THE COMPARATIVE MORPHOLOGY OF THE PENIS
IN THE LIBELLULID GENERA CELITHEMIS,
LEUCORRHINIA, AND LIBELLULA (ODONATA)

A Thesis

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by

Robert Anthony Restifo, B.S.

The Ohio State University
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Approved by

[Signature]
Advisor
Department of Entomology
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INTRODUCTION

The reproductive system of male dragonflies internally consists of a pair of testes, a pair of vas deferentia, a sperm sac, and an ejaculatory duct. Externally, it is composed of a genital pore and a pair of valves on the ninth sternite, a pair of superior appendages, an inferior appendage, and a pair of paraprocts on the tenth segment, and the accessory genitalia, or copulatory apparatus, on the venter of the second abdominal segment.

The accessory genitalia consists of a number of variable structures frequently used for taxonomic purposes. These structures include an anterior lamina (LA, Figs. 1-6), a pair of hamules (Hib, Hoh, Figs. 1-6), a pair of genital lobes (GL, Figs. 1-6), a penis sheath (SP, Figs. 2, 4, 6), and a penis (Figs. 7-72). These structures have been used in the systematics of several anisopteran groups (Bennifield, 1965; Borror, 1931, 1942; Cowley, 1937; Fraser, 1940; Kennedy, 1922b, 1923; Tai, 1967; and Walker, 1912, 1953, 1957), and have been the subjects of morphology studies (Chao, 1953; Currie, 1958; Goddard, 1896; Kennedy, 1922a; Poonawalla, 1966; Prasad and Srivastava, 1960, 1964; Swinebroad, 1954; and Watson, 1965).

This study is concerned with the structure of the penis in three libellulid genera: Celithemis; Leucorrhina;
and Libellula. The terminology used is that of Borror (1942), with slight modification.

The purposes of this study are: (1) to examine the penes of the North American species of the above mentioned genera; (2) to determine whether the penes can provide taxonomic characters; and (3) to propose the relationships between the species within each genus.
MATERIALS

The material used in this study represents the species in North America north of Mexico. With a few exceptions, the species are those recognized by Needham and Westfall (1954). When enough specimens were available, at least four specimens of each species were studied.

The species studied are listed below. The number in parentheses is the number of specimens dissected and the pelves cleared for study.

**Celithemis Hagen**

- amanda (Hagen) (7)
- bertha Williamson (4)
- elisa (Hagen) (4)
- eponina (Drury) (5)
- fasciata Kirby (5)
- martha Williamson (5)
- monomelaena Williamson (4)
- ornata (Rambur) (5)
- verna Pritchard (2)

**Leucorrhinia Brittinger**

- borealis Hagen (2)
- frigida Hagen (4)
- glacialis Hagen (4)
- hudsonica (Selys) (4)
intacta (Hagen) (4)
patricia Walker (1)
proxima Calvert (4)

Libellula Linnaeus

auripennis Burmeister (6)
axilena Westwood (4)
comanche Calvert (4)
composita (Hagen) (5)
croceipennis Selys (5)
cyanea Fabricius (4)
flavida Rambur (5)
forensis Hagen (4)
incesta Hagen (3)
luctuosa Burmeister (5)
nechami Westfall (7)
nodisticta Hagen (4)
pulchella Drury (5)
quadrimaculata Linnaeus (4)
saturata Uhler (4)
semita Burmeister (4)
vibrans Fabricius (4)
TECHNIQUES

Before removing the penes, the specimens were relaxed. Two methods of relaxation were used. Specimens of Celithe
dmis and Libellula were placed in a relaxing chamber for
three to five days; specimens of Leucorrhinia were placed
in a solution of Aerosol OT (sodium dioctyl sulfosuccinate),
diluted by a factor of three drops to 125 ml. of distilled
water, for five to ten minutes. Each specimen was then
placed on a small sheet of balsa wood, and a right lateral
view of the second abdominal segment drawn. The specimen
was then placed on its dorsal surface with the wings spread
and held down by strips of paper. A ventral view of the
second segment was drawn, after which the penis was dis-
sected out by first cutting the membranes on either side
of the first segment of the penis with a sharpened number
one insect pin. The median ridge of the third sternite
was then grasped with a pair of fine-pointed jeweler's
tweezers, and the sternite cut just proximad to the base
of the first segment with a piece of razor blade on an
applicator stick. The first segment was then grasped with
the tweezers, and the penis pulled out. The penis was
then placed in a pH cup containing glycerine and preliminary
drawings of the ventral and lateral views made. The penis
was then placed in a pH cup containing fifteen per cent
potassium hydroxide for three to six days, until sufficiently
cleared for study. The penis was placed in a pH cup containing glycerine and the ventral and lateral views drawn.

When the drawings were completed, the penis was placed in a glycerine-filled four by ten millimeter genitalia vial, which was put in the envelope with the specimen.

All drawings were made with a camera lucida. The drawings of the second abdominal segments and peres of the species of *Celithemis* were made at 22.5X and 45X, respectively. All the drawings of *Leucorrhinia* and *Libellula* were made at 22.5X.
GENERAL STRUCTURE OF THE MALE GENITALIA
OF THE SECOND ABDOMINAL SEGMENT

The accessory genitalia of male dragonflies lie in the genital fossa, a depression on the venter of the second abdominal segment. The structures associated with the fossa have been named (vide supra).

