25.	Basic wing pattern of <u>Tipula fraterna</u>	72
26.	Variation in basic wing pattern of <u>Tipula fraterna</u> with white in cell R 4+5.. . . .	75
27.	Variation in basic wing pattern of <u>Tipula fraterna</u> with white in cell M ₁	75
28.	Variation in basic wing pattern of <u>Tipula fraterna</u> with white in cell M ₂	75
29.	Variation in basic wing pattern of <u>Tipula fraterna</u> with white in cells R ₃ and R 4+5.. . . .	75
30.	Variation in basic wing pattern of <u>Tipula fraterna</u> found in Stone County, Mississippi, and the Little Escambia River in Escambia County, Alabama	78
31.	Variation in wing venation of <u>Tipula fraterna</u> showing spur at angle of Rs.	78
32.	Basic wing pattern of <u>Tipula confraterna</u>	80
33.	Variation in basic wing pattern of <u>Tipula confraterna</u> with white in cell M ₁	80
34.	Variation in basic wing pattern of <u>Tipula confraterna</u> with white in cell M ₂	80

LIST OF ILLUSTRATIONS--continued

Figure

35.	Variation in wing venation of <u>Tipula confraterna</u> with extra vein in cell M_2	80
36.	Comparison of tergo-lobe angles of <u>Tipula fraterna</u> and <u>Tipula confraterna</u>	82
37.	Basic wing pattern of <u>Tipula strepens</u>	84
38.	Variation in basic pattern of <u>Tipula strepens</u>	84
39.	Inner dististyle of <u>Tipula strepens</u>	88
40.	Inner dististyle of <u>Tipula fraterna</u>	88
41.	Sketch of aedeagus and lateral arms of <u>Tipula</u> <u>strepens</u>	88
42.	Tergo-lobe and outer dististyle of neotype of <u>Tipula fraterna</u>	95
43.	Holotype of <u>Tipula confraterna</u> , tergo-lobe and outer dististyle	95
44.	Position of genital structures of male and female <u>Tipula fraterna</u> during copulation	100
45.	Egg of <u>Tipula fraterna</u>	109
46.	<u>Tipula fraterna</u> , spiracular disk of first instar larva	109
47.	<u>Tipula fraterna</u> , anal lobes of first instar larva.	109
48.	<u>Tipula fraterna</u> , head capsule of first instar larva.	109
49.	<u>Tipula fraterna</u> , maxillary plate of first instar larva	113
50.	<u>Tipula fraterna</u> , clypeal-labral region of first instar larva	113

LIST OF ILLUSTRATIONS--continued

Figure

51.	<u>Tipula fraterna</u> , mandible of first instar larva.	113
52.	<u>Tipula fraterna</u> , lateral view of fourth instar larva	116
53.	Setal type which gives partial black coloration to anterior body segments of <u>Tipula fraterna</u> larva.	116
54.	Chaetotaxy of segments of <u>Tipula fraterna</u> fourth instar larva	116
55.	<u>Tipula fraterna</u> , spiracular disk of fourth instar larva	120
56.	<u>Tipula fraterna</u> , mandible of fourth instar larva	120
57.	<u>Tipula fraterna</u> , prosthecal tuft of mandible	120
58.	<u>Tipula fraterna</u> , maxilla of fourth instar larva	120
59.	<u>Tipula fraterna</u> , antenna of fourth instar larva	120
60.	<u>Tipula fraterna</u> , maxillary plate of fourth instar larva	123
61.	<u>Tipula fraterna</u> , prementum of fourth instar larva	123
62.	<u>Tipula fraterna</u> , pupa	128
63.	<u>Tipula confraterna</u> , wing pad of pupa	128
64.	Diagram showing relationship of <u>fraterna</u> complex to other complexes	132

INTRODUCTION

There are within the Tipulidae several groups of closely related species which are called species complexes by the workers in this field. These species are nearly the same with respect to morphological appearances, and many times overlap almost completely in all other details of their biology. On the basis of slight morphological differences, new species have been named and, in other cases, species have been synonymised with no certainty as to the validity of some forms within these species complexes. Such a situation is found in many genera of crane-flies, including the genus Tipula itself. Rogers (1942) calls attention to this situation within the genus Tipula by stating that, "the not infrequent existence in the Tipulidae of two closely similar species that have identical or very similar geographical ranges and habitats merits further study." He goes on to mention, as examples, the group composed of T. hirsuta and T. valida within the subgenus Lunatipula, T. eluta and T. furca within the subgenus Yamatotipula, and the T. triplex group, also within the subgenus Lunatipula. He believed that the possibility of genetic dimorphism within one species could not be "absolutely dismissed."

Within the genus Tipula and subgenus Yamatotipula, the tricolor group includes several species complexes, which in turn appear to be very closely related. The so-called fraterna complex is one of these. Through the study of the species making up the fraterna complex, further knowledge might be gained about the taxonomic standings of the various

species which, in turn, might yield some perspective to the relationships of this group and with groups closely related to it. Although this work is primarily concerned with the fraterna complex, it is impossible not to refer to species of the other complexes for background or supporting evidence, and this has been done quite freely throughout this paper.

The species of the genus Tipula in North America with which this paper is concerned are shown in Table 1,

TABLE 1,

SPECIES OF THE GENUS TIPULA
IN NORTH AMERICA WITH WHICH
THIS PAPER IS CONCERNED

<u>Complex</u>	<u>Species</u>
<u>sayi</u>	<u>T. sayi</u> <u>T. ludoviciana</u> <u>T. osceola</u>
<u>furca</u>	<u>T. furca</u> <u>T. vicina</u> <u>T. eluta</u>
<u>caloptera</u>	<u>T. caloptera</u> <u>T. noveboracensis</u>
<u>tricolor</u>	<u>T. tricolor</u> <u>T. manahatta</u> <u>T. subeluta</u> <u>T. sackeniana</u>
<u>concava</u>	<u>T. concava</u>
<u>fraterna</u>	<u>T. fraterna</u> <u>T. floridensis</u> <u>T. maculipleura</u> <u>T. strepens</u> <u>T. calopteroideis</u>

The subgenus Yamatotipula was first defined by Matsumura (1916)

as having generic rank and later reduced to subgeneric rank, broadened, and redefined by Alexander (1935). The characters which separate this subgenus from others of the genus Tipula are adequately described in Alexander (1935, 1942). The subgenus is holarctic in distribution and probably contains between sixty and seventy species. T. (Y.) jamaicensis Alex., a neotropical species from the Greater Antilles, is the only non-holarctic species. Alexander (1951) believes T. jamaicensis to be closely related to T. (Y.) ludoviciana Alex., found in the southeastern United States.

The subgenus has evidently evolved along two alternative lines, one having wings with a pattern of brown and pale white longitudinal stripes, and the other without any pattern on the wings. The former line is known as the so-called tricolor group in the nearctic region.

Rogers (personal communication) stated that the tricolor group could be still further divided into several more or less natural species complexes and, before his death, did mention the species which he believed made up the various complexes; however, he did not specify what he considered to be the limitations or definitions of each. I agree with Rogers about the composition of most of the complexes and have, in the following paragraphs, attempted to give the characteristics by which I believe each can be separated. The main characteristics used to separate these complexes are the wing patterns, especially at the tips beyond the cord, and details of the genitalia. The usefulness of these complexes will be shown later during the discussion of the relationships of the species involving the fraterna complex. In the eastern United States the tricolor group diverges into two general lines. One is

characterized by the wings having only one dark brown stripe along the costal border of the wing ending at the Sc2 and R 1+2 cells of the wings. Members of the sayi complex fall into this group in which Rogers placed the species T. sayi, T. osceola, and T. ludoviciana, stating that the areas along the Gulf Coast and inland Florida flatwoods have many apparently intermediate populations between sayi and osceola. He believed ludoviciana to be clearly related but apparently quite distinct from the others. The genitalia of the species within this complex have a basic pattern with the outer dististyle ovate, the inner dististyle with the basal lobe elongate as in ludoviciana, or shorter and bulbous as in osceola (Fig. 1). The dististyles of all the species are weakly chitinated.

The second divergent line of the tricolor group involves several complexes, all having a dark brown stripe or vitta along the costal edge of the wing. The stripe is sometimes broken at the cord, then continues into cells Sc2 and R 1+2. Another stripe of dark brown occurs along the veins Cu and m-cu of the wing.

The caloptera complex has two distinct species. These are T. (Y.) caloptera and T. noveboracensis. In both, the pale areas of the wing occur in the anterior two-thirds of the cell M, along the cord, dipping around the edge of the m-cu into the inner half of the cell M₁ and the distal two-thirds of the cell 1st M₂, then along the inner portions of the cells M₃, M₂, the inner fourth of cell M₁ and the distal half of the cell R 4+5, giving the pale whitish stripe pattern from the cell M to R 4+5 a sinuate appearance at the cord. The basic pattern of the ninth tergo-lobes are similar, having one prominent medial lobe and two smaller lateral lobes. In T. caloptera the medial lobe only is well

developed and moderately chitinized, while in T. noveboracensis all the lobes are heavily chitinized and appear black. Details of the dististyles leave no doubt that the two are definitely separate species.

The furca complex contains three species of which one, T. (Y.) vicina, is distinctly northern. The others, T. (Y.) furca and eluta are not as distinct and their validity was questioned by Rogers. The general wing pattern of all the species within the furca complex is characterized by the pale white stripe of the wing extending more or less in a straight line from the cell M to the distal edge of the cell R 4+5 with no sinuate appearance at the cord. In furca a dark area dips into the pale white area of cell R, giving the stripe at this point a bisinuate appearance, whereas eluta does not have this character. I have been unable to obtain specimens of T. eluta for study and cannot comment further on this species. The genitalia of vicina and furca are similar, with the outer dististyle lobed at the base, the distal portions nearly the same; that of furca longer and more slender than that of vicina. The inner dististyle and tergo-lobe are also of the same basic shape (Fig. 2).

The tricolor complex (not to be confused with the tricolor group) includes at least four species: T. tricolor, T. subeluta, T. sackeniana, and T. manahatta. These are characterized by the presence of a pale white area of varying length beyond the cord which gradually disappears as it runs into the lower portion of cell R5, completely through the cell 1st M2 and along either side of vein M1. The genitalia of this complex are very similar to those of the fraterna complex described below. The details of the genitalia of this complex cannot be discussed here because I do not have available representatives of all the species.

Plate 1

Figure 1. Genital structure of Tipula ludoviciana as representative of sayi complex. From left to right: outer dististyle, tergo-lobe, inner dististyle.

Figure 2. Genital structure of Tipula furca as representative of furca complex. From left to right: outer dististyle, tergo-lobe, inner dististyle.

Plate 1

1

2

There is, however, in the specimens available, some indication that this complex could be subdivided into two lesser groups on the basis of the presence or absence of pencils of setae on the lateral margins of the tergo-lobe.

The fraterna complex was considered by Rogers to be one of the more difficult in which to determine the validity of the species. In this complex he included T. strepens, T. calopteroides, T. fraterna, T. floridensis, and T. maculipleura. Along with these described species several other specimens had been collected through the years which definitely belonged to this complex but whose affinities with any of the described species were difficult to determine. Both Alexander (1942) and Rogers (personal communication) questioned the validity of calopteroides, saying that it probably was only a variant of strepens. In addition, Rogers proposed the possibility that with a large enough series of strepens and fraterna available for study the differences between the two might be shown to intergrade completely. T. fraterna, floridensis, and maculipleura were possibly conspecific, being instead subspecies, or the results of many overlapping clines radiating out of the north and Appalachian areas. With these factors in mind, it was decided that extensive collecting in the southeastern United States might well shed light upon the speciation of the fraterna complex and related complexes as well. The wing patterns of the various species within this complex vary but have, in common, the pale whitish pattern extending transversely along or just before the cord of the wing from the stigmal area to the base of the wing and into the cells M3 and M4. The differences of the genitalia of the species of the fraterna complex are nearly

negligible, or were thought to be so by Rogers, and will be described in detail later. T. strepens and calopteroides have, in addition to the above, whitish areas in the inner portions of the cells R 4+5, M1, and M2. Other specimens of this complex were taken occasionally which were similar to fraterna except for a pale white area to be found in the cell R 4+5. Rogers also collected specimens from the Mountain Lake region of Virginia which at the time were labeled "strepens near fraterna" or "fraterna near strepens." Possibly, for this reason, Rogers began to think that the two were intergrading or hybridizing in certain areas. T. strepens is a distinctly northern and Appalachian species, however, while fraterna was reported from both the north and the south.

T. (Y.) floridensis was described by C. P. Alexander (1926). The holotype was taken at Gainesville, Florida, and was thought to occur only in the southern portion of the southeastern United States. Alexander described T. (Y.) maculipleura one year later from one specimen taken by Rogers in the mountains of Fentress County, Tennessee (Alexander, 1927). The holotype of Tipula fraterna, described by Hermann Loew (1864) from Washington, D. C., has apparently been lost and has not been available for study.

The remaining species of the tricolor group in the southeast are not easily placed in any of the above complexes. T. (Y.) concava possesses a wing pattern close to that of some specimens of strepens, but the size, and especially the characteristics of the larval forms, show that this species might belong close to furca. Details of the tergo-lobe separate concava from the other complexes as a very distinct species.

Little was known about the ecology, distribution, and life

histories of the species of the fraterna complex, and it was decided therefore to add to the primary problem of the systematics as much information as possible about the biology of this complex.

METHODS AND MATERIALS

In order to determine the systematic status of the fraterna complex and the species within that complex, more specimens and many more aspects of their biology had to be investigated than had ever before been attempted. In 1953, Dr. Lewis Berner of the University of Florida received a United States Public Health Grant for the purpose of studying the mayflies of the southeastern United States. I was fortunate in receiving an assistantship to help with this work, for it allowed me to collect craneflies of the fraterna complex at the same time. The southeastern states sampled were: Tennessee, North Carolina, South Carolina, Georgia, Louisiana, Alabama, Mississippi, and Florida. The total mileage traveled approximated fifty-two thousand miles, with about four hundred and twenty-one collections made, of which one hundred and twelve resulted in the collection of some seven hundred and sixty-eight specimens of the fraterna complex. The areas in which collections and observations were made are shown in Figure 3.

Approximately one hundred and sixty-four specimens of the fraterna complex were also received from the University of Michigan Museum of Zoology through the kindness of Dr. T. H. Hubbell, who also allowed me to use the late Dr. J. S. Rogers' notes on the fraterna complex, the main portion of which was distributional data. Dr. H. T. Townes also donated several specimens of this complex from the vicinity of Greenville, South Carolina.

Occasional specimens of the fraterna or other complexes of the tricolor group were also obtained from many of the colleges and universities of the southeast visited during the course of this investigation.

