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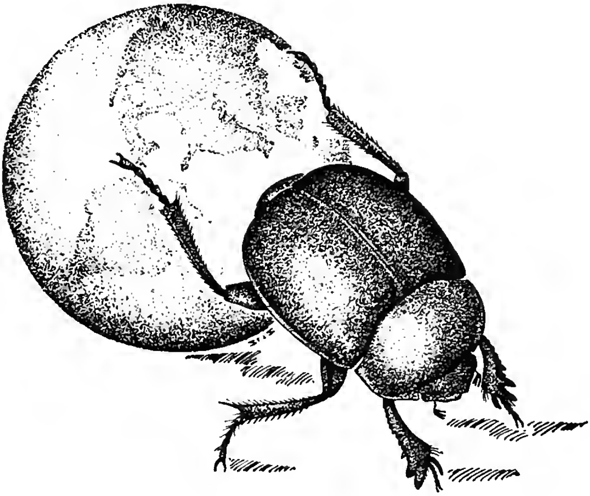

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# REVISION AND CLADISTIC ANALYSIS OF THE WORLD GENERA OF THE FAMILY HEMEROBIIDAE (INSECTA: NEUROPTERA)

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*Abstract.*—The extant world genera of the family Hemerobiidae are revised; and the literature on fossil hemerobiids is reviewed. A key is provided to the 25 extant genera recognized. An intergeneric cladistic analysis utilizing 107 characters, 24 ingroup genera, and 3 outgroup species provides a basis for (1) justifying the holophyly of the family, (2) recognizing holophyletic subgroups within the family, (3) proposing a new nine-subfamily classification of the family, and (4) identifying putative synapomorphies for nearly all recognized named taxa. Traits used in the cladistic analysis include characters from the head, forewing, and male and female terminalia. The biogeographic patterns exhibited within the family are discussed in light of the cladistic classification.

For each genus, a synonymical listing, a differential diagnosis, a list of proposed synapomorphies, and notes on distribution and included species are given. To the extent possible from the material available for study, representative forewings, hind wings, and several aspects of the male and female terminalia, are illustrated for each genus.

Phylogenetically important character complexes are analyzed in the comparative framework of the familial classification. The hemerobiid genitalic structure previously termed the "parameres" is here considered a unique evolutionary novelty of the family, and renamed the parabaculum. This structure is not a homologue of the "parameres" (=9th gonocoxites sensu Adams) of other neuropterous families. A new terminology is proposed for the putatively homologous regions of the gonarcus, facilitating comparative analysis of this complex sclerite.

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The family Hemerobiidae, brown lacewings, contains approximately 550 species which are collectively distributed on all continents except Antarctica. Several genera, e.g., *Hemerobius*, *Micromus*, and *Sympherobius*, are, or are nearly, themselves cosmopolitan. All known hemerobiid larvae are strictly predaceous. Adults are generally believed to be principally predaceous, but at least one recent work (Stelzel, 1990) documents unexpectedly high levels of honeydew feeding. All species apparently inhabit, both as larvae and adults, the surfaces of emergent terrestrial vegetation, upon which their foodstuffs are found.

The fragmented taxonomic literature on the Hemerobiidae consists largely of descriptive treatments, and accounts of local and regional faunas. Very few works of both broad taxonomic and broad geographic scope have been published. This situation has hindered the recognition of phylogenetically meaningful (i.e., holophyletic sensu Ashlock, 1971) groups on a global scale, and has discouraged the pursuit of studies such as comparative biology and biogeography, which are dependent upon the recognition of such groups.

This paper is a comprehensive revision of the family Hemerobiidae at, and above, the rank of genus. Its single most important objective has been to reorganize the family into a set of nested holophyletic taxa. To accomplish this, an extensive morphological survey was undertaken to identify characters of potential phylogenetic significance. The cladogram resulting from the cladistic analysis of the characters identified during this survey represents the first detailed hypothesis of hemerobiid intergeneric relationships. Although the cladistic relationships proposed here are subject to future corroboration, as are all hypotheses, the putative synapomorphies expressed on the cladogram support and identify specific clades which are capable of being confirmed or refuted by future work. In addition, the cladogram provides a much needed initial framework of sister-group relationships within the family. These relationships, in conjunction with the autapomorphies identified for most genera, provide a logical basis from which to begin comprehensive revisionary studies of individual genera.

In addition to its phylogenetic component, this work contains: (1) the first comprehensive key to world hemerobiid genera, (2) a new subfamily classification of the family, (3) a preliminary analysis of hemerobiid biogeography, and (4) a summary of available information on hemerobiid fossils. For each genus, diagnostic and distributional data are presented, and citations to published information on immature stages are given.

When this project was begun in 1986, the family Hemerobiidae contained approximately 45 valid genera and subgenera. Several of these have since been either formally removed from the family (*Nyrma* [to the Berothidae], by U. Aspöck, 1989), or synonymized with other hemerobiid genera (e.g., *Anotiobiella* [with *Hemerobius*], by Gonzalez-Olazo, 1987; *Oxybiella* and *Drepanomina* [with *Megalomina*], and *Kimminsiella* [with *Psectra*], by New, 1988; *Sympheromima* [with *Sympherobius*], by Oswald, 1988b; and *Idiomicromus* [with *Micromus*], by Monserrat, 1990). The changes proposed herein further restrict the number of valid genera to 25, and eliminate all previously recognized subgenera. This substantial reduction in the number of genus-group taxa results from the recognition of only demonstrably holophyletic taxa.

## MATERIALS AND METHODS

*Material.* This study is based on the examination of specimens of approximately 185 hemerobiid species borrowed from the following collections: American Museum of Natural History, New York, NY (AMNH); Bernice P. Bishop Museum, Honolulu, HI (BPBM); British Museum (Natural History), London, England (BMNH); California Academy of Sciences, San Francisco, CA (CAS); Cornell University Insect Collection, Ithaca, NY (CUIC); Florida State Collection of Arthropods, Gainesville, FL (FSCA); James B. Johnson, private collection (JOHNSON); Muséum National d'Histoire Naturelle, Paris, France (MNHP); Ellis G. MacLeod, private collection (MacLeod); Museum of Comparative Zoology, Harvard University, Cambridge, MA (MCZ); National Collection of Insects, Pretoria, South Africa (NCIP); National Museum of Natural History, Washington, DC (NMNH); Norman D. Penny, private collection (PENNY).

*Specimen Preparation and Examination.* Head capsules and terminalic structures were cleared in a cold 10 percent solution of KOH, generally overnight, then rinsed in 70 percent EtOH or a dilute solution of acetic acid. Most terminalic preparations were, in addition, stained for ca. 1–2 minutes in a saturated solution of 70 percent EtOH and Chlorazol Black, then rinsed in 70 percent EtOH. Structures were transferred directly from 70 percent EtOH to glycerine for examination under dissecting and/or compound light microscopes.

This procedure yielded generally satisfactory results. However, care was taken not to overstain multilayered structures, as overstained preparations may not be sufficiently translucent to allow examination with transmitted light. Such examination was found to be critical for accurately distinguishing the attachments of membranes to male genitalic structures (particularly to the gonarcus and parabaculum) and for obtaining a detailed understanding of the morphological configurations of complex genitalic structures.

*Illustrations.* Drawings were prepared with the aid of camera lucidas attached to Wild M5 dissecting and Olympus CH compound microscopes. Wings were detached and held flat between a pair of glass slides for illustration. To simplify wing figures, marginal trichosores have been omitted throughout. All hemerobiids possess prominent trichosores on the wing margins, although in a few taxa they are poorly developed or absent proximally. Wing flexion and fold lines are indicated by dashed lines.

Terminalic structures were mounted in glycerine jelly on depression slides to prevent rotation during illustration. Lateral views of male and female terminal abdominal segments are illustrated with little or no sclerite overlap. In actual preparations, telescopic foreshortening of these segments is commonplace. The trichobothria-bearing callus of the ectoproct is outlined only; individual trichobothria are not shown. Surface micro-ornamentation and setae are shown only where particularly diagnostic.

The gonarcus and parabaculum of one species of each genus are illustrated in dorsal and lateral views. These figures are oriented with anterior to the right, and dorsal (lateral view figures) or left side (dorsal view figures) up. An attempt has been made in many of these figures to show where the membranes associated with these sclerites are attached. This feature should aid in interpreting these structures, particularly with respect to the new terminologies proposed herein. To minimize hidden lines and maximize views of sclerotized surfaces, the free membrane margins in these figures are shown in artificially cropped and stretched positions.

Most terminalic figures have been drawn from material stained with Chlorazol Black. Some details shown in the illustrations may not be apparent in unstained material. This is particularly true of minute structural details of the gonarcus and parabaculum. It should also be noted that the edges of internal terminalic apodemes (e.g., those of the intragonarcus, the parabacular apophysis, and the anteroventral angles of some male 9th tergites) show evidence of adult growth. The absolute shapes of these structural components may vary as a function of post-ecdysial age.

Text references to figures found in this work are cited with a upper case "F" ("Fig."), those in other works with a lower case "f" ("fig.").

*Ordinal Nomenclature.* The following system of "neuropteroid" ordinal names is used here (after Kristensen, 1981): Neuropterida (adjective, neuropterid) = Neuroptera + Megaloptera + Raphidioptera; Neuroptera (adjective, neuropterous) = the lacewings and their allies (Planipennia); Megaloptera = Sialidae + Corydalidae; Raphidioptera = Inocelliidae + Raphidiidae.

*Terminology.* The general entomological terminology employed here follows The Torre-Bueno Glossary of Entomology (Nichols, 1989). Most terms used for particular character systems are explained below under the heading *Adult Morphology.*

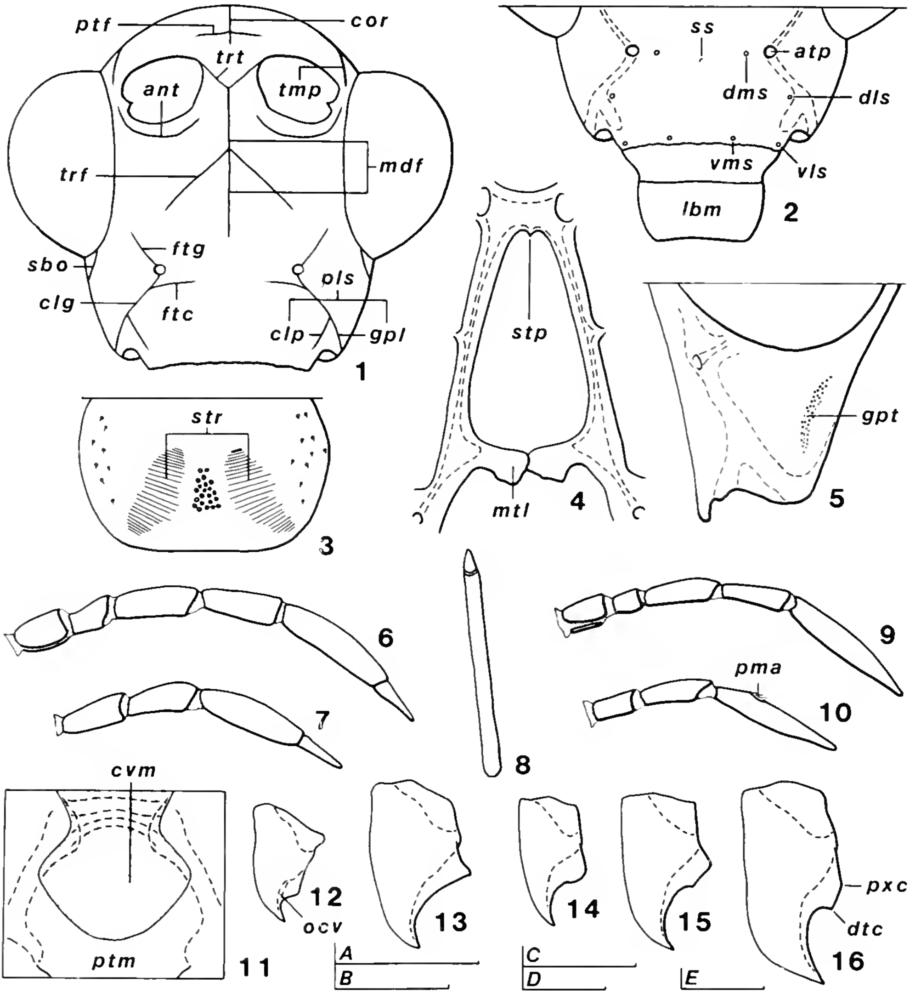
*Abbreviations and Annotations.* Collection acronyms are recorded above under *Material.* The following annotations are used in the synonymical listings: A, adult description or characterization; Bdy, body; Bio, biology; Dst, distribution; FT, female terminalia; ITSD, incorrect type species designation; Key, key or keyed; Lst, list or listed; Msc, miscellaneous notes; MT, male terminalia; Nom, nomenclature; OD, original description; RD, redescription; Syn, synonymy, synonymized; Tax, taxonomy (synonymy, homonymy, type data, etc.); W, wing. An asterisk (*) following an annotation indicates a figure (e.g., FW*, forewing figure).

## ADULT MORPHOLOGY

This section presents pertinent information on general hemerobiid morphology. It is intended primarily to supplement the characters used in the cladistic analysis (see below), not as a comprehensive morphological analysis or survey. The treatment by Killington (1936:13–44) is still the best general review of hemerobiid morphology, although some of its terminology is now out-of-date. Discussions of character polarities in this section are based on the results of the cladistic analysis presented in the next section.

### Head

*Cranium.* Well sclerotized; posterior surface with complete or incomplete postocular carinae running ventrally from the dorsolateral aspects of the occipital foramen to the posterior articulations of the mandibles; a variety of internal costae may be present (Fig. 1), these may or may not be evidenced by external sulci; frons unmodified externally, except in *Neosympherobius* which bears a pair of lateral cavities connected by a transverse depression, and a pair of low prominences above the anterior tentorial pits (Fig. 78); clypeus planate, bearing several pairs of homologizable primary setae (Fig. 2) in addition to more irregular setae; eyes prominent, pulvinate (Fig. 78) to hemispherical (Fig. 1); ocelli always absent; antennae moniliform, scape large, its shape variable but generally somewhat flattened (with a medially directed process in one *Zachobiella* species), pedicel somewhat larger than first flagellomere; tentorium strongly sclerotized, anterior arms with prominent mesal lobes (Fig. 4, mtl), devel-



Figs. 1–16. Head terminology. 1, Cranium, anterior (diagrammatic, showing principal costae). 2, Lower cranium, anterior (diagrammatic, showing insertions of principal clypeal setae). 3, Epipharyngeal surface of labrum (*Megalomus tortricoides*) [Scale bar E]. 4, Tentorium, anterodorsal (*Notiobiella multifurcata*) [A]. 5, Lower cranium, lateral (*Drepanacra binocula*) [B]. 6, Maxillary palpus (*Hemerobius humulinus*) [B]. 7, Labial palpus (*Hemerobius humulinus*) [B]. 8, Penicilliform sensillum of galea (*Megalomus tortricoides*) [C]. 9, Maxillary palpus (*Megalomus tortricoides*) [D]. 10, Labial palpus (*Megalomus tortricoides*) [D]. 11, Ventral part of occipital foramen, posterior (*Micromus montanus*) [B]. 12–16, Right mandibles, anterior. 12, *Carobius pulchellus* [B]. 13, *H. humulinus* [B]. 14, *Sympherobius amiculus* [B]. 15, *Psectra diptera* [B]. 16, *Psychobiella sordida* [B]. Abbreviations: ant, antennal costa; atp, anterior tentorial pit; clg, clypeogenal costa; clp, clypeopleurostomal costa; cor, coronal costa; cvm, cervical membrane; dls, dorsolateral seta; dms, dorsomedial seta; dtc, distal convexity; ftc, frontoclypeal costa; ftg, frontogenal costa; gpl, genopleurostomal costa; gpt, genal punctulae; lbm, labrum; mdf, midfrontal costa; mtl, mesal tentorial lobe; ocv, orad cavity; pls, pleurostomal costa; pma, palpi-

opment of dorsal arms highly variable, absent to very long, posterior tentorial bridge stout, generally with a short anteromedian process (Fig. 4, stp).

*Mouthparts.* Labrum approximately rectangular, aboral surface prominently setose, oral surface bearing sensory organs and, in *Megalomus*, two columns of transverse strigae (Fig. 3, str); mandibles moderately asymmetrical, left mandible modified to receive and overlap right mandible when opposed, both mandibles rarely with well-developed molar ridges (some *Megalomus*); mesal surface of left mandible with dorsal and ventral blades enclosing a groove which receives opposed right mandible, dorsal blade always bearing a prominent basal tooth; mesal surface of right mandible with a well-developed dorsal blade bearing one or two prominent cusps or a rounded lobe (Figs. 12–16), ventral blade vestigial (Fig. 12) or absent; maxillary palpus (Figs. 6, 9) 5-segmented, basal palpomere longitudinally divided, 5th palpomere simple (Fig. 9) or bisubsegmented (Fig. 6); galea 2-segmented, distal segment bearing several types of sensilla and an apical sensillar knob, the latter often minute and concealed by adjacent trichoid sensilla; laciniae attenuate and prominently setose; labial palpus (Figs. 7, 10) 3-segmented, 3rd palpomere simple (Fig. 10) or bisubsegmented (Fig. 7), 3rd palpomere always bearing a palpimacula (Fig. 10, pma) on its outer surface, the palpimacula is composed of a small group of recumbent setae overlying a shallow depression; glossae and paraglossae fused into a rounded ligula of variable shape.

## Thorax

*Prothorax.* Pronotum generally transverse, i.e., wider than long, occasionally more produced anteriorly; usually with a pair of distinguishable parasagittal calli.

*Pterothorax.* Very homogeneous throughout the family, see Killington (1936) for a general morphological account.

*Legs.* Procoxa elongate and subcylindrical, meso- and metacoxae short and conical; pro- and mesotibiae subequal or somewhat longer that pro- and mesofemora, protibia generally with an antennal comb composed of elongate, aligned, setae located distally on its anteromesal face; metatibia much longer that metafemur; all tarsi with five tarsomeres, all but the ultimate generally bearing a row of stout spines ventrodistally; pretarsus always with a pair of simple, lateral, arched claws and a median empodium.

## Wings

*General.* Trichosores always present, but sometimes vestigial or absent on proximal wing margins. Wing membranes always microtrichose, never macrotrichose (except very rarely along some wing veins). Nygmata never present. Pterostigma never sharply defined, but a 'pterostigmal area', marked by altered subcostal veinlets, is almost always identifiable in the distal portion of the costal space. Marginal end-twigging of longitudinal veins generally pronounced.

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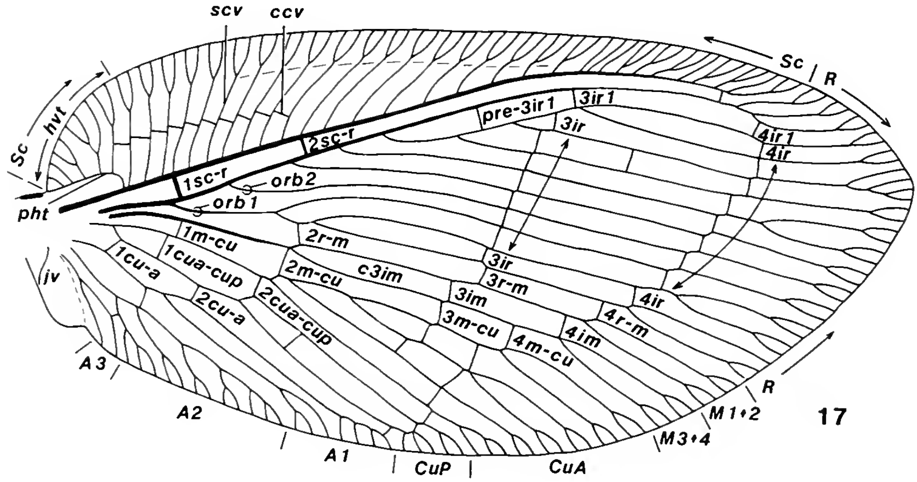
macula; ptf, postfrontal costa; ptm, postmentum; pxc, proximal convexity; sbo, subocular costa; ss, sagittal seta; stp, sagittal tentorial process; str, strigae; tmp, temporal costa; trf, transfrontal costa; trt, transtorular costa; vls, ventrolateral seta; vms, ventromedial seta. Scale bars (mm): A = 0.2; B = 0.2; C = 0.02; D = 0.2; E = 0.1.



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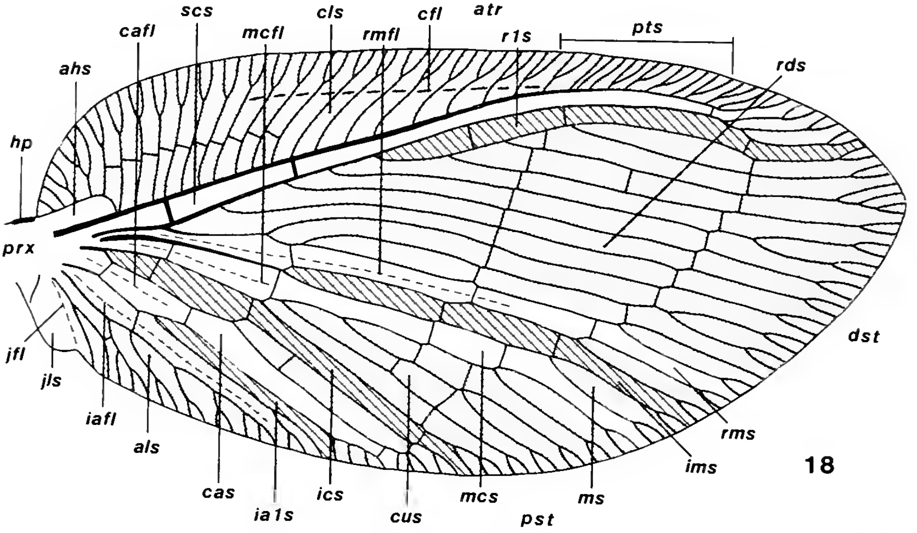

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Figs. 17–18. Forewing terminology. 17, Venation (composite). 18, Wing spaces, flexion lines, and miscellaneous (composite). Abbreviations: A1, A2, A3, anal veins; ahs, antehumeral space; als, anal space; atr, anterior; cafl, cubitoanal flexion line; cas, cubitoanal space; ccv, costal crossvein; cfl, costal flexion line; cls, costal space; CuA (cua), anterior cubitus; CuP (cup), posterior cubitus; cus, cubital space; dst, distal; hp, humeral plate; hvt, humeral veinlet; i, intra; ia1s, intra-A1 space; iafl, intraanal flexion line; ics, intracubital space; ims, intramedial space; jfl, jugal fold line; jls, jugal space; jv, jugal vein; M (m), media; mcfl, mediocubital flexion line; mcs, mediocubital space; ms, medial space; orb#, oblique radial branch of anterior radial trace = "radial sector"; pht, proximal humeral trace; prx, proximal; pst, posterior; pts, pterostigmal space; R (r), radius; r1s, R1 space; rds, radial space; rmfl, radiomedial flexion line; rms, radiomedial space; Sc (sc), subcosta; scs, subcostal space; scv, subcostal veinlet.

*Venation.* Three categories of wing veins are differentiated here: (1) *longitudinal veins*—longitudinal or oblique, setose, veins, (2) *veinlets*—longitudinal veins of the costal space, and (3) *crossveins*—asetose veins joining adjacent longitudinal veins. All veins are composed of one or more simple *internodes* bounded by *nodes* where they fork or intersect other veins. Crossveins always consist of a single internode. The vein expanse between two adjacent forks of a longitudinal vein is called an *interramus.* An interramus will consist of more than one internode if intersected by one or more crossveins.

*Longitudinal Veins.* The terminology adopted for the principle longitudinal veins of the forewing is given in Fig. 17. No "MA" arising from the apparent R is assumed present (see discussion under Characters 29–33 below).

*Traces.* Any continuous sequence of vein internodes may be referred to as a *trace.* This new venational concept allows great flexibility, precision, and conciseness in describing venational features, particularly in defining axes of vein pectinations and wing space boundaries. The major traces are the anterior and posterior traces of the principle longitudinal veins. These traces may be defined, respectively, as the most anterior and posterior sequences of internodes of each principle longitudinal vein. Other traces, e.g., the proximal humeral trace (Fig. 17, pht [="recurrent vein" of authors]), may be defined in a similar manner.

*Gradate Series.* Crossveins are frequently arranged in more or less aligned tracts called gradate series. Up to five gradate series are commonly found in hemerobiid forewings (Fig. 17), these are the *costal gradate series,* and up to four series posterior to the anterior radial trace. In this work, the number and position of the latter series are based on the inferred plesiomorphic number (4) and positions of the m-cu crossveins. These series are numerically designated 1 to 4 starting at the base of the wing. Crossveins belonging to each series are prefixed with the same numerical designator. The serial assignment of individual crossveins is sometimes problematic; and extra, short, interpolated, series are occasionally developed in some large-winged taxa (e.g., Fig. 166). The proper assignment of crossveins lying behind the anterior cubital trace to the 3rd or 4th gradate series is often especially difficult.

The numerical designation of gradate series is preferred here over the common prior practice of using relative positional designators (i.e., "inner", "middle" and "outer"). The numerical system proposed here is intended to imply specific crossvein (for some crossveins) and series homologies. The relative positional designator system has generally been used as a system of convenience, without specific regard for homologies. Specific hypotheses about principle crossvein homologies are required here to facilitate critical assessment of gradate series variations, particularly, to infer gains or losses of entire gradate series and gains or loses of individual principle crossveins.

*Crossveins.* The principle crossveins joining different principle longitudinal veins are designated by a numerical prefix and a pair of vein abbreviations in lowercase letters, e.g., the four principle mediocubital crossveins are designated 1m-cu, 2m-cu, 3m-cu, and 4m-cu (Fig. 17). The number indicates the gradate series association of the crossvein, and the letters the longitudinal veins it intersects. Crossveins joining different branches of the same longitudinal vein are designated by a numerical prefix, the letter "i" ['intra-'], and one lowercase vein abbreviation, e.g., the two principle intramedial crossveins are designated 3im and 4im (Fig. 17).

*Membranes.* Two categories of wing membrane divisions are differentiated: (1) *cells*, unbroken expanses of membrane bounded by veins and/or the wing margin, and (2) *spaces*, aggregates of cells (and vein segments) bounded by veins and the wing margin.

*Cells.* Wing cell designations are formed from the designation of the crossvein bounding the cell distally and the prefix "c" ['cell'], e.g., the intramedial cell bounded distally by crossvein 3im is designated c3im (Fig. 17).

*Spaces.* Ten principle, and five secondary, wing spaces are differentiated here. The principle spaces are bounded by the anterior and posterior traces of most of the principle longitudinal veins. Secondary spaces are subdivisions of principle spaces. All spaces used herein are illustrated in Fig. 18.

*Flexion and Fold Lines.* Flexion and fold lines are designated after the wing space in which they occur. Up to five flexion lines are present (Fig. 18): (1) *costal* (cfl), (2), *radiomedial* (rmfl), (3) *mediocubital* (mcfl), (4) *cubitoanal* (cafl), and (5) *intraanal* (iafl). A single fold line, the *jugal* (jfl), is always present.

*Forewing.* Always macropterous. Membrane frequently hyaline, but more often darkly mottled with browns or blacks on a more or less hyaline ground, rarely secondarily coriaceous. Veins whitish, yellowish, reddish, blackish, brownish, or green (rare), frequently with alternating light and dark regions. Forewing outlines extremely variable, continuously convex shapes vary from narrowly elliptical (Fig. 115) to nearly circular (Fig. 132), shapes with one or more marginal concavities (especially on the posterior wing margin) have been independently derived in several lineages.

Costa prominent. Costal space of variable width, attenuating distally; humeral area extremely broad (Fig. 132) to very narrow (Fig. 124); *humeral veinlet* (most proximal subcostal veinlet) simple to many branched; *proximal humeral trace* (="recurrent vein" of authors) strongly recurrent to simply transverse; posthumeral subcostal veinlets simple or branched, but only rarely all simple. Subcostal space generally with 2 or 3 crossveins, 1 substigmal and 1 (Fig. 17, 1sc-r) or 2 (Fig. 17, 1sc-r and 2sc-r) proximal, rarely with proliferated supernumeraries (Fig. 174); proximal width wider than adjacent subcosta, except in *Notiobiella*. Radius highly modified, with one or more branches (the ORB's [oblique radial branches] or "radial sectors") of ancestral Rs origin, secondarily originating from the anterior radial trace (see discussion under Characters 29–33 below). CuA and M3+4 fused in *Nusalala* and many *Micromus*. Jugal lobe well formed, one jugal vein present.

*Hind Wing.* Shorter than forewing, usually macropterous, rarely brachypterous, micropterous, or absent [lost]. Membrane generally pale, sometimes weakly mottled, never coriaceous. Humeral plate generally forming an oblique strut at base of wing (e.g., Fig. 34), and often with a short distal lobe bearing several stout, frenulum-like, bristles. Humeral veinlet (most proximal subcostal veinlet), and most or all posthumeral subcostal veinlets, simple. Subcosta stout. Crossveins absent proximally in subcostal space. Radius not modified as in forewing, but occasionally with Rs stem closely associated with or briefly fused to R1. R1 space frequently with a prominent proximal ir1 crossvein which mimics a second "radial sector" (Fig. 99). Remnant of inferred MA always present as a well-developed, generally sigmoid, vein which terminates on the posterior radial trace. CuA stout. CuP well developed to absent, possibly size correlated, with greater development in larger wings. A1 usually deeply forked. Jugal lobe vestigial, jugal vein present.

*Additional Terminological Considerations.* The phrase "radial sectors" is used here in its traditional sense, i.e., to collectively refer to the two or more prestigmal oblique branches of the forewing anterior radial trace. Although technically incorrect, this phrase is used in several places in this work (e.g., in the generic key) because it is concise and widely understood in the intended sense. The "radial sectors" are called "oblique radial branches" (ORB's), when a designation relatively free of implications of homology is necessary or convenient. ORB's are counted consecutively from the base of the wing.

### Abdomen

*General.* 10-segmented; segments 1–8 with paired lateral spiraculae; 10th tergite always bipartite, each half (*ectoproct*) bearing an oval aggregation of trichobothria set in rosettiform alveoli and borne on a low callosity; segments 8–10 always sexually dimorphic, more proximal segments only occasionally sexually dimorphic.

*Basal Segments (1–6).* Tergites 1–6 and sternites 2–6 free and hemiannular; each sternite generally with a transverse costa internally, costae gradually decreasing in prominence on more posterior segments, sternite 1 reduced to a transverse strip; male tergites 3–4 (sometimes other tergites also) frequently notched posteromedially; male tergites 4–6 rarely (some *Psectra*) with marginal posteromedian processes.

### Female Terminalia (Abdominal Segments 7–10)

*7th Segment.* Tergite free and hemiannular; sternite free and normally hemiannular, rarely divided (*Anapsectra*).

*8th Segment.* Lateral tergite margins produced ventrally below, and enclosing, spiraculae of 8th segment (Fig. 26), contralateral margins often lying closely adjacent ventrally or, rarely, fused; 8th sternite (*subgenitale*) variously developed, large and prominent to absent, when prominent, its apex usually enclosed at rest by a pair of small concave or rod-like sclerites, the *gonapophyses posteriores*, which are associated with the anteroventral angles of the 9th gonocoxites.