The descriptions appearing in this paper refer to the structures in their normal position, i.e. facing ventrad with the lobes of the penis directed caudad.

The anterior lamina is a sclerotized plate which occupies the anterior one-fourth of the genital fossa. It projects ventrad in its posterior one-third and bears a fringe of long setae on its postero-median edge. It is quite uniform in shape in Libellula and Celithemis but varies in a few species of Leucorrhinia.

The hamules are a pair of heavily sclerotized structures which extend beyond the ventral edges of the second tergite. They lie posterior to the anterior lamina, laterad of the midline, and anterior to the genital lobes. Distally each hamule is bifid, with a relatively narrow, ventrally directed, hooked inner branch (Hih, Figs. 1-6) and a broader, shorter, bluntly rounded outer branch (Hob, Figs. 1-6). The inner branch is anterior to the outer branch in Celithemis and Leucorrhinia but posterior to the outer branch in Libellula. Hagen (1890) states that in
Leucorrhinia the inner branch is moveable, the line of flexion running diagonally across the base of the inner branch. The shape of the hamules varies little in Celithe-mis and Libellula but shows good specific variation in Leucorrhinia.

The genital lobes are rounded prolongations of the postero-ventral edges of the second tergite. These lobes project caudad and mesad over the first segment of the penis and bear a fringe of long setae along their apical edges. The shape of these lobes does not vary in the three genera studied.

The sheath of the penis is a thin U-shaped flap arising on the ceiling of the genital fossa between the bases of the hamules. It is directed cephalad but does not bend ventrad as in other anisopteran families (Currie, 1958; Swinebroad, 1954). It does not vary in shape in the three genera studied.

The penis is a four segmented structure which bears at its distal end a set of lobes which are highly variable in shape. The penis arises from the anterior end of the third sternite and extends cephalad between the hamules and ventrad to the sheath. Anterior to the hamules it bends ventrad and then caudad, so that the terminal lobes lie between the hamules and are directed caudo-ventrally.

The terminology used for the various segments, as well as the lobes, varies from author to author and from
group to group. The terminology used in this study follows that used by Borror (1942). In Figures 7-72, the basal portion of segment II and all of segment I are omitted.

The first or basal segment (vesicle of some authors) is a large flask-shaped structure which is heavily sclerotized on its ventral surface but membranous on its dorsal surface. Its wide basal end articulates with the third sternite. The narrow distal end lies between the bases of the hamules. The shape of the first segment varies little in the genera studied.

The second segment is cylindrical, elongate and terminates with a short, dorsally directed protuberance (spur of Kennedy, 1922a) on its dorsal surface. This segment varies little in the genera studied.

The third segment is short, triangular, and bears an opening, the proximal meatus of the seminal duct, on its cephalo-median surface. The shape and orientation of this segment allows the fourth segment to be directed caudo-ventrad. The shape of the third segment varies little in the genera studied.

The fourth segment consists of a heavily sclerotized basal portion and a set of highly variable lobes distally. The basal portion is roughly triangular in shape and often protrudes ventrad in what is called the hood. According to Kennedy (1922a) there may be as many as nine lobes
associated with the distal end of the penis. The majority of the lobes are evagination of the walls of the basal portion (Borror, 1942).

The hood (H, Figs. 25-72) is a ventrally directed prolongation of the caudo-ventral edge of the fourth segment of the penis. A distinct hood is not present in all libellulid genera; it shows variable development in some. In shape, it varies from bilobed to laterally compressed. A hood is not present in Celithemis. In Leucorrhinia the hood is well developed into a bilobed structure; it is similar in shape in most species (pointed caudo-dorsally); but in L. frigida it is bifid and directed caudad, and in L. patricia and L. proxima it is rounded. The hood in Libellula shows various degrees of development, from a low triangular projection to a high, laterally compressed projection.

The lateral lobes (L, Figs. 7-72) are a pair of usually heavily sclerotized, somewhat laterally flattened structures which arise from the lateral walls of the fourth segment. These lie laterad of the other lobes. They are fairly uniform in shape in Celithemis and Leucorrhinia, but vary significantly in Libellula.

The medial lobes (M, Figs. 7-72) are a pair of lightly sclerotized, slightly erectile lobes which form the ventral and part of the lateral walls of the distal end of
the seminal duct (SD, Figs. 7-72). They are the ventral-most lobes. Their shape varies little in *Celithemis* and *Leucorrhinia*, but significantly in *Libellula*.

The median process (MP, Figs. 7-72) is the most variable of the lobes. It is lightly sclerotized, erectile, usually rounded, and lies dorsad of the medial lobes, mesad of the lateral lobes, and ventrad of the apical lobe. It may bear as many as three cornua. A cornu (C, Figs. 7-72) is any non-erectile process or prolongation arising from the median process. It may be lightly or heavily sclerotized, usually arises medially, and usually extends at least to the apices of the medial lobes. The cornua correspond to the structures termed "cornua" by Kennedy (1922a, b) and those termed "median process" by Borror (1947). The median process in *Celithemis* is sac-like and extends to the apices of the medial lobes. It bears a median, sclerotized cornu, which is emarginate apically. In *Leucorrhinia* it is large, sac-like, and bears a pair of sclerotized cornua, which are bent ventrad apically. In *Libellula* it is highly variable and may bear as many as three cornua. The number, degree of sclerotization, and length of the cornua vary significantly.

