

A PRELIMINARY CLADISTIC ANALYSIS OF ODONATE WING VENATION*

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A data matrix comprising 96 selected wing venation characters from each of 15 fossil and 32 extant spp. was analysed using cladistic parsimony algorithms. The results indicate that suborder Anisoptera is a natural (i.e. monophyletic) grouping, but that both Anisozygota and Zygotera are paraphyletic. Within the extant order, coenagrionoid and lestoid families occupy the basal branches of the phylogenetic tree. Next comes Calopterygoidea as a monophyletic group, then Amphipterygidae, then Anisozygota, and finally Anisoptera as a monophyletic group. The Australian endemic species *Hemiphysalis mirabilis* Selys is indicated as sister to a clade comprising the whole remainder of the modern order, plus the Permian suborders Protozygota and Archizygota and the Triassic suborder Triadophlebiomorpha. If this phylogenetic estimate is correct, the conservation value of *H. mirabilis* is far greater than its current taxonomic status as a monotypic superfamily would suggest.

INTRODUCTION

At August 1991 (the date of the XI Symposium of Odonatology) two cladistic estimates (BRAUCKMAN & ZESSIN, 1989; ZESSIN, 1991) of higher-level relationships in Odonata had been published. Since that time a small number of others (PFAU, 1991; NEL et al., 1993; NEL et al., 1993; BECHLY, 1995) also have appeared. Nel et al. and Nel & Martinez-Delclos used computer-cladistic methods to examine relationships in Anisozygota and Anisoptera. The other analyses are based on manual cladistic methods (phylogenetic systematics) and deal with a small number of taxa or a small part of the order. Order Odonata as a whole has not been

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examined using cladistic parsimony analysis. The objective of such a study would be to improve on current estimates of the higher taxon groupings. I report early progress toward that objective.

Several long-standing problems in the higher classification in Odonata appear to be resistant to traditional taxonomic methods. One concerns the relationships at suborder level. Conflicting hypotheses have been suggested, including that

- (1) Zygoptera arose from Protozygoptera, and Anisoptera from Protanisoptera (TILLYARD & FRASER, 1938-40),
- (2) Anisoptera arose from within Zygoptera (meaning the suborder Zygoptera is paraphyletic: FRASER, 1957; HENNIG, 1981), and
- (3) Zygoptera and Anisoptera arose separately from anisozygopteran ancestors (CARLE, 1982).

Related problems occur at the family level. For example, CARLE (1982) has questioned whether the broad-winged or narrow-winged Zygoptera form the most basal zygopteran lineage, and CARLE & WIGHTON (1990) have suggested that wing-narrowing has occurred convergently, and thus that the narrow-winged families do not form a monophyletic group. An older debate concerns the position of *Hemiphysalis mirabilis* Selys, a rare species restricted to a few sites in south-eastern Australia (TRUEMAN et al, 1992; ENDERSBY, 1993). MUNZ (1919) considered *Hemiphysalis* an advanced coenagrionid. TILLYARD (*in* TILLYARD & FRASER, 1938-40: 149) raised a new, monotypic superfamily, placed "at the very base of the whole Suborder". FRASER (1957) retained this superfamily status but argued, in effect, for a sister-group relationship between *H. mirabilis* and the whole remainder of the modern order, including the suborders Anisozygoptera and Anisoptera.

A clear resolution of odonate higher relationships is needed to achieve a classification which reflects the phylogeny of the order, and to facilitate progress in evolutionary, ecological and biological studies, which rely on phylogenetic estimates for purposes such as modelling past relationships, making a distinction between the ecological correlation and co-inheritance of traits, and determining whether instances of apparent co-variation are statistically independent or historically linked.

Cladistic systematic methods avoid some of the errors of logic which affect other methods for reconstructing phylogenies. In cladistic systematics, taxa are arranged on the basis of their shared, derived character states (synapomorphies). In other methods, including traditional taxonomic techniques, taxa may be grouped partly or wholly on the basis of overall similarity (including shared primitive states; symplesiomorphies) and names may be assigned on the basis of either symplesiomorphies or unique characters (autapomorphies), neither of which are indicative of relationships. The current ordinal classification in Odonata is that of FRASER (1957), who's work is based in part on explicit grouping by symplesiomorphy (called 'persistent archaic characters' in FRASER, 1954) in preference to synapomorphy. Fraser's classification cannot be considered a valid estimate of relationships in the order.

This is not to say that cladistic procedures necessarily will give the correct phylogenetic tree. In particular, cladistics can be misled by either reticulation (hybridization, horizontal gene transfer, etc. between species) or by convergence in character states. In addition, the various cladistic techniques each have their own biases. Manual cladistic analysis (phylogenetic systematics as described in HENNIG, 1966) suffices to recover a hierarchic signal when the number of taxa is small, there is no homoplasy (inconsistency in the signal from different characters), and each character can be polarised with certainty prior to analysis. When there is much homoplasy, when the primitive states of some characters are unknown, and when the problem to be addressed involves a moderate to large number of terminal taxa, manual cladistic methods become unreliable and computer-based parsimony analysis becomes the cladistic method of choice.