*9th Segment.* Lateral portions of tergite greatly expanded ventrally, and extended posteriorly to subtend ectoprocts, contralateral margins generally closely adjacent on ventral midline; tergite sometimes (e.g., most Microminae) sagittally divided; tergite often narrowed, sometimes divided (e.g., some *Psectra*, Fig. 110), laterally; sternite absent; paired gonocoxites always prominent and usually free, elongated (e.g., some *Wesmaelius*, Fig. 52), rarely partially fused to each other (e.g., *Anapsectra*, some *Hemerobius*) or to adjacent ipsilateral margins of 9th tergite (e.g., *Zachobiella*, Fig. 126), stylus present (Fig. 26) or absent [lost] (Fig. 35).

*10th Segment.* Ectoprocts rarely strongly lobed or ornamented (in contrast to males); sternite absent.

*Internal Reproductive Tract.* Vulva opening between paired 9th gonocoxites, leading into a broad, membranous (rarely partially sclerotized), genital chamber (*bursa*), which is presumed to receive male's spermatophore, and into which open the colleterial gland, bursal glands, and the proximal end of the insemination-fertilization

Table 1. General terminology for gonarcus and associated membranes.

| | Gonarcus[1] | | |
|---|---|---|---|
| | Paleogonarcus | | Neogonarcus |
| | Intragonarcus | Extragonarcus | Neogonarcus |
| Gonopons | Intragonopons | Extragonopons | Neogonopons |
| Hemigonarcus | Intrahemigonarcus | Extrahemigonarcus | Neohemigonarcus |
| Associated membranes | Paragonosaccal | Paragonosaccal & Gonosaccal | Paragonosaccal [& Gonosaccal] |

[1] See also Figures 19, 20. Unfortunately, proper orthography dictates that the singular and pleural forms of words based on the Latin work "arcus," arch, bear the same ending, -us.

canal. The latter canal opens at a small rounded pore (not a slit) at the anterior end of the bursa, its distal end presumably emptying into the common oviduct. The shape of the canal is highly variable, generally a narrow, more or less irregularly convoluted tubule, rarely helical (e.g., some *Noius*), often with an expanded area somewhere along its length. The term "spermatheca", which has been used in prior literature to indicate either any well-sclerotized portion of the insemination-fertilization canal, or a prominently expanded region along its length, requires clarification and standardization within neuropterous taxa. Consequently, this term is not used here.

## Male Terminalia (Abdominal Segments 7–10)

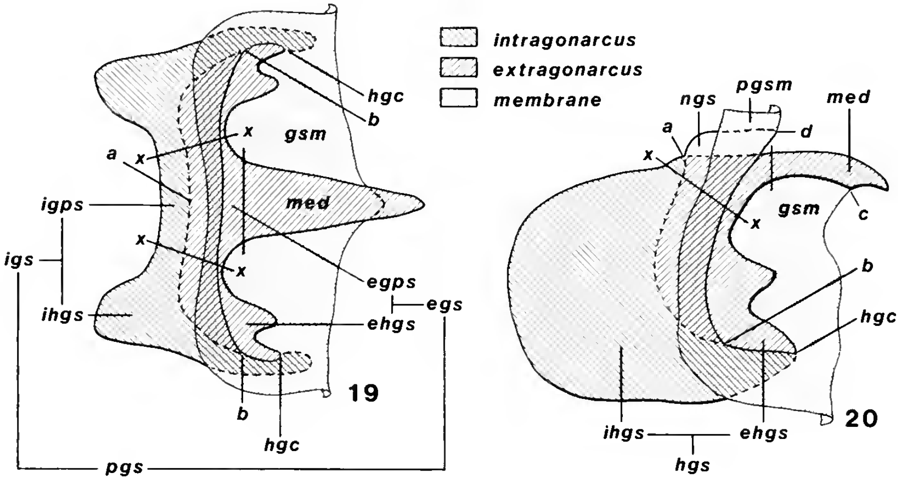
### Tergites and Sternites

*7th Segment.* Tergite and sternite nearly always free and hemiannular, tergite occasionally with processes (some *Megalomus, Psectra, Zachobiella*).

*8th Segment.* Tergite and sternite normally free and hemiannular; tergite rarely with processes (some *Psectra*, *Zachobiella*), or linked to 8th sternite (some *Zachobiella*, Fig. 127) or 7th tergite; sternite rarely (some *Zachobiella*, Fig. 127) with a posteromedian projection (=?fused 9th sternite); spiraculae rarely opening through prolonged lateral margins of tergite (some *Notiobiella* and *Zachobiella*) or sternite (some *Zachobiella*, Fig. 127).

*9th Segment.* Tergite generally free, and approximately hemiannular overall, but with numerous modifications in different taxa, including: (1) anteroventral angles produced internally as apodemes (e.g., *Nesobiella*, Fig. 47; *Anapsectra*, Fig. 117), (2) posteroventral angles produced as distinct processes (e.g., Sympherobiinae, Fig. 69; *Psectra*, Fig. 108; *Zachobiella*, Fig. 127), (3) posterior margin produced as an elongate process (some *Psectra*), (4) a sagittal dorsal division (most Microminae), (5) a transverse dorsal division, separating anterior antecostal portion of tergite from posterior portion (some *Psectra*), or (6) partial fusion with ectoproct (most Microminae); sternite extremely variable in shape, from small, flat or hemiannular plates to prominently produced tubular structures (e.g., Fig. 47), occasionally (1) with distinctive ornamentation (Fig. 194), or (2) apparently lost or fused with 8th sternite (some *Zachobiella*, Fig. 127); 9th gonocoxites prominent in *Carobius*, absent in all other taxa.

*10th Segment.* Ectoprocts articulating with (Fig. 27), or fused to (Fig. 222), posterior margins of 9th tergite, and very diversely ornamented within in the family; orna-



Figs. 19–20. Male gonarcus terminology. 19, Gonarcus, dorsal (diagrammatic). 20, Gonarcus, lateral (diagrammatic). Abbreviations: a, b, c, d, reference points; egps, extragonopons; egs, extragonarcus; ehgs, extrahemigonarcus; gsm, gonosaccal membrane; hgc, hemigonarcal conjunction; hgs, hemigonarcus; igps, intragonopons; igs, intragonarcus; ihgs, intrahemigonarcus; med, mediuncus; ngs, neogonarcus; pgs, paleogonarcus; pgsm, paragonosaccal membrane; x-x, reference line.

mentation types include (1) broad, hollow, cuticular lobes, (2) solid projecting spines, and (3) numerous modifications of setae and their bases.

### Gonarcus

The hemerobiid gonarcus is a highly variable and frequently complex sclerite. It's morphology has been extensively studied for this work. To provide a foundation for accurately assessing the homologies of its parts, and to clear up earlier misinterpretations, its structural morphology is treated in detail below. Some of the terminology employed was proposed earlier by Oswald (1988b), but much is new. The terms used below for the principal divisions of the gonarcus are summarized in Table 1; and most are identified in Figs. 19—20.

*Commissures, Intragonarcus and Extragonarcus.* The hemerobiid gonarcus is a complex sclerite composed of surface (external) and apodemal (internal) components, which are freely suspended in the membranous posterior body wall of the abdomen. Gonarcal components are membranously attached to the body wall along lines, called *commissures*, which constitute the principal landmarks for delimiting putatively homologous gonarcus regions. There are three primary commissures: (1) the antextragonarcal, (2) the postextragonarcal, and (3) the neogonarcal.

The *antextragonarcal commissure* (Figs. 19, hgc-b-a-b-hgc; 20, hgc-b-a) marks the line of attachment of the *paragonosaccal membrane* (Fig. 20, pgsm) to the *paleogonarcus* (Fig. 19, pgs). This commissure divides the posterior (external) components of the paleogonarcus (collectively the *extragonarcus* [Fig. 19, egs]), from its anterior (apodemal) components (collectively the *intragonarcus* [Fig. 19, igs]). The antextragonarcal commissure extends dorsad from its pair of termini at the *hemigonarcal conjunctions* (Figs. 19–20, hgc), which are the two ventrolateral points on the gonarcus where the free margin of the intragonarcus meets the ventral margin of the extragonarcus. The hemigonarcal conjunctions are important gonarcal landmarks and are generally easily located in stained preparations. The path of the antextragonarcal commissure may be obscured by secondary sclerotization of the paragonosaccal membrane (see *Neogonarcus and Neogonarcal Commissure* below).

The *postextragonarcal commissure* (Figs. 19, hgc-hgc; 20, hgc-c) marks the line of attachment of the *gonosaccal membrane* (Fig. 20, gsm) to the *extragonarcus* (Fig. 19, egs). Like the antextragonarcal commissure, the postextragonarcal commissure terminates ventrally at the hemigonarcal conjunctions. The path of the postextragonarcal commissure is generally distinct, but may be discontinuous (when the mediuncus is membranously separated from the gonarcus arch), highly convoluted, or obscure (when the posterior margin of the extragonarcus is poorly defined).

*Gonopons and Hemigonarcus.* The gonarcus arch has historically been partitioned into three parts, a pair of lateral "wings", the *hemigonarcus* (Fig. 20, hgs), and a dorsomedial connecting "bridge", the *gonopons* (Fig. 19, igps + egps). These regions are approximately delimited in Figs. 19–20 by lines marked "x-x". Although the positions of these boundaries are sometimes imprecise, they are generally clear enough to be of use descriptively, and this tripartite division is retained here.

By combining the two preceding gonarcal division schemes (intragonarcus/extragonarcus, and gonopons/hemigonarcus), the paleogonarcus can be partitioned into six basic regions (see Table 1): (1) an anterodorsal, apodemal *intragonopons* (Fig. 19, igps), (2) a posterodorsal, external *extragonopons* (Fig. 19, egps), from which the *mediuncus* (Fig. 19, med) extends posteriorly, (3) a pair of anterolateral, apodemal *intrahemigonarcus* (Fig. 20, ihgs), and (4) a pair of posterolateral, external *extrahemigonarcus* (Fig. 20, ehgs).

*Neogonarcus and Neogonarcal Commissure.* In addition to sclerites of paleogonarcal origin (i.e., the intragonarcus + extragonarcus), many hemerobiid gonarcus contain sclerotized structural elements derived from the secondary sclerotization of the plesiomorphically membranous paragonosaccal membrane. The term *neogonarcus* (Fig. 20, ngs) is used here to collectively refer to these elements. It is sometimes convenient to partition the neogonarcus into a dorsomedian *neogonopons* and a pair of lateral *neohemigonarcus*, named for the analogous portions of the paleogonarcus.

The *neogonarcal commissure* (Figs. 19, b-b; 20, b-d) marks the line of attachment of the membranous (distal) portion paragonosaccal membrane (Fig. 20, pgsm) to the margin of its sclerotized (proximal) part, the neogonarcus (Fig. 20, ngs). In almost all cases, the ends of the neogonarcal commissure are confluent with some part of the antextragonarcal commissure. The neogonarcal commissure is discontinuous when lateral neohemigonarcal plates are developed without a dorsally connecting neogonopons (e.g., Fig. 72). Poor definition of the posterior margin of the neogonarcus sometimes prevents precise definition of the neogonarcal commissure.

*Intragonarcus.* The intragonarcus (Fig. 19, igs) is the internal, apodemal, portion of the paleogonarcus. It is bounded posteriorly by the antextragonarcal commissure. It is generally divisible into a narrowly transverse, dorsomedial bar, the intragonopons (Fig. 19, igps), and a pair of broad lateral lobes, the intrahemigonarcus (Fig. 19, ihgs);

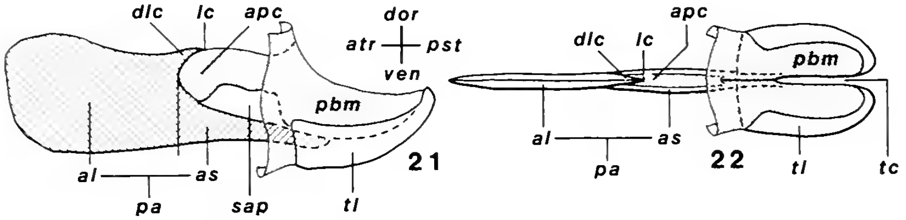
although, the boundary between these regions is not always clear, particularly when the intrahemigonarcus are poorly developed. Surface irregularities of the intragonarcus include localized depressions and occasional carinae. Although well sclerotized, the intragonarcus is usually poorly pigmented; consequently, the details of its structure may not be fully apparent in unstained preparations. The intragonarcus generally exhibits evidence of growth along its free margin in the form of sequentially arranged sclerotized arcs. Since the margin of the intrahemigonarcus appears to grow at a greater rate than that of the intragonopons, the shape of the intragonarcus may vary as a function of adult age.

*Extragonarcus.* The extragonarcus (Fig. 19, egs) is the externally exposed portion of the paleogonarcus. It is bounded anteriorly by the antextragonarcal commissure and posteriorly by the postextragonarcal commissure. The conformation of the extragonarcus is extremely variable within the Hemerobiidae. It is generally composed of a sclerotized, anterior (proximal), arch which bears one or more posteriorly directed processes. The proximal arch is generally divisible into a dorsomedial area, the extragonopons (Fig. 19, egps), and a pair of lateral areas, the extrahemigonarcus (Fig. 19, ehgs). The frequently prominent dorsomedian process of the extragonarcus is called the *mediuncus* (Fig. 19, 20, med). The approximate division of the mediuncus from the extragonopons is shown in Figs. 19 and 20 by a heavy vertical line.

*Neogonarcus.* The term neogonarcus (e.g., Fig. 20, ngs [a-b-d-a]) is used here to collectively refer to any secondary sclerotization(s) of the paragonosaccal membrane which is(are) attached to the gonarcus along the antextragonarcal commissure (Fig. 20, a-b-hgc). Non-homologous neogonarcal elements of varying configuration and complexity have evolved independently in different hemerobiid lineages. In some cases these elements considerably alter the overall appearance of the gonarcus.

In some genera, the neogonarcus is present as a prominent arched plate, which extends roof-like over the base of the clearly identifiable mediuncus (as is shown in Fig. 20, also in some *Megalomina*, Fig. 211, ngs; *Neuronema*, Fig. 170, ngs; *Psychobiella,* Fig. 97, ngs). Occasionally, prominent neogonarcus bear attenuate, posteriorly directed, processes (e.g., *Micromus*, Figs. 219, ngs, ngsp; 220). The extent of lateral development of the neogonarcus is highly variable, but frequently the neohemigonarcus enclose much of the extrahemigonarcus (Figs. 96–97). In some cases the structural role of the extrahemigonarcus are taken over by the neohemigonarcus, and the extrahemigonarcus are reduced. In a few extreme cases (e.g., *Megalomus flinti* and *nigratus*, and some *Neuronema*) the ventral portions of the extrahemigonarcus are entirely lost and the gonosaccal membrane is attached directly to the internal surface of the neohemigonarcus (not the posterior margin of the extragonarcus). In these cases, it is imperative to make reference to the gonarcal commissures to establish the correct homology of gonarcal elements.

In *Sympherobius* (Fig. 84), the extragonopons and mediuncus are absent [lost]; and the gonosaccal membrane terminates transversely on the ventral surface of the gonopons. The structure which occupies the position of the mediuncus in this genus is actually a narrow neogonarcal element, the *pseudomediuncus* (pmd). This sclerite articulates with the posterior margin of the gonopons and, at rest, generally lies partially suspended below the gonopons. Less-developed pseudomediunci are present in the genera *Nomerobius* (Fig. 72) and *Neosympherobius* (Fig. 76).



Figs. 21–22. Male parabaculum terminology. 21, Parabaculum, dorsal (diagrammatic). 22, Parabaculum, lateral (diagrammatic). Abbreviations: al, apophyseal lamella; apc, apophyseal cavity; as, apophyseal shaft; atr, anterior; dlc, dorsolamellar cusp; dor, dorsal; lc, lamellar conjunction; pa, parabacular apophysis; pbm, parabacular membrane; pst, posterior; sap, supraapophyseal plate; tc, terminal cleft; tl, terminal lobe; ven, ventral.

## Parabaculum

The hemerobiid genitalic structure previously called the "parameres" is here renamed the *parabaculum* (name from the Greek *para*, near, and the Latin *baculum*, rod, in reference to the inferred plesiomorphic shape of its apodeme; plural, *parabaculi*). A new name is required for this structure because, as argued below under *Homology*, it is not a homologue of the 9th gonocoxites (sensu Adams, 1969), which have been frequently called "parameres" in other Neuroptera. The fine structure of the parabaculum is highly variable and frequently of taxonomic value. Below, I discuss the general morphology and structural variability of the parabaculum.

*General Morphology* (Figs. 21–22). The parabaculum is composed of two fundamental sclerotized regions: an anterior *parabacular apophysis* (pa), and a pair of posterior *terminal lobes* (tl). The terminal lobes are separated medially by an anteriorly convergent space, the *terminal cleft* (tc). The parabaculum is freely suspended in the membranous body wall at the posterior end of the abdomen. The terminal lobes lie parasagittally, below the gonarcus-mediuncus complex, and above the 9th sternite and hypandrium internum. The membrane adjacent and attached to the parabaculum is called the *parabacular membrane* (pbm). The parabacular apophysis is generally elongate, and usually extends medially for a considerable distance between the hemigonarcus. Although freshly preserved material was not examined, it seems likely that the muscles which control the motion of the parabacular apophysis insert principally on the inner surfaces of the hemigonarcus.

*Orientational Terminology*. The parabaculum is composed of external surface sclerites and sclerotized apodemal components. Its suspension in the membranous abdominal body wall allows it great range of motion and orientation. These factors make it difficult to conveniently apply self-evident descriptors of relative position (e.g., proximal, posterior) to the parabaculum, because the terms would lack a clearly evident orientational basis. The orientational basis arbitrarily imposed upon the parabaculum for the descriptive purposes of this work is shown associated with Fig. 21.

*Parabacular Apophysis*. The plesiomorphic condition of the parabacular apophysis is presumed to be that of a simple elongate apodeme composed of two subregions: a posterior, baculiform, *apophyseal shaft* (as), and an anterior, sagittally oriented plate, the *apophyseal lamella* (al). The apophyseal lamella is an apodemal process which extends freely into the body cavity. The generally narrower apophyseal shaft connects the apophyseal lamella to the terminal lobes.

The point at which the free dorsal margin of the apophyseal lamella meets the parabacular membrane is called the *lamellar conjunction* (lc). The parabacular membrane is plesiomorphically attached to the parabacular apophysis along two contiguous lines which begin at the lamellar conjunction and extend parasagittally along the dorsal margin of the apophyseal shaft. The lamellar conjunction is frequently located at the apex of an acute process of the posterodorsal margin of the apophyseal lamella, the *dorsolamellar cusp* (dlc). The dorsolamellar cusp frequently extends posteriorly over a portion of the dorsal surface of the apophyseal shaft. When this occurs, a compressed space, the *apophyseal cavity* (apc), becomes dorsally enclosed by the dorsolamellar cusp, ventrally enclosed by the apophyseal shaft, and laterally enclosed by the parabacular membrane.

Apophyseal cavity configurations exhibit varying degrees of complexity and development within the family. A compressed, shallowly concave space with membranous lateral walls is the putative plesiomorphic condition. In a slightly more derived condition, the cavity remains shallow and compressed, but the lateral walls become partly or entirely sclerotized. In a still more derived condition, the lateral walls are well sclerotized with the dorsolamellar cusp reaching, or nearly reaching, the terminal lobes. This results in a condition in which an elongate and compressed tube is enclosed within a baculiform apophysis (Fig. 70, 71).

The parabacular apophysis often bears prominent sclerotized structures of secondary origin. Collectively, these structures are referred to as *supraapophyseal plates* (Fig. 21, sap), but they are almost certainly not homologous among the genera which exhibit them. These plates represent secondarily sclerotized portions of the parabacular membrane associated with the dorsal surface of the parabacular apophysis. They are generally more or less bilaterally symmetrical and may be articulated or rigidly fixed to the parabacular apophysis.

Supraapophyseal plates may be erect and parasagittally adpressed (e.g., *Drepanacra*, Figs. 155–156; some *Micromus*), or laterally splayed (e.g., *Megalomus*, Figs. 164–165; *Nusalala*, Figs. 205–206, lbc; some *Wesmaelius* and *Neuronema*). Close inspection of parasagittally adpressed supraapophyseal plates usually reveals some of evidence of an apophyseal cavity, or its remnant, between them. Splayed supraapophyseal plates may or may not be associated with a compressed apophyseal cavity, and may additionally bear prominent processes or spines (e.g., some *Nusalala*, *Neuronema*).

Several genera (e.g., *Nusalala, Gayomyia*, most *Neuronema*) possess supraapophyseal sclerites which articulate with the parabacular apophysis. In *Nusalala* and *Gayomyia*, these appear to represent novel secondary sclerotizations of the parabacular membrane which have developed in close functional association with the parabacular apophysis, and have maintained a plesiomorphic articulation. The structures in these genera have been given separate names, *laterobacula* in *Nusalala* (Fig. 205, lbc) and *penniform sclerites* in *Gayomyia* (Fig. 179, pen), to indicate their presumed independent origin.

*Modifications of the Apophyseal Shaft.* The plesiomorphic, slender, apophyseal shaft may exhibit one or more of several types of modifications. The following are exemplary, not exhaustive. The apophyseal shaft may be: (1) deeply (e.g., *Drepanepteryx*, Fig. 189; *Nesobiella*, Fig. 48) or entirely (*Hemerobius*, Fig. 37) divided sagittally, (2) superficially unrecognizable due to secondary sclerotization of the adjacent parabacular membrane, which may obscure the dorsal surface of the apophyseal shaft (e.g., some *Micromus* and *Megalomus*), (3) modified as a broad horizontal plate with the parabacular membrane attached along its lateral margins (e.g., some *Micromus*; *Zachobiella*, Fig. 128), or (4) prominently grooved medioventrally (e.g., some *Neuronema* and *Micromus*).

*Modifications of the Apophyseal Lamella.* The apophyseal lamella is, with very few exceptions, always a distinct structure. In the few taxa where the lamella is vestigial or lost (e.g. some *Megalomus*), its muscle insertions have apparently shifted to adjacent apophyseal plates, which are always well developed when the lamella is absent. In *Hemerobius*, where the parabaculum is composed of a pair of independent, bilaterally symmetrical, halves, each half bears a small anterior lamella (Figs. 37–38). In other species, the ventral groove of the apophyseal shaft may extend anteriorly onto the apophyseal lamella resulting in a tricuspidate cross-section.

*Terminal Lobes.* The configurations of the terminal lobes of the parabaculum are extremely diverse within the family, and are of considerable taxonomic value. In their presumed plesiomorphic condition they are a small bilaterally symmetrical pair of lobes with limited dorsal sclerotization. More derived conditions include such diverse modifications as spinose or multiply-lobed structures or, in the one *Zachobiella* male examined, with the lobes apparently fused into a single median process (Fig. 128). The terminal lobes are external sclerites and often bear surface micro-ornamentation.

*Parabaculum Homology.* Adams (1969:8–10) discussed the homology and origin of the principal components of the male terminalia in the Neuropterida. He homologized neuropterid male "parameres" with the 9th gonocoxites of other insects, and traced the evolution of neuropterid 9th gonocoxites from their putative ancestral association with the 9th tergite (retained in Raphidioptera, most Megaloptera, and a few Neuroptera) to their derived association with the gonarcus (found in most Neuroptera and a few Megaloptera). According to Adams' interpretation, which is adopted here, the structures previously called "parameres" in most neuropterous families are 9th gonocoxite homologues.

Based on Adams' discussion (pp. 9–10), three general recognition criteria can be stated for neuropterous 9th gonocoxites: (1) proximal association with the posterior margin of the extragonarcus, (2) prominent setation, and (3) clear evidence of paired ancestral structure. If the hemerobiid parabaculum is also a 9th gonocoxite homolog (sensu Adams), one could reasonably expect to recognize it on the basis of one or more of these criteria; the hemerobiid parabaculum, however, fails all three.

Criterion 1: *Proximal Association with Extragonarcus.* The hemerobiid parabaculum is never fused to or articulated with the extragonarcus. In only a few clearly derived cases are parts of the parabaculum even closely associated with the posterior margin of the extragonarcus. For example: (1) in a few *Micromus* the posterior margins of the hemigonarcus are strongly bent medially, and encroach upon the parabaculum, and (2) in some *Megalomus* (e.g., Figs. 164–165) the supraapophyseal plates are well developed and laterally splayed, and their margins may approach the extragonarcus laterally.

Criterion 2: *Setation.* Hemerobiid parabaculi frequently bear minute microtrichia or microspines, but they are apparently never setose.

Criterion 3: *Paired Ancestral Structure.* All previous authors appear to have regarded the hemerobiid parabaculum as a structure derived from a pair of independent ancestral sclerites. This assumption is implicit in frequent statements in the hemerobiid literature regarding "fused parameres". This idea appears to have drawn support from two primary observations: (1) the nearly universal presence of paired terminal lobes on hemerobiid parabaculi, and (2) the presence of a completely bipartite parabaculum in the genus *Hemerobius.* This apparent support is examined below.

Although paired terminal lobes of the parabaculum are apparently present in all hemerobiid genera except *Zachobiella,* this condition does not necessarily imply derivation of this structure from a pair of incompletely fused ancestral sclerites (where the terminal lobes would represent a remnant of paired structure). If the fusion hypothesis was true, evidence of a suture marking the line of sagittal fusion between the ancestral sclerites could reasonably be expected. I have been unable to find any such suture in the parabaculum. The apophyseal lamella is always a simple lamellate apodeme; it never exhibits a sagittal suture. This structure is a plate-like ingrowth of the integument of the outer body surface (as indicated by the concentric growth rings generally visible on its lateral surfaces), not a remnant of fused sclerites. Likewise, no suture is evident sagittally along the apophyseal shaft. In some taxa, the supraapophyseal plates are adpressed sagittally and may appear to form a suture. However, this is a secondary condition involving secondarily sclerotized portions of the parabacular membrane, not the true apophyseal shaft. The absence of a distinguishable sagittal suture in the parabaculum seems strong evidence against any hypothesis suggesting its origin from a pair of ancestral sclerites.

The fact that *Hemerobius*—the oldest and one of the best known, most speciose, and most widespread of hemerobiid genera—possesses a completely bipartite parabaculum (Fig. 37) has clearly biased the interpretation of the homology of the parabaculum. As the type genus of the Hemerobiidae, *Hemerobius* was the natural focal point of comparative studies involving hemerobiid taxa. This comparative bias led to two intertwined misconceptions. First, that the paired "parameres" (parabaculum) in *Hemerobius* were homologous with the paired "parameres" (9th gonocoxites) of other neuropterous families; and second, that the unpaired "parameres" (parabaculum) in non-*Hemerobius* hemerobiids were "fused" (note the twice implied polarity, "parameres" [pleural, implying ancestral pairing] and "fused" [implying ancestral separation]). The first conclusion misinterpreted the homology of the parabaculum within the order Neuroptera, whereas the second misinterpreted the polarity of the parabaculum states "fused" and "not fused" (or, more clearly, "not divided" and "divided").

In the genus *Carobius,* both the 9th gonocoxites and parabaculum are present (Figs. 29–32). The gonocoxites fit criteria 1 and 3, but are not setose (criterion 2). This clearly demonstrates that these structures are not homologs. Furthermore, the cladistic analysis (see below) strongly supports the polarity "not divided" [plesiomorphic] and "divided" [apomorphic] for the parabacular states.

To summarize, the principal evidence supporting recognition of the parabaculum as a hemerobiid novelty not homologous with the 9th gonocoxites of other Neuroptera are: (1) the absence of a sagittal parabacular suture, (2) the rarity of close associations between the parabaculum and the posterior margin of the extragonarcus, and (3) the joint presence of paired 9th gonocoxites and a parabaculum in the genus *Carobius*.

### Hypandrium Internum

Always present, membranously associated with the ventral surface of the parabaculum near the anterior end of the terminal lobes; in dorsal view an approximately triangular sclerite with a depressed median keel and more or less revolute lateral margins (e.g., Tjeder 1961, figs. 480–481, 578–579, 685–686). The configuration of this sclerite varies only slightly within the family; and it is of little taxonomic value.

## CLADISTIC ANALYSIS

### Methods and Data

### Overview

Hemerobiid intergeneric relationships were investigated cladistically. Twenty-four ingroup genera and three outgroup species were evaluated for 107 characters. The resulting data matrix was analyzed using the cladistic computer program HENNIG86 (Farris, 1988).

### Cladistic Methodology

Cladistic methods seek to identify (i.e., estimate) the cladogenetic component of phylogeny by analysis of the distributions of putatively synapomorphic (shared derived) characters exhibited by collections of studied taxa (Hennig, 1966; Sneath and Sokal, 1973; Wiley, 1981). Numerical formulations of cladistic methods—generally intended for implementation on computers—are designed to construct trees containing internodes justified by putative synapomorphies from Taxon × Character matrices of numerically coded character state data. On the basis of a parsimony criterion, the tree which minimizes the number of character state changes required to explain the observed state distributions is regarded as the best estimate of the relative genealogical relationships among the studied taxa. In cases where multiple equally parsimonious cladograms are found to exist, selection among these, if desirable, must employ one or more secondary criteria, for example, biogeography or posthoc character weighting. Cladogram rooting and character state polarization are generally accomplished by some form of outgroup comparison (Watrous and Wheeler, 1981; Maddison et al., 1984). The outgroup may consist of one or more real taxa, or of a hypothetical taxon whose character state array is composed of individually justified plesiomorphic states.

### Data

For the present analysis, approximately 185 hemerobiid species were examined (ca. one third of the currently valid world species). An exact species tally is not possible due to the presence of unidentifiable, questionably identified, and undescribed species among the material examined. Because of the impracticability of scoring all species for all 107 characters (see *Characters* below), one or more representative species of each genus were selected for comprehensive examination. These species are indicate by "+" symbols in Appendix 2. To the extent allowed by the available material, three criteria were adopted to limit geographic and/or taxonomic bias in the selection of representative species: (1) samples were selected to include species from geographically distant and/or disjunct portions of generic ranges, (2) samples were selected to include species from presently or formerly differentiated taxonomic subgroups (i.e., species from different subgenera, or species from subjectively synonymous genera), (3) larger samples were generally taken from larger genera. Species not selected for comprehensive scoring were subsequently examined for the presence of the synapomorphic characters identified by the cladistic analysis of the representative species; these additional species provided a means of more broadly assessing the distribution of putative synapomorphies.

After scoring each representative species, the character states of congeners were evaluated, and a single state adopted for each character/genus. These character states were used in the cladistic analysis, and are given in matrix form in Appendix 5.

Selection of a single state was trivial in cases where all congeners possess the same state. However, where intrageneric variation was present among congeners the choice of a representative state was problematic. In each such case the state interpreted as plesiomorphic within the genus was adopted as representative; however, no general methodology—short of independently analyzing each polymorphic genus—can ensure identification of the correct plesiomorphic state.

The following approach was used here to address this problem: (1) the state initially considered plesiomorphic was that which was most widespread of among other hemerobiid genera; then, (2) a preliminary cladistic analysis was run using this state; then, (3) the initially selected state of the polymorphic genus was compared to the state exhibited by its sister group; finally, (4) if the outgroup state matched one of the states exhibited by the polymorphic genus, the latter was (if necessary) reset to match the outgroup state, and the analysis was rerun. Under this methodology, the initial selection of character states may have some biasing effect on the topology of the tree finally adopted; however, since the number of intragenerically polymorphic characters in this analysis is low (64/2889 = 2.2%), it is believed that any such bias is minimal.

