

A new phylogenetically basal subfamily of brown lacewings from Chile (Neuroptera: Hemerobiidae)

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A new genus and species, *Adelphohemerobius enigmarum*, is described from Chile and assigned to a new subfamily, Adelphohemerobiinae, of the neuropterous family Hemerobiidae (brown lacewings). A cladistic analysis of morphological data derived from the unique female holotype of *A. enigmarum* supports the conclusion that it represents the sister-group of the family Hemerobiidae *sensu* Oswald (1993a). The holotype of *A. enigmarum* is interpreted to be the first non-teratological hemerobiid specimen known to possess a single 'radial sector', i.e., only the true ancestral Rs.

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Introduction

The family Hemerobiidae, brown lacewings, is a cosmopolitan clade of approximately 550 species (Monserrat 1990a) of small predaceous insects in the order Neuroptera. Oswald (1993a) recently reviewed the phylogeny, taxonomy, and biogeography of the world genera of this family. Three additional genera have subsequently been described, or were described while this monograph was in press: *Biramus*, by Oswald (1993b), and *Navasius* and *Falcomegalomus*, by Gonzalez-Olazo (1992; *Navasius* Gonzalez-Olazo is a junior homonym of *Navasius* Esben-Petersen, 1936 [Myrmeleontidae] and *Navasius* Yang & Yang, 1990 [Chrysopidae]). This paper describes another new genus and species, *Adelphohemerobius enigmarum*, which is of special interest as the sister-group to all other previously known brown lacewings. Because of the basal phylogenetic position of this new species, a new subfamily has been required to place it within the sequenced classification scheme of Oswald (1993a). Morphological terminology follows Oswald (1993a).

New taxa

Subfamily ADELPHOHEMEROBIINAE,
subfam. n.

Type genus: *Adelphohemerobius* gen. n. (No other genera are included.)

Diagnosis. - As given below for *Adelphohemerobius* gen. n.; the apomorphies of this subfamily are identical to those given below for *A. enigmarum*.

Genus *Adelphohemerobius*, gen. n.

Type species: *Adelphohemerobius enigmarum* sp. n.

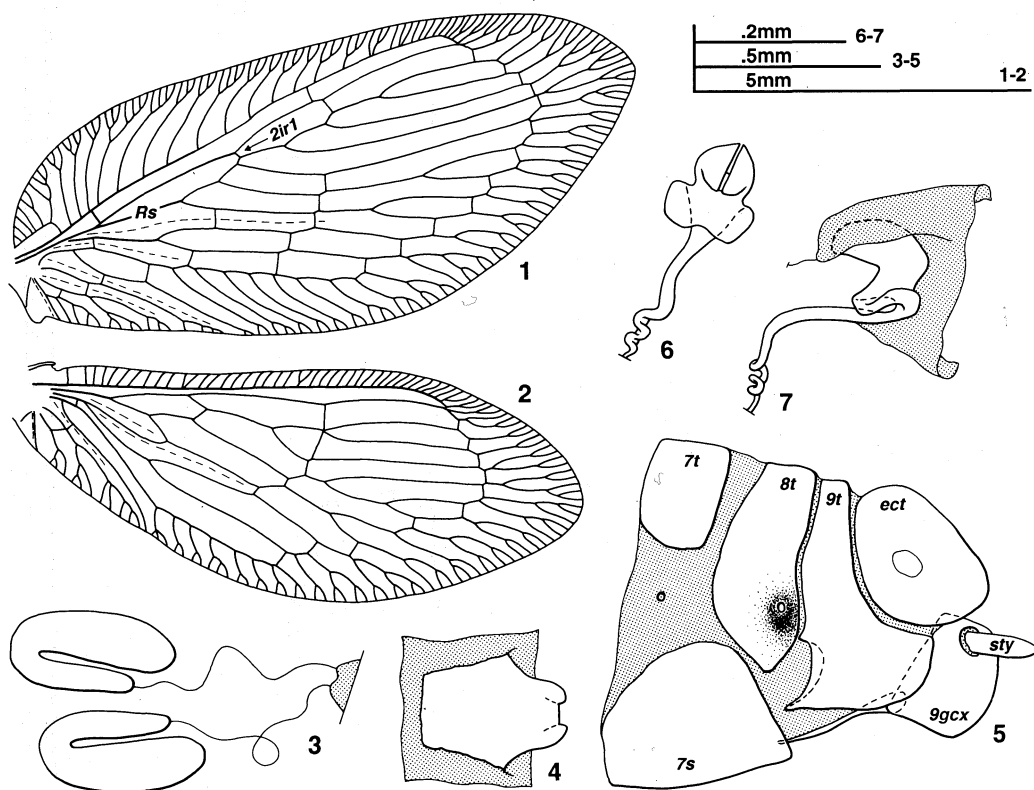
Diagnosis. - Readily differentiated from all other hemerobiid genera (and subfamilies) by any of the following characters: (1) forewing radius bearing a single oblique radial branch (Fig. 1, Rs) [not two or more], (2) female insemination/fertilization canal of the slit-entry type (Fig. 6) [not pore-entry type], (3) female with a distinct subanale [not absent], or (4) female 9th gonocoxite stylus elongate (Fig. 5, sty) [not short or absent]. The apomorphies of this genus are identical to those given below for *A. enigmarum*.

