EVOLUTION, TAXONOMY, AND BIOGEOGRAPHY OF ANCIENT GONDWANIAN LIBELLULOIDES, WITH COMMENTS ON ANISOPTEROID EVOLUTION AND PHYLOGENETIC SYSTEMATICS (ANISOPTERA: LIBELLULOIDEA)*

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New phylogenetic systematic methodologies are presented and the terms 'neapomorphy', 'coapomorphy', 'exapomorphy' and 'apophyletic' introduced. Results are presented in sorted character state matrices which show the outcome of character state evaluation while depicting phylogenetic arrangement. Higher classification, phylogeny, and biogeography of Anisoptera are reviewed and keys provided for superfamilies and families. The pattern of anisopteroid neapomorphy supports the superfamily arrangement proposed by F.L. CARLE (1986, *Odonatologica* 15: 275--326), while indicating polyphyly for Cordulegasteroidea [sic] of F.C. FRASER (1957, *A reclassification of the order Odonata*, R. Zool. Soc NSW, Sydney) and both "Neanisoptera" and "Petaluroidea" of H.-K. PFAU (1991, *Adv. Odonatol.* 5: 109-141). Paraphyletic groupings include Aeschnidae [sic] of R.J. TILLYARD (1917, *The biology of dragonflies*, Cambridge Univ. Press), and Cordulegastroidea of D.A.L. DAVIES (1981, *Soc. int. odonatol. rapid Comm.* 3: 1-60). *Nothomacromia* nom.n. is proposed as a replacement for *Pseudomacromia* Carle & Wighton, 1990, nec. *Pseudomacromia* Kirby, 1890. Congruence between phylogenetic and biogeographic patterns indicates two or more distinct mesozoic utilizations of a trans-pangaeian montane dispersal route. Incorrect association of *Neopetalia* with austropetaliids for the past 137 years has obscured the gondwanian origin and subsequent radiation of non-cordulegastrid Libelluloidea, a process which began at least 140 million years ago on the now frozen continent of Antarctica. – Chlorogomphid evolution was largely influenced by unknown vicariant events related to the combined forces of mountain building and rapid drift of India toward the equator, coupled with a 40-60 million year insular isolation.

insular isolation. Classification is revised as follows: Chlorogomphidae: Chloro-
petaliinae subfam.n.: (Chloropetaliini trib. n.): *Chloropetalia* gen.n. [type *C. selysi*
Fraser]; – Chlorogomphinae comb. n.: (Eorogomphini trib. n.): *Eorogomphus* gen.n.
[type *O. preciosus* Fraser]; (Sinorogomphini trib. n.): *Sinorogomphus* gen.n. [type *C.
nasutus* Needham]; (Chlorogomphini comb. n.): *Neorogomphus* gen.n. [type *C. fraseri*
St. Quentin], *Indorogomphus* gen.n. [type *O. xanthoptera* Fraser], *Orogomphus* Selys,
Aurorachlorus gen.n. [type *C. papilio* Ris], *Chlorogomphus* Selys. – Early synthemistid
evolution was largely influenced by unknown vicariant events in Antarctica related to
the combined forces of mountain building and drift of Antarctica-Australia toward the
south pole, coupled with a 60 million year isolation. Resulting selective pressures
produced the largest set of congruent neapomorphy and exapomorphy known in the
Anisoptera. Classification is revised as follows: Synthemistidae: (Synthemiopsini
trib.n.): *Synthemiopsis* Tillyard; (Palaeosynthemistini trib.n.): *Palaeosynthemis* Förster,
Archaeosynthemis gen.n. [type: *S. leachii* Selys]; (Synthemistini comb.n.): *Synthemis*
Selys, *Parasynthemis* gen.n. [type *S. regina* Selys], *Calesynthemis* gen.n. [type *S.
miranda* Selys]; (Eusythemistini trib.n.): *Austrosynthemis* gen.n. [type: *S. cyanitincta*
Tillyard], *Choristhemis* Tillyard, *Eusynthemis* Förster.

INTRODUCTION

Currently only a modicum of agreement exists concerning anisopteran classifi-
cation. Disagreement is not primarily between so called "splitters and lumpers",
but is rather a result of different methodologies based on diverse perceptions con-
cerning the function of classifications. Phenetic and hybrid phenetic-phylogenetic,
based methodologies such as that utilized by TILLYARD & FRASER (1940) and
FRASER (1957) are inherently anthropogenic and allow paraphyletic and in the
former case polyphyletic groupings. The objective of phylogenetic systematics is
to determine phylogeny upon which taxonomy is based, a consequence is that
phenotypically similar groups may not be grouped together if obvious similarities
are due to plesiomorphy. Because phylogenetic keys, like phylogenetic classifica-
tions are inherently more stable and confer more information than artificial phenetic
constructs, the following descriptive phylogenetic keys are presented in place of
isolated descriptions.

Phylogenetic methodologies potentially offer tremendous predictive power, but
without careful character evaluation information content can be severely reduced.
Character weighting is then the crucial issue: in phenetic classification characters
are either weighted 0 if not recognized, and 1 if recognized, or greater depending
on how finely a "character" is split; in Hennigian phylogenetic classification char-
acters are weighted 0 if unrecognized or plesiomorphic, and 1 if apomorphic. How-
ever, in phylogenetic systematics as developed and utilized by myself, in addition
to plesiomorphy being weighted 0, apomorphy is considered to be either neapo-
morphic, coapomorphic, or exapomorphic, with relative weights 1, 0, and maximally
½, respectively. Categorization of apomorphy is required to eliminate false con-
gruence based on correlated characters (coapomorphy), and to minimize false
synapomorphy based on convergent losses (exapomorphy). Neapomorphy then,

represents a very small proportion of the total character states studied, in particular it represents a character (or correlated character set) representing a unique evolutionary solution to a specific set of selective pressures.

The objective of the new approach is to discover congruent neapomorphy upon which a classification comprising monophyletic groups is based, with groups ranked according to relative geologic age as determined from the geologic record and biogeographic vicariance. Determination of neapomorphy through the elimination of coapomorphy necessitates a keen understanding of function, as seemingly uncorrelated character states may be part of a single functional system. For example, loss of the male hind wing angulation and anal brace is associated with the loss of abdominal auricles, this has occurred three separate times in the Anisoptera (Tab I, apomorphy set 4), and presumably reflects a change in the method used to establish the copulatory position. Genuine congruent neapomorphy typically involves different systems, sexes, or life stages. For example, gomphid neapomorphy includes larval antennal segment 3 enlarged, larval proventriculus with rasplike lobes, adult head with postocellar ridge, adult palpal end hook apically spinelike, and male posterior hamuli engaging female sternum 9 with an anterior stroke.

HENNIG (1966) introduced the term paraphyletic to describe the class of nonmonophyletic taxa based on symplesiomorphy, but unfortunately his definition also applies to certain polyphyletic groups. A more direct approach is to describe the group whose elevation in rank results in the creation of a polyphyletic or paraphyletic group; here paraphyletic is limited to a group that includes a most recent common ancestor but not all of its descendants. For groups of relatively exaggerated taxonomic rank the term apophyletic is introduced. Apophyletic groups are typically based on obvious phenetic differences and ignorance of congruent neapomorphy, and although they are often monophyletic they are responsible for most of the controversy concerning anisopteroid classification. A classic apophyletic group is the "class" Aves which is thought to be part of the Dinosaur suborder Theropoda. In the present study apophyletic groups include *Choristhemis* Tillyard and *Chlorogomphus* Selys (if *Orogomphus* Selys is recognized).

The new methodlogy is not rigid, but because all tree topologies can be reduced to a pectinate series of monophyletic groups, a table of nested character state possibilities can be initially constructed. Homologous character state distributions are then tabulated with the order of taxonomic groups rearranging as examples of each character state pattern are discovered. Note that some patterns may not match the initial pectinate approximation and can be added if it is not desired to combine groups as for character set 9 of Table I. Ten or more taxonomic groups should be included so that the probability of a reversed topology is minimal; note that if only three groups are considered polarity is confounded. Polarity is not predetermined with fossil evidence, ontogeny, or out groups, but is an automatic outcome of nested congruent neapomorphy as long as the number of groups is greater than 3, but preferably greater than 10. While examples for each character state pattern are

discovered, apomophic character states are evaluated by determining if they are neamorphic, exapomorphic, or coapomorphic.

Careful character state evaluation generally eliminates the need to utilize parsimony analyses to determine the best topology from several likely incorrect possibilities, exceptions are situations involving excessive exapomorphy. Because the statistical robustness of nested congruent neapomorphy is so high, an estimated phylogeny will generally stand or fall based on character state evaluation; this is best presented in a sorted data matrix which not only shows the results of character state evaluation, but also depicts the estimated phylogeny. In the present paper neapomorphy is denoted by N, plesiomorphy by –, exapomorphy by X, and coapomorphy by C; lower case letters are used to indicate conditions within groups. In each apomorphy set neapomorphy is listed first with each neapomorphy followed by respective coapomorphy; exapomorphy is listed last.

Numerical evaluation can be achieved by simply adding neapomorphic character sets although the information content from possibly convergent character states is more difficult to discern. Apparent neapomorphic convergence often coincides with the letter n in the data matrices and typically involves poorly understood (10f, Tab. I), superficial (16c, Tab. I), or obviously nonhomologous characters (4c, Tab. I). Experienced systematists are actually quite adept at discerning homologous and nonhomologous similarity, but reinterpretation is always possible. Therefore, apparent neapomorphic convergence should be listed even though it is given no weight in an analysis. In contrast, the probability of exapomorphic convergence is always relatively high due to difficulties in distinguishing exapomorphic similarity, therefore, resulting noncongruent exapomorphic character patterns are expected and of little concern. However, the formula $1/(X+1)$, where X is the number of loss events, can be utilized to weight congruent exapomorphy sets or congruent neapomophy-exapomorphy sets; for example it is 1/5 for exapomoprhy set 14d of Table I, and 1/2 for neapomorphy-exapomorphy set 12g of Table I. The apomorphy score for Table I is as follows: apomorphy set 1 (3.0), 2 (7.0), 3 (5.5), 4 (4.3), 5 (6.0), 6 (1.8), 7 (6.0), 8 (4.8), 9 (2.0), 10 (6.5), 11 (7.3), 12 (5.8), 13 (5.3), 14 (3.7), 15 (8.0), 16 (2.5), 17 (4.0), 18 (9.7), 19 (1.3), 20 (4.0), 21 (1.5), 22 (5.0); total score = 107.0, average score = 4.9. Other arrangements of Table I are of course possible, but the added exapomorphy required to make observed neapomorphic character sets congruent significantly reduces the total score. Note that much coapomorphy has been removed from the tables to save space and that coapomorphic exapomorphy is sometimes listed with respective neapomorphy (e.g. Table I, character 5g).

KEY TO THE SUPERFAMILIES AND FAMILIES OF ANISOPTERA, EXCLUDING FAMILIES OF NON-CORDULEGASTRID LIBELLULOIDEA

1   Adult labium with palpal end hook as long as ligula, ligula entire; postfrons with postocellar ridge; supratriangles similar in shape and with anterior side concave posteriorly; posterior hamuli

engaging female sternum 9, apical hooks directed anteriorly; ovipositor reduced to fused progonocoxae and progonapophyses, metagonopodites at most represented by small sternal plates. Larval antennae 3 or 4 segmented, third segment more than ½ antennal length; second mandibular segment movable; mesotarsi 2-segmented; abdominal segments 4 or 5 to 6 with linear transverse muscles and anterolateral sternal apodemes; sclerotized proventricular lobes elongate--rasplike, with 8-20 scattered teeth .... Gomphoidea – **Gomphidae**

— Adult labium with palpal end hook shorter than ligula, ligula variable; postfrons without postocellar ridge; supratriangles either not similar in shape or with anterior side straight; posterior hamuli engaging female sternum 8, apical hooks directed posteriorly or medially; ovipositor complete or reduced, metagonopodites at least represented by small peglike structures. Larval antennae 6 to 8 segmented, third segment less than ½ antennal length; second mandibular segment not movable; mesotarsi 3-segmented; abdominal segments 4 and 5 with vestigial or phragmatic transverse abdominal muscles and without anterolateral apodemes; sclerotized proventricular lobes mound or toothlike, with 0-8 posteriorly clustered teeth 2

2 Adult compound eyes widely separated dorsally, anterodorsal surface of occiput trapezoidal; pterostigmata concave posteriorly and longer than distance between costal braces; ligula with wide medial cleft; male epiproct typically divaricate, and cerci strongly expanded distally; ovipositor complete and strongly upturned. Larval tibiae with apical borrowing hooks; terminalia forming dorsally directed vent; labial palps with robust dorsolateral spur at base of endhook; molar lobe with teeth; transverse abdominal muscles 4 and 5 vestigial; proventriculus with 8 sclerotized lobes each with 0-6 similar blunt teeth .... Petaluroidea – **Petaluridae**

— Adult compound eyes contiguous or approximate dorsally, anterodorsal surface of occiput triangular; pterostigmata not concave posteriorly, shorter than distance between costal braces; ligula with medial cleft variable; male epiproct typically quadrate or triangular, and cerci not strongly expanded distally; ovipositor variable, not upturned. Larval tibiae without apical burrowing hooks; terminalia not forming dorsally directed vent; labial palps without robust dorsolateral spur at base of endhook; molar lobe without teeth; transverse abdominal muscles 4 or 5 phragmatic or obsolete; proventriculus with 4 sclerotized lobes each with 2-8 sharp teeth, apical tooth largest 3

3 Adult pterostigmal brace thickened and oblique; anterior lamina with elongate medial cleft, anterior hamuli directed medially, posterior hamuli vestigial; median process of male abdominal segment 2 short L-shaped; ovipositor complete, suited for endophytic oviposition. Larval prementum flat, dorsal surface of labium without long premental and palpal setae, labrum not concealed by triangular labial palps, labial endhook distinctly longer than base of palp; epiproct typically bifurcate apically; proventriculus radially symmetrical, sclerotized lobes small-lobelike with 8 or fewer clustered teeth .... Aeshnoidea – 4

— Adult pterostigmal brace obsolete, (present in *Neopetalia*); anterior lamina without elongate medial cleft, anterior hamuli directed posteroventrally or absent, posterior hamuli well developed; median process of male abdominal segment 2 long J-shaped; ovipositor reduced, suited for exophytic oviposition. Larval prementum scooplike, dorsal surface of labium typically with long premental and palpal setae, labrum concealed by triangular labial palps, labial endhook distinctly shorter than base of palp; epiproct acuminate; proventriculus bilaterally symmetrical, sclerotized lobes large-toothlike, edged with 2-8 teeth .... Libelluloidea – 5

4 Adult wings with costal series of 5-8 reddish blotches; compound eyes approximate or meeting at point dorsally; abdomen without dorsal or lateral carinae, 7 or 8 often with lateral expansions; wings without planates; fore wing triangle with proximal side more than ½ anterior side; penis laterally exposed, prepuce well developed, segment 4 pendulous with huge paired flagellae directed posteroventrally. Larval abdominal segments 1-10 with lateral lobes; prementum slightly widened distally; labrum widened distally to ca width of prementum; ventrolateral occipital ridge massive; paraprocts shorter than ½ width of abdominal segment 9; femora dorsally excrescent; transverse abdominal muscles obsolete; body surface extensively granulate ... **Austropetaliidae**

— Adult wings without costal series of 5-8 reddish blotches; compound eyes meeting along dorsal

seam; abdomen with dorsal and lateral carinae, without lateral expansions; wings with planates; fore wing triangle with proximal side less than ½ anterior side; penis laterally concealed, prepuce obsolete, segment 4 swablike without huge paired flagellae directed posteroventrally. Larval abdominal segments 3-9 at most with lateral spines; prementum greatly widened distally; labrum ca. ½ width of prementum; ventrolateral occipital ridge low; paraprocts longer than ½ width of abdominal segment 9; femora dorsally smooth; transverse abdominal muscle 5 phragmatic, 6 linear; body surface not extensively granulate .... **Aeshnidae**