When collecting along a stream, I took every possible adult specimen of the fraterna complex present for a distance of approximately one hundred yards in order to determine the numbers of individuals present at a particular time along a particular stream. To better understand the ecological and taxonomic relations in one population, I concentrated my efforts in one stream at various periods in the summer of 1956. This stream, located about six miles south of Chattahoochee, Florida, is called Flat Creek. The series of specimens collected there are referred to henceforth as the Gadsden County series.

Adults were collected with a sweep net and killed in cyanide bottles or preserved in alcohol. Those placed in cyanide jars were transferred to small druggists' envelopes (No. 3) and allowed to dry in this manner with the wings folded back over the body. Adults to be kept alive were placed immediately in plastic containers (3 1/2" x 3 1/2" x 2 1/2") which were then put in a portable ice-box until such time as the specimens could be observed for various behaviors or could be used for obtaining eggs.

Observation of the adults was much improved by the use of a screen cage (20" x 16" x 18"), so constructed as to allow a large flat pan of water for maintaining high humidity to be placed in the bottom. Many times a large piece of clay with attached vegetation from the stream bank was also placed in this pan for watching oviposition behavior of the female. The lighting was kept at a minimum when the cage was used

indoors. The adults were then watched to determine their normal behavior. After observation, the females were either preserved or eggs obtained from them. The males were preserved as described above.

Two methods were used to obtain fertilized eggs. The first was to place the female in a vial containing a little water so that the abdomen was immersed. This condition often stimulated the female to oviposit into the water. The other method was to remove the head of the female with a very small, fine pair of scissors. This operation was done with care so as not to damage any other portion of the insect. When the female was damaged in such a way as to tear out portions of the nervous or digestive systems from the thorax, no eggs were released. However, if the head was removed properly, the female, in a few minutes, began to lay eggs. The reason for this activity may be explained by the presence of an inhibitory action of the brain upon the ovipositors, but when the brain is removed, the valves of the female are activated (Wigglesworth, 1950).

The second method of obtaining eggs was decidedly preferable to the first. As many as one hundred and twenty eggs could be obtained from a single female by the decapitation method, while only a few to perhaps a dozen could be obtained by the other method. The more frequently the females mated, the easier oviposition occurred, and the larger the number of fertilized eggs produced. I found that teneral females do not respond to either treatment.

After the eggs were laid, I placed them in one or two situations depending upon whether I wanted only the egg and early stages up to and including the first instar larvae, or whether I wanted the larvae to

continue their development. When put in containers with clay, particles would stick to the chorion of the egg blocking observation of its development. Maximal visibility in viewing the developing eggs was obtained when the eggs were put into containers supplied with about an eighth of an inch of water in the bottom. A small piece of clay was added to groups of the eggs which were to hatch, and larvae were allowed to continue their development. This procedure was initiated, when as a result of transfer from containers supplied only with water to those containing clay, many or all of the recently hatched first instar larvae would die. For some undetermined reason, when the clay was added before the eggs hatched, the larvae lived. Specimens of the desired age were preserved in F.A.A. or in 95 per cent alcohol. The advantage of the former was that if sectioning were desirable at a future date, the specimens would be suitably preserved.

Collecting the immature stages in the field was restricted, by necessity, to the second, third, fourth instar larvae, and the pupae. The eggs and first instar larvae were too small to be caught by the strainer used to wash soil of the habitat away from the specimens. If not preserved, the larval specimens were placed in containers along with clay, moss, and liverworts from the habitat. Enough water was added to dampen the soil thoroughly, but not saturate it enough to make it fall apart. If too much water was added to the containers, the larvae would climb up the sides of the cage and eventually die. This was especially true of the first, and sometimes of the second, instar. The later instars are also affected by the presence of too much water in the rearing containers, but they did not die as readily under such conditions. A

large supply of food material (clay and contained materials from the habitat) was made available to the larger instars. If enough food was not present, the usually detritus-eating larvae turned cannibalistic, damaging or eating the other larvae within the cage. Usually no more than four of the last instar larvae were placed in any one container at the same time.

The pupae were always reared away from the larvae in the containers because they too would sometimes be attacked by the larvae. Pupating larvae and fully formed pupae were reared in two manners: by placing them on moistened paper, or by placing them in a cage with a small amount of damp soil in it. The advantage of the former method was that it resulted in keeping the exuviae or pupal case clean and free from particles of clay, providing better study specimens. The advantage of the second method was that it showed the more normal position of the larval exuviae near the pupa, and that the behavior of the pupa in its natural environment could be more readily observed. Pupating larvae were separated from all other individuals so that the exuviae from the last larval molt could be preserved, as other larvae when present would almost immediately consume the cast off skin.

The only way in which the genital or wing structures could be viewed in detail was to mount them on microscope slides. The genitalia were treated by first immersing the detached terminal segments in water to which had been added a trace of detergent as a wetting agent. The specimen was then placed in 10 per cent sodium hydroxide solution and allowed to stand until the tissue had been dissolved. The genitalia

were then washed in water and placed in glacial acetic acid. After fifteen to twenty minutes they were transferred to a solution composed of one part of clove oil and two parts of glacial acetic acid. After an additional twenty minutes, the specimen was again transferred into another clove oil and acetic acid solution, composed of one part of each. The specimen was left in this solution until dissected and mounted on the slide. Euparal was used as the mounting medium. The wings were processed in much the same way as the genitalia, but the step in which the specimen was put into the hydroxide was omitted. The hydroxide made the wing too soft to work with and, in addition, caused decoloration of the wing pattern. Decoloration was especially to be avoided as it is one of the characteristics under study in this complex. The right wing and the genitalia were mounted on the same slide. The genitalia were oriented with the tergo-lobe and the left side of the ninth segment left intact, the right side with the outer and inner dististyles completely separated. The eighth sternite and tergite were also included on the slide as were the aedeagus, the basal bulb of the penis, and a large U-shaped structure, discussed in the section on the morphology of T. fraterna.

Most of the structures were measured by the use of an ocular micrometer. The ninth tergo-lobe was outlined by use of a camera lucida and lines drawn along the sides until they met. The angle formed was then measured with a protractor.

GEOGRAPHIC DISTRIBUTION OF THE COMPLEXES

The geographic distributions of the complexes within the subgenus Yamatotipula which are closely related to the fraterna complex are shown in Figures 4, 5, 6, 7, and 8; however, as there still remains some question concerning certain boundaries, particularly the western extension of these ranges, these distribution maps must be considered as only tentative.

A look at the distributions of the various complexes may shed some light on possible trends in the fraterna complex, such as the center or centers of distribution, and also give further evidence of the relationship of this complex to other complexes and, consequently, to the species involved.

The gavi complex has been found in the entire eastern portion of the United States and as far west as Arkansas. The complex is represented by one species, T. jamaicensis, in the Greater Antilles.

Members of the furca complex are found as far westward as New Mexico, where Alexander (1946) reports the occurrence of T. (Y.) vicina. T. (Y.) furca is found in Texas and Missouri and into northern Florida. The northern limit of all species in the complex is southeastern Canada. T. (Y.) eluta has not been reported outside of the geographic limits of the two other species. The southern range of the furca complex can now be extended into the mid-central peninsula of Florida, as I have taken specimens of furca from there.

Plate 2

Figure 3. Map showing areas collected in southeastern states.

Figure 4. Distribution of sayi complex.

Figure 5. Distribution of furca complex.

Figure 6. Distribution of caloptera complex.

Plate 2

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Plate 3

Figure 7. Distribution of tricolor complex.

Figure 8. Distribution of concava complex.

Plate 3

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The caloptera complex is widely distributed, ranging from southeastern Canada in the north, Missouri in the west, and certainly as far south as the Weekiwachee River in Florida. Other specimens of caloptera have been taken in abundance in southeastern Louisiana. T. (I.) noveboracensis has not been reported previously south of Maryland and only as far west as Ohio (Foote, 1956). Subsequently, a single specimen has been reared from a larva collected in the mountains of North Carolina.

The range of the tricolor complex, based on records reported by Alexander (1942), extends into Labrador in the north and Florida in the south. The western range is known to extend at least into Arkansas, and I have taken T. tricolor, of (a form) closely related to it, in southern Louisiana and Mississippi.

The geographic distribution of the concava complex covers the least area. Rogers, in a personal communication, said that this species had not been taken farther south than Tennessee and South Carolina. I have taken many specimens in northern Alabama and northern Georgia, but not south of the Piedmont. Alexander (1942) states that this species occurs in Missouri and gives its northern range, based on his records, as Connecticut and Michigan. The northern range will undoubtedly be extended into the lower portion of Ontario on the basis of the known distribution of a plant, Justica americana, the roots of which Rogers (1930) states compose the "typical and almost exclusive habitat of this species." This plant grows along the sides of the rivers and in shallow streams from Texas to Canada (Fernald, 1952).

The following changes in the taxonomy are introduced here for clarification, but will be treated at greater length in the section

entitled "Taxonomy of the Tipula fraterna complex":

T. floridensis = T. fraterna

T. maculipleura = T. fraterna

T. confraterna, new species

The fraterna complex is found in the eastern part of the United States. The distribution of strepera is definitely northern, the species never having been taken south of North Carolina (Alexander, 1941). Alexander (1942) also reports this species to be in the northeastern United States and southeastern Canada. The western limit is reported to be Wisconsin and Kansas (Fig. 9).

Alexander (1942) reports T. fraterna to be found in New Hampshire, Connecticut, and Pennsylvania in the north, with the southern range in Georgia and northern Florida. Rogers (1942) reports it in Michigan and in 1933 in Tennessee as T. (Y.) maculipleura. I have taken specimens of fraterna in every state of the southeast, including Tennessee, Mississippi, Louisiana, Alabama, Georgia, North Carolina, South Carolina, and Florida.

The northern and western limits of the range of Tipula fraterna are poorly known, and I shall, therefore, concern myself only with its southeastern distribution. The distribution of fraterna and confraterna follows, to a large extent, the Piedmont of North Carolina, South Carolina, and Georgia, following the Apalachicola or Chattahoochee river system from the Piedmont into the western pan-handle of Florida and from there into the north central and central portions of Florida, leaving the entire Coastal Plain area from eastern North Carolina, South Carolina, central and eastern Georgia, and northeastern Florida unpopulated (Fig. 10).

Rogers (1933) believes that one of the major barriers preventing

northern species of Tipulidae from spreading into the Coastal Plains of this area is the lack of "clear, fairly rapid, pebble-bottom streams," and "the scarcity of persistent, cool, moist shade . . .," usually afforded by hardwood formations. With the data I have now, I can see no other explanation for the limitation of T. fraterna from this area. Rogers (1933) also indicates that the spread of northern species of craneflies into Florida via the Apalachicola River system could be explained by the close similarity of ecological conditions of this area to the Piedmont areas.

I have not taken fraterna in the northeastern part of Florida nor in the southeastern portion of Georgia even after several trips to that area, and I doubt that the species lives in this region at all. Bellamy (1947), in a careful study of the Tipulidae of the University of Florida Conservation Reserve at Welaka, was unable to find any species of the fraterna complex.

T. fraterna has not been found south of Marion County, Florida, where it was reported by Bellamy (1936). I have not taken it south of Alachua County. Although there are numerous lakes and swamps in central Florida, there are few perennial surface streams (Anon., 1938). The lack of these streams may account, at least partially, for the absence of T. fraterna from this region.

The southern limit in southeastern Louisiana, Mississippi, Alabama, and west Florida, parallels closely the beginning of the interzonal soils, which typically are considered poorly drained (Fig. 11).

The western limits of the range stop parallel to the beginning of the Mississippi-Alluvial soils and, to a lesser degree, the Memphis-Grenada

Plate 4

Figure 9. Distribution of Tipula strepens. Localities from which specimens were studied are indicated.

Figure 10. Distribution of Tipula fraterna. Localities from which specimens were studied are indicated.

Plate 4

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10

soils. Collecting was extremely poor in this region. The streams are predominantly intermittent, and those which are not do not possess suitable banks or over-hanging vegetation for immature or adult stages of T. fraterna. In Tennessee T. fraterna was found in few of the streams near the Mississippi, as most of them were dried up or canalized.

This distribution would appear consistent with the hypothesis that fraterna has a northern center of dispersal. If we look again at the distribution of the species complexes, we find that every species within these complexes occurs in the north. The tricolor group as a whole gives evidence of a northern center of dispersal with the species spreading to the west and to the south. The distribution as a whole then would give further evidence of a migration of the fraterna complex southward.

Records of T. (Y.) confraterna reveal a distribution very similar to that of fraterna. Specimens of this species are in the University of Michigan Museum of Zoology collections from southern Maine, Michigan, northern Indiana, southern Ohio, and Florida. I have taken specimens in Tennessee, North Carolina, South Carolina, and Alabama. Several specimens were also acquired from collections made by H. T. Townes near Greenville, South Carolina. Locations from which specimens have been collected are shown in Figure 12.

SEASONAL DISTRIBUTION

The seasonal distribution of T. (Y.) fraterna in the eastern United States varies considerably from Florida to Michigan, representing the southern and northern parts of the range. At Flat Creek near Chattahoochee fraterna begins to emerge in the middle or latter part of March. Where adults occurred, the number obtained per one hundred yards of collecting was between three and five. By the middle of May a maximal population was reached. The number of adults taken at Flat Creek at this time was the highest taken anywhere in the southeast, numbering forty-one adults per one hundred yards. During the summer, a low level was noted during the month of July, when about seven adult specimens per one hundred yards were taken. The early part of August again showed a peak population, as shown by a collection of twenty-seven adults per one hundred yards. By the latter part of October, no specimens were taken from this area. The data from other collections from Alabama, Mississippi, and Louisiana east of the Mississippi River follow this trend with some, but little, variation.

North of Alabama seasonal emergence seems to be the same as that found in Michigan. In Tennessee fraterna does not emerge until late May or early June. After the month of June, no adults were collected in most of the state. In many places, however, larvae which corresponded to the age one would expect had the eggs been laid in June were found; but none were collected which would show a later summer emergence. Only

in the southeastern portion of Tennessee were adults taken in the middle of August, but then only in very small numbers.

In North Carolina the appearance of fraterna is nearly the same as that in Tennessee, but the emergence extends throughout most of the summer. However, the numbers of adults taken numbered less towards the end of the summer with no definite peaks occurring after the spring or early summer emergence. In most streams the population peaks were quite abrupt. In some streams I collected from fifteen to twenty adults per one hundred yards and later, within less than a week, found practically no adults present at all. Rogers (1942) reports that only one generation per year is found at areas near the E. S. George Reserve in Livingston County, Michigan. The emergence took place there during the early part of the month of June. Alexander (1942) records the appearance of fraterna only in the months of June and July.