Cladistic parsimony techniques scan many possible arrangements of the taxa in an attempt to find the one which best fits the given data. With a moderate number of taxa (up to about 15-20), it is possible to consider every tree. With larger data sets, the tree space can be searched using heuristic algorithms. Provided a search has been done competently, the shortest (ie, most-parsimonious) tree discovered by parsimony analysis can be regarded as a best phylogenetic estimate of the relationships amongst taxa, given the original data.

Parsimony analysis can, however, give a biased or unreliable result in some circumstances. First, the algorithm always will prefer some branching pattern over none at all, even where the input data does not warrant a cladistic estimate. Second, the algorithm may favour the wrong tree if there is pattern in convergent states (FAITH, 1989) (i.e., where there is more than one hierarchic signal in the data). Third, the algorithm can favour the wrong tree if convergence is common and if some branches on the tree are much longer than others (HENDY & PENNY, 1989). This latter bias occurs mainly with molecular sequence data, for which the number of possible states is small and convergent states are absolutely equal (i.e., in principle not separable by a re-inspection of specimens).

Currently available parsimony packages PAUP 3.0 (SWOFFORD, 1990) and Hennig86 (FARRIS, 1988) provide a reliable means for finding shortest trees for data matrices of the size here used. The Permutation Tail Probability (PTP) test protocol (FAITH & CRANSTON, 1991; FAITH, 1991) provides a means by which the statistical significance of computer-generated phylogenetic hypotheses (but not of manually generated hypotheses) can be tested.

The analysis reported here is based on morphological data from a range of extant and fossil species, representing a wide range of odonatoid families. The data is analysed using PAUP 3.0 and Hennig86, and the results are subjected to PTP testing. The choice of widely separated species as terminal taxa ensures that the pattern to be estimated truly is hierarchic and not reticulate, the number of taxa is within the capacity of the heuristic search algorithms, and the data selected for analysis is not of a type commonly prone to the 'long branches' effect. Thus, the

resulting trees are *prima facie* interpretable as a phylogeny.

TAXA AND CHARACTERS

Forty-seven selected taxa (14 fossil odonatoids/Odonata, 32 extant Odonata, 1 fossil Palaeodictyopteroidea as outgroup) were scored for each of 96 wing vein characters.

Extant taxa were chosen to represent families across the whole order. Locally available species were used where possible, and character states were scored from five or more pinned specimens of each species. Fossil taxa were selected to cover the extinct suborders Archizygoptera, Protanisoptera, Protozygoptera and Triadophlebiomorpha, the almost-extinct Anisozygoptera and the putative odonate stem, ancestral or sister taxon Meganeuridae (Protodonata). Further selection criteria for the fossils were (i) a sufficient quality of wing preservation to allow at least 50% of characters to be scored, and (ii) ready access to the fossil itself or to a good quality illustration from which the data could be coded.

The analysis is restricted to wing vein characters because (i) wing veins are extensively used at all levels in odonate systematics, and are critical to the existing classification, and (ii) most fossils consist of wing impressions alone. No other character systems can be scored for the majority of fossil species in the present analysis.

A fossil palaeodictyopteran was chosen as outgroup. An outgroup is needed to convert the product of the parsimony algorithm into a phylogenetic estimate, by showing where the most parsimonious undirected tree should be rooted. An outgroup must lie clearly outside of the group under study, but must not be so distant that it cannot be reliably placed in relation to the ingroup taxa. At least some characters which inform about relationships amongst the ingroup must be scorable for the outgroup if it is to be reliably placed. Extant taxa could not be used as outgroups in the current analysis because all are too distant. Odonate wings are highly autapomorphic and, in spite of recent progress (e.g. RIEK & KUKALOVÁ-PECK, 1984; KUKALOVÁ-PECK, 1991), a full homologisation of the wing veins across pterygote orders has yet to be achieved. The alternative was to take a species from Palaeodictyopteroidea. This extinct palaeopteran superorder can be reliably placed outside Odonatoidea, but the wings are sufficiently similar to allow many of the same characters to be scored. The type species of family Calvertiellidae was selected to represent the group. This family was once placed in Odonatoidea on the evidence of wing vein characters, but is now firmly placed in Palaeodictyopteroidea on the basis of a complex of shared characters of the mouthparts (KUKALOVÁ, 1964).

The species selected for analysis are listed in Appendix 1.