The apical lobe (A, Figs. 7-72) is lightly sclerotized, trough-shaped, and occupies a dorso-median position relative to the rest of the lobes. It may be small or large, round
or elongate. In *Celithemis* it is large and rounded, and
does not vary in shape. In *Leucorrhinia* it is elongate,
bent ventrad, and varies in shape in only two species. In
*Libellula* the apical lobe varies from small to fairly large
but is consistently rounded.

The internal lobes (I, Figs. 7-24) are paired, lightly
sclerotized, erectile, and lie laterad of the apical lobe
and median process, from which they arise. They are present
in *Celithemis* as elongate lobes but are apparently not
present in *Leucorrhinia* and *Libellula*.

The posterior lobe (P, Figs. 39-72) is sac-like,
lightly sclerotized, erectile, and is situated dorsad of
the median process, from which it arises. It is present in
*Libellula* but apparently not in *Celithemis* or *Leucorrhinia*. 
MALE GENITALIA OF THE SPECIES OF CELITHEMIS

The structure of the genitalia of the species of Celithemis (Figs. 1-2, 7-24) shows little variation. The anterior lamina projects slightly, is broadly U-shaped in ventral view, and bears a fringe of long setae on its caudo-median edge. The inner branch of the hamules is relatively short and bears a small, laterally directed hook apically. The outer branch is shorter and broadly rounded. The sheath of the penis is small, U-shaped, and lies horizontally on the ceiling of the genital fossa between the bases of the hamules. The genital lobes extend ventrad as far as the outer branch of the hamules. The penes are very similar in all the species.

There is no hood. The lateral lobes are usually fairly narrow and curved mesad apically. The medial lobes are broad, almost reach the apices of the lateral lobes, lie roof-like ventrad of the sclerotized, tubular seminal duct, and have a constriction on their lateral edges near the bases in ventral view. The median process is broad, emarginate apically, extends to the apices of the lateral lobes, and bears a median cornu. The cornu is sclerotized, usually narrow and elongate, emarginate apically, usually bent ventrad in profile, and has its base round in ventral view. The internal lobes are elongate, usually broad, and
extend distally at least to the apices of the lateral lobes, often beyond. The apical lobe is trough-shaped, bent ventrad apically, and usually does not extend to the apices of the lateral lobes.

The structure of the penis in this genus does not vary enough to draw any conclusions about the relationships between the species. The following are descriptions of the penes of the species of *Cellithemis* as they vary from the general structure (vide supra).

*C. amanda* (Figs. 7-8). The lateral lobes are fairly elongate and bent slightly dorsad in profile. The cornu is short, relatively broad, very slightly bent ventrad, and broadly emarginate apically. The internal lobes extend slightly beyond the apices of the lateral lobes.

*C. berthae* (Figs. 9-10). The lateral lobes are fairly elongate and bent slightly dorsad in profile. The cornu extends distally beyond the apices of the internal lobes. The internal lobes are relatively narrow.

*C. elisa* (Figs. 11-12). The lateral lobes are broader and not bent dorsad. The cornu is broader than that of *bertha* and does not extend to the apices of the internal lobes. The apical lobe extends distally beyond the apices of the lateral lobes.

*C. eponina* (Figs. 13-14). The lateral lobes are relatively short and broad and not bent dorsad. The cornu extends
beyond the apices of the internal lobe, is strongly bent ventrad, and is acutely emarginate apically. The apical lobe extends beyond the apices of the lateral lobes.

C. *fasciata* (Figs. 15-15). The lateral lobes are abruptly bent cephalad at their apices in ventral view. The cornu extends beyond the apices of the internal lobes. The apical lobe extends to the apices of the lateral lobes.

C. *martha* (Figs. 17-18). The lateral lobes are relatively short and broad and not bent dorsad. The cornu does not reach the apices of the internal lobes and is not bent ventrad. The apical lobe extends to the apices of the lateral lobes.

C. *monomelaena* (Figs. 19-20). The lateral lobes are short and broad. The cornu is broad, slightly bent ventrad, and does not extend to the apices of the internal lobes.

C. *ornata* (Figs. 21-22). The lateral lobes are very broad, short, humped on their ventral edges in profile, and very wide basally in ventral view. The cornu does not extend to the apices of the internal lobes. The internal lobes are hidden laterally by the lateral lobes.

C. *verna* (Figs. 23-24). The lateral lobes are not bent dorsad. The cornu extends almost to the apices of the internal lobes. The apical lobe does not extend to the apices of the lateral lobes.
MALE GENITALIA OF THE SPECIES OF LEUCORRHINIA

The genitalia of the species of Leucorhinia (Figs. 3-4) show some specific variation. The anterior lamina usually projects slightly ventrad and is roughly U-shaped in ventral view. The anterior lamina in intacta is distinctly bilobed in its apical half, each lobe being quadrate in profile, oval in ventral view, and bears short, thick, black spines. The shape of the hamules in this genus is a good character for separating the species. The inner branch is well developed ventrad and often broadly bent caudad. The outer branch is broadly rounded in profile and overlaps the anterior edge of the genital lobes. In ventral view the outer branch varies from acutely angulate to rounded where it overlaps the genital lobes laterally, and bears on its caudo-medial edge a projection which varies from a sharp, cephalad directed hook to a broadly rounded lobe. Since it is not the purpose of this study to evaluate the hamules as a taxonomic character, they will not be described in any detail. The sheath of the penis is U-shaped and lies on the ceiling of the genital fossa between the bases of the hamules. It is directed cephalad and is not bent ventrad. The genital lobes are rounded apically, narrowed basally, and bent caudad. They do not project ventrad as far as the outer branch of the hamules. They bear a fringe of long
setae along their caudo-medial edges. The shape of the genital lobes does not vary. The penis varies in shape enough to separate the species into groups.