The sixty-degree isotherm (Kincer, 1941) agrees favorably with that area in which I consider the periodicity of emergence of T. fraterna to change. Generally, north of this line, the insects show only one maximal period of emergence during the early summer. South of this line (Figure 11) there is a continual emergence, corresponding to that described above. Berner (1950) states that, in general, species of northern origin are non-seasonal in Florida. The fact that T. fraterna shows a similar behavior does not disagree with the hypothesis that it has a northern origin and center of distribution and may be considered to be added evidence of this phenomenon.

Plate 5

Figure 11. Map showing soil groups, fall-line and 60°, 65°, and 70° isotherms. (Adapted from Yearbook of Agriculture 1938, 1941. (A) Mississippi alluvial soils, (B) Interzonal soils, (C) Norfolk-Blanton soils.

Figure 12. Distribution of Tipula confraterna. Localities from which specimens were studied are indicated.

11

12

HABITAT RELATIONSHIPS

The habitat of adult Tipula fraterna has been described briefly by Rogers (1930, 1933, 1942) as being confined to streams. This restricted association has been confirmed by my collections. For the habitat of the larval stages, Rogers (1942) noted that, "the larvae of what appears to be the same species have been taken from submerged patches of filamentous algae in sand bottom brooks in northern Florida."

The fact remains that prior to this study no investigator had made a definite association of the immature stages with the adult of Tipula fraterna. The larvae of T. fraterna were never taken by me in any aquatic situations such as reported by Rogers, and I am sure that the larvae of which he wrote was another tipuline, but perhaps still within the tricolor group. Indeed, in areas such as he described, I have taken a tipuline larva, probably the one to which he was referring, altogether different from those of the fraterna complex.

In correlating the type of stream and stream bank with the occurrence of T. fraterna, the following characteristics were considered: intermittance or permanency, rate of flow, pH, color, width, depth, slope of the bank, soil, and vegetation of the bank.

Intermittent streams are common in the western parts of Mississippi and Tennessee. Streams in which water had very slow or no perceptible flow along the major portion of their course were considered stagnant. All others examined varied in having a slow but steady flow, a common type in the Coastal Plain, to the cascading streams in the mountainous areas.

The beds of streams in which Tipula fraterna occurs range from sand-bottom streams, common in the Coastal Plains, to the rocky-bedded streams of the mountains. This character, while important in describing the habitats of other members of the tricolor group, has little importance with respect to the fraterna complex.

The most favorable type of stream bank has an almost vertical slope from the water surface varying from a few inches to several feet. Tipula fraterna seldom occurs on banks which have a very gradual slope. The soil of the bank in which the immature stages occur is red-yellow or brown-yellow clay loam. The eggs, larvae, and pupae were not found in banks composed largely of silt or sand.

The stream banks where T. fraterna occurs might be considered as ecotones, because they have transitional conditions between strictly aquatic and terrestrial habitats. Many of these stream banks are divisible into three layers or zones, which grade into each other, but which, for the purposes of description and discussion, will be considered here as distinct.

The first or lowest zone is closest to the water surface and has the most soil water as shown by the slight film of water on the clay. This layer is usually without macroscopic vegetation, although there are occasional patches of mosses and liverworts present. The root systems of the overhanging vegetation are partially exposed with some clay adhering to them. Erosion of the bank in this layer may be so great as to cause extreme undercutting of the bank forming a cavity behind the exposed roots. The roots below the water line may be well-washed or with a fine silt collected in them, but this was generally found to be a poor

crane-fly habitat.

The second zone is characterized by an abundance of mosses and liverworts. It may contact the water when the first layer is missing. It is relatively more stable than the first layer and resists periodic flooding and erosion. The soil is held tightly together by roots so that it is extremely difficult to wash out the larvae. The common mosses found are Mnium rostratum, M. cuspidatum, M. affine, Hypnum acutatum, H. patensiae, H. curvifolium, Plagiothecium micans, Sphagnum palustre, S. subsecundum, Thuidium delicatulum, and Bryum sp. Some common liverworts are Marchantia sp. and Porella sp. Byers (1952) reported that specific Bryophytes were important food materials and indicators of habitat moisture content suitable for species of Dolichopeza. I have found no correlation of T. fraterna larvae with any particular species of moss, and, if there is any importance to be attached to the presence of Bryophytes with these larvae, it would be as indicators of stability and suitable moisture content of the bank.

The third layer of the stream bank includes herbaceous plants, grasses, and shrubs. This zone may be adjacent to the water surface in the absence of the first and second zones, but this condition rarely occurs. Generally, this zone is drier than the other zones. A plant common to this zone, especially in the Piedmont and mountains, is yellow root, Xanthorhiza simplicissima. Vines, such as Smilax sp., and species of Hypericum also occur in abundance. These appear much more commonly, however, in the Piedmont and the Coastal Plain areas as do members of the family Vitaceae (Vitis sp.). In all areas Rubus sp. and poison ivy, Rhus toxicodendron occur. Sometimes trees form a part of this layer and

influence its composition by shading. Among these, especially in the Coastal Plains, are Alnus rugosa, Cyrilla racemiflora, Cyrilla sp., Magnolia sp., Ilex sp., Betula nigra, Crataegus marchalli, and Ulmus alata. Many of the mountain streams have Rhododendron thickets and mountain laurel, Kalmia sp., along the banks.

Regardless of the kinds of trees and shrubs, the ideal stream for the larvae and adults of T. fraterna has branches from these trees and shrubs that arch over the bank and the water. The height of these varies, some even touching the water's surface or dipping below it. These branches not only provide shade for the bank but also protect this area from the wind, rain, sun, and help maintain a high humidity.

There are no apparent differences in habitats between T. fraterna and T. confraterna, various stages of both occurring in identical situations. No larval specimens of strepens were found in habitats of T. fraterna in the Carolinas, although farther north they may occur together. However, I have not been able to verify this as I have not had the opportunity to visit localities where T. strepens is known to occur. Alexander's (1941) description of the adult habitat leads me to believe that they will not be found very far from T. fraterna in all cases where the ranges overlap.

The eggs of Tipula fraterna are laid in the first zone of the stream bank where they hatch into the first instar larvae and are found here more commonly than in the second and third layers. It appears that as the larvae grow, they extend their wanderings into the second and third layers, where I usually found more third and fourth instar larvae.

The larval stages rarely occurred in the third layer, and when I have taken them in this area, it has usually been after a heavy rain. The rain makes the soil more moist, and the larvae would then move into this usually drier area. Pupation occurs in the second and third layers, and no pupae were ever taken from the first layer.

There is no predictable distance from the water surface to the larval sites, but generally ten to twelve inches above the water line is the uppermost limit. The presence of some of the mosses in this area, especially Sphagnum, indicates that the water of the habitat is acid. The correlation of the distribution of T. fraterna and T. confraterna with the soil types in the southeastern regions also indicates that the soils have a slightly acid reaction. Larvae may sometimes be found in the bank beneath the surface of the water, and I believe that the reason for this may be a sudden rise in the water level so that larvae have not yet had time to move to drier soil. If larvae are left in containers of water for longer than a week, they will become very sluggish and finally die, but if able to crawl out of the water, they leave it and survive. Larvae may be found in barely moist soil on rare occasions, but are most abundant in soil which is damp. The larvae of T. fraterna do not burrow laterally very far and are found no deeper in the banks than one to one and a half inches. The spiracular disks can often be seen extended to the surface of the soil. In some cases burrows can be seen which may have been made by other animals as well as those made by the crane fly larvae and air is made available to the larvae through these open tunnels. An interesting corollary to the stratification of the banks is that one

does not usually see these burrows in the zone nearest the surface of the water, probably because the larger larvae do not require the degree of moisture needed by the smaller larvae. This is probably because of the surface-mass relationship and the increased thickness of the integument, which means that there would be less water loss from the surface of the larger forms.

The larvae in the rearing cages expel their fecal pellets from the clump of clay in which they have been placed. These fecal pellets are expelled with considerable force and land on the sides of the cage which may be as much as three inches away from the clay. There is evidence that this may be a protective measure to avoid pollution, because larvae do not live as long in cages from which the pellets have not been removed.

The larvae of T. fraterna have also been taken from clay-impregnated logs and branches partially lying the stream or next to the edge of the clay bank. Larvae have never been taken at streams in which the banks were composed only of sand, as common in northeastern Florida. Some streams of the Atlantic and Gulf coastal areas of the Coastal Plain have banks with a gray to pepper-colored soil containing a large amount of humic materials, and larvae have not been found in this type of bank. In streams with banks of clay, but which are barren and have no overhanging vegetation, fraterna larvae or adults were not present.

Pupae of T. fraterna are found in relatively drier parts of the second or third zone. Great numbers of pupal cases can be seen in those areas just after the spring peak of emergence in the vicinity of Chatahoochee, Florida. The larvae evidently work themselves to within a few

millimeters of the surface and then pupate, leaving the larval exuviae packed just behind. The pupae, immediately prior to emergence, go to the surface of the bank, anchor themselves by the spines at the posterior portion of the body and arch upward, lying with the major portion of the body exposed. It is quite evident that with the pupa in this position the newly emerged adult, when still not separated from the pupal case, will be helplessly exposed to predators, as well as to rain and wind. This condition probably reduces the number of surviving adults.

The adults are rarely found resting in branches over six feet above the water line. Tipula fraterna may still be found where there is no overhanging vegetation if something replaces it, to maintain a high humidity and provide resting places, such as rocks jutting out over the bank of streams. On windy or rainy days adults rest close to the surface of the bank and in the thickest portions of the overhanging vegetation. Even so, rains evidently take a tremendous toll of the insects. On several occasions I collected in streams which had a large population of fraterna one day; the next day, after a heavy rain, few or no adults were found.

LIFE HISTORY

The egg of T. fraterna would be ideal for the study of embryology of tipulids for two reasons: the egg is fairly large, and the chorion is pale yellow and nearly transparent making it possible to observe some aspects of the growing embryo as development takes place. I am here considering that the time of oviposition is approximately the time of fertilization. The total period for larval development within the egg is from seven to ten days. Eggs from the same female, although laid within five to ten minutes of each other, do not hatch at the same times. Most hatch within one or two hours following the first hatching, but some will not hatch for at least an additional twenty-four hours.

Briefly, the embryonic development shows that at the end of the first twenty-four hour period, there is no noticeable change in the appearance of the egg. The end of the second twenty-four hour period reveals a contraction of the contents with obvious pulling away from the chorion, especially at the ends of the egg. At the end of seventy-two hours, segmentation is noticeable on the dorsal side of the embryo. Yolk material is collected in a ventral area, but segmentation here is vague or obscured. Indentations of organ buds are now seen at both the anterior and posterior ends of the embryo.

A red to dark brown spot forms on the anterior and lateral sides of the embryo between the fourth and sixth days. This area corresponds roughly to the darkened areas surrounding the eyes of the first instar head capsule. By this time, the mouth parts have formed, but the

mandibles are not hardened. Segmentation is visible, although the yolk mass is still noticeably large. During the sixth and seventh days the yolk mass diminishes in size; the dark areas occurring on the head capsule become much larger than before. During the eighth to tenth days the mandibles harden, and the head capsule becomes clearly defined.

Prior to hatching the larva exhibits movement at its anterior end. The posterior end of the larva does not move at all or moves so little as to be hardly discernible. The actions of the mandibles of the enclosed larva are most striking -- opening widely and then apparently scraping the inner edge of the chorion as they close. The head capsule may be twisted so that the mandibles rest nearly dorsally or ventrally to the median lateral plane of the egg. The egg splits along the side opposite the micropyle which is here considered the ventral side. What causes the split is not known, although it could be partially due to the expansion of the embryo and to the scraping of the mandibles. As the larva emerges from the chorion it immediately swells to about two or three and one-half times its size while in the egg. This rapid expansion probably causes further splitting of the egg. The larva then uses its mandibles to grip any available object and pulls against the egg which is held in place by its holdfast. By alternating the gripping of the object with its mandibles and contracting its entire body, the larva proceeds to pull itself out of the shell and into the surrounding soil. Sections show that yolk cells are still present in the gut of the newly hatched larva. These are evidently used up within another twenty-four hours, for sections of the day old larva reveal that the gut is now full of soil debris.

I have not been able to rear the first instar larva completely

through the life cycle to the adult stage. From larvae collected in the field I was able to rear second instar to third instar and third instar to fourth instar. First instar larvae hatched from eggs in the laboratory have been carried through the second instar during a period of thirty to thirty-five days. Fourth instar larvae were reared with ease to the pupal and finally to the adult stages.

During the larval molts a split in the integument occurs dorsally and just posterior to the head capsule of the exuviae of the prior instar. The new instar then proceeds to crawl out of the old integument. The process of shedding the exuviae takes no more than a minute or two after the splitting occurs. The scarcity of exuviae from the various instars is due to the fact that they are eaten very soon by the new instar or by other larvae near by. Byers also mentions this behavior in the genus Dolichopeza and suggests that this may serve as one of the first meals of the new instar, serving also as a rich source of food materials.

A few hours prior to pupation, the larva becomes very sluggish and weak. In addition, there are no typical larval movements, and pupal movement, a whipping motion, is now evident. The head capsule is pushed forward with the mouthparts pointing ventrally. Dorsally, through the integument, the mesonotal breathing horns can be seen developing and ventrally the leg sheaths of the pupa are also seen forming. The lobes of the spiracular disk become soft and, just before pupation proper, are empty of any larval structure. In some specimens the tergal spines of the pupa were seen in the lobes of the spiracular disk, suggesting that these structures are homologous.

At the time of pupation, the organism becomes slightly flattened dorso-ventrally and appears contracted, much like an accordion. The abdominal region appears slightly inflated. The region of the thorax also is the scene of rapid pulsating movements. A split occurs just dorsal and posterior to the head capsule. The pupa then proceeds to move out of the larval exuviae. The newly emerged pupa is pale yellow, the only darkened areas being on the mesonotal breathing horns. Hardening of the remainder of the body is completed after four to six days. The wing pads are the last structures to achieve full coloration, the characteristic white areas in pupae of the fraterna complex occurring a day or two before emergence of the adult. The time for pupal development takes from six to eight days at room temperatures.

I have not seen the emergence of the adult of T. fraterna from beginning to end; however, I have observed individuals as they were nearly free of the pupal case. The coloration of the teneral adult is extremely pale with a greenish tint. Byers has described the process of emergence for Dolichocheza, and I feel after having watched other species of the tricolor group emerging from their pupal cases that the emergence of fraterna closely follows that pattern.