Ninety-six characters were identified, mostly from higher taxon definitions and existing keys to higher level relationships in Odonata. Character and states definitions are given in Appendix 2. The veins are referred to using a modified version of the Tillyard-Fraser wing vein naming system (O'FARRELL, 1970). This system is used for convenience only, and does not indicate acceptance of the implied inter-ordinal homologies, some of which are directly contradicted by alternative naming schemes (e.g. RIEK & KUKALOVÁ-PECK, 1984).

The data matrix is given in Table I.

RESULTS

Originally, the data matrix was analysed using parsimony programs PAUP 3.0q (SWOFFORD, 1990) and Hennig86 (FARRIS, 1988). It has since been re-analysed using PAUP 3.1.1 (SWOFFORD, 1993). Each program and version gives the same set of four most-parsimonious trees (length=365 excluding uninformative characters, CI=.288, with multistate characters treated as unordered). These four

Table 1
Data matrix – Full taxon names are listed in Appendix 1, character state codings in Appendix 2. ("?" = missing or inapplicable)

Character:	1	2	3	4	5	6	7	8	9	9
Calvertiella	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
Proteron	00000000??	7100700070	0007007710	0077007777	00000000??	7700000000	0070000000	0000010100	0000000000	010700
Ditaxineura	1001001011	1100001110	0000110101	0000010000	1100000000	7700110000	7777701020	0000077777	0000000000	001700
Polystixineura	1001010111	1010001100	0000101000	0000010700	1100000000	7700001000	0070000000	0000000100	0000000000	000100
Tupus	0000000071	1100100070	0000177711	7777000000	1100000000	7771100000	0077701001	00000002100	0000000000	011307
Trisagrion	1000071100	0000000070	0000110100	0000000000	0170700000	7700071001	0070100000	1100100001	0001100000	000100
Procrummalcon	1000071100	0100000070	0000177000	0000000070	0170700000	7700071001	0070100000	1100100001	0001100000	000100
Triadophlebia	0070101011	0100171100	0000177100	0000017711	0177010000	0110000000	0070000000	0100100010	0001111110	000000
Kennedyia	1000001100	0000000070	0000000000	0077011100	0110000000	0000000000	0070000000	0000000000	0001100000	000100
Pernalestes	1000001101	1000001100	0000101101	0077011177	0110000070	7700011001	0070000000	0000000000	0001100000	000100
Fernagrion	1000001100	0000001101	0000100100	0077011177	0110000070	7700011001	0070000000	0000000000	0001100000	000100
Zanaphlebia	1000071000	0000000100	0000101000	0101011100	0110000000	7701000000	0070000000	0000000000	0001100000	000100
Xanthagrion	1000071000	0000001101	1100100000	0101011100	0110000000	7701000000	0070000000	0000000000	0001100000	000100
Platynema	1000011100	0000000101	1100100000	0101010000	0110000000	7701000000	0070000000	0000000000	0001100000	000100
Neoticta	1000001100	0000001101	1100101000	0101010000	0110000000	7701000000	0070000000	0000000000	0001111110	000000
Platydictya	1000071100	0000000101	1000101000	0101010000	0110000000	7701000000	0077000000	0000000000	0001111110	000000
Proconeura	1000071100	0000000101	1000101000	0101010000	0110000000	7701000000	0077000000	0000000000	0001111110	000000
Pseudostigma	1000001100	0000000111	1100100000	0101010000	0110000000	7701000000	0077000000	0000000000	0001111110	000000
Austroargiolestes	1000001100	0000000111	1100100000	0101010000	0110000000	7701000000	0077000000	0000000000	0001100000	000100
Perilestes	1000001100	0000000111	1100100000	0101010000	0110000000	7701000000	0077000000	0000000000	0001100000	000100
Chorismagrion	1000011100	0000000101	1100100000	0001011100	0110010000	7700011001	0070000000	0000000000	0001100000	000100
Synlestes	1000011100	0000000101	1100100000	0001011100	0110010000	7700011001	0070000000	0000000000	0001100000	000100
Austolestes	1000011100	0000000101	1100100000	0001011100	0110010000	7700011001	0070000000	0000000000	0001100000	000100
Pseudolestes	1000001100	0000000100	0000100000	0101011100	0110000000	7701010001	0070000000	0000000000	0001100000	000100
Leptoides	1000001100	0000000101	0000100000	0101010000	0110000000	7701010001	0070000000	0000000000	0001100000	000100
Amblypteryx	1000001101	1010000100	0000100100	0101010000	0110000000	7701010001	0070000000	0000000000	0001100000	000000
Dipblebia	1000011001	1010000100	0000100100	0101011100	0110000000	7701010001	0070000000	0000000000	0001100000	000000
Chalcopteryx	1000001101	1010111100	0000077110	0101010000	0110000000	7701010001	0070000000	0000000000	0001100000	000100
Phallage	1000001101	1010111100	0000077110	0101010000	0110000000	7701010001	0070000000	0000000000	0001100000	000100
Heliocharis	1000001001	1000000100	0000100100	0101010000	0110000000	7701010001	0070000000	0000000000	0001100000	000100
Neurobasis	1000001001	1011111100	0000100100	0101010000	0110000000	7701010001	0070000000	0000000000	0001100000	000100
Petallura	1000001001	1011111100	0000100100	0101010000	0110000000	7701010001	0070000000	0000000000	0001100000	000100
Setorophlebia	1000001001	1000000100	0000100100	0101010000	0110000000	7701010001	0070000000	0000000000	0001100000	000100
Liasophlebia	1000001001	1000000100	0000100100	0101010000	0110000000	7701010001	0070000000	0000000000	0001100000	000100
Varophlebiopsis	1000071001	1000000100	0000100100	0077011170	0117700000	7701010001	0070000000	0000000000	0001100000	000100
Phlebiopsis	1000001001	1000000100	0000100100	0077011170	0117700000	7701010001	0070000000	0000000000	0001100000	000100
Wightonia	7007071001	1010000100	0000100100	7701010000	0077011110	0077011110	0070000000	0000000000	0001100000	000100
Autroptetalia	1010701001	1010000100	0000100100	0101010000	0077011110	0077011110	0070000000	0000000000	0001100000	000100
Heinania	1010701001	1010000100	0000100100	0101010000	0077011110	0077011110	0070000000	0000000000	0001100000	000100
Chlorogomphus	1000001001	1010000100	0000100100	0101010000	0077011110	0077011110	0070000000	0000000000	0001100000	000100
Ichthyogomphus	1010001001	1010000100	0000100100	0101010000	0077011110	0077011110	0070000000	0000000000	0001100000	000100
Synthesia	1000001011	1010000100	0000100100	0101010000	0077011110	0077011110	0070000000	0000000000	0001100000	000100
Cordulephya	1000001011	1010000100	0000100100	0101010000	0077011110	0077011110	0070000000	0000000000	0001100000	000100
Hemicordulia	1000001011	1010000100	0000100100	0101010000	0077011110	0077011110	0070000000	0000000000	0001100000	000100
Dipterodes	1000001011	1010000100	0000100100	0101010000	0077011110	0077011110	0070000000	0000000000	0001100000	000100
Nannophlebia	1000000101	1010101100	0001177100	1010101000	0001111100	1011100011	1110101000	0001000101	1100000001	000110

