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Phylogeny of *Libellula* Linnaeus (Odonata: Insecta)

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Abstract

Phylogenetic analysis was performed on a set of 242 morphological characters. The taxon sample included 31 *Libellula*, and representative species from selected libeluline tribes, from all libellulid subfamilies, from all libelluloid families, from all anisopteran superfamilies, and *Epiophlebia*. Corduliinae was shown to be paraphyletic even among genera characterized by a well developed anal loop bisector. Sympetrini was found to be polyphyletic with *Crocothemis* the sister group to Libellulini. The traditional placement of Trameini, far from Libellulini is in doubt, because it is here placed as the sister group to *Crocothemis* + Libellulini. Kennedy's phylogeny of *Libellula* was largely corroborated, with the following exceptions: the subgenera *Libellula*, *Eolibellula,* and *Syntetrum* form a monophyletic group which is the sister group to a clade including *Belonia*, *Holotania*, *Neotetrum*, and *Eotainia* subgenus nov. [type species *Mesothemis composita* Hagen]; and *Eurothemis* is determined to be the sister group of *Ladona* instead of *Neotetrum*. In addition we confirm *Belonia* to be monophyletic, and find *Platetrum* + *Plathemis* to form a monophyletic group, sister to *Ladona* + *Eurothemis;* these four subgenera together form the sister group to *Libellula sensu stricto (s.s.).*

Key words: Libellulidae, *Libellula*, *Eotainia* subgenus nov., phylogeny

Introduction

Libellula Linnaeus was established in 1758 to include all known Odonata, and has been redefined both through removal of species into newly established genera, and by addition of newly described *Libellula*. At present approximately 33 species are recognized within *Libellula s. l.* (Bridges 1994), and all but *L. melli* Schmidt and *L. niphonica* Kobayashi of China are included in this study (Fig. 1). Several subgenera have been established within *Libellula* and include: *Platetrum* Newman, *Plathemis* Hagen, *Ladona* Needham, *Eurothemis* Kennedy, *Libellula* Linnaeus, *Eolibellula* Kennedy, *Syntetrum* Kennedy, *Belonia* Kirby, *Holotania* Kirby, and *Neotetrum* Kennedy. In addition, our phylogenetic analysis

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supports the establishment of a monotypic subgenus for *Mesothemis composita* Hagen, which is found to be the sister of the *Neotetrum* + *Holotania* clade. *Libellula* are common and widespread in the northern hemisphere with *Platetrum*, *Eurothemis*, and *Synetrum* endemic to the Palearctic, with *Libellula quadrimaculata* L. holoarctic in distribution, and with the remaining 26 species distributed among 7 subgenera all restricted to the Nearctic (including Central America).

A debate concerning the generic status of *Plathemis* Hagen (1861) and *Ladona* Needham (1897) has persisted due to the apparent close relationship of these taxa to *Platetrum* and *Eurothemis*, respectively; and to uncertainty as to the type species of *Libellula* (Walker and Corbet 1975, Carle 1982). We follow Calvert (1901-1908), Ris (1910), and Kennedy (1922b) in recognizing *Libellula quadrimaculata* L. as the generotype of *Libellula*, but note that Kirby (1889) lists *Libellula depressa* L. as the type. Ris (1910), Kennedy (1922b), and Walker and Corbet (1975) avoided the problem by including *Plathemis* and *Ladona* within *Libellula*. However, Garman (1927), Needham and Westfall (1955), Carle (1982), and Needham, Westfall, and May (2000) accorded generic status to *Plathemis* and *Ladona*. A study by Kambhampati and Charlton (1999) utilizing mitochondrial 16S rRNA sequence data found evidence that *Plathemis* and *Ladona* are monophyletic and basal to Nearctic *Libellula*. Furthermore, a study by Artiss *et al.* (2001) using combined mitochondrial CO1 and 16S rRNA sequence data places *Orthemis* between *Plathemis* and remaining *Libellula* , and groups *Platetrum* and *Eurothemis* with *Ladona*, basal to remaining *Libellula*.

In the present study we infer a phylogeny for *Libellula* utilizing 242 morphological characters. The most useful characters are from the wing venation and penis. Terminology used for venation is that of Needham, Westfall, and May (2000), and for the external morphology of the penis that of Bartenef (1915) and Kennedy (1922a). Nomenclature of libelluloids is unstable, and the terms “Libelluloidea, Libellulidae, and Libellulinae” require definition. We consider basal libelluloids to include Cordulegastridae, Neopetaliidae, and Chlorogomphidae (Carle 1995), and the higher libelluloids to include Synthemistidae, Gomphomacromiidae, and Libellulidae. Needham, Westfall, and May (2000) was followed in applying the rank of subfamily to Macromiinae, Corduliinae, and Libellulinae, rather than elevating them to family level. Recently, many other corduliine taxa have also been elevated to family status (Bechly 1996, Lohman 1996), but for stability, they are here considered Corduliinae until further evidence is presented regarding their status.

Materials and methods

Outgroup taxa were selected to include the anisozygopteran, *Epiophlebia*, and a representative from each of the anisopteran superfamilies *sensu* Carle (1982). The taxon sample included 31 *Libellula*, and represenative species from selected libeluline tribes, from all libellulid subfamilies, and from all libelluloid families. Characters for the libelluloid study were taken from Carle and Louton 1994, Carle (1995,1996), to which new characters for Libellulinae were added, based in part on Kennedy (1922b) and Carle (1982). Most characters are binary, and coding follows Carle's (1995) numbering and method of evaluating correlated characters (coapomorphies) and loss characters (exapomorphies). Putative apomorphies are coded as "1"s, with rows of taxa containing "1"s shuffled to the bottom of the matrix, so that taxa are bisected into those possessing plesiomorphy on the top, and apomorphy on the bottom (Appendix 2). Like patterns of characters are placed next to one another in an attempt to identify highly correlated characters and to therefore uncover independent congruent character sets. When an apomorphy was hypothesized to be highly correlated with another character, the column was moved directly to the right of its "partner," and the 1s were replaced with Cs. By convention, blocks of autapomorphic character sets for smaller groups such as families (e.g., Appdx. 2, block 3 for Epiophlebiidae), are positioned to the upper right of the larger, relatively basal synapomorphy blocks (Appdx. 2, block 2 defining all Anisopteroids), and character sets defining the backbone of the tree positioned to the lower right (e.g., Appdx. 2, block 4 defining all Anisoptera). In this arrangement, putative polarities can be readily evaluated. If incongruence can be justifiably coded as losses, either because they are deeply nested inside strongly supported nodes, or because there is morphological evidence of loss, then zeros were replaced with Xs. Loss events were counted in the column, and the character weighted by 1/(number of loss events +1). Phylogenetic analysis was performed via character-based parsimony using PAUP 4 (Swofford, 1999).