Since the present analysis addresses the resolution of intergeneric relationships, detailed analyses of intrageneric variation in the characters examined are not presented. However, intragenerically variable characters are identified in the character treatments, and are indicated by bold values in Appendix 5. Future intrageneric analyses incorporating these characters will provide further information on their polarities, and allow for reassessment of their effects on inferred intergeneric relationships.

## Computational Methods

The coded character state data given in Appendix 5 was analyzed with the microcomputer program HENNIG86 (Version 1.5; Farris, 1988). Minimum length cladograms were computed by sequentially applying options "mhennig*" (a tree calculation command which constructs several trees, each by a single pass through the data matrix, followed by branch-swapping on each tree) and "bb*" (which applies extended branch-swapping to all trees in the current tree file). As a means of identifying common elements among equally parsimonious cladograms, Nelson consensus trees were calculated using the "Nelsen" option. Output from the "xsteps" option was used in character and cladogram analysis. Cladograms were rooted using the outgroups defined below.

### Outgroup Taxa

Three outgroup species, *Nothochrysa californica* (Chrysopidae: Nothochrysinae), *Psychopsis birmana* (Psychopsidae), and *Polystoechotes punctatus* (Polystoechotidae), were included as terminal taxa in the overall cladistic analysis as a check on the holophyly of the Hemerobiidae, and as a means of polarizing character states within the family. These outgroup species were selected as available representatives of the three families most often included with the Hemerobiidae in the neuropterous superfamily Hemerobioidea (Withycombe, [1925]; Riek, 1970; Henry, 1982; Schlüter, 1986).

### Characters

The 107 characters used in the cladistic analysis include 11 multistate (3 or 4 states) characters (10, 12, 23, 24, 26, 53, 56, 78, 86, 96, and 106); all others are binary. Characters 10, 12 and 106 were analyzed as nonadditive (unordered); all others were treated as additive (ordered). Binary characters have the plesiomorphic state coded "0", and the derived state coded "1". Transformation series for additive multistate characters are presented under the appropriate character treatments. Any descriptive or analytical information concerning characters, their states, or polarities, determined prior to the analysis are given under the subheading *Comments*. Post-analysis notes on the polarities of character states, and the fits and lengths of characters to the preferred cladogram (see *Cladistic Analysis: Results: Cladograms*, below, and Fig. 23) are given under the subheading *Results*.

Character lengths are reported in the format "L = #", where # is the numerical length of each character on the preferred cladogram. These values are taken from the HENNIG86 output of the preferred cladogram and represent the number of times each character exhibits a character state change on the cladogram.

Nonterminal lineages are identified by the reference numbers given on the preferred cladogram.

## HEAD (Characters 1–22)

### Cranial Costae (Characters 1–4)

The relative positions of most cranial costae are shown in Fig. 1. Internal costae are not always marked by external sulci, and vice versa.

Character 1: *Temporal costae.*

(0) absent or poorly developed;
(1) well developed (Fig. 1, tmp).

*Comments:* The genera *Hemerobius* (1), *Psectra* (1), and *Zachobiella* (1) are polymorphic for this character. The states used in the cladistic analysis for these genera are given in parentheses.

*Results:* L = 4. State (1) is uniquely derived in lineage 2, but is independently reversed (1→0) in lineages 19, 22, and *Conchopterella.*

Character 2: *Transtorular costa.*

(0) absent or poorly developed;
(1) well developed (Fig. 1, trt).

*Comments:* Tjeder (1961, e.g., fig. 467) noted the presence of a "postfrontal suture" in several hemerobiid taxa. This "suture" is certainly not homologous with the orthopteroid postfrontal sutures of Snodgrass (1935, fig. 57B), which diverge laterally from the coronal suture and pass behind the ocelli and antennal toruli. The hemerobiid "suture" is never continuous with the coronal suture and always extends between, not behind, the toruli. As Tjeder's "postfrontal suture" appears to be only a secondary internal thickening of the cranium between the toruli, it is treated here under the name transtorular costa. The genus *Micromus* is polymorphic for this character; state (1) was used in the cladistic analysis.

*Results:* L = 2. State (1) is uniquely derived in lineage 21, but is reversed (1→0) in *Megalomina.*

Character 3: *Midfrontal costa.*

(0) absent or weakly developed;
(1) well developed (Fig. 1, mdf).

*Comments:* The *midfrontal costa* is a simple internal costa of the midline of the frons. It is frequently expressed as a ventral extension of the median cusp of the transtorular costa. The genus *Micromus* is polymorphic for this character; state (1) was used in the cladistic analysis.

*Results:* L = 2. State (1) is uniquely derived in lineage 21, but is reversed (1→0) in *Megalomina.*

Character 4: *Frontoclypeal costa.*

(0) entirely absent, or present only as a pair of spurs arising from the clypeogenal costae near the anterior tentorial pits, spurs not united medially (Fig. 1, ftc);
(1) present, a strong, transversely continuous, costa across the frontoclypeus below the anterior tentorial pits.

*Comments:* The genus *Micromus* is polymorphic for this character; state (0) was used in the cladistic analysis.

*Results:* L = 1. State (1) is a unique autapomorphy of *Noius.*

Mouthparts (Characters 5–12)

Character 5: *Columns of transverse strigae on epipharyngeal surface of labrum.*

(0) absent;
(1) two columns present (Fig. 3, str).

*Results:* L = 1. State (1) is a unique autapomorphy of *Megalomus.* The function of this structure, noted here for the first time, is unknown.

Character 6: *Penicilliform sensilla of galea.*

(0) absent;
(1) present (Fig. 8).

*Comments:* The apices of hemerobiid galeae possess a distinctive type of penicilliform sensillum. These sensilla consist of an elongate proximal rod terminated by a small distal cone (Fig. 8).

*Results:* L = 1. State (1) is a unique, unreversed, synapomorphy of lineage 2. This character, first reported here, is considered a tentative synapomorphy of the Hemerobiidae. Similar sensilla are lacking in the outgroups examined.

Character 7: *5th palpomere of maxillary palpus.*

(0) not subsegmented (Fig. 9);
(1) composed of two subsegments (Fig. 6).

*Comments:* Prior works have characterized the hemerobiid maxillary palpus as 5- or 6-segmented. Similarly, the labial palpus (Character 8) has been characterized as 3- or 4-segmented. The "subsegmentation" terminology adopted here is preferred because it explicitly states the inferred homology of the added palpal unit. There is no doubt that the extra palpal units, the "6th" maxillary and "4th" labial, have been derived respectively from the 5th maxillary and 3rd labial palpomeres. This is best illustrated by the labial palpus, where the palpimacula (Fig. 10, pma) always occurs on the ultimate palpomere in taxa with "3-segmented" palpi (Fig. 10), but always on the penultimate "segment" in taxa with "4-segmented" palpi.

Tjeder (1961:340) reported that the ultimate palpomeres of South African *Sympherobius* species lack subsegmentation. I have examined material from this area and have found subsegmentation to be present.

*Results:* L = 3. State (1) is uniquely derived in lineage 3, but is independently reversed (1→0) in lineages 12 and 17. State changes of characters 7 and 8 occur identically on the cladogram. Although these characters are logically independent, their identical state-change patterns and similar natures suggest that they may share a common functional or developmental origin.

Character 8: *3rd palpomere of labial palpus.*

(0) not subsegmented (Fig. 10);
(1) composed of two subsegments (Fig. 7).

*Comments:* See *Comments* under Character 7.

*Results:* L = 3. State (1) is uniquely derived in lineage 3, but is independently reversed (1→0) in lineages 12 and 17. See also *Results* for Character 7.

Character 9: *Dorsal (cervical) margin of postmentum.*

(0) transverse or irregularly parabolic and poorly defined;
(1) regularly parabolic and well defined (Fig. 11).

*Comments:* The genus *Nusalala* is polymorphic for this character; state (1) was used in the cladistic analysis.

*Results:* L = 2. State (1) is uniquely derived in lineage 21, but is reversed (1→0) in *Megalomina.*

Character 10: *Orad cavity of right mandible.*

(0) absent [lost];
(1) present, inconspicuous (Fig. 12, ocv);
(2) present, prominent.

*Comments:* The states of this character were analyzed as nonadditive.

*Results:* L = 3. State (0) is independently derived (1→0) in lineage 3 and the outgroup *Psychopsis birmana*; state (2) is uniquely derived (1→2) in the outgroup *Polystoechotes punctatus. Carobius pulchellus* was the only hemerobiid examined which possessed an orad cavity on the right mandible. This cavity is enclosed by the prominent dorsal mandibular blade and a smaller ventral shelf. In this analysis, this character is interpreted as plesiomorphic within the Hemerobiidae. In all other hemerobiids this cavity has apparently been lost through the atrophy of the ventral shelf. Additional study of this character in other *Carobius* species and other neuropterous families is warranted.

Character 11: *Proximal convexity of orad margin of right mandible.*

(0) prominently convex, rounded (Fig. 16, pxc);
(1) prominently convex, strongly angulate (Figs. 13, 15).

*Results:* L = 3. State (1) is independently derived in lineages 4, 12, and *Noius.*

Character 12: *Distal convexity of orad margin of right mandible.*

(0) absent (Fig. 13) or poorly developed;
(1) well developed, rounded (Fig. 14);
(2) well developed, strongly angulate (Fig. 15; 16, dtc).

*Comments:* The states of this character were analyzed as nonadditive.

*Results:* L = 3. State (1) is uniquely derived (0→1) in lineage 7; state (2) is independently derived (0→2) in lineage 12 and *Psychobiella.*

Clypeal Setae (Characters 13–17)

The relative positions and terminology applied to the principal long setae of the clypeus are illustrated in Figure 2. These setae may be identified by their size, and their positions relative to each other, the anterior tentorial pits, and the clypeogenal and clypeopleurostomal costae. Additional setae are generally present on the clypeus, but are too variable in size and/or position to be of taxonomic value. The four main pairs of principal clypeal setae—the dorsolaterals, dorsomedials, ventrolaterals, and ventromedials—are broadly homologous throughout the Hemerobiidae.

Character 13: *Paired dorsolateral setae of clypeus.*

(0) absent;
(1) present (Fig. 2, dls).

*Results:* L = 1. State (1) is a unique, unreversed, synapomorphy of lineage 2.

Character 14: *Sagittal seta of clypeus.*

(0) absent;
(1) present (Fig. 2, ss).

*Results:* L = 1. State (1) is an autapomorphy of *Hemerobius.*

Character 15: *Paired mesolateral setae of clypeus.*

(0) absent or short;
(1) present and long.

*Comments:* Species of the genus *Notiobiella* possess an extra pair of prominent clypeal setae just dorsad of the ventrolaterals, herein called the *mesolaterals.* The genus *Neuronema* is polymorphic for this character; state (0) was used in the cladistic analysis.

*Results:* L = 1. State (1) is an autapomorphy of *Notiobiella.*

Character 16: *Paired ventrolateral setae of clypeus.*

(0) absent;
(1) present (Fig. 2, vls).

*Results:* L = 1. State (1) is a unique, unreversed, synapomorphy of lineage 2.

Character 17: *Paired ventromedial setae of clypeus.*

(0) absent;
(1) present (Fig. 2, vms).

*Results:* L = 2. State (1) is uniquely derived in lineage 2, but is reversed (1→0) in *Psychobiella.*

Tentorium (Characters 18–19)

Character 18: *Sagittal process of tentorial bridge.*

(0) present (Fig. 4, stp);
(1) absent [lost].

*Results:* L = 3. State (1) is independently derived in lineages 1, 20, and *Noius.*

Character 19: *Mesal lobes of anterior tentorial arms.*

(0) widely separated;
(1) very closely adjacent or overlapping (Fig. 4, mtl).

*Results:* L = 1. State (1) is an autapomorphy of *Notiobiella.*

Head Miscellaneous (Characters 20–22)

Character 20: *Setal foveae of cranium.*

(0) absent or few (<10) and inconspicuous;
(1) numerous (>10) and prominent.

*Comments:* In *Gayomyia falcata* most of the cranium is prominently punctate. Prominent punctures are rare or absent in other hemerobiids.

*Results:* L = 1. State (1) is an autapomorphy of *Gayomyia.*

Character 21: *Field of punctulae on posterior margin of gena.*

(0) absent;
(1) present (Fig. 5, gpt).

*Results:* L = 1. State (1) is a unique, unreversed, synapomorphy of lineage 16.

Character 22: *Bilobed cavity of male frons.*

(0) absent;
(1) present (Fig. 78).

*Results:* L = 1. State (1) is an autapomorphy of *Neosympherobius.*

FOREWING (Characters 23–49)

General forewing structure and terminology are given in Figures 17 and 18.

Costal Space (Characters 23–26)

Character 23: *Trichosores of anterior wing margin.*

(0) present proximally and distally;
(1) lost proximally, present distally;
(2) lost proximally and distally.

*Comments:* Pre-analysis transformation hypothesis: 0→1→2. This transformation suggests that trichosores are lost sequentially from the wing margin, beginning at the base of the wing and proceeding distally. This idea is supported by trichosore distributions in other Neuroptera (e.g., Mantispidae, see Lambkin, 1986), where proximal trichosores appear to be lost before those located more distally.

*Results:* L = 4. State (1) is independently derived (0→1) in lineage 21, *Zachobiella*, and the outgroup *Nothochrysa californica*, and further uniquely derived (1→2) in *Nothochrysa*. This pattern corroborated the pre-analysis transformation hypothesis of this character.

Character 24: *Humeral veinlet.*

(0) branched, proximal humeral trace recurrent and with 3 or more rami (Fig. 18, pht);
(1) branched, proximal humeral trace recurrent but with only 1 or 2 rami (Fig. 115);
(2) simple, branching absent [lost], straight or slightly bent.

*Comments:* Pre-analysis transformation hypothesis: 0→1→2. This transformation assumes sequential reduction in the prominence of the humeral veinlet, particularly in association with reduction in the width of the humeral area. The genera *Micromus*

(1), *Noius* (1), *Psectra* (0), *Sympherobius* (0), and *Zachobiella* (1) are polymorphic for this character. The states used in the cladistic analysis for these genera are given in parentheses.

*Results:* L = 5. State (1) is independently derived (0→1) in lineages 13, 21, and the outgroup *Nothochrysa californica*, but is reversed (1→0) in *Megalomina* and further derived (1→2) in *Nothochrysa*. The pre-analysis transformation hypothesis of this character was corroborated, except for the anomalous reversal in *Megalomina*.

Character 25: *Humeral marginal silhouette.*

(0) convex (Fig. 17);
(1) linear or shallowly concave (Fig. 191).

*Results:* L = 3. State (1) is independently derived in lineages 21, *Zachobiella*, and the outgroup *Nothochrysa californica*.

Character 26: *Crossveins [not veinlets] of costal space.*

(0) numerous (>4/wing) and regularly positioned, forming a distinct gradate series in costal space (Fig. 182);
(1) absent (Fig. 24) or few in number (rarely >4/wing);
(2) numerous (>4/wing) but irregular in position, forming, with costal veinlets, a reticulate network in costal space at base of wing (Fig. 174).

*Comments:* Pre-analysis transformation hypothesis: 1→0; 1→2. This transformation suggests the independent acquisition of numerous costal crossveins in *Drepanepteryx* and *Gayomyia* based on their different arrangements. The genera *Conchopterella* (1), and *Micromus* (1) are polymorphic for this character. The states used in the cladistic analysis for these genera are given in parentheses.

*Results:* L = 2. State (0) is uniquely derived in *Drepanepteryx*; state (2) is uniquely derived in *Gayomyia*. The pre-analysis transformation hypothesis was corroborated.

Subcostal Space (Characters 27–28)

Character 27: *Prestigmal width of subcostal space.*

(0) narrow to broad, but > width of adjacent Sc throughout (Fig. 17);
(1) very narrow, ≤ width of adjacent Sc throughout (Fig. 98) (sometimes slightly wider immediately adjacent to crossvein 1sc-r).

*Results:* L = 1. State (1) is an autapomorphy of *Notiobiella*.

Character 28: *Subcostal crossvein 2sc-r.*

(0) absent (Fig. 24);
(1) present (Figs. 17, 90).

*Comments:* The genera *Notiobiella* (1), and *Zachobiella* (1) are polymorphic for this character. The states used in the cladistic analysis for these genera are given in parentheses.

Table 2. State transformations for Characters 29–33.

| Character | Transformation[1] |
|---|---|
| 29 | 0→1 |
| 30 | 0→2 |
| 31 | 1→3 |
| 32 | 1→4 |
| 33 | 3→5 |

[1] Unit length transformations.

*Results:* L = 2. State (1) is uniquely derived in lineage 9, but is reversed (1→0) in lineage 22. In *Noius*, the sister-group to lineage 22, crossvein 2sc-r is frequently poorly developed or vestigial. This state may be transitional between a fully developed 2sc-r crossvein and its loss in lineage 22.

Radial Space (Characters 29–37)

Characters 29–33: *Radial vein configuration.*

(0) 1 ORB, the true radial sector.
(1) 2 ORB's, ORB1 deeply forked (Fig. 66).
(2) 2 ORB's, ORB1 shallowly forked (Fig. 24).
(3) 3 ORB's, ORB1 deeply forked (Fig. 90).
(4) 3 ORB's, ORB1 shallowly forked (Fig. 33).
(5) 4+ ORB's (e.g., Fig. 207). All genera characterized by 4 or more "radial sectors" are placed here.

*Comments.* Interpret "deeply forked" as: most proximal anterior branch of ORB1 arising from proximal half of posterior ORB1 trace, "shallowly forked" as: most proximal anterior branch of ORB1 arising from distal half of posterior ORB1 trace.

Characters 29–33 involve transformations among the six states listed above. The following pre-analysis transformation series were hypothesized: (Series 1) 0→2; (Series 2) 0→1→3→5; (Series 3) 1→4. The transformation assigned to each character is given in Table 2. Data matrix values for characters 29–33 (columns 29–33 in Appendix 5) contain additive binary coding sequences encoding the preceding transformation series. The binary coding sequence of each state is given in Table 3. The homologies and polarities of radial vein states are discussed below.

*Discussion.* The homologies of the oblique radial branches (ORB's) of the forewing have been difficult to assess. Three principle areas of ambiguity are involved. Phrased in the form of questions, these are: (1) Do the ORB's contain veins homologous with the MA?, (2) Do the ORB's contain veins homologous with the R1?, and (3) What is the correspondence between individual ORB's and portions of the ancestrally pectinate neuropterous Rs. These questions are addressed below. In the discussion, the following definitions are employed: (1) the *apparent R* is taken to be the longitudinal vein posterior to the Sc and anterior to the apparent M, (2) the *apparent M* is taken to be the longitudinal vein immediately anterior to the Cu, which is always clearly identifiable, and (3) the *apparent Rs* is taken to be the most proximal ORB.

Table 3. Additive binary coding values for characters 29–33.

| | Character | | | | |
|---|---|---|---|---|---|
| State | 29 | 30 | 31 | 32 | 33 |
| (0)[0] | 0 | 0 | 0 | 0 | 0 |
| (1)[1] | 1 | 0 | 0 | 0 | 0 |
| (2)[2] | 0 | 1 | 0 | 0 | 0 |
| (3)[3] | 1 | 0 | 1 | 0 | 0 |
| (4)[4] | 1 | 0 | 0 | 1 | 0 |
| (5)[5] | 1 | 0 | 1 | 0 | 1 |

[0] *Nothochrysa, Polystoechotes, Psychopsis* (outgroups).
[1] All sympherobiine and notiobielline genera.
[2] *Carobius.*
[3] *Psychobiella.*
[4] All hemerobiine genera.
[5] All drepanacrine, megalomine, drepanepterygine, and micromine genera.

## Do the ORB's Contain Veins Homologous with the MA?

Many, if not most, present neuropterists implicitly or explicitly accept the hypothesis that an ancestral anterior branch of the media, the MA, has fused anteriorly with the R, *and* that its remnant is represented in the fore- and hind-wings of most extant Neuroptera by the most proximal branch of the apparent R or apparent Rs. This acceptance is reflected in the terminological conventions commonly adopted for forewing venation. Martynov (1928) first introduced the idea that the apparent neuropterous R is a hybrid R+MA, an idea subsequently adopted by Carpenter (e.g., 1936, 1940), and his students (e.g., Adams, [1960]; Adams, 1967; MacLeod and Adams, [1968]; Adams, 1970). Unfortunately, a comprehensive review of this concept is beyond the scope of this work, and its applicability to the Hemerobiidae is judged here solely on the basis of evidence found in hemerobiid taxa.

At least two general lines of supportive evidence have been advanced to suggest the existence of a hybrid forewing R+MA in the Hemerobiidae. These are: (1) the presence of a sigmoid vein (Fig. 167, sv) connecting the apparent M and R in the hind wings of all hemerobiids, and (2) the presence of a "basal" or "b" crossvein in some hemerobiids (Kevan and Klimaszewski, 1987: fig. 2, "b").

The presence of a sigmoid vein connecting the apparent M and R in the hind wing is very widespread within the Neuropterida (see, for example, the wing illustrations in Aspöck et al., 1980). Tillyard (1916, text-fig. 4) interpreted this vein as the basal portion of the ancestral Rs which had become secondarily fused to the base of the M. Martynov, however, interpreted it as a basal branch of the M, which he designated the MA. A substantial body of evidence seems to support Martynov's interpretation. For example: (1) the invariable origin of this vein from the base of the apparent M, (2) its frequently long uncrossvein-like appearance, and (3) its broad distribution within the Megaloptera (Van der Weele, 1910b) and Raphidioptera (Aspöck et al., 1980), where the identity of the true Rs appears to be clear, as well as in the Neuroptera. If this hind wing vein is the MA (which seems likely), and if one is willing to assume parallel venational development of the forewing and hind wing, the fusion of MA in the hind wing could be used as evidence of a similar fusion in the forewing. However, because differential development of other forewing and hind wing venation is common within the Neuroptera, there is little a priori reason to suspect that the second premise of this argument is true.

Carpenter (1940) reported that a "basal" or "b" crossvein (Kevan and Klimaszewski, 1987: fig. 2, "b") was present in most *Hemerobius* species, and occasionally present in other North American hemerobiids. I have found the "b" crossvein only in species of *Hemerobius*. Occasionally, in other genera, forewing cell c2r-m is somewhat darkly pigmented or sclerotized proximally in the cleft between the apparent R and apparent M. This may falsely give the impression of a crossvein at that position. This manner of modification could be misinterpreted as a "b" crossvein.

Carpenter interpreted the "b" crossvein as the vestigial remnant of the basal piece of the forewing MA. I interpret it as forewing crossvein 2r-m, which is lost, or proximally displaced, in *Hemerobius*. The latter interpretation seems better supported: (1) the "b" crossvein in *Hemerobius* possesses all of the characteristics normally associated with true crossveins, i.e., it is transverse, weakly sclerotized, nontracheate, and asetose; (2) the "b" crossvein is present only in *Hemerobius*; and (3) *Hemerobius* is the only hemerobiid genus apparently lacking a forewing 2r-m crossvein. The coincidence of the last two points appears to be particularly compelling evidence supporting the homology of the "b" crossvein with crossvein 2r-m of other hemerobiids.

In conclusion, I find no clear evidence to support the hypothesis that the most proximal branch of either the apparent R or apparent Rs in the hemerobiid forewing has been derived from the M. Consequently, in this work, I adopt the terminological convention of calling the apparent M the media (M) and the apparent R the radius (R). This terminology implies that if an anterior branch of the M did fuse anteriorly with the R, its terminal branchings have subsequently been suppressed, and its stem entirely lost.

### Do the ORB's Contain Veins Homologous with the R1?

Previous workers have not discussed the possibility that at least some ORB's may represent branches of the R1 that have been displaced proximally by the basad "migration" of distal R1 forks. Comstock (1918) regarded a similar fork "migration" mechanism, operating on the "R2", to have produced the pectinate Rs found in many Neuroptera.

The principal evidence opposing the evolution of such a mechanism on the hemerobiid anterior radial trace is the presence in most genera of a long *substigmal interramus*, i.e., the portion of the anterior radial trace located between the most distal prestigmal ORB and the most proximal terminal fork of the R1. The ubiquitous presence of this long interramus is difficult to reconcile with branching patterns expected from the operation of an R1 fork migration mechanism. Such a mechanism would be expected to produce veins separated by interrami of subequal length along the entire distal portion of the anterior radial trace. But, veins nearly meeting this expectation are found in only a few genera, e.g., *Austromegalomus* and *Drepanepteryx*, which contain species characterized by especially numerous ORB's. Therefore, I conclude that R1 fork "migration" has not been an important mechanism in producing hemerobiid ORB's. Although the distal ORB's in some *Austromegalomus* and *Drepanepteryx* species may originate from this source, taxa possessing 2 to 4 ORB's (the ORB states of most concern here) are regarded as not containing ORB's of R1 origin.

## How do the ORB's Correspond to the Branches of the Ancestral Rs?

Having outlined above my reasons for dismissing possible claims of partial homology of the ORB's with the R1 and/or M, it seems clear that the ORB's must be collectively homologous with the Rs, since the R1 and M bound the Rs anteriorly and posteriorly. This interpretation supports the homologies of Comstock (1918) over those proposed by Tillyard (1916) or Carpenter (1940).

## Radial State Polarities

Tillyard (1916:290) proposed that forewing states with few (2–3) "radial sectors" (ORB's) were derived through reduction from ancestral states with numerous "radial sectors". This opinion was quoted and accepted by Nakahara (1960b:1–2). Although I agree that a morphocline in "radial sector" number is clear, I disagree with Tillyard's assessment of its polarity. I suggest that evolution in "radial sector" number has generally (although not necessarily exclusively) increased, not decreased, within the Hemerobiidae, and that convergence toward higher "radial sector" numbers (4+) is more prevalent than convergence toward lower numbers. At least two lines of evidence suggest the latter polarity.

First, since a single ORB, the Rs, is clearly plesiomorphic within the Neuroptera, an increase in ORB number must, at some level, be derived within the family. Logically, a sequential increase in ORB number, 1→2→3→4+, would appear to be reasonable.

Second, independent increases in radial sector number are evident within some hemerobiid genera. For example: (1) most *Wesmaelius* are characterized by 3 ORB's (apparently the plesiomorphic number within the Hemerobiinae), but several species normally possess 4 (e.g., *quadrifasciatus*, *concinnus*), and (2) Oswald (1988b:400) suggested, based on a cladistic analysis of Nearctic *Sympherobius* species, that the 3-ORB state found in the four species of the European *fuscescens* species group is derived, relative to the 2-ORB state predominant within that genus and apparently plesiomorphic within the Sympherobiinae.

Confirmation of a general trend toward increase in ORB number cannot, however, completely establish ORB homologies, since portions of the ancestrally pectinate neuropterous Rs may have become secondarily associated with the anterior radial trace at different times and/or at different points. Starting with a plesiomorphic forewing radial configuration consisting of a pectinately branched Rs, a simple R1, and one or more crossveins joining the two, at least three general classes of mechanisms can be imagined which could account for the shifting of the origins of ancestral Rs branches to the anterior radial trace.

The first class of mechanisms postulates the partial basal fusion of the Rs with the R1. In simple formulations, these mechanisms would appear to result in a distal "migration" of the origin of the Rs along the anterior radial trace. However, it is possible to escape this difficulty by suggesting concurrent or subsequent basal "migration" of individual branches following the partial anastomosis of R1 and the anterior sectoral trace.

The second class of mechanisms invokes a concept which might be called "crossvein capture". These mechanisms require the existence of one or more crossveins joining the ancestral R1 and Rs. These crossveins may "capture" a portion of the Rs by rotating from a transverse to an oblique orientation and coming to serve as the functional base of a portion of the Rs, or by decreasing in length and thus "pulling" a segment of the anterior sectoral trace toward the anterior radial trace. In the latter case, eventual elimination of the crossvein after a period of shortening could result in the attachment an Rs fragment directly to the anterior radial trace.

The third mechanism, adventitious fragmentation of the Rs, with subsequent reassociation of the fragments along the anterior radial trace, is not theoretically or mechanistically satisfying, but may account for much of the intraspecific variability in ORB numbers and origination positions observed in taxa which generally possess 5 or more ORB's. This mechanism cannot be conclusively differentiated from a mechanism which supposed the adventitious origin of entirely new branches from the R1.

All three types of mechanisms have been discussed by several previous authors (e.g., Carpenter, 1940; Comstock, 1918; Tillyard, 1916). Each general mechanism appears plausible; but, none appear to leave behind an unambiguous "signature". Consequently, the evolution of radial configurations in the Hemerobiidae is likely to remain ambiguous.

Three principal criteria were used to define and polarize the radial states recognized here. First, the observed number of ORB's [up to 4] was used to divide radial states into four groups. As a working hypothesis, the state adopted for each taxon (species or genus) was the one most frequently observed in the taxon. However, since taxa characterized by four or more ORB's generally exhibit high levels of intraspecific and intrageneric variation in ORB number, these taxa were grouped under a single state. Second, the observed location of the most proximal fork of the most proximal ORB was used to divide the 2-ORB and 3-ORB groups into two states each, two in which the most proximal ORB was deeply forked (Figs. 66, 90), and two in which this vein was only shallowly forked (Figs. 24, 33). Third, and finally, the six states were polarized by assuming a sequential increase in ORB number and a progression from deeply forked to shallowly forked states.

*Results:* Character 29: L = 1. State (1) is a unique, unreversed, synapomorphy of lineage 3.

Character 30: L = 1. State (1) is an autapomorphy of *Carobius.*

Character 31: L = 2. State (1) is independently derived in lineages 14 and *Psychobiella.*

Character 32: L = 1. State (1) is a unique, unreversed, synapomorphy of lineage 4.

Character 33: L = 1. State (1) is a unique, unreversed, synapomorphy of lineage 14.

These results generally corroborate the pre-analysis polarities. In particular, the assumption that ORB numbers generally increase within the family is borne out. The subfamilies Carobiinae, Hemerobiinae, Sympherobiinae, and Notiobiellinae, which are characterized by low (2–3) ORB numbers, clearly cluster at the base of the cladogram, while those possessing higher ORB numbers (Drepanacrinae, Megalominae, Drepanepteryginae, Microminae) are grouped further from the base. The parallelism of character 31 in lineages 14 and *Psychobiella*, and the occurrence of both characters 31 and 33 on lineage 14, are the only two apparently anomalous features of this character with regard to the pre-analysis polarities.

Character 34: *Most proximal fork of posterior sectoral trace.*

(0) located in proximal one-third of posterior sectoral trace (Fig. 66);
(1) located in distal two-thirds of posterior sectoral trace (Fig. 24).

*Comments:* The genera *Megalomus* (0), *Neuronema* (0), and *Sympherobius* (0) are polymorphic for this character. The states used in the cladistic analysis for these genera are given in parentheses.

*Results:* L = 5. State (1) is independently derived in lineages, 4, 21, *Carobius*, *Notiobiella*, and *Gayomyia*. Post-analysis consideration of this character suggests that the derived state (1) has evolved by several independent mechanisms. In *Notiobiella*, the basally simple posterior sectoral trace appears to have resulted from the lengthening of the Rs stem due to the distal migration of its most proximal fork (Fig. 98). In all other taxa, a simple posterior sectoral trace appears to have resulted from a shift in the origin of its anterior branches to the anterior radial trace; however, this association is inferred to have occurred at different times in different lineages. Thus, these states are probably not homologous, and this character should be dropped or revised in subsequent analyses. This character may also not be completely independent from characters 29–33.

Character 35: *Pre-3ir1 intraradial crossveins.*

(0) present (Figs. 17, 166);
(1) absent (Fig. 50).