I did not feed the adults as Byers reported doing, so I did not gather data showing the difference in longevity of the adult when fed as compared to that of the adult unfed. The latter period is, for T. fraterna, about three to four days, which is less than the expected life span of the tipuline estimated by Rogers to be three weeks and by Byers half that for Dolichocheza. I believe Byers' estimation to be the more nearly correct, based on my observations of T. fraterna. Byers found that

adults when fed live half again as long as unfed adults, and presumably the adults should live a little longer in their natural habitat than in the laboratory; therefore, I feel certain that the life span of the adult of T. fraterna is no more than ten to fourteen days, and this only under ideal conditions.

Rogers (1933) reports that there are generally three to five instars in the larval stage of Tipulidae. Byers (1952) reported the possibility of pupal development directly from the third instead of the usual fourth instar in Dolichopeza. I did not observe, or at any time suspect, that this behavior was happening in Tipula fraterna. There are four apparent instars in the larval development based on the lengths of larval body and head capsule measurements shown in Table II. The larval length was subject to variation in growth and age. The manner of preservation also affected length, but I feel that these measurements represent closely the actual lengths of the instars. I assume that, due to the heavy chitinization, there is little or no growth of the head capsule during a particular instar. The head capsule measurements are, in my opinion, the better guide to the determination of the instar. In only one case was there overlap between instars in the measurements of the larval body, and in this case a larva considered to be in the fourth instar was poorly preserved with a resulting length which would have placed it in the third instar. However, the head capsule definitely showed it to be within the range of the fourth instar group to which it properly belonged. The variation of the head capsule is considerable in the last instar. This is also true of the larval length measurements. There was only a slight indication that the measurements of the head

capsule also indicate the relative size of the larval body. The largest head capsule of the group measured was 2.08 mm. in length, the larval body of which was 22.53 mm. long; the longest larva measured 28.08 mm., and this specimen had a head capsule measuring only 1.96 mm. The smallest larvae of the fourth instar group, measuring 16.80 mm. and 19.95 mm., did have smaller head capsules measuring 1.53 mm. and 1.65 mm. in length respectively. Byers states that in the genus Dolichopeza the last instar takes the longest portion of the life cycle, and that the second instar takes the shortest time. I believe the same is also true of T. fraterna, which requires from ten to twelve months to complete its life cycle.

The graphic representation of sizes of the immature stages is shown in Figure 13. The number of individuals measured is shown in parentheses and the extreme measurements of length (in mm.) are shown in Table 2.

TABLE 2.

LENGTHS IN MM. OF ALL STAGES OF T. FRATERNA
AND LARVAL HEAD CAPSULE LENGTHS

(Numbers of specimens measured are given in parentheses.)

	<u>Body length</u>	<u>Head capsule length</u>
Egg	0.84 - 0.93 (9)	
First instar	1.51 (just hatched) - 4.52 (10)	0.26 - 0.39 (11)
Second instar	4.69 - 7.20 (8)	0.46 - 0.81 (10)
Third instar	12.60 - 17.55 (8)	1.02 - 1.35 (13)
Fourth instar	16.80 - 28.08 (12)	1.53 - 2.08 (13)
Pupa	15.45 - 22.58 (11)	
Adult	14.00 - 17.00 (10)	

Plate 6

Figure 13. Graphic representation of lengths of all stages of Tipula fraterna, larval head, capsule lengths, and longevity of all stages.

Plate 6

LENGTH IN DAYS OF STAGES

MORPHOLOGICAL FEATURES OF THE ADULT

The description of the morphology of the Tipula fraterna adult described below includes only those structures used in the study of variation and the description of species within the fraterna complex. The following details are based on a study of specimens of Tipula fraterna, but may also serve for T. confraterna and T. strepens. Inclusion of a detailed morphological description is not necessary here for the discussion of the species involved, and the differences that occur between these species will be mentioned in the section on the taxonomy of these species.

Male: The structure of the head of the male is shown in Figure 14. The major portion is occupied by two large compound eyes. Slightly anterior to the eyes is a pronounced ridge, the anterior vertex, from which the antennae originate. The fronto-clypeal region is relatively short and stout, and the nasus is long. The antennae are composed of thirteen segments: a scape, the pedicel, the eleven flagellar segments. The mouth-parts of the tipulid are well described in Alexander (1942), Crampton (1942), Rees and Ferris (1939), and Byers (1952). Byers claims that Dolichopeza has four palpal segments and a palpifer, or five palpal segments, while the other authors report only four in Tipulidae. My observations agree with those of Byers.

In studying variability of the thorax, the most important structures to be considered are the episternum, the anepisternum, the sternopleurite, and the propleurite, all of which have been adequately described

by Alexander (1942). These structures are shown in Figure 14. The interpretation of the wing venation followed here is also that of Alexander (Figure 15).

The male abdomen is characterized by the first abdominal segment being much shorter than the other segments. The second segment is between three and four times the length of the first and is the longest segment of the abdomen. The remainder of the segments become shorter posteriorly.

The ninth tergite is fused with the ninth sternite, but on the posterior portions of this segment is a light area, which may correspond to the pleural suture. Details of the hypopygium, including the outer dististyle, inner dististyle, aedeagus, seminal bulb, and ninth tergo-lobe, are shown in Figure 16, A,B,C,D,E. To facilitate the discussion of the functions of the various lobes of the inner dististyle, I have designated them as lobes 1, 2, 3, and 4. The tenth segment has been considered by other investigators to be the membranous portion surrounding the anal opening, an interpretation with which I am in agreement. In T. fraterna there are two sclerotized plates immediately dorsal to the anal opening which may be remnants of the tenth tergite. There is some question as to what the U-shaped structure shown in Figure 16F may be. It may possibly be referred to the epimere as described in Tipula reesi by Rees and Ferris (1939). Perhaps a more likely possibility is that this structure represents a vestige of the tenth sternite. The ninth sternite has at its anterior edge a thickened area, heavily chitinized. The structure in question might correspond to this particular area on the tenth sternite. The position of the structure is such that it occurs at

Plate 7

Figure 14. Structures of head and thorax of Tipula fraterna.

aes - anepisternum
 e - eye
 es - episternum
 n - nasus
 pn - pronotum
 psc - praescutum
 P - pedicel
 sc - scape
 spl - sternopleurite
 V - vertex

Figure 15. Wing venation of Tipula fraterna.

c - costal
 cu - cubitus
 M - medial
 Rs - radial sector
 R - radial

14

15

the base of a membrane which surrounds the anus ventrally and laterally and thus would correspond to the area in which one would expect the tenth sternite to be located.

Female: The external morphology of the female agrees, generally, with that of the male except for shorter antennae and the genital segments. The eighth sternite is now considered by most students of the Tipulidae to be projected into the hypovalves of the ovipositor. The ninth segment is characterized by having a thin dorsal plate or tergite. Ventral to this plate a lobular area occurs which is just dorsal to the gonopore. This area is strongly sclerotized and articulates with the ninth tergite, and so is considered to be the ninthsternite. Immediately below and anterior to the gonopore is a long sclerotized blade which, in a lateral view, curves ventrally and, toward the anterior tip, again curves slightly dorsad. The posterior tip of this blade is compressed dorso-ventrally and becomes much broader. Medially on this broader portion, there occurs a notch which gives the whole structure a Y-shaped appearance. This corresponds to the Y-shaped structure described by Byers in Dolichopesa, that of T. fraterna differing slightly in size and shape from that of the former. Because of confusion in the interpretation of the morphology of the terminal segments of the female, those up through the tenth have been labeled in Figure 17.

The region beyond the tenth tergite, i.e., the cerci and a bilobed structure beneath and posterior to the anus, is indistinct. The bilobed structure corresponds favorably to that structure marked as the tenth sternite in Tipula reesi (Rees and Ferris, 1939); however, these same

Plate 8

Figure 16. Male hypopygial structures of Tipula fraterna.

- A. Inner dististyle
- B. Outer dististyle
- C. Lobe of ninth tergite
- D. Aedeagus
- E. Seminal bulb
- F. U-shaped structure

Plate 8

A

B

C

D

E

F

workers have considered this structure plus the cerci to be structures of the eleventh segment in Limonia sciophila.

Plate 9

Figure 17. Female hypopygium. Segments numbered through tenth.

TAXONOMY

T. fraterna

The following characters show continuous variations which do not appear to have geographical significance, nor do they appear to separate into a fraterna, floridensis, or maculipleura type. Some are also modified by conditions of preservation.

Loew describes the antennae of Tipula fraterna as being pale yellow with the apical segments somewhat brownish and the basal segments hairy. Alexander (1942) describes the antennae of T. fraterna as being relatively long and bicolorous. He also described the antennae of T. floridensis (Alexander, 1926) with the first basal segment dark brown and sparsely pruinose; the second basal segment a little paler; the flagellar segments bicolorous, with the long pedicel of each yellow, the basal portion darker. The distal flagellar segments are described as becoming uniformly brown or infuscated. Specimens of the Gadsden County series, and from the southeast generally, show that in coloration the antennae range from the second to the distal flagellar segments being almost entirely yellow and lightly bicolorous, to all segments appearing infuscated with the bicolorous condition nearly obliterated. In any case the bicolorous condition is not seen on the first or second basal segment and only vaguely if at all on the first flagellar segment. Loew describes the rostrum of T. fraterna as being pale yellow. Alexander states that this is also true of T. floridensis. I have many specimens

from the southeast which show the rostrum as light brown. The palpi of the two species are considered dark brown by both investigators and, while not so stated by Alexander (1927), those of T. maculipleura (holotype) are also brown. The coloration of this structure in the Gadsden County series and the southeast generally show considerable variation with yellow and brown mixtures.

The head of T. floridensis is described as dark gray with anterior vertex paler and in the female with a capillary median vitta. Loew also described such a vitta in the female of T. fraterna which he used as the type. The males which I have examined also have a dark median vitta in this area; however, there is a gradation from complete obliteration of this vitta, due to the dark coloration of the parietal region, to a distinct line running from the anterior vertex to the occiput.

The praescutal stripes have a similar degree of variation, ranging from being distinctly visible to almost obliterated. The type of T. maculipleura is very discolored in this region but does show the presence of these stripes. In all areas of the pro-, meso-, and meta-thorax, the markings of the sclerites vary in color from light to dark brownish-yellow or brown. The only apparent character difference between T. fraterna and T. maculipleura is in the characteristic coloration of the pleura. Alexander separated T. maculipleura from T. fraterna and T. floridensis by the occurrence of brown markings on the ventral half of the sternopleurite and on the anterior portion of the anepisternum as well as the propleurite. This condition can often be seen on specimens through the normal amounts of pruinose material present. Even in the topotypes of floridensis, faint suggestions of this condition can be seen

on the pleura. These spots become very distinct as soon as the pruinose material is matted or in some way neutralized by the various methods of relaxing or preservation of the specimen, or by the oils from the specimens themselves. I decided to see what would result by taking specimens at random which were preserved in alcohol and observing the spots which occur in these areas. In nearly all cases these spots showed through the pruinosity, and the specimens would have been considered to be T. maculipleura. I also selected two specimens of T. fraterna which did not show the brown through the pruinosity of these areas and subjected them to treatment in a relaxing jar and found that the same markings became apparent. The legs of all the specimens also agree in range of coloration. Normally the distal end of the femur has the tip dark brown, but sometimes the coloration is so intense as to obliterate this character altogether.

The abdominal tergites are dark brown on the sublateral margins giving the insect the appearance of having two stripes on the abdomen. These sublateral stripes may expand over the tergites until the dorsum becomes unicolorous, except on the second which remains lighter. In view of my findings, I can see no valid reason for considering T. maculipleura to be distinct from T. fraterna and I am, therefore, placing maculipleura as a synonym of fraterna.

There appears to be no orderly distribution of these variations that would suggest geographical influence. Byers states that coloration in the genus Dolichocheza must be used with extreme caution as a taxonomic criterion. This is certainly true within the fraterna complex and may apply to the entire tricolor group.

Characteristics of the fraterna complex which show suggestions of geographic as well as population differences include features of the wings of both sexes and the genitalia of the males.

The wings and the genitalia of these species, as is generally true for the Tipulidae, play an important part in the determination of species in this complex. The unfortunate fact is, however, that Loew did not describe the male of fraterna and the type (female) has been lost. Alexander and Rogers have built the concept of fraterna, floridensis, and maculipleura on specimens which occur in the north, in Florida, or in Tennessee. Rogers noted also that fraterna exists in Florida, along with the species that he considered to be floridensis. One Florida population known to have both types was sampled by me for the major portion of a summer in order to study the variation within it and to determine the validity of floridensis as a species. T. floridensis supposedly had several slight differences separating it from fraterna. The outer dististyle and the tergo-lobe differences were considered to be the most diagnostic. On the outer dististyle, two extremes were noted -- the occurrence of a tuft of setae on the apical caudal edge of the outer dististyle in specimens considered to be good floridensis; the absence of this tuft or the even distribution of setae were considered as characteristic of fraterna.

Five samples were taken from Flat Creek south of Chattahoochee, Florida, of which one was eliminated because it was collected within a few days of another. I assumed, therefore, that any possible differences between the two samples would be negligible. Adults that I might have missed in the first collection might possibly appear in the second

collection, thus a distinct break between the two samples would not be present. Samples considered were collected on the following dates: March 30, May 28, July 16, and August 22, 1956. The collections were spaced more than a month apart so that adults alive at the previous time of collection would not be alive for the next sampling, and overlap was thus avoided.

All of these specimens were dissected and mounted in euparal according to the method outlined previously. The outer dististyles were then classified according to three types. The first consisted of specimens whose dististyles were considered to be typical for fraterna, based on Rogers' experience (personal communication) and Alexander's description of this species. This type is characterized by the even distribution of setae or the absence of a tuft of setae on the apical caudal edge of the dististyle (Figure 18). The floridensis type of outer dististyle was picked following Rogers' and Alexander's ideas of floridensis plus a study of specimens which were named by Rogers as floridensis. This type had a tuft of setae on the apical caudal margin of the outer dististyle (Figure 19). The third type is composed of specimens whose outer dististyles are gradations between the two extremes. All intermediates were assigned here. The results of the examinations of the Gadsden County series are shown in Table III.

Within the individual samples the percentage of fraterna type individuals decreased as the summer progressed, while the floridensis type individuals increased in frequency. The intermediate types tended to become progressively more numerous during the summer. The presence or absence of a tuft of setae on the apical caudal edge of the outer dististyle

may then be due, in part, to seasonal differences and is not considered a valid character for separation of the two species.

TABLE 3.