5   Adult with supplementary sector arising near bridge crossvein; paraglossal spines present; lateral clypeal lobes not inflated; occellar lobe vestigial; pterostigmata parallel sided, length typically ca. 8 times width; male protibiae with short apical keels and meso- and metatibiae with outer spines peglike; anterior hamuli large erect-foliate; progonopodites appressed into elongate gently tapered spade. Larval cerci vestigial, less than ½ midventral length of abdominal segment 10; vulvar lamina more than 6/10 length of sternum 9 .... **Cordulegastridae**

–   Adult without supplementary sector arising near bridge crossvein; paraglossal spines obsolete; lateral clypeal lobes inflated; ocellar lobe present; pterostigmata not parallel sided with length ca 8 times width; male without small protibial padlike keels and meso- and metatibial peglike spines; anterior hamuli vestigial or elongate-triangular with incurved end hook; progonopodites not appressed into elongate gently tapered spade. Larval cerci well developed, more than ½ midventral length of segment 10; vulvar lamina less than ½ length of sternum 9 ....:
.... **Non-cordulegastrid Libelluloidea**

KEY TO THE GENERA OF ANCIENT GONDWANIAN LIBELLULOIDES (NEOPETALIIDAE, CHLOROGOMPHIDAE, SYNTHEMISTIDAE AND GOMPHOMACROMIIDAE)

1   Adult with pterostigmal brace thickened and oblique; wings with costal series of 4 reddish blotches, apical blotch divided by yellowish orange pterostigmata; abdominal terga 5-8 with ventroapical tufts of long black hair; male tibial keels ca 1/3 length of protibiae and 1/5 length of meso- and metatibiae; anterior hamuli contiguous and L-shaped; female sternum 10 expanded into huge circular splash plate. Larval labial palpi bilobate with 5-6 irregular medial teeth; prementum with 2-6 vestigial setae; palpi with 1 short dorsomedial setae near base of palpal end hook; antennae 6--segmented, third segment more than twice length of second segment; antefrons moundlike; male epiproctal tubercle acuminate; vulvar lamina ca 1/3 length of sternum 9 ....
.... Neopetaliidae – *Neopetalia* Cowley

–   Adult with pterostigmal brace vestigial; wings without costal series of 4 reddish blotches; abdominal terga 5-8 without ventroapical tufts of long black hair; male tibial keels typically more than 1/3 length of protibiae and 1/5 length of meso- and metatibiae (obsolete in Libellulinae); anterior hamuli not contiguous or L-shaped; female sternum 10 without splash plate. Larval labial palpi not bilobate with 5-6 irregular medial teeth; prementum with 4-30 elongate setae; palpi with 2-8 elongate dorsomedial setae; antennae typically 7 segmented, third segment less than twice length of second segment; antefrons not moundlike; male epiproctal tubercle not acuminate; vulvar lamina not typically 1/3 length of sternum 9 2

2   Adult ligula longer than wide and with apical cleft; labial palps with well developed movable end hook and apical spine; sectors of the arculus separated at base; supratriangles slightly convex anteriorly; antenodal crossveins of hind wing not aligned, with two costal braces; subtriangular interspace dilated basally; anterior hamuli elongate, with interhamular spur. Larval labial palpi with elongate irregular medial teeth; ligula with glossal and paraglossal lobes; mesosternum without paracoxal lobes; metasternum with transverse sulci joined by medial sulcus; ventral proventricular sclerotized lobes without large subapical tooth, dorsal lobes without posteromedial edge strongly

inclined laterally; sternum 6 without anterolateral apodemes; epiproct apically needlelike .... Chlorogomphidae – 5

– Adult ligula wider than long and without apical cleft; labial palps with vestigial movable end hook and apical spine; sectors of the arculus fused basally; supratriangles strongly convex anteriorly; antenodal crossveins of hind wing mostly aligned or with 3 or more costal braces; subtriangular interspace not dilated basally; anterior hamuli short or obsolete, without interhamular spur. Larval labial palpi without elongate irregular medial teeth; ligula with distal margin entire; mesosternum with paracoxal lobes; metasternum with transverse sulci contiguous, medial sulcus obsolete; ventral proventricular sclerotized lobes with large subapical tooth, dorsal lobes with posteromedial edge strongly inclined laterally; sternum 6 with anterolateral apodemes; epiproct not apically needlelike 3

3 Adult median space with 1-5 crossveins; hind wings with 3-5 costal braces alternating with poorly aligned antenodals; wings with 3-10 cubital-anal crossveins; abdomen cylindrical, segments 3-6 typically more than 5 times as long as wide, male segment 7 cylindrical without well developed middorsal ridge or lateral carinae. Larval ligula represented by a medial triangular lobe; metasternum with transverse sulci meeting at point; wing pads divergent; hind femur ca 1.5 times length of front femur; abdomen typically 2.0-2.5 times as long as wide ..... Synthemistidae – 12

– Adult median space without crossveins; hind wings with antenodal crossveins aligned and progressively more bracelike proximally; wings with 1-4 cubital-anal crossveins; male abdomen triquetrous, at least on segments 7 and 8, segments 3-6 less than 5 times as long as wide, tergum 7 with well developed middorsal ridge or lateral carinae. Larval metasternum with transverse sulci fused; wing pads typically parallel; hind femur typically more than 1.6 times length of front femur; abdomen less than 2.1 times as long as wide 4

4 Anal loop elongate with gaff shorter than base; sectors of arculus diverging basally; male without genital lobe, male tergum 1 with ventrolateral hamulelike spines (obsolete in Pseudocordulia). Larval labial palpi without setae along medial margin; metasternum with transverse sulci fused at short seam; dorsal proventricular lobes not united by medial chutelike sclerotization; ventral proventricular lobes with posterior face ca as wide as that of dorsal lobes; ventral proventricular lobes with teeth separated by ca twice width of posterior face of dorsal lobes; lateral prothoracic lobes shelflike .... Gomphomacromiidae – 20

– Anal loop rounded or elongate with gaff longer than base; sectors of arculus often stalked; male with genital lobe and without hamulelike ventrolateral spines on segment 1. Larval labial palpi typically with setae along medial margin; metasternum with transverse sulci typically fused along long seam; dorsal proventricular lobes united by medial sclerotization; ventral proventricular lobes with posterior face ½, or less than as wide as that of dorsal lobes; ventral proventricular lobes typically with teeth separated by less than width of posterior face of dorsal lobes; lateral prothoracic lobes not shelflike .... macromiid-corduliid-libellulid complex

5 Dorsal mesanepisternal yellow stripes wedge shaped, wider dorsally; lateral mesanepisternal stripes absent; mesanepimeral yellow stripes well developed; metanepisternal stripes vestigial or absent; metanepimera with wide yellow stripe; antefrons slightly inflated dorsally, with dorsolateral carinae well developed; compound eyes separated by ca 1/6 width of medial ocellus in male, and by ca 1/3 width in female; male cerci dorsoventrally flattened, ca 3 times as long as wide, with outer edge evenly curved with midventral spine, and with inner apical tooth acute and directed posteromedially; anterior hamuli directed posteroventrally, without well developed posterobasal lobe; ventroapical penile lobes (cornua) elongate, more than 6 times as long as wide; vulvar lamina as long as wide with midventral keel. Larval ligula flattened with glossa and paraglossa fused into paired rounded medial lobes; palpal end hook with dorsal row of small setae; ventral proventricular teeth with scattered dorsal denticles; dorsal abdominal setae peglike; abdominal segment 9 without lateral carinae .... Chloropetaliinae subfam.n., type genus *Chloropetalia* gen.n., type species *Chlorogomphus selysi* Fraser; also includes *Orogomphus atkinsoni* Selys, *O. dyak* Laidlaw, and *C. olympicus* Fraser

– Dorsal mesanepisternal yellow stripes linear; lateral mesanepisternal yellow stripes well developed; mesanepimeral stripes narrow or absent; metanepisternal pale stripes well developed; metanepimeral stripes narrow or absent; antefrons strongly inflated dorsally, with dorsolateral carinae vestigial or absent; compound eyes separated by at least 1/3 width of medial ocellus in male, and by at least 2/3 width in female; male cerci not as above; anterior hamuli directed ventrally, with well developed posterobasal lobe; ventroapical penile lobes stout, less than 4 times as long as wide, vulvar lamina wider than long without midventral keel. Larval ligula[2] scooplike with glossa and paraglossa distinct; ventral proventricular teeth with denticles limited to tooth edges; dorsal abdominal setae hairlike; abdominal segment 9 with lateral carinae ....
.... Chlorogomphinae comb.n., type genus *Chlorogomphus* Selys – 6

6   Anterior half of mesanepimera and metanepimera with yellow stripe; labrum with submedial pale areas; male compound eyes separated by ca 2/5 width of median ocellus; male hind wing as long as abdominal segments 1-6, hind wing to abdominal length ratio of male greater than 1.40, that of female greater than 1.23; male cerci ca 2.5 times as long as wide, with outer edge abruptly curved subapically without midventral spine, and with inner apical tooth blunt and directed medially .... Eorogomphini trib.n., type genus *Eorogomphus* gen.n., type species *O. preciosus* Fraser; also includes *O. speciosus* Selys, *C. fernandi* Asahina, and *C. schmidti* Asahina

– Anterior half of mesanepimera without or with a vestigial yellow stripe, anterior half of metanepimera without yellow stripe; labrum predominantly brown or black; male compound eyes separated by at least 2/3 width of medial ocellus; male hind wing as long as abdominal segments 1-8 or longer, hind wing to abdominal length ratio of male less than 1.32, that of female less than 1.22; male cerci not as above 7

7   Dorsal mesanepisternal pale stripes dorsally expanded into transverse oval; meso- and metakatepisterna with yellow spots; abdominal tergum 3 more than twice as high basally as apically; female abdominal segments 3-7 subcylindrical, segment 4 more than 3 times as long as high; female abdominal segment 6 or 7 with paired apical yellow spots ca as long as wide; hind wing triangle with costal side longer than proximal side; hind wing to abdominal length ratio of female more than 1.13; first penile segment without medial groove; wings typically without opaque markings .... Sinorogomphini trib.n., type genus *Sinorogomphus* gen.n., type species *C. nasutus* Needham; also includes   *C. tunti* Needham, *C. infuscatus* Needham, *O. suzukii* Oguma, *C. kitawakii* Karube, and *C. urolobatus* Chen

– Dorsal mesanepisternal pale stripes not dorsally expanded into transverse oval; meso- and metakatepisterna brown or black; abdominal tergum 3 less than 1.7 times as high basally as apically in male, less than 1.5 times in female; female abdominal segments 3-7 laterally compressed, segment 4 less than 3 times as long as high; female abdominal segment 6 and 7 with paired apical yellow spots less than 1/2 as long as wide or obsolete; hind wing triangle with costal side shorter than proximal side or subequal in male; hind wing to abdominal length ratio of female less than 1.13; first penile segment with medial groove; wings typically with apical or basal opaque markings .... Chlorogomphini comb.n. – 8

8   Labrum with U-shaped central greenish yellow spot; lateral mesanepisternal yellow stripes narrow, only slightly wider than dorsal mesanepisternal yellow stripes; basal abdominal segments with broad lateral oblique yellow stripe extending from ventral edge of metanepimera to antecostal suture of segment 3; abdominal tergum 7 with paired basal yellow spots ca as long as wide; male hind wing to abdominal length ratio 1.20-1.26; male with bases of abdominal segments 8 and 9 constricted basally; cerci reduced, in female ca 1/2 length of tergum 10, in male with blunt basolateral spine; male epiproct strongly upcurved apically .... *Neorogomphus* gen.n.,

[2] Larval characters based on FRASER's (1929) supposed larva of *C. campioni*. However, larval characters described by MATSUKI, et al. (1995) for *C. brunneus* do not agree. If Fraser's larvae are cordulegastrid, listed characters are likely diagnostic for Chlorogomphidae.

type species *C. fraseri* St. Quentin; also includes *C. auratus* Martin, *C. arooni* Asahina, and *C. vietnamensis* Asahina

– Labrum black without U-shaped central greenish yellow spot; lateral mesanepisternal yellow stripes wide, at least 4 times as wide as dorsal mesanepisternal yellow stripes at midlength; basal abdominal segments with broad lateral oblique yellow stripe extending from ventral edge of metanepimera to apex of segment 2 only; abdominal tergum 7 without paired basal yellow spots ca as long as wide; male hind wing to abdominal length ratio 0.95-1.19; male with bases of abdominal segments 8 and 9 constricted basally; cerci well developed, in female ca 2/3 length of tergum 10, in male without blunt basolateral spine; male epiproct not strongly upcurved apically 9

9 Dorsal and lateral mesanepisternal pale stripes confluent dorsally; antefrons bilobate, without well developed ventrolateral carinae; male hind wing triangle with proximal side subequal to costal side; male abdominal segment 2 longer than high; abdomen to hind wing length ratio of male ca 1.16, of female ca 0.97; anterior hamuli directed ventrally, end hooks directed posteromedially, separated apically by ca length of hamuli; fourth penile segment elongate with lateral keels forming acute apex; anterior lamina slightly bilobate; male cerci with lateral spine subequal to apical spine and located just beyond midlength; male epiproct with deep wide U--shaped apical notch .... *Indorogomphus* gen.n., type species *O. xanthoptera* Fraser; also includes *O. campioni* Fraser

– Dorsal and lateral mesanepisternal pale stripes not confluent dorsally; antefrons flattened, with well developed ventrolateral carinae; male hind wing triangle with proximal side longer than costal side in male; male abdominal segment 2 shorter than high; abdomen to hind wing length ratio of male and female at most 12% different; anterior hamuli directed posterolaterally, end hooks directed medially, separated apically by more than length of hamuli; fourth penile segment short with lateral keels forming obtusely rounded apex; anterior lamina strongly bilobate; male cerci with lateral spine larger than apical spine and located subapically, spines occasionally obsolete; male epiproct without deep wide U-shaped apical notch 10

10 Metasternum black medially; posterior third of metanepimera above ventrolateral carinae predominantly yellow; submedial apical abdominal spots increasing in size on segment 7; male abdominal segments 4-7 cylindrical; male hind wing to abdominal length ratio more than 1.08; male epiproct with small apical notch and apically truncate rami; female occiput not depressed; female abdominal tergum 3 with ventrolateral stripe not confluent with apical ring; female abdominal segments 5 and 6 more than two times as long as high .... *Orogomphus* Selys, type species *O. splendidus* Selys; also includes *C. brevistigma* Oguma, *C. okinawensis* Ishida, *C. brunneus* Oguma, *C. costalis* Asahina, *C. keramensis* Asahina, *C. iriomotensis* Ishida, and *C. risi* Chen

– Metasternum yellow medially; posterior third of metanepimera above ventrolateral carinae narrowly yellow; submedial apical abdominal spots decreasing in size on segment 7; male abdominal segments 4-7 triquetrous; male hind wing to abdominal length ratio less than 1.08; male epiproct not as above; female occiput depressed; female abdominal tergum 3 with ventrolateral stripe confluent with apical ring; female abdominal segments 5 and 6 less than two times as long as high 11

11 Anal loop with 28-35 cells; fore and hind wings with extensive basal opaque markings; male with posterobasal wing margin slightly angulate; male and female abdomen to hind wing length ratio dissimilar; female abdominal segment 4 ca 1.5 times as long as high; lateral mesanepisternal yellow stripes obsolete; male cerci triangular, basally expanded, with well developed lateral and subapical spines; male epiproct divaricate with shallow U-shaped apical notch ....
.... *Aurorachlorus* gen.n., type species *C. papilio* Ris

– Anal loop with 8-17 cells; male wings and female fore wings without basal opaque markings; male with posterobasal wing margin evenly rounded; male and female abdomen to hind wing

length ratio similar; female abdominal segment 4 ca 2.0 times as long as high; lateral mesanepisternal yellow stripes well developed; male cerci elongate, laterally compressed, without lateral or subapical spines; male epiproct narrowed subapically with divaricate apices, and with V-shaped apical notch .... *Chlorogomphus,* type species *C. magnificus* Selys; also includes *C. mortoni* Fraser

12   Wings with spots at nodus; fore wing arculus with posterior portion ca 1/3 its length; hind wing triangle and anal loop elongate, base of anal loop, distal side of triangle, and gaff subequal; proximal side of hind wing triangle perpendicular to longitudinal veins, distal side more than 1.5 times length of proximal side; male epiproct with wide V-shaped apical notch; prepuce ca as long as base of penile segment 3; ovipositor knoblike apically ....
.... Synthemiopsini trib.n., type genus *Synthemiopsis,* monotypic *S. gomphomacromioides* Tillyard