Included species (1). - *A. enigmarum* sp. n.: Chile.

Etymology and gender. - Adelpho- [from Gr. *adelphē*, sister] + *Hemerobius*, in reference to the position of this taxon as the sister-group to other known hemerobiids. Gender: masculine.

Adelphohemerobius enigmarum sp. n.

(Figs 1-7)



Figs 1-7. *Adelphohemerobius enigmaramus* sp. n. (holotype, ♀): (1) forewing; (2) hind wing; (3) bursal accessory glands and apex of bursa; (4) subgenitale, ventral; (5) apex of abdomen, lateral; (6) insemination/fertilization canal, anterodorsal; (7) same, lateral. Abbreviations: 2ir1, gradate series two crossvein of R1 space; 7s, 7th sternite; 7t, 8t, 9t, tergites; 9gcx, 9th gonocoxite; ect, ectoproct; Rs, radial sector; sg, subgenitale; sty, 9th gonocoxite stylus.

Description. – Proposed apomorphies are marked below with an asterisk (*). Adult female medium-sized, forewing length from base of tegula to wing apex 9.7 mm ($n = 1$ wing).

Head: Eyes small; temporal costae well developed; epicranial suture absent; clypeus with paired dorsomedial, dorsolateral, ventromedial, and ventrolateral setae; prominent unpaired dorsomedian seta absent; maxillary palp with five palpomeres, ultimate (fifth) palpomere without an apical subsegment, basal (first) palpomere cylindrical, not divided longitudinally on its medial face (*?, see 'Character notes' below); labial palp with three palpomeres, ultimate (third) palpomere with a palpicula but without an apical subsegment.

Thorax: Pronotum transverse, lateral margins produced as prominent ventrally sclerotized lobes.

Forewing (Fig. 1): Margin convex throughout,

not falcate; trichosores prominent proximally and distally (not shown in figure); proximal humeral trace recurrent and pectinately branched; stigmal region indistinct; subcostal space broad proximally and only slightly narrowed distally before stigmal region; posterior subcostal trace rather abruptly recurved in stigmal region to terminate on (or very near) anterior radial trace (*); two Sc-R crossveins present, one proximal (=1sc-r) and one beyond midpoint of subcostal space (see 'Character notes'); anterior radial trace with a single oblique radial branch, the Rs (similar in both forewings; see 'Character notes'); anterior cubital trace pectinately branched, iCuL crossveins lacking; third (=inner) and fourth (=outer) gradate series well developed in precubital portion of wing; ground membrane coloration hyaline with faint brownish mottling, veins hyaline to light brown with irregular

darker markings, the most prominent fuscous wing markings are as follows (in descending order of prominence; not shown in Fig. 1): (1) a large macula posterior to crossvein 3m-cu, (2) a small macula enclosing several 4ir crossveins just posterior to the apex of the fourth gradate series, (3) a small macula enclosing crossvein 4ir1, and (4) a row of small spots along the forewing margin.