There is a well developed hood in all species; it varies from pointed and directed caudad to rounded in profile, and is usually bilobed with a thin, lightly sclerotized median portion in ventral view. The lateral lobes are large, usually bent ventrad in profile, and directed mesad in ventral view. The medial lobes are small, inconspicuous, rounded, and not variable in shape. The seminal duct is sclerotized and nearly tubular distally where it is covered by the medial lobes. The median process is a large sac-like, trough-shaped lobe located mesad to the lateral lobes. It is lightly sclerotized and bears a pair of sclerotized, pointed cornua. Each cornu is directed dorsad in its basal one-third within the median process and lies sub-parallel to the midline, extending distally slightly past the apices of the medial lobes, and bent ventrad apically in ventral view. The apical lobe is elongate, broadly bent ventrad, and usually extends to the apices of the lateral lobes.

Based on penis structure, there appear to be three groups into which the North American species fall. These groups are indicated by the shapes of the hood, lateral lobes, and apical lobe. The following are descriptions of the groups and of the species as they vary from the general
structures of the groups.

The first group includes only *frigida*. The group is characterized by: (1) the hood being bifid, with each point being directed caudad, and with no lightly sclerotized membrane between the points; (2) the lateral lobes being short and triangular in profile; and (3) the apical lobe being broad, bent ventrad, and extending well beyond the apices of the lateral lobes.

*L. frigida* (Figs. 27-28). The medial lobes are narrow and relatively elongate. The median process is small and extends to the apices of the lateral lobes. The cornua are not bent ventrad apically.

The second group includes *borealis*, *glacialis*, *hudsonica*, and *intacta*. It is characterized by: (1) the hood being bilobed, each lobe rounded on its caudo-ventral edge and pointed caudo-dorsad, and with a lightly sclerotized membrane between the lobes; (2) the lateral lobes being broad, elongate, slightly bent ventrad, and rounded apically; and (3) the apical lobe being broad, bent ventrad, and extending to or beyond the apices of the lateral lobes.

*L. borealis* (Figs. 25-26). The cornua are bent laterad apically and extend to the apex of the median process.

*L. glacialis* (Figs. 29-30). The cornua are bent laterad apically and do not extend to the apex of the median process.
**L. hudsonica** (Figs. 31-32). The cornua are bent slightly laterad apically and do not extend to the apex of the median process. The apical lobe has an angular projection on its dorsal edge basally.

**L. intacta** (Figs. 33-34). The lateral lobes are narrow, approaching those of group 3 in shape. The cornua are bent laterad apically and extend to the apex of the median process.

The third group includes *patricia* and *proxima*. It is characterized by: (1) the hood being bilobed, each lobe rounded apically, and with a lightly sclerotized membrane between the lobes; (2) the lateral lobes being narrow, elongate, bent ventrad, and rounded apically; and (3) the apical lobe being small, narrow, bent ventrad, and extending only three-fourths the length of the lateral lobes.

**L. patricia** (Figs. 35-36). The lateral lobes are slightly convergent in ventral view. The median process is relatively small. The cornua extend beyond the apex of the median process.

**L. proxima** (Figs. 37-38). The lobes of the hood are broader than those of *patricia*. The median process is small. The cornua extend beyond the apex of the median process.
MALE GENITALIA OF THE SPECIES OF LIBELLULA

Except for the penis, the genitalia of the species of Libellula (Figs. 5-6) are fairly uniform in shape and do not serve to differentiate the species. The anterior lamina projects ventrad, slightly at its base and with its apex extending as far as the apices of the genital lobes. It is broadly U-shaped in ventral view and bears a fringe of long setae along its caudo-medial edge. The hamules are relatively short and broad and are directed caudo-ventrad. The inner branch is usually triangular in profile and has its apex slender and bent laterad into a small hook. The outer branch is usually a low shoulder in profile and rounded, projecting slightly caudo-lateral in ventral view. The shape of the hamules varies in a few species: in croceipennis the outer branch projects laterad, making the hamules appear elongate mesad to laterad in ventral view; in quadrimaculata the hamules are C-shaped in profile; in saturata the hamules are similar to those of croceipennis; and in semifasciata the outer branch strongly projects caudo-laterad. The sheath of the penis is U-shaped, directed cephalad, does not project ventrad, and lies between the bases of the hamules. The genital lobes are rounded, over-lie slightly caudad, project ventrad slightly beyond the outer branch of the hamules, and bear a fringe of long
setae along their ventral edges. They vary in shape only in \textit{croceipennis}, in which they are enlarged, project beyond the apices of the outer branches of the hamules, and strongly overlie caudal. The penes of the species of \textit{Libellula} have already been described and a phylogeny proposed (Kennedy, 1922a,b). The lobes on the fourth segment are highly variable and serve as a basis on which the species can be separated. Because the drawings in Kennedy's papers are so sketchy, and because there have been some modifications in the status of certain species, it seems desirable to re-examine the penis of each species, make more detailed drawings, and re-evaluate the proposed phylogeny.