–   Wings without spots at nodus; fore wing arculus with posterior portion less than 1/3 its length; hind wing triangle and anal loop not elongate, base of anal loop, distal side of triangle, and gaff unequal; proximal side of hind wing triangle oblique to longitudinal veins, distal side less than 1.5 times length of proximal side; male epiproct without wide V-shaped apical notch; prepuce at most 1/3 as long as base of penile segment 3; ovipositor not knoblike apically 13

13   Midbasal space typically with 1 crossvein; posterior hamuli of boxing glove type with denticles at apex of thumb and along knuckles; abdominal segment 1 of male with spinose ventrolateral spurs; penile segment 2 gently curved basally and longer than segment 1; penile segment 3 at least twice as long as wide; ovipositor extended beyond cerci; larvae as far as known with trilobate labial palps .... Palaeosynthemistini trib.n., type genus *Palaeosynthemis* Förster – 14

–   Midbasal space typically with 2-5 crossveins; posterior hamuli not of boxing glove type with denticles at apex of thumb and along knuckles; abdominal segment 1 of male without spinose ventrolateral spurs; penile segment 2 abruptly bent basally and shorter than segment 1; penile segment three less than twice as long as wide; ovipositor not extended beyond cerci, reduced to vulvar laminae; larval labial palps with medial margin entire or with small rounded teeth.... 15

14   Pterostigmata as long as hind wing supratriangle; fore wing triangle distant from arculus by less than length of proximal side of triangle; abdominal segments 3-8 with paired submedian oval spots subequal and divided by antecostal suture; penile filament shorter than penile segment 1 .... *Archaeosynthemis* gen.n., type species *S. leachii* Selys; also includes *S. macrostigma* Selys, and *S. spiniger* Tillyard

–   Pterostigmata shorter than hind wing supratriangle; fore wing triangle distant from arculus by more than length of proximal side of triangle; abdominal segments 3-7 with transverse dashes along antecostal suture; penile filament longer than penile segment 1 ....
....*Palaeosynthemis* Förster, type species *P. primigenia* Förster; also includes *S. alecto* Lieftinck, *S. cervula* Lieftinck, *S. feronia* Lieftinck, *S. cyrene* Lieftinck, *S. evelynae* Lieftinck, *S. gracilenta* Lieftinck, *S. wollastoni* Campion, and *S. kimminsi* Lieftinck

15   Hind wing with 3-5 midbasal crossveins; posterior hamuli without posteromedially directed end hook, hamuli clasping vulvar lamina with ventro-dorsal action; base of penile cornua expanded into medial septumlike plate; penile filament directed dorsally at base; male cerci without basolateral spine; vulvar lamina bilobate and at least 1/2 as long as segment 10 ....
.... Synthemistini comb.n., type genus *Synthemis* Selys – 16

–   Hind wing with 1-2 midbasal crossveins; posterior hamuli with posteromedially directed end hook, hamuli not clasping vulvar lamina with ventro-dorsal action; base of penile cornua not expanded into medial septumlike plate; penile filament directed posteriorly at base; male cerci with basolateral spine; vulvar lamina vestigial or appressed and shorter than 1/2 as long as segment 10 .... Eusynthemistini trib.n., type genus *Eusynthemis* Förster – 18

16   Sectors of the arculus arising at 1/4-1/3 length of arculus; posterior hamuli chisellike with apical transverse row of denticles; ventrolateral margin of male abdominal tergum 2 with coarse setal

brush; male tergum 10 with laterally compressed posteriorly directed spine; male epiproct parallel sided and apically truncate; vulvar lamina extended beyond abdominal segment 9 ....
.... *Synthemis* **Selys,**
type species *E. eustalaca* Burmeister; also includes *S. tasmanica* Tillyard

– Sectors of the arculus arising at ca 1/5 length of arculus; posterior hamuli with posteriorly directed spine, without apical transverse row of denticles; ventrolateral margin of male abdominal tergum 2 without coarse setal brush; male tergum 10 without laterally compressed posteriorly directed spine; male epiproct triangular; vulvar lamina bilobate and ca 1/2 as long as sternum 9 17

17 Thorax laterally predominantly pale; abdominal segment 7 predominantly yellow dorsally; posterior hamuli stublike with lateral groove and posteriorly directed spine; penile cornua recurved thick-hooklike with medial plates displaced posteriorly on cornua; penile filament not apically recurved; vulvar lamina apically flattened with U-shaped medial notch as wide as long, and prominent midbasal swelling; larvae with 7 lateral palpal setae .... *Parasynthemis* **gen.n.,** type species *S. regina* Selys, monotypic

– Thorax laterally predominantly dark; abdominal segment 7 predominantly dark dorsally; posterior hamuli falcate, posteriorly tapered to fingerlike apices; penile cornua thin and erect; penile filament apically recurved; vulvar lamina inflated, without U-shaped medial notch as wide as long or prominent midbasal swelling; larvae with 2-4 lateral palpal setae ....
.... *Calesynthemis* **gen.n.,** type species, *S. miranda* Selys; also includes *S. campioni* Lieftinck, *S. montaguei* Campion, *S. serendipita* Winstanley, *S. flexicauda* Campion, *S. fenella* Campion, and *S. ariadne* Lieftinck

18 Midbasal space typically with 1 crossvein; male epiproct less than 2/3 length of cerci; cerci undulate, longer than combined length of segments 9 and 10, down curved basally, and with basolateral spines lobelike; penile segment 1 erect moundlike; penile segment 2 without ventrobasal lobes or U-shaped medial notch; penile cornua erect thin forklike; penile filament longer than penile segment 2; female sternum 8 not produced ventrally; vulvar lamina ca 1/5 length of sternum 9 without paired medial spurs .... *Austrosynthemis* **gen.n.,** type species *S. cyanitincta* Tillyard; also includes *S. claviculata* Tillyard, and *S. ofarrelli* Theischinger & Watson

– Midbasal space with 2-3 crossveins; male epiproct more than 2/3 length of cerci; cerci straight, shorter than combined length of segments 9 and 10, not down curved basally, and with basolateral spines spinelike; penile segment 1 not erect moundlike; penile segment 2 with ventrobasal lobes forming U-shaped medial notch; penile cornua not erect thin forklike; penile filament shorter than penile segment 2; female sternum 8 produced ventrally; vulvar lamina ca 1/10 length of sternum 9 and with paired medial spurs 19

19 Antefrons narrower than distance from base of labrum to top of antefrons; membranule vestigial; penile cornua fused into erect finlike keel; penile segment 4 with lateral keels; penile filament shorter than penile segment 3; male cerci nearly straight, slightly shorter than abdominal segments 9 and 10 combined, and with rounded apices; epiproct triangular, ca twice as long as wide and 7/10 length of cerci; sternum 8 produced to apex of abdominal segment 9, vulvar lamina represented by paired posteriorly directed lobes .... *Choristhemis* **Tillyard,** type species *S. flavoterminata* Martin; also includes *S. olivei* Tillyard, and *C. barbarae* Moulds

– Antefrons wider than distance from base of labrum to top of antefrons; membranule well developed; penile cornua with thick stem and slightly bifoliate apex; penile segment 4 without lateral keels; penile filament longer than penile segment 3; male cerci incurvate, slightly longer than abdominal segment 9, and with pointed apices; epiproct quadrate, ca 1.5 times as long as wide and 9/10 length of cerci; sternum 8 not produced posteriorly; vulvar lamina with paired erect spurs .... *Eusynthemis* **Förster,** type species *S. brevistyla* Selys; also includes *E. deniseae* Theischinger, *E. frontalis* Lieftinck, *S. guttata* Selys, *S. nigra* Tillyard, and *S. virgula* Selys

20 Wings with costal brace at arculus; fore wing triangle with anterior side longer than proximal side; hind wing with second Cu-A crossvein distal to arculus; male mesotibial keels well developed; posterior hamuli with posterior lobe erect-chisellike; female sterna 9 with medial carina and 10 with lateral carinae. Larvae with depressed lateral prothoracic shelf .... *Pseudocordulia* Tillyard
– Wings without costal brace at arculus; fore wing triangle with anterior side shorter than proximal side; hind wing with second Cu-A crossvein proximal to arculus; male mesotibial keels absent; posterior hamuli with posterior lobe directed posteriorly and rounded; female sterna 9 and 10 without carinae. Larvae with erect lateral prothoracic shelf 21
21 Pterostigmata more than 4 times as long as wide; hind wing triangle with costal side ca 1.5 times length of proximal side; anal triangle less than twice as long as wide at base; posterior hamuli with thumb erect-hooklike; male epiproct ca 1.7 times as long as wide; ovipositor obsolete, metagonapophyses nipplelike fused to sternum 9. Larval labial palpi with ca 6 small medial teeth .... *Archaeophya* Fraser
– Pterostigmata less than 3 times as long as wide; hind wing triangle with costal side ca 1.3 times length of proximal side; anal triangle more than twice as long as wide at base; posterior hamuli with thumb appressed; male epiproct ca. 1.3 times as long as wide; ovipositor with progonapophyses extended beyond cerci, metagonapophyses straplike. Larval labial palpi with 3 large medial teeth .... *Gomphomacromia* Brauer

DISCUSSION

THE PANGAEIAN ANISOPTERAN RADIATION

Anisoptera probably originated after the great Permian-Triassic extinction as evidenced by the diverse array of anisopteroids existing by the Jurassic (CARLE, 1982a). Repeated extinction events have undoubtedly trimmed palaeopteran evolution to favor K selected inhabitants of the homothermal environments and detritivore based ecosystems of seepages and small streams (CARLE, 1982b). During stable periods lentic habitats have been reinvaded with the relaxation of selective pressures leading to bewildering arrays of morphological diversity typified by considerable homoplasy. Dragonflies of most extant anisopteran families are predominantly obligate inhabitants of streams or seepage areas; extant anisopteroid families including groups which have independently colonized lentic habitats are Gomphidae, Aeshnidae, and the macromiid-corduliid-libellulid (MCL) complex. Unfortunately, small stream inhabitants are unlikely to become fossilized due to relatively low vagility, small population sizes, and the high energy nature of streams, rendering odonate fossil assemblages biased toward the bizarre evolutionary dead ends of R selected lentic communities (CARLE, 1982a, 1982b). Fortunately, many anisopteran inhabitants of seepages and small streams have persisted to the present, perhaps representing the most outstanding assemblages of living fossils known.

Extant anisopteran superfamilies (sensu CARLE, 1986) were well established before the break up of Pangaea as evidenced by the distribution of montane and temperate lotic Anisoptera and associated communities. Dispersal of these groups was facilitated by the trans-pangaeian mountain system (Fig. 1), with subsidence
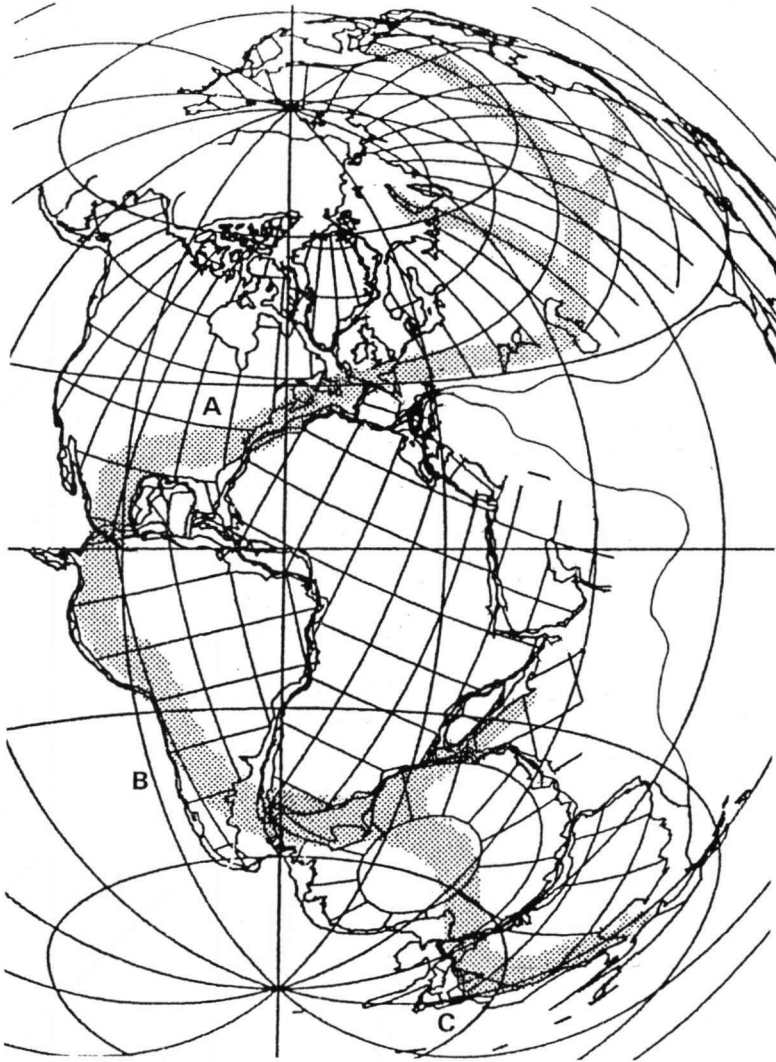
Fig. 1. Paleocontinental map for Early Jurassic (ca 180 million years ago) modified from SMITH & BRIDEN (1977), shaded areas indicate likely location of trans-pangaeian mountain system: (A) North American refugium; – (B) South American refugium; – (C) Tasmanian refugium.

resulting in contemporary northern-southern hemisphere vicariant distributions of ancient lotic Anisoptera. Repeated north-south congruences with early anisopteran phylogeny (Tab. I), indicate that the trans-pangaeian montane dispersal route was persistent yet tenuous. Utilization of this dispersal route varied among anisopteran superfamilies and may be involved in the origin of Aeshnoidea and Libelluloidea

(CARLE, 1983). During the early Mesozoic the Appalachian mountains were situated at the equator with climatological conditions perhaps similar to the mountains of the west African rift system of today. Therefore, it is not unexpected that three anisopteran superfamilies have their most archaic extant genera endemic to eastern North America; these are *Hagenius, Tachopteryx,* and *Zoraena* (CARLE, 1983, 1986). The fourth superfamily has as its most archaic genus the Tasmanian endemic *Archipetalia*, however, the most archaic aeshnid genus *Gomphaeschna*, is again an eastern North American endemic.

It is evident from the sorted character matrix for anisopteran families (Tab. I) that the "Cordulegastroidea" of DAVIES (1981) is paraphyletic, and that the "Neanisoptera" and "Petaluroidea" of PFAU (1991) are polyphyletic. Clearly, the weakest grouping in the present analysis is proposed monophyly for non-gomphid Anisoptera, it is supported by the moundlike denticulate proventricular lobes (6a and 6b), loss of anterolateral apodemes on segments 4 and 5 (however, presence of these apodemes may represent a gomphid neapomorphy), and loss in articulation of the second molar segment (note its independent loss in Epiophlebiidae, suggesting that its loss in Petaluridae might also be independent). If two or more neapomorphies are discovered for non-petaluroid Anisoptera, position reversal of Gomphoidea and Petaluroidea would be required.

Gomphoid monophyly is supported by apomorphy set 5. Supposed affinity between Gomphidae and the macromiid-corduliid-libellulid complex based on reduction of the ovipositor is extremely doubtful not only because of phylogenetic remoteness revealed in the nested pattern of neapomorphy (Tab. I), but because it is based on exapomorphy in which the actual losses are not equivalent. In Gomphoidea the vulvar lamina is composed of fused progonocoxae and progonapophyses, and the metagonopodites are plesiotypically represented by paired sternites which are hooked by the posterior hamuli during copulation. In Libelluloidea the progonocoxae are not apparent and the progonapophyses are plesiotypically elongate, and the metagonopodites are strap- or rodlike and apparently have a tactile function related to egg extrusion. Various developments of the anisopteroid postfrons are superficially similar, however, development of the gomphoid postocellar ridge is related to the tandem grip, where as development of the interocellar ridge of *Epiophlebia* and the intraocellar lobe of aeshnoids and libelluloids is apparently related to differential shading of ocelli. Fossorial larval concealment is also a similarity between Gomphoidea and at least ancient Libelluloidea, but gomphoid specializations (5a, 5b, and 5e) are unique and arose in a different manner. Early Gomphidae likely concealed themselves beneath the decomposing leaves and other detrital material of pool areas, and utilized the antennae to elevate the substrate just before the labial strike as in extant Hageniinae (pers. obs.). The wide third antennal segment and distal antennal atrophy, rasplike proventricular lobes, and reduced tarsal segments were evidently suitable preadaptations to a fossorial mode of life. Exophytic oviposition and larval concealment have enabled Gomphoidea to re-

peatedly invade lentic habitats, and not surprisingly, Gomphoidea are well represented throughout the Jurassic fossil record. The most rheophilic of temperate gomphoids are the octogomphines, which include the Octogomphini and Trigomphini of the northern hemisphere and the Hemigomphini of southwestern South America and Australia (CARLE & COOK, 1984; CARLE, 1986).