Hind wing: As in Fig. 2; sinuous vein (=MA stem) present; CuP present, prominent, reaching posterior margin as an unbranched vein; coloration: hyaline with a few small brownish spots in stigmal region.

Female terminalia (Figs 3-7): Tergite 8: hemianular, prolonged laterally to enclose spiracles of 8th somite; spiracles borne on prominent tubercles (*). Tergite 9: apparently not divided sagittally, but dorsomedial portion of tergite narrow and weakly sclerotized; lateral regions expanded ventrally and posteriorly to subtend ectoprocts, as in other hemerobiids; anteroventral corners each marked by a prominent concavity (*); distoventral surfaces bearing macrotrichia modified as short thickened spines (*). Ectoproct: outline oval, callus cercus and trichobothria present. Subanale: present (see 'Character notes'). 9th gonocoxites: D-shaped; styli present, long relative to other hemerobiids (see 'Character notes'), inserted on upper surfaces of gonocoxites. Subgenitale: prominent, in ventral view a large hexagonal plate, apex bilobed. Gonapophyses posteriores: well developed. Insemination/fertilization canal: of the slit-entry type, consisting of a compact, arched, and dorsosagittally slit 'proximal body', from the distal end of which protrude (1) a broadened and flattened semi-membranous shelf, and (2) a relatively straight tubular duct that terminates in several fine arched loops (see 'Character notes'). Bursa copulatrix: entirely membranous, bearing a simple, unpaired, colleterial gland proximodorsally and a pair of bursal accessory glands distally; each bursal accessory gland consists of a large looped chamber/reservoir (tanned brownish and heavily sclerotized) and a fine filiform duct linking it to the bursa (see 'Character notes').

Natural history and immature stages. - Unknown. A predatory adult habit is suggested by the presence of numerous sclerotized fragments of insect cuticle among the gut contents of the holotype.

Distribution. - Presently known only from Osorno Prov., Chile.

Material examined. - Holotype ♀ (NMNH). Type locality: Chile, Osorno Province, near Aguas Calientes (a small hot springs resort community, ca. 40°40'S 72°20'W). Verbatim label data: 'CHILE: Osorno Prov[ince]. / P[arque]. N[acional]. Puyehue, 600m / Ag[ua]s. Calientes to 3kmW. / 12-20 Dec. 1981 / D[onald]. R. Davis' [white rectangular label], 'Holotype / Adelphohemerobius / enigmaramus Oswald / J.D. Oswald 1993b' [red rectangle]. Condition: good, right flagellum missing, otherwise complete. Pinned through mesothorax, right wings glued to small card pinned below specimen. The following structures have been macerated in KOH and placed in a glycerin-filled microvial pinned below specimen: head (left flagellum separated), prothorax, right hind leg, abdomen (terminalia separated and stained with Chlorazol Black).

Etymology. - enigma- [from L. *aenigma*, a riddle or something obscure] + -ramus [from L. *ramus*, branch], in reference to the form of the forewing radial vein.

Comments. - The pivotal phylogenetic position of *Adelphohemerobius enigmaramus* has prompted me to describe this species based on the single available female specimen, in order to bring its existence to the attention of South American entomologists and to facilitate the discovery the male. The single oblique branch of the forewing radius possessed by this species should allow unambiguous association of conspecific males.

Character notes

Basal maxillary palpomere. - In many (most?) hemerobiids the sclerotized outer cylinder of the first maxillary palpomere is divided longitudinally by a membranous channel on its ventromedial face. Functionally, this scrobe probably acts to increase the range of motion of the first maxillary palpomere by allowing it to partially surround and overlap the base of the galea (which is inserted on the stipes directly below the insertion of the maxillary palpus). *Adelphohemerobius* lacks this scrobe; however, whether this condition is ancestral or derived is unclear. Some non-hemerobiid taxa also possess this scrobe, suggesting that it is sufficiently widespread to be a possible ancestral state within the Hemerobiidae; however, absence of the scrobe would seem to be a more logical *a priori* choice for the ancestral condition. This character deserves further study over a wider range of neuropterous taxa.