*Results:* L = 3. State (1) is uniquely derived in lineage 2, but is independently reversed (1→0) in *Neuronema* and *Gayomyia*.

Character 36: *Intraradial crossvein 4ir1.*

(0) present (Figs. 17, 33);
(1) absent [lost] (Fig. 74).

*Comments:* The genera *Conchopterella* (0), *Micromus* (0), and *Psectra* (1) are polymorphic for this character. The states used in the cladistic analysis for these genera are given in parentheses.

*Results:* L = 2. State (1) is independently derived in lineage 12 and *Neosympherobius*.

Character 37: *Posterodistal marginal silhouette.*

(0) convex (Fig. 24);
(1) concave (Figs. 149, 174).

*Comments:* The genera *Conchopterella* (0), *Drepanepteryx* (0), *Hemerobius* (0), *Megalomina* (0), *Micromus* (0), and *Sympherobius* (0) are polymorphic for this character. The states used in the cladistic analysis for these genera are given in parentheses.

*Results:* L = 2. State (1) is independently derived in *Drepanacra* and *Gayomyia*. The derived state is also independently derived in some species of other genera.

### Radiomedial Space (Characters 38–40)

Character 38: *Radiomedial crossvein 2r-m.*

(0) present (Figs. 17, 24);
(1) absent [lost] (Fig. 33) or displaced proximad of crossvein 2m-cu.

*Comments:* In *Hemerobius* crossvein 2r-m is absent or displaced toward the base of the wing. When present, it always lies proximal to the position of crossvein 2m-cu, and generally lies proximal to fork M1+2/M3+4. The genus *Notiobiella* is polymorphic for this character; state (0) was used in the cladistic analysis.

*Results:* L = 2. State (1) is independently derived in *Hemerobius* and the outgroup *Psychopsis birmana.*

Character 39: *Radiomedial crossvein 3r-m.*

(0) present (Figs. 17, 33);
(1) absent [lost] (Fig. 24).

*Comments:* The genus *Micromus* is polymorphic for this character; state (0) was used in the cladistic analysis.

*Results:* L = 2. State (1) is independently derived in *Carobius* and the outgroup *Nothochrysa californica.*

Character 40: *Radiomedial crossvein 4r-m.*

(0) present (Figs. 17, 41);
(1) absent [lost] (Fig. 66).

*Comments:* The genus *Notiobiella* is polymorphic for this character; state (1) was used in the cladistic analysis.

*Results:* L = 3. State (1) is independently derived in lineages 7, 11, and the outgroup *Nothochrysa californica.*

### Media Posterior Space (Characters 41–42)

Character 41: *Intramedial crossvein 2im.*

(0) absent (Fig. 24);
(1) present (Fig. 182).

*Comments:* The genera *Conchopterella* (0), *Megalomina* (0), and *Micromus* (0) are polymorphic for this character. The states used in the cladistic analysis for these genera are given in parentheses.

*Results:* L = 2. State (1) is independently derived in lineage 19 and the outgroup *Nothochrysa californica.*

Character 42: *Intramedial crossvein 4im.*

(0) present (Figs. 17, 41);
(1) absent [lost] (Fig. 98).

*Results:* L = 3. State (1) is independently derived in lineage 11, *Sympherobius*, and the outgroup *Nothochrysa californica*.

Mediocubital Space (Characters 43–46)

Character 43: *Mediocubital crossvein 2m-cu.*

(0) present (Figs. 17, 41);
(1) absent [lost] (Figs. 199, 207).

*Results:* L = 1. State (1) is a unique, unreversed, synapomorphy of lineage 22.

Character 44: *Mediocubital crossvein 3m-cu.*

(0) present (Figs. 17, 41);
(1) absent [lost] (Fig. 24).

*Comments:* The genera *Hemerobius* (0), *Megalomus* (0), and *Micromus* (0) are polymorphic for this character. The states used in the cladistic analysis for these genera are given in parentheses.

*Results:* L = 4. State (1) is independently derived in lineage 6, *Carobius*, *Nusalala*, and the outgroup *Nothochrysa californica*.

Character 45: *Mediocubital crossvein 4m-cu.*

(0) present (Figs. 17, 41);
(1) absent [lost] (Fig. 82).

*Comments:* The genus *Micromus* is polymorphic for this character; state (0) was used in the cladistic analysis.

*Results:* L = 3. State (1) is independently derived in lineage 11, *Sympherobius*, and the outgroup *Nothochrysa californica*.

Character 46: *Mediocubital flexion line.*

(0) present (Figs. 18, 33);
(1) absent [lost] (Fig. 174).

*Results:* L = 2. State (1) is independently derived in *Gayomyia* and the outgroup *Nothochrysa californica*. Loss of the mediocubital flexion line in *Gayomyia* is associated with the proliferation of finely reticulate veins at the base of the forewing in this genus.

Cubital Space (Characters 47–48)

Character 47: *Intercubital crossvein 1cua-cup.*

(0) absent (Figs. 17, 50);
(1) present (Fig. 199).

*Comments:* The genus *Neuronema* is polymorphic for this character; state (1) was used in the cladistic analysis.

*Results:* L = 2. State (1) is independently derived in lineages 19 and 22.

Character 48: *Depth of most proximal fork of forewing CuP.*

(0) fork absent or shallow, length of CuP stem before fork > length of posterior CuP trace beyond fork (Fig. 41);
(1) deep, length of CuP stem before fork ≤ length of posterior CuP trace beyond fork (Figs. 17, 98).

*Comments:* The genus *Conchopterella* is polymorphic for this character; state (1) was used in the cladistic analysis.

*Results:* L = 4. State (1) is independently derived in lineage 14, *Notiobiella*, and the outgroup *Polystoechotes punctatus*, but is reversed (1→0) in lineage 22.

### Anal Space (Character 49)

Character 49: *Depth of most proximal fork of forewing A1.*

(0) absent or shallow, length of A1 stem before fork > length of posterior A1 trace beyond fork (Fig. 24);
(1) fork deep, length of A1 stem before fork ≤ length of posterior A1 trace beyond fork (Figs. 17, 149).

*Comments:* The genera *Conchopterella* (1), *Megalomus* (0), and *Neuronema* (0) are polymorphic for this character. The states used in the cladistic analysis for these genera are given in parentheses.

*Results:* L = 3. State (1) is independently derived in lineages 15, 20, and the outgroup *Psychopsis birmana*.

## MALE TERMINALIA (Characters 50–95)

### 9th Tergite (Characters 50–55)

Character 50: *9th tergite.*

(0) not completely divided sagittally (anterior and/or posterior margin may be sagittally emarginate);
(1) completely divided sagittally.

*Results:* L = 2. State (1) is independently derived in lineage 22 and *Gayomyia.*

Character 51: *Antecosta of 9th tergite (lateral view).*

(0) not obliquely crossing tergite from anterior to posterior margin (Fig. 36);
(1) obliquely crossing tergite from anterior to posterior margin (Fig. 148).

*Results:* L = 2. State (1) is independently derived in lineage 16 and *Psychobiella.*

Character 52: *Cusps of posterolateral margins of male 9th tergite.*

(0) absent (Fig. 47);
(1) present (Fig. 69, cus).

*Results:* L = 1. State (1) is an autapomorphy of *Nomerobius.*

Character 53: *Posteroventral angle of 9th tergite.*

(0) produced as a narrow membrane-margined lobe (Fig. 69);
(1) not prominently produced (Fig. 47) or, if somewhat produced, expanded as a broad membrane-margined lobe;
(2) produced as an elongate subectoproctal lobe (usually) with a free distal process (Fig. 108, 117).

*Comments:* Pre-analysis polarity hypothesis: 1→0; 1→2.

*Results:* L = 2. State (0) is uniquely derived in lineage 7; state (2) is uniquely derived in lineage 12. The pre-analysis hypotheses of polarity were corroborated.

Character 54: *Horizontal costae of inner lateral surfaces of 9th tergite.*

(0) absent;
(1) present (Fig. 65, cos).

*Results:* L = 1. State (1) is an autapomorphy of *Hemerobiella.*

Character 55: *9th and 10th tergites.*

(0) not fused (Fig. 27);
(1) fused (Fig. 222).

*Results:* L = 2. State (1) is independently derived in lineage 22 and the outgroup *Nothochrysa californica.*

9th Sternite (Characters 56–63)

Character 56: *9th sternite.*

(0) absent [lost] (Fig. 127);
(1) present, a free sclerite (Fig. 27);
(2) present, fused with 8th sternite.

*Comments:* Pre-analysis polarity hypothesis: 1→0; 1→2.

*Results:* L = 2. State (0) is uniquely derived in *Zachobiella*; state (2) is uniquely derived in the outgroup *Nothochrysa californica*. The pre-analysis polarity hypotheses were corroborated.

Character 57: *Sagittal costa of dorsal surface of 9th sternite.*

(0) absent;
(1) present (Fig. 144, cos).

*Comments:* The midline of the male 9th sternite *Austromegalomus insulanus* is marked in its anterior ⅓ to ½ by a low sagittal costa. This costa appears to be restricted to *Austromegalomus.*

*Results:* L = 1. State (1) is an autapomorphy of *Austromegalomus.*

Character 58: *Apex of 9th sternite* (A).

(0) not produced as a long, straight, attenuate tube;
(1) produced as a long, straight, attenuate tube (Fig. 47).

*Results:* L = 1. State (1) is an autapomorphy of *Nesobiella.*

Character 59: *Apex of 9th sternite* (B).

(0) not tubularly produced and abruptly upturned distally;
(1) tubularly produced and abruptly upturned distally (Fig. 69).

*Results:* L = 2. State (1) is independently derived in *Nomerobius* and the outgroup *Polystoechotes punctatus.*

Character 60: *Digitiform posterior process of 9th sternite.*

(0) absent;
(1) present (Fig. 194).

*Comments:* Each of the three species of *Noius* examined possess a narrow sclerotized process issuing medially from the posteroventral margin of the male 9th sternite. This derived state is unique to *Noius.* It differs from the drawn-out 9th sternite processes of *Nomerobius* and *Nesobiella* by lacking sclerotization proximodorsally and/or laterally, and by differences in setation. The last trait is particularly diagnostic. In *Nomerobius* the apical portion of the 9th sternite has lost its setae or bears only modified spine-like or peg-like setae (Oswald, 1990). In *Nesobiella,* the attenuate apex bears normal, unmodified macrotrichia along its entire length. In *Noius oceanicus* and *noumeanus* the posteroventral process bears a small field of unmodified setae apically and a dense tuft of setae posterobasally. An undescribed species of *Noius* from Samoa has the apical setae thickened and arranged in a fan-like array, and the basal setal tuft absent (?lost). The protruded apices of the male 9th sternite in *Noius, Nomerobius,* and *Nesobiella,* are considered here to be parallel, analogous developments, a hypothesis supported by their distant cladistic relationships (Fig. 23).

*Results:* L = 1. State (1) is an autapomorphy of *Noius.*

Character 61: *Posterior margin of 9th sternite.*

(0) without a pair of acute cusps;
(1) with a pair of acute cusps (Fig. 53).

*Comments:* The posterior margin of the male 9th sternite in *Wesmaelius* bears a pair of cusps, which are frequently drawn out as slender processes. Less prominent cusps are found in some *Hemerobius* species. These are considered parallel developments; and absence of such cusps (state 0) is presumed plesiomorphic in *Hemerobius.*

*Results:* L = 1. State (1) is an autapomorphy of *Wesmaelius.*

Character 62: *Posterolateral lobes of 9th sternite.*

(0) absent;
(1) present (Fig. 194).

*Results:* L = 1. State (1) is an autapomorphy of *Noius.*

Character 63: *Paired elongate setae of 9th sternite.*

(0) absent;
(1) present (Fig. 69).

*Comments:* In addition to normal unmodified macrotrichia, all known species of *Nomerobius* possess a pair of elongate, chalazate macrotrichia posterolaterally on the male 9th sternite.

*Results:* L = 1. State (1) is an autapomorphy of *Nomerobius.*

10th Tergite [Ectoproct] (Characters 64–68)

Character 64: *Mesal surfaces of ectoprocts.*

(0) largely membranous (excluding narrowly protruding lobes);
(1) largely sclerotized (narrowly protruding lobes absent) (Fig. 136).

*Comments:* The male ectoprocts of *Conchopterella* are large, planar, setose, structures which are broadly sclerotized on their mesal surfaces. In all other genera, the mesal surfaces of the ectoprocts are largely membranous, with mesal sclerotization restricted to the inner surfaces of narrowly protruding lobes and/or the revolute margins of outer surfaces.

*Results:* L = 1. State (1) is an autapomorphy of *Conchopterella.*

Character 65: *Fusiform setae of ectoproct.*

(0) absent;
(1) present (Fig. 46).

*Results:* L = 1. State (1) is an autapomorphy of *Nesobiella.*

Character 66: *Pecten of ectoproct.*

(0) absent;
(1) present (Fig. 59, pec).

*Comments:* The male ectoprocts of *Wesmaelius* each possess a row of contiguous cuticular pegs. These pegs are apparently not derivatives of modified setae and are borne on a mesal process of varying length (sometimes very long).

*Results:* L = 1. State (1) is an autapomorphy of *Wesmaelius.*

Character 67: *Articulated posteroventral lobe of ectoproct.*

(0) absent;
(1) present (Fig. 108, 109).

*Comments:* In *Psectra*, each male ectoproct possesses a small hinged or articulated posteroventral lobe which carries near its apex a row of variously modified setae.
*Results:* L = 1. State (1) is an autapomorphy of *Psectra*.

Character 68: *Modified subapical seta of ectoproct.*

(0) absent;
(1) present (Fig. 69).

*Comments:* The ectoprocts of the four known species of *Nomerobius* each possess a single distinctive subapical seta, which is thickened, elongate and borne on a short pedicel.
*Results:* L = 1. State (1) is an autapomorphy of *Nomerobius*.

Gonarcus and Associated Structures (Characters 69–83)

Character 69: *Sagittal emargination of posterior margin of extragonopons [not mediuncus].*

(0) absent;
(1) present (Fig. 195).

*Comments:* All three species of *Noius* examined possess a peculiarly modified gonopons in which a pair of small parasagittal plates protrude posteriorly, resulting in the formation of a sagittal emargination between them.
*Results:* L = 1. State (1) is an autapomorphy of *Noius*.

Character 70: *Ventral margins of extrahemigonarcus.*

(0) not turned outward;
(1) distinctly turned outward (Fig. 77).

*Comments:* In *Neosympherobius cinereus* the ventral portions of the reduced extrahemigonarcus are strongly flared laterally.
*Results:* L = 1. State (1) is an autapomorphy of *Neosympherobius*.

Character 71: *Horizontal costae of inner surfaces of intrahemigonarcus.*

(0) absent;
(1) present (Fig. 177, cos).

*Results:* L = 1. State (1) is an autapomorphy of *Gayomyia*.

Character 72: *Horizontal costae of outer surfaces of intrahemigonarcus.*

(0) absent;
(1) present (Fig. 76, cos).

*Results:* L = 1. State (1) is an autapomorphy of *Neosympherobius*.

Character 73: *Lateral neogonarcal carinae of gonarcus.*

(0) absent;
(1) present (Fig. 72, car).

*Comments:* Each of the four species of the genus *Nomerobius* possesses a pair of small neogonarcal carinae or plates. These are oriented perpendicular to their respective extrahemigonarcus and are located ventrally along the antextragonarcal commissure.

*Results:* L = 1. State (1) is an autapomorphy of *Nomerobius*.

Character 74: *Gonofenestra.*

(0) absent (Fig. 28);
(1) present (Fig. 153, gfa).

*Results:* L = 4. State (1) is uniquely derived on lineage 10, but is reversed (1→0) on lineages 20, 23, and *Zachobiella*.

Character 75: *Gonofenestral plate.*

(0) absent (or gonofenestra absent);
(1) present (Fig. 134, gfp).

*Comments:* In *Conchopterella* the anteromedian portion of the gonofenestral membrane has become secondarily sclerotized and forms a broad gonofenestral plate, which is separated from the mediuncus by a constricted gonofenestral membrane.

*Results:* L = 1. State (1) is an autapomorphy of *Conchopterella*.

Character 76: *Secondary gonopons of gonarcus.*

(0) absent;
(1) present (Fig. 73, sgp).

*Comments: Nomerobius* is unique among hemerobiid genera in possessing a secondarily derived sclerotized bridge, the secondary gonopons, joining the posteroventral margins of the extrahemigonarcus. All four known species of *Nomerobius* possess this structure (Oswald, 1990). The transverse bar joining the hemigonarcus of some *Psectra* species is interpreted here as a derivative of the mediuncus.

*Results:* L = 1. State (1) is an autapomorphy of *Nomerobius*.

Character 77: *Transverse subbasal costa of ventral surface of mediuncus.*

(0) absent;
(1) present (Fig. 96, cos).

*Comments:* In *Psychobiella* the mediuncus is narrowed and bears a transverse costa on its ventral surface near the base.

*Results:* L = 1. State (1) is an autapomorphy of *Psychobiella*.

Character 78: *Apex of mediuncus.*

(0) mediuncus absent (Fig. 76);
(1) apex pointed or rounded (not emarginate) (Figs. 19, med; 176);
(2) emarginate (Fig. 153);
(3) terminating in a pair of long, slender, pliable processes (Fig. 162, med).

*Comments:* Pre-analysis polarity hypothesis: 1→0; 1→2→3.

*Results:* L = 7. State (1) is most plesiomorphic. State (2) is independently derived (1→2) on lineage 10 and in the outgroup *Psychopsis birmana*. State (0) is uniquely derived (1→0) on lineage 8. State (3) is uniquely derived (2→3) in *Megalomus*. State (2) is independently reversed (2→1) on lineages 18 and *Anapsectra*, and rereversed (1→2) in *Megalomina*. Although the pre-analysis transformations were generally upheld, the configuration of the apex of the mediuncus seems particularly plastic in the Hemerobiidae, and convergence among some of these states may be expected.

Character 79: *Pseudomediuncus.*

(0) absent;
(1) present (Fig. 84, pmd).

*Results:* L = 1. State (1) is a unique, unreversed, synapomorphy of lineage 7.

Character 80: *Base of pseudomediuncus.*

(0) narrow (or pseudomediuncus absent) (Fig. 73);
(1) laterally expanded (Fig. 85).

*Results:* L = 1. State (1) is an autapomorphy of *Sympherobius.*

Character 81: *Pseudomediuncus divisions.*

(0) absent, pseudomediuncus absent or undivided (Fig. 72, pmd);
(1) present, divided into two sclerites (Fig. 84).

*Results:* L = 1. State (1) is an autapomorphy of *Sympherobius.*

Character 82: *Gonosaccal membrane below mediuncus.*

(0) without a scabriculous region (Fig. 143) (or mediuncus absent);
(1) with a scabriculous region (Fig. 135, sbr).

*Results:* L = 3. State (1) is independently derived on lineage 15 and in *Psychobiella* (poorly developed), but is reversed (1→0) in *Austromegalomus.*

Character 83: *Phallolingua.*

(0) absent;
(1) present.

*Comments:* Nakahara (1960b) coined the term phallolingua for a tubular, eversible, structure found in species of the genus *Notiobiella*. At rest the phallolingua is telescopically withdrawn below the mediuncus and above the parabaculum; and it appears to be a modification of part of the gonosaccal membrane. Its external surface (when everted) is often extensively ornamented with small spicules.

*Results:* L = 1. State (1) is an autapomorphy of *Notiobiella.*

Parabaculum and Associated Structures (Characters 84–92)

Character 84: *Parabaculum* (A).

(0) absent;
(1) present (Fig. 21).

*Results:* L = 1. State (1) is a unique, unreversed, synapomorphy of lineage 2.

Character 85: *Parabaculum* (B).

(0) not deeply divided, or if deeply divided not as described for state (1) below (or parabaculum absent);
(1) deeply (entirely or nearly entirely) divided, composed of a pair of adjacent, narrow sclerotized straps, which are enlarged posteriorly as small sclerotized surfaces surrounded by membrane, sagittal apophyseal lamella absent (Figs. 37, 48).

*Results:* L = 1. State (1) is a unique, unreversed, synapomorphy of lineage 5.

Character 86: *Sagittal division of parabaculum.*

(0) terminal cleft complete, parabaculum comprised of a pair of laterally adjacent sclerites (Fig. 37);
(1) terminal cleft incomplete (Fig. 22, tc) (or parabaculum absent);
(2) terminal cleft absent, parabaculum with a single undivided terminal lobe (Fig. 128).

*Comments:* Pre-analysis polarity hypothesis: 1→0; 1→2.

*Results:* L = 2. State (0) is uniquely derived in *Hemerobius*; state (2) is uniquely derived in *Zachobiella*. The pre-analysis hypotheses of polarity were corroborated.

Character 87: *Dorsal subapical spinose processes of parabaculum.*

(0) absent;
(1) present, superposed over small terminal lobes (Figs. 95, 156).

*Comments:* Spiniform processes derived from the terminal lobes of the parabaculum are sporadically distributed throughout the Hemerobiidae. Such processes may be apical or subapical. Well-sclerotized distal processes found in genera such as *Drepanepteryx*, *Wesmaelius*, and *Micromus*, appear to represent simple, convergent, modifications of the terminal lobes (by elongation, attenuation, and increased sclerotization). Distinctly spiniform subapical processes occur in *Drepanacra*, *Psychobiella*, and some *Megalomus*. Only those of found in *Drepanacra* and *Psychobiella* were assumed homologues for this character. In these genera the processes arise from the dorsal margin of the terminal lobes and project posteriorly over small, terminal lobe remnants. In *Megalomus*, analogous processes arise ventrally or laterally from the terminal lobes. *Megalomus* is polymorphic for such processes and their absence is presumed plesiomorphic.

*Results:* L = 2. State (1) is independently derived in *Psychobiella* and *Drepanacra*. This result suggests that the processes in *Drepanacra* and *Psychobiella* are not homologous, as coded above.

Character 88: *Ventrodistal region of parabaculum.*

(0) not expanded as a pair of rounded bulbous lobes (or parabaculum absent);
(1) expanded as a pair of rounded bulbous lobes (Fig. 112).

*Results:* L = 1. State (1) is an autapomorphy of *Psectra.*

Character 89: *Bow in apophyseal shaft of parabaculum immediately anterior to terminal lobes.*

(0) absent;
(1) present (Fig. 139).

*Results:* L = 1. State (1) is an autapomorphy of *Conchopterella.*

Character 90: *Penniform sclerites.*

(0) absent;
(1) present (Fig. 179, pen).

*Comments: Gayomyia falcata* possesses a pair of penniform (narrow, arched, and toothed) sclerites attached dorsally to the parabaculum at the base of the terminal cleft.

*Results:* L = 1. State (1) is an autapomorphy of *Gayomyia.*

Character 91: *Supra-penniform sclerite.*

(0) absent;
(1) present (Fig. 178, spn).

*Comments:* The supra-penniform sclerite is a small triangular sclerite located dorsal to the penniform sclerites in *Gayomyia.*

*Results:* L = 1. State (1) is an autapomorphy of *Gayomyia.*

Character 92: *Laterobacula.*

(0) absent;
(1) present (Fig. 205, lbc).

*Comments:* The laterobacula are a pair of small sclerites which flank the dorsal surface of the parabaculum in *Nusalala.*

*Results:* L = 1. State (1) is an autapomorphy of *Nusalala.*

Male Terminalia Miscellaneous (Characters 93–95)

Character 93: *Gonosaccal accessory sclerite.*

(0) absent;
(1) present (Figs. 190, acs; 186).

*Comments:* This sclerite is a small bilobed structure lying in the gonosaccal membrane above the parabaculum in *Drepanepteryx.*

*Results:* L = 1. State (1) is an autapomorphy of *Drepanepteryx.*

Character 94: *Supragonopontal setal group.*

(0) absent;
(1) present.

*Comments:* This feature is a small group of generally well-developed setae which lie medially in the paragonosaccal membrane adjacent to the anterior margin of the extragonopons. The genus *Wesmaelius* is polymorphic for this character; state (1) was used in the cladistic analysis.
*Results:* L = 1. State (1) is a unique, unreversed, synapomorphy of lineage 4.

Character 95: *9th gonocoxites.*

(0) present, articulating with or fused proximally to gonarcus (Fig. 29, 9gcx; 30);
(1) absent [lost];

*Results:* L = 1. State (1) is a unique, unreversed, synapomorphy of lineage 3. For a discussion of this character see above under the heading *Adult Morphology: Abdomen: Male Terminalia: Parabaculum.*

FEMALE TERMINALIA (Characters 96–107)

Tergites and Sternites (Characters 96–98)

Character 96: *7th Sternite.*

(0) posterior margin sagittally emarginate;
(1) not divided and posterior margin not emarginate;
(2) sternite completely divided sagittally (Fig. 121).

*Comments:* Pre-analysis polarity hypothesis: 1→0; 1→2. The genus *Psectra* is polymorphic for this character; state (1) was used in the cladistic analysis.
*Results:* L = 2. State (0) is uniquely derived in the outgroup *Psychopsis birmana*; state (2) is uniquely derived in *Anapsectra*. The pre-analysis hypotheses of polarity were corroborated.

Character 97: *Ventral margins of 9th tergite.*

(0) without chalazate setae;
(1) with chalazate setae (Fig. 118).

*Comments:* The genus *Micromus* is polymorphic for this character; state (0) was used in the cladistic analysis.
*Results:* L = 1. State (1) is an autapomorphy of *Anapsectra*.

Character 98: *Anteroventral lobes of 9th tergite.*

(0) absent (Fig. 52);
(1) present (Fig. 64, avl).

*Comments:* In *Hemerobiella* the anteroventral angle of the 9th tergite is prominently produced anteriorly as a broad, nonapodemal, lobe.
*Results:* L = 1. State (1) is an autapomorphy of *Hemerobiella*.

9th Gonocoxites (Characters 99–102)

Character 99: *9th gonocoxites.*

(0) membranously separated from ipsilateral 9th tergite margins (Fig. 26, 9gcx);
(1) fused with ipsilateral 9th tergite margins (Fig. 126, 9t+9gcx).

*Comments:* All hemerobiid females except those of *Zachobiella* possess free 9th gonocoxites, i.e., the gonocoxites are membranously separated from the adjacent posteroventral margins of the 9th tergite. New (1988, figs. 229, 237, 247) published the first illustrations of *Zachobiella* female terminalia and showed free gonocoxites to be present in the Australian species *Zachobiella lobata*, *pallida* and *submarginata*. However, in the four *Zachobiella* females examined for this analysis (including specimens of *pallida* and *submarginata*) the 9th gonocoxites were found to be fused to the adjacent ipsilateral margins of the 9th tergite. This results in a condition in which the gonocoxites appear to be lacking. This configuration should be verified in other species of *Zachobiella*.

*Results:* L = 1. State (1) is an autapomorphy of *Zachobiella*.

Character 100: *Styli of 9th gonocoxites.*

(0) present (Fig. 26, sty);
(1) absent [lost] (Fig. 35).

*Results:* L = 5. State (1) is independently derived in lineages 4, 12, 21, *Drepanepteryx*, and the outgroup *Nothochrysa californica*. The polarity of this character seems well established by outgroup comparison with other neuropterid taxa, particularly the Megaloptera and Raphidioptera, where styli are nearly universally present. However, recognizable styli are present in only a few neuropterous families, e.g., Psychopsidae, Polystoechotidae, Osmylidae, Ithonidae, and Hemerobiidae, having apparently been lost in most other families. Within the Hemerobiidae, 13 of 25 genera possess styli, and styli have been lost independently in four lineages: (1) the subfamily Hemerobiinae, (2) the clade *Psectra* + *Anapsectra* + *Zachobiella*, (3) the genus *Drepanepteryx*, and (4) the subfamily Microminae.

Character 101: *Sclerotized sulcus dividing 9th gonocoxites.*

(0) absent;
(1) present (Fig. 118, sul).

*Comments:* The genera *Neuronema* (0), *Noius* (0), *Notiobiella* (0), and *Psectra* (0) are polymorphic for this character. The states used in the cladistic analysis for these genera are given in parentheses.

*Results:* L = 1. State (1) is an autapomorphy of *Anapsectra*. In females of *Anapsectra medleri* the 9th gonocoxites are partially joined by secondary sclerotization of their dividing membrane, the channel between them taking the form of a deep sclerotized sulcus.

Character 102: *Ventral lobes of 9th gonocoxites.*

(0) absent;
(1) present (Fig. 118, vlb).

*Comments:* The genera *Hemerobius* (0), *Megalomus* (0), and *Micromus* (0) are polymorphic for this character. The states used in the cladistic analysis for these genera are given in parentheses.

*Results:* L = 1. State (1) is an autapomorphy of *Anapsectra*.

### Female Terminalia Miscellaneous (Characters 103–107)

Character 103: *Gonapophyses posteriores.*

(0) present;
(1) absent [lost].

*Comments.* The term gonapophyses posteriores is applied here to the pair of small, concave, sclerites which border or enclose the apex of the female subgenitale. These structures tend to be poorly developed or absent when the subgenitale is reduced or absent. The genera *Megalomus* (0), *Micromus* (0), *Notiobiella* (0), and *Sympherobius* (0) are polymorphic for this character. The states used in the cladistic analysis for these genera are given in parentheses.

*Results:* L = 5. State (1) is independently derived on lineages 5, 12, *Carobius*, *Nomerobius*, and *Noius*.

Character 104: *Insemination-fertilization canal.*

(0) slit-entry type;
(1) pore-entry type.

*Comments:* All hemerobiid females possess an elongate, generally well sclerotized, duct joining the bursa to the median oviduct. This duct is here called the insemination-fertilization canal. During insemination, sperm are presumed to pass from the male's spermatophore (implanted in the female's bursa during copulation) into the canal, where they are temporarily stored (frequently in an enlarged "spermathecal" region) before passing to the oviduct, where fertilization occurs. The presence, or likely presence, of similar canals of equivalent function have been reported in most other families of Neuroptera (e.g., Chrysopidae [Philippe, 1972: fig. 5, "canal de la spermatheque" + "spermatheque" + the short duct between the bursa and spermatheca]; Osmylidae [Adams, 1969: fig. 6, "fertilization canal"]; Mantispidae [Lambkin, 1986: figs. 30–31, "spermatheca" + "fertilization canal"]) and Raphidioptera (Raphidiidae [Achtelig, 1978: fig. 6, "ductus receptaculi seminis" + "receptaculum seminis" + "ductus seminalis").

The hemerobiid insemination-fertilization canal differs from those found in the outgroups examined in the configuration of the entrance to the canal. In all hemerobiids the canal entrance is a small circular opening located at or near the anterior end of the bursa. In the outgroups, the entrance to the canal is by means of an elongate dorsal slit. It seems likely that the "slit-entry" canal type arose from a plesiomorphically membranous bursa in which a narrow midventral strip became secondarily sclerotized; subsequent revolution and opposition of the lateral margins of the sclerotized strip could create an elongate hollow cleft possessing a narrow dorsal slit ringed by bursal membrane. From this "slit-entry" configuration, the "pore-entry" configuration found in hemerobiids could be easily derived through progressive closure of one end of the slit. Such closure would simultaneously account for the small size of the opening into, and the elongate form of, hemerobiid insemination-fertilization canals.

The comparative morphology of the neuropterous insemination-fertilization canal has not been well studied. A detailed survey of females of representative neuropterous families is needed to clarify homologies and standardize terminological conventions for this structure. Particularly problematic is the term "spermatheca", which has been (1) loosely applied to any sclerotized portion of the insemination-fertilization canal (e.g., many Neuroptera), (2) restricted to some prominently enlarged portion of the canal (if one is present) (e.g., Chrysopidae, some Hemerobiidae), or (3) applied to a pair of bulbs each joined to the canal by an elongate duct (Osmylidae). All these structures are not homologous and should not bear the same name.