trees do not differ in deep-level topology. The strict consensus tree is shown in Figure 1. The CI value is low, indicating much homoplasy in the data, but is well above the value which would be expected from a matrix of this size if there were no significant hierarchic signal in the data (SANDERSON & DONOGHUE, 1989).

The consensus tree resolves the Protagrionidae with Odonatoidea rather than with Palaeodictyopteroidea. Other key results are as follows:

- (1) The 11 Anisoptera form a monophyletic group which is sister to one or more

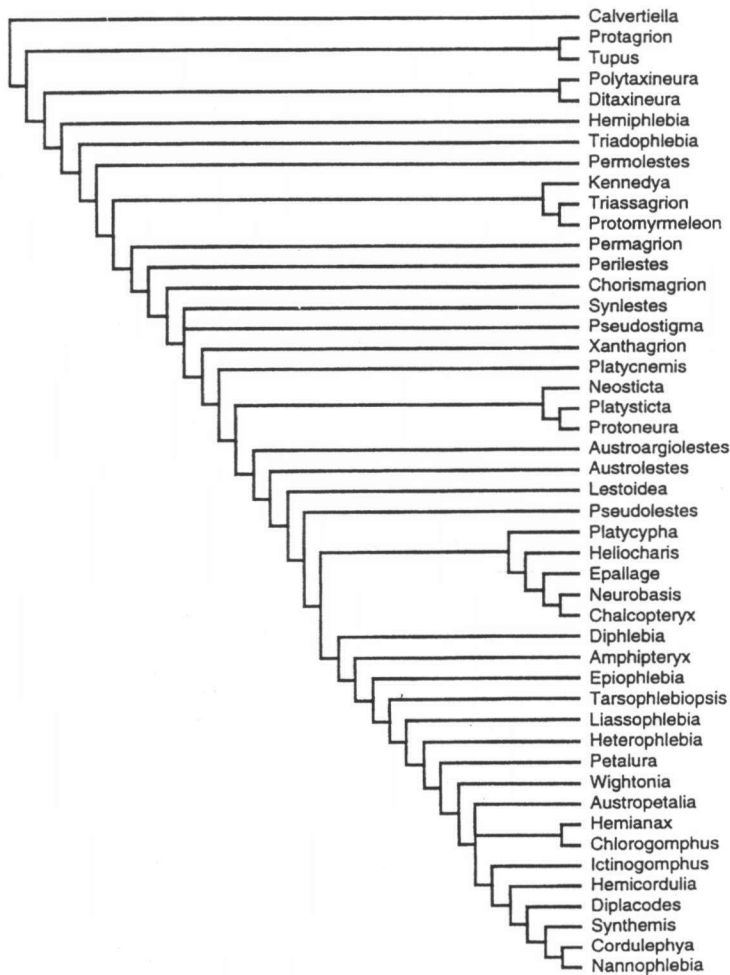


Fig. 1. Strict consensus of trees obtained by parsimony analysis of the data matrix shown in Table I.

fossil Anisozygoptera, but Anisozygoptera and Zygoptera are paraphyletic groupings.