***Eotania* subgenus nov.**

Type Species: *Mesothemis composita* Hagen

Length: 42-49mm; abdomen 30-32mm; hind wing 35-37mm.

Distribution: USA (AZ, CA, KS, NV, NM, OR, TX, UT, WY).

Adult - Face white with anterior edge of labrum black, dorsum of vertex and occiput white, compound eyes pearly white. Posterior margin of prothorax low and rounded. Middorsal pterothoracic white stripe extended over 1/2 of mesanepisterna, pterothorax laterally white with black stripes along meso- and metapleural sulci, interpleural suture black to level of spiracle, legs black with basal half of outer femoral face pale. Wings hyaline with saffron stain extended outward to about arculus, female with nodal brown spots, costa white, and pterostigmata brown. Triangles 2-3/1-2 celled, fore wing subtriangle 3-4 celled, bridge crossveins 2-3, hind wing antenodals 10-12, and forewing cubital planate wth 2 cell rows. Abdomen black with submedian row of pale spots on segments 1-3 in male, and 1-8 in female. Abdominal sternum 1 without hooks, anterior lamina angled ventrally at about 30 degrees, and posterior hamuli with well developed endhook and shoulder. Tergum 9 without lateral carinae. Male cerci only slightly widened distally. Penis with low hood, with elongate lateral lobes with apices curved dorsally, with cornual base expanded with dense dorsal cover of erectile hair, and with lateral cornua short-robust.

Larvae- Head expanded posterior to compound eyes. Abdomen with apical submedian brown stripes, dorsal abdominal hooks absent or at most humplike, and lateral abdominal spines obsolete.

Morphological characters

The principal characters utilized in our analysis are those of the wing venation and coloration, and those of the male secondary genitalia. Many of the characters utilized are well illustrated in Needham, Westfall, and May (2000), and will be referred to in the following format: (NWM Fig.00x-z). Head characters are used only three times in the analysis of Libelluloid phylogeny with the most important, (Character 27c in Appendix 1), involving the posterior border of adult compound eye (NWM Fig.28c-d). Leg characters are used to distinguish Macromiinae, which are characterized by a long ventral tarsal claw (NWM Fig.430d). Two thoracic characters are utilized;, they are the sinuous mesoplueral sulci (Garman 1927, Fig.40a-b), and the bilobate hind margin of the prothorax (Borror 1945, Figs. 37-43). Abdominal characters involve the shape of the abdomen and the development of transverse and lateral carinae. In addition, eight abdominal coloration characters are utilized and an additional three are concerned with the degree of pruinosity, a waxy covering which typically obscures the color patterns of males. The submedian abdominal pale spots are used in four characters (NWM Fig.29b).

The terminology of wing venation used in this analysis is basically that of Needham, Westfall, and May (2000), (NWM Fig.7). The costal pleat is well developed between the wing base and nodus, and crossveins within this space are referred to as antenodals and, when these are aligned and strengthened, they are called costal braces. Hind wing with 9 plus costal braces (character 33a), is a conservatively stated character, as most Libelulini have more than 11 costal braces. Beyond the nodus the subcostal vein fuses to the costa so that postnodal crossveins are located to either side of the radial vein. Character 35b, forewing with 4-5 unmatched postnodals, refers to the missing basal crossveins of the second postnodal series (compare NWM Fig. 10 to 444). The pterostigma is located near the end of the postnodal space, and characters include the number of crossveins beyond the hind wing pterostigma, position of the pterostigmal brace (the pterostigmal brace is located in the second postnodal interspace typically at the proximal end of the pterostigma), pterostigmal shape (NWM Fig. 428), and the relative length of the pterostigma. Perhaps the most distinctive feature of Anisopteran venation are the triangles: characters utilized include base of hind wing triangle at or near arculus (NWM Fig. 26), cubital vein arises from outer side of triangle, (compare NWM Fig. 426 to 427), and forewing subtriangle with more than 3 cells. The anal loop of Libelulidae forms a strong pleat which supports the anal region of the wing, and in higher Corduliinae and Libellulinae the anal loop has a well developed midrib (NWM Fig. 426). Further characters involve development of the anal loop toe, development of the "heel angle" of anal loop bisector, and development of the spur (NWM Fig. 426). Other venational characters include the number of bridge crossveins (NWM Fig. 10), vein M_2 strongly undulate (compare NWM Fig. 425 to 485), and forewing cubital planate with 2-3 cell rows (labeled as Mpl on NWM Fig. 425). In addition, fifteen wing coloration characters are utilized; they involve the presence, color, and relative size of basal, nodal, and apical wing spots; and the color of the costa and pterostigma.

The male secondary genitalia are unique to the Odonata and include the most important systematic characters in the group; in Libellulidae the anterior hamuli and apical penile segment are reduced (compare NWM Fig. 12 to 435). The penile terminology used in this analysis is basically that of Kennedy (1922a), and because many of the characters utilized are well illustrated in Kennedy (1922b) his drawings will be referred to in the following format: (K Plate 0 Fig.00). Of the 31 genitalic characters utilized to determine libellulid phylogeny only five do not involve penile characters. Among these are the unique ventral process on abdominal segment 1 of male *Plathemis* and *Platetrum* (NWM Fig. 528). In addition, the degree of uplift of the anterior lamina distinguishes *Eotania* from *Neotetrum-Holotania* (NWM Fig. 489). The shape of the posterior hamuli is also quite distinctive among subgenera of *Libellula*: the stubby boxing-glove-like type is characteristic of the *Platetrum-Ladona* groups, in other *Libellula* it is more hook-like with a reduced shoulder (compare NWM Fig. 489 to 528). The penile characters utilized in this analysis primarily involve the shape of the apical segment, the shape of the lateral lobes, and the development of the cornua (Kennedy 1922a,b).

Phylogenetic results

Figure 1 shows the results of our phylogenetic analysis. Corduliinae is divided into a paraphyletic group by character sets 25 and 26. Sympetrini (Tillyard 1917, Tillyard and Fraser 1940, Fraser 1957, Davies 1981, Bridges 1994) is found to be polyphyletic and not the sister group of Libellulini. Trameini is rather closely related to Libellulini, and *Orthemis* is the sister group of *Libellula sensu lato (s.l.)* within our taxon sample. *Libellula (s.l.)* is divided into four basal monophyletic groups: *Platetrum-Plathemis*, *Eurothemis-Ladona*, *Libellula-Syntetrum-Eolibellula*, and *Belonia-Neotetrum-Holotania-Eotania* subgen. nov. *Belonia* is found to be monophyletic and the sister group of the remaining subgenera of group four, and *Eotania* subgen. nov. is found to be the sister group of *Neotetrum-Holotania*. Monophyly for most named taxa are well supported as indicated by both high bootstrap values (Fig. 1) and the high congruence of independent character sets shown in the sorted data matrix (Appendix 2).