Petaluroid monophyly is supported by apomorphy set 7. Most petaluroid neapomorphy is related to construction and use of a semi-terrestrial larval retreat, except that the use of the dorsobasal end hook spur is not understood. Adult neapomorphy includes the spatulate palpal end hooks, elongate pterostigmata, and upturned ovipositor which is likely correlated with oviposition conditions in the larval habitat. At least one fossil petalurid is known from the Jurassic of Europe (*Protolindenia wittei*). Subsidence of the trans-pangaeian dispersal route split Petaluridae into two monophyletic groups, the northern Tachopteryginae, and the southern Petalurinae. The most ancient representatives of these subfamilies inhabit the northern and southern remnants of the dispersal route, *Phenes* in Chile, and *Tachopteryx* in eastern North America. Although petaluroid seeps occur most abundantly along mountain ranges and fall lines, unlike octogomphines petaluroids are able to colonize isolated lowland habitats. Therefore, the probable flat topography of proto New Zealand could explain the occurrence of *Uropetala* and the absence of octogomphines on these islands.

Monophyly for Aeshnoidea + Libelluloidea is supported by apomorphy set 8. Three fully congruent neapomorphy sets are listed, although shape of the male epiproct is possibly correlated with dorsal development of the compound eyes. The proventricular lobes are toothlike, although those of Libelluloidea are much larger and more specialized. The loss of teeth on the second molar segment is of course an exapomorphy, but it is congruent with listed neapomorphy suggesting that convergent losses are not involved. Evolution of the transverse abdominal muscles is not certain because of apparent losses and specializations in several families. Losses in the Petaluridae and Austropetaliidae are possibly related to semi-terrestrial larval habitats which do not require jet propulsion. Here it is assumed that the similar elongate transverse abdominal muscles of segments 4-6 in Gomphoidea are serially homologous and represent the plesiotypic state. The loss of muscles 4 and 5 in petaluroids is considered an independent exapomorphy. However, it is not known if these muscles were elongate or phragmatic (barrierlike), if phragmatic apomorphy 8f would need to be changed to 6e, and would add support to non-gomphoid monophyly. Cordulegastrids apparently have both muscles 4 and 5 phragmatic and this is apparently the plesiotypic condition for Aeshnoidea + Libelluloidea. The loss of muscles 4-6 in austropetaliids is considered an independent exapomorphy. Additional losses include the absence of muscle 4 in Aeshnidae, and the loss of muscle 5 in later Libelluloidea. The Austropetaliidae are the most plesiotypic members of this group and are limited to Chile, Tasmania, and eastern Australia, again suggesting north-south vicariance, in this instance between ancient Petaluroidea

(i.e. *Tachopteryx*) and ancient Aeshnoidea + Libelluloidea.

Aeshnoid monophyly is supported by apomorphy set 9, and is primarily based on specializations of the secondary genitalia, although additional larval specializations such as the characteristic trapezoidal head shape are not listed. Perhaps the most prominent specialization is the anterior splitterlike development of the ligula (i.e. the homologue of the zygopteran penis). Most of these genitalic specializations are likely correlated with the heavily musculated ovipositor which is designed to place eggs deeply into hard substrates. However, PFAU (1991) considered them plesiomorphic and placed all non-aeshnid Anisoptera in a newly created group the "Neanisoptera". Monophyly for Neanisoptera was based on a single supposed apomorphy, medial fusion of the ventral penile groove of segment 3. The penile groove is evident in petaluroids and plesiotypic libelluloids, but these groups lack the open basal slit and associated lateral ridges of austropetalids and plesiotypic aeshnids. The basal slit and lateral ridges match the uniquely shortened L-shaped aeshnoid ligula and are therefore likely coapomorphic. Petaluroids and plesiotypic libelluloids have an elongate ligula similar to that of Zygoptera perhaps representing the plesiotypic anisopteroid condition. An alternate scenario to that proposed by Pfau is realized if reduction or loss of an original biphasic sperm pump is initially directed by expansion of the apical erectile system to improve sperm competitiveness and subsequently directed by utilization of the apical erectile system and vagina as a highly efficient secondary sperm pump. Replacement of the original method of sperm removal (which apparently relied upon washing and swamping of previously deposited sperm) with an erectile removal system based on physical exclusion has apparently occurred independently in Aeshnoidea and Libelluloidea.

In Aeshnidae replacement of the original sperm removal method has led to the loss of both the primary sperm pump and apical sperm tube. The plesiotypic *Gomphaeschna* exemplifies the first step in this transition, exhibiting a highly specialized raised opening in the proximal half of the third penile segment; reduction in this apomorphic feature and third penile segment in later Aeshnidae led PFAU (1991) to incorrectly consider this the plesiotypic anisopteroid condition. However, austropetaliid Aeshnoidea retain the prepuce, which may be used to rock the hinged fourth segment (apical penile flagellae of Aeshnoidea and the MCL complex are probably derived from the articulated penile cornua of plesiotypic Anisoptera) forward during the erectile phase aiding in the aspiration of sperm; distal migration of sperm may occur due to favorable pressure differentials during the deflationary phase as in Libellulidae. In Macromiidae the prepuce and hinged fourth segment are analogous to that of austropetaliids, however, the primary sperm pump is not lost. In the Libellulidae the favorable pressure differential created by elastic collapse of the seminal chamber and hydraulic deflation of the fourth penile segment leads to highly efficient copulation as evidenced by the 3-10 second copulation period of various Libellulinae. Although these conclusions are speculative they seem highly probable and are at least consistent with listed congruent

neapomorphy. Monophyly for both Austropetaliidae and Aeshnidae is well supported by the numerous neapomorphies listed in Table I, and North-South vicariance is again evident with the plesiotypic *Gomphaeschna*, restricted to eastern North America, and austropetaliids, restricted to the Southern Hemisphere.

Libelluloid monophyly is supported by apomorphy set 12, and is primarily based on specialization of the larval labium. Unlike larval Gomphoidea which seek prey within the bottom substrates, or larval Aeshnoidea which stalk their prey, larvae of plesiotypic libelluloids utilize their legs to kick material out from under the body and up over the abdomen and thorax so that only the eyes protrude above the bottom, from where they lie and wait for prey within the water column (pers. obs.). The labium is scoop shaped with raptorial setae and triangular labial palpi. Medially the labial palpi are plesiotypically trilobate with ca three elongate teeth per lobe; this may represent a triplication of the original zygopteroid condition. In addition the proventriculus is no longer radially symmetrical and the lobes are large toothlike with denticles arranged serially along posterior edges. The ovipositor is modified for exophytic oviposition with the metagonapophyses at least nipplelike. The most ancient Libelluloidea are the cordulegastrids which are restricted to the northern hemisphere with their most plesiotypic genus, *Zoraena* endemic to eastern North America (CARLE, 1983).

Cordulegastrid monophyly is supported by apomorphy set 13, and is primarily based on adult specializations. The wings are unique in possessing a supplementary sector or branch which arises near the bridge crossvein, and the male legs are also unique in that the meso- and metatibiae have the outer spines peglike; a characteristic correlated to a reduction of these spines in all Anisoptera and likely related to establishment of the copulatory position in flight (CARLE, 1982c). Male protibiae also have small apical pads which are apparently derived from the intersegmental membrane; these pads are apparently homologous with the tibial keels of other Libelluloidea, but not with subapical protibial pads of various Gomphidae. The Cordulegasteroidea [sic] of TILLYARD & FRASER (1940) is paraphyletic based on nested congruent neapomorphy listed in Tables I and II. The Cordulegastroidea could be made monophyletic by limiting the group to the Cordulegastridae, however, the intermediate position of Neopetaliidae and lack of cordulegastrids in the southern hemisphere suggest that a restricted Libelluloidea would be considerably less ancient than other anisopteran superfamilies. Retaining Cordulegastridae within the Libelluloidea results in similar biogeographical patterns within anisopteran superfamilies. Additional cordulegastrid neapomorphy includes the elongate spadelike ovipositor which FRASER (1957) thought supported an affinity with extinct Aeschnidiidae. However, the revised Cordulegasteroidea [sic] of FRASER (1957) is polyphyletic due to the inclusion of the Aeschnidiidae which CARLE (1982a) and CARLE & WIGHTON (1990) considered an extinct lentic adapted sister group to extant Anisoptera; true fossil Cordulegastridae remain unknown. The unique distal placement of the discal brace and unique fossil larvae tentatively associated with this group, (i.e. *Nothomacromia* Carle

nom. nov. and Nothomacromiidae nom. nov. for *Pseudomacromia* Carle & Wighton, 1990, nec. *Pseudomacromia* Kirby, 1890), does not support a phylogenetic position near the Cordulegastridae. The North-South vicariance pattern between Austropetaliidae and Aeshnidae (i.e. *Gomphaeschna*) is mirrored by the relationship between Cordulegastridae and early non-cordulegastrid Libelluloidea. However, in the latter case phylogenetic polarity is reversed; *Zoraena* is endemic to eastern North America, and the most plesiotypic non-cordulegastrid libelluloid, *Neopetalia*, is endemic to Chile.

In summary, the pattern of anisopteroid neapomorphy supports the superfamily arrangement proposed by CARLE (1986), while showing the "Neanisoptera" of PFAU (1991) to be polyphyletic. Although larval and adult Gomphoidea are quite specialized, fossil evidence and biogeography of Gomphoidea, and neapomorphy of non-gomphoid Anisoptera indicate that gomphoid specializations occurred during the early Mesozoic; Gomphoidea representing the sister group to remaining extant Anisoptera. Petaluroidea larvae and adults are also quite specialized and neapomorphy for Aeshnoidea + Libelluloidea is substantial, including both larval and adult characters. Aeshnoidea are relatively unspecialized with monophyly supported by only two listed neapomorphies. Obvious plesiomorphy apparently explains repeated incorrect phylogenetic placement of Aeshnidae. Libelluloidea is distinguished by amazing larval specializations, but in the adult only by unique reductions in the ovipositor and possible presence of male protibial "keels". Not surprisingly adult male Austropetaliidae and Cordulegastridae appear quite similar, indeed the austropetaliids had been placed within the Neopetaliidae until recently (CARLE & LOUTON, 1994). Evolution of the libelluloid larval type led to great stability in larval evolution of early libelluloid families where most neapomorphy is limited to the adult stage. Early Mesozoic evolution of lotic Anisoptera was strongly influenced by repeated formation and subsidence of the trans-pangaeian mountain system. Congruence between phylogenetic and biogeographic patterns is substantial, and indicates two or more distinct Mesozoic utilizations of a trans-pangaeian montane dispersal route. Phylogenetic relationships indicate that all early dispersal was in a southerly direction, but later northward migration also occurred. Relict generic pairs of the Jurassic fauna exhibiting north-south vicariance at the tribal level are *Octogomphus-Neogomphus*, at the subfamily level *Tachopteryx--Phenes*, at the family level *Archipetalia-Gomphaeschna*, and *Zoraena-Neopetalia*, and at the superfamily level *Tachopteryx-Archipetalia*, and *Archipetalia-Zoraena*.

THE GONDWANIAN LIBELLULOID RADIATION

Incorrect association of *Neopetalia* with austropetaliids for the past 137 years has greatly confused efforts to unravel libelluloid evolution, in particular it has obscured the gondwanian origin and subsequent radiation of non-cordulegastrid Libelluloidea. Monophyly for non-cordulegastrid Libelluloidea is supported by

apomorphy set 14 of Table I. Adult neapomorphy is substantial and includes infla-
tion of lateral clypeal lobes, inflation of intraocellar lobe, short wide pterostigmata,
and presence of male meso- and metatibial keels; exapomorphy includes loss of
glossal spines, and reduction of the ovipositor. Placement of *Neopetalia* at the base
of the non-cordulegastrid Libelluloidea is supported by apomorphy set 16 of Table
I, which indicates monophyly for (Chlorogomphidae + Synthemistidae +
Gomphomacromiidae + the MCL complex). Neapomorphy includes dorsal
proventricular lobes with inner denticular row directed medially, male tibial keels
long (considered to be secondarily lost in Libellulinae), divergent larval wing pads
(a variable character state typically correlated with burrowing), and median space
with 1-5 crossveins (convergently present in some Zygoptera and Aeshnidae, and
lost in Gomphomacromiidae and the MCL complex); exapomorphy includes loss
of the pterostigmal brace (considered to be convergently lost in Cordulegastridae
and in several additional Odonata). The many exapomorphies required to make
apomorphy set 16 congruent certainly weaken the case for monophyly, but the
most likely alternative, monophyly for Neopetaliidae + Chlorogomphidae, is ap-
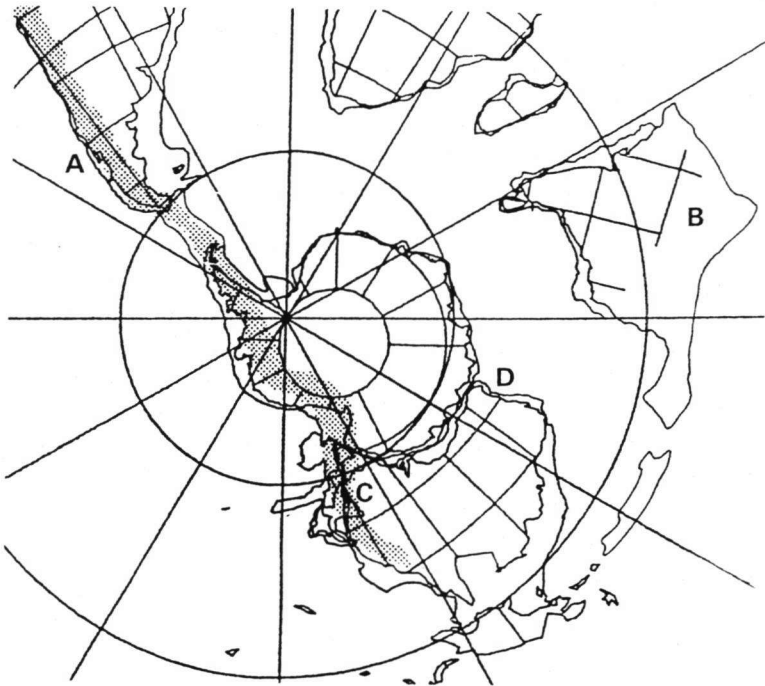
Fig. 2. Paleocontinental map for Late Cretaceous (ca 80 million years ago) modified from SMITH &
BRIDEN (1977), shaded areas indicate likely location of trans-Antarctic mountain system: (A) South
American refugium; – (B) Indian refugium; – (C) Tasmanian refugium; and – (D) Southwest Austral-
ian refugium.

parently not supported by neapomorphy. In addition to neapomorphy listed in apomorphy set 15 (Tab. I), female *Neopetalia* have a "genital lobe" on tergum 2, and have elongate curved cerci which support the lateral rims of the splash plate. The sole representative of this family, *Neopetalia punctata* Selys, is restricted to central Chile. However, its range is nearly as extensive as the combined ranges of all South American Austropetaliidae, indicating less restrictive habitat requirements and higher vagility. These characteristics likely spurred the most dramatic adaptive radiation of extant Anisoptera, a process which began at least 140 million years ago on the now frozen continent of Antarctica (Fig. 2).