Based on penis structure, there appear to be five groups into which the North American species of \textit{Libellula} fall. These groups correspond to Kennedy's subgenera, excluding \textit{Plathemis} and \textit{Ladona}. The following are descriptions of the groups and of the species as they vary from the general structure of the groups.

The first group includes \textit{croceipennis} and \textit{saturata}. It is characterized by: (1) a caudo-ventrally directed hood; (2) small, relatively undeveloped lateral lobes; and (3) two or three long, well developed cornua. \textit{L. croceipennis} (Figs. 39-40). The hood is well developed, laterally compressed, and overlies the bases of the medial lobes. The lateral lobes are lightly sclerotized,
narrow, arise at the dorsal edge of the fourth segment, and are bent laterad apically. The medial lobes extend beyond the hood, diverge slightly apically, and bear a lateral ridge which runs horizontally from the distal meatus to the walls of the fourth segment; this ridge forms the lateral extent of the medial lobes in ventral view. The median process is sac-like, extends slightly beyond the apices of the medial lobes, and bears a pair of cornua. The cornua arise from the caudo-dorsal edge of the median process, are sparcely fringed with short setae, and bear a very lightly sclerotized, ventrally directed spine on their bases. The posterior lobe (shown partially inflated) usually extends to the apex of the median process. The apical lobe is inconspicuous, lying along the dorsal edge of the fourth segment.

L. saturata (Figs. 41-42). The hood is not well developed, as in croceipennis. The lateral lobes are heavily sclerotized, directed caudo-ventrad, bent mesad, and abruptly widened basally in ventral view. The medial lobes are broad in profile, with a narrow band on each lobe extending dorsad along the edges of the fourth segment to the lateral lobes. The median process is sac-like and bears three cornua. Two of the three cornua are long, fairly well sclerotized, directed caudo-dorsad in profile and laterad in ventral view. The third cornu
is less sclerotized and shorter; it arises from the membranous portion of the median process; the other two have a common, sclerotized base. Kennedy (1922a) states that, "the right one is asymmetrical", referring to the less sclerotized, shorter cornu. In two of the three specimens which had not lost the cornua, the shorter one was to the left, as shown in the drawings. A larger series of specimens will have to be studied before any conclusions can be drawn as to this variation. The posterior lobe is sac-like and fused with the median process. The apical lobe is larger and extends from the dorsal edge of the fourth segment to the bases of the lateral lobes.

The second group includes only _semifasciata_. None of the lobes in this species are well developed. Kennedy interpreted this condition as primitive and designated this species as the ancestor from which the other species developed. Assuming this condition to be primitive, there are four branches of development diverging from this base; these branches correspond to the other groups.

_L. semifasciata_ (Figs. 43-44). There is no distinct hood. The lateral lobes are heavily sclerotized, short, and arise from the caudo-dorsal edges of the fourth segment. Basally they are directed ventrad but are bent so that they are directed caudad through most of their length.
in profile. They are slightly divergent in ventral view. The medial lobes are short and broad in profile, with apical projections around the seminal duct, and are widened basally in ventral view. The median process is short, not extending to the apices of the medial lobes, and bears a pair of cornua. The cornua are well sclerotized, extend past the apices of the lateral lobes, are pointed and directed caudo-dorsad in profile; in ventral view they are directed laterad, with their apices bent caudad. The posterior lobe is sac-like and small. The apical lobe is small and lies well dorsad to the lateral lobes.

The third group includes only *quadrimaculata*. The lateral lobes are shorter and wider in profile than those of *semifasciata*; the medial lobes are more developed; and there is a third cornu present. Kennedy regards this species as "highly specialized in its intense activity".

*L. quadrimaculata* (Figs. 45-46). There is no distinct hood. The medial lobes are narrow bands along the distal edges of the fourth segment, extending from the dorsal edges of the lateral lobes, where they are slightly expanded, to slightly ventrad of the ventral edge of the fourth segment. The median process is broad and tapers to the median cornu in ventral view. The two lateral cornua are fairly heavily sclerotized, bent dorsad in profile,
parallel in ventral view, and sharply pointed. The median cornu is less sclerotized, half as long as the lateral cornua, sharply bent dorsad, and pointed. The posterior lobe is large and extends dorsad to the dorsal edges of the lateral lobes.

The fourth group includes \textit{forensis}, \textit{nodisticta}, and \textit{pulchella}. It is characterized by: (1) a well developed, cephalo-ventrally directed hood with three carinae; (2) lightly sclerotized, short, slender lateral lobes; (3) large, broad medial lobes which cover most of the median process; (4) an elongate median process which is fused with the posterior lobe basally; and (5) a short, stout, lightly sclerotized, median cornu.

\textit{L. forensis} (Figs. 47-48). The apical lobe is relatively small and has its ventral edge extending ventrad to the base of the median process.

\textit{L. nodisticta} (Figs. 49-50). The apical lobe is larger, extending almost to the apices of the lateral lobes, and has its ventral edge extending ventrad just past the dorsal edge of the median process.