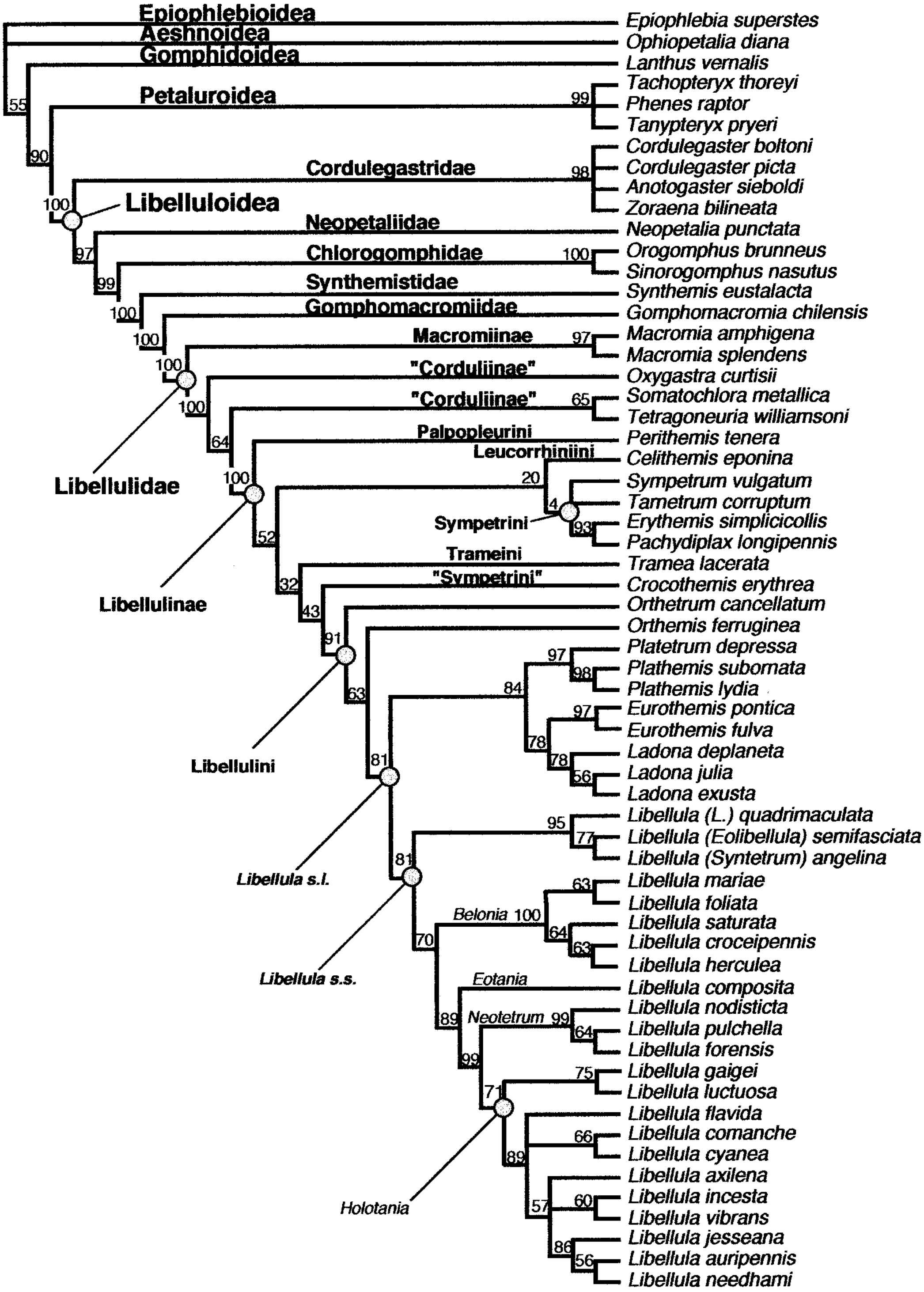

FIGURE 1. Phylogenetic topology for the major groups of Libelluloidea and species of *Libellula*. Strict consensus of 18 trees of 256.59 steps with bootstrap values (Felsenstein, 1985). Bootstrap analysis was performed with 1000 heuristic searches, including all trees compatible with a 50% majority- rule consensus.

Discussion

The phylogenetic topology of basal libelluloides closely mirrors the breakup of Pangaea (Carle 1995). Cordulegastridae are limited to Laurasia; Neopetaliidae to Chile; Chlorogomphidae to India, Southeast Asia, and Japan; Synthemistidae to Tasmania, Australia, New Guinea, and New Caledonia; and the gomphomacromiids and basal corduliines to Australia, Andean South America, South Africa, and Madagascar. In tropical Africa and Southeast Asia basal Corduliinae are not represented, and in contrast, the Libellulinae, the species of which comprise nearly 70% of all Libelluloidea, exhibits its greatest diversity (Davies 1981). Determining what corduliine group has given rise to Libellulinae will undoubtedly effect the placement of Libellulini within Libellulinae.

Unlike Corduliinae, Libellulinae are a monophyletic group well defined by uncorrelated apomorphic character states; these include: posterior margin of compound eye evenly curved, mesopleural sulci sinuous, and abdominal terga 2 and 3 with transverse carinae (Carle 1995). An additional apomorphy not included in our analysis is secondary genitalia with a unique filling and ejaculatory mechanism (Pfau 1991). Characteristics most often utilized to define Libellulinae are the well developed toe of the anal loop, and in males, the lack of tibial keels, lack of the hind wing angulation, and lack of auricles (denticulate lateral tubercles of abdominal segment 2). However, the anal loop is typically obsolete in Tetrathemini, and the toe of the anal loop is typically obsolete in Brachydiplacini. In addition, the loss characters of libelluline males are correlated and also typical of Hemicordulia (Corduliinae), Anatogaster (Cordulegastridae), and Anax (Aeshnidae). The well developed lateral abdominal carinae and elongate bisectored anal loop of higher Corduliinae combined with the loss of male auricles, hind wing angulation, and mesotibial keels in Hemicordulia, suggest that even the higher corduliines are paraphyletic as implied by the classifications of Bechly (1996) and Lohman (1996). In addition, the occurrence of Hemicordulia from Tasmania to Southeast Asia and Madagascar, support the evolution of Libellulinae from the higher vagile Corduliinae, and not from the peripherally isolated gomphomacromiid-like corduliines.