- (2) Although many relationships in Zygoptera are not well resolved by the analysis (branch lengths are short and in parts the consensus is close to being bush-like), it does appear that the broad-winged families are not basal. They are placed as sister to a paraphyletic Amphipterygidae, one part of which is sister to the Anisoptera + Anisozygoptera clade.
- (3) There is considerable evidence for the TILLYARD & FRASER (1938-40) and FRASER (1957) view that the ancestral odonate had narrow, zygoteran-like wings. This would imply that the peculiar autapomorphies of anisopteran wing venation can be explained, at least in part, as a means for re-evolving broad wings and strong flight after the primitive venation of the odonatoid ancestor had been partially lost. It also implies that wing vein naming systems which depend on the primitiveness of anisopteran venation to homologue veins in the posterior part of the wing, e.g., the Comstock-Needham system (NEEDHAM, 1903) and the Riek & Kukalová-Peck system (RIEK & KUKALOVÁ-PECK, 1984), cannot be entirely correct.
- (4) The Permian suborders Protozygoptera and Archizygoptera form a monophyletic group, as previously reported by ZESSIN (1991).
- (5) The enigmatic Australian species *Hemiphlebia mirabilis* is placed well basal of the other extant species. This species appears to share none of the derived states of other extant odonates, and on the characters used in the present analysis is placed not merely as sister to the rest of the extant order but basal with respect to the Upper Permian zygoteran family Permagrionidae, the Permian suborders Protozygoptera and Archizygoptera, and the Triassic suborder Triassophlebiomorpha.

The above consensus tree is not changed when multistate characters are respecified as ordered, when the transformation matrices amongst character states are made asymmetric by including single-step loss functions for the wing field width measures, or when the logically linked characters (13-14, 21-32, 33-34, 84-86, 87-88) are each downweighted by 50% to reflect their inter-dependent status.

The statistical robustness of the tree topology was tested using permutation tail probability (PTP and T-PTP) tests (FAITH & CRANSTON, 1991; FAITH, 1991). Each test was based on 100 randomisations of the data. All test searches were performed in PAUP 3.1.1 using the TBR branch swapping algorithm and five random-addition-sequence starting trees, as for the original searches. The hierarchic information content of the matrix is confirmed (PTP<0.01) and the monophyly of Anisoptera is strongly supported (T-PTP<0.01).

The basal position of *Hemiphlebia* was examined using an a priori T-PTP test for monophyly of a group comprising Anisoptera, Anisozygoptera, Protozygoptera, Archizygoptera, Triadophlebiomorpha, and Zygoptera excluding *Hemiphlebia*. The basal position of *Hemiphlebia* was confirmed (T-PTP<0.01: tree length difference

+3, range of length differences from 100 randomisations of the matrix -26 to -4). The proposition that *Hemiphlebia* might belong with the other extant suborders was examined using an a priori T-PTP test for the non-monophyly of a group comprising Zygoptera plus Anisozygoptera plus Anisoptera. The non-monophyly of this grouping is confirmed (T-PTP<0.01: tree length difference -1, range of length differences from 100 randomisations of the matrix -33 to -9).

Taken together, these results suggest that the basal position of *Hemiphlebia* cannot be attributed to any chance co-variation among character states.

DISCUSSION

The overall pattern of relationships shown in Figure 1 is generally consistent with the results of traditional taxonomy as expressed in the classification of FRASER (1957). The non-monophyly of Zygoptera and the derivation of Anisoptera through an intermediate anisozygopterous stage are consistent with the 'narrow-winged ancestor' model of TILLYARD & FRASER (1938-40).

The fact that the consensus tree is insensitive to several unavoidably arbitrary aspects of the present analysis is welcome as it increases confidence in the results. Confirmation of the monophyly of Anisoptera is not surprising and is in line with the predictions of traditional taxonomy.