*Results:* L = 1. State (1) is a unique, unreversed, synapomorphy of lineage 2.

Character 105: *Subgenitale.*

(0) present;
(1) absent [lost].

*Comments:* When present, the female subgenitale is generally a small, apically bilobed, sclerite arising from the medioventral body wall between the ventrally expanded lobes of the 9th tergite. The subgenitale is probably a remnant of the female 8th sternite. The genera *Megalomus* (0), and *Micromus* (0) are polymorphic for this character. The states used in the cladistic analysis for these genera are given in parentheses.

*Results:* L = 2. State (1) is independently derived in lineages 5 and 12.

Character 106: *Sclerotizations of female bursa.*

(0) bursa membranous, without sclerotized areas;
(1) bursa broadly but weakly sclerotized dorsally;
(2) bursa with lateral walls prominently sclerotized;
(3) bursa with a sclerotized dorsal arch transversely connecting lateral margins of 8th sternite.

*Comments:* The states of this character were analyzed as nonadditive. Secondary sclerotizations of the female bursa are rare in hemerobiids. The genera *Micromus* (0), *Neuronema* (0), and *Notiobiella* (0) are polymorphic for this character. The states used in the cladistic analysis for these genera are given in parentheses.

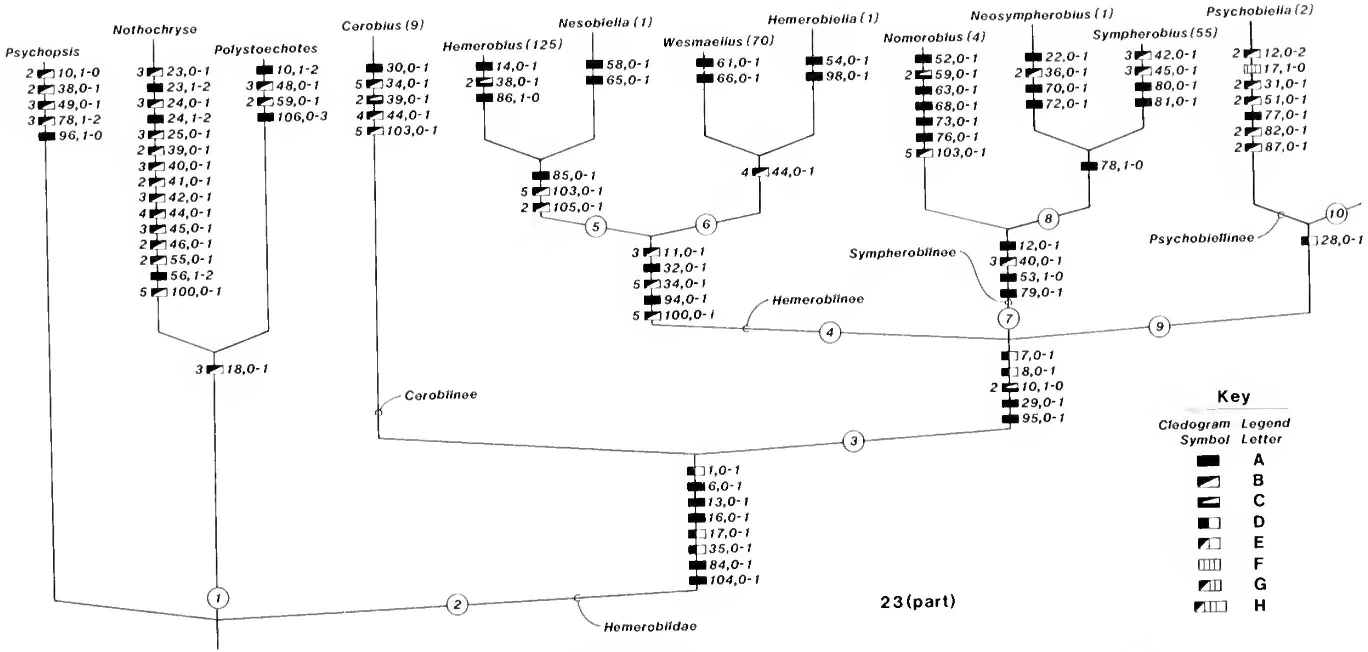
*Results:* L = 3. State (1) is uniquely derived (0→1) in *Gayomyia*; state (2) is uniquely derived (0→2) in *Nusalala*; state (3) is uniquely derived (0→3) in the outgroup *Polystoechotes punctatus*.

Character 107: *Distal diverticulum of insemination-fertilization canal.*

(0) absent;
(1) present.

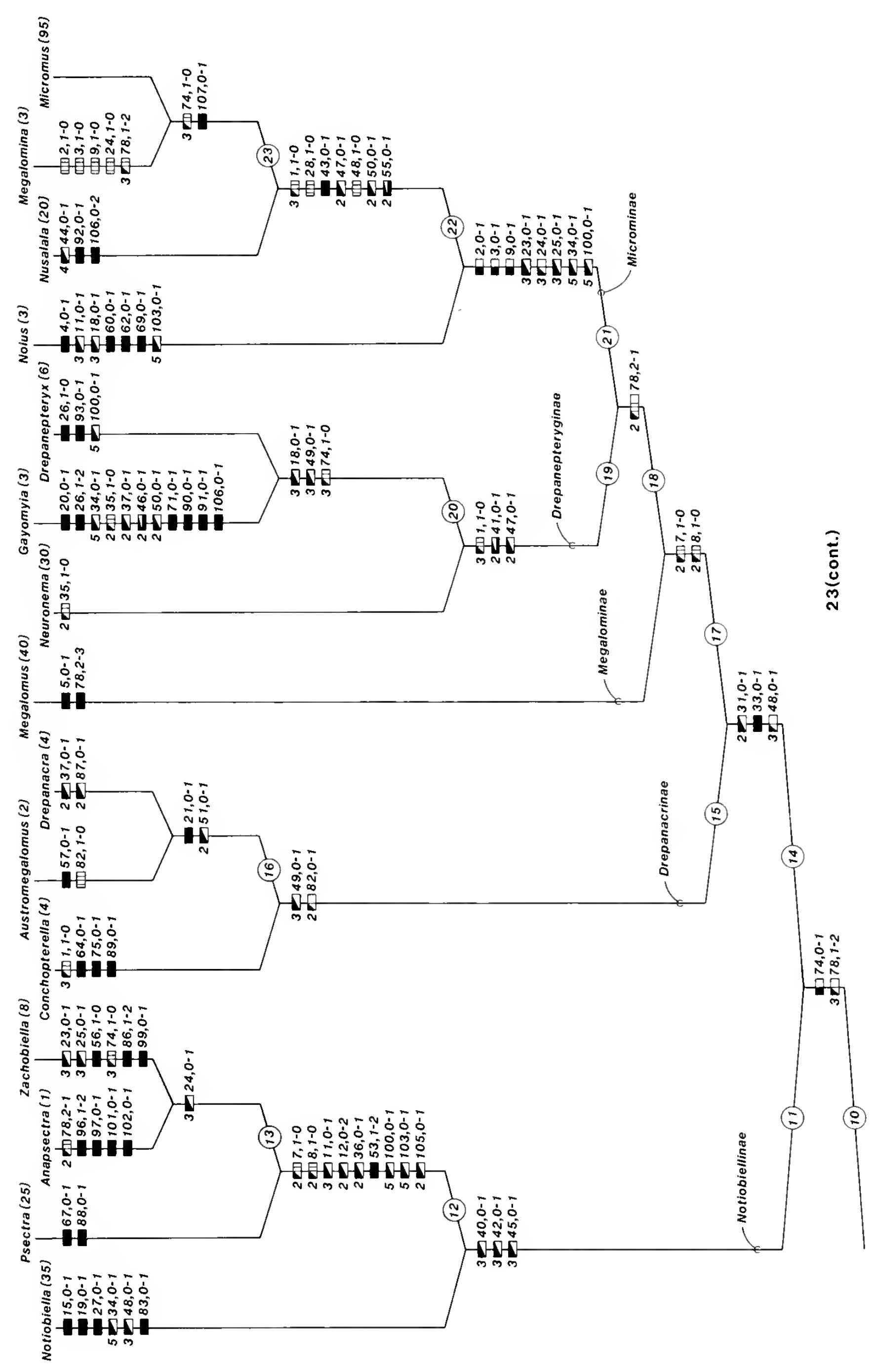
*Comments:* In many Microminae the distal end of the insemination-fertilization canal possesses a distinct constriction, setting off a small diverticular lobe.

*Results:* L = 1. State (1) is a unique, unreversed, synapomorphy of lineage 23.



23(part)

Fig. 23. Preferred cladogram of hemerobiid intergeneric relationships (# outgroups = 3, # ingroups = 24, # characters = 107, L = 196, CI = 0.61, RI = 0.70). Nonterminal lineages are numbered for reference. The number of species in each ingroup genus is given in parentheses following the generic name (approximate for larger genera). Proposed synapomorphies are mapped on the cladogram lineages in the following format: (1) the number to the left of the lineage symbol, if any, gives the number of occurrences of the indicated character state transformation on the cladogram, including outgroups [given only if > 1], (2) the lineage symbol [see below], (3) the character number, and (4) the character state transformation (plesiomorphic → apomorphic). LINEAGE SYMBOLS: The indicated character state transformation is: [A] unique and unreversed on the cladogram, [B] convergent on the cladogram, including outgroups, [C] unique within the Hemerobiidae, but convergent when outgroups are also considered, [D] unique on the cladogram, but reversed within the supported clade, [E] convergent on the cladogram, and reversed within the supported clade, [F] a unique reversal of an earlier character state transformation, [G] convergent on the cladogram, and a reversal of an earlier character state transformation, [H] convergent on the cladogram (outside the supported clade), a reversal of an earlier character state transformation, and rereversed within the supported clade.


Micromus (95)
Megalomina (3)
Nusalala (20)
Notius (3)
Drepanepteryx (6)
Gayomyia (3)
Neuronema (30)
Megalomus (40)
Drepanacra (4)
Austromegalomus (2)
Conchopterella (4)
Zachobiella (8)
Anapsectra (1)
Psectra (25)
Notiobiella (35)
3 74,1-0
107,0-1
2,1-0
3,1-0
9,1-0
24,1-0
3 78,1-2
4 44,0-1
92,0-1
106,0-2
23
3 1,1-0
28,1-0
43,0-1
2 47,0-1
48,1-0
2 50,0-1
2 55,0-1
4,0-1
3 11,0-1
3 18,0-1
60,0-1
62,0-1
69,0-1
5 103,0-1
22
2,0-1
3,0-1
9,0-1
3 23,0-1
3 24,0-1
3 25,0-1
5 34,0-1
5 100,0-1
Microminae
21
2 78,2-1
26,1-0
93,0-1
5 100,0-1
20,0-1
26,1-2
5 34,0-1
2 35,1-0
2 37,0-1
2 46,0-1
2 50,0-1
71,0-1
90,0-1
91,0-1
106,0-1
3 18,0-1
3 49,0-1
3 74,1-0
2 35,1-0
20
3 1,1-0
2 41,0-1
2 47,0-1
Drepanepteryginae
19
18
2 7,1-0
2 8,1-0
5,0-1
78,2-3
Megalominae
17
2 31,0-1
33,0-1
3 48,0-1
15
2 37,0-1
2 87,0-1
57,0-1
82,1-0
21,0-1
2 51,0-1
16
3 1,1-0
64,0-1
75,0-1
89,0-1
3 49,0-1
2 82,0-1
Drepanacrinae
14
74,0-1
3 78,1-2
3 23,0-1
3 25,0-1
56,1-0
3 74,1-0
86,1-2
99,0-1
2 78,2-1
96,1-2
97,0-1
101,0-1
102,0-1
3 24,0-1
13
67,0-1
88,0-1
2 7,1-0
2 8,1-0
3 11,0-1
2 12,0-2
2 36,0-1
53,1-2
5 100,0-1
5 103,0-1
2 105,0-1
12
15,0-1
19,0-1
27,0-1
5 34,0-1
3 48,0-1
83,0-1
3 40,0-1
3 42,0-1
3 45,0-1
Notiobiellinae
11
10

23(cont.)

## Results

### Cladograms

Two minimal length tree topologies were identified by the HENNIG86 analysis (L = 196, CI = .61, RI = .70). The Nelson consensus tree of these topologies was identical to one of the two original trees. This tree is illustrated in Fig. 23, and is adopted as the preferred cladogram of hemerobiid intergeneric relationships. The lineage numbers cited in the following sections refer to the lineage reference numbers given in Fig. 23. The second original tree differs from the preferred tree only by its dichotomous resolution of the trichotomy formed by lineages 4, 7, and 9 on the preferred tree, though this resolution is very tenuous. The two tree topologies differ only due to two different equally parsimonious optimizations for character 34 (see Appendix 3). This character has a length of five steps, with three steps the same for both optimizations: 34(0→1) on lineages 21, *Gayomyia*, and *Notiobiella*. The other two steps differ in the two optimizations. In optimization 1 the transformation 34(0→1) occurs also on lineages 4 and *Carobius*; in optimization 2 the transformation 34(0→1) would occur on lineage 2 and be reversed [34(1→0)] on a lineage uniting lineages 7 and 9, but not 4. The tree specified by optimization 1 is preferred here. This choice appears conservative in preferring a trichotomous resolution of clades 4, 7, and 9, over a fully dichotomous resolution supported only by a single transformation of character 34, which post-analysis evaluation suggests consists of several nonhomologous character states (see *Results* under this character above).

### Characters

The fit of each character to the preferred cladogram is given under the heading *Results* in the appropriate character treatment above. These fits are summarized by character in Appendix 3, and by lineage in Appendix 4.

### Classification

A new generic and subfamily classification of the Hemerobiidae is proposed here, based on the holophyletic groups of genera identified by the cladistic analysis. This classification is given in full in Appendix 1. Its subfamily taxa are compared to earlier hemerobiid classifications in Table 4. This new classification was constructed using the conventions recommended by Wiley (1981) for annotated Linnaean classifications. The most important of these conventions is the adoption of a phyletic sequencing scheme.

Phyletic sequencing is a method for converting cladograms into classifications. Using this method, one or more pectinately branched cladogram lineages are selected as "axes" for the classification. The sequential branches originating along these "axes" are named and given equal categorical rank. A sequential listing of taxa (a classification) formulated in this manner has the following desirable properties: (1) each named taxon is holophyletic; (2) each named taxon which is linked to the "axis" at a dichotomous node is the sister-group of the collection of taxa of equal rank below it. The phrase *sedis mutabilis*, sequence interchangeable, is used to identify taxa stemming from polytomous nodes. Adjacent taxa in the classification which bear

Table 4. Family-group classifications of the Hemerobiidae proposed since 1916.

| Comstock (1918) | Krüger (1922) | Navás ([1925], 1933) | Nakahara (1960) | Present classification |
|---|---|---|---|---|
| — | — | — | — | Carobiinae |
| Hemerobiidae | Hemerobiinae | Hemerobiini | Hemerobiinae | Hemerobiinae, *s.m.*[1] |
| Sympherobiidae | Sympherobiinae | Sympherobiini | — | Sympherobiinae, *s.m.* |
| — | — | — | — | Psychobiellinae |
| — | — | — | Notiobiellinae | Notiobiellinae |
| — | — | — | — | Drepanacrinae |
| — | Megalominae | Megalomini | — | Megalominae |
| — | Drepanepteryginae | Drepanopteryini | — | Drepanepteryginae |
| — | Microminae | Micromini | — | Microminae |
| — | — | Nyrmini | — | — |

[1] *s.m.*: *sedis mutabilis*, sequence interchangeable.

this annotation are of interchangeable position in the classification, since the sister-group relationships among such taxa are unresolved.

The "axis" selected as the basis of the subfamily classification proposed here was chosen to balance the conflicting desiderata of: (1) maximizing the number of subfamily taxa recognized, thereby increasing the specificity of the classification, and (2) minimizing the number of new family-group names to be proposed. The chosen lineage—composed of preferred cladogram lineages 2, 3, 9, 10, 14, 17, and 18—bears 9 pectinate branches. Six of these possess available family-group names (Hemerobiinae, Sympherobiinae, Notiobiellinae, Megalominae, Drepanepteryginae, and Microminae); new names are proposed here for the other three (Carobiinae, Psychobiellinae, and Drepanacrinae). Formal names are not proposed at this time for the two clades within the Hemerobiinae (*Hemerobius* + *Nesobiella*, and *Wesmaelius* + *Hemerobiella*); but these groups may be informally called, respectively, the *Hemerobius* and *Wesmaelius* genus-groups.

## Discussion

Numbers enclosed in brackets in the following discussion are character numbers keyed to the character treatments above.

### Holophyly of the Hemerobiidae

Tillyard (1916) appears to be the only previous author to have attempted to differentiate critically the Hemerobiidae from other neuropterous families on the basis of explicitly defined characters. Other authors have described or characterized the family, but they have not fully differentiated it from other families. The 10 characters forming the basis of Tillyard's concept of the Hemerobiidae are reviewed below, followed by an assessment of the putative synapomorphies of the family proposed here.

Character 1: "The presence of more than one radial sector in the forewing". In the terminology used here, this statement is equivalent to "anterior radial trace with two or more ORB's". This character is clearly apomorphic within the Hemerobiidae; however, it is not synapomorphic at the level of the entire family. Two different forewing radial vein configurations characterized by two ORB's appear to have evolved independently in the Hemerobiidae, one in *Carobius*, and one in its sister-group, lineage 3.

Character 2: "The absence of unspecialised cross-veins". Tillyard observed that hemerobiids possess fewer forewing crossveins than most other families of Neuroptera, e.g., Ithonidae, Dilaridae, Osmylidae, and the myrmeleontoid families. The latter families possess crossveins which are both more numerous, and of more indeterminate wing position. Although hemerobiids possess fewer, and by implication more "specialised", forewing crossveins than many neuropterous families, the phylogenetic implications, if any, of this trait are difficult to assess, particularly since Tillyard proposed no specific crossvein homologies which could be subjected to testing. Other neuropterous families possessing relatively few forewing crossveins include the Coniopterygidae, Sisyridae, and Berothidae.

Character 3: "The presence of at least one false or secondary origin for the radial sector in the hindwing". Tillyard (1916: text-fig. 4) misinterpreted the sigmoid vein (Fig. 175, sv) which joins the hind wing M to the Rs as the basal segment of the Rs. This vein is now generally interpreted as the MA. Under the latter interpretation, adopted here, the true Rs is (as expected) the most proximal branch of the R, and does not originate on the M. Thus, Tillyard's first false origin of the Rs is actually its true origin. Since this Rs configuration is plesiomorphic within the pterygote Insecta, it cannot justify the holophyly of the Hemerobiidae.

Character 4: "The presence. . .of a coupling apparatus at the base of the wings". Tillyard believed that the jugal lobe of the forewing and the "jugal process" of the anteroproximal aspect of the hind wing (see Tjeder, 1961, figs. 460–466, "frenulum") functioned as a coupling mechanism in flight. To the best of my knowledge, such a function for these structures remains unconfirmed. Furthermore, as noted by Tillyard, similar putative coupling mechanisms are present in other neuropterous families, and thus would not appear to constitute a synapomorphy at the level of the Hemerobiidae.

Character 5: "The absence of any distal fusion between Sc and R". Fusion of the Sc and R is clearly derived within the Neuroptera. Lack of fusion, which is characteristic of the Hemerobiidae, is plesiomorphic, and therefore not evidence for hemerobiid holophyly.

Character 6: "The archaic, unspecialised form of Rs". Tillyard misinterpreted the collective homology of the Rs. He assumed that only the most distal prestigmal branch of the anterior radial trace (which is itself typically pectinately branched) represented the homologue of the Rs of other neuropterous families (Tillyard, 1916: 276). Under this interpretation, hemerobiids, and all other neuropterous families, have an "unspecialized" pectinately branched Rs. This interpretation of the forewing Rs is considerably at odds with the interpretation adopted here (see Characters 29–33 above). All ORB's in aggregate are treated here as veins of ancestral Rs origin, and the retention of a pectinately branched most distal prestigmal ORB is interpreted as a plesiomorphic remnant of a once more extensively branched Rs. This character, therefore, cannot justify the holophyly of the Hemerobiidae.

Character 7: "The retention of the archaic branchings of the veins as they approach the wing-border". This character refers to the 'marginal twigging' of hemerobiid longitudinal veins. Since similar states are present in most other families of Neuroptera, as was well known to Tillyard, 'marginal twigging' is certainly plesiomorphic at the level of the Hemerobiidae, and is not evidence for the holophyly of the family.

Character 8: "The fusion of M with R basally in the forewing, and the fusion of M in the hindwing with the weakly formed, original, basal portion of Rs". As noted above (see Characters 29–33), Tillyard's interpretations of the forewing R and hind wing Rs are here regarded as erroneous. Consequently, this character is not relevant to the question of hemerobiid holophyly.

Character 9: "The unspecialised form of the antennae". The moniliform character of hemerobiid antennae was considered by Tillyard to be "unspecialized" (i.e., plesiomorphic), relative to antennal configurations in the families Psychopsidae, Chrysopidae, and Nymphidae. There is currently no reason to doubt this polarity; however, as a plesiomorphic trait, it cannot be used to support the holophyly of the family.

Character 10: "Position of [the wings at] rest". Tillyard proposed this character to distinguish hemerobiids, in which the wings are held at rest in a nearly vertical rooflike orientation over the thorax and abdomen, from the Psychopsidae and Ithonidae, in which the wings are oriented at rest in a more horizontal plane. The orientation found in Hemerobiidae is widespread within the Neuroptera and is certainly plesiomorphic at the level of the Hemerobiidae.

In summary, I conclude that none of the 10 traits used by Tillyard to characterize the Hemerobiidae is synapomorphic at the level of this family. In view of this, it seems remarkable that Tillyard's concept of the family is essentially identical to that adopted in this work. The present cladistic analysis strongly supports the holophyly of the family on the basis of eight entirely different characters (Fig. 23). The most significant of these are the presence of: penicilliform sensilla on the galea [6]; prominent paired setae on the clypeus [13, 16, 17]; a parabaculum in the male genital complex [84]; and a pore-entry type of female insemination-fertilization canal [104].

## Notes on Other Clades

Carobiinae: This subfamily contains only the Australian genus *Carobius*. This genus is the sister-group to the rest of the Hemerobiidae, and occupies an isolated position within the family. The holophyly of *Carobius* is justified on the basis of five characters [30, 34, 39, 44, 103], three of which [34, 44, 103] lend only weak support to this clade, since they each occur independently four or five times within the Hemerobiidae. The most convincing synapomorphy of the genus is the configuration of the forewing radius [30], which is unique to *Carobius* (Fig. 24). Species of *Carobius* are also the only hemerobiids which retain, plesiomorphically, the 9th gonocoxites as clearly recognizable elements of the male genitalia.

Lineage 3: This clade is well supported by five characters [7, 8, 10, 29, 95]. The subsegmentation of the distal segment of both the labial and maxillary palpi [7, 8], the altered configuration of the radius [29], and the loss of 9th gonocoxites in the male [95] are the most significant characters.

Hemerobiinae (Lineage 4): This grouping is justified on the basis of five characters [11, 32, 34, 94, 100], three of which [11, 34, 100] occur independently three to five times within the Hemerobiidae. The most convincing synapomorphies of the group are the presence of a distinctive group of macrotrichia, the supragonopontal setal group, located medially on the paragonosaccal membrane above the gonopons [94]; and the configuration of the typically three forewing "radial sectors" [32]. Hemerobiine species with four or five "radial sectors" are known, but are uncommon and clearly derived within the subfamily.

Sympherobiinae (Lineage 7): The Sympherobiinae is justified on the basis of four characters [12, 40, 53, 79]. The presence of a pseudomediuncus associated with the male gonarcus [79], and the elongated posteroventral angle of the male 9th tergite [53], are particularly good synapomorphies of this clade.

Lineage 9: The single putative synapomorphy of this clade is the presence of forewing crossvein 2sc-r [28]. Although this character involves the presence/absence of a wing crossvein, a character type which has historically been accorded low weight in Neuropteran taxonomy, this crossvein exhibits minimal intraspecific and intrageneric variation, and appears to be a phylogenetically significant trait. Within the clade, this crossvein is prominent in all taxa except (1) *Noius*, where it is present but vestigial, (2) lineage 22 (*Nusalala* + *Megalomina* + *Micromus*) and some *Zachobiella*, where it is secondarily lost, and (3) *Notiobiella*, where it is secondarily shortened or lost due to the extreme narrowing of the subcostal space. As one of the relatively few venational traits synapomorphic on the principal "classificatory axis" of the family, this character could prove important in assessing the phylogenetic positions of fossil hemerobiids, which are known almost entirely from preserved wings.

Psychobiellinae: This subfamily contains only the Australian genus *Psychobiella*, whose holophyly is justified on the basis of seven characters [12, 17, 31, 51, 77, 82, 87]. Of these, only the proximal transverse costa of the ventral surface of the male mediuncus [77] is unique to *Psychobiella*, although five of the six remaining characters occur only twice within the Hemerobiidae. It is interesting to note that four of the latter characters [31, 51, 82, 87] co-occur in the Drepanacrinae or on the lineages between the Psychobiellinae and Drepanacrinae. This suggests the possibility of a closer relationship between these two subfamilies than is indicated in the current analysis.

Lineage 10: Of the two characters supporting this clade [74, 78], the opening of a membranous gonofenestra at the base of the mediuncus [74] appears most significant, although this structure has apparently been independently and secondarily lost several times within this clade.

Notiobiellinae (Lineage 11): This clade is supported by three homoplasious characters [40, 42, 45]. The observations (1) that all three of these characters involve the loss of individual forewing crossveins, and (2) that these losses co-occur in the apparently distantly related genus *Sympherobius*, cast some doubt upon the robustness of the grouping of *Notiobiella* with the clade *Psectra* + *Anapsectra* + *Zachobiella*. The holophyly of the latter clade is, however, particularly well supported.

Lineage 14: This clade is supported by three characters [31, 33, 48], of which, those involving alteration in the configuration of the radius [31, 33] appear most significant.

Drepanacrinae: This grouping is defined on the basis of two homoplasious characters [49, 82]. One of these, a scabriculous membrane surface on the venter of the mediuncus [82] is also characteristic of the Psychobiellinae, and is part of a complex of characters suggesting a closer relationship between these two subfamilies than is indicated by the present analysis. The second character, a deeply forked forewing A1

[49], occurs twice within the Hemerobiidae at the level of this generic analysis, but also occurs sporadically in other genera. This character may be partially dependent on wing size, with larger wings showing more deeply forked A1 veins.

Lineages 17 and 18: These two clades are relatively weakly supported. Lineage 17 is justified solely on the basis of the presumed secondary fusion of the two subsegments of the ultimate labial and maxillary palpomeres [7, 8]. The separation of the Megalominae from the Drepanepteryginae + Microminae, Lineage 18, is even more tenuous, being supported only by a change in the distal shape of the mediuncus [18]. Based on the length of this character [L = 7] on the preferred cladogram, this feature appears to be especially plastic within the Hemerobiidae; and it may not provide convincing phylogenetic evidence at the present level of analysis.

Megalominae: This subfamily contains only the genus *Megalomus*, whose holophyly is justified by two unique synapomorphies [5, 78]. The male genitalia of *Megalomus*, particularly the convoluted mediuncus, are distinctive (Figs. 159, 162). The holophyly of this genus seems well established.

Drepanepteryginae: This clade is justified on the basis of three characters [1, 41, 47], two of which [1, 47] are homoplasious within the Hemerobiidae. The members of this group are all large hemerobiids, which may account for the presence of forewing 2im [41] and 1cua-cup [47] crossveins in these taxa. This grouping should be reexamined after a more comprehensive survey of the very poorly supported genus *Neuronema*, the putative sister-group to other drepanepterygines, has been undertaken.

Microminae: This grouping is supported by eight characters [2, 3, 9, 23, 24, 25, 34, 100]. On the simple basis of the number of supporting characters, the Microminae is the best supported subfamily in this analysis; however, all eight characters are either paralleled elsewhere in the Hemerobiidae, or are reversed within the Microminae. The subordinate grouping *Nusalala* + *Megalomina* + *Micromus* is almost certainly holophyletic; however, the relationships among these three genera require further analysis. I was not able to identify any synapomorphies for the large, cosmopolitan, genus *Micromus*, and I regard as very tentative the cladistic relationships shown in Fig. 23 between it and the genera *Nusalala* and *Megalomina*. In particular, the possibility that *Nusalala* may be a derived clade falling within the broad *Micromus* concept accepted here should be investigated. The sister-group to these three genera, *Noius*, appears distantly related both on the basis of venational and terminalic characters.

## Posterior Processes of the Male Extragonarcus

The establishment of homologies among the posterior processes of the hemerobiid male extragonarcus has been an especially difficult problem; one which is only partially resolved here. Previous authors have applied a variety of terms to these processes (e.g., aedeagus, arcessus, entoprocesses, epimeres, mediuncus). But, uncertainties about homologies have often prevented critical application of these terms. Due to this uncertainty, extragonarcal process characters, with the exception of the mediuncus, were excluded from the present cladistic analysis. The discussion below is a retrospective look at the question of the homologies of these processes, based on the intergeneric relationships reflected in the preferred cladogram.

Carobiinae: In *Carobius*, the sister-group to all other hemerobiids, three extragonarcal processes are typically present: (1) an unpaired dorsomedian process, the *mediuncus* (Fig. 28, med), and (2) a pair of ventrolateral processes called here the *paramediunci* (Fig. 28, pmed) [Etymology: para-, from Greek *para*, near, + mediuncus; pleural, paramediunci]. The male terminalic figures given by New (1988) show that this generalized arrangement is found in eight of the nine known species of *Carobius*. One species, *C. elongatus*, apparently lacks a mediuncus. This tripartite extragonarcal configuration is assumed here to be plesiomorphic within the Hemerobiidae.

Hemerobiinae: Both the mediuncus and paramediunci are retained in *Nesobiella* and *Wesmaelius*. In *Wesmaelius* a prominent mediuncus (Fig. 56, med) is present, flanked by a pair of paramediunci (Fig. 56, pmed) which have retained their plesiomorphic ventrolateral positions. In *Nesobiella* the paramediunci (Fig. 43, pmed) have converged medially to become partially fused sagittally, but the mediuncal remnant is distinctly visible as an acute cusp dividing the bases of the paramediunci. In *Hemerobius* the paramediunci (Fig. 39) have assumed the form of a pair of ventrally directed appendages, which are generally only narrowly attached to the posterior margin of the extragonarcus. In many *Hemerobius* species the paramediunci are medially convergent (not uncommonly partially fused sagittally), and the mediuncus is generally vestigial or lost. In *Hemerobiella* (Fig. 62), a simple but prominent mediuncus has been retained, but the paramediunci are entirely lost.

Sympherobiinae: In *Nomerobius* (Figs. 72–73) the paramediunci are present as a pair of small posteriorly directed lobes which are flexibly associated with the lateral margins of a small, triangular mediuncus. In *Neosympherobius* (Fig. 76) and *Sympherobius* (Fig. 84) both the mediuncus and paramediunci are entirely lost. In all three of these genera, but particularly in *Sympherobius*, a pseudomediuncus (a neogonarcal, not extragonarcal, structure) is present projecting from the gonopons.