Subcostal crossveins. - Both forewings of the holotype of *A. enigmaramus* possess two prominent crossveins in the subcostal space. The proximal crossvein is considered here to be a homolog of

crossvein 1sc-r of Oswald (1993a), based on its basal position; however, the homology of the distal crossvein is more difficult to assess. Because of its far distal position, i.e., more than halfway between the position of the 1sc-r and the stigmal region, I regarded this crossvein as an analog, not a homolog, of crossvein 2sc-r of Oswald (1993a: 170, Character 28). This interpretation is consistent with the finding of Oswald (1993a) that in no hemerobiid genus in which crossvein 2sc-r is present is it consistently located beyond the halfway point mentioned above (although occasional exceptions may occur in individual species with secondarily abbreviated wing apices, e.g., *Conchopterella kuscheli* Handschin, see Oswald 1993a: 236, fig. 132). The distal crossvein in *Adelphohemerobius* could, alternatively, be considered either a plesiomorphically or an apomorphically distally placed 2sc-r crossvein. Both of these latter interpretations would require a reevaluation of the homology and phylogenetic history of crossvein 2sc-r.

Radial sector. – *Adelphohemerobius enigmaramus* is interpreted here to be the first hemerobiid species known to possess a single oblique radial branch (ORB) diverging from the anterior radial trace – a branch that is homologous with the single ancestral radial sector that is characteristic of nearly all non-hemerobiid Neuroptera. The occurrence of this radial vein state in *Adelphohemerobius* is of considerable importance because the presence of multiple 'radial sectors' has for many years been accepted as a diagnostic feature of the family Hemeroibiidae.

It can, however, be argued that the vein internode interpreted here as crossvein 2ir1 (Fig. 1) is the stem of a second ORB. Although it is probably impossible to conclusively disprove this alternative interpretation based on an examination of the veins themselves (see discussions of radial vein evolution in Oswald 1993a, 1993b), the interpretation adopted here appears more plausible given the following observations: (1) the internodes interpreted as 2ir1 crossveins are crossvein-like in appearance (i.e., short, aetose, and approximately transverse), although not as long as most other crossveins of the forewing, (2) a single radial sector is plesiomorphic within the Neuroptera, and it is therefore a plausible condition for the sister-group to other hemerobiids, (3) the interpretation of a single Rs in *Adelphohemerobius* is not contradicted by any of the synapomorphic characters which support its

basal position within the Hemeroibiidae, and (4) if the internode interpreted here as crossvein 2ir1 is instead interpreted as the basal segment of a second ORB (=ORB2), ORB1 would exhibit a condition otherwise unknown in the Hemeroibiidae, i.e., with the anterior trace of ORB1 giving rise to two branches proximal to the origin of ORB2.

Subanale. – *Adelphohemerobius* is unique in the family Hemeroibiidae in possessing a distinct subanale (present in the female holotype and expected also in the male). This structure – a small, setose, medial plate located immediately below the anus – is usually interpreted as a remnant of the 10th sternite and is found in several neuropterous families. Its presence in *Adelphohemerobius*, although distinctive, is interpreted here as plesiomorphic. A similar, but apparently non-homologous structure, the supragonopontal setal group (Oswald 1993a: 188, Character 94), is found in many species of the subfamily Hemeroibiinae.

9th gonocoxite stylus. – Ninth gonocoxites that bear styli are present in approximately one-half of all hemerobiid genera, are plesiomorphic within the family, and have been lost independently in four different hemerobiid lineages (Oswald 1993a). The stylus of *A. enigmaramus* is the longest that I have observed in any hemerobiid, and stylus elongation might be interpreted as a synapomorphy of *Adelphohemerobius*. However, given the relatively long styli found in species of the subfamily Carobiinae (genus *Carobius*; see figures in New 1988), the elongate stylus of *Adelphohemerobius* would appear to be more plausibly interpreted as a plesiomorphic condition. Given the relatively small size or loss of the stylus in most hemerobiid genera, this latter polarity is also more consistent with the apparently common trend toward reduction of the stylus within this family.