Chlorogomphid monophyly is supported by apomorphy set 17 (Tab. I), and is primarily based on adult specializations. Chlorogomphid neapomorphy includes the basally widened subtriangular interspace which is abruptly narrowed distally at the origin of a strong posterior sector, basally the interspace is from 2-4 times as wide as the section from the distal furcation to the wing margin. Additional adult neapomorphy involves the secondary genitalia which possess a stout lateral spur posterior to uniquely triangular elongate anterior hamuli which have incurvate apices. The larvae are superficially quite similar to those of *Neopetalia* and cordulegastrids, but the toothlike proventricular lobes are smaller and the terminalia are much more acuminate. Protochlorogomphids likely migrated along the windward side of the Pampean-cape mountains (at about 50° latitude), and into eastern Antarctica from where they spread northward along mountains associated with the Afro-Indian rift system. Southward drift of Antarctica-India-Australia had likely already limited the chlorogomphids to India by the mid-Cretaceous and rapid northward drift of India during the late Cretaceous permanently separated them from their nearest relatives.

Dramatic evolutionary change would involve those libelluloids remaining in Antarctica. During the Cretaceous progressive movement of Antarctica toward the south led to increased adaptation to temperate conditions as evidenced by the presence of tree rings (DOTT & BATTEN, 1971), and possibly to the 6 month day and night conditions south of the Antarctic Circle. The most obvious, a reduction in size, is still evident in the plesiotypic genera *Synthemiopsis* and *Gomphomacromia* which are barely ½ the size of their chlorogomphid counterparts. These groups were relatively r selected, with less restrictive larval habitat requirements and relatively high adult vagility, which may have included migratory tendencies. Monophyly for Synthemistidae + Gomphomacromiidae + the MCL complex is based on the largest set of congruent neapomorphy and exapomorphy known in the Anisoptera; these are listed as apomorphy set 18 of Table I. Most neapomorphy occurred in the larval stage with adult neapomorphy limited to alignment of antenodal crossveins and basal fusion of the arcular sectors with associated anterior convexity of supratriangles. Larval neapomorphy involved the development of a large subapical tooth on the ventral proventricular lobes and medial inclination of the posteromedial edge of the dorsal lobes; the latter character state may represent coapomorphy. Additional larval neapomorphy includes development of mesosternal paracoxal lobes which apparently help hold the labium in the

retracted position, fusion of anterior and posterior metasternal transverse sulci which indicates a shorter and wider abdomen, and transverse abdominal muscle 6 attached to flat-elongate anterolateral apodemes; these changes are adaptations to a more cursorial larval existence. Labial modification involved the daggerlike palpal teeth which became smaller and more regular in response to increased dependence on smaller prey. Most exapomorphy occurred in the adult stage with larval exapomorphy limited to the loss of paraglossal lobes. Adult exapomorphy includes the wide ligula with entire apical margin, labial palpi with apical spine and movable end hook vestigial, and anterior hamuli vestigial or absent.

Synthemistid monophyly is supported by apomorphy set 19, and is solely based on adult specializations. Neapomorphy includes formation of additional well developed costal braces which alternate with non-aligned antenodals, and development of an elongate abdomen (e.g. male abdominal segment 4 ca 5 times as long as high). However, the latter character state may have developed within the Synthemistidae because the abdomen of *Synthemiopsis* is not elongate (male abdominal segment 4 only ca 3 times as long as high). In addition, the arcular sectors are stalked; this character state is also shared with macromiids and libellulids, but since it is achieved through the loss of a vein base it is considered an exapomorphy. The diversity of ancient synthemistids in Tasmania, and the presence of *Gomphomacromia* in Chile and its closest relative *Archaeophya* in southeastern New South Wales indicates late Cretaceous or early Cenozoic dispersal along the rejuvenated Andean-Antarctic-Tasman mountain chain. However, already by the late Cretaceous almost all of Antarctica was south of the Antarctic Circle (Fig. 2), suggesting that its utility as a dispersal route and evolutionary center was nearing an end.

Monophyly for Gomphomacromiidae and the MCL complex is supported by apomorphy set 20 of Table I. Adult neapomorphy includes the alignment of all or nearly all antenodals with associated weakening of original costal braces and strengthening of secondarily aligned antenodals, and the development of the triquetrous abdomen at least on male abdominal segments 7 and 8 with development of associated middorsal and lateral carinae. Larval neapomorphy includes fusion of transverse metasternal sulci and possibly correlated shortening of the abdomen, and a relative lengthening of the hind femora. Reversals of the latter two character states are known and are related to a return to the fossorial mode of larval life. Monophyly for Gomphomacromiidae is supported by apomorphy set 21 of Table I. Neapomorphy includes base of anal loop subequal to the gaff coupled with arcular sectors not stalked, and larval pronotum typically laterally shelflike. Gomphomacromiidae is here restricted to three genera that are primarily defined by plesiomorphy (i.e. adult abdominal segment 1 with lateral spurs and larval labial palpi without medial setae); the group is likely paraphyletic. Monophyly for the MCL complex is supported by apomorphy set 21 of Table I. Adult neapomorphy includes development of the male genital lobe with the correlated opposable posterior hamuli, and basal asymmetry of penile flagellae (MAY & COOK, 1993; apparently lost in libellulines). Larval neapomorphy includes

Table I

Sorted character state matrix for anisopteran families; ZYG=Zygoptera, – EPI=Epiophlebiidae, –
GOM=Gomphidae, – PET=Petaluridae, – AUS=Austropetaliidae, – AES=Aeshnidae, –

Apomorphy	
1a	Larvae with caudal gills
1b	Median process of male abdominal sternum 2 with apical sperm removal organ
1c	Tandem hold achieved with male cerci
1d	Adult epiproct obsolete
2a	Fore and hind wings dissimilar in shape
2b	Male and female hind wings dissimilar in shape
2c	· Arculus between costal braces
2d	Larva with well developed rectal gill chamber
2e	Proventriculus located anteriorly, anterior of abdominal segment 2
2f	Tandem hold achieved with male cerci and epiproct
2g	Tandem hold with male terminalia grasping female occipital region
2h	Antefrons inflated
2i	Larva with frontal shelf developed
3a	Larva with stridulating file on abdominal segments 3-6
3b	Adult with hyperdeveloped interocellar ridge
3c	Adult with flattened elongate-ovoid pedicel with lateral hair fringe
3d	Male occipital region with antitandem lobes
3e	Male ventral epiproctal spurs engaging anterior lamina
3f	Pyramidal genital pore injects sperm between long contiguous posterior hamuli
3g	Secondary genitalia with medial organs vestigial
4a	Median process of abdominal segment 3 developed into 4 segmented penis
4b	Trachea RA with posterior branch extended into "IR3"
4c	Anterior end of discal brace tilted distally
4d	Wings with crossvein dividing quadralateral into triangle and supratriangle
4e	Larvae with transverse abdominal muscles, with jet propulsion
4f	Male abdomen with auricles
4g	Male hind wings with anal brace
4h	Male hind tibiae with spines at least slightly reduced relative to female
4i	Proventriculus with 4-8 sclerotized lobes
5a	Larval antennae with third segment enlarged, 4 segmented
5b	Proventriculus with 4 elongate rasplike sclerotized lobes
5c	Posterior hamuli engaging female sternum 9 with anterior stroke
5d	Adult palpal end hook spinelike apically, ca as long as ligula
5e	Adult with ridgelike postocellar lobe
5f	Larval mesotarsi 2 segmented
5g	Progonopods fused, metagonopods obsolete
5h	Male with subapical protibial pads
6a	Proventriculus with denticles grouped posteriorly
6b	Sclerotized proventricular lobes mound or toothlike
6c	Larval abdominal segments 4 and 5 secondarily without anterolateral apodemes
6d	Larval second molar segment with basal articulation lost
7a	Larval tibiae with apical burrowing hooks
7b	Larval labial palps quadrate with robust spur at base of end hook
7c	Larval terminalia forming dorsally directed vent
7d	Larval terminalia with ventromedial hair brush

Table I

COG=Cordulegastridae, – NEO=Neopetaliidae, – CHL=Chlorogomphidae, – SYN=Synthemistidae, – GMA=Gomphomacromiidae, and – MCL=macromiid-corduliid-libellulid complex

Character		ZYG	EPI	GOM	PET	AUS	AES	COG	NEO	CHL	SYN	GMA	MCL
1a	Larval abdomen	N	–	–	–	–	–	–	–	–	–	–	–
1b	Male genitalia	N	–	–	–	–	–	–	–	–	–	–	–
1c	Terminalia	N	–	–	–	–	–	–	–	–	–	–	–
1d	Terminalia	C	–	–	–	–	–	–	–	–	–	–	–
2a	Adult wing	–	N	N	N	N	N	N	N	N	N	N	N
2b	Adult wing	–	N	N	N	N	N	N	N	N	N	N	N
2c	Adult wing	–	N	N	N	N	N	N	N	N	N	N	N
2d	Larval abdomen	–	N	N	N	N	N	N	N	N	N	N	N
2e	Proventriculus	–	N	N	N	N	N	N	N	N	N	N	N
2f	Terminalia	–	N	N	N	N	N	N	N	N	N	N	N
2g	Terminalia	–	C	C	C	C	C	C	C	C	C	C	C
2h	Adult head	–	N	N	N	N	N	N	N	N	N	N	N
2i	Larval head	–	C	C	C	C	C	C	C	C	C	C	C
3a	Larval abdomen	–	N	–	–	–	–	–	–	–	–	–	–
3b	Adult head	–	N	–	–	–	–	–	–	–	–	–	–
3c	Adult head	–	N	–	–	–	–	–	–	–	–	–	–
3d	Adult head	–	N	–	–	–	–	–	–	–	–	–	–
3e	Terminalia	–	N	–	–	–	–	–	–	–	–	–	–
3f	Male genitalia	–	C	–	–	–	–	–	–	–	–	–	–
3g	Male genitalia	–	X	–	–	–	–	–	–	–	–	–	–
4a	Male genitalia	–	–	N	N	N	N	N	N	N	N	N	N
4b	Larval thorax	–	–	N	N	N	N	N	N	N	N	N	N
4c	Adult wing	n	–	N	N	N	N	N	N	N	N	N	N
4d	Adult wing	–	–	C	C	C	C	C	C	C	C	C	C
4e	Larval abdomen	–	–	N	N	x	N	N	N	N	N	N	N
4f	Adult abdomen	–	–	N	N	N	x	x	N	N	N	N	x
4g	Adult wing	–	–	C	C	C	x	x	C	C	C	C	x
4h	Adult legs	–	–	C	C	C	x	x	C	C	C	C	x
4i	Proventriculus	–	–	X	X	X	X	X	X	X	X	X	X
5a	Larval head	–	–	N	–	–	–	–	–	–	–	–	–
5b	Proventriculus	–	–	N	–	–	–	–	–	–	–	–	–
5c	Male genitalia	–	–	N	–	–	–	–	–	–	–	–	–
5d	Adult head	–	–	N	–	–	–	–	–	–	–	–	–
5e	Adult head	–	–	N	–	–	–	–	–	–	–	–	–
5f	Larval thorax	–	–	X	–	–	–	–	–	–	–	–	–
5g	Ovipositor	–	–	X	–	–	–	–	–	–	–	–	–
5h	Adult legs	–	–	n	–	–	–	–	–	–	–	–	–
6a	Proventriculus	–	–	–	N	N	N	N	N	N	N	N	N
6b	Proventriculus	–	–	–	C	C	C	C	C	C	C	C	C
6c	Larval abdomen	–	–	–	X	X	X	X	X	X	X	X	X
6d	Larval head	–	X	–	X	X	X	X	X	X	X	X	X
7a	Larval thorax	–	–	–	N	–	–	–	–	–	–	–	–
7b	Larval head	–	–	–	N	–	–	–	–	–	–	–	–
7c	Terminalia	–	–	–	N	–	–	–	–	–	–	–	–
7d	Terminalia	–	–	–	N	–	–	–	–	–	–	–	–

Table I, continued

	Apomorphy
7e	Adult palpal end hooks spatulate
7f	Pterostigmata concave posteriorly and longer than distance between costal braces
7g	Female ovipositor strongly upturned
8a	Adult compound eyes approximate or contiguous dorsally
8b	Adult postfrons with intraocellar lobe
8c	Male epiproct quadrate or triangular
8d	Proventriculus with 4 sclerotized toothlike lobes, apical denticle largest
8e	Molar lobe without teeth
8f	Larva anterior transverse abdominal muscles phragmatic
9a	Larval epiproct bifurcate apically
9b	Posterior hamuli vestigial
9c	Median process of abdominal segment 2 L-shaped and acute anteriorly
9d	Anterior hamuli small-laminate with apices approximate medially
9e	Anterior lamina with elongate medial cleft
10a	Adult wings with series of 5-8 reddish brown blotches along costa
10b	Larva with lateral abdominal lobes on segments 1 through 10
10c	Penile segment 4 pendulous with paired sicklelike flagella
10d	Larval labrum strongly widened distally, to ca apical width of prementum
10e	Larval ventrolateral occipital ridge massive
10f	Larval femora dorsally excrescent
10g	Larval transverse abdominal muscles obsolete
11a	Adult compound eyes meeting dorsally along eye seem
11b	Fore wing triangle longer than that of hind wing
11c	Adult abdomen with weak dorsal and well developed lateral carinae
11d	Penile segment 4 swablike
11e	Larval anal pyramid hyperattenuate
11f	Larval transverse abdominal muscle 5 phragmatic
11g	Wings with planate in triangular interspace
11h	Penile prepuce obsolete
12a	Larval labrum concealed by triangular-shaped labial palps
12b	Proventricular lobes with denticles arranged serially along posterolateral edges
12c	Proventriculus bilaterally symmetrical
12d	Larval labial palp with elongate dorsal setae
12e	Larval labium with premental setae
12f	Larval posterior margin of abdominal segments with long hair setae
12g	Larval palpi with elongate irregular medial teeth
12h	Gonocoxae vestigial, gonapophyses blunt tipped, oviposition exophytic
13a	Supplementary sector arising near bridge crossvein
13b	Male meso- and metatibiae with outer spines peglike
13c	Male with apical protibial pads
13d	Anterior hamuli large erect-foliate
13e	Progonopodites appressed into elongate gently tapered spade
13f	Larval cerci relatively vestigial
14a	Adult lateral clypeal lobes inflated
14b	Adult intraocellar lobe with at least small posterior inflation
14c	Male tibial keels keellike
14d	Adult glossal processes obsolete