In the remaining six subfamilies (Psychobiellinae, Notiobiellinae, Drepanacrinae, Megalominae, Drepanepteryginae, and Microminae), only the homology of the mediuncus is here regarded as well established. Detailed assessments of the homologies of other extrahemigonarcal processes present in these subfamilies must await more comprehensive analyses of individual genera and subfamilies. In recent years the term *entoprocess* (*-es*) has been used extensively as a term of convenience to designate any paired posterior process of unknown homology on the neuropterous gonarcus. Until homologies (and appropriate new names) for paired extragonarcal processes can be established in these six subfamilies, I recommend that this term, or the phrase "extrahemigonarcal process(es)", be applied to such structures. Use of the term "entoprocess" should be accompanied by a statement indicating that no homologies are to be inferred among the structures so designated.

I also recommend that the term *arcessus* be abandoned in the Hemerobiidae. Most structures given this designation in prior literature are mediuncus homologs. Tjeder (1931:4) proposed the term *mediuncus* for the unpaired, posteriorly directed, dorsomedian, process of the extragonarcus in several species of *Wesmaelius* (as *Boriomyia*). This term has subsequently been very widely applied to processes of similar location throughout the Neuroptera. Tjeder (1936:7) proposed the term *arcessus* for the small sclerotized structure located below the "mediuncus" in some *Neuronema* species. Unfortunately, the membranous attachments to the gonarcus in *Neuronema* clearly reveal that Tjeder's "mediuncus" and "arcessus" in *Neuronema* are in fact the neogonarcus and mediuncus respectively. Thus, Tjeder's term "arcessus", in its original sense, is a synonym of "mediuncus". Similar misinterpretations have also been made for some *Micromus* species which possess well-developed neogonarcus (e.g., *perelegans*: Tjeder, 1936: pl. 10, figs. f, h; *africanus*: Tjeder, 1961:322, figs. 519–520).

Although the homologies of extragonarcus processes remain problematic in the remaining six subfamilies (Psychobiellinae, Notiobiellinae, Drepanacrinae, Megalominae, Drepanepteryginae, and Microminae), three other gonarcal developments present in some of these taxa deserve mention here. First, the mediuncus in these subfamilies is often modified as a broad, elongate, dorsal plate, which supports an extensive gonosaccal membrane. This contrasts with the generally small mediunci of the three preceding subfamilies. Usually associated with such mediuncal enlargements are structural modifications which facilitate dorsoventral motion of the distal end of the mediuncus. Second, neogonarcal sclerites are extensively developed in some genera of these subfamilies (e.g., some *Megalomus*, *Neuronema*, and *Micromus*). The addition of a prominent neogonarcus in some of these taxa has resulted in considerable alteration in the overall appearance of the gonarcus. Third, in nearly all genera of these subfamilies, a small membranous "window" is present dorsomedially at the base of the mediuncus. This structure, named here the *gonofenestra* (Fig. 153, gfa) [Etymology: Greek *gono*, seed, + Latin *fenestra*, window], is interpreted as a secondarily desclerotized area at the base of the mediuncus, developed, perhaps, as one mechanism to facilitate movement of the mediuncus.

Psychobiellinae: The gonarcal configuration in *Psychobiella* is highly modified. In *P. sordida* (Figs. 96–97), much of the extragonarcus is enclosed within a helmet-like neogonarcus. The mediuncus is prominently produced; and the paramediunci are apparently lost. The extrahemigonarcus are deeply cleft laterally along a pair of lines which begin near the hemigonarcal conjunctions and follow the trend of the antextragonarcal commissure. These clefts result in the production of a pair (one above each cleft) of flat extragonarcal lobes which flank the mediuncus. No gonofenestra is present.

Notiobiellinae: Gonofenestra present or absent. In *Notiobiella* (Figs. 100–101) the mediuncus is prominent and the posterolateral margins of the extragonarcus frequently bear one or more processes of uncertain homology. The posteroventral angles of the extrahemigonarcus (=?paramediunci) are frequently produced to support the eversible phallolingua. In *Psectra* the mediuncus may be distinct (Figs. 113–114) or vestigial; lateral extragonarcal processes are absent. In *Anapsectra medleri* (Figs. 119–120) the mediuncus is distinctly tricuspate; lateral extragonarcal processes are absent. In *Zachobiella* (Figs. 130–131) the mediuncus is distinct and divided apically; lateral extragonarcal processes are sometimes present.

Drepanacrinae: Gonofenestra always prominent. In all three genera, *Conchopterella* (Figs. 134–135), *Austromegalomus* (Figs. 142–143), and *Drepanacra* (Figs. 153–154), the mediuncus forms a large, dorsal plate which is apically emarginate. The posteroventral margins of the extragonarcus are variously lobed.

Megalominae: Gonofenestra present. In *Megalomus* the mediuncus (Fig. 162, med) is distinctively modified. It's proximal portion is directed sharply downward at the gonopons, and its distal portion is bent along a transverse flexion line to project posteriorly. The distal portion is composed of a pair of filiform processes divided by a deep sagittal emargination. From the proximolateral angles of the base of the mediuncus arise a pair of long narrow entoprocesses (Fig. 162, ent), the "epimeres" of Carpenter (1940). The homology of these processes remains uncertain, but they may represent a pair of ancestrally lateral extragonarcal processes, that have become secondarily associated with the base of the mediuncus. The posteroventral corners of the extragonarcus are sometimes produced. Neogonarcal sclerotization is often well developed in *Megalomus*, particularly in the South American species *flinti* and *nigratus*, a factor which has undoubtedly facilitated the observed general reduction in the prominence of the extragonarcus.

Drepanepteryginae: In *Neuronema* the structure of the paleogonarcus (Fig. 170, pgs) is highly variable. The mediuncus (Fig. 170, med) may be well developed as a large, posteriorly directed plate or reduced as a small, ventrally directed lobe, but it is generally only membranously associated with the remainder of the gonarcus. The extragonarcus is poorly developed or absent ventrally, but is usually developed as a pair of fixed lobes (frequently large) dorsally. A neogonopons (Fig. 170, ngs) is often present over the base of the mediuncus. A gonofenestra is present. In *Gayomyia* (Figs. 176–177) the mediuncus is prominent and laterally continuous with the extrahemigonarcus. Situated laterally near the base of the mediuncus are a pair of elongate, movable processes of uncertain homology which articulate with the posterior margins of the extragonarcus; the neogonarcus and gonofenestra are absent. In *Drepanepteryx* (Figs. 184–185) the mediuncus is prominent and flanked by a pair of stout extragonarcal processes; again, the neogonarcus and gonofenestra are absent.

Microminae: In *Noius* (Figs. 195–196) a large gonofenestra is present and the extrahemigonarcus are reduced to a pair narrow sclerotized straps which join the mediuncus to the gonarcus arch. The extragonopons is represented by a pair of plates divided by a sagittal incision. In *Nusalala* (Figs. 201—202) the mediuncus is flanked by two pairs of processes, an inner pair associated with the proximolateral angles of the mediuncus, and an outer pair extending as posteriorly directed outgrowths of the dorsal portion of the extrahemigonarcus. A gonofenestra is present. The extrahemigonarcus are generally well developed, but are frequently partially overlain by extensive but inconspicuous neogonarcal plates. In *Megalomina* (Figs. 211–212) the mediuncus is prominent, generally emarginate distally, and laterally continuous with the extrahemigonarcus. The posterolateral margins of the extrahemigonarcus are produced as inwardly revolute plates. The gonofenestra is absent. A neogonopons (Fig. 211, ngs) may be developed over the base of the mediuncus. In *Micromus* (Figs. 219–220) the mediuncus is always prominent, but the relative development of the extrahemigonarcus and neogonarcus are extremely variable. In some species the mediuncus is broadly connected at its base to well-developed lateral extrahemigonarcus (presumably the plesiomorphic condition). In other taxa the extrahemigonarcus are largely or entirely lost, their structural functions apparently having been taken over by neogonarcal sclerites. Posterior processes of the gonarcus are particularly diverse in *Micromus*. However, many of these arise from the posterior margin of the neogonarcus (e.g., the dorsomedian processes in *variegatus* [Fig. 220, ngsp] and *multipunctatus*, and the paired lateral processes in *dissimilis*, *numerosus*, and *timidus*), not the extragonarcus. Thus, these processes are not homologous with other extragonarcal processes in *Micromus* or other genera. In *Micromus*, true extrahemigonarcal processes generally take the form of broad posterior lobes rather that acute prominences. Well-developed shelf-like neogonopontes are present in many *Micromus* species.

## TAXONOMIC HISTORY AND EARLY CLASSIFICATIONS

The modern era of hemerobiid taxonomy began with Tillyard's 1916 revision of the Australian hemerobiid fauna, in which he formulated the first modern concept of the family. Pre-Tillyardian concepts, from Latreille (1802) to Handlirsch (1906–1908), and the early formulations of Banks (1892, 1907, 1913), were considerably broader in scope and are not discussed here. Since Tillyard's seminal work, four subsequent authors have advanced proposals to subdivide the Hemerobiidae. Each of these is briefly reviewed below. Table 4 summarizes these classifications, and contrasts them with the subfamily classification used here. The latter classification is presented in full in Appendix 1, and is substantiated above under the heading *Cladistic Analysis: Results: Classification.*

Based on his extensive studies of wing venation, Comstock (1918) proposed a division of the Hemerobiidae into two families: (1) the Sympherobiidae, to include *Sympherobius*, *Psectra*, *Notiobiella* and other (unnamed) genera possessing only two "radial sectors", and (2) the Hemerobiidae, to include all genera possessing three or more "radial sectors". Although a similar division was proposed at lower rank in the subsequent classifications of Krüger and Navás, very few later workers (e.g., Brues and Melander, 1932; Kuwayama, 1962) followed Comstock in recognizing the Sympherobiidae at family rank. Comstock's concept of the Sympherobiidae is rejected here because it is not a holophyletic grouping. The preferred cladogram (Fig. 23) shows that a suprageneric hemerobiid taxon based solely on the dichotomy 2 vs. 3+ "radial sectors" (i.e., a grouping of Carobiinae + Sympherobiinae + Notiobiellinae vs. the remaining genera) would be clearly polyphyletic.

Krüger (1922) proposed a five subfamily classification based on another detailed venational study. Several pieces of evidence suggest that Krüger was unaware of Comstock's prior work. First, Comstock's work is not cited in Krüger's paper; second, the genera *Annandalia*, *Psectra*, and *Notiobiella*, which were noted by Comstock are not mentioned by Krüger; and, third, Krüger cites himself (pp. 170–171) as the author of the names Hemerobiinae and Sympherobiinae. This evidence suggests that Krüger's proposal of family-group names based on the type genera *Hemerobius* and *Sympherobius* was independent of Comstock's proposal. Several factors have contributed to the rejection of Krüger's classification by subsequent workers, principal among these are: (1) the eccentric format of Krüger's paper, which has made the identification and critical assessment of any diagnostic subfamilial characters extremely difficult, (2) the fact that an important intended companion paper was never published, and (3) the small number of genera upon which the classification was based. Furthermore, a comparison of Krüger's subfamily concepts (as revealed by the taxonomic listings given by Krüger, 1922:170–172) against the preferred cladogram (Fig. 23), suggests that at least his subfamilies Drepanepteryginae, Megalominae, and Hemerobiinae do not appear to be holophyletic.

Navás ([1925b]) divided the Hemerobiidae of the Iberian Peninsula into four tribes: Sympherobiini, Hemerobiini, Megalomini, and Micromini. It is not clear whether Navás was aware of Krüger's earlier subfamily proposals, or whether he independently proposed his nearly identical tribal groupings. In 1933, however, Navás explicitly recognized Krüger's Drepanepteryginae at tribal rank (as Drepanopterygini [sic]), and also proposed a sixth tribe, Nyrmini, for the enigmatic genus *Nyrma*. The latter tribe was recently removed to the family Berothidae as the subfamily Nyrminae (U. Aspöck, 1989). Navás's remaining subfamilies exhibit problems similar to those of Krüger's classification, e.g., foundation on few—mostly European—genera, and implicit recognition of some groupings which are not holophyletic.

Nakahara (1960b) proposed a division of the Hemerobiidae into two subfamilies: (1) the Notiobiellinae, for the genus *Notiobiella* (based on the presence of a distinctive derived genitalic feature, the phallolingua) and (2) the Hemerobiinae, for all other genera. Nakahara's work is significant for its shift in emphasis from venational to male terminalic characters as the primary basis for hemerobiid family-group classification, and as the first attempt to extensively survey hemerobiid diversity at the generic level beyond the confines of a regional or continental boundary. However, its classification is unsatisfactory for at least two reasons: (1) although the genus *Notiobiella* is certainly holophyletic, its elevation to subfamily status clearly renders Nakahara's Hemerobiinae paraphyletic; (2) the recognition of only two subfamilies, one of which is monogeneric, leaves intergeneric relationships within the bulk of the family entirely unresolved.

Shortly following the publication of Nakahara's work, Tjeder (1961) criticized and rejected all previously proposed classifications of the Hemerobiidae. No critical defenses of earlier classifications have subsequently been advanced; and few works published following Tjeder's influential paper have formally recognized family-group subdivisions within the Hemerobiidae.

The new classification proposed here has been formulated with the deficiencies of earlier arrangements in mind. It's principle advantages over older classifications are: (1) foundation on a most parsimonious cladistic hypothesis of intergeneric relationships, (2) recognition of only phylogenetically meaningful—demonstrably holophyletic—taxa based on putative synapomorphies, (3) incorporation of the phyletic sequencing convention, thereby allowing the estimated phylogeny upon which it is based to be retrieved from the classification, (4) expansion of the character base upon which the classification is based, and (5) inclusion of as many extant hemerobiid genera as practicable.

## Taxonomic Treatments

*Format.* The following taxonomic treatments are divided into subheadings as follows (some treatments do not contain all subheadings):

(1) *Synonymical Listing.* A listing of all supraspecific names which are considered synonyms of the treated taxon name, with relevant nomenclatural data and references. References cited as authoritative sources of subjective synonyms are generally recent revisionary works, not necessarily the first reference in which the synonymy was proposed.

(2) *Differential Diagnosis.* A synoptic statement giving a character combination diagnostic for the treated taxon.

(3) *Proposed Synapomorphies.* A listing of synapomorphic characters of the treated taxon (and unnamed subordinated clades, if any), as inferred from the cladistic analysis. Clades are identified by name or the lineage reference number given on the preferred cladogram (Fig. 23). Characters are identified by their numbers, in brackets [], and listed in numerical order.

(4) *Included Genera or higher taxa.* A listing of family- and/or genus-group taxa included within each treated higher taxon.

(5) *Species.* For genera containing 15 or fewer species, an alphabetical listing is given of all species and their known distributions. For larger genera, the approximate number of valid species currently placed in the taxon is given; for more detailed species level data on these genera, the references cited under the heading *Principal Revisions and Regional Faunas* should be consulted. See also Appendix 2.

(6) *Distribution.* A description of the known distribution of the treated taxon.

(7) *Principal [Revisions and] Regional Faunas.* A reference list of revisional and faunal works which include data on species in the treated taxon. The geographic scope of each work is indicated in brackets. Generally, only the most recent faunal treatment for any area is cited. Some older works may be taxonomically out-of-date. Citations to faunal studies of individual European countries may be found in Aspöck et al. (1980), and are not repeated here.

(8) *Preimaginal Stages.* A reference list of literature pertaining to the preimaginal stages of the treated genus grouped by species.

(9) *Synonymical Notes.* Justifications for newly proposed synonyms.

(10) *General Notes.* Comments and discussion not conveniently treated under any other heading.

## FAMILY HEMEROBIIDAE LATREILLE, 1802

Hemerobini Latreille, 1802:288 (Type genus: *Hemerobius* Linnaeus).
Hemerobida Leach in Brewster, 1815:138.
Hemerobides Leach in Brewster, 1815:138.
Hemerobiides Billberg, 1820:95.
Hemerobidae Stephens, 1829:310.
Hemerobioides Burmeister, 1829:22.
Hemerobites Brullé, 1832:275.
Hemerobiina Newman, 1835:380.
Hemerobiites Newman, 1835:380.
Hemerobii Ehrenberger, 1836:17.
Hemerobiidae Westwood, [1838]:48.
Hemerobiinae Swainson and Shuckard, 1840:356.
Hemerobioidae Agassiz, [1842] 1842–1846:176.
Hemerobina Schneider, 1851:35.
Hemerobiidea Costa, 1855:1.
Hemerobinae Handlirsch, [1906]:42.
Hemerobiini Nakahara, 1915:13.

*Differential Diagnosis.* Very small to small, generally brown or brownish, Neuroptera. Forewing length 3–18 mm. Distinguished from other Neuroptera by the forewing character combination: (1) anterior radial trace bearing 2 or more (up to ca. 12) "radial sectors" and (2) nygmata absent.

*Proposed Synapomorphies.* Hemerobiidae (Lineage 2): [1] Temporal costae well developed (sometimes secondarily reduced); [6] galeae bearing penicilliform sensilla; [13, 16, 17] clypeus bearing several pairs of homologizable primary setae; [35] pre-

3ir1 intraradial crossveins lost (occasionally secondarily regained); [84] parabaculum present in male; [104] female insemination-fertilization canal opening of pore-entry type.

Lineage 3: [7, 8] 5th maxillary and 3rd labial palpomeres bisubsegmented; [10] orad cavity of right mandible absent [lost]; [29] forewing radial sector segments Rs(stem) and Rs(b) branching from anterior radial trace; [95] male 9th gonocoxites absent [lost].

Lineage 9: [28] Forewing subcostal crossvein 2sc-r present.

Lineage 10: [74] Male gonarcus with gonofenestra; [78] apex of mediuncus emarginate.

Lineage 14: [31, 33] Forewing radial sector segments Rs(stem), Rs(a), Rs(b), and Rs(c) branching from anterior radial trace; [48] forewing CuP deeply forked, most proximal fork located in proximal half of posterior CuP trace.

Lineage 17: [7, 8] 5th maxillary and 3rd labial palpomeres simple, bisubsegmentation absent [lost].

Lineage 18: [78] Apex of male mediuncus simple, emargination absent [lost].

*Included Higher Taxa.* Nine subfamilies containing 24 valid genera are recognized here, see Appendix 1. One additional genus, *Notherobius* New (1988), is also considered valid, but was not examined and is not placed to subfamily.

*Species* (ca. 550). Species richness for all recognized family- and genus-group taxa is summarized in Appendix 2.

*Distribution.* Cosmopolitan, absent only from very high latitudes, nonvegetated deserts, and some remote oceanic islands.

*Principle Regional Faunas.* Only complete, or nearly complete, faunal studies are listed below. Taxonomically limited works are listed under the individual genera treated. For faunas of individual European countries, and some adjacent areas see Aspöck et al. (1980).

NEARCTIC REGION: Carpenter, 1940 [Nearctic (keys)].

NEOTROPICAL REGION: Alayo, 1968 [Cuba (keys)]; Penny and Monserrat, [1985] [Amazon Basin (keys)]; Stange, 1967 [Argentina and Uruguay (list)].

PALEARCTIC REGION: Aspöck et al., 1980 [Europe (keys)]; Kuwayama, 1962 [Japan (keys)]; Makarkin, 1985, 1986 [USSR (keys)].

ETHIOPIAN REGION: Fraser, 1951 [Madagascar (keys)]; Tjeder, 1961 [southern Africa (keys)].

ORIENTAL REGION: Ghosh and Sen, 1977 [India (list)].

AUSTRALIAN REGION: New, 1988 [Australia (keys)]; New, 1988 [New Guinea (keys)].

ISLAND FAUNAS: See Table 10.

*General Notes. Comments on hemerobiid subgenera.* Many recent revisionary and regional faunistic works which treat hemerobiids have recognized subgenera within the genera *Hemerobius* [(*Hemerobius*), (*Monorobius*), (*Brauerobius*)], *Megalomus* [(*Megalomus*), (*Pirionus*)], *Micromus* [(*Micromus*), (*Nesomicromus*)], *Sympherobius* [(*Sympherobius*), (*Niremberge*)], and *Wesmaelius* [(*Wesmaelius*), (*Kimminsia*)]. The use of these subgenera clearly results from the desire to nomenclaturally distinguish intrageneric groupings within these large genera. Unfortunately, justification for these subgenera is available only in the form of restricted regional studies. Since all of the genera involved are quite broadly distributed, formal recognition of these subgenera is, in my view, premature.

The subdivision of large genera on the basis of restricted regional studies is apt to result in the recognition of subgenera which are small paraphyletic splinter groups, large paraphyletic stem-groups, or both. If our classifications are to reflect our best hypotheses (estimates) of phylogeny (a position taken here), then all named taxa should represent demonstrably holophyletic groups. A corollary of this position is the necessity of removing taxa, including subgenera, which are not demonstrably holophyletic.

Detailed analyses of intrageneric relationships within the five genera mentioned above were beyond the scope of this work. However, I have examined a sufficient number of species in each of these genera, encompassing distant portions of their ranges, to conclude that no good evidence exists to support the supposition that their pairs (or triplets) of subgenera represent pairs of holophyletic taxa. Although some of these subgenera represent small, apparently closely related, possibly holophyletic groups of species (e.g., (*Brauerobius*), (*Pirionus*), (*Niremberge*), (*Wesmaelius*)), formal nomenclatural recognition of each of these subgenera would require the coordinate recognition of a larger subgenus which appears to be paraphyletic. Lacking comprehensive phylogenetic studies upon which to base demonstrably holophyletic subdivisions of these genera, the removal of their paraphyletic subgenera seems best achieved for the present by treating all of their existing subgeneric names as synonyms. For these reasons, no subgenera are formally recognized in this work.

Rather than continue to use subgenera of unsubstantiated holophyly, I suggest that neuropterists expand their use of the informal "species-group" convention as a means of expressing preliminary intrageneric groupings within regional faunas. Formal subgeneric taxa should be proposed only for demonstrably holophyletic groups in connection with an explicit phylogenetic analysis, preferably accompanying a comprehensive revision of the larger genus involved.

## Key to World Hemerobiid Genera (Adults)

*Notes and Instructions.* The following key to the 25 genera recognized in this work is the first attempt to facilitate generic identifications for the entire family Hemerobiidae. Although it should allow the identification of most specimens, some alterations may be necessary after intrageneric variability has been more completely analyzed. The key is intentionally artificial (i.e., holophyletic groups are not always keyed as units), and utilizes forewing characters almost exclusively for maximum ease of use. Because hemerobiid venation is notoriously variable, the choice and sequence of couplets have been carefully considered to minimize errors from this source. However, some specimens with exceptionally abnormal venation may not key correctly. Distributional information is given in brackets. The genus *Notherobius* (not seen) is included based on information published by New (1988).

1. Both forewings with 2 or fewer prestigmal "radial sectors" (Fig. 82) [widespread] .......... 27

1′. One or both forewings with 3 or more prestigmal "radial sectors" (Fig. 33) [widespread] .......... 2

2(1′). Both forewings with 0 [rare] or 1 prestigmal sc-r crossveins (Fig. 33) [widespread] ..... 16

2′. One or both forewings with 2 or more prestigmal sc-r crossveins (Fig. 157) [widespread] ..... 3

3(2′). Both forewings with 2 or fewer prestigmal sc-r crossveins [widespread] ..... 7

3′. One or both forewings with 3 or more prestigmal sc-r crossveins [widespread] ..... 4

4(3′). Both forewings with 10 or more prestigmal sc-r crossveins; forewings partly or entirely finely reticulate [southern South America and Pacific islands] ..... 5

4′. One or both forewings with 9 or fewer prestigmal sc-r crossveins; forewings without fine reticulations (discal area sometimes coarsely reticulate) [widespread] ..... 6

5(4). Forewings falcate and finely reticulate proximally (Fig. 174); subcostal space with one row of cells; hind wing macropterous [southern South America and adjacent islands] ..... *Gayomyia*

5′. Forewings falcate or not, but entirely finely reticulate; subcostal space, at least proximally, with 2 or more irregularly parallel rows of cells; hind wing micropterous or absent [Hawaiian Islands] ..... *Micromus* (part)

6(4′). Forewings short and very broadly oval, nearly circular; "membrane" coriaceous; humeral area extremely broad (Fig. 132) [Juan Fernandez Islands] ..... *Conchopterella* (part)

6′. Forewings elongate, not nearly circular; "membrane" usually membranous; humeral area broad or narrow [widespread] ..... 7

7(3, 6′). Forewing costa continued proximally toward humeral plate as a simple vein segment beyond its intersection with proximal humeral trace (Fig. 199); forewing humeral area narrow, humeral veinlet simple or branched [widespread] ..... 23

7′. Forewing costa terminating proximally at its point of intersection (sometimes incomplete) with distal end of proximal humeral trace, this point lying closely adjacent to humeral plate (Fig. 17); forewing humeral area broad, humeral veinlet always branched [widespread] ..... 8

8(7′). Both forewings with 3 or fewer m-cu crossveins (count any closely adjacent "doubled" crossveins as one) AND Forewing CuP simple or shallowly forked (i.e., most proximal fork of CuP lying in distal half of posterior CuP trace) [widespread] ..... 19

8′. One or both forewings with 4 or more m-cu crossveins OR Forewing CuP deeply forked (i.e., most proximal fork of CuP lying in proximal half of posterior CuP trace) [widespread] ..... 9

9(8′, 18′). Forewing crossvein 1cua-cup present (Fig. 182) AND Forewing costal space with a gradate series containing at least 5 (usually more) crossveins (not veinlets) [Palearctic] ..... *Drepanepteryx*

9′. Forewing crossvein 1cua-cup absent (Fig. 33) OR Forewing costal space with 4 or fewer crossveins (not veinlets) [widespread] ..... 10

10(9′). Forewing distinctly falcate (Fig. 149) [South America, Australia, and eastern Asia] ..... 11

10′. Forewing not falcate, posterior margin convex throughout (Fig. 166) [widespread] ..... 12

11(10). Antecubital portion of forewing 3rd gradate series strongly sigmoid [South America] ..... *Conchopterella* (part)

11′. Antecubital portion of forewing 3rd gradate series linear or only weakly sigmoid (Fig. 149) [Australia, eastern Asia] ..... *Drepanacra*

12(10′). Forewing with 2 or fewer ir1 crossveins (Fig. 90) (1 or fewer if R1 fused distally with most distal "radial sector"; count closely adjacent "doubled" crossveins as one) OR R1 area ill-defined because of proliferation of "radial sectors" (Fig. 140) [widespread] .................... 13

12′. Forewing with 3 or more ir1 crossveins (Fig. 166) (occasionally 2 if R1 fused distally with most distal "radial sector"; count closely adjacent "doubled" crossveins as one) [eastern Asia] .................... *Neuronema*

13(12). Both forewings with 4 or fewer prestigmal "radial sectors" [widespread] 14

13′. One or both forewings with 5 or more prestigmal "radial sectors" [widespread] 15

14(13). Both hind wings with 2 or fewer ir1 crossveins [widespread, but not Australia] 15

14′. One or both hind wings with 3 ir1 crossveins (Fig. 91) [Australia] ... *Psychobiella*

15(13′, 14). Posterior margins of genae each with a field of minute punctulae (Fig. 5) [Tahiti Is., Rapa Is.] .................... *Austromegalomus*

15′. Posterior margins of genae without fields of minute punctulae [widespread, but not Tahiti or Rapa] .................... *Megalomus*

16(2). Forewing costa continued proximally toward humeral plate as a simple vein segment beyond its intersection with proximal humeral trace (Fig. 199); forewing humeral area narrow, humeral veinlet simple or branched; forewing crossvein 2m-cu present or absent [widespread] .................... 23

16′. Forewing costa terminating proximally at its point of intersection (sometimes incomplete) with distal end of proximal humeral trace, this point lying closely adjacent to humeral plate (Fig. 17); forewing humeral area narrow or broad; forewing crossvein 2m-cu present (Fig. 157) [widespread] .................... 17

17(16′). Hind wing 4th (outer) gradate series with 3 or more (rarely 2) intraradial crossveins (Fig. 34) [widespread] .................... 18

17′. Hind wing 4th (outer) gradate series with 1 or fewer (rarely 2) intraradial crossveins (Fig. 42) [widespread] .................... 21

18(17). Both forewings with 3 or fewer m-cu crossveins (1 eastern Asian species with 4, but then with a long sagittal clypeal seta; count closely adjacent "doubled" crossveins as one) AND Forewing CuP simple or shallowly forked (i.e., most proximal fork of CuP lying in distal half of posterior CuP trace) [widespread] 19

18′. One or both forewings with 4 or more m-cu crossveins (long sagittal clypeal seta never present) OR Forewing CuP deeply forked (i.e., most proximal fork of CuP lying in proximal half of posterior CuP trace) [widespread] ......... 9

19(8, 18). Anterior border of forewing cell c3r-m strongly bowed anteriorly (Fig. 60); forewing radial veins between 3rd gradate series and wing margin distinctly sinuate (Fig. 60) [South America] .................... *Hemerobiella*

19′. Anterior border of forewing cell c3r-m straight or only very weakly bowed anteriorly (Fig. 50); forewing radial veins between 3rd gradate series and wing margin not sinuate (Fig. 33) [widespread, including South America] ....... 20

20(19′). Clypeus with a long sagittal seta (Fig. 2); crossvein 2r-m absent, or if present, positioned proximad of crossvein 2m-cu; intersection of crossvein 2m-cu with M3+4 located more than the crossvein's length distal to fork M1+2/M3+4, resulting in cell c2m-cu narrow distally (Fig. 33); male parabaculum completely divided (Fig. 37); male ectoproct without a pecten (Fig. 36) [widespread] .................... *Hemerobius*

20′. Clypeus without a long sagittal seta; crossvein 2r-m present and positioned distad of crossvein 2m-cu (Fig. 50); intersection of crossvein 2m-cu with M not more than the crossvein's length distal to fork M1+2/M3+4 (sometimes anterior to this fork), resulting in cell c2m-cu broad distally (Fig. 50); male parabaculum not completely divided (Fig. 57); male ectoproct with a pecten (Fig. 59) [widespread] ........................................ *Wesmaelius*

21(17′). Forewing with 3 m-cu crossveins [widespread, including South America and the Hawaiian Islands] ................................ *Sympherobius* (part)

21′. Forewing with 4 m-cu crossveins [South America and the Hawaiian Islands] 22

22(21′). Posterior sectoral trace giving rise to 1 side-branch along its proximal half (Fig. 74); male frons with a deep bilobed cavity (Fig. 78) [South America] ................................................ *Neosympherobius* (part)

22′. Posterior sectoral trace simple along its proximal half (Fig. 41); male frons without a deep bilobed cavity [Hawaiian Islands] .................. *Nesobiella*

23(7, 16). Forewing crossvein 2m-cu present, separated from crossvein 1m-cu by a distance approximately equal to the combined lengths of both crossveins (Fig. 191) [southwestern Pacific islands] .................................. *Noius*

23′. Forewing crossvein 2m-cu absent, if apparently present then distance separating crossvein 1m-cu from next apparent m-cu crossvein much greater than their combined lengths (Fig. 207) [widespread, including Pacific islands] ... 24

24(23′). Both forewings with M3+4 and CuA free (not fused), assume no fusion if a transverse 3m-cu crossvein is present (Fig. 207) (it may be very short) [widespread] .............................................................. 26

24′. One or both forewings with M3+4 and CuA fused, assume fusion if: (1) fusion is clear, or (2) no 3m-cu crossvein is apparent, (3) apparent 2m-cu or 3m-cu crossvein is strongly inclined or setose (Fig. 199), or (4) continuation of apparent CuA beyond its intersection with apparent 2m-cu or 3m-cu crossvein is unbranched except for small marginal forks (Fig. 215) [widespread] ..... 25