Insemination/fertilization canal. – *Adelphohemerobius* is the only hemerobiid known to possess an insemination/fertilization canal of the slit-entry type, although this condition is common in non-hemerobiid neuropterans. The short, compact, form of the dorsally slit proximal body and the tubular distal portion of the canal found in *A. enigmaramus* can be readily interpreted as an intermediate state between the more elongate slit-entry canals of many non-hemerobiid neuropterans and the pore-entry canals characteristic of other hemerobiid taxa.

Bursal accessory glands. – The form and distribution of bursal accessory glands within the Hemerobiidae is poorly known. Only a few descriptions and/or illustrations of these structures presently exist in the hemerobiid literature (e.g., Monserrat 1990b: 71, figs. 11, 12, 14 [*Notiobiella*]; Monserrat 1992: 126, fig. 5 [*Anapsectra*, ducts only]), but it is uncertain whether this lack of information is attributable to a true absence of these glands in most hemerobiids, or to a failure to locate and describe them. The existing techniques commonly used to prepare the internal female terminalia of dried specimens for examination may hinder the discovery of these structures. Particular care must be taken when flushing macerated female abdomens to avoid damage to these glands; excessively vigorous flushing can easily break the slender ducts that join the gland reservoirs to the bursa. The glands and ducts also become easily entangled in the abdominal tracheae during flushing and can be accidentally removed when separating the bursa from these tracheae.

In the hemerobiid taxa in which I have observed bursal accessory glands, the reservoirs of these glands were ovoid, translucent, and membranous. Such reservoirs are usually inconspicuous, although they occasionally become conspicuous through inflation, presumably due to osmotic pressures generated during the transfer of specimens among the different fluids used in the maceration and staining process. The reservoirs of *Adelphohemerobius*, on the other hand, are prominent structures: shaped like sharply bent tapered tubes (Fig. 3), darkly tanned, and well sclerotized. Whether this condition is ancestral or derived is currently unknown, but neuropterous bursal accessory glands may have considerable potential phylogenetic value and additional study of their structure and distribution is warranted.

Oswald (1993a, 1993b) were maintained in the present analysis.

Data. – The input data matrix contained numerically coded morphological data from three sources: (1) Oswald (1993a: appendix 5), for all genera except *Biramus* and *Adelphohemerobius*, (2) Oswald (1993b: table 1), for *Biramus*, and (3) a row of newly coded data (Table 1) for *Adelphohemerobius*. Two modifications of the data originally used by Oswald (1993a) were incorporated into the data matrix: (1) character 34 of Oswald (1993a) was deleted, and (2) characters 29-33 of the hemerobiine genera *Hemerobius*, *Nesobiella*, *Wesmaelius*, and *Hemerobiella* were recoded using 'transformation series 2' of Oswald (1993b: table 2). These two changes were made by Oswald (1993b) and are justified therein.

Characters 50-95 in Table 1, which pertain to the unknown male of *Adelphohemerobius*, were coded as unknown data ('?'). Crossvein 1cu-a-cup (Character 47) is present (state 1) in one forewing of the holotype, but absent (state 0) in the other. Consequently, this character was also coded as unknown; however, adventitious crossveins occa-

Table 1. Coded character state data for *Adelphohemerobius enigmaramus*. Characters (upper numbers) and states (lower numbers) are identical to those given by Oswald (1993a: 164-191), except as noted under 'Phylogenetic analysis: Data'. Characters 50-95 pertain to the male sex and are currently unknown.

										1	1	1	1	1	1	1	1	2	
1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
1	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	1	0	0	0
2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	4
1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5	5	5	6
1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
0	0	0	0	0	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?
6	6	6	6	6	6	6	6	6	7	7	7	7	7	7	7	7	7	7	8
1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
8	8	8	8	8	8	8	8	8	9	9	9	9	9	9	9	9	9	9	9
1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
1	1	1	1	1	1	1	1	1											
0	0	0	0	0	0	0	0	0											
0	1	2	3	4	5	6	7												
0	0	0	0	0	0	0	0												

Phylogenetic analysis

Overview. – A cladistic analysis was used to estimate the phylogenetic position of *Adelphohemerobius* relative to other hemerobiid genera.