\textit{L. pulchella} (Figs. 51-52). The apical lobe is small, extending half the length of the lateral lobes, and has its ventral edge extending ventrad just past the dorsal edge of the median process.
The fifth group includes *composita, axilena, auripennis, luctuosa, needhami, comanche, cyanea, flavida, incesta* and *vibrans*. It is a highly variable group; the relationships are not clear and are very confusing. The only characters common to all the species are the heavily sclerotized, elongate lateral lobes and the lightly sclerotized, median cornu arising from a broadly elongate median process. The following relationships are proposed.

*Composita* does not appear to be closely related to any other species in this subgroup.

*L. composita* (Figs. 53-54). There is no distinct hood. The lateral lobes are slightly sinuate, have their dorsal and ventral edges sub-parallel, and are slightly enlarged apically. In ventral view they are bulged laterad, enlarged in their apical half, and have the apices bent mesad and overlapping. The medial lobes are small, narrow bands along the distal edges of the fourth segment and have their ventral ends expanded caudad. The median process extends three-fourths the length of the lateral lobes and has its base covered ventrally by the medial lobes and laterally by ventrally directed basolateral projections from the posterior lobe. The cornu extends dorsad just beyond the dorsal edges of the lateral lobes. The posterior lobe is elongate, extends to the base of the cornu, and has a pair of ventrally
directed baso-lateral projections which extend almost to the midline, making it appear scoop-shaped in posterior view.

Axilena is also not closely related to any other species in this group, differing by several characters (vide infra). L. axilena (Figs. 55-56). There is no distinct hood. The lateral lobes are narrowed basally and bent dorsad in profile, and are sinuate, with their apices bent mesad in ventral view. The medial lobes are confined to the medio-ventral surface of the median process, pyramidal in shape, extend ventrad as far as the ventral edge of the fourth segment, and extending distally one-third the length of the median process. The median process is elongate and has a pair of baso-lateral bulges in ventral view. The cornu is short, thick, and bent cephalad, extending as far as the middle of the narrowed portion of the lateral lobes. The posterior lobe is not well defined; its ventral limits are inconspicuous, being hidden by the median process. The apical lobe is small and dorso-ventrally elongate.

Auripennis, needhami, and luctuosa are closely related, having the following characters in common: (1) a low, cephalo-ventrally directed hood; (2) heavily sclerotized, sinuate lateral lobes which have their apices bent ventrad; (3) medial lobes which extend as narrow bands along the
distal edges of the fourth segment from the bases of the lateral lobes ventrad and are widened ventrally; (4) the posterior lobe is as long as the median process and has a pair of ventrally directed, base-lateral projections which make it appear scoop-shaped in posterior view; and (4) an elongate cornu.

_L. auripennis_ (Figs. 57-58). The lateral lobes are nearly parallel-sided and bent mesad but with the apices usually not crossing. The medial lobes extend from the ventral edges of the bases of the lateral lobes to ventrad of the other lobes; their caudo-dorsal edges are very thin and difficult to see. The apical lobe extends from the caudo-dorsal edge of the fourth segment to between the bases of the lateral lobes.

_L. needhami_ (Figs. 59-60). The lateral lobes are abruptly widened at two-thirds their length, with the apices much narrowed and bent mesad, usually crossing. The medial lobes extend from the caudo-dorsal edges of the fourth to half the length of the hood and are widened ventrally. The apical lobe extends along the dorsal edge of the fourth segment to dorsad of the bases of the lateral lobes.

_L. luctuosa_ (Figs. 61-62). The hood is very low, not well developed. The lateral lobes are abruptly widened at two-thirds their length, with their apices much
narrowed, bent mesad, and crossing. The medial lobes extend from the caudo-dorsal edges of the fourth segment, where they are slightly widened, to the ventral edge of the hood and are widened ventrally. The apical lobe extends from the dorsal edges of the fourth segment to between the bases of the lateral lobes.

*Comanche, cyanea,* and *flavida* are closely related, sharing the following characters: (1) a low, caudo-ventrally directed hood; (2) heavily sclerotized, sinuate lateral lobes; (3) small, inconspicuous medial lobes which appear as very narrow bands along the distal edges of the fourth segment; (4) an elongate cornu; and (5) a pair of ventrally directed, baso-lateral projections on the posterior lobe, making it appear scoop-shaped in posterior view.

*L. comanche* (Figs. 63-64). The middle portions of the lateral lobes, that part directed caudo-dorsad, is broader than either the bases or the apices. The medial lobes are the largest of any species in this subgroup. The ventrally directed, baso-lateral projections of the posterior lobe extend ventrad two-thirds the length of the medial lobes.

*L. cyanea* (Figs. 65-66). The lateral lobes are nearly parallel-sided and strongly bent ventrad apically. The ventrally directed, baso-lateral projections of the posterior lobe extend ventrad as far as the ventral
edges of the medial lobes. The apical lobe is somewhat larger than those of the other species in this subgroup. *L. flavida* (Figs. 67-68). The lateral lobes are very long and nearly parallel-sided. The medial lobes are very inconspicuous; they apparently lie along the distal edges of the fourth segment and are hidden by the hood ventrally and the posterior lobe laterally. The ventrally directed, baso-lateral projections of the posterior lobe usually overlap the distal ends of the fourth segment and extend ventrad to the ventral edge of the median process.

*Incesta* and *vibrans* are closely related, having a characteristically well developed, ventrally directed hood and well developed medial lobes which extend ventrad at least half of the length of the hood.