The T-PTP test result for the extreme basal placement of *Hemiphlebia mirabilis* suggests that this species may indeed be a "living fossil". If the true relationships are as shown in Figure 1, the species is far more taxonomically isolated than has previously been suggested. The line which leads to *Hemiphlebia* must have branched from the rest of Odonata no later than the early Permian, about 280 Myr ago. If this is so, the current taxonomic placement of *H. mirabilis* in a monotypic superfamily seriously understates the taxonomic isolation and conservation value of this species. Separate subordinal placement would be more appropriate. A name, Archaeoptera, is available (BELYSHEV & KHARITONOV, 1985). This suborder takes *Hemiphlebia* as type genus, although Belyshev & Kharitonov also included the genus *Chorismagrion*, which appears somewhat further up in the Figure 1 tree.

However, great caution is needed when dealing with potential nomenclatural change. In the first place, too much should not be made of an analysis based only on one structure and one life stage. Wing venation is subject to an unknown amount of evolutionary convergence which could bias this phylogenetic estimate. Other character sets are available for the extant taxa and it may be that these will contradict the placement of *Hemiphlebia* suggested by this analysis. It is especially worrying that many of the wing vein states displayed by *Hemiphlebia* can be interpreted either as primitive absence or as secondary loss. In the second place, the extreme basal position of *Hemiphlebia* was an unexpected outcome of the analysis, and in this circumstance the a priori T-PTP test gives an over-estimate of statistical confidence in the result. A bias-free, a posteriori form of the test has been

described (FAITH, 1991), but its application to a 6/40 partition of a 46/taxon matrix (outgroup excluded) is not feasible using conventional computing facilities. The apparent placement of *Hemiphysalia* basal of Protozygota, Archizygota, Triadophlebiomorpha and Permagrionidae may not be as well supported as would appear.

The tree in Figure 1 is suggestive of possible broad patterns in odonate evolution, and may provide a useful basis for evolutionary and ecological research, but it would be unwise to base any nomenclatural change on these preliminary results. The cladistic approach holds a promise that difficult parts of the odonate phylogenetic tree eventually will be resolved, but the current analysis is no more than an early step in a long process. Much work remains to be done.

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APPENDIX 1

SPECIES AND FAMILY REPRESENTATION

† Superorder

PALAEODICTYOPTEROIDEA

Calvertiella permiana Tillyard (Calvertiellidae)
– Designated as outgroup taxon in the analysis.

Protagrion audouini Brongniart (Protagrionidae) – Originally described in Odonatoidea: removed to Palaeodictyoptera by CARPENTER (1943) but placed under the heading “Palaeoptera: Order Uncertain” by CARPENTER (1992).

Superorder ODONATOIDEA

† Order PROTANISOPTERA

Ditaxineura anomalostigma Tillyard (Ditaxineuridae)

Polytaxineura stanleyi Tillyard (Polytaxineuridae)

† ORDER PROTODONATA

Tupus permianus Sellards (Meganeuridae)

ORDER ODONATA

† Suborder Archizygoptera

Triassagrion australiense Tillyard (Protomyrmeleontidae)

Protomyrmeleon handlirschi Martynov (Protomyrmeleontidae)

† Suborder Protozygoptera

Kennedyia mirabilis Tillyard (Kennedyidae)

Permolestes gracilis Martynov (Permolestidae)

Suborder Zygoptera

Permagrion falklandicum Tillyard († Permagrionidae)

Hemiphebia mirabilis Selys (Hemiphebiidae)

Xanthagrion erythroneurum (Selys) (Coenagrionidae)

Platynemesis pennipes (Pallas) (Platynemididae)

Neosticta canescens Tillyard (Isostictidae)

Platysticta maculata (Selys) (Platystictidae)

Protoneura capillaris (Rambur) (Protoneuridae)

Pseudostigma aberrans Selys (Pseudostigmatidae)

Austroargiolestes icteromelas (Selys) (Megapodagrionidae)

Perilestes fragilis Hagen (Perilestidae)

Chorismagrion risi Morton (Synlestidae: Chorismagrioninae)

Synlestes weyersii Selys (Synlestidae: Synlestinae)

Austrolestes cingulatus (Burmeister) (Lestidae)

Pseudolestes mirabilis Kirby (Pseudolestidae)

Lestoidea conjuncta Tillyard (Lestoideidae)

Amphipteryx agrioides Selys (Amphipterygidae: Amphipteryginae)

Diphlebia lestoides (Selys) (Amphipterygidae: Diphlebiinae)

Chalcopteryx rutilans Rambur (Polythoridae)

Epallage fatime Charpentier (Euphaeidae)

Heliocharis amazona Selys (Dicteriastidae)

Neurobasis chinensis (L.) (Calopterygidae)

Platycypha caligata Selys (Chlorocyphidae)

Suborder Anisozygoptera

Heterophlebia buckmani (Brodie) († Heterophlebiidae)

Liassophlebia magnifica Tillyard († Liassophlebiidae)

Tarsophlebiopsis mayi Tillyard († Tarsophlebiidae)

Epiophlebia superstes (Selys) (Epiophlebiidae)