At least 13 tribes are currently recognized within Libellulinae and in this analysis we have included representative genera from Leucorrhiniini *(Celithemis)*, Libellulini *(Orthetrum, Orthemis, Libellula)* , Sympetrini *(Sympetrum, Tarnetrum, Pachydiplax, Erythemis, Crocothemis)*, Palpopleurini *(Perithemis)*, and Trameini *(Tramea)*. Needham and Broughton (1927) presented a genealogical tree of Libellulinae based on venation and placed the Sympetrini as the sister group of Libellulini according to similarities in the anal loop. A more basal clade of their tree included *Perithemis, Celithemis,* and *Crocothemis,* and yet a more basal clade included *Tramea*. Within the Libellulinae sampled here *Perithemis, Celithemis, Sympetrum, Tarnetrum, Pachydiplax*, and *Erythemis* are characterized by an erect bilobate posterior margin of the prothorax and most are also characterized by a well developed spur vein or heel area of the anal loop. In stark contrast to the results of Needham and Broughton (1927), this group forms the sister group to a clade composed of

Tramea, *Crocothemis*, and Libellulini (Fig. 1). Fraser (1957) placed *Celithemis* in Leucorrhiniini and considered it near Sympetrini; this is consistent with its position as shown in Fig. 1. Again in contrast to our results, Needham and Broughton (1927) removed *Celithemis* from Sympetrini, and placed it within a newly established Celithemini composed of Palpopleurini, Macrodiplacini, and other assorted genera including *Crocothemis.* Based on the 9 plus antenodals in the hind wing, *Crocothemis* in this taxon sample actually forms the sister group to Libellulini.

Apomorphies of Libellulini include an undulate M_2 vein, male abdomen pruinose, abdomen short and wide, reduction in width of anal field, and an increase in venational density. The Neotropical *Cannaphila* Kirby also fits quite well within Libellulini, but lacks a strongly undulate M_2 vein. Based on 5 or more crossveins beyond the pterostigma, *Orthemis* rather than *Orthetrum* is the sister group to *Libellula s.l.* within this taxon sample. *Orthemis* also shares short robust penile segments with *Libellula*, has the posterior hamuli somewhat boxing-glovelike, and has paired lateral cornua which are similar to those of *L. (Eolibellula) semifasciata* Burmeister, *L. (Libellula) quadrimaculata*, and *L. (Syntetrum) angelina* Selys. Placement of *Orthemis* together with *Plathemis* as the sister group of remaining *Libellula s. l.* (Artiss *et al.* 2001), is not supported by our analysis. Synapomorphies of *Libellula* include fore wing with 4-5 unmatched postnodals, wings with 2-6 bridge crossveins, basal brown area of fore wing extended to first antenodal (reversed at least 3 times), and abdomen wide (abdominal segment 5 wider than long, reversed at least 4 times). Our analysis divides the genus *Libellula s.l.* into three basal groups of 3 to 5 species which are laurasian in distribution and one basal group of 20 species that is nearctic in distribution. The first two groups are *Eurothemis-Ladona*, and *Platetrum-Plathemis;* they comprise the sister group to *Libellula s.s.* and are characterized by boxing glove-like posterior hamuli, lateral cornua which are short and wide at least basally, short wide lateral penile lobes (convergent to *L. quadrimaculat*a), and short wide abdomens with a white pruinessence (grayish in *L. deplanata* Rambur). *Eurothemis* and *Ladona* share similar wing and abdominal patterns and the dorsal fusion of the cornua. *Eurothemis* exhibits a remarkable expansion of the fused cornua and an associated apical elongation of the lateral lobes, this led Kennedy (1922b) to place it as the sister taxon to *Neotetrum.* Although superficially similar, the cornual expansion in *Neotetrum* has its apex directed dorsally as opposed to anteroventrally in *Eurothemis*, suggesting that these expansions are not homologous. Although Artiss *et al.* (2001) did not confirm a close relationship between *Platetrum* and *Plathemis,* this, our second basal group is characterized by several synapomorphies including: male with ventral processes on abdominal sternum one, lateral penile lobes widened apically, third penile segment with a transverse trough, and abdominal segment 9 with lateral carinae. Both the *Ladona-Eurothemis* and *Plathemis-Platetrum* subgeneric pairs are separated by the North Atlantic Ocean; because none of these species are unusually vagile it is likely that they represent the isolated remnants of a transatlantic Miocene faunal split.

The third and fourth basal subgeneric groups of basal *Libellula* are*: Eolibellula-Libellula-Syntetrum,* and *Belonia-Eotania-Holotania-Neotetrum.* This group of seven subgenera share the presence of a medial penile cornua, have 2-3 cell rows subtended by the fore wing cubital planate (convergent to *Plathemi*s), and typically have nodal wing spots (lost three times). Kennedy (1922b) considered the penis of our third group to be the most plesiotypic within *Libellula* and treated the group as paraphyletic. Accordingly Kennedy established two new subgenera so that all three subgenera in our basal group three are monotypic. Synapomorphies of group three include posterior hamuli hook-like, basal abdominal segments translucent, abdomen swollen basally and acuminate apically, and costa white (convergent to *Eotania).* However, the lateral penile cornua in group three are shorter than in either *Orthemis* or *Belonia* indicating that intermediate length cornua may also be a genuine synapomorphy for the group. Group three has a circumpolar distribution with *Eolibellula* found throughout eastern North America, with *Synetrum* restricted to Japan, and with *Libellula quadrimaculata* circumpolar. Similar wing patterns indicate that *Eolibellula* and *Syntetrum* might form a subgeneric pair with a distribution similar to the gomphid genus *Lanthus,* however it seems more likely that *Syntetrum* represents a peripheral isolate of *Libellula quadrimaculata* which later also dispersed into North America where it is now sympatric with *Eolibellula*.