25(24′). Hind wing M3+4 not fused to CuA (Fig. 200) AND Forewing CuA simple (not forked) proximal to its fusion with M3+4 (proximal segment of M3+4 appearing as a long, oblique, setose "crossvein") (Fig. 199); male parabaculum with a pair of articulated sclerites developed in the parabacular membrane adjacent to the apophyseal shaft (Fig. 205) [South and Central America, West Indies] ........................................................ *Nusalala*

25′. Hind wing M3+4 fused to CuA (Fig. 216) OR Forewing CuA forked proximal to its fusion with M3+4 (proximal portion of anterior branch of CuA usually appearing to be crossvein 2m-cu or 3m-cu) (Fig. 215); male parabaculum without sclerites developed in the parabacular membrane adjacent to the apophyseal shaft (Fig. 217) [widespread] .................... *Micromus* (part)

26(24). Most proximal hind wing ir1 crossvein intersecting anterior sectoral trace (1) in interramus 4 AND (2) proximal to pterostigmal region (Fig. 208) (interrami are vein segments located between sequential longitudinal vein branching points) [Australia and New Guinea] .......................... *Megalomina*

26′. Most proximal hind wing ir1 crossvein not intersecting anterior sectoral trace in interramus 4 (Fig. 216) OR not proximal to pterostigmal region (usually intersecting in interramus 2 or 3, or near distal end of pterostigma) [widespread, including Australia and New Guinea] ............... *Micromus* (part)

27(1). Forewing CuP forked proximal to crossvein 2cua-cup (Fig. 98) [widespread] 34

27′. Forewing CuP not forked proximal to crossvein 2cua-cup (Fig. 82) [widespread] .............................................................. 28

28(27′). Posterior sectoral trace giving rise to 1 side-branch along its proximal half (Fig. 82) [widespread] ............................................ 29

28′. Posterior sectoral trace simple along its proximal half (Fig. 24) [Australia] . ........................................................... *Carobius*

29(28). Forewing costal space narrow or broad; some posthumeral costal veinlets branched (or, if none branched, then trichosores evident in humeral area) AND proximal humeral trace recurrent and with at least 1 side-branch [widespread] .......... 30

29′. Forewing costal space very narrow; posthumeral costal veinlets unbranched; proximal humeral trace unbranched (or, if with at least 1 side-branch, then trichosores not evident in humeral area) [Australia, southeast Asia] *Zachobiella*

30(29). Forewing 4th (outer) gradate series with 3 or more (usually 4) intraradial crossveins (Fig. 82) [widespread] .......... 31

30′. Forewing 4th (outer) gradate series with no more than 2 (usually 0) intraradial crossveins (Fig. 106) [widespread] .......... 32

31(30). Forewing crossveins 4m-cu and 4im absent (Fig. 82); intraradial crossveins of forewing 4th (outer) gradate series frequently stepped alternately [widespread, including South America] .......... *Sympherobius* (part)

31′. Forewing crossveins 4m-cu and 4im present (Fig. 66) (rarely one absent); intraradial crossveins of forewing 4th (outer) gradate series always stepped in one direction (Fig. 66) [South America] .......... *Nomerobius*

32(30′). Forewing crossvein 2sc-r present (Fig. 106); male frons without a deep bilobed cavity [widespread, but not South America] .......... 33

32′. Forewing crossvein 2sc-r absent (Fig. 74); male frons with a deep bilobed cavity (Fig. 78) [South America] .......... *Neosympherobius* (part)

33(32). Male ectoproct with a small, articulated, posterior lobe, bearing a distal row of modified setae or setal pegs (Figs. 108–109); antecosta of male 9th tergite entire; female 9th gonocoxites small reniform plates, without prominent marginal lobes or spinose setal bases (Fig. 110) [widespread, including Africa] .......... *Psectra*

33′. Male ectoproct with a lanceolate posterior process, not bearing a distal row of modified setae (Fig. 117); antecosta of male 9th tergite divided by an internal sagittal sulcus; female 9th gonocoxites greatly enlarged, each ornamented ventrally with a prominent ventral lobe and spines derived from modified setal bases (Fig. 118) [Africa] .......... *Anapsectra*

34(27). All or part of prestigmal length of forewing subcostal space much wider than width of adjacent subcosta (New, 1988, fig. 192) [Australia] ...... *Notherobius*

34′. Entire prestigmal length of forewing subcostal space no wider than width of adjacent subcosta (sometimes slightly wider immediately adjacent to crossvein 1sc-r) (Fig. 98) [primarily pantropical, including Australia] .... *Notiobiella*

## Subfamily Carobiinae Oswald, new subfamily

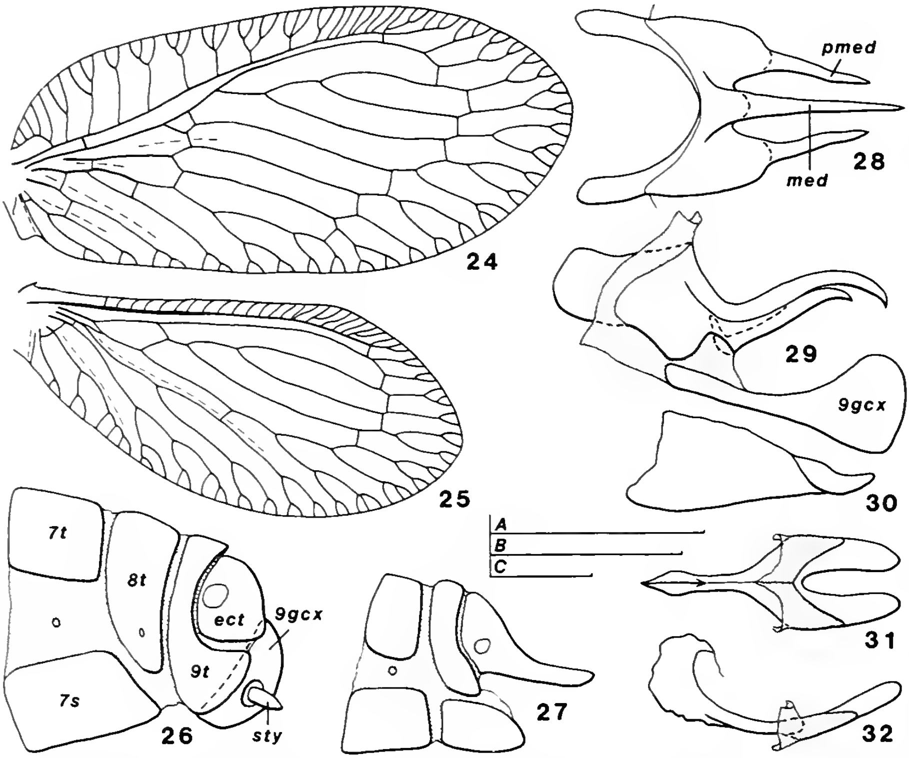
Carobiinae Oswald, new subfamily (Type genus: *Carobius* Banks).

*Included Genera. Carobius.*

## Genus Carobius Banks

(Figs. 12, 24–32)

*Carobius* Banks, 1909:78 (Type species: *Carobius pulchellus* Banks, 1909:79, by original designation. Etymology: Unexplained, probably Caro- [from Latin *carus*, dear or precious] + -bius [from Greek *bios* (masculine), life]. Gender: Masculine.): Tillyard, 1916 (RD, A, Dst, Key, W*, Tax); New, 1988 (RD, A, Dst, Key, FT*, MT*, W*, Tax).



Figs. 24–32. *Carobius pulchellus* (except as noted). 24, Forewing [Scale bar A]. 25, Hind wing [A]. 26, Female terminalia (*Carobius* sp.), lateral [B]. 27, Male terminalia, lateral [B]. 28, Gonarcus, dorsal [C]. 29, Gonarcus and 9th gonocoxite, lateral [C]. 30, 9th gonocoxite, dorsal [C]. 31, Parabaculum, dorsal [C]. 32, Parabaculum, lateral [C]. Abbreviations: 7t, 8t, 9t, tergites; 7s, 7th sternite; 9gcx, 9th gonocoxite; ect, ectoproct; med, mediuncus; pmed, paramediuncus; sty, stylus. Scale bars (mm): A = 2.0; B = 0.5; C = 0.1.

*Differential Diagnosis.* Recognized by the forewing character combination (Fig. 24): (1) anterior radial trace bearing 2 prestigmal "radial sectors" and (2) posterior sectoral trace simple for at least the proximal two-thirds of its length.

*Proposed Synapomorphies.* [30] Forewing with 2 ORB's, ORB1 shallowly forked; [34] most proximal fork of most proximal "radial sector" located in distal two-thirds of posterior sectoral trace; [39] forewing radiomedial crossvein 3r-m absent; [44] forewing mediocubital crossvein 3m-cu absent; [103] female gonapophyses posteriores absent.

*Species* (9). *angustus* Banks: Queensland, New South Wales; *curvatus* New: South Australia; *elongatus* New: New South Wales; *lateproctus* New: Northern Territory; *pectinatus* New: Northern Territory; *pedicellatus* New: South Australia and southwestern Australia; *pulchellus* Banks: Queensland, New South Wales; *spinosus* New: southwestern Australia; *trifurcatus* Kimmins: Queensland.

*Distribution.* Australia.

*Preimaginal Stages.* Unknown.

## Subfamily Hemerobiinae Latreille (revised)

Hemerobini Latreille, 1802:288 (Type genus: *Hemerobius* Linnaeus). See also the *Synonymical Listing* for the family Hemerobiidae.

*Differential Diagnosis.* Recognized by the forewing character combination (Fig. 33): (1) crossveins 2sc-r and 1cua-cup absent, (2) anterior radial trace bearing 3 to 5 prestigmal "radial sectors", and (3) crossvein 4r-m present.

*Proposed Synapomorphies.* Hemerobiinae (Lineage 4): [11] Proximal convexity of orad margin of right mandible strongly angulate; [32] forewing with 3 ORB's, ORB1 shallowly forked; [34] most proximal fork of most proximal "radial sector" located in distal two-thirds of posterior sectoral trace; [94] male supragonopontal setal group present; [100] styli of female 9th gonocoxite lost.

*Hemerobius* genus-group (Lineage 5): [85] Parabaculum deeply divided; [103] female gonapophyses posteriores lost; [105] female 8th sternite (subgenitale) lost.

*Wesmaelius* genus-group (Lineage 6): [44] Forewing mediocubital crossvein 3m-cu lost.

*Included Genera. Hemerobius*, *Nesobiella*, *Wesmaelius*, and *Hemerobiella*.

*Distribution.* All continents except Antarctica, but poorly represented in Australia (1 *Hemerobius* sp.). Present on numerous islands in the Atlantic, Indian and Pacific oceans.

## Genus Hemerobius Linnaeus

(Figs. 6–7, 13, 33–40)

*Hemerobius* Linnaeus, 1758:549 (Type species: *Hemerobius humulinus* Linnaeus, 1758:550, by subsequent designation by the International Commission on Zoological Nomenclature, Opinion 211 (ICZN, 1954):3. Etymology: See Navás, [1924b] 1923:199; Hemero- [from Greek *hemera*, day] + -bius [from Greek *bios* (masculine), life]. Gender: Masculine.): Latreille, 1810 (ITSD); Curtis, 1828 (ITSD).

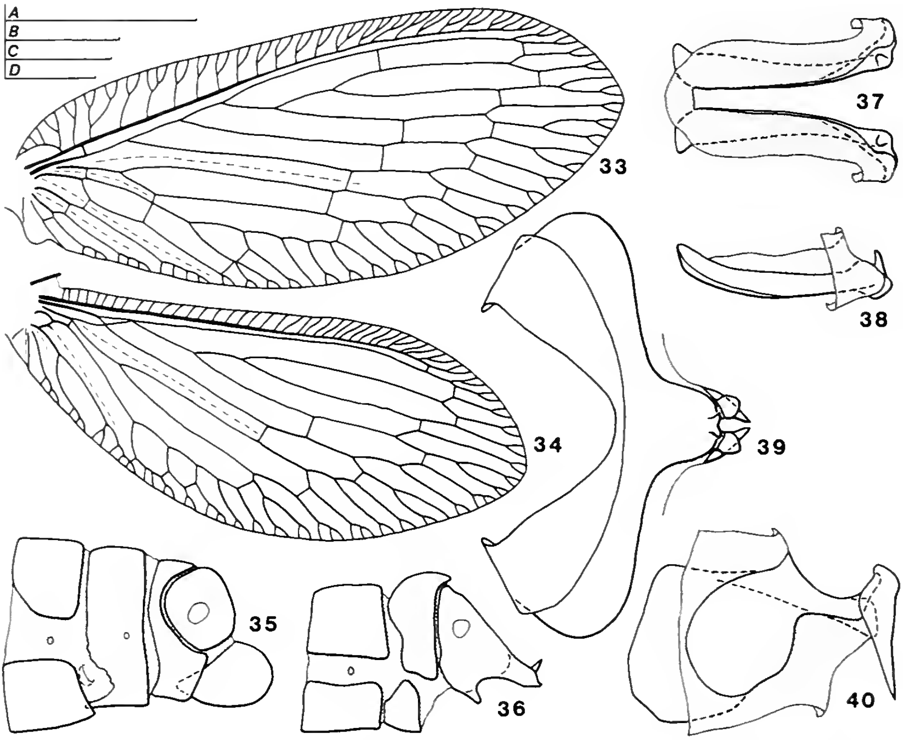
*Egnyonyx* Wesmael, 1836:167 (Type species: *Hemerobius humulinus* Linnaeus, 1758: 549 [as *humuli* (sic)], by subsequent designation by Kimmins, 1963:202. Etymology: Unexplained, probably Egny- [origin unknown] + -onyx [from Greek *onyx* (masculine), claw]. Gender: Masculine.): Kimmins, 1963 (Syn).

*Mucropalpus* Rambur, 1842:420 (Type species: *Hemerobius lutescens* Fabricius, 1793: 84, by subsequent designation by Aspöck et al., 1980:208. Etymology: Unexplained, probably Mucro- [from Latin *mucro*, sharp point] + -palpus [from Latin *palpus* (masculine), feeler]. Gender: Masculine.): McLachlan, 1863 (ITSD); Banks, 1905 (ITSD); Leraut, [1981] 1980 (ITSD); Klimaszewski and Kevan, 1985 (Syn).

*Stenolomus* Navás, 1906:701 (Type species: *Stenolomus cabrerai* Navás, 1906:701 [=*Hemerobius eatoni* Morton, 1906:147], by subsequent designation by Aspöck et al., 1980:208. Etymology: See Navás, 1906:701; Steno- [from Greek *stenos*, narrow] + -lomus [from *(Mega)lomus*]. Gender: Masculine.): Klimaszewski and Kevan, 1985 (Syn).

*Hemerodomia* Navás, 1909b:215 (Type species: *Hemerodomia buyssoni* Navás, 1909b: 217 [=*Hemerobius stigma* Stephens, 1836:112], by monotypy. Etymology: See Navás, 1909b:216; Hemero- [from *Hemero(bius)*] + -domia [from Puy-de-Dome, a region in France]. Gender: Feminine.): Klimaszewski and Kevan, 1985 (Syn).

*Brauerobius* Krüger, 1922:171 (Type species: *Hemerobius marginatus* Stephens, 1836:



Figs. 33–40. *Hemerobius humulinus*. 33. Forewing [Scale bar A]. 34, Hind wing [A]. 35, Female terminalia, lateral [C]. 36, Male terminalia, lateral [C]. 37, Parabaculum, dorsal [B]. 38, Parabaculum, lateral [B]. 39, Gonarcus, dorsal [D]. 40, Gonarcus, lateral [D]. Scale bars (mm): A = 2.0; B = 0.1; C = 0.5; D = 0.1.

109, by original designation. Etymology: Unexplained, probably Brauer- [from the surname of Austrian entomologist Friedrich Moritz Brauer (1832-1904)] + -obius [from Greek *bios* (masculine), life]. Gender: Masculine.): Klimaszewski and Kevan, 1985 (Tax). NEW STATUS

*Hagenobius* Krüger, 1922:171 (Type species: *Hemerobius citrinus* Hagen, 1861:204 [=*Hemerobius conjunctus* Fitch, [1855] 1854:798], by original designation. Etymology: Unexplained, probably Hagen- [from the surname of German entomologist Hermann August Hagen (1817–1893)] + -obius [from Greek *bios* (masculine), life]. Gender: Masculine.): Klimaszewski and Kevan, 1985 (Syn).

*Reuterobius* Krüger, 1922:171 (Type species: *Hemerobius pini* Stephens, 1836:111, by original designation. Etymology: Unexplained, probably Reuter- [from the surname of Finnish entomologist Odo Morannal Reuter (1850–1913)] + -obius [from Greek *bios* (masculine), life]. Gender: Masculine.): Klimaszewski and Kevan, 1985 (Syn).

*Schneiderobius* Krüger, 1922:171 (Type species: *Hemerobius nitidulus* Fabricius, 1777:244, by original designation. Etymology: Unexplained, probably Schneider-

[from the surname of German entomologist Wilhelm Gottlieb Schneider (1814–1889)] + -obius [from Greek *bios* (masculine), life]. Gender: Masculine.): Klimaszewski and Kevan, 1985 (Syn).

*Anotiobiella* Kimmins, 1928:364 (Type species: *Anotiobiella withycombei* Kimmins, 1928:365, by monotypy. Etymology: Unexplained, probably A- [from Greek *a*-, not] + *Notiobiella*. Gender: Feminine.): Gonzalez-Olazo, 1987 (Syn).

*Allemerobius* Banks, 1940:183 (Type species: *Allemerobius flaveolus* Banks, 1940: 184, by monotypy. Etymology: Unexplained, probably All- [from Greek *allos*, other] + -emerobius [from *(H)emerobius*]. Gender: Masculine.): Yang, 1981 (RD, MT*). NEW SYNONYM

*Dyshemerobius* Tjeder, 1961:352. Type species: *Dyshemerobius productus* Tjeder, 1961:354, by original designation. Etymology: Unexplained, probably Dys- [from Greek *dys*, bad or with difficulty] + *Hemerobius*. Gender: Masculine.): Tjeder, 1961 (OD, Dst, Fig, Key, Not); Tjeder, 1963a (Tax, Dst); Monserrat, 1990 (Dst, Fig, MT, Tax). NEW SYNONYM

*Mesohemerobius* Nakahara, 1966:202 [not *Mesohemerobius* Ping, 1928:42 (a fossil hemerobiid)] (Type species: *Mesohemerobius subacutus* Nakahara, 1966:202, by original designation. Etymology: Unexplained, probably Meso- [from Greek *mesos*, middle] + *Hemerobius*. Gender: Masculine.). NEW SYNONYM

*Semohemerobius* Yang, 1983:128 [an objective replacement name for *Mesohemerobius* Nakahara, 1966; not *Mesohemerobius* Ping, 1928] (Type species: *Mesohemerobius subacutus* Nakahara, 1966:202, by original designation [for *Mesohemerobius* Nakahara, 1966]. Etymology: See Yang, 1983:128; An anagram of *Mesohemerobius*. Gender: Masculine.). NEW SYNONYM

*Monorobius* Makarkin, 1985:167 (Type species: *Hemerobius lutescens* Fabricius, 1793:84, by original designation. Etymology: Unexplained, probably Mono- [from Greek *monos*, one] + -robius [from *(Heme)robius*]. Gender: Masculine.). NEW SYNONYM

*Differential Diagnosis*. Recognized by the presence of a prominent sagittal seta on the clypeus (Fig. 2), and the completely divided male parabaculum (Fig. 37). Differentiated venationally from other Hemerobiinae by the absence of crossvein 2r-m (Fig. 33), or its displacement proximad of crossvein 2m-cu.

*Proposed Synapomorphies*. [14] Prominent sagittal seta of clypeus present; [38] forewing radiomedial crossvein 2r-m absent or lying proximad of crossvein 2m-cu; [86] male parabaculum longitudinally divided into a pair of parasagittal sclerites.

*Species* (ca. 125). No recent comprehensive listing is available.

*Distribution*. Cosmopolitan. Widespread on all continents except Australia (1 sp.; New Guinea, 3 spp.) and Antarctica (absent), but apparently most diverse in northern temperate areas. Present also on numerous islands in the Atlantic, Indian and Pacific oceans.

*Principle Revisions and Regional Faunas*. Alayo, 1968 [Cuba]; Aspöck et al., 1980 [Europe]; Klimaszewski and Kevan, 1985, Kevan and Klimaszewski, 1987 [Canada and Alaska]; Kuwayama, 1962 [Japan]; MacLeod, 1964 [Hawaiian Islands]; Makarkin, 1985 [USSR]; New, 1988 [Australia]; New, 1988 [New Guinea]; Penny and Monserrat, [1985] 1983 [Amazon Basin]; Stange, 1967 [Argentina and Uruguay]; Tjeder, 1961 [southern Africa].

*Preimaginal Stages.* (1) *atrifrons*—Killington, 1937; (2) *humulinus*—Smith, 1923 (as *humuli*); Withycombe, 1923; Killington, 1936, 1937; Nakahara, 1954 (as *obtusus*); Agekjan, 1973; (3) *japonicus*—Nakahara, 1954; (4) *lutescens*—-Withycombe, 1923; Killington, 1937; (5) *marginatus*—-Killington, 1937; (6) *micans*—Withycombe, 1923; Killington, 1936, 1937; (7) *nitidulus*—Withycombe, 1923; Killington, 1936, 1937; Bansch, 1964; (8) *pacificus*—Quayle, 1912; Moznette, 1915a, 1915b; (9) *perelegans*—Killington, 1934, 1936, 1937; (10) *pini*—Killington, 1936, 1937; (11) *simulans*—-Killington, 1936, 1937; (12) *stigma*—Withycombe, 1922, 1923; Smith, 1925 (as *stigmaterus*); Killington, 1936, 1937; Miller and Lambdin, 1982, 1984.

*Synonymical Notes. Allemerobius.* Banks (1940) diagnosed *Allemerobius* on the basis of the slightly falcate forewing and several other minor venational features. These characters are variable within the revised concept of *Hemerobius* adopted here. I have examined two specimens (both females, MCZ) of the type species, *Allemerobius flaveolus.* These specimens exhibit the proposed synapomorphies of *Hemerobius* found in females, i.e., characters [14] and [38]. The male terminalia of *flaveolus* were figured by Yang (1981: figs. 62–65). They are in all respects characteristic of *Hemerobius.* For example, the ectoprocts bear acute processes distally, the gonarcus possesses a pair of median paramediunci, and the parabaculum is completely divided sagittally. The latter characteristic is a unique synapomorphy of *Hemerobius* [character 86].

*Dyshemerobius.* Tjeder (1961) originally diagnosed *Dyshemerobius* on the basis of several unusual characteristics of the female terminalia (particularly the partially fused and ventrally produced 9th gonocoxites) of its type species, *D. productus.* Tjeder (1963a) described a second species, *falciger*, and added the male terminalic character "gonarcus split in the middle-line" to the generic diagnosis of *Dyshemerobius.* Monserrat (1990) described the male of *productus* and showed that the split gonarcus of *falciger* was not characteristic of *productus.* In fact, all three of Tjeder's diagnostic features appear to be derived relative to the homologous states found in other *Hemerobius* species. Although *falciger* and *productus* may yet prove to form a distinctive species group within *Hemerobius*, its exclusion from *Hemerobius* s.l. would render the latter paraphyletic. I have examined the male holotype of *falciger.* It possesses all three of the synapomorphies proposed here for *Hemerobius* [characters 14, 38, and 86], and the two genera are synonymized on this basis.

*Mesohemerobius* Nakahara [nec Ping] and *Semohemerobius.* Nakahara (1966) diagnosed *Mesohemerobius* on the basis of the fused paramediunci (fused "processes of aedeagus") of the male gonarcus. Within *Hemerobius*, this condition is clearly derived relative to the presence of a pair of independent paramediunci. Excluding a group of species from *Hemerobius* on the basis of this character alone would leave the taxon comprising the remaining *Hemerobius* species paraphyletic. I have examined a male of *Mesohemerobius subacutus*, the type species of *Mesohemerobius*, and found it to possess the three *Hemerobius* synapomorphies proposed here, and the two genera are synonymized on this basis. *Semohemerobius* is an objective replacement name for *Mesohemerobius* Nakahara, 1966 (not *Mesohemerobius* Ping, 1928).

*Brauerobius.* Several recent authors have followed Aspöck et al. (1980) in recognizing *Brauerobius* as a subgenus distinct from *Hemerobius* (*Hemerobius*). In my view, recognition of *Brauerobius* as a formal subgenus is premature. Although the males of the *marginatus* species group (i.e., *costalis*, *marginatus*, and *tristriatus*) possess a distinctive synapomorphy, i.e., a field of setal bases modified as recurved denticles on the mesodistal surfaces of the male ectoprocts, removal of these species from *Hemerobius* likely leaves the remaining group of *Hemerobius* species paraphyletic. If the *marginatus* group forms the sister group to the rest of *Hemerobius* (the presence of acute prominences on the male ectoprocts, absent in the *marginatus* group, is a possible although unconfirmed synapomorphy of this grouping) there may be justification for recognizing *Brauerobius* at subgeneric rank. However, the analyses needed to demonstrate this possibility have yet to be undertaken.

*Monorobius*. Makarkin (1985:101 [of English translation]) diagnosed the subgenus *Hemerobius* (*Monorobius*) on the basis of two characters: (1) "ectoproct with single tip (kataprocessus), anaprocessus in form of spine or lacking" and (2) "paired parts of arcessus [paramediunci] fused at base". These characters do not appear to divide *Hemerobius* into a pair of holophyletic subgenera, consequently, the subgenus *Hemerobius (Monorobius)* is not recognized here.

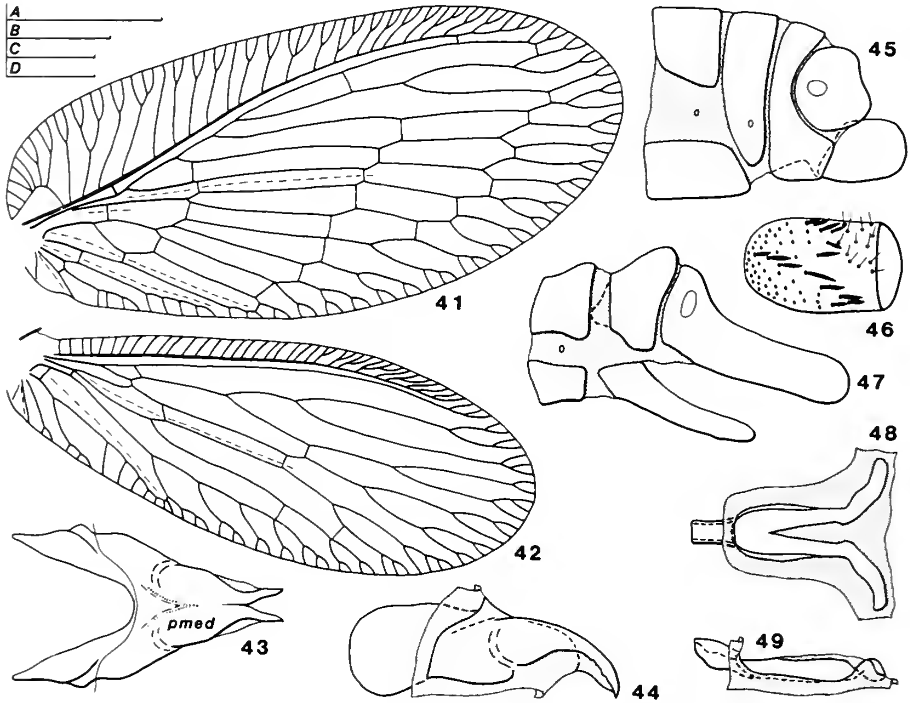
There are currently insufficient data to establish the homologies of the male ectoproct processes of *Hemerobius*. This is especially true when processes of highly divergent ectoprocts, such as those characteristic of Makarkin's subgenera, are compared. Even if Makarkin's homologies are accepted, it is difficult to accept that this character constitutes a synapomorphy for (*Monorobius*), since both processes ("anoprocessus" and "katoprocessus") are distinctly present in most species of both *Hemerobius* (*Monorobius*) and *H.* (*Hemerobius*) sensu Makarkin (see Makarkin (1985: figs. 10–27).

Makarkin's second character, proximal fusion of the paramediunci, is the same as that proposed by Nakahara for his genus *Mesohemerobius*. For a discussion of this character see under the heading *Mesohemerobius and Semohemerobius* above. It should be noted that a tendency for the paramediunci to migrate medially along the posterior margin of the extragonarcus may be a common convergent trait in the Hemerobiinae and Sympherobiinae. Paramediunci which lie closely adjacent, or are fused, medially along the posterior margin of the extragonarcus occur in *Hemerobius*, *Nesobiella*, and *Nomerobius*. The possibility that such a configuration has evolved convergently in independent lineages of *Hemerobius* cannot be presently ruled out. This tends to argue against the diagnostic use of this character for a subgeneric taxon.

*General Notes*. Among hemerobiid genera, *Hemerobius* is second only to *Micromus* in its number of generic synonyms. This reflects a long history of attempts to subdivide this large and broadly distributed genus. Adequate faunistic treatments of *Hemerobius* are currently available for most regions of the world (South and Central America and southeast Asia being notable exceptions). Future advances in our understanding of this genus will only come from concerted efforts to expand phylogenetic and revisionary studies across regional and continental boundaries. Such studies are the only satisfactory basis upon which stable, holophyletic, intrageneric groupings can be based.

## Genus Nesobiella Kimmins
(Figs. 41–49)

*Nesobiella* Kimmins, 1935:618 (Type species: *Megalomus hospes* Perkins, 1899:36, by original designation. Etymology: Unexplained, probably Neso- [from Greek *nesos*, island] + -bi- [from Greek *bios*, life] + -ella [from Latin diminutive suffix



Figs. 41–49. *Nesobiella hospes*. 41, Forewing [Scale bar A]. 42, Hind wing [A]. 43, Gonarcus, dorsal [C]. 44, Gonarcus, lateral [C]. 45, Female terminalia, lateral [B]. 46, Apex of male ectoproct, mesal [C]. 47, Male terminalia, lateral [B]. 48, Parabaculum, dorsal [D]. 49, Parabaculum, lateral [D]. Abbreviations: pmed, paramediuncus. Scale bars (mm): A = 2.0; B = 0.5; C = 0.2; D = 0.1.

-*ellus*]. Gender: Feminine.): Perkins, 1913 (Bio); Esben-Petersen, 1937 (Dst, Lst); Zimmerman, 1940 (Dst, Key, Lst); Zimmerman, 1957 (Dst, Key); MacLeod, 1964 (Mis).

*Differential Diagnosis.* Differentiated from other Hawaiian hemerobiids by the character combination: (1) forewing anterior radial trace bearing 3 or 4 prestigmal "radial sectors" (Fig. 41), (2) forewing proximal humeral trace strongly recurrent (Fig. 41), and (3) 2 or fewer (usually 0 or 1) intraradial crossveins in hind wing 4th (outer) gradate series.

*Proposed Synapomorphies.* [58] Apex of male 9th sternite produced as a long, straight, attenuate tube; [65] inner distal surface of male ectoproct bearing a field of shortened, fusiform setae.

*Species* (1). *hospes* (Perkins): Hawaiian Islands.

*Distribution.* Hawaiian Islands.

*Preimaginal Stages.* Unknown.