Computational methods. – Cladograms were generated by sequential application of the HENNIG86 (Farris 1988) tree calculation commands 'mhennig*' and 'bb*' to an input data file (see below). The parameters (e.g., tree rooting, character additivities) used in the earlier analyses of

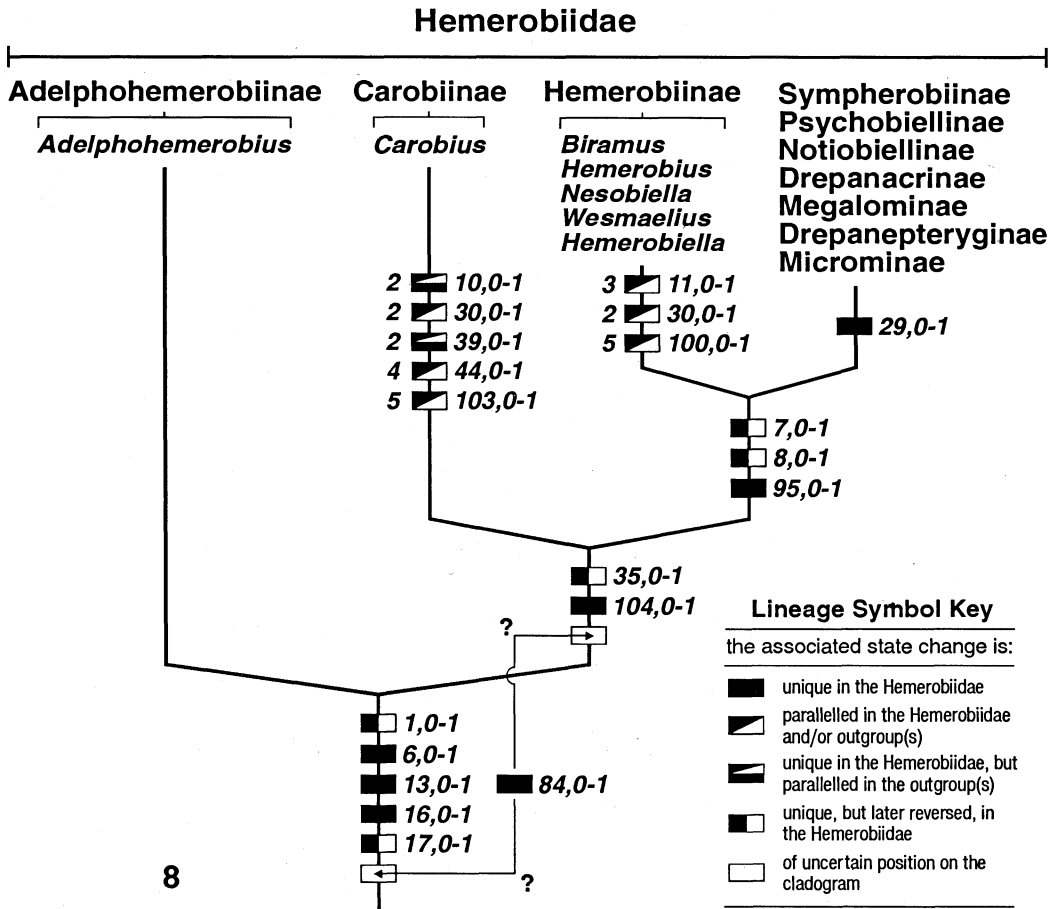


Fig. 8. Cladogram of basal relationships within the family Hemerobiidae. Character state changes are mapped in the following format [left to right]: (1) number of occurrences [if ≠ 1] of the state change on the complete cladogram of hemerobiid intergeneric relationships (not fully shown here), with outgroups, (2) lineage symbol, (3) character number, (4) state numbers [ancestral - derived]. Character and character state numbers are as in Oswald (1993a: 164-191). The position of character 84 is uncertain because the male of *Adelphohemerobius* is unknown.

sionally occur in this position in other hemerobiid taxa, and, given the apparent basal position of *Adelphohemerobius* within the Hemerobiidae, state 0 will probably be found to be characteristic for *Adelphohemerobius*.