Table I, continued

Character		ZYG	EPI	GOM	PET	AUS	AES	COG	NEO	CHL	SYN	GMA	MCL
7e	Adult head	–	–	–	N	–	–	–	–	–	–	–	–
7f	Adult wing	–	–	–	N	–	–	–	–	–	–	–	–
7g	Adult abdomen	–	–	–	N	–	–	–	–	–	–	–	–
8a	Adult head	–	–	–	–	N	N	N	N	N	N	N	N
8b	Adult head	–	–	–	–	N	N	N	N	N	N	N	N
8c	Terminalia	–	–	–	–	N	N	N	N	N	N	N	N
8d	Proventriculus	–	–	–	–	N	N	N	N	N	N	N	N
8e	Larval head	–	–	–	–	X	X	X	X	X	X	X	X
8f	Larval abdomen	–	–	–	X	X	N	N	N	N	N	N	N
9a	Terminalia	–	–	–	–	N	N	–	–	–	–	–	–
9b	Male genitalia	–	–	–	–	N	N	–	–	–	–	–	–
9c	Male genitalia	–	–	–	–	C	C	–	–	–	–	–	–
9d	Male genitalia	–	–	–	–	C	C	–	–	–	–	–	–
9e	Male genitalia	–	–	–	–	C	C	–	–	–	–	–	–
10a	Adult wing	–	–	–	–	N	–	–	–	–	–	–	–
10b	Larval abdomen	–	–	–	–	N	–	–	–	–	–	–	–
10c	Male genitalia	–	–	–	–	N	–	–	–	–	–	–	–
10d	Larval head	–	–	–	–	N	–	–	–	–	–	–	–
10e	Larval head	–	–	–	–	N	–	–	–	–	–	–	–
10f	Larval thorax	–	n	–	n	N	–	–	–	–	–	–	–
10g	Larval abdomen	–	–	–	–	X	–	–	–	–	–	–	–
11a	Adult head	–	–	–	–	–	N	–	–	–	–	–	–
11b	Adult wing	–	–	–	–	–	N	–	–	–	–	–	–
11c	Adult abdomen	–	–	–	–	–	N	–	–	–	–	–	–
11d	Male genitalia	–	–	–	–	–	N	–	–	–	–	–	–
11e	Terminalia	–	–	–	–	–	N	–	–	–	–	–	–
11f	Larval abdomen	–	–	–	–	–	N	–	–	–	–	–	–
11g	Adult wing	–	–	n	–	–	N	–	–	–	–	–	n
11h	Male genitalia	–	–	–	–	–	X	–	–	–	X	X	X
12a	Larval head	–	–	–	–	–	–	N	N	N	N	N	N
12b	Proventriculus	–	–	–	–	–	–	N	N	N	N	N	N
12c	Proventriculus	–	–	–	–	–	–	N	N	N	N	N	N
12d	Larval head	n	–	–	–	–	–	N	N	N	N	N	N
12e	Larval head	n	–	–	–	–	n	N	N	N	N	N	N
12f	Larval abdomen	–	–	–	–	–	–	N	N	N	x	X	X
12g	Larval head	–	–	–	–	–	–	N	N	N	X	X	X
12h	Ovipositor	–	–	–	–	–	–	X	X	X	X	X	X
13a	Adult wing	–	–	–	–	–	–	N	–	–	–	–	–
13b	Adult legs	–	–	–	–	–	–	N	–	–	–	–	–
13c	Adult legs	–	–	–	–	–	–	N	–	–	–	–	–
13d	Male genitalia	–	–	–	–	–	–	N	–	–	–	–	–
13e	Adult abdomen	–	–	–	–	–	–	N	–	–	–	–	–
13f	Larval abdomen	x	–	–	–	X	–	X	–	–	–	–	–
14a	Adult head	–	–	–	–	–	–	–	N	N	N	N	N
14b	Adult head	–	–	–	–	N	N	–	N	N	N	N	N
14c	Adult legs	–	–	–	–	–	–	–	N	N	N	N	x
14d	Adult head	x	–	X	–	–	x	–	X	X	X	X	X

Table I, continued

	Apomorphy
15a	Adult wings with 4 reddish costal blotches
15b	Adult abdominal segments 5-8 with ventroapical tufts of long hair
15c	Anterior hamuli contiguous and L-shaped
15d	Female sternum10 expanded into huge circular splash plate
15e	Larval male epiproctal tubercle large acute-pyramidal
15f	Larval mesonotum with postspiracular spines
15g	Larval antefrons moundlike with lateral patches of spinelike setae
15h	Prementum with 4-6 vestigial setae, labial palpi with one small dorsal setae
16a	Proventriculus with inner denticles of dorsal lobes directed medially
16b	Male with metatibial keels longer than 1/5 length of tibia
16c	Larval wing pads divergent
16d	Median space with 1-5 crossveins, (also with 3-10 Cu-A crossveins)
16e	Oblique pterostigmal brace obsolete
17a	Subtriangular interspace dilated basally
17b	Secondary genitalia with interhamular spur
17c	Anterior hamuli elongate-triangular with incurved end hook
17d	Larval epiproct needlelike apically
18a	Hind wing antenodal crossveins in alignment (with 3 or more costal braces)
18b	Proventriculus with subapical tooth on ventral lobes
18c	Dorsal proventricular teeth with posteromedial edge inclined medially
18d	Larval mesosternum with paracoxal lobes
18e	Larval metasternum with anterior and posterior transverse sulci contiguous
18f	Larval abdominal sternum 6 with flat-elongate anterolateral apodemes
18g	Sectors of arculus fused at least basally
18h	Wings with posterior arcular portion short, supratriangle distinctly convex anteriorly
18i	Adult intraocellar lobe with shelflike overhang of medial ocellus
18j	Adult labial palpi with movable end hook and apical spine vestigial
18k	Anterior hamuli vestigial or absent
18l	Larval ligula with distal margin entire, without paraglossal lobes
18m	Adult ligula with distal margin entire
18n	Adult ligula wider than long
19a	Hind wing with 3-5 costal braces alternating with non-aligned antenodals
19b	Sectors of arculus stalked
19c	Male abdomen attenuate, (male segment 4 typically 5 times as long as high)
20a	Larval metasternum with anterior and posterior sulci fused medially
20b	Adult hind wings with antenodals all weakly bracelike
20c	Male abdomen triquetrous at least on segments 7 and 8
20d	Male tergum 7 with well developed middorsal ridge or lateral carinae
20e	Larval abdomen less than twice as long as wide
20f	Larval hind femora more than 1.5 times length of front femora
21a	Anal loop elongate with gaff shorter than base
21b	Pronotum laterally shelflike
22a	Male with well developed genital lobe
22b	Larvae with medial edge of palpal lobes setose
22c	Dorsal proventricular lobes with medial chutelike sclerotization
22d	Ventral proventricular lobes less than ½ as wide as dorsal lobes
22e	Ventral proventricular lobes with teeth separated by less than width of dorsal lobes

Table I, continued

Character	ZYG	EPI	GOM	PET	AUS	AES	COG	NEO	CHL	SYN	GMA	MCL
15a Adult wing	–	–	–	–	–	–	–	N	–	–	–	–
15b Adult abdomen	–	–	–	–	–	–	–	N	–	–	–	–
15c Male genitalia	–	–	–	–	–	–	–	N	–	–	–	–
15d Adult abdomen	–	–	–	–	–	–	–	N	–	–	–	–
15e Terminalia	–	–	–	–	–	–	–	N	–	–	–	–
15f Larval thorax	–	–	–	–	–	–	–	N	–	–	–	–
15g Larval head	–	–	–	–	–	–	–	N	–	–	–	–
15h Larval head	–	–	–	–	–	–	–	N	–	–	–	–
16a Proventriculus	–	–	–	–	–	–	–	–	N	N	N	N
16b Adult legs	–	–	–	–	–	–	–	–	N	N	N	x
16c Larval thorax	n	–	n	–	–	–	x	–	N	N	X	X
16d Adult wing	n	–	–	–	–	n	–	–	N	N	X	X
16e Adult wing	x	X	x	–	–	–	X	–	X	X	X	X
17a Adult wing	–	–	–	–	–	–	–	–	N	–	–	–
17b Male genitalia	–	–	–	–	–	–	–	–	N	–	–	–
17c Male genitalia	–	–	–	–	–	–	–	–	N	–	–	–
17d Terminalia	–	–	–	–	–	–	–	–	N	–	–	–
18a Adult wing	n	–	–	–	–	–	–	–	–	N	N	N
18b Proventriculus	–	–	–	–	–	–	–	–	–	N	N	N
18c Proventriculus	–	–	–	–	–	–	–	–	–	N	N	N
18d Larval thorax	–	–	–	–	–	–	–	–	–	N	N	N
18e Larval thorax	–	–	–	–	–	–	–	–	–	N	N	N
18f Larval abdomen	–	–	–	–	–	–	–	–	–	N	N	N
18g Adult wing	–	–	–	–	–	–	–	–	–	N	N	N
18h Adult wing	–	–	–	–	–	–	–	–	–	C	C	C
18i Adult head	–	–	–	–	–	n	–	–	–	N	N	N
18j Adult head	–	–	–	–	–	–	–	–	–	X	X	X
18k Male genitalia	–	–	–	–	–	–	–	–	–	X	X	X
18l Larval head	o	–	o	–	–	–	–	–	–	X	X	X
18m Adult head	–	–	X	–	–	–	–	–	–	X	X	X
18n Adult head	–	–	X	–	–	X	–	–	–	X	X	X
19a Adult wing	–	–	–	–	–	–	–	–	–	N	–	–
19b Adult wing	–	–	–	–	–	–	–	–	–	X	–	x
19c Adult abdomen	n	–	–	–	–	–	–	–	–	o	–	–
20a Larval thorax	–	–	–	–	–	–	–	–	–	–	N	N
20b Adult wings	–	–	–	–	–	–	–	–	–	–	N	N
20c Adult abdomen	–	–	–	–	–	–	–	–	–	–	N	N
20d Adult abdomen	–	–	–	–	–	–	–	–	–	–	C	C
20e Larval abdomen	–	–	–	–	–	–	–	–	–	–	N	x
20f Larval thorax	–	–	–	–	–	–	–	–	–	–	N	x
21a Adult wing	–	–	–	–	–	–	–	–	–	–	N	–
21b Larval thorax	–	–	–	–	–	–	–	–	–	–	o	–
22a Male genitalia	–	n	–	–	–	–	–	–	–	–	–	N
22b Larval head	–	–	–	–	–	–	–	N	–	–	–	N
22c Proventriculus	–	–	–	–	–	–	–	N	–	–	–	N
22d Proventriculus	–	–	–	–	–	–	–	–	–	–	–	N
22e Proventriculus	–	–	–	–	–	–	–	–	–	–	–	N

development of raptorial setae on the medial edge of the labial palpi, development of medial chutelike sclerotization between dorsal proventricular lobes, and ventral proventricular lobes less than ½ as wide as dorsal lobes with teeth separated by less than width of dorsal lobes. In addition, most larvae of these groups have dorsal abdominal spines, and female progonaphophyses and metagonaphophyses are vestigial. Absence of plesiotypic genera of the MCL complex from Tasmania suggests that the group originated on the Australian portion of the Antarctica-Australia continent during the early Cenozoic. Northward drift of Australia during the Eocene and afterward led to dispersal of the MCL complex along the Indonesian island arc into Laurasia, this was accompanied by a further invasion of lentic habitats and higher vagility, leading to a rapid spread and an almost random distribution of the MCL complex throughout the world.

THE CHLOROGOMPHID RADIATION

Rapid northward drift of India during the late Cretaceous and early Cenozoic undoubtedly led to the formation of the Proto-Himalaya in northern India analogous to the mountains of present day New Guinea. The combined forces of mountain building and rapid drift toward the equator evidently created a dynamic mix of dispersal and vicariance which favored rapid evolution as all ancient chlorogomphid genera trace their origins to the Himalayas. The realization that neopetaliids represent the sister group to chlorogomphids greatly increases congruent neapomorphy listed in Table II. For example, the following character states could be considered apomorphic if cordulegastrids are considered the nearest out group: compound eyes contiguous dorsally, dorsolateral carinae of antefrons well developed, male cerci flattened and elongate, epiproct longer than wide, and fourth penile segment elongate. These are the conditions in *Neopetalia* and not surprisingly the sorted character state matrix predicts that they are plesiomorphic relative to chlorogomphids. Monophyly for chloropetaliines is supported by apomorphy set 3 of Table II and monophyly for chlorogomphines is supported by apomorphy set 4 of Table II. Most unexpected is the thoracic color patern reversal exhibited in derived chlorogomphines. The plesiotypic thoracic color pattern of chloropetaliines indicates that Chlorogomphidae could be paraphyletic, i.e. Chlorogomphinae may form a monophyletic group with remaining libelluloids. Also the scattered denticles of chloropetaliine ventral proventricular lobes suggest the plesiotypic gomphoid condition. However, the bidentate ventral lobes of the MCL complex is likely derived from a similar plesiotypic condition. The apparent Himalayan-Indonesian split distribution of chloropetaliines is also problematic and implies that Borneo may indeed represent a piece of the Gondwanian puzzle, however it seems more likely that northeast India may have been in contact with Borneo via Sumatra-Java during the Eocene.

Monophyly for Eorogomphini is supported by apomorphy set 5 of Table II and

monophyly for remaining Chlorogomphinae is supported by apomorphy set 6 of Table II. *Eorogomphus* is unique in that it combines the thoracic color patterns of Chloropetaliinae and Chlorogomphinae being much more extensively yellow than other Chlorogomphidae. In addition, the compound eyes are slightly more separated than in Chloropetaliinae, but the hind wing to abdominal length ratio remains unchanged, i.e. at 1.40-1.50 in males and 1.25-1.35 in females. Neapomorphy of remaining Chlorogomphinae includes compound eyes separated by at least the width of the median ocellus, meso- and metanepimeral yellow stripes vestigial or absent, and hind wing to abdominal length ratio of male less than 1.32, and of female less than 1.22. The Eorogomphines appear to be Himalayan endemics.

Monophyly for Sinorogomphini and Chlorogomphini is supported by apomorphy set 7 and 8 of Table II, respectively. Adult neapomorphy of Sinorogomphini includes the dorsal expansion of the dorsal mesanepisternal yellow stripes into a transverse oval club, male meso- and metakatepisterna with yellow spots, abdominal segment 6 or 7 with paired apical subtriangular yellow spots ca as long as wide, and abdominal segment 3 strongly constricted apically. Neapomorphy of Chlorogomphini is primarily based on non-coapomorphic wing character states, these include wings often with apical or basal opaque markings, female hind wing to abdominal length ratio less than 1.13, and a narrowing of the hind wing triangles. Specifically, costal side of triangle shorter than proximal side or occasionally subequal in male. In addition, female abdominal segments 3-7 are laterally compressed and abdominal segment 4 is less than three times as long as high, and in the male the fourth penile segment has distinct lateral keellike ridges. The Sinorogomphini has apparently spread northward into China from the Himalayan region, with one species reaching Taiwan.

Phylogenetic arrangement within Chlorogomphini is somewhat uncertain in that *Indorogomphus* shares only one neapomorphy and one exapomorphy (Tab. II, apomorphy set 10), with *Orogomphus, Aurorachlorus*, and *Chlorogomphus*. Additional study may show *Neorogomphus* and *Indorogomphus* to form a monophyletic group, in which case the biogeography of Chlorogomphini might be more understandable. Monophyly for *Neorogomphus* is supported by apomorphy set 9 of Table II. Neapomorphy includes labrum typically with U-shaped central spot, abdominal segments with paired spots ca as long as wide and in the basal position, lateral mesanepisternal yellow stripes narrow, male with bases of abdominal segments 8 and 9 constricted basally, and male cerci with blunt lateral spine. *Neorogomphus* has apparently spread southeastward into southeast Asia from the Himalayan region.

Monophyly for *Indorogomphus* is supported by apomorphy set 11 of Table II. Neapomorphy includes dorsal and lateral mesanepisternal pale stripes confluent or nearly confluent dorsally; antefrons inflated bilobate, without well developed ventrolateral carinae; and abdomen to hind wing length ratio of male ca 1.16 and that of female ca 0.97. This large difference between male and female body form is

most closely approximated in *Neorogomphus*, and may represent a synapomorphy for these two genera. *Indorogomphus* is restricted to western and southern India, and it is either a southwestern hill country vicariant paired with *Neorogomphus* which is parapatric, or with *Orogomphus* as indicated in Table II.

Monophyly for *Orogomphus* + *Aurorachlorus* + *Chlorogomphus* is supported by apomorphy set 12 of Table II. Neapomorphy includes male hind wing triangle with costal side shorter than proximal side so that the posterior angle of the triangle is acute, fourth penile segment with well developed lateral keels forming a short obtusely rounded apex, anterior hamuli triangular and directed ventrolaterally with end hooks directed medially, and anterior lamina distinctly bilobate. Monophyly for *Orogomphus* is supported by apomorphy set 13 of Table II. Neapomorphy includes female occiput transverse ridgelike, and male epiproct with small apical notch with epiproctal rami apically truncate. *Orogomphus* has apparently spread northward from Borneo to the Philippines, Taiwan, the Ryukyu islands, and eventually to Japan. North-South vicariance between *Orogomphus* and *Chlorogomphus* is apparent across the Karimata straight, again suggesting former contact between India and Indonesia. Formation of an Eocene dispersal route along a south Tethyan mountain range extending from the proto-Himalaya in eastern India to Indonesia via Sumatra is supported by the split distributions of *Chloropetalia* and *Chlorogomphus*, and by the apparent vicariant generic pairs, *Indorogomphus-Chlorogomphus* and *Chlorogomphus-Orogomphus*.