The forth and largest basal group of *Libellula,* includes the subgenera *Belonia, Eotania*, *Holotania* and *Neotetrum,* is characterized by having the median cornua longer than the lateral cornua. All four subgenera are restricted to North America and the most basal species in each is found in either the south western United States or Central America, suggesting that this area was an important refugium for *Libellula* during glacial maxima. In contrast to the findings of Artiss *et al.* (2001) we do not find *Belonia* to be paraphyletic. Synapomorphies for *Belonia* include the reddish abdominal and wing color, and the unique penile cornua which are elongate, asymmetrical, and lined with short papillae. Based on shorter cornua and darker coloration, *L. foliata* (Kirby) and *L. mariae* Garrison, are the most basal *Belonia*. The penis of *Eotania, Holotania,* and *Neotetrum* is unique in that the lateral lobes are elongate and curved dorsally, and the cornual base is greatly expanded with a dense dorsal covering of erectile hair. Additional synapomorphies for this group include the erect posterior hamuli with a reduced shoulder, and the submedian line of pale abdominal spots. Kennedy (1922) considered *Eotania* to be the sister taxon to *Holotania*, probably based on the relatively short lateral penile lobes of *Neotetrum*. However several apomorphies are shared between *Holotania* and *Neotetrum,* these include: submedian pale areas confluent and contiguous with the lateral carina of terga 6-10, anterior lamina angled at about 45 degrees, third penile segment hood-like, lateral penile cornua obsolete, and forewing subtriangle typically with more than 3 cells. Therefore, *Eotainia* is here considered to be the sister taxon to *Holotania - Neotetrum. Neotetrum* and *Holotania* are distinguished primarily on the basis of penile characters, *Neotetrum* has the lateral penile lobes reduced to small up-curved rods and has a sharp medial ridge on the posterior face of the penile hood, *Holotania* is characterized by having the lateral penile lobes curved ventrally at apex, by having the penile hood produced posteroventrally, and by having the medial cornua elongate-recumbent. The less extensive wing markings and less reduced medial cornua indicate that *L. nodisticta* Hagen represents the most basal *Neotetrum*. *Libellula luctuosa* Burmeister and *L. gaigei* Gloyd comprise the sister group to remaining *Holotania*, synapomorphies for this pair include base of the wings opaque black or brownish red out to the nodus, and medial penile lobe of segment 3 hoodlike. Remaining *Holotania* are characterized by having an enlarged pterostigma which is about one half as long as the postnodal space. *Libellula flavida* Rambur, *L. cyanea* Fabricius, and *L. comanche* Calvert exhibit bicolored pterostigma, and in the latter two species the pterostigma are about half black and half white. Remaining *Holotania* are characterized by having the submedian abdominal pale areas confluent and contiguous with the lateral carina on segments 3-10. Speciation has apparently been quite rapid in the remaining *Holotania* so that many taxonomic characters involve reproductive isolation, and are quite homoplastic. *Libellula axillena* Westwood may be basal in this group due to its darker coloration, more robust build, and more extensive wing markings. Of the remaining species, *Libellula incesta* Hagen and *L. vibrans* Fabricius share a fingerlike extension of the penile hood, and *L. jesseana* Williamson, *L. auripennis* Burmeister, and *L. needhami* Westfall have red costa and the submedian abdominal pale areas confluent and contigious with the lateral carinae of segments 1-10. *Libellula jesseana* and *L. auripennis* share bright red pterostigmata in the mature male.

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Appendix 1

Apomorphic character states for Libellulidae, character state descriptions for nodes 1-22 are described in Carle (1995). Many of the characters utilized are well illustrated in Needham, Westfall, and May (2000), and will be referred to in the following format (NWM Fig.00x-z). The penile terminology used in this analysis is basically that of Kennedy (1922a), and because many of the characters utilized are well illustrated in Kennedy (1922b) his drawings will be referred to in the following format (K Plate 0 Fig.00).

HEAD, LEGS, THORAX and ABDOMEN
23a Ventral tarsal claw longer than dorsal claw (NWM Fig.430d)
23b Larval frons with horn (NWM Fig.322)
27c Posterior border of adult eye not sinuous (NWM Fig.28c-d)
27d Mesopleural sulci sinuous (Garman 1927, Fig.40a-b)
27e Abdominal terga 2 & 3 with supplementary transverse carina (NWM Fig.29b)
27f Hind margin of prothorax bilobate (Borror 1945, Figs. 37-43)
29a Abdominal tergum 4 with supplementary transverse carina
35a Abdominal segment 5 wider than long
41a Abdominal terga 9 with lateral carina
45c Abdomen swollen basally and acuminate apically
51a Eyes pearly white

WINGS - VENATION and PTEROSTIGMATA
24b Base of hind wing triangle at or near arculus (NWM Fig. 26)
24c With 5 or more cross veins beyond hind wing pterostigma
24d With 2-6 bridge cross veins (NWM Fig.7)
24e Pterostigmal brace displaced distally and aslant
31a Cubital vein arises from outer side of triangle (NWM Figs. 426 and 427),
32b Pterostigma trapezoidal (NWM Fig. 428)
33a Hind wing with 9+ costal braces
34a M_2 strongly undulate (NWM Figs. 425 and 485)
35b Forewing with 4-5 unmatched postnodals (NWM Figs. 10 and 444).
44b Forewing cubital planate with 2-3 cell rows (labeled as Mpl on NWM Fig. 425)
52b Forewing subtriangle with more than 3 cells (some intraspecific variation) (NWM Fig. 485)
58a Pterostigma about 1/2 the length of the postnodal space

WINGS - ANAL LOOP
24a Anal loop with midrib (NWM Fig. 426)
25a Anal loop with hoof-like toe (NWM Fig. 326)
26a Anal loop with toe
27a Anal loop with well developed toe (NWM Fig. 426)
27b Toe of anal loop with midrib (coapomorphy of 27a)
28a Loss of the "heel angle", resulting in nearly straight midrib (NWM Fig. 521)
30a Anal loop with well developed spur (NWM Fig. 426)
32a Bisector arises near 1/4 of anal loop base or less

GENITALIA - HAMULI and ANTERIOR LAMINA

36a Posterior hamuli boxing-glovelike (NWM Figs. 489 and 528)
41b Male with ventral process on abdominal segment 1 (NWM Fig. 528)
45d Posterior hamuli hooklike (NWM Figs. 489 and 528)
50c Posterior hamuli erect with small shoulder
52c Anterior lamina angled at about 45 degrees (NWM Fig. 489)