PERCENTAGE OF INDIVIDUALS FROM THE GADSDEN COUNTY
SERIES SHOWING FRATERNA, FLORIDENSIS, AND
INTERMEDIATE TYPES OF SETAE DISTRIBUTION
ON OUTER DISTISTYLES

Type	March 30	May 28	July 16	August 22	TOTAL
<u>fraterna</u>	71% n=15	59% n=24	14% n=1	21% n=5	48% n=45
<u>floridensis</u>	5% n=1	5% n=2	43% n=3	37% n=9	16% n=15
intermediate	24% n=5	36% n=15	43% n=3	42% n=10	36% n=33
TOTAL SPECIMENS IN SAMPLE	21	41	7	24	93

% = percentage in each sample falling into this category.

n = actual number of specimens in each sample falling into a particular category

Table 4 shows the results of lumping thirty-three southeastern collections. It is interesting to note that if, in Table 4, I had merely lumped all of the specimens together without regard to month of collection the results could be interpreted as representing two species with a number of intergrades present. However, presenting this material in the same manner as in Table 3, the data in Table 4 can be more correctly interpreted, i.e., with the percentage of fraterna type individuals decreasing, the percentage of floridensis type individuals increasing, and always some intergrades between the two extremes during the summer. Table 4 includes samples from all states in the southeast.

TABLE 4.

PERCENTAGE OF INDIVIDUALS FROM SEVERAL SOUTHEASTERN SAMPLES GROUPED TOGETHER SHOWING FRATERNA, FLORIDENSIS, AND INTERMEDIATE TYPES OF SETAL DISTRIBUTION ON OUTER DISTISTYLES

Type	June	July	August	TOTAL
<u>fraterna</u>	73% n=40	40% n=2	6% n=7	39% n=49
<u>floridensis</u>	14% n=8	40% n=2	72% n=45	14% n=55
intermediate	13% n=7	20% n=1	22% n=14	17% n=22
TOTAL SPECIMENS IN SAMPLE	55	5	66	126

Another fact, not shown in Table 3, is that I have in this population at least one individual which shows the fraterna type dististyle on one side and the floridensis type dististyle on the other side. The normal situation, however, is to have both dististyles alike.

Because of the variability, it seems useless to analyze a mean type of outer dististyle to be found in a particular locality in the southeast. To do this, summer-long samples must be had from each location, and such samples are not available.

The shape of the outer dististyle was studied to see whether any condition in this structure used by Alexander and Rogers for systematic separation of the two supposed species would be valid. This structure, along with that of the tergo-lobe, appears to have the greatest amount of variation of any of the structures studied. There also appears to be as

much variation within the Gadsden County series as is found in the entire southeastern distribution of T. fraterna. The same is true of the number of setae which occur on the tergo-lobe, a character suggested by Rogers (personal communication) as a possible one for use in the separation of the species. The variations in shape of the outer dististyle were: (1) the width of the stem of the outer dististyle; (2) the curve of the apical end of the dististyle; and (3) the shape of the apical end of the dististyle. The width of the stem was indirectly considered by Rogers when he suggested that the shape of the outer dististyle was strap-like. This would, in my opinion, indicate a shape such as shown in Figure 20. I have found all gradations between this condition and the development of a bulge, giving an irregular shape to the stem, as shown in Figure 21. The curve of the outer dististyle was also considered and again the variations were continuous and did not show the possibility of two species being present (Figure 22 and Figure 23). The shape of the distal end of the outer dististyle of T. floridensis was described by Alexander as truncate and by Rogers as having no apical cephalo lobe. The shapes to be found in one of the samples of the Gadsden County series are shown in Figure 24. Both lobed and lobeless dististyles were seen in all samples. A condition of similar scope is seen in the shape of the distal tip of the ninth tergo-lobe. One extreme has the tip almost truncate, the other has the distal tip rounded. In both the outer dististyle and tergo-lobe, northern and southern specimens show similar variations.

Variation in size of the insect was also considered, but only in the Gadsden County series. The sampling was not complete enough for comparison of measurements of populations from north to south. Body length

Plate 10

Figure 18. Setal distribution of fraterna type outer dististyle.

Figure 19. Setal distribution of floridensis type outer dististyle.

Figure 20. Strap-shaped stem of outer dististyle.

Figure 21. Irregular stem of outer dististyle.

Figure 22. Nearly straight outer dististyle.

Figure 23. Curved outer dististyle.

Plate 10

18

19

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and wing length are correlated, the larger the wing, the longer the body and vice versa. It was evident that the first three measurements indicate one factor alone: that the wing length and body size change with the time of collection of the specimen. The fourth measurement indicates the variation to be found in the angle of the ninth tergo-lobe of T. fraterna. The measurements are as follows: (1) The distance from the arcum (arcual point) to the tip of the wing: the arcual point is that point at which a depression in the wing is formed in the arcum. (2) The distance from the arcual point to the inner base of the tegula. The total of the above characters, (1) and (2), is considered to equal the approximate length of the wing. During the process of removing the wing from dried specimens the tegula was sometimes destroyed. For this reason both measurements were taken, the first being more important to variation studies because of its availability. The changes during the summer, of each, were closely matched. (3) The length of the ninth tergite, measured along its mid-line. This confirmed the conclusion that the body size decreases from early to late summer. (4) The angle of the tergo-lobe. After mounting the tergo-lobe on a slide an outline drawing was made with a camera lucida. Lines were then drawn along the two sides of the lobe and projected until they met. The angle was then measured with a protractor. The results are shown in Table V.

The means of the first character show that the relative size, as reflected in this structure, decreases as the summer progresses. This condition is found commonly in many other insects and was reported by Byers to be true also for Dolichopeza. The range of the approximate wing lengths for the month of March is 18.33 mm. to 15.50 mm.; for May, 17.67 to 14.72 mm.; for July, 16.41 to 13.24 mm.; for August, 16.11 to 13.86 mm.

TABLE 5

RESULTS AND ANALYSIS OF WING AND BODY MEASUREMENTS

Character	Statistic	March 30	May 28	July 16	August 23	t-test Mar. 30 & August 23
Distance from areual point to wing tip	n	20	40	7	24	
	range	15.75 - 13.35	15.15 - 12.60	13.95 - 11.15	13.65 - 11.78	
	$\bar{X}$	14.44 ± 3.23	13.78 ± 2.18	12.85 ± 4.86	12.82 ± 2.62	
	s	.7390	.5170	.7180	.5771	
	S/ $\bar{X}$	5.12 ± .809	3.75 ± .419	5.59 ± 2.113	4.50 ± .650	.597
Distance from areual point to base of tegula	n	17	38	5	23	
	range	2.65 - 22.15	2.52 - 2.21	2.52 - 2.09	2.49 ± 2.03	
	$\bar{X}$	2.436 ± .5891	2.359 ± 3.827	2.286 ± 1.022	2.277 ± .4748	
	s	.0424	.0098	.2012	.1286	
	S/ $\bar{X}$	6.41 ± 1.099	4.20 ± .482	8.80 ± 2.783	5.66 ± .835	.54
Length of ninth tergite	n	20	41	7	23	
	range	1.12 - 9.60	1.12 - .990	1.054 - .960	1.054 - .930	
	$\bar{X}$	1.063 ± .2377	1.059 ± .1653	.992 ± .3749	.995 ± .20746	
	s	.0018	.0013	.0316	.0361	
	S/ $\bar{X}$	3.99 ± .631	3.05 ± .337	3.19 ± 1.206	3.62 ± .534	.448
Angle of tergo- lobe	n	20	40	7	24	
	range	29 - 43	25 - 47	24 - 40	17 - 42	
	$\bar{X}$	35.55 ± 7.949	34.85 ± 5.510	26.86 ± 10.15	31.04 ± 6.336	
	s	4.370	4.775	7.420	5.757	
	S/ $\bar{X}$	12.29 ± 1.943	13.70 ± 1.532	27.62 ± 10.438	18.55 ± 2.678	1.89
Approximate wing length	range	18.33 - 15.50	17.67 - 14.72	16.41 - 13.24	16.11 - 13.86	

The measurement of the angle of the tergo-lobe reveals that the range of means is 35.55 degrees at the beginning of the summer to 31.04 degrees at the end of the summer. This measurement also shows the highest coefficient of variation of any of the measurements. In other samples tested but not shown in the figure, this measurement constantly has a much higher coefficient of variation than all other structures measured, varying from a coefficient of nine to that of twenty-seven; the latter, was found in those specimens of the Gadsden County series. The data show that in the samples of this series, there appears to be an increase of the coefficient of variation as the summer progresses; however, by computing the standard error and the standard error of the difference (Bader, 1955) and comparing the latter to the actual difference of the means as in an *_____*, there was found to be no significant difference between the first and last samples.

The shape of the outer dististyle, the presence or absence of the tuft of setae, and the angle formed by the sides of the tergo-lobe did not in any manner correlate, leading me to believe that two separate species were not present. I am, therefore, considering T. floridensis to be a synonym of T. fraterna.

It was realized that in order to understand the differences in color patterns present in the wings of species of the fraterna complex a basic color pattern must be recognized. This was accomplished for T. fraterna by taking a summer-long series of specimens to determine the basic pattern. This pattern was then compared to other specimens within the geographic range being considered. Again the Gadsden County series supplied much of the information about the basic wing pattern, which is

here described as that pattern in which whitish fascia always appears along the cord and on the outer wing cells (Figure 25). The figure shows that portion of the pattern which remains most constant in shape throughout the summer. The pattern consists of the pale whitish fascia extending from the stigmal area, along the cord of the wing, into the cells M3 and M4. Figures 26, 27, and 28 show wing patterns from the same population with the areas of the distal portion of the wing which become very light and in some cases nearly white. The basic pattern remains unaffected. The frequency of these variations within the samples of this population during the summer is shown in Table VI. Cells M3 and M4 always have the pale white fascia. The other cells possess lighter areas at much lesser frequencies. No change from this condition is seen in any of the samples within the southeast. In only one case the wing possessed a lighter or whitish area in cell R3 along with lighter areas in cell R 4+5 (Figure 29).

Table VI also indicates that the occurrence of a lighter area in cell M2 is much greater than the occurrence of such areas in cells M1 and R4+5. The information suggests that the appearance of these lighter areas is genetically determined, but it is also subject to ecological influences.

The basic pattern also shows some variation within the southeast; however, there is no indication that a cline involving this character is present. The most striking variation of the wing pattern within the southeast was found in two areas, one near the Alabama-Florida state line on the Little Escambia River and in Stone County, Mississippi. In both cases the normal basic pattern was present in some specimens, but in others the pattern was nearly obliterated, merely being suggested

Plate 11

Figure 24. Variation in distal tips of outer dististyle of specimens of Gadsden County Series. (A) March 30, (B) August 22.

Figure 25. Basic wing pattern of Tipula fraterna.

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within the cells M3 and M4 (Figure 30).

TABLE 6

THE PERCENTAGE OF INDIVIDUALS IN GADSDEN COUNTY SERIES
SHOWING WHITE OR LIGHT AREAS IN WING CELLS

Variation	March 30	May 28	July 16	August 22
White or light areas in cell:				
R ₄₊₅	0% n=0	12% n=5	29% n=2	4% n=1
M ₁	0% n=0	17% n=7	29% n=2	4% n=1
M ₂	0% n=0	29% n=12	57% n=4	21% n=5
M ₃	100% n=20	100% n=41	100% n=7	100% n=24
M ₄	100% n=20	100% n=41	100% n=7	100% n=24
TOTAL NUMBER OF SPECIMENS EXAMINED	20	41	7	24

Another type of variation also occurring in the Stone County, Mississippi, sample is the presence of a spur on the angle of the vein R₅ before it reaches the distal tip of the wing (Figure 31). This variation also is found in the Gadsden County series, occurring near the end of the summer, and found in about twelve per cent of the specimens. The Stone County population also was collected near the end of the summer. These three regions were the only ones in the southeast in which variations of this type were found.

T. confraterna

The basic wing pattern to be found in available specimens of T.

Plate 12

Figure 26. Variation in basic wing pattern of Tipula fraterna with white in cell R 4+5.

Figure 27. Variation in basic wing pattern of Tipula fraterna with white in cell M₁.

Figure 28. Variation in basic wing pattern of Tipula fraterna with white in cell M₂.

Figure 29. Variation in basic wing pattern of Tipula fraterna with white in cells R₃ and R 4+5.

Plate 12

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confraterna shows a similar development. In this species the basic pattern to be found at the tip of the wing (the cord and the region beyond the cord) is a patch of white in cell R 4+5 as well as in cells M3 and M4 (Figure 32). This pattern varies slightly as does the basic pattern of T. fraterna, but the patch of white in the cell R 4+5 covers nearly all, except the proximal half and an extreme distal portion, of the cell. This patch is also characteristically rectangular. Variations which occur much less frequently include lighter brown to nearly white areas in cells M1 and M2 (Figures 33 and 34). Although no data are available to substantiate the conclusion, the latter color variations may be due to the same factors suggested as affecting T. fraterna, i.e., ecological conditions and genetic inheritance.

In one specimen of T. confraterna collected near Mountain Lake, Virginia, by J. S. Rogers, the cell M2 has an extra vein extending from the proximal tip of vein M3 into cell M2 (Figure 35).

Differences and similarities of the ninth tergo-lobe are equally as subtle as those of the wings, but a measurement is here considered which, in my opinion, will serve as one of the valid characters for the separation of the two species. This measurement is the same as that described for T. fraterna in which lines are projected along the tergo-lobe until they meet and the angle measured. Although not many specimens of T. confraterna are available, I am convinced that this angle, coupled with the basic wing pattern, can be used for the separation of T. fraterna and T. confraterna. As shown in Figure 36, the angles of T. fraterna range from 15 degrees to 52 degrees, with a mean of 35 degrees in a total of 218

Plate 13

Figure 30. Variation in basic wing pattern of Tipula fraterna found in Stone County, Mississippi, and the Little Escambia River in Escambia County, Alabama.

Figure 31. Variation in wing venation of Tipula fraterna showing spur at angle of Rs.

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Plate 14

Figure 32. Basic wing pattern of Tipula confraterna.

Figure 33. Variation in basic wing pattern of Tipula confraterna with white in cell M_1 .

Figure 34. Variation in basic wing pattern of Tipula confraterna with white in cell M_2 .

Figure 35. Variation in wing venation of Tipula confraterna with extra vein in cell M_2 .

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Plate 15

Figure 36. Comparison of tergo-lobe angles on (A) Tipula fraterna and (B) Tipula confraterna. Angle of tergo-lobe indicated in degrees.

Plate 16

Figure 37. Basic wing pattern of Tipula strepens.

Figure 38. Variation in basic wing pattern of Tipula strepens.

37

38

specimens measured; while the angle of the tergo-lobe of T. confraterna ranges from fifty-three degrees to eighty-four degrees, with a mean of sixty-nine degrees in a total of twelve specimens measured. Other specimens considered to be confraterna which were examined but not dissected and measured are obviously within the range of confraterna.