Monophyly for *Chlorogomphus* + *Aurorachlorus* is supported by apomorphy set 14 of Table II. Neapomorphy includes submedial apical abdominal spots decreasing in size posteriorly so that of tergum 7 does not increase in size, male abdominal segments 4-7 triquetrous and abdomen to hind wing length ratio less than 1.08, female abdominal tergum 3 with ventrolateral stripe confluent with apical ring and abdominal segments 5 and 6 less than 2 times as long as high, and female occiput depressed. However, other similarities such as development of the anal loop and spined male cerci suggest that *Aurorachlorus* may have been derived from *Orogomphus*. Monophyly for *Chlorogomphus* is supported by apomorphy set 15 of Table II. Neapomorphy is apparently limited to adult male character states and includes epiproct narrowed subapically with divergent apices, cerci slender ca 4 times as long as wide in dorsal view, widely separated basally, and without lateral or apical spines, and posterobasal wing margin evenly rounded with the anal brace weakly developed. In addition, the male and female abdomen to wing length ratios are similar, and the number of cells in the anal loop are low, 8-10 in the male, and 11-18 in the female; the latter character state may represent a reversal to the plesiotypic state. Monophyly for *Aurorachlorus* is supported by apomorphy set 16 of Table II. Neapomorphy includes lateral mesanepisternal yellow stripes obsolete, anal loop elongate with 28-35 cells, female abdomen very short and compressed with abdominal segment 4 ca 1.5 times as long as high, and all wings with extensive basal opaque brown markings, that of hind wing divided by wide golden yel-

low band. *Aurorachlorus* and *Chlorogomphus* apparently form an East-West vicariant pair.

In summary, chlorogomphid evolution was largely influenced by unknown vicariant events related to the combined forces of mountain building and rapid drift toward the equator, coupled with a 40-60 million year insular isolation. All chlorogomphid genera with the possible exception of *Aurorachlorus* trace their origins to a southern Tethyan mountain range, which allowed East-West dispersal as far as Java and western India during the Eocene. Even now all ancient chloro-gomphid genera are represented in the eastern Himalaya. Following closure of the Tethyan sea (Oligocene) chlorogomphids spread throughout Asia; *Sinorogomphus* and *Aurorachlorus* to China, *Neorogomphus* to Southeast Asia, and *Orogomphus* from Borneo to Japan. The realization that neopetaliids represent the ancient Gondwanian sister group to chlorogomphids greatly increases both phylogenetic and biogeographic understanding of their evolution.

THE SYNTHEMISTID RADIATION

During the Cretaceous Antarctica drifted southward to eventually lie almost com-pletely within the Antarctic Circle, exposing early synthemistids to increasingly temperate conditions, and apparently to the 6 month day and night conditions of the antarctic region. Selective pressures were undoubtedly extreme producing the largest set of congruent neapomorphy and exapomorphy known in the Anisoptera. Ancient libelulloides of the Antarctic were relatively r selected, which resulted in smaller size, less restrictive larval habitat requirements, and relatively high adult vagility which may have included migratory flights. Tasmanian diversity of an-cient synthemistids suggests that considerable evolution occurred in Antarctica before dispersal into Australia. Establishment of apophyletic groups within Synthemistidae, i.e. *Eusynthemis* Förster (= *Metathemis* Tillyard) and *Choristhemis* Tillyard, and non-recognition of *Palaeosynthemis* Förster have obscured phylo-genetic relationships, although even TILLYARD (1910) remarked concerning *Syn-themis* that they are "certainly the most archaic members of the group still extant".

Discovery of a Tasmanian synthemistid of decided gomphomacromiid facies led TILLYARD (1917) to apply the name *Synthemiopsis gomphomacromioides*. The monotypic Synthemiopsini is the only ancient synthemistid tribe restricted to Tas-mania, where it inhabits the small pools and rivulets of seepage areas. Monophyly for *Synthemiopsis* is supported by apomorphy set 1 of Table III. Adult neapomorphy is unexpectedly pronounced and includes wings with spots at nodus and wing base, prepuce tonguelike and ca as long as base of penile segment 3, ovipositor knoblike apically, base of anal loop, distal side of triangle, and gaff subequal, and proximal side of hind wing triangle perpendicular to longitudinal veins. Congruent neapo-morphy of remaining Synthemistidae is also substantial suggesting that *S. gompho-macromioides* is a relict of early synthemistid evolution that occurred in the Ant-

Table II

Sorted character state matrix for neopetaliid and chlorogomphid genera: NEO=*Neopetalia*, –
CHP=*Chloropetalia*, – EOR=*Eorogomphus*, – SIN=*Sinorogomphus*, – NOR=*Neorogomphus*, –

	Apomorphy
1a	Adult wings with 4 reddish costal blotches
1b	Adult abdominal segments 5-8 with ventroapical tufts of long hair
1c	Anterior hamuli contiguous and L-shaped
1d	Female sternum 10 expanded into huge circular splash plate
1e	Larval male epiproctal tubercle large acute-pyramidal
1f	Larval mesonotum with postspiracular spines
1g	Larval antefrons moundlike with lateral patches of spinelike setae
1h	Prementum with 4-6 vestigial setae, labial palpi with one small dorsal setae
2a	Proventriculus with inner denticles of dorsal lobes directed medially
2b	Male with metatibial keels longer than 1/5 length of tibia
2c	Larval wing pads divergent
2d	Median space with 1-5 crossveins, (also with 3-10 Cu-A crossveins)
2e	Oblique pterostigmal brace obsolete
3a	Anterior hamuli directed posteroventrally
3b	Ventroapical penile lobes more than 6 times as long as wide
3c	Vulvar lamina with midventral keel
3d	Larval palpal end hook with dorsal row of small setae
3e	Ventral proventricular teeth with scattered dorsal denticles
3f	Male compound eyes separated by ca 1/3 width of medial ocellus
3g	Female compound eyes separated by ca 2/3 width of medial ocellus
4a	Dorsal mesanepisternal pale stripes linear
4b	Lateral mesanepisternal and metanepisternal pale stripes well developed
4c	Mesanepimeral pale stripes narrow or obsolete
4d	Antefrons strongly inflated dorsally, with dorsolateral carinae vestigial
4e	Male cerci not dorsoventrally flattened, less than 2.5 times as long as wide
4f	Vulvar lamina wider than long
4g	Male compound eyes separated by at least 1/2 width of medial ocellus
4h	Female compound eyes separated by more than width of medial ocellus
5a	Labrum with submedian yellow areas
5b	Male compound eyes separated by ca 1/2 width of median ocellus
5c	Adult with yellow stripe on anterior half of metanepimera
5d	Adult with narrow yellow stripe on anterior half of mesanepimera
6a	Adult compound eyes separated by at least width of median ocellus
6b	Adult meso- and metanepimeral pale stripes vestigial or obsolete
6c	Hind wing to abdominal length ratio of male less than 1.32
6d	Hind wing to abdominal length ratio of female less than 1.22
7a	Dorsal mesanepisternal pale stripes dorsally expanded to transverse club
7b	Male meso- and metakatepisterna with yellow spots
7c	Abdominal tergum 3 twice as high basally as apically
7d	Abdominal segment 6 or 7 with paired apical yellow spots ca as long as wide
8a	Wings often with apical or basal opaque markings
8b	Fourth penile segment with lateral keels
8c	Female hind wing to abdominal length ratio less than 1.13
8d	Female abdominal segment 4 less than 3 times as long as high
8e	Female abdominal segments 3-7 laterally compressed

Table II

IND= *Indorogomphus*, – ORO=*Orogomphus*, – CHG=*Chlorogomphus*, – AUR=*Aurorachlorus*

Character		NEO	CHP	EOR	SIN	NOR	IND	ORO	CHG	AUR
1a	Adult wings	N	–	–	–	–	–	–	–	–
1b	Adult abdomen	N	–	–	–	–	–	–	–	–
1c	Male genitalia	N	–	–	–	–	–	–	–	–
1d	Adult abdomen	N	–	–	–	–	–	–	–	–
1e	Terminalia	N	–	–	–	–	–	–	–	–
1f	Larval thorax	N	–	–	–	–	–	–	–	–
1g	Larval head	N	–	–	–	–	–	–	–	–
1h	Larval head	N	–	–	–	–	–	–	–	–
2a	Proventriculus	–	N	N	N	N	N	N	N	N
2b	Adult legs	–	N	N	N	N	N	N	N	N
2c	Larval thorax	–	N	N	N	N	N	N	N	N
2d	Adult wings	–	N	N	N	N	N	N	N	N
2e	Adult wings	–	X	X	X	X	X	X	X	X
3a	Male genitalia	–	N	–	–	–	–	–	–	–
3b	Male genitalia	–	N	–	–	–	–	–	–	–
3c	Ovipositor	–	N	–	–	–	–	–	–	–
3d	Larval head	–	N	–	–	–	–	–	–	–
3e	Proventriculus	–	N	–	–	–	–	–	–	–
3f	Adult head	–	N	–	–	–	–	–	–	–
3g	Adult head	–	C	–	–	–	–	–	–	–
4a	Adult thorax	–	–	N	N	N	N	N	N	N
4b	Adult thorax	–	–	N	N	N	N	N	N	N
4c	Adult thorax	–	–	N	N	N	N	N	N	N
4d	Adult head	–	–	N	N	N	N	N	N	N
4e	Terminalia	–	–	N	N	N	N	N	N	N
4f	Ovipositor	–	–	N	N	N	N	N	N	N
4g	Adlt head	–	–	N	N	N	N	N	N	N
4h	Adult head	–	–	C	C	C	C	C	C	C
5a	Adult head	–	–	N	–	–	–	–	–	–
5b	Adult head	–	–	N	–	–	–	–	–	–
5c	Adult thorax	–	–	N	–	–	–	–	–	–
5d	Adult thorax	–	–	C	–	–	–	–	–	–
6a	Adult head	–	–	–	N	N	N	N	N	N
6b	Adult thorax	–	–	–	N	N	N	N	N	N
6c	Adult wing	–	–	–	N	N	N	N	N	N
6d	Adult wing	–	–	–	C	C	C	C	C	C
7a	Adult thorax	–	–	–	N	–	–	–	–	–
7b	Adult abdomen	–	–	–	N	–	–	–	–	–
7c	Adult thorax	–	–	–	N	–	–	–	–	–
7d	Adult abdomen	–	–	–	N	–	–	–	–	–
8a	Adult wing	–	–	–	–	N	N	N	N	N
8b	Male genitalia	–	–	–	–	N	N	N	N	N
8c	Adult wing	–	–	–	–	N	N	N	N	N
8d	Adult abdomen	–	–	–	–	N	N	N	N	N
8e	Adult abdomen	–	–	–	–	C	C	C	C	C

Table II, continued

	Apomorphy
8f	Male hind wing triangle with costal side subequal or shorter than proximal side
8g	Female hind wing triangle with costal side shorter than proximal side
9a	Labrum with U-shaped central greenish yellow spot
9b	Lateral mesanepisternal yellow stripes only slightly wider than dorsal stripes
9c	Lateral yellow band extended from metanepimera to antecostal suture of segment 3
9d	Abdominal segment 7 with paired basal yellow spots ca as long as wide
9e	Male with bases of abdominal segments 8 and 9 constricted basally
9f	Male cerci with blunt lateral spine
10a	Male hind wing to abdominal length ratio less than 1.20
10b	Adult labrum brown or black
11a	Dorsal and lateral mesanepisternal pale stripes confluent dorsally
11b	Antefrons bilobate, without well developed ventrolateral carinae
11c	Abdomen to hind wing length ratio of male ca 1.16, of female ca 0.97
12a	Male hind wing triangle with costal side shorter than proximal side
12b	Fourth penile segment with lateral keels forming short obtusely rounded apex
12c	Anterior hamuli directed ventrolaterally, end hooks directed medially
12d	Anterior lamina distinctly bilobate
13a	Female occiput transverse ridgelike
13b	Male epiproct with small apical notch
13c	Male epiproctal rami apically truncate
14a	Submedial apical abdominal spots decreasing in size posteriorly.
14b	Male abdominal segments 4-7 triquetrous
14c	Male abdomen to hind wing length ratio less than 1.08
14d	Female abdominal tergum 3 with ventrolateral stripe confluent with apical ring
14e	Female abdominal segments 5 and 6 less than 2 times as long as high
14f	Female occiput depressed
15a	Male and female abdomen to wing length ratio similar
15b	Male epiproct narrowed subapically with divergent apices
15c	Male cerci dorsally ca 4 times as long as wide
15d	Male cerci without lateral or apical spines
15e	Male with posterobasal wing margin evenly rounded
16a	Anal loop with 28-35 cells
16b	Female abdominal segment 4 ca 1.5 times as long as high
16c	Fore wings with extensive basal opaque markings
16d	Male hind wing with extensive opaque markings
16e	Lateral mesanepisternal yellow stripes obsolete

arctic. Monophyly for remaining Synthemistidae is supported by apomorphy set 2 of Table III. Adult neapomorphy includes hind wing triangle with distal side less than 1.5 times length of proximal side, and fore wing arculus with posterior portion less than 1/3 its length. Congruent exapomorphy includes epiproct without wide V-shaped apical notch.

Palaeosynthemistines are characterized by pronounced plesiomorphy, although monophyly is supported by apomorphy set 3 of Table III. Neapomorphy is apparently limited to penile segment 2 gently curved basally and longer than penile

Table II, continued

Character	NEO	CHP	EOR	SIN	NOR	IND	ORO	CHG	AUR
8f Adult wing	--	–	–	–	N	N	N	N	N
8g Adult wing	–	–	–	–	C	C	C	C	C
9a Adult head	–	–	–	–	N	–	–	–	–
9b Adult thorax	–	–	–	–	N	–	–	–	–
9c Adult abdomen	–	–	–	–	N	–	–	–	–
9d Adult abdomen	–	–	–	–	C	–	–	–	–
9e Adult abdomen	–	–	–	–	N	–	–	–	–
9f Terminalia	–	–	–	–	N	–	–	–	–
10a Adult wing	–	–	–	–	–	N	N	N	N
10b Adult head	–	–	–	X	–	X	X	X	X
11a Adult thorax	–	–	–	–	–	N	–	–	–
11b Adult head	–	–	–	–	–	N	–	–	–
11c Adult abdomen	–	–	–	–	–	N	–	–	–
12a Adult wing	–	–	–	–	–	–	N	N	N
12b Male genitalia	–	–	–	–	–	–	N	N	N
12c Male genitalia	–	–	–	–	–	–	N	N	N
12d Male genitalia	–	–	–	–	–	–	N	N	N
13a Adult head	–	–	–	–	–	–	N	–	–
13b Terminalia	–	–	–	–	–	–	N	–	–
13c Terminalia	–	–	–	–	–	–	C	–	–
14a Adult abdomen	–	–	–	–	–	–	–	N	N
14b Adult abdomen	–	–	–	–	–	–	–	N	N
14c Adult abdomen	–	–	–	–	–	–	–	N	N
14d Adult abdomen	–	–	–	–	–	–	–	N	N
14e Adult abdomen	–	–	–	–	–	–	–	N	N
14f Adult head	–	–	–	–	–	–	–	N	N
15a Adult abdomen	–	–	–	–	–	–	–	N	–
15b Terminalia	–	–	–	–	–	–	–	N	–
15c Terminalia	–	–	–	–	–	–	–	N	–
15d Terminalia	–	–	–	–	–	–	–	C	–
15e Adult wing	–	–	–	–	–	–	–	X	–
16a Adult wing	–	–	–	–	–	–	–	–	N
16b Adult abdomen	–	–	–	–	–	–	–	–	N
16c Adult wing	–	–	–	–	–	–	–	–	N
16d Adult wing	–	–	–	–	–	–	–	–	C
16e Adult thorax	–	–	–	–	–	–	–	–	X

segment 1, and larvae with trilobate labial palpi. However, the trilobate labial palps may represent a plesiomorphic condition because similar labial palpi also characterize at least some *Gomphomacromia*. Synthemistini + Eusynthemistini are characterized by substantial neapomorphy and exapomorphy, these are listed as apomorphy set 6 of Table III. Neapomorphy includes midbasal space with 2-5 crossveins, posterior hamuli not of boxing glove type, and penile segment three less than twice as long as wide. Exapomorphy includes ventral margin of male abdominal tergum 1 without spinose ventrolateral spurs, and ovipositor reduced with apex

not extended beyond cerci. Palaeosynthemistines exhibit the most widespread distribution of synthemistid tribes, they have dispersed from Tasmania (or Antarctica) to eastern and western Australia, New Guinea, and Fiji.