Suborder Anisoptera

Wightonia araripina Carle († Aeshnidiidae)

Petalura gigantea Leach (Petaluridae)

Austropetalia patricia (Tillyard) (Neopetaliidae)

Hemianax papuensis (Burmeister) (Aeshnidae)

Chlorogomphus campioni Fraser (Cordulegastriidae)

Ictinogomphus australis (Selys) (Gomphidae)

Synthemis eustalacta (Burmeister) (Corduliidae: Synthemistinae)

Cordulephya pygmaea Selys (Corduliidae: Cordulephyinae)

Hemicordulia tau (Selys) (Corduliidae: Corduliinae)

Diaplacodes bipunctata (Brauer) (Libellulidae: Sympetrinae)

Nannophlebia risi Tillyard (Libellulidae: Tetrathemistinae)

APPENDIX 2

CHARACTER SET

Vein names and abbreviations follow O'FARRELL (1970). Abbreviations: C costa, Sc subcosta, R radius, M median vein, Cu cubitus, 1A anal vein, Ax antenodal, Px postnodal, N nodus, Sn subnodus, Pt pterostigma, Arc arcus, Dc discoidal cell. The names of main veins apply to the stem portion, the branches of R are numbered from the most anterior, the other branched veins are divided into anterior (A) and posterior (P) sectors.

The following variations and additions are made to O'Farrell's nomenclature: Vein Sc is identified as ScP, R1 as RA, the stem of R2-R4 as RP with major branching points T (proximal) and U (distal). The branches of RP are identified as RP1 (R2), RP2 (R3) and RP3 (R4+5). The "intercalated" veins IR3 and IR2 are labelled IT and IU respectively. MA is treated as M.

- (1) Pt in C-R1 space; absent (0), present (1)
- (2) Pt in RA-RP1 space; absent (0), present (1)
- (3) Pt length $\leq 4 \times$ width (0), $> 4 \times$ width (1)
- (4) Forward sloping (i.e., anterior distal, posterior proximal) crossvein bracing Pt in forewing; absent (0), present (1)
- (5) Backward sloping vein in RA-RP before Pt; absent (0), present (1)
- (6) Forward sloping crossvein bracing Pt in hindwing; absent (0), present (1)
- (7) Nodus (N) formed by ScP terminating sharply on C; absent (0), present (1)
- (8) N decidedly less than 1/2 wing length from base (1), otherwise (0)
- (9) N decidedly more than 1/2 wing length from base (1), otherwise (0)
- (10) Two or fewer antenodals (Ax) in costal space (0), 3 or more (1)
- (11) Two or fewer Ax in subcostal space basal of Sn (0), 3 or more (1)
- (12) Two or more Ax aligned (0), less than 2 (1)
- (13) More than 2 Ax aligned (1), otherwise (0)
- (14) More than 4 Ax aligned (1), otherwise (0)
- (15) One or more subcostal Ax before 1st complete Ax; absent (0), present (1)
- (16) Primary Ax distinguishable (0), primaries indistinguishable (1)
- (17) Distal subcostal Ax oblique to RA; absent (0), present and forming anterior Sn (1)
- (18) Oblique RA-RP vein at Sn; absent (0), present (complete Sn formation) (1)
- (19) Sn normal (0), misaligned with the RA-RP crossvein abnormally distal (1)
- (20) Postnodals (Px) in C-RA-RP1 field mostly unaligned (0), aligned (1)
- (21) Px mostly not aligned with RP1-RP2 crossveins (0), aligned (1)
- (22) Px mostly not aligned with RP2-RP3-M crossveins (0), aligned (1)
- (23) Px mostly not aligned with veins behind M (0), aligned (1)
- (24) No more than 1 basal costal Px before first radial Px (0), more than 1 (1)
- (25) M leaving radial stem vein before RP (0), RP+M leaving stem vein as a single unit (1)
- (26) M leaving stem vein at or after Ax2 (0), well before Ax2 (1)
- (27) M leaving stem vein at or before Ax2 (0), well after Ax2 (1)
- (28) RA-RP space not crossed proximal to end of ScP (0), crossed (1)
- (29) Median (basal) space open (0), crossed (1)
- (30) Longitudinal (+) vein in median space; absent (0), present (1)
- (31) Crossvein closing forewing Arc at or before divergence of M from RP; absent (0), present (1)
- (32) Crossvein closing fwg Arc after divergence of M from RP; absent (0), present (1)
- (33) Crossvein closing hindwing Arc at or before divergence of M from RP; absent (0), present (1)
- (34) Crossvein closing hwg Arc after divergence of M from RP; absent (0), present (1)