The variation of the outer dististyle of confraterna closely parallels that of T. fraterna, with some specimens having a pronounced tuft of setae along the apical caudal edge of the outer dististyle and others without this feature.

Size and coloration are virtually identical with that of T. fraterna. Again no definite clines can be determined from the available specimens.

Intergradation of T. fraterna and T. strepens

Rogers' speculation (see page 8) that T. fraterna and T. strepens intergrade, especially in the area of Mountain Lake, Virginia, can be understood more clearly in the light of the range of variations that I have discovered in T. fraterna. The basic wing pattern of T. strepens is defined as always having the whitish fascia in cells R5, M1, M2, M3, and M4. The variation of this condition is the size of the area within each cell (Figure 37 and 38). This area may be quite narrow in some specimens, quite broad in others. The basic pattern, however, remains the same. The Mountain Lake series collected by Rogers agrees with this basic pattern and all specimens fall within the normal range of variation of T. strepens. The tergo-lobe of strepens is thick at the base, extending caudad for a short distance, then abruptly curving inward at both sides

to produce a small lobe resembling that of T. confraterna. In undissected specimens, the thick base of the tergo-lobe is only vaguely seen and might be mistaken for the main portion of the ninth tergite.

The outer dististyles of T. strepens are similar to those of T. fraterna and confraterna, but with much more pronounced apical cephalo and apical caudal lobes at the distal tips than either of these species. The setae are evenly distributed in all specimens examined. The inner dististyle also shows similarities but the ventral lobe is much smaller than that of either T. fraterna or T. confraterna. In addition, the articulation of the inner dististyle to the tergite faces much more forward than in T. fraterna or T. confraterna (compare Figures 39 and 40).

The lateral arms of the aedeagus give finality to the above evidence when compared to those of T. fraterna and T. confraterna. The lateral arms of the two latter species are blade-like without any abrupt widening at the tips of the blades. Those specimens of the Mountain Lake area show the strepens condition of an abrupt broadening of the distal portion of the blade as is shown in Figure 41. I can find no evidence that would lead me to believe that intergradation has occurred between T. fraterna or T. confraterna and T. strepens.

It is interesting that the color patterns of the wings of T. fraterna and T. confraterna vary to the extent that some overlap may be seen between theirs and those of T. strepens. Along with this basic color pattern the shape of the tergo-lobe can be used with ease to separate the species. The similarities only serve to emphasize the close relationship of the three species.

Plate 17

Figure 39. Inner dististyle of Tipula strepens (articulation black).

Figure 40. Inner dististyle of Tipula fraterna (articulation black).

Figure 41. Sketch of aedeagus and lateral arms of Tipula strepens.

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Description of Neotype of *T. fraterna*

The type material from which *Tipula fraterna* was described has been reported as lost (Alexander, 1915). Dr. Alexander (personal communication) informed me that the late Dr. Nathan Banks had since examined the type material of certain species described by Loew (1864) in an attempt to find some of those types which were evidently lost. I wrote to Dr. P. J. Darlington at the Museum of Comparative Zoology, where this material is located, asking if Dr. Banks had been successful in locating the insects, particularly *Tipula fraterna*. This letter was answered by Dr. W. O. Brown, in the absence of Dr. Darlington, who informed me that he was "unable to find any material among the tipulids that is in any way marked as related to *Tipula fraterna*, or that one might reasonably take as type material of that species." Since both Dr. Alexander and Dr. Banks had examined this material and could find no type which referred to *T. fraterna*, I must assume that the type of *Tipula fraterna* is indeed lost.

As a result of the lack of a type and of the study on variability of adult structures, I believe that a neotype for the species *Tipula fraterna* should now be erected. In picking the specimen to serve as the neotype, I used my conception of the species and also followed as closely as possible that, which in my opinion, Loew, Alexander, and Rogers had in mind.

In the following description and that of the new species, *T. confraterna*, I will follow closely that form which has been set by Dr. C. P. Alexander, whose descriptions of *T. floridensis* or *T. maculipleura*,

would serve, for the most part, as a description of T. fraterna; however, some modifications are deemed necessary.

Due to the lack of T. fraterna adults from the type locality at Washington, D. C., a specimen was chosen from among a lot taken in Macon County, North Carolina. This region is the closest locality to Washington from which specimens are available.

Tipula fraterna Loew (neotype)

Wing length:¹ 16.50 mm. Body length: 15.80 mm.

Head: Frontal prolongation of head obscure yellow, nasus long, slender, dorsal surface sparsely pruinose; palpi brown. Antennae, if bent backward, extending slightly beyond base of abdomen; basal segment dark yellowish-brown, second segment concolorous, both segments sparsely pruinose; the first flagellar segment yellow with base vaguely darker. Remainder of flagellar segments bicolorous, nearly black at base with distal portion of each segment yellow. Bicolorous condition becoming obscure at distal flagellar segments gradually becoming more infuscated and darker. Head dark gray pruinose, vertex lighter; head with dark median vitta extending from vertex to occiput.

Thorax: Pronotum brown, mesonotal praescutum brownish-gray with three brown stripes, all indistinctly bordered with darker brown; the median stripe with a dark brown median vitta which becomes obscure before the suture; scutum brownish-gray pruinose; scutellum paler yellowish-brown gray pruinose. Pleura light gray pruinose, slightly darker at

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¹Wing length is measured from the inner margin of the tegula to the tip of the wing.

propleura, sternopleurite, anterior anepisternum, and episternum. Halteres pale brown with knobs darker. Legs with coxae yellow, faintly black at posterior base; femora brownish-yellow, darkening slightly at distal tips, tibiae darker brownish-yellow; remainder of leg segments becoming darker with terminal segments of tarsi brownish-black. The entire apex of the wing dark brown; the inner end of the stigma yellow, the distal end dark brown; cell M paler; a narrow but conspicuous whitish band transversing wing at or a little before the cord, extending from the stigmal area into cells M₃ and M₄, and the inner end of cell 1st M₂. Veins dark brown except in area of the whitish band. Venation, basal section of R₂ about 1/2 r; cell 1st M₂ relatively long and narrow; petiole of cell M₁ about one-third the cell M₁.

Abdomen: Abdominal tergites pale yellowish brown, with broad dark brown sublateral stripes, lateral margins paler, the former vague at the second abdominal segment, darker in first and other segments. Sternites pale yellow-brown anteriorly, becoming dark brown at terminal segments. Hypopygium with caudal margin of ninth tergite bearing a conspicuous, strongly depressed and slightly triangular, median lobe, the tip of the lobe bluntly rounded, the sides narrowing to an angle of thirty-nine degrees (Figure 42). The outer dististyle compressed, with vague apical-cephalo and apical-caudal lobes; setae slightly tufted in appearance at apical-caudal edge. Ninth sternite with a deep, V-shaped notch, the margins fringed with conspicuous elongate setae.

Neotype: Male; Macon County, North Carolina, at Highlands, altitude 3,800 feet. June 11, 1934, J. S. Rogers, No. 50 (Slide no. 684, Hynes).

Topotypes: Five males; Macon County, North Carolina at Highlands, June 11, 1934, J.S.R., no. 50 (Slide no. 6660, J.S.R.). Six males; Macon County, North Carolina at Highlands, 3,800 feet. June 12, 1934, J. S. Rogers, no. 58 (Slides nos. 6658, 6659, J.S.R.). The neotype will be deposited at the University of Michigan Museum of Zoology, Ann Arbor, Michigan. Topotypes are deposited at the University of Michigan Museum of Zoology, and in the University of Florida Collections, Gainesville, Florida.

Description of *Tipula confraterna* sp. n.

Wing length: 16.50 mm. Body length: 16.50 mm.

Head: Frontal prolongation yellow-brown with dorsal area sparsely pruinose, nasus long, slender, and some color; palpi brown. Antennae of moderate length, in male if bent backward would extend to base of abdomen. Basal segment yellow-brown, sparsely pruinose; second segment concolorous; first flagellar segment yellow; second flagellar segment with mere suggestion of black at base, remainder of segment yellow; remaining segments bicolorous, with more distal segments becoming more uniformly infuscated. Head gray, pruinose, anterior vertex lighter, dark median vitta from anterior vertex to occiput.

Thorax: Pronotum brown. Mesonotal praescutum brownish-gray with three brown to gray pruinose stripes, all distinctly bordered with darker brown, the median stripe with a dark brown medial line becoming obsolete before suture; scutum brownish-gray pruinose; scutellum gray pruinose. Postnotal mediotergite light gray, pruinose. Pleura gray pruinose, episternum darker. Halteres dark brown, knobs darker. Legs with coxae pale gray pruinose, trochanters yellow, the tips narrowly and slightly darkened; tibiae brownish-yellow; tarsi brownish-yellow darkening gradually

to brownish-black at terminal segments. The apex of the wing dark brown except for cell R 4+5 which has an elongate pale white patch located distally in the cell, the remainder of the wing dark brown except for cell Cu, which is largely whitish, basal portion of M and first anal cell also whitish. Proximal portion of stigmal area yellow, distal area dark brown; conspicuous, whitish, obliterative band crosses the wing extending from the yellow stigma to the base of M3 and including the basal portion of cell 1st M2 and a major portion of cell M4.

Abdomen: Tergites pale yellowish-brown with broad, dark, sub-lateral stripes; lateral margins broadly paler and pruinose; posterior tergites with dark brown spreading across entire tergite; sternites pale yellow anteriorly, becoming dark brown at posterior end. Male hypopygium with the caudal margin of ninth tergite bearing a conspicuous, broadly triangular-shaped, strongly depressed, median lobe; tip truncate, the sides of the lobe narrowing to an angle of seventy-seven degrees (Figure 43). Outer dististyles with slight apical-cephalo and apical-caudal lobes at distal tips; slightly tufted setae occurring on apical-caudal lobe.

Holotype: 1 male; Hickman County, Tennessee, at Centerville. June 15, 1956; Hynes # 6-1556-1. Slide of genitalia (Hynes # 683).

Paratypes: 2 males; Tuscaloosa County, Alabama, at Gin Creek. June 16, 1954; Hynes # 6-1654-1. Slide of genitalia (Hynes # 349). Four males (one teneral): Hardin County, Tennessee, at Second Creek. June 9, 1956. Hynes # 6-956-2.

Holotype will be deposited at the University of Michigan Museum of Zoology, Ann Arbor, Michigan. Paratypes will be deposited at the University of Florida Insect Collection, Gainesville, Florida.

Plate 18

Figure 42. Neotype of T. fraterna. Left: tergo-lobe. Right: outer dististyle.

Figure 43. Holotype of T. confraterna. Left: tergo-lobe. Right: outer dististyle.

42

43

REPRODUCTIVE BEHAVIOR

Pre-copulatory and copulatory behavior of T. fraterna and T. confraterna, although not basically different from that described by Rogers (1933) for the general mating behavior of tipulids, or Byers (1952) for the genus Dolichopeza, did show some variations.

No difference in behavior could be noted between the species, T. fraterna and T. confraterna. At no time was swarming of males or females noted, and I feel certain that swarming, in the sense that is commonly thought of in Tipulidae, does not take place in this complex. Rogers also mentioned that males would remain near a pupa of the female which, upon emergence, would be seized for copulation. I have not seen this type of behavior. Rogers does report having seen both swarming and early seizure of females in T. caloptera. Indeed, the results of mating-cage experiments lead me to believe that males of T. fraterna will seldom copulate with a teneral female.

When the two species are mixed, the behavior, regardless of the sex, varies from a neutral to avoidance reaction. In only one case have I seen an attempt by a male of T. fraterna to approach the female of T. confraterna, and in this case the behavior on the part of the female was not active rejection, but passive avoidance as will be described later. In no case did I observe a male of T. confraterna approach the female of T. fraterna.

A distinction has been made between pre-copulatory and copulatory

behavior not only for clarity in the following discussion, but because there seem to be minor activities which take place during each phase. Pre-copulatory activity begins with the approach of the male to the female. If the female is receptive, she remains passive, occasionally fluttering her wings in order to maintain balance. The male approaches from behind and drapes his legs over the female. Usually the prothoracic legs alone, and rarely the mesothoracic legs, are placed over the anterior edge of the wings of the female to prevent the female from flying. If the female does vibrate her wings, the male becomes very active, attempting to maintain a hold on her wings to keep her immobile. Simultaneously the male curves the abdomen under that of the female and clasps it with the outer dististyles of his genitalia. The dististyles now work back along the female's abdomen alternately grasping and releasing it until his genitalia reach the posterior end of the female, finally coming to rest at the angle of the cerci and the hypovalves. The posterior end of the male's abdomen is now curved in such a manner as to place the hypovalves in an area ventral to the tergo-lobe. At the same time, the inner dististyles fit into the hypovalves so that the inner lobe #1 fits into the medial inner groove, and the smaller lobe #2 fits along the outer edge, while lobe #3 fits the opposite edge and is nearly in line with lobe #2. How the cerci and the hypovalves are forced apart by the genitalia of the male has not been determined. Byers reported that the gonopophysis of Dolichocheza served this function. The further separation of the cerci, however, is done by the ventral edges of the ninth sternite and the ventral lobes of the inner dististyle, i.e., lobe #4. Meanwhile, the tips of the lobe #1 of the inner dististyle are now located in a cavity

just ventral and anterior to the hypovalves. The tergo-lobe is then lowered into a depression just dorsal and anterior to the hypovalves, in order to maintain a vise-like grip on the area. The grasping of the hypovalves appears to be the function of the tergo-lobe. The ventral lobe #4, of the inner dististyle comes to rest at the medial margin of the cerci, while the dorsal lobes, #2 and #3, retain a grip on each of the blades of the hypovalve (Figure 44). The legs of the male now release their hold on the female and he swings downward with the female supporting him. This results in the ventral surface of the female and the dorsal surface of the male being oriented in the same direction with wings held outward in the normal position. The penis is now inserted into the genital pore of the female, and pre-copulatory behavior is considered to be at an end, and copulation has begun.

After watching many pairs of crane-flies in copulation, I feel certain that there is a type of behavior present, not previously recorded, in which the males during copulation jerk one or two legs in a rhythmic motion occurring at the rate of about one movement per second. Later during copulation, this jerking stops. After the termination of this unique motion, the male may attempt to release itself from the copulatory position, or may continue to hang from the female with no visible motion from either. If the male and female are disturbed during copulation, they will separate, and the jerking motion of the male continues for some time even though there is no contact with the female. This activity has been observed both in nature and in the laboratory. It has also been observed in other species of the tricolor group in addition to T. fraterna and T. confraterna.

Plate 19

Figure 14. Position of genital structures of male and female Tipula fraterna during copulation.