Palaeosynthemistini is divided into two genera, *Archaeosynthemis* which inhabits seepage areas of Australia and Fiji, and *Palaeosynthemis* which is restricted to New Guinea, both genera are defined by congruent neapomorphy. Monophyly for *Archaeosynthemis* is supported by apomorphy set 4 of Table III. Adult neapomorphy includes pterostigmata elongate, typically at least as long as hind wing supratriangle, and abdomen with submedial paired oval spots subequal on segments 3-8. Monophyly for *Palaeosynthemis* is supported by apomorphy set 5 of Table III. Adult neapomorphy includes fore wing triangle distant from arculus by more than length of proximal side of triangle, penile filament longer than penile segment 1, and abdominal segments 3-7 with transverse dashes along antecostal suture. Although it is likely that *A. macrostigma* has spread from Tasmania to eastern Australia and then to western Australia and Fiji, East-West vicariance between *A. macrostigma* and *A. leachi* may have occurred in Antarctica with *A. leachi* invading western Australia via east Antarctica during the Eocene or earlier. *Archaeosynthemis spiniger* is likely a regional vicariant of *A. leachi*.

Monophyly for Synthemistiini is supported by apomorphy set 7 of Table III. Adult neapomorphy is substantial and includes hind wing with 3-5 midbasal crossveins, vulvar lamina bilobate and at least ½ as long as segment 10, posterior hamuli clasping vulvar lamina with ventro-dorsal action and apices denticulate or spinelike, base of penile cornua expanded into medial septumlike plate, and penile filament basally directed dorsally and abruptly curved posteriorly. Congruent exapomorphy includes male cerci without basolateral spine or lobe. Synthemistini are known from Tasmania, eastern Australia, and New Caledonia. As in Palaeosynthemistini it is likely that Synthemistini spread from Tasmania to eastern Australia, but unlike any other synthemistid group, then dispersed to New Caledonia.

Monophyly for *Synthemis* is supported by apomorphy set 8 of Table III. Adult neapomorphy is substantial and includes posterior hamuli chisellike with apical transverse row of denticles, ventrolateral margin of male abdominal tergum 2 with coarse setal brush, male tergum 10 with laterally compressed posteriorly directed spine, and male epiproct elongate and distally parallel sided with truncate apex. Monophyly for *Parasynthemis* + *Calesynthemis* is supported by apomorphy set 9 of Table III. Adult neapomorphy is diverse and includes sectors of the arculus arising at near its posterior end (at ca 1/5 length of arculus), posterior hamuli with posteriorly directed spine, and vulvar lamina bilobate and ca 1/2 as long as sternum 9. *Synthemis* inhabit seepage areas of Tasmania and eastern Australia. North-South vicariance across Bass Strait includes an earlier event involving *Synthemis*-*Parasynthemis* and a later event involving *S. tasmanica* and *S. eustalacta*.

Monophyly for *Parasynthemis* is supported by apomorphy set 10 of Table III. Adult neapomorphy is substantial and includes abdominal segment 7 predomi-

nantly yellow dorsally, posterior hamuli stublike with lateral groove and short posteriorly directed spine, vulvar lamina flattened with wide U-shaped notch and prominent midbasal swelling, penile segment 3 with ventroapical spines (cornua) hooklike with medial plates displaced distally on cornua, and larvae with 7 lateral palpal setae. Monophyly for *Calesynthemis* is supported by apomorphy set 11 of Table III. Adult neapomorphy is striking, but is apparently limited to the male secondary genitalia, it includes posterior hamuli falcate and posteriorly tapered to fingerlike apices and penile filament apically recurved. *Parasynthemis* is a monotypic endemic of the eastern Australian mainland which has successfully invaded sluggish streams, riverine pools, and swamps. *Calesynthemis* is endemic to New Caledonia and many species are known to be semi-terrestrial. Although *Calesynthemis* is quite diverse the above neapomorphy supports a single vicariant pair, *Parasynthemis-Calesynthemis.*

Monophyly for Eusynthemistini is supported by apomorphy set 12 of Table III. Adult neapomorphy includes hind wing with 1 or 2 midbasal crossveins, and posterior hamuli prolonged posteriorly with posteromedially directed end hook and minute notch. Exapomorphy includes vulvar lamina vestigial, i.e. shorter than ½ as long as segment 10. Eusynthemistini inhabit the streams and rivers of eastern Australia with one plesiotypic species, *Austrosynthemis cyanitincta* known from southwest Australia, and one derived species, *Eusynthemis frontalis* known from the Solomon Islands. Eusynthemistid biogeography is somewhat problematic in that the synthemistine-eusynthemistine vicariant pair could be related to North-South vicariance across Bass Strait or to East-West vicariance in Antarctica. The latter possibility is supported by the absence of *Austrosynthemis* is southeastern Australia, but would require at least two separate invasions of eastern Australia via southwestern Australia.

Monophyly for *Austrosynthemis* is supported by apomorphy set 13 of Table III. Adult neapomorphy is substantial and includes penile segment 1 erect moundlike, penile cornua erect thin-forklike, and male cerci down curved basally with basolateral spine lobelike. Exapomorphy includes vulvar lamina bilobate and ca 1/5 length of sternum 9. Monophyly for *Choristhemis + Eusynthemis* is supported by apomorphy set 14 of Table III. Adult neapomorphy is substantial and includes midbasal space of fore wing with 2-3 crossveins, male cerci straight or incurvate, penile segment 2 with ventrobasal lobes forming U-shaped medial notch, and vulvar lamina with paired medial spurs and sternum 8 produced ventrally. Congruent exapomorphy includes penile filament shorter than penile segment two. *Austrosynthemis* occurs in southwestern and northeastern Australia. If East-West Antarctic vicariance did indeed lead to the synthemistine-eusynthemistine pair, then it is apparent that East-West Australian vicariance led to the *Austrothemis-Choristhemis* pair, although relatively recent dispersal had led to the reestablishment of *Austrosynthemis* in north-eastern Australia.

Monophyly for *Choristhemis* is supported by apomorphy set 15 of Table III.

Table III

Sorted character state matrix for synthemistid genera: SYP=*Synthemiopsis*, – ARC=*Archaeosynthemis*, – PAL=*Palaeosynthemis*, – SYN=*Synthemis*, – PAR=*Parasynthemis*, – CAL=*Calesynthemis*, –

Apomorphy

1a	Wings with spots at nodus
1b	Prepuce ca as long as base of penile segment 3
1c	Ovipositor knoblike apically
1d	Base of anal loop, distal side of triangle, and gaff subequal
1e	Proximal side of hind wing triangle perpendicular to longitudinal veins
2a	Hind wing triangle with distal side less than 1.5 length of proximal side
2b	Fore wing arculus with posterior portion less than 1/3 its length
2c	Epiproct without wide V-shaped apical notch
3a	Penile segment 2 longer than penile segment 1
3b	Penile segment 2 gently curved basally
3c	Larvae with trilobate labial palpi
4a	Pterostigmata as long as hind wing supratriangle
4b	Abdomen with submedial paired oval spots subequal on segments 3-8
5a	Fore wing triangle distant from arculus by more than length of proximal side of triangle
5b	Penile filament longer than penile segment 1
5c	Abdominal segments 3-7 with transverse dashes along antecostal suture
6a	Midbasal space with 2-5 crossveins
6b	Posterior hamuli not of boxing glove type
6c	Penile segment three less than twice as long as wide
6d	Abdominal segment 1 of male without spinose ventrolateral spurs
6e	Ovipositor not extended beyond cerci
7a	Hind wing with 3-5 midbasal crossveins
7b	Vulvar lamina bilobate and at least 1/2 as long as segment 10
7c	Posterior hamuli clasping vulvar lamina with ventro-dorsal action
7d	Base of penile cornua expanded into medial septumlike plate
7e	Penile filament directed dorsally at base
7f	Male cerci without basolateral spine or lobe
8a	Posterior hamuli chisellike with apical transverse row of denticles
8b	Ventrolateral margin of male abdominal tergum 2 with coarse setal brush
8c	Male tergum 10 with laterally compressed posteriorly directed spine
8d	Male epiproct elongate and distally parallel sided with truncate apex
9a	Sectors of the arculus arising at ca 1/5 length of arculus
9b	Posterior hamuli with posteriorly directed spine
9c	Vulvar lamina bilobate and ca 1/2 as long as sternum 9
10a	Abdominal segment 7 predominantly yellow dorsally
10b	Posterior hamuli stublike with lateral groove and short posteriorly directed spine
10c	Vulvar lamina flattened with wide U-shaped notch, and prominent midbasal swelling
10d	Penile cornua hooklike, medial plates displaced distally on cornua
10e	Larvae with 7 lateral palpal setae
11a	Posterior hamuli falcate, posteriorly tapered to fingerlike apices
11b	Penile filament apically recurved
12a	Hind wing with 1 or 2 midbasal crossveins
12b	Posterior hamuli with posteromedially directed end hook
12c	Vulvar lamina shorter than 1/2 as long as segment 10
13a	Penile segment 1 erect moundlike

Table III

AUS=*Austrosynthemis*, – CHO=*Choristhemis*, – EUS=*Eusynthemis*

Character		SYP	ARC	PAL	SYN	PAR	CAL	AUS	CHO	EUS
1a	Adult wings	N	–	–	–	–	–	–	–	–
1b	Male genitalia	N	–	–	–	–	–	–	–	–
1c	Ovipositor	N	–	–	–	–	–	–	–	–
1d	Adult wings	N	–	–	–	–	–	–	–	–
1e	Adult wings	C	–	–	–	–	–	–	–	–
2a	Adult wings	–	N	N	N	N	N	N	N	N
2b	Adult wings	–	N	N	N	N	N	N	N	N
2c	Terminalia	–	X	X	X	X	X	X	X	X
3a	Male genitalia	–	N	N	–	–	–	–	–	–
3b	Male genitalia	–	C	C	–	–	–	–	–	–
3c	Larval head	–	N	?	–	–	–	–	–	–
4a	Adult wings	–	N	–	–	–	–	–	–	–
4b	Adult abdomen	–	N	–	–	–	–	–	–	–
5a	Adult wings	–	–	N	–	–	–	–	–	–
5b	Male genitalia	–	–	N	–	–	–	–	–	–
5c	Adult abdomen	–	–	N	–	–	–	–	–	–
6a	Adult wings	–	–	–	N	N	N	N	N	N
6b	Male genitalia	–	–	–	N	N	N	N	N	N
6c	Male genitalia	–	–	–	N	N	N	N	N	N
6d	Adult abdomen	–	–	–	X	X	X	X	X	X
6e	Ovipositor	–	–	–	X	X	X	X	X	X
7a	Adult wings	–	–	–	N	N	N	–	–	–
7b	Vulvar lamina	–	–	–	N	N	N	–	–	–
7c	Male genitalia	–	–	–	N	N	N	–	–	–
7d	Male genitalia	–	–	–	N	N	N	–	–	–
7e	Male genitalia	–	–	–	N	N	N	–	–	–
7f	Terminalia	–	–	–	X	X	X	–	X	–
8a	Male genitalia	–	–	–	N	–	–	–	–	–
8b	Adult abdomen	–	–	–	N	–	–	–	–	–
8c	Adult abdomen	–	–	–	N	–	–	–	–	–
8d	Terminalia	–	–	–	N	–	–	–	–	–
9a	Adult wings	–	–	–	–	N	N	–	–	–
9b	Male genitalia	–	–	–	–	N	N	–	–	–
9c	Vulvar lamina	–	–	–	–	N	N	–	–	–
10a	Adult abdomen	–	–	–	–	N	–	–	–	–
10b	Male genitalia	–	–	–	–	N	–	–	–	–
10c	Vulvar lamina	–	–	–	–	N	–	–	–	–
10d	Male genitalia	–	–	–	–	N	–	–	–	–
10e	Larval head	–	–	–	–	N	–	–	–	–
11a	Male genitalia	–	–	–	–	–	N	–	–	–
11b	Male gentialia	–	–	–	–	–	N	–	–	–
12a	Adult wings	–	–	–	–	–	–	N	N	N
12b	Male genitalia	–	–	–	–	–	–	N	N	N
12c	Vulvar lamina	–	–	–	–	–	–	X	X	X
13a	Male genitalia	–	–	–	–	–	–	N	–	–

Table III, continued

Apomorphy
13b Penile cornua erect thin-forklike
13c Male cerci down curved basally
13d Male cerci with basolateral spine lobelike
13e Vulvar lamina bilobate, ca 1/5 length of sternum 9
14a Midbasal space with 2-3 crossveins
14b Male cerci not undulate
14c Penile segment 2 with ventrobasal lobes forming U-shaped medial notch
14d Vulvar lamina with paired medial spurs, sternum 8 produced ventrally
14e Penile filament shorter than penile segment two
15a Antefrons narrower than distance from base of labrum to top of frons
15b Male cerci nearly straight with rounded apices
15c Penile segment 4 with lateral keels
15d Penile cornua fused into erect finlike keel
15e Penile filament shorter than penile segment 3
15f Membranule vestigial
16a Penile cornua with thick stem and slightly bifoliate apex
16b Ovipositor with erect spurs
16c Male cerci and epiproct slightly longer than abdominal segment 9
16d Male epiproct ca 1.5 times as long as wide and truncate apically

Adult neapomorphy includes antefrons narrower than distance from base of labrum to top of frons, male cerci nearly straight with rounded apices, penile segment 4 with lateral keels, penile cornua fused into erect finlike keel, and penile filament shorter than penile segment 3. Congruent exapomorphy includes the vestigial membranule. Monophyly for *Eusynthemis* is supported by apomorphy set 16 of Table III. Adult neapomorphy includes penile cornua with thick stem and slightly bifoliate apex, ovipositor with erect spurs, male cerci and epiproct slightly longer than abdominal segment 9, and male epiproct ca 1.5 times as long as wide and truncate apically. *Choristhemis* and *Eusynthemis* are restricted to eastern Australia with *Choristhemis* centered in the North (NSW) and *Eusynthemis* centered in the South (Queensland). A lack of total sympatry suggests that the *Choristhemis-Eusynthemis* pair resulted from North-South vicariance in eastern Australia.

In summary, early synthemistid evolution was largely influenced by unknown vicariant events in Antarctica related to the combined forces of mountain building and drift toward the south pole, coupled with a 60 million year isolation. Resulting selective pressures produced the largest set of congruent neapomorphy and exapomorphy known in the Anisoptera. The diversity of ancient Tasmanian synthemistids and the presence of ancient synthemistids in southwest Australia suggests that considerable evolution occurred in Antarctica before dispersal into Australia. Synthemiopsini is the most plesiotypic extant synthemistid group and is endemic to Tasmania. Palaeosynthemistini and Synthemistini are also represented in Tasmania, but both have invaded eastern Australia and various islands beyond.

Table III, continued

Character	SYP	ARC	PAL	SYN	PAR	CAL	AUS	CHO	EUS
13b Male genitalia	–	–	–	–	–	–	N	–	–
13c Terminalia	–	–	–	–	–	–	N	–	–
13d Terminalia	–	–	–	–	–	–	C	–	–
13e Vulvar lamina	–	–	–	–	–	–	X	–	–
14a Adult wings	–	–	–	–	–	–	–	N	N
14b Terminalia	–	–	–	–	–	–	–	N	N
14c Male genitalia	–	–	–	–	–	–	–	N	N
14d Vulvar lamina	–	–	–	–	–	–	–	N	N
14e Male genitalia	–	–	–	–	–	–	–	X	X
15a Adult head	–	–	–	–	–	–	–	N	–
15b Terminalia	–	–	–	–	–	–	–	N	–
15c Male genitalia	–	–	–	–	–	–	–	N	–
15d Male genitalia	–	–	–	–	–	–	–	C	–
15e Male genitalia	–	–	–	–	–	–	–	X	–
15f Adult wings	–	–	–	–	–	–	–	X	–
16a Male genitalia	–	–	–	–	–	–	–	–	N
16b Ovipositor	–	–	–	–	–	–	–	–	N
16c Terminalia	–	–	–	–	–	–	–	–	N
16d Terminalia	–	–	–	–	–	–	–	–	C

Palaeosynthemistini and the sister group of Synthemistini, the Eusynthemistini, have both apparently invaded southwestern Australia via Antarctica. If these groups did evolve before the northward drift of Australia then they would have been extant at least 50 million years ago.

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