- (35) Sectors of Arc not confluent (0), confluent (1)
- (36) Strong M-CuP crossvein (Q) closing Dc distally; absent (0), present (1)
- (37) Fwg QM inner Dc angle $\gg 90$ deg. (1), otherwise (0)
- (38) Hwg QM inner Dc angle $\gg 90$ deg. (1), otherwise (0)
- (39) Fwg QM inner Dc angle $\ll 90$ deg. (1), otherwise (0)
- (40) Hwg QM inner Dc angle $\ll 90$ deg. (1), otherwise (0)
- (41) CuP lacking strong forward curve at or before position of Arc (0), with such a curve (1)
- (42) Fwg CuP more or less straight at Arc (0), turning backward (1)
- (43) Hwg CuP more or less straight at Arc (0), turning backward (1)
- (44) Fwg CuP not turning sharply back at mid Dc (0), turning sharply back (1)
- (45) Hwg CuP not turning sharply back at mid Dc (0), turning sharply back (1)
- (46) CuP more or less straight at Q (0), turning sharply fwd (1)
- (47) Strut S dividing fwg Dc into triangle and supertriangle; absent (0), present (1)
- (48) Strut S dividing hwg Dc into triangle and supertriangle; absent (0), present (1)
- (49) Other (weaker) crossveins in undivided Dc or in triangle; absent (0), present (1)
- (50) Other (weaker) crossveins in supertriangle; absent (0), present (1)
- (51) S joining M, costal side of triangle kinked (1), otherwise (0)
- (52) S joining Q, supertriangle four-sided (1), otherwise (0)
- (53) Crossveins in RP-M before distal end of Dc or supertriangle; absent (0), present (1)
- (54) First fork (T) of RP located at or after N (0), at least marginally before N (1)
- (55) First fork (T) of RP located well before N (1), otherwise (0)
- (56) First fork (T) of RP located well after N (1), otherwise (0)
- (57) T fork asymmetric, the anterior branch straight (1), otherwise (0)
- (58) T fork asymmetric, the posterior branch straight (1), otherwise (0)
- (59) Second fork (U) of RP located after N (0), at N (1)
- (60) U fork asymmetric, the anterior branch straight (1), otherwise (0)
- (61) IT located at or after N (0), at least marginally before N (1)
- (62) IT located well before N (1), otherwise (0)
- (63) Crossveins in RP-IT space proximal to N; absent (0), present (1)
- (64) IT strongly joined to RP1 (1), otherwise (0)
- (65) IT strongly joined to RP3 (1), otherwise (0)
- (66) Oblique vein (O) joining RP2-IT; absent (0), present (1)
- (67) RP1 unbranched (0), branched (1)
- (68) RP1-IU field not expanded (0), expanded (1), moderately wide (2)
- (69) IU-RP2 field not expanded (0), expanded (1)
- (70) RP2 unbranched (0), branched (1)
- (71) RP2 apparently stemming from IT (1), otherwise (0)
- (72) RP2-IT field not expanded (0), expanded (1)
- (73) IT unbranched (0), branched (1)
- (74) IT-RP3 field not expanded (0), expanded (1), moderately wide (2)
- (75) RP3 unbranched (0), branched (1)
- (76) RP3-M field not expanded (0), expanded (1), moderately wide (2), very wide (3)
- (77) M unbranched (0), branched (1)
- (78) M-CuP field not expanded distally (0), expanded (1), moderately wide (2), very wide (3), extremely wide (4)
- (79) CuP-1A field not expanded (0), expanded (1)
- (80) M-CuP field proximally narrow (0), 2 or more cells wide against vein Q (1)
- (81) CuP-1A field not constricted at Q (0), at least partly constricted (1)
- (82) CuP-1A field not or partly constricted at Q (0), 1A nearly meeting CuP at Q (1)
- (83) CuP of normal length (0), shortened distally and not extending far beyond Q (1)

- (84) 1A separate from wing border at base of wing (0), fused to wing border (1)
- (85) 1A separate from wing border at a point just short of Ac (0), basally fused to wing border (1)
- (86) 1A separate from wing border at points beyond Ac (0), basally fused to wing border (1)
- (87) 1A of normal length (0), shortened distally and not extending far beyond Q (1)
- (88) 1A normal or somewhat shortened distally (0), very short and not extending to Q (1)
- (89) 1A either normal or reduced but at some point separate from wing border (0), 1A entirely coincident with wing border (1)
- (90) Branch of fwg 1A running into CuP corner at S (subtriangle formation); absent (0), present (1)
- (91) Branch of hwg 1A running into CuP corner at S (subtriangle formation); absent (0), present (1)
- (92) Hwg 1A branches before Sq; absent (0), present (1)
- (93) 1A branches distal of Sq; absent (0), present (1)
- (94) Anal field distal of Sq undeveloped (0), 1-4 cells wide (1), more than 4 cells wide (2)
- (95) Hwg Anal loop; absent (0), present (1)
- (96) Hwg basal corner not angulated in male (0), angulated (1)