*L. incesta* (Figs. 69-70). The hood is directed caudo-ventrally. The lateral lobes are sinuate in profile, with the apices bent ventrad and the middle portions slightly wider than the bases or apices; the apices cross in ventral view. The medial lobes are thin, project ventrad half the length of the hood, and are bent caudad apically, appearing C-shaped in profile. The cornu is short, usually hidden by the lateral lobes in profile. The posterior lobe has a pair of ventrally directed, baso-lateral projections which extend ventrad to the
ventral edge of the median process. The apical lobe is small.

*L. vibrans* (Figs. 71-72). The hood is directed ventrally. The lateral lobes are bent dorsad and slightly widened apically in profile, with the apices divergent in ventral view. The medial lobes are fairly broad, extending ventrad three-fourths the length of the hood and caudad half the length of the lateral lobes; they are flask-shaped in ventral view, the bases as wide as the hood. The median process is relatively narrow in ventral view and fused with the posterior lobe basally. The cornu is elongate. The apical lobe is large and round, extending from the dorsal edge of the fourth segment to the bases of the lateral lobes.
DISCUSSION

The structure of the genitalia, especially the penis, shows little variation within a species. The variations observed were due to either distortion during clearing in potassium hydroxide or to the erection of the penis. The greatest variability occurred in the penes which had the erectile lobes fully inflated. The median process and posterior lobe showed the greatest inflatability, thus the greatest variation in structure.

Variation between the species in a given genus seems to depend on the genus involved. The genitalia of the species of Celithemis show little inter-specific variation; the genitalia of the species of Leucorrhinia, especially the shape of the hamules, do show inter-specific variation; and the genitalia of the species of Libellula, especially the penes, show inter-specific variation.

As taxonomic character, the genitalia, especially the hamules and penes, are of little use to differentiate the species of Celithemis. In Leucorrhinia, the hamules show good inter-specific variation, but the penes can serve to only differentiate the species groups. In Libellula, the hamules are of little value to separate the species, but the penes provide excellent characters for separating the species and have been used to indicate relationships
between the species.
SUMMARY

The penis of nine species of Celithemis, seven species of Leucorrhinia, and seventeen species of Libellula, representing the North American species of those genera, were cleared in potassium hydroxide and studied. The purposes of this study were to examine the penes in the above mentioned genera, to determine whether the penes can provide taxonomic characters, and to attempt to describe the relationships between the species in each genus based on the structure of the penes. The terminology used was that of Borror (1942), with some modifications. General descriptions of the accessory genitalia are given for each genus, and detailed descriptions of the penes are given for the species.

The structure of the penis cannot be used to separate the species in the genus Celithemis. The species of Leucorrhinia can be separated into groups, but the relationships within the groups cannot be determined by penis structure. The species of Libellula can be separated into groups, and the relationships within those groups can be determined by penis structure. Kennedy (1922 a,b) proposed a phylogeny of the species of Libellula based on the penis structure and supported by other characters. The relationships proposed in this study correspond with those of Kennedy, with only a few differences.
LITERATURE CITED


PLATE I
(Mag. 22.5X)

Fig. 1. Second abdominal segment of *Celithemis monomelaena* (ventral view).

Fig. 2. Second abdominal segment of *C. monomelaena* (lateral view).

Fig. 3. Second abdominal segment of *Leucorrhinia glacialis* (ventral view).

Fig. 4. Second abdominal segment of *L. glacialis* (lateral view).

**LEGEND**

GL -- genital lobe

Hib -- inner branch of hamule

Hob -- outer branch of hamule

LA -- anterior lamina

SP -- sheath of the penis

I -- first segment of penis

II -- second segment of penis

III -- third segment of penis

IV -- fourth segment of penis
PLATE II

(Mag. Figs. 5-6 22.5X; Figs. 7-10 46X)

Fig. 5. Second abdominal segment of *Libellula pulchella* (ventral view).

Fig. 6. Second abdominal segment of *L. pulchella* (lateral view).

Fig. 7. Penis of *Celithemis amanda* (ventral view).

Fig. 8. Penis of *C. amanda* (lateral view).

Fig. 9. Penis of *C. bertha* (ventral view).

Fig. 10. Penis of *C. bertha* (lateral view).

LEGEND

A --- apical lobe
C --- cornu
DM --- distal meatus
GL --- genital lobe
H --- hood
Hib - inner branch of hamules
Hob - outer branch of hamules
I --- internal lobe
L --- lateral lobe
LA --- anterior lamina
M --- medial lobe
MP --- median process
SD --- seminal duct
SP --- sheath of the penis
I --- first segment of penis
II --- second segment of penis
III --- third segment of penis
IV --- fourth segment of penis
PLATE III
(Mag. 45X)

Fig. 11. Penis of *Celithemis elisa* (ventral view).
Fig. 12. Penis of *C. elisa* (lateral view).
Fig. 13. Penis of *C. eponina* (ventral view).
Fig. 14. Penis of *C. eponina* (lateral view).
Fig. 15. Penis of *C. fasciata* (ventral view).
Fig. 16. Penis of *C. fasciata* (lateral view).
Fig. 17. Penis of *C. martha* (ventral view).
Fig. 18. Penis of *C. martha* (lateral view).