GENITALIA - PENIS

36c Lateral cornua short and flattened (K Plate II Fig. 11)
37a Lateral penile lobes short and wide (K Plate II Figs. 8,11,12)
38c Cornua fused into U-shaped ridge (K Plate IV Fig. 7)
39a Apex of penis inflated (K Plate II Fig. 9)
40a Lateral penile lobes directed ventrally (K Plate IV Figs. 7,8,9,26)
41c Lateral penile lobes doubled in width apically (K Plate II Figs. 11,12)
41d Apical penile segment with transverse ventral trough (K Plate IV Figs. 10,25)
42a Lateral penile lobes bifurcate (K Plate II Fig. 12)
43a Lateral penile lobes spoonlike (K Plate II Fig. 11)
44a Penis with medial cornua (K Plate II Figs. 3,5,8)
47a Lateral penile lobes broad flattened and elongate (K Plate II Figs. 5,7)
48a Medial cornua longer than lateral cornua (K Plate II Fig. 3)
49a Penis with 3 long cornua (K Plate II Fig. 8)
49c Lateral cornua asymmetrical (K Plate II Fig. 3)
49d Cornua with line of short papillae (K Plate II Fig. 3)
50a Apical penile lobes with internal hair plumes (K Plate III Fig. 26)
50b Base of cornua expanded (K Plate II Fig. 4,6,10)
50d Lateral penile lobes more than 10 times as long as wide at base (K Plate II Figs. 4,6,10)
52a Apical penile segment hoodlike (K Plate II Figs. 6,10)
52e Penis with lateral cornua obsolete (K Plate II Fig. 6,10)
54a Penile hood with sharp medial ridge (K Plate II Fig. 6)
54b Lateral penile lobes reduced to small up curved rod (K Plate II Fig. 6)
56a Lateral penile lobes curved ventrally at apex (K Plate II Fig. 10)
56b Penile hood produced posteriorly (K Plate II Fig. 10)
56c Medial cornua elongate recumbent (K Plate IV Fig. 18,21,24)
61a Penile hood fingerlike (K Plate IV Figs. 23,24).
65a With lateral cornua longer than third penile segment
66a Lateral penile lobes strongly curved posterodorsally

COLOR - WINGS

35c Basal brown area of forewing extended to the first antenodal
38d Forewing with dark streaks along midbasal space only, hind wing with basal black triangular area posterior to anal vein
43b Male with nodal and apical wing spots confluent
44c Nodal wing spot present
45a Costa white
46a Forewing with basal marking limited to streaks bordering supratriangle
46b Apical wing band much wider than nodal band
49b Basal 1/3 to 2/3 of wings saffron

53a	Male with white band beyond basal brown spot
55a	Nodal wing band extended across 3/4 of wing
57a	Basal 1/2 of wing shaded with black
59a	Pterostigma bicolored white and black
62b	Costa red
63a	Pterostigma of mature male yellow to orange
64a	Pterostigma of mature male red

COLOR - ABDOMEN

34b	Male abdomen pruinose
36b	Male abdomen with white pruinosity
38a	Male abdomen pruinose with black apex
38b	Female abdomen with triangular abdominal spots
45b	Abdomen translucent
49e	Male abdomen completely red
50e	Abdomen with submedian pale areas (NWM Fig.29b)
52d	submedian pale areas confluent and contiguous with the lateral margins of segments 6-10
58b	Submedian pale areas confluent and contiguous with the lateral margins of segments 4-10
60a	Submedian pale areas confluent and contiguous with the lateral margins of segments 3-10
62a	Submedian pale areas confluent and contiguous with the lateral margins of segments 1-10

Appendix 2

Apomorphic character states are indicated with 1's; or 1's, 2's, and 3's for multistate characters. Lossesare indicated with x's or x's, y's, and z's for putative non homologous loss events. Highly correlated characters are listed as c's and placed to the right of the character to wich they are correlated.

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                                                1      777 111111111111          888881          11111111
                      1111222222222 333333344444444440 99999NNN 000000111111 555556555NNNNN3666 777777722222222
                      abcdabcdefghi abcdefgabcdefghijg abcdeabc abcdefabcdef abcdecfghabcdedabd abcdefgabcdefgh
Zygoptera             111C......... .................. ........ ............ ..........1....... ...............
Epiophlebia           ....111111C1C 11111CX........... .....2.. .....1...... .................X ...............
Austropetaliidae      ....111111C1C .......111CX1CCX1X 11CCC... 111111...... ...............1CX ...............
Anax                  ....111111C1C .......111C1ZCCX11 11CCC... ......111111 ...............1CX ...............
Other aeshnids        ....111111C1C .......111C11CCX11 11CCC... ......111111 ...............1CX ...............
Hagenius              ....111111C1C .......111C11CCXX1 .....111 ............ 111111XX.......... ..............X
Ophiogompus           ....111111C1C .......111C11CCXX1 .....111 ............ 111111XX1......... ..............X
Other gomphids        ....111111C1C .......111C11CCXX1 .....111 ............ 111111XX1......... ..............X
Tachopteryx/Petalura  ....111111C1C .......111C11CCXX1 .....111 ............ .........1111111CX 1111111........
Tanypteryx            ....111111C1C .......111C11CCXX1 .....111 ............ .........1111111CX 1111111........
Phenes                ....111111C1C .......111C11CCXX1 .....111 .....1...... .........1111111CX 1111111........
Zoraena/Kalyptogaster ....111111C1C .......111C11CCXX1 .....111 ............ .........1111111CX .......1111111X
Anotogaster           ....111111C1C .......111C1YCCXX1 .....111 ............ .........1111111CX .......1111111X
Cordulegaster         ....111111C1C .......111C11CCXX1 .....111 ............ .........1111111CX .......1111111X
Neopetalia            ....111111C1C .......111C11CCXX1 .....111 ............ .........1111121CX .......1111111X
Chloropetalia         ....111111C1C .......111C11CCXX1 .....111 ............ .........1111121CX .......1111111X
Sinorogomphus         ....111111C1C .......111C11CCXX1 .....111 ............ .........1111121CX .......1111111X
Synthemis             ....111111C1C .......111C11CCXX1 .....111 ............ .........1X111X1CX .......111111XX
Gomphomacromia        ....111111C1C .......111C11CCXX1 .....111 ............ .........1X111X1CX .......11111XXX
Macromiinae           ....111111C1C .......111C11CCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Macromiinae           ....111111C1C .......111C11CCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Oxygastra             ....111111C1C .......111C11CCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Tetragoneuria         ....111111C1C .......111C11CCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Somatochlora          ....111111C1C .......111C11CCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Perithemis            ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Celithemis            ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Sympetrum             ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Tarnetrum             ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Pachydiplax           ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Erithemis             ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Tramea                ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Crocothemis           ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Orthetrum cancellatum ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Orthemis ferruginea   ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Eurothemis fulva      ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Eurothemis pontica    ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Ladona julia          ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Ladona exusta         ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Ladona deplanata      ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Platetrum depressa    ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Plathemis lydia       ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Plathemis subornata   ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
L.quadrimaculata      ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
L.semifasciata        ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Syntetrum angelina    ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Belonia mariae        ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Belonia foliata       ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Belonia saturata      ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Belonia croceipennis  ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Belonia herculea      ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Eotania composita     ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Neotetrum nodisticta  ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Neotetrum forensis    ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Neotetrum pulchella   ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Holotania luctuosa    ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Holotania gaigei      ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Holotania flavida     ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Holotania comanche    ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Holotania cyanea      ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Holotania axilena     ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Holotania vibrans     ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Holotania incesta     ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Holotania needhami    ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Holotania auripennis  ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
Holotania jesseana    ....111111C1C .......111C1XCCXX1 .....11X ............ .........1X111X1CX .......11111XXX
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Appendix 2 (Cont.)