44

There are some additional observations and facets of the behavior of T. fraterna and T. confraterna which I feel deserve more attention than I was able to give them during the course of this investigation. Mating and copulation of T. fraterna and T. confraterna begins at dusk or twilight and in the early morning. The length of time required for copulation in nature is not known, but in the laboratory some pairs continued for as long as three hours. Copulation does not take place until the light diminishes. Pairs that are found in copulation in early morning will separate before the morning is far advanced. Behavior of oviposition also appears to stop about this time. Both males and females then assume the resting position until the light again recedes. Resting may be interrupted intermittently by the insects' flying from one resting place to another.

Putting several males and females of one or both species of the fraterna complex into a cage usually resulted in a haphazard series of flights around the cage. No attempt to seek the male or the female on the part of the opposite sex could be seen. Only when the males and females approached each other closely was there any positive reaction or attempt to mate. The close proximity of the two sexes in nature may be due to the habitat requirements (Rogers, 1933; Byers, 1952). However, in experiments using T. furca, a behavior is seen which might provide an answer to this problem of how males and females locate each other. A male of T. furca was put into a cage and allowed to settle. When a female was introduced, the noise produced by her wings stimulated the male to leave his perch immediately and fly directly to the female engaging her in copulation. This might suggest that wing vibration is one method used by

male crane-flies to find females.

Usually when a female of T. confraterna was introduced into the cage along with a male of T. fraterna no movement was seen on the part of either individual; nor did the reverse situation in which a T. fraterna female and T. confraterna male were brought together result in any noticeable behavioral differences. In only one case did a T. fraterna male attempt to begin mating with a female of T. confraterna. The female, however, merely sidled away. Normal rejection of the male by the female in either species consists of a violent kicking and vibration of the wings. If this does not produce the desired effect, the female flies violently to the bottom of the cage, at the same time kicking her legs, so that both individuals, upon hitting the bottom, are immediately separated. This act may be repeated several times before the male ceases the attempts to mate.

In another observation of a T. fraterna female and the male of another species of tricolor group, Tipula sp. (close to tricolor), the male was able to assume a mating position with the female but was unable to hold her genitalia, apparently for mechanical reasons. These two types of reaction indicate that behavior may serve to keep some species apart, while in others, the mechanical connections of the genitalia are not suitable for the two to carry on normal copulation.

Several times the following situation was observed in the cage. One pair of T. fraterna individuals was in the state of active copulation and would be approached by another male of fraterna. The unattached male would then attempt to copulate with the female who was already engaged in this activity. Sometimes this resulted in the copulating male's being

pushed away from the female; other times the male would successfully maintain his hold on the female. Such attacks may indicate aggressive behavior on the part of males. It would be interesting to set up a hierarchy study with the female as the goal to determine whether such a phenomenon does exist in Tipulidae. No attempt to collect such data was made, as this lies beyond the present scope of this problem.

Various combinations of matings between the species T. fraterna and T. confraterna were attempted with observations from eight separate groups of individuals taken from as many locations. In any one group, males and females of T. fraterna and then of T. confraterna were put into the cage to determine if they would mate with each other. If they did, they were then returned to small containers until used in later experiments. This served as a control to test whether an individual was mature and ready to mate. Then combinations of T. fraterna males and T. confraterna females were tried, but no attempts to mate resulted. The reverse combination was also tried with only the one case, recorded above, in which the T. fraterna male approached the T. confraterna female. At no time during experiments with any combination in single pairs or in groups of one sex of one species with a single individual of the opposite sex of the other species did T. fraterna or T. confraterna mate with each other, although they mated freely among themselves prior to this time. After such combinations had been observed, as a further check, the males and females of both species were put into the cage at the same time. In every case where mating was observed, the male of fraterna went to the fraterna females, and males of confraterna went to the females of T. confraterna. The selectivity of males and females of these two groups

furnishes additional evidence of their specificity.

Oviposition usually follows soon after mating. The female, during oviposition, can be seen to bounce continuously. During the bouncing, the body is oriented with its ventral side parallel with and toward the bank, its head up and forward toward the bank, and the abdomen curved down and forward. The female flies to within three to six inches of the side of the bank and about two to four inches above the water level. She then moves toward the bank, touching it with her tarsi, and at the same time swings her abdomen forward so that the hypovalves and cerci enter the soil horizontally. She then flies away from the bank aided by a springing action of her legs. This action is repeated about eighty times per minute. The greatest length of time that this activity was observed to continue was twenty-five minutes. I do not know if, or how many times, this sequence of behavior may be repeated. Occasionally the valves become stuck in the soil. When this happens, the female increases the speed of her wing vibrations and pushes vigorously against the soil with her legs. The female has never been observed pushing its abdomen deeply into the soil or penetrating more than the length of the valves themselves.

Sometimes the female will bounce in a vertical fashion over the surface of the water. This may occur just prior to or immediately after oviposition. I could not determine whether or not eggs were being laid at this time.

After completing oviposition, the female flies to the low branches overhanging the stream and assumes the resting position.

To determine the number of eggs ejected at one time, I allowed the female to continue the bouncing dance for as long as possible, then

that portion of the bank was cut away for observation under a microscope. Examination of this material revealed that one, sometimes two, and rarely three, eggs would be found at any one point in the site. Several of these extirpated ova were kept in the laboratory until they hatched so that identification could be confirmed. Observation of the hypopygium of the decapitated females in the laboratory revealed that the rhythmical action of the ovipositor corresponded to the rhythm or bouncing action of the oviposition flight. The eggs were usually ejected one at a time, but occasionally one adhered to the hypovalves and the ejection of the following egg would then force both eggs out onto the damp bottom of the cage. Such a situation would explain finding eggs in two's and three's at one point together in the habitat.

The eggs are ejected with considerable force. In containers, four inches square, with the decapitated specimen at one side, the eggs are sometimes ejected with such force that they are thrown to the opposite wall. I was never able to determine whether the depression or raising of the cerci was responsible for the force with which the eggs were eliminated.

When the eggs are ejected into water in the bottom of the container, the hold-fast soon becomes uncoiled and attaches to any debris or to the hold-fasts of other eggs. The advantage of this structure is especially evident when one considers that the area in which the eggs are laid is that in which the greatest amount of erosion takes place. The egg will be held in the area by the filament to roots within the soil. Syers (1952) also reports this structure to be present on the eggs of Dolichopeza and

it is present on the eggs of all species of the tricolor group which I have examined to date. Hemmingsen (1952) has associated the hold-fast with ova deposited in water. The presence of the structure on fraterna eggs leads to the conclusion that this group is basically aquatic except in the adult stage, and even though eggs are now laid above the water line this characteristic has been retained.

IMMATURE STAGES

The immature stages of T. fraterna have been collected and associated with the adult for confirmation of identification. Of the immature stages of T. confraterna, only the pupa can be differentiated from those of T. fraterna. The first and fourth larval stages are described; as the second and third instars follow closely that of the fourth instar, except for size differences, these stages are not treated separately.

Egg

The egg possesses a long filamentous hold-fast at the end opposite the micropyle. It is yellow, elongate, slightly concave at the ventral surface, and bluntly rounded at the ends; the micropyle is prominent. Length: 0.84 - 0.93 mm.; width: 0.28 - 0.31 mm. Figure 45.

First instar larva

The first instar larva, upon hatching, is nearly translucent and white, with many short and a few long setae covering the body. A short time after hatching the color changes to that characteristic of the later instars. The body is terete and stout. The spiracular disk appears as shown in Figure 46. The anal lobes are milk white, and, have six lobes present with the posterior ventral lobes appearing only slightly (Figure 47). Sometimes the posterior ventral lobes cannot be seen at all. The length of the larva varies from 1.59 mm. to 4.52 mm., depending on age. The head capsule ranges from .26 mm. to .39 mm. The head capsule (Figure 48) does

Plate 20

Figure 45. Egg of T. fraterna.

Figure 46. T. fraterna, spiracular disk of first instar larva.

Figure 47. T. fraterna, anal lobes of first instar larva.

Figure 48. T. fraterna, head capsule of first instar larva.

(A) ventral view, (B) dorsal view.

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A

B

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not darken or harden completely. The mandibles, the areas surrounding the ocular plate, the labium, the labrum, and the areas from the ocular plate to the clefts of the head capsule are moderately dark. The edges of the dorsal portion of lateral cranial fragment and the lateral edge of the dorsal cranial fragment plus the coronal suture are dark, as well as the strip extending from the basal mandibular articulation to the maxillary plate. The maxillary plate (Figure 49) has seven teeth. The apical tooth is the longer, but, unlike those in the fourth instar, the teeth appear much sharper. The prementum is also toothed, but appears to have two less than that of the later instars, and the remainder also much sharper than those of the later instars. The labrum of the first instar larva is separated from the clypeal region by a suture which is located directly in front of the antennal plate. The clypeal-labral region is shown in Figure 50. The margin of the labrum appears to be only feebly trilobed. The lateral areas are fringed with setae which project forward and slightly mesad. Also lateral to the central area, on either side, occur two thick setae which originate on the dorsal portion of the chitinized plate. These setae also project forward and slightly mesad, and as far as the fringe of setal hairs described above. The central lobe possesses many very tiny setae. Mesad to the antennae and just caudad to the clypeal-labral suture is a relatively large papilla which points obliquely cephalad. Directly mesad to the papilla there is one long setal hair. On the rest of the clypeal-labral region, especially the lateral portions there are five or six areas which appear to be sensory pits. Another structure, here unnamed, on the clypeal-labral region,

originates just posterior to the clypeal-labral suture on the mid-line of the head capsule. The structure then projects posteriorly and gives off two arms, one to either side, which then end about level to the posterior lateral sutures of the ocular plate. I have found no evidence of the presence of this structure in the other larval instars. No reference is made to this structure by any of the previous authors. I have also found this structure in every first instar larva of other species of the tri-color group which I have examined. What the origin of this structure is, or what its function may be, remains unknown. I thought at one time that it might aid in the escape from the egg, but there is no proof.

The mandible (Figure 51) is yet another structure which varies greatly from that of the later larval instars. The apical portion of the mandible has three teeth which are acute and elongate and point directly forward along the medial line. Just basal and mesad to the apical teeth, occurs another arm at the tip of which are two sharp teeth. There are other smaller lobes on the mandible, but I am not sure whether these appear as variations or are constant in the structure of the mandible.

Fourth instar larva

The fully mature larva (Figure 52) when alive may have slight coloration due to the habitat from which it is collected, because of small particles of clay which adhere to the exoskeleton. When preserved most of the particles are washed off by the alcohol and the true color is seen to be white with yellowish casts. The anterior segments sometimes are a pale, golden yellow, flecked with black due to the presence of setae of the type shown in Figure 53. The body becomes darker at the

Plate 21

Figure 49. T. fraterna; maxillary plate of first instar.

Figure 50. T. fraterna; clypeal-labral region of first instar larva.

Figure 51. T. fraterna; mandible of first instar larva.

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posterior end, especially on the dorsal side. This is due to a heavier concentration of setae. The pleural region sometimes becomes noticeably darkened, giving the larva the appearance of possessing lateral stripes. This condition may occur naturally, or may occur as a result of preservation. The posterior end is truncate, with six conspicuous lobes of the spiracular disk present; the six whitish anal lobes present on the tenth segment are subdivided into a pair of lateral anterior lobes and two ventral anterior lobes which are subequal in length, and directly posterior to the latter are a pair of posterior ventral lobes which are slightly smaller than the other two pairs. There are no creeping welts occurring on either the dorsal or ventral surface of the body. The chaetotaxy of the long setal hairs and pencils of setal hairs are shown in Figure 54 A, B, C, and D.

The boundaries between the tergal and pleural and sternal and pleural areas are indistinct except under high magnification. Under such conditions it is possible to see abrupt differences in the arrangement of the setae in these regions. The pleura have smaller and different arrangements of setae than the sternal or tergal areas. The latter are very similar. There are tufts of small setae surrounding long, single setae which occur at the posterio-lateral edges of the tergal and sternal areas of abdominal segments two through seven. The numbers of setae increase on the tergal and sternal areas of the abdominal segments six and seven. The eighth abdominal tergal area has a noticeably increased number of setae, in which the long single setae, so prominent in the other segments, are no longer present or have been obscured by the presence of

Plate 22

Figure 52. Tipula fraterna, lateral view of fourth instar larva.

Figure 53. Setal type which gives partial black coloration to anterior body segments of Tipula fraterna larva.

Figure 54. Chaetotaxy of segments of Tipula fraterna fourth instar larva. Tergal, pleural, and sternal areas shown from left to right. (A) First thoracic segment. (B) Second and third thoracic segments. (C) First abdominal segment. (D) Second through seventh abdominal segments.

52

53

A

B

C

D

54

the others. The eighth sternal area has four evenly spaced, long, single setae placed slightly posterior to the middle of the segment; tufts of moderately long setae are absent. The ninth tergal area has setae appearing in dense quantity just previous to the tergal lobes of the spiracular disk. This also gives a very dark appearance to the tergal area.

The spiracular disk (Figure 55) has six lobes, the lateral and ventral pair being subequal. The dorsal pair of lobes are small; all lobes bear a fringe of short setae on their margins. At the tips of the ventral pair of lobes occurs a single, long, sensory hair, the length of which is slightly less than half that of the lobe. The ventral lobes are marked with a chitinous plate with a medial stripe, extending from the base of the sensory hair to about mid-length of the plate. At the basal margin of the plate are three heavily chitinized spots, which become smaller laterally. The lateral lobes have a triangular plate which abuts basally almost to the spiracle. The ventral margin of this plate is more deeply colored forming a stripe. The dorsal lobes have triangular plates, the ventral medial margin lying close to the spiracle. The medial and lateral margins of the plate are more heavily chitinized than the remainder of the plate giving the appearance of two stripes; the medial broader than the lateral, on each plate.

The tenth segment of the abdomen is subterminal, surrounding the anal opening and possessing six anal lobes described above. The entire segment is sparsely armed with setae, and much whiter than the rest of the body. A long setal hair is located in the area which is probably the pleural region of this segment.

The head capsules of several tipulines have been described by several authors including Alexander (1920), Oldham (1929), Cook (1949), and Byers (1952). Of these descriptions, that of Cook, treating the head capsules of various Diptera, among them the crane fly, Holorusia rubiginosa, is the most complete and useful in interpreting the phylogenetic significance of the dipteran head capsules. His terminology and that of Alexander's are used in the following description.

The head capsule of the fourth instar has the following dimensions: length, 1.53 - 2.08 mm.; width, 0.74 - 0.93 mm. The head capsule is massive and compact. The mandible (Figure 56) with a pair of teeth at the apical margin, which are prominent, deflected ventrally, separated slightly from another pair of teeth along the ventral edge. The dorsal edge possesses indistinct teeth. Prosthecal tuft shown in Figure 57; the body of the mandible is heavily chitinized.