Results. - A single most parsimonious tree (length = 198; ci = 0.60, ri = 0.70) was found. This tree - which places *Adelphohemerobius* as the sister-group to all previously known genera of the family Hemerobiidae - is shown in Fig. 8 in a collapsed form that fully illustrates only the most basal rela-

tionships within the Hemerobiidae. The topologies of those parts of the tree not shown in detail in Fig. 8 are identical to those illustrated previously by Oswald (1993a: fig. 23; as modified by Oswald 1993b: fig. 13).

Classification

Because it represents the sister-group to all other known hemerobiids, *Adelphohemerobius* might be assigned to a new family; however, its possession of

a habitus generally similar to that of other hemerobiids (e.g., in size, coloration, wing shape, and body form), as well as its possession of several of the autapomorphies attributed by Oswald (1993a) to the hemerobiid stem lineage (i.e., the stem of the clade Hemerobiidae), argue for its inclusion in a slightly expanded concept of the Hemerobiidae. In adopting this second taxonomic option, a new subfamily, Adelphohemerobiinae, has been required to incorporate *Adelphohemerobius* into the earlier sequenced classification of Oswald (1993a).

Discussion

Adelphohemerobius enigmarum is a remarkable hemerobiid. Its morphology combines the plesiomorphic traits of a single Rs and a slit-entry insemination/fertilization canal together with most of the autapomorphies identified by Oswald (1993a) as characteristic of the stem lineage of the Hemerobiidae (i.e., temporal costae well developed, and penicilliform galear sensilla and three pairs of prominent clypeal setae present). This mosaic of characters supports the conclusion that *Adelphohemerobius* constitutes the sister-group of all other known hemerobiids, and marks it as an important transitional form in the order Neuroptera.

It is unfortunate that no males of *Adelphohemerobius* were available for inclusion in the cladistic analysis. The states of its male 9th gonocoxites and parabaculum are of particular interest. Based on the present cladistic analysis, and that of Oswald (1993a), paired 9th gonocoxites should be present in *Adelphohemerobius*. The presence of these structures is a plesiomorphic feature currently known in the Hemerobiidae only in the genus *Carobius*. If male 9th gonocoxites are present in *Adelphohemerobius*, they will strengthen the conclusion that the loss of these structures is a synapomorphic feature of the vast majority of brown lacewing taxa (see Fig. 8, character 95).

Oswald (1993a) reinterpreted the hemerobiid male terminalic structure commonly called the 'parameres' to be an evolutionary novelty of the family Hemerobiidae, and renamed this structure the parabaculum. Because the male of *Adelphohemerobius* is currently unknown, the lineal position of the origin of this trait within the Hemerobiidae is now uncertain (Fig. 8, character 84). If a parabaculum is present in *Adelphohemerobius* the interpretation of Oswald (1993a) will be supported; if it is absent, the presence of a parabaculum would

constitute a synapomorphy of only the non-*Adelphohemerobius* hemerobiids. The latter condition (parabaculum absent) might prove to be the more interesting of these two cases, since it would clearly imply that the parabaculum was gained *within* the family Hemerobiidae and not inherited from a more distant common ancestor (Although Oswald [1993a] interpreted the parabaculum as a hemerobiid synapomorphy, its inheritance from a non-hemerobiid ancestor must still be considered a possibility because the true sister-groups of the Hemerobiidae remain speculative.)

It is interesting to note that although the male of *A. enigmarum* is of considerable phylogenetic interest (as discussed above), the conclusion that this species represents the sister-group of all other hemerobiids is well supported even in the absence of any knowledge of male structure. This seemingly paradoxical result, given the typical importance of male terminalic traits for inferring phylogenetic relationships within the Hemerobiidae, stems from the fact that few of the autapomorphies occurring on the basalmost lineages within the family Hemerobiidae involve traits of the male terminalic character complex.

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