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                      111111111 11111111111111 11111111111111111111 1112222222 22222222 22221222 2 2222222 2233
                      333334444 55555555666666 77778888888888888881 9990000000 11222222 33441444 6 5777777 8901
                      abcefabcd abcdefghabcdef abcdabcdefghijklmnoh acbbcdaefg ababcdef ababgcde a aabcdef aaaa
Zygoptera             ......... .............. .................... .1........ ........ ........ . ....... ....
Epiophlebia           ......... ............X. .................... .......... ..1..... ........ . ....... ....
Austropetaliidae      ....X.1.. .............. .................... .......... ........ ........ . ....... ....
Anax                  ......1.Z .............. ............1....Y.Y .......... ........ ....1... . ....... ....
Other aeshnids        ......1.. .............. ............1....Y.Y .......... ........ ....1... . ....... ....
Hagenius              ........Y .............. ...............YYY.. .......... ........ ....1... . ....... ....
Ophiogompus           ........Y ..........1... ...............YYY.. .......... ........ ........ . ....... ....
Other gomphids        ........Y .............. ...............YYY.. .......... ........ ........ . ....... ....
Tachopteryx/Petalura  ......... .............. .................... .......... ........ ........ . ....... ....
Tanypteryx            ......... .............. .................... .......... ........ ........ . ....... ....
Phenes                ......... .............. .................... .......... ........ ........ . ....... ....
Zoraena/Kalyptogaster 1111X.... ............X. .................... .......... ........ ........ . ....... ....
Anotogaster           1111X.... ............X. .................... .......... ........ ........ . ....... ....
Cordulegaster         1111X.... ............X. .................... .......... ........ ........ . ....... ....
Neopetalia            .....111X 11111111...... .................... .......... ........ ........ . ....... ....
Chloropetalia         .....111X ........1111X1 1111................ .......... ........ ........ . ....... ....
Sinorogomphus         .....111X ........1111X1 1111................ .......... ........ ........ . ....... ....
Synthemis             .....111X ........1111X1 ....1111111C1XXXXXXX 11X....... ........ .....X.. . ....... ....
Gomphomacromia        .....111X ........11XXX1 ....1111111C1XXXXXXX ..111C1CC1 11...... .....X.. . ....... ....
Macromiinae           .....111X ........11XXX1 ....1111111C1XXXXXXX ..X11C1CC1 ..1111C1 11...... . ....... ....
Macromiinae           .....111X ........11XXX1 ....1111111C1XXXXXXX ..X11C1CC1 ..1111C1 11...... . ....... ....
Oxygastra             .....111X ........11XXX1 ....1111111C1XXXXXXX ..111C1CC1 ..1111C1 ..111XX1 . ....... ....
Tetragoneuria         .....111X ........11XXX1 ....1111111C1XXXXXXX ..111C1CC1 ..1111C1 ..111XX1 1 1...... ....
Somatochlora          .....111X ........11XXX1 ....1111111C1XXXXXXX ..111C1CC1 ..1111C1 ..111XX1 1 1...... ....
Perithemis            .....11XX ........1XXXX1 ....1111111C1XXXXXXX ..111C1CCX ..1111C1 ..111X.1 1 .1CX111 X1..
Celithemis            .....11XX ........1XXXX1 ....1111111C1XXXXXXX ..111C1CCX ..1111CX ..111XXX 1 .1CX111 X.1.
Sympetrum             .....11XX ........1XXXX1 ....1111111C1XXXXXXX ..X11C1CCX ..1111CX ..111XXX 1 .1CX111 ..1.
Tarnetrum             .....11XX ........1XXXX1 ....1111111C1XXXXXXX ..X11C1CCX ..1111CX ..111XXX 1 .1CX111 .11.
Pachydiplax           .....11XX ........1XXXX1 ....1111111C1XXXXXXX ..X11C1CCX ..1111CX ..111XXX 1 .1CX111 ..11
Erithemis             .....11XX ........1XXXX1 ....1111111C1XXXXXXX ..X11C1CCX ..1111CX ..111XXX 1 .1CX111 ..11
Tramea                .....11XX ........1XXXX1 ....1111111C1XXXXXXX ..X11C1CCX ..1111CX ..111XXX 1 .1CX11X ....
Crocothemis           .....11XX ........1XXXX1 ....1111111C1XXXXXXX ..X11C1CCX ..1111CX ..111XXX 1 .1CX11X ..1.
Orthetrum cancellatum .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..X11C1CC1 ..1111CX ..111XXX 1 .1CX11X ....
Orthemis ferruginea   .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..X11C1CC1 ..1111CX ..1111XX 1 .1CX11X ....
Eurothemis fulva      .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Eurothemis pontica    .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Ladona julia          .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Ladona exusta         .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Ladona deplanata      .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Platetrum depressa    .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Plathemis lydia       .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Plathemis subornata   .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
L.quadrimaculata      .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
L.semifasciata        .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Syntetrum angelina    .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Belonia mariae        .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Belonia foliata       .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Belonia saturata      .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Belonia croceipennis  .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Belonia herculea      .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Eotania composita     .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Neotetrum nodisticta  .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Neotetrum forensis    .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Neotetrum pulchella   .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Holotania luctuosa    .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Holotania gaigei      .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Holotania flavida     .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Holotania comanche    .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Holotania cyanea      .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Holotania axilena     .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Holotania vibrans     .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Holotania incesta     .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Holotania needhami    .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Holotania auripennis  .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
Holotania jesseana    .....11XX ........1XXXX1 ....1111111C1XXXXX1X ..211C1CC1 ..1111CX ..11111X 1 .1CX11X ....
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Appendix 2 (Cont.)