The maxilla (Figure 58) is quadrate, with the cardo nearly triangular but curving cephalad just before union with other small plates. There are two short, thick, setae present at the bend of this curve. The stipes is seen as an irregular shaped plate. The maxillary palpus is prominent and membranous, except for a chitinous ring at the tip; mesad to the palpus occurs a brush of thick setae, and mesal to this brush on the dorsal surface of the maxilla there is a median large papilla. Another brush of setae occurs along the central lateral margin of the maxilla. The lateral margin and some other portions of the maxillae are covered with numerous short setae.

The antennae are two segmented and chitinized except near the apex where the apical sensory papilla is located (Figure 59). The basal

Plate 23

- larva.
- Figure 55. Tipula fraterna, spiracular disk of fourth instar larva.
- Figure 56. Tipula fraterna, mandible of fourth instar larva.
- Figure 57. Tipula fraterna, prosthecal tuft of mandible.
- Figure 58. Tipula fraterna, maxilla of fourth instar larva.
- Figure 59. Tipula fraterna; antenna of fourth instar larva.

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segment is membranous, attaching to the antennal plate adjacent to the labrum. The length is four times the width, and curved slightly mesad and dorsad.

The maxillary plate (Figure 60) has seven teeth; the apical median tooth is the longest; all the teeth are rounded at the tips, not sharp. The prementum has five teeth, none sharp (Figure 61); the apical median tooth is the longest; the most lateral teeth are very small. On the ventral surface of the labral region are several rows of flattened heavy setae, and on either side of the mid-line are two small spinous papillae. On the anterior and mesal margin of the lateral lobes there is a papilla with two long sensory hairs. Lateral to the papilla and dorsally on the anterior edge there is another sensory papilla.

Pupa

Length, 14.3 mm.; width at the base of the wing-pad, 2.70 mm.; depth at the base of the wing-pad, 2.85 mm.

Body (Figure 62 A, B) pale yellow to rust-brown; eyes, wing-pads, and leg sheaths, dark brown; a conspicuous pale-yellow stripe along the carinate margin of the pleura from the upper edge of the wing-pad at the first abdominal segment to the seventh abdominal segment. Antennal sheaths yellow, ending at the anterior fourth of the lower edge of the wing-pad. Labial sheaths brown, fleshy, touching the leg sheaths of the prothorax. Sternal plates of thorax yellow-brown. Maxillary sheaths brown, touching the antennal sheaths at an oblique angle, recurving caudad, ending about one-half the distance back along the main trunk.

Wing-pads ending just before the apex of the second abdominal segment,

Plate 24

Figure 60. Tipula fraterna, maxillary plate of fourth instar larva.

Figure 61. Tipula fraterna, prementum of fourth instar larva.

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61

dark brown except for a pale yellow transverse mark near the distal fourth of the wing-pad, a small pale yellow area just anterior to this, and another irregular, small, pale yellow mark just below and slightly caudad of the base of the wing-pad corresponding to the markings of the adult wing. Venation usually obscure.

Leg sheaths ending midway between the anterior edge of the fourth abdominal segment and the false division of the segment. Metathoracic leg sheaths slightly longer than the mesothoracic leg sheaths. The cephalic crest bilobed with one or no setae present.

Mesonotal breathing horns thick at base, becoming narrower towards the tip and then suddenly expanding; annulated, pointing at an oblique angle laterad, recurving dorsad at the tips; a delicate, dark brown line occurs along the entire length of the mesonotal breathing horn. Length of horns, 0.81 - 0.87 mm.

The prothorax is yellow, weakly inflated, bilobed or with mid-dorsal area depressed, dark brown and sculptured.

Mesothorax at the anterior third is sculptured in the dorsal area, weakly carinate at the mid-dorsal line, and dark brown; also, with a more flattened appearance. The rest of the mesothorax is rounded, appearing humped. Extending from the carinate region to the posterior third of the mesothorax is a medial stripe which is weakly sculptured; on either side of this is another stripe also weakly sculptured, beginning just caudad of the mesonotal breathing horns, nearly converging at the most dorsal point of the mesothorax into a flat, oval tubercle. One lateral, blunt tubercle occurs mesad and about midway between the median line of the mesothorax and the base of each wing-pad.

The metathorax is small; with an inconspicuous ridge with three setae on each lateral anterior margin of tergal plate. The anterior margin of the tergal plate concave; the posterior margin with a small V-shaped projection into the anterior edge of the first abdominal segment.

The first abdominal segment dull yellow-brown with darker areas forming obscure stripes on either side of the mid-line. A row of four tubercles occurs on either side of the mid-line and about one-third the distance cephalad of the posterior margin. Dark brown pits are on either side of the anterior division of the tergal plate. The entire tergal plate rimmed with dark brown. Abdominal segments two through seven are subdivided, the posterior portion slightly less in length than the anterior; posterior section of the segment possessing several spined tubercles; three transverse dark brown markings on either side of the anterior section.

The pleura of the second segment has two spines on its carinate edge, the anterior much smaller than the posterior. The pleura of the third through seventh segments with anterior spine slightly larger, occurring caudad of anterior margin of segment; the tip of the spine with one setal hair; posterior spine just cephalad of posterior edge of segment, tip with one heavy setal hair, and also one delicate setal hair just posterior to it.

The eighth abdominal segment with tergal plate having no spines or tubercles; pleura having one spinous tubercle below and slightly cephalad of base of anterior tergal arm of ninth segment; sternite having four tubercles, two on each side, the mesal pair larger, all pointing slightly caudad.

The male cauda with anterior pair of tergal arms smaller than others, blunt, pointing directly dorsad. Lateral pair diverging slightly laterad, spinous tips curving mesad. Anterior tergal lobes with bases pointing caudad, curving until spined tips pointing dorsad and slightly mesad. Spinous tubercles of sheath enclosing inner dististyle curving dorsad and slightly mesad. Sheath for outer dististyle truncate or slightly lobed, pointing caudad and slightly-mesad, indicative of the shape of the adult structure and following closely the variation found in the adult. Female cauda with tergal arms much as in the male; caudal valves not curved, pointing directly caudad.

Pupa of *T. confraterna*

The only difference observed between the pupal stages of *T. fraterna* and *T. confraterna* is in the wing-pad of the latter species. In addition to the transverse whitish area described in the pupa of *fraterna*, there occurs in the distal region of the wing-pad of *T. confraterna* a white patch corresponding to that found in the cell R5 of the wing of the adult (Figure 63).

Plate 25

Figure 62. Tipula fraterna, pupa. (A) dorsal view, (B) lateral view.

Figure 63. Tipula confraterna, wing pad of pupa.

Plate 25

A

B

62

63

STATUS OF THE FRATERNA COMPLEX IN RELATION TO THE OTHER
COMPLEXES OF THE TRICOLOR GROUP

The analysis of the various characters and structures of the fraterna complex shows rather conclusively the close relationships of T. fraterna, T. confraterna, and T. strepens. The status of these species in relation to other species has been only briefly considered in descriptions of the new form and has remained somewhat obscured by the inability to explain certain characters, i.e., the wing patterns of the adult forms. Tentative answers to this problem are provided by examination of these species when put into their various complexes and especially by examination of the immature forms. The status of the fraterna complex in relation to the other complexes is described but briefly below. It is based on observations made of the immature stages of the tricolor group while stressing the fraterna complex. It is recognized that a much more complete analysis could be made of the tricolor group as a whole, but I intend only to show what I believe to be the position of the fraterna complex in relation to the other complexes.

Immature stages of the tricolor group, exclusive of the sayi complex, were studied. The position of this complex has not been determined because of lack of material. Alexander (1920) stated that the eggs of the species within the genus Tipula possessed black chorions. It became apparent in studying the various complexes that some complexes had eggs with black chorions or heavily chitinized chorions, and others had eggs with pale yellow or lightly chitinized chorions. Certain correlations of

the type of chorion could also be made with the larval forms. Those species with the black chorioned eggs developed into larvae which were heavily marked by setae producing dark patterns such as occur on the larvae of T. caloptera, T. eluta (Malloch, 1917; Plate XXIX, Fig. 2), and T. furca, and which have, generally, a gray-green coloration. With one exception, eggs with yellow chorions developed into larvae which were characterized by the absence of such markings and were generally pale yellow, as in the fraterna and tricolor complexes. The exception was the concava complex, which Alexander (1926) considers as being closely related to T. eluta, a member of the furca complex. This relationship was based tentatively on similarity of the wing patterns. The immature stages of T. concava are peculiar in that the eggs have a yellow chorion and the larvae are pale yellow, but also possess feeble markings forming stripes extending from the second or third abdominal segments to the dorso-anterior margin of the spiracular disk. This striped pattern is very characteristic of that found in eluta and furca. Thus, coloration of the eggs and the body pattern of the larvae give further evidence of a relationship which can be seen in the adult stages, especially in the details of the genitalia, as the outer dististyles of species in both the fraterna and tricolor complexes are strap-like. The genitalia of T. concava are more like those of the furca complex than any other. The probable relationship of the furca and caloptera complexes is shown by the dark chorions of the eggs. The phylogenetic relationships of the complexes might be as drawn in Figure 64.

Plate 26

Figure 64. Diagram showing relationship of fraterna complex to other complexes within tricolor group of subgenus Yamatotipula.

SUMMARY AND CONCLUSIONS

Within the family Tipulidae there are several groups composed of closely related species, forming species complexes which are similar in most details of morphology, coloration, geographical distribution, and habitats. Within the genus Tipula and the subgenus Yamatotipula, the tricolor group is composed of several of these species complexes, one of which is the fraterna complex.

Originally the fraterna complex was believed to be composed of five species; T. fraterna, T. floridensis, T. maculipleura, T. strepens, and T. calopteroides. Of these the validity of T. maculipleura and T. floridensis was questioned. Specimens had also been collected which had a patch of white in the cell R 4+5 of the wings. The status of this form was uncertain but believed to be included within the species T. fraterna by previous workers.

This problem was primarily concerned with the determination of the status of these species, with the exception of T. calopteroides which was not considered for lack of material, and the elucidation of their biological relationships.

In order to answer questions as to the validity of the species and the relationship of the fraterna complex to the other species complexes, I traveled extensively collecting adults and immature stages within the southeastern area. The distribution of all the complexes, and especially that of fraterna, was studied. Some of the ecological requirements and

the life history of T. fraterna and related forms were determined and the reproductive behaviors observed. The morphological and color variations were studied, both within a single population for a complete season, and in different populations. The following are the conclusions drawn from this study.

1. All of the species complexes and all of the species within those complexes are found in the northeastern United States and in southeastern Canada. It is proposed that the complexes and consequently T. fraterna, T. strepens, and T. confraterna had this area as their center of dispersal. Available data indicate that they spread from this center out to the west and southeast.

2. The distribution of T. fraterna and T. confraterna within the southeast follows closely the margin of the Piedmont from North Carolina to west-central Georgia, then dips southward into western and north-central Florida. Tipula fraterna exists in nearly all areas from this eastern limit to the Mississippi River. It is suspected that edaphic factors along the coastlines and inland may not be compatible for the development of the immature stages of the two species and may partially explain this distribution. It was shown that T. fraterna and T. confraterna follow the same pattern of distribution.

3. In Michigan, there is only one emergence of T. fraterna, during the month of June. This seasonal limitation is evidently characteristic southward to southern Tennessee and northern Alabama. In North and South Carolina the peak emergence occurs in June and tapers off toward the end of the summer. Southward to Florida the emergence is continuous throughout the summer, but two peaks are observed, one in May, the other

in August. This may not necessarily mean that there are two generations per year in this region.

4. A study of the ecology of T. fraterna adults and immature stages does not suggest any correlation with types of vegetation, major or minor. Mosses and liverworts with which the immatures may be associated are thought to be more indicative of the stability of the stream banks.

5. Physical characteristics of southeastern streams considered necessary for the presence of T. fraterna are:

- (a) some flow, neither stagnant nor swampy.
- (b) a steep bank, not a slowly rising bank.
- (c) a bank in which the soil is composed of clay with roots and a certain amount of organic debris in it; the immature stages were never found in gray- to pepper-colored soils nor in banks composed completely of sand.
- (d) a bank which is relatively stable.
- (e) a stream in which low overhanging vegetation is present for resting areas, to supply protection, and to help maintain a high humidity for the adults.

6. The eggs and first instar larvae occupy that area nearest the water surface. It appears that as the larvae increase in size and age, they migrate upward from the water surface. The pupae are found in the relatively drier areas higher on the bank.

7. Differences between adults of T. fraterna and those of T. floridensis were found to be merely variations and not constant, and, for

that reason, T. floridensis is considered to be conspecific with T. fraterna.

8. The characteristics separating T. maculipleura from T. fraterna were found to be due largely to methods of preservation and care of the specimens and of no taxonomic significance. Tipula maculipleura is therefore considered a synonym of T. fraterna.

9. In as much as the type specimen of T. fraterna has been lost or destroyed, a neotype has been designated.

10. There are very few differences between T. fraterna and the spot-winged form, T. confraterna, in habitat, behavior, morphology, or distribution; but two differences in the morphology are constant: (1) the angle of the tergo-lobe, and (a) the presence of a patch of white in cell R_2 of the wing. In addition, the two forms do not mate. Consequently, I consider T. confraterna to be a new species.

11. Some overlap exists in the wing patterns of T. fraterna, T. confraterna, and T. strepens and may explain why Rogers thought that T. fraterna and T. strepens were intergrading. However, the basic wing patterns remain constant and are correlated with constant differences of the tergo-lobes. All specimens, including those from the so-called areas of intergradation, were found to lie within the normal range of variation of the species involved.

12. Based on evidence from the immature stages, the fraterna complex is most closely related to the tricolor complex. This conclusion is confirmed by the details of the genitalia of the adult forms.

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BIOGRAPHY

Claude Dennis Hynes was born in Winnebago, Minnesota, July 10, 1929. He received his primary and secondary education in the Winnebago public schools and was graduated from Winnebago High School in 1947. He attended Macalester College, St. Paul, Minnesota, from 1947 to 1951, receiving the Bachelor of Arts degree in June, 1951.

He began his graduate studies in 1951 at the University of Michigan from which he received the Master of Science degree in 1953. His graduate work was continued at the University of Florida from 1953 to 1957, during which time he held successively a Research Assistantship and a Teaching Assistantship.

He is a member of the Phi Sigma Society, the Society for the Study of Evolution, and the Florida Entomological Society.

This dissertation was prepared under the direction of the chairman of the candidate's supervisory committee and has been approved by all members of the committee. It was submitted to the Dean of the College of Arts and Sciences and to the Graduate Council and was approved as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August 10, 1957

B. J. Byers
Dean, College of Arts and Sciences

_____
Dean, Graduate School

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