LEGEND

A --- apical lobe
C --- cornu
DM -- distal meatus
I --- internal lobe
L --- lateral lobe
M --- medial lobe
MP -- median process
SD -- seminal duct
I --- first segment of penis
II -- second segment of penis
III - third segment of penis
IV -- fourth segment of penis
PLATE IV
(Mag. Figs. 19-24 45X; Figs. 25-30 22.5X)

Fig. 19. Penis of Celithemis monomelaena (ventral view).
Fig. 20. Penis of C. monomelaena (lateral view).
Fig. 21. Penis of C. crnata (ventral view).
Fig. 22. Penis of C. ornata (lateral view).
Fig. 23. Penis of C. verna (ventral view).
Fig. 24. Penis of C. verna (lateral view).
Fig. 25. Penis of Leucorrhinia borealis (ventral view).
Fig. 26. Penis of L. borealis (lateral view).
Fig. 27. Penis of L. frigida (ventral view).
Fig. 28. Penis of L. frigida (lateral view).
Fig. 29. Penis of L. glacialis (ventral view).
Fig. 30. Penis of L. glacialis (lateral view).

LEGEND

A --- apical lobe                      MP --- median process
C --- cornu                           SD --- seminal duct
DM --- distal meatus                  I --- first segment of penis
H --- hood                            II --- second segment of penis
I --- internal lobe                   III --- third segment of penis
L --- lateral lobe                    IV --- fourth segment of penis
M --- medial lobe
PLATE V
(Mag. 22.5X)

Fig. 31. Penis of *Leucorrhinia hudsonica* (ventral view).
Fig. 32. Penis of *L. hudsonica* (lateral view).
Fig. 33. Penis of *L. intacta* (ventral view).
Fig. 34. Penis of *L. intacta* (lateral view).
Fig. 35. Penis of *L. patricia* (ventral view).
Fig. 36. Penis of *L. patricia* (lateral view).
Fig. 37. Penis of *L. proxima* (ventral view).
Fig. 38. Penis of *L. proxima* (lateral view).
Fig. 39. Penis of *Libellula croceipennis* (ventral view).
Fig. 40. Penis of *L. croceipennis* (lateral view).
Fig. 41. Penis of *L. saturata* (ventral view).
Fig. 42. Penis of *L. saturata* (lateral view).

**LEGEND**

A --- apical lobe
C --- cornu
DM --- distal meatus
H --- hood
L --- lateral lobe
M --- medial lobe
MP --- median process
P --- posterior lobe
SD --- seminal duct
I --- first segment of penis
II --- second segment of penis
III --- third segment of penis
IV --- fourth segment of penis
PLATE VI
(Mag. 22.5X)

Fig. 43. Penis of Libellula semifasciata (ventral view).
Fig. 44. Penis of L. semifasciata (lateral view).
Fig. 45. Penis of L. quadriraculata (ventral view).
Fig. 46. Penis of L. quadriraculata (lateral view).
Fig. 47. Penis of L. forensis (ventral view).
Fig. 48. Penis of L. forensis (lateral view).
Fig. 49. Penis of L. nondisticta (ventral view).
Fig. 50. Penis of L. nondisticta (lateral view).
Fig. 51. Penis of L. pulchella (ventral view).
Fig. 52. Penis of L. pulchella (lateral view).
Fig. 53. Penis of L. composita (ventral view).
Fig. 54. Penis of L. composita (lateral view).

LEGEND

A --- apical lobe  P --- posterior lobe
C --- cornu       SD --- seminal duct
DM --- distal meatus  I --- first segment of penis
H --- hood        II --- second segment of penis
L --- lateral lobe III --- third segment of penis
M --- medial lobe  IV --- fourth segment of penis
MP --- median process
PLATE VII
(Mag. 22.5X)

Fig. 55. Penis of Libellula axilena (ventral view).
Fig. 56. Penis of L. axilena (lateral view).
Fig. 57. Penis of L. auripennis (ventral view).
Fig. 58. Penis of L. auripennis (lateral view).
Fig. 59. Penis of L. needhami (ventral view).
Fig. 60. Penis of L. needhami (lateral view).
Fig. 61. Penis of L. luctuosa (ventral view).
Fig. 62. Penis of L. luctuosa (lateral view).
Fig. 63. Penis of L. comanche (ventral view).
Fig. 64. Penis of L. comanche (lateral view).

LEGEND

A --- apical lobe
C --- cornu
DM --- distal meatus
H --- hood
L --- lateral lobe
M --- medial lobe
MP --- median process
P --- posterior lobe
SD --- seminal duct
I --- first segment of penis
II --- second segment of penis
III --- third segment of penis
IV --- fourth segment of penis
PLATE VIII
(Mag. 22.5X)

Fig. 65. Penis of *Libellula cyanea* (ventral view).
Fig. 66. Penis of *L. cyanea* (lateral view).
Fig. 67. Penis of *L. flavida* (ventral view).
Fig. 68. Penis of *L. flavida* (lateral view).
Fig. 69. Penis of *L. incesta* (ventral view).
Fig. 70. Penis of *L. incesta* (lateral view).
Fig. 71. Penis of *L. vibrans* (ventral view).
Fig. 72. Penis of *L. vibrans* (lateral view).

LEGEND

A --- apical lobe
C --- cornu
DM -- distal meatus
H --- hood
L --- lateral lobe
M --- medial lobe
MP -- median process
P --- posterior lobe
SD -- seminal duct
I --- first segment of penis
II -- second segment of penis
III -- third segment of penis
IV -- fourth segment of penis