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                      333 33 333 3333444 33334444 34 444 44444 44 4 4444455555 666 555555 555555 5 555 56 66 66
                      223 44 555 6667444 88881111 90 233 55558 66 7 9999900000 625 122222 344666 5 788 90 12 34
                      aba ab abc abcaabc abcdabcd aa aab abcda ab a abcdeabcde aba aabcde aababc a aab aa aa aa
Zygoptera             ... .. ... ....... ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Epiophlebia           ... .. ... ....... ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Austropetaliidae      ... .. ..1 ......1 ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Anax                  ... .. ... .....1. ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Other aeshnids        ... .. ... .....1. ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Hagenius              ... .. ... .....1. ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Ophiogompus           ... .. ... ....... ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Other gomphids        ... .. ... ....... ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Tachopteryx/Petalura  ... .. ... ....... ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Tanypteryx            ... .. ... ....... ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Phenes                ... .. ... ....... ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Zoraena/Kalyptogaster ... .. ... ....... ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Anotogaster           ... .. ... ....... ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Cordulegaster         ... .. ... ....... ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Neopetalia            ... .. ..1 ......1 ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. 1.
Chloropetalia         ... .. ... ....... ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Sinorogomphus         ... .. ... ....... ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Synthemis             ... .. ... ....... ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Gomphomacromia        ... .. ... ....... ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Macromiinae           ... .. ... ....... ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Macromiinae           ... .. ... ....... ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Oxygastra             ... .. ... ....... ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Tetragoneuria         ... .. ... ....... ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Somatochlora          ... .. ... ....... ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Perithemis            ... .. 1.. ....... ....1... .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Celithemis            ... .. ... ....... ........ .. ... ..... .1 . .......... ... ...... ...... . ... .. .. .1
Sympetrum             ... .. ... ....... ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Tarnetrum             ... .. ... ....... ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Pachydiplax           ... .1 ... ....... 1...1... .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Erithemis             ... .1 ... ....... ....1... .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Tramea                11. .. ... ....... ........ .. ... ..... .. . .......... ... ..1... ...... . ... .. .. ..
Crocothemis           ..1 .. ... ....... ........ .. ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Orthetrum cancellatum ..1 11 ... ....... 1....... .. ... 1.... .. . .......... ... ...... ...... . ... .. .. ..
Orthemis ferruginea   ..1 11 ... ....... ........ .. ... ..... .. . .......... ... ..1... ...... . .1. .. .. ..
Eurothemis fulva      ..1 11 111 11X.... 11X1.... 1. ... ..... .. . .......... ... .....X ...... . ... .. .. ..
Eurothemis pontica    ..1 11 111 11X.... 11X1.... 1. ... ..... .. . .......... ... .....X ...... . ... .. .. ..
Ladona julia          ..1 11 111 1111... 1X11.... .1 ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Ladona exusta         ..1 11 111 1111... 1X11.... .1 ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Ladona deplanata      ..1 11 111 1X11... X111.... .1 ... ..... .. . .......... ... ...... ...... . ... .. .. ..
Platetrum depressa    ..1 11 111 1111... ....1111 .. 1.. ..... .. . .......... ... ..1..X ...... . ... .. .. ..
Plathemis lydia       ..1 11 111 1111.11 ....1111 .. .11 ..... .. . .......... ... ..1... 1..... . .1. .. .. ..
Plathemis subornata   ..1 11 111 1111.11 ....1111 .. .11 ..... .. . .......... ... ...... 1..... . .1. .. .. ..
L.quadrimaculata      ..1 1X 11X ...1111 ........ .1 ... 1111. .. . .......... ... ...... ...... . ... .. .. ..
L.semifasciata        ..1 1X 11X ....111 ........ .. ... 1111. 11 . .......... ... ..1... ...... . ... .. .. ..
Syntetrum angelina    ..1 1X 111 ..1.111 ....?... .. ... 1111. 11 1 .......... ... ...... ...... . ... .. .. ..
Belonia mariae        ..1 1X 11X ....11X ........ .. ... ....1 .. . 11111..... 1.. ..1... ...... . ... .. .. ..
Belonia foliata       ..1 1X 11X ....11X ........ .. ... ....1 .. . 11111..... 1.. ..1... ...... . ... .. .. ..
Belonia saturata      ..1 1X 11X ....11X ........ .. ... ....1 .. . 11111..... .1. ..1... ...... . ... .. .. ..
Belonia croceipennis  ..1 1X X1X ....11X ........ .. ... ....1 .. . 11111..... .11 ..1... ...... . ... .. .. ..
Belonia herculea      ..1 1X X1X ....11X ........ .. ... ....1 .. . 11111..... .11 ..1... ...... . ... .. .. ..
Eotania composita     ..1 11 X1X ....111 ........ .. ... 1...1 .. . .....11111 ... 1..... ...... . ... .. .. ..
Neotetrum nodisticta  ..1 11 111 ....111 ........ .. ... ....1 .. . .....111X1 ... .1111X 111... . ... .. .. ..
Neotetrum forensis    ..1 11 111 ....111 ........ .. ... ....1 .. . .....111X1 ... .1111X 111... 1 ... .. .. ..
Neotetrum pulchella   ..1 11 111 ....111 ........ .. ... ....1 .. . .....111X1 ... .1111X 111... 1 ... .. .. ..
Holotania luctuosa    ..1 11 X11 ....11? ........ .. ... ....1 .. . .....11111 ... .1111X 1..111 . 1.. .. .. ..
Holotania gaigei      ..1 11 X11 ....11? ........ .. ... ....1 .. . .....11111 ... .1111X 1..111 . 1.. .. .1 ..
Holotania flavida     ..1 11 X1X ....11X ........ .. ... ....1 .. . .....11111 ... .1111X ...111 . .11 .. .. 1.
Holotania comanche    ..1 11 X1X ....11X ........ .. ... ....1 .. . .....11111 ... .1111X ...111 . .11 1. .. ..
Holotania cyanea      ..1 11 X11 ....11X ........ .. ... ....1 .. . .....11111 ... .1111X ...111 . .11 1. .. ..
Holotania axilena     ..1 11 X11 ....111 ........ .. ... ....1 .. . .....11111 ... .1111X ...111 . .11 .1 .. ..
Holotania vibrans     ..1 11 X11 ....111 ........ .. ... ....1 .. . .....11111 ... .1111X ...X11 . .11 .1 1. ..
Holotania incesta     ..1 11 X1X ....11X ........ .. ... ....1 .. . .....11111 ... .1111X ...11X . .11 .1 1. ..
Holotania needhami    ..1 1X X1X ....11X ........ .. ... ....1 .. . ....111111 .1. .1111X ...111 . .11 .1 .1 1.
Holotania auripennis  ..1 1X X1X ....11X ........ .. ... ....1 .. . ....111111 .1. .1111X ...111 . .11 .1 .1 .1
Holotania jesseana    ..1 11 X1X ....11X ........ .. ... ....1 .. . .....11111 .1. .1111X ...111 . .11 .1 .1 .1
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