## Genus Wesmaelius Krüger
(Figs. 50–59)

*Wesmaelius* Krüger, 1922:170 (Type species: *Hemerobius concinnus* Stephens, 1836: 106, by original designation. Etymology: Unexplained, probably from the surname of Belgian entomologist Constantin Wesmael (1798–1872). Gender: Masculine.).

*Kimminsia* Killington, 1937:254 (Type species: *Hemerobius betulinus* Strom, 1788: 387, by original designation. Note: The identity of *H. betulinus* is uncertain. Aspöck et al., 1980:409, list this name as a nomen dubium, and treat usages of "*betulinus*" by subsequent authors under the junior name *nervosus* Fabricius (1793:85); see also Tjeder (1941:28–29) and Esben-Petersen (1925:54) for discussions of the identity of *betulinus*. Etymology: See Killington, 1937:254; From the surname of British entomologist Douglas Eric Kimmins (1905–1985). Gender: Feminine.): Tjeder, 1941 (ITSD); Klimaszewski and Kevan, 1987, 1987 (Tax). NEW STATUS

*Differential Diagnosis.* Recognized by the character combination: in the forewing (Fig. 50), (1) crossvein 2sc-r absent, (2) anterior radial trace bearing 3 or more (up to ca. 6) prestigmal "radial sectors", (3) proximal humeral trace strongly recurrent, (4) crossvein 2r-m present and positioned adjacent or distal to crossvein 2m-cu, (5) anterior border of cell c3r-m not strongly bent, and, in the hind wing (Fig. 51), (6) 4th (outer) gradate series with 3 or more intraradial crossveins. Distinguished from the similar and largely sympatric genus *Hemerobius* by the presence of forewing crossvein 2r-m in its normal position adjacent or distal to crossvein 2m-cu, and, in the male genitalia, by the presence of a pecten (Fig. 59, pec) on the mesal process of the male ectoproct, and the male parabaculum never completely divided. See also key couplet 20.

*Proposed Synapomorphies.* [61] Posterior margin of male 9th sternite bicuspate; [66] pecten of male ectoproct present.

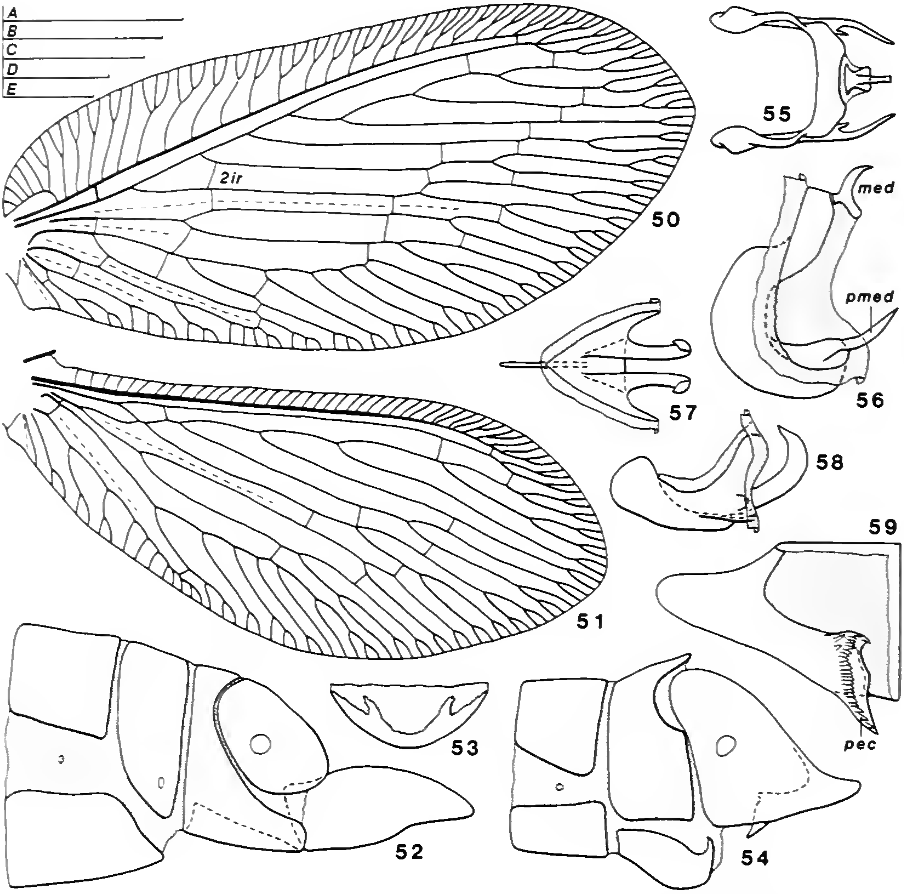
*Species* (ca. 70). No recent comprehensive listing is available.

*Distribution.* Widely distributed in North America, Africa, Europe and Asia. Most diverse in the temperate regions of North America and Eurasia. Many early records are recorded under the generic names "*Kimminsia*" and "*Boriomyia*" (sensu Banks, 1905).

*Principle Revisions and Regional Faunas.* Aspöck et al., 1980 [Europe]; Klimaszewski and Kevan, 1987, 1987 [Canada and Alaska]; Kuwayama, 1962 [Japan]; Makarkin, 1986 [USSR]; Tjeder, 1961 [southern Africa].

*Preimaginal Stages.* (1) *bihamita*—Yang, 1980a; (2) *concinnus*—Withycombe, 1923 (in *Boriomyia*); Killington, 1937; (3) *navasi*—Monserrat, 1983; (4) *nervosus*—Withycombe, 1923 (in *Boriomyia*); Miles, 1924 (in *Boriomyia*); Killington, 1934, 1936, 1937 (as *Boriomyia betulina*); (5) *quadrifasciatus*—-Withycombe, 1923 (in *Boriomyia*); Killington, 1934, 1936, 1937; (6) *rava*—Killington, 1937 (in *Boriomyia*); (7) *subnebulosus*—Withycombe, 1923 (in *Boriomyia*); Killington, 1936, 1937 (in *Boriomyia*); Laffranque and Canard, 1975; (8) spp.—-Gurney, 1947.

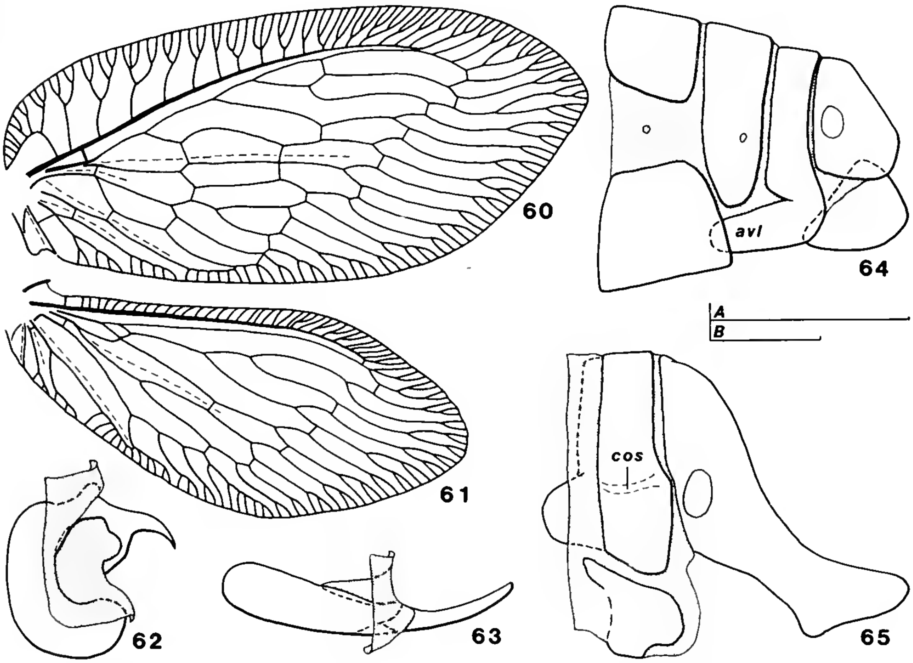
*Synonymical Notes. Kimminsia.* Recent works treating Nearctic and Palearctic *Wesmaelius* have generally followed Aspöck et al. (1980) in recognizing two subgenera, (*Wesmaelius*) and (*Kimminsia*). Klimaszewski and Kevan (1987:163, 263) diagnosed the smaller subgenus (*Wesmaelius*) on four principal characters: (1) fore-



Figs. 50–59. *Wesmaelius concinnus*. 50, Forewing [Scale bar B]. 51, Hind wing [B]. 52, Female terminalia, lateral [D]. 53, Male 9th sternite, posterior [D]. 54, Male terminalia, lateral [D]. 55, Gonarcus, dorsal [C]. 56, Gonarcus, lateral [C]. 57, Parabaculum, dorsal [A]. 58, Parabaculum, lateral [A]. 59, Ventrodistal portion of male ectoproct, mesal [E]. Abbreviations: 2ir, 2nd series intraradial crossvein; med, mediuncus; pec, pecten; pmed, paramediuncus. Scale bars (mm): A = 0.5; B = 2.0; C = 0.5; D = 0.5; E = 0.2.

wing broadly oval, (2) a forewing 2ir crossvein present (Fig. 50; "$r+m_A$" in their terminology), (3) male ectoprocts triangular, and (4) female 9th gonocoxites ("gonapophyses laterales") elongate. The subgenus (*Kimminsia*) was characterized as possessing the corresponding characters: (1) forewing narrowly oval to oval, (2) forewing 2ir crossvein absent, (3) male ectoproct rectangular, and (4) female 9th gonocoxites short.

I regard the polarities of characters (1) and (3), forewing and male ectoproct shapes, as unresolved, and therefore not currently adequate to demonstrate the holophyly of



Figs. 60–65. *Hemerobiella sinuata* (except as noted). 60, Forewing [Scale bar A]. 61, Hind wing [A]. 62, Gonarcus, lateral [B]. 63, Parabaculum, lateral [B]. 64, Female terminalia (*Hemerobiella* sp.), lateral [B]. 65, Male terminalia, lateral [B]. Abbreviations: avl, anteroventral lobe of 9th tergite; cos, costa. Scale bars (mm): A = 2.0; B = 0.5.

either group. By outgroup comparison to other hemerobiine genera, the states of characters (2) and (4) in (*Wesmaelius*) are clearly derived; and, the plesiomorphic states in (*Kimminsia*) cannot justify its holophyly. Although (*Wesmaelius*) appears to be holophyletic, its removal from *Wesmaelius* s.l. appears to render (*Kimminsia*) paraphyletic; for this reason neither subgenus is recognized here.

## Genus Hemerobiella Kimmins
(Figs. 60–65)

*Hemerobiella* Kimmins, 1940:232 (Type species: *Hemerobiella sinuata* Kimmins, 1940:233, by original designation. Etymology: Unexplained, probably Hemero- [from Greek *hemera*, day] + -bi- [from Greek *bios*, life] + -ella [from the Latin diminutive suffix *-ellus*]. Gender: Feminine.).

*Differential Diagnosis.* Differentiated from other New World hemerobiids by the character combination: in the forewing (Fig. 60), (1) crossvein 2sc-r absent, (2) anterior radial trace bearing 3 or more prestigmal "radial sectors", (3) proximal humeral trace strongly recurrent, (4) anterior border of cell c3r-m strongly bent, and, in the hind wing (Fig. 61), (5) 4th (outer) gradate series with 3 or more intraradial crossveins.

The last character, and the distinctly sinuate distal portions of the forewing radial veins (Fig. 60), will distinguish this genus from other Hemerobiinae, including the similar genus *Wesmaelius*. The male ectoproct lacks a pecten.

*Proposed Synapomorphies*. [54] Horizontal costae of inner lateral surfaces of male 9th tergite present; [98] anteroventral angles of female 9th tergite prominently produced anteriorly.

*Species* (1). *sinuata* Kimmins: Ecuador. A female specimen from Venezuela examined for this study (NMNH) is presumed to belong to this genus, but may not be conspecific with *sinuata*.

*Distribution*. Northwestern South America.

*Preimaginal Stages*. Unknown.

### Subfamily Sympherobiinae Comstock (revised)

Sympherobiidae Comstock, 1918:179 (Type genus: *Sympherobius* Banks).
Sympherobiinae Krüger, 1922:171.
Sympherobini Navás, [1925b]:91.

*Differential Diagnosis*. Recognized by the forewing character combination: (1) crossvein 2sc-r absent, (2) anterior radial trace bearing 2 prestigmal "radial sectors" (3 in a few *Sympherobius*), and (3) proximal third of posterior sectoral trace bearing one side branch, and (4) trichosores evident on humeral margin.

*Proposed Synapomorphies*. Sympherobiinae (Lineage 7): [12] Distal convexity of orad margin of right mandible rounded; [40] forewing radiomedial crossvein 4r-m absent; [53] posteroventral angle of male 9th tergite produced as a narrow, membrane-margined lobe; [79] male pseudomediuncus present.

Lineage 8 (*Neosympherobius* + *Sympherobius*): [78] Mediuncus lost.

*Included Genera*. *Nomerobius*, *Neosympherobius*, and *Sympherobius*.

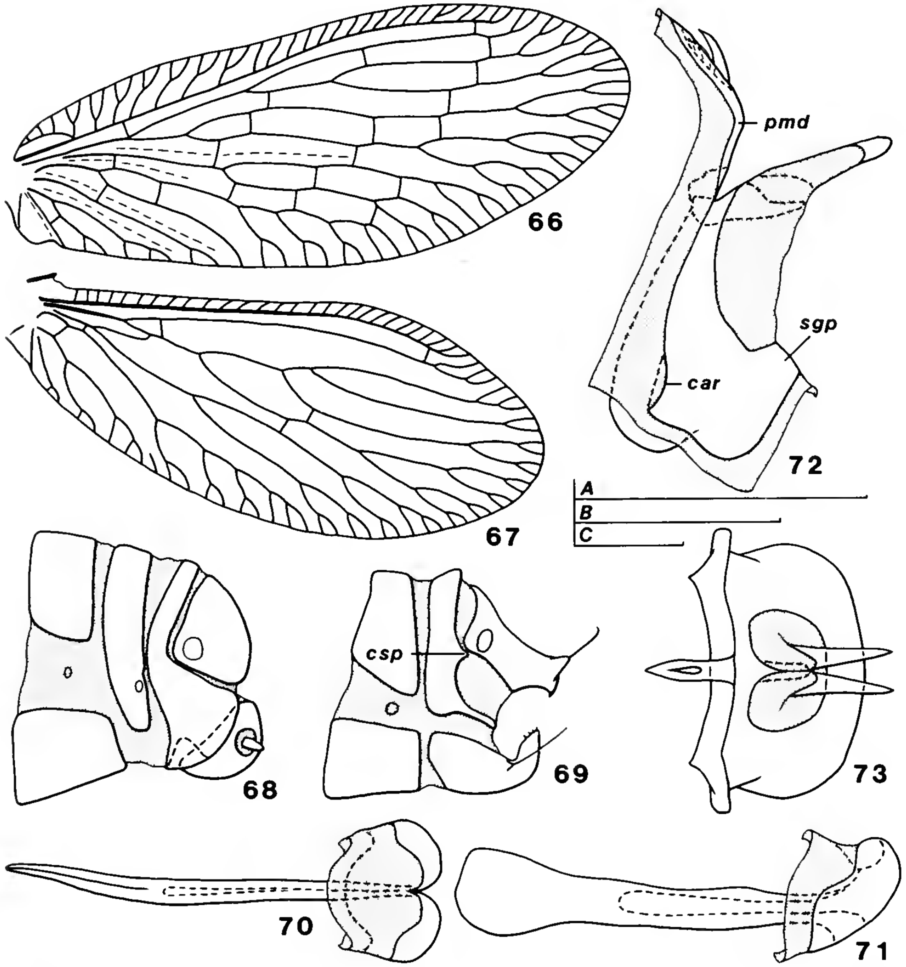
*Distribution*. North, South and Central America, Europe, Africa, and Asia. Apparently absent from Australia, India and most or all of tropical southeast Asia.

### Genus Nomerobius Navás
(Figs. 66–73)

*Nomerobius* Navás, 1915a:130 (Type species: *Megalomus psychodoides* Blanchard in Gay, 1851:127, by monotypy. Etymology: Unknown. Gender: Masculine.): Stange, 1967 (Lst); Penny and Monserrat, [1985] 1983 (Tax); Oswald, 1990 (Tax).

*Differential Diagnosis*. Distinguished from other South American hemerobiids by the forewing character combination (Fig. 66): (1) anterior radial trace bearing 2 prestigmal "radial sectors", (2) intramedial space with 2 (rarely 1) crossveins, and (3) mediocubital space with 4 (rarely 3) crossveins. The posterolateral cusps of the male 9th tergite (Fig. 69) and the secondary medioventral connection between the extrahemigonarcus of the male gonarcus (Figs. 72–73) are also diagnostic.

*Proposed Synapomorphies*. [52] Posterolateral margins of male 9th tergite cuspate; [59] apex of male 9th sternite tubularly produced and abruptly upturned; [63] male 9th sternite bearing a pair of elongate lateral setae; [68] male ectoproct with an elongate subapical seta borne on a short pedicel; [73] male gonarcus with lateral



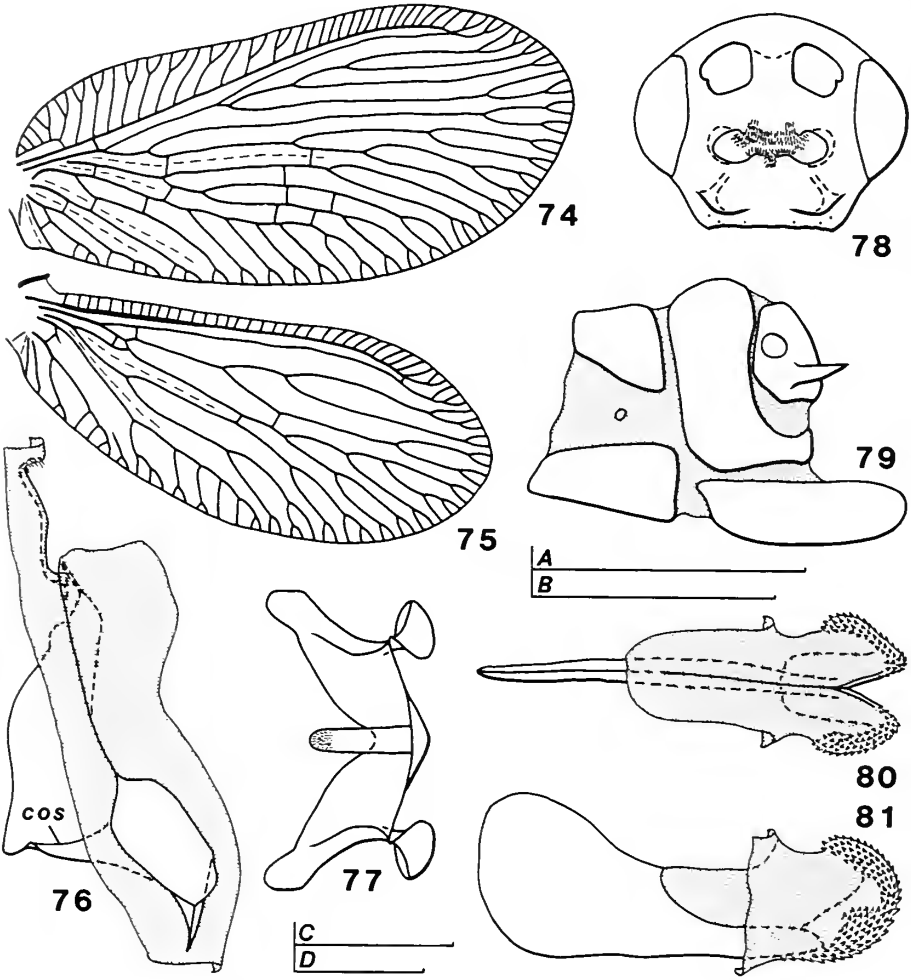
Figs. 66–73. *Nomerobius psychodoides.* 66, Forewing [Scale bar A]. 67, Hind wing [A]. 68, Female terminalia, lateral [B]. 69, Male terminalia, lateral [B]. 70, Parabaculum, dorsal [C]. 71, Parabaculum, lateral [C]. 72, Gonarcus, lateral [C]. 73, Gonarcus, dorsal [C]. Abbreviations: car, carina; csp, cusp of 9th tergite; pmd, pseudomediuncus; sgp, secondary gonopons. Scale bars (mm): A = 2.0; B = 0.5; C = 0.1.

neogonarcal carinae; [76] secondary gonopons of male gonarcus present; [103] female gonapophyses posteriores lost.

*Species* (4). *signatus* (Hagen): Argentina, Chile, Peru; *cuspidatus* Oswald: Argentina, Chile, Bolivia; *psychodoides* (Blanchard in Gay): Argentina, Chile, Peru; *spinosus* Oswald: Chile.

*Distribution.* Central and southern South America.

*Preimaginal Stages.* Unknown.



Figs. 74–81. *Neosympherobius cinereus*. 74, Forewing [Scale bar A]. 75, Hind wing [A]. 76, Gonarcus, lateral [D]. 77, Gonarcus, dorsal [D]. 78, Cranium, anterior [C]. 79, Male terminally, lateral [B]. 80, Parabaculum, dorsal [D]. 81, Parabaculum, lateral [D]. Abbreviations: cos, costa. Scale bars (mm): A = 2.0; B = 0.5; C = 0.5; D = 0.1.

## Genus Neosympherobius Kimmins
(Figs. 74–81)

*Neosympherobius* Kimmins, 1929:187 (Type species: *Neosympherobius cinereus* Kimmins, 1929:187, by original designation. Etymology: Unexplained, probably Neo- [from Greek *neos*, new] + *Sympherobius*. Gender: Masculine.): Stange, 1967 (Lst).

*Differential Diagnosis.* Distinguished from other South American hemerobiids by the forewing character combination (Fig. 74): (1) anterior radial trace bearing 2 (occasionally 3) prestigmal "radial sectors", (2) CuP not forked proximal to crossvein 2cua-cup, and (3) 4th (outer) gradate series lacking crossveins in intraradial space. The paired frontal cavities of the male (Fig. 78) are unique within the family. The highly derived configuration of the male gonarcus is also diagnostic (Fig. 76).

*Proposed Synapomorphies.* [22] Male with a bilobed frontal cavity; [36] forewing intraradial crossvein 4ir1 lost; [70] ventral margins of extrahemigonarcus prominently turned outward; [72] each intrahemigonarcus with a more or less horizontal costa or keel ventrally.

*Species* (1). *cinereus* Kimmins: Argentina.

*Distribution.* Southern South America.

*Preimaginal Stages.* Unknown.

## Genus Sympherobius Banks
(Figs. 14, 82–89)

*Sympherobius* Banks, 1904:209 (Type species: *Hemerobius amiculus* Fitch, [1855] 1854:799, by monotypy. Etymology: Unexplained, probably Symphero- [from Greek *sympheron*, useful] + -bius [from Greek *bios* (masculine), life]. Gender: Masculine.): Sharp, [1908] 1906 (ITSD); Oswald, 1988b (Rev).

*Spadobius* Needham, 1905:16 (Type species: *Hemerobius occidentalis* Fitch, [1855] 1854:799, by original designation. Note: Carpenter (1940:227) indicates that the *H. occidentalis* of Needham, 1905, is a misidentification (of *H. occidentalis* Fitch) conspecific with *H. amiculus* Fitch, [1855] 1854, the type species of *Sympherobius* Banks. This is a case of a misidentified type species which may at a later date require submission to the Commission for type designation under ICZN Article 70b. Etymology: Unexplained, probably Spado- [from Latin *spadix*, frond or palm-tree branch] + -bius [from Greek *bios* (masculine), life]. Gender: Masculine.): Oswald, 1988b (Syn).

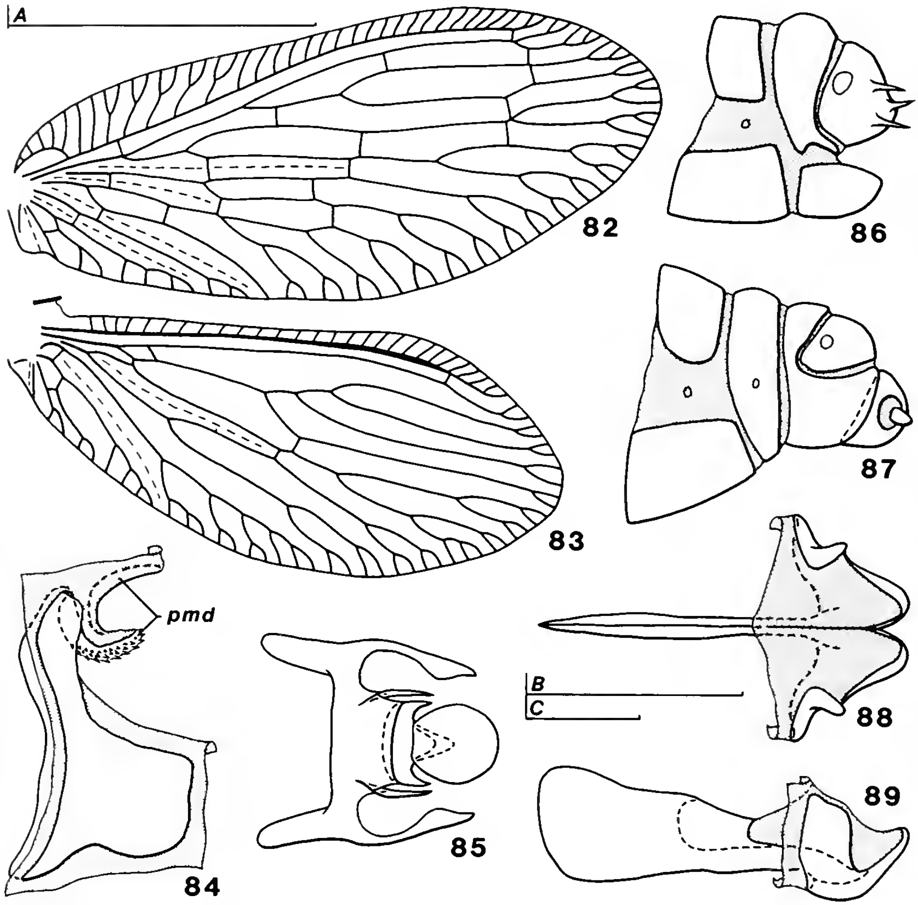
*Palmobius* Needham, 1905:17 (Type species: *Hemerobius amiculus* Fitch, [1855] 1854:799, by original designation. Etymology: Unexplained, possibly Palmo- [from Latin *palma*, hand or palm-tree] + -bius [from Greek *bios* (masculine), life]. Gender: Masculine.): Oswald, 1988b (Syn).

*Niremberge* Navás, 1909a:377 (Type species: *Niremberge limpida* Navás, 1909a:377 [=*Hemerobius fuscescens* Wallengren, 1863:22], by monotypy. Etymology: See Navás, 1909a:377; An anagram of the surname of the early Spanish naturalist V. P. Juan Eusebio Nieremberg, S. J. (1590–1658). Gender: Feminine (implied from originally included species).): Navás, [1924b] 1923 (ITSD); Oswald, 1988b (Tax, Syn). NEW STATUS

*Coloma* Navás, 1915a:129 (Type species: *Megalomus marmoratipennis* Blanchard in Gay, 1851:127, by original designation. Etymology: See Navás, 1915a:129; From the surname of R. P. Luis Coloma, S. J. Gender: Feminine.): Oswald, 1988b (Syn).

*Nefasitus* Navás, 1915a:131 (Type species: *Sympherobius amicus* Navás, 1915b:332 [=*Sympherobius fallax* Navás, 1908:408], by original designation. Etymology: See Navás, [1924b] 1923:196; From Nefasit, a locality in Eritrea, Ethiopia. Gender: Masculine.): Oswald, 1988b (Syn).

*Eurobius* Krüger, 1922:171 (Type species: *Hemerobius elegans* Stephens, 1836:113, by original designation. Etymology: Unexplained, probably Euro- [from Europe



Figs. 82–89. *Sympherobius amiculus*. 82, Forewing [Scale bar A]. 83, Hind wing [A]. 84, Gonarcus, lateral [C]. 85, Gonarcus, dorsal [C]. 86, Male terminalia, lateral [B]. 87, Female terminalia, lateral [B]. 88, Parabaculum, dorsal [C]. 89, Parabaculum, lateral [C]. Abbreviations: pmd, pseudomediuncus. Scale bars (mm): A = 2.0; B = 0.5; C = 0.1.

or Europa] + -bius [from Greek *bios* (masculine), life]. Gender: Masculine.): Oswald, 1988b (Syn).

*Lachlanius* Krüger, 1922:171 (Type species: *Hemerobius inconspicuus* McLachlan, 1868:177 [=*Hemerobius fuscescens* Wallengren, 1863:22], by original designation. Etymology: Unexplained, probably from the surname of British entomologist Robert McLachlan (1837–1904). Gender: Masculine.): Oswald, 1988b (Syn).

*Sympheromima* Kimmins, 1928:363 (Type species: *Sympheromima marginata* Kimmins, 1928:363, by original designation. Etymology: Unexplained, probably Sympheron- [from Greek *sympheron*, useful] + -mima [from Greek *mimos*, imitator or actor]. Gender: Feminine.): Oswald, 1988b (Syn).

*Differential Diagnosis.* Small hemerobiids recognized by the forewing character combination (Fig. 82): (1) crossvein 2sc-r absent, (2) anterior radial trace bearing 2 prestigmal "radial sectors" (3 in a few Eurasian spp.), (3) CuP not forked proximal to crossvein 2cua-cup, (4) proximal half of posterior sectoral trace bearing one side branch (simple in a few Eurasian spp.), (5) trichosores evident on humeral margin, and proximal humeral trace prominently recurrent, (6) 4th (outer) gradate series with 3 or more intraradial crossveins, and (7) crossveins 4m-cu and 4im absent. In males, the distinctive bipartite pseudomediuncus (Fig. 84) and processes of the ectoproct (Fig. 86) are diagnostic.

*Proposed Synapomorphies.* [42] Forewing intramedial crossvein 4im lost; [45] forewing mediocubital crossvein 4m-cu lost; [80] base of pseudomediuncus laterally expanded; [81] pseudomediuncus distinctly bipartite.

*Species* (ca. 55). For a recent world listing see Oswald (1988b).

*Distribution.* Widely distributed in the temperate and tropical areas of North and South America, and the temperate areas of Europe, Africa, and Asia. Apparently absent from Australia, India and most or all of tropical southeast Asia.

*Principle Revisions and Regional Faunas.* Alayo, 1968 [Cuba]; Aspöck et al., 1980 [Europe]; Kuwayama, 1962 [Japan]; Makarkin, 1986 [USSR]; Oswald, 1988b [Nearctic]; Penny and Monserrat, [1985] 1983 [Amazon Basin]; Stange, 1967 [Argentina and Uruguay]; Tjeder, 1961 [southern Africa]; Zimmerman, 1957 [Hawaiian Islands].

*Preimaginal Stages.* (1) *amiculus*—Smith, 1923; (2) *californicus*—Essig, 1910 (as *angustus*); (3) *domesticus*—Nakahara, 1954; (4) *elegans*—Withycombe, 1923; (5) *fallax*—Bodenheimer, 1930 (as *amicus*); (6) *fuscescens*—Withycombe, 1923 (as *inconspicuus*); Killington, 1931, 1937; (7) *masucocciphagus*—Yang, 1980b; (8) *pellucidus*—New, 1967a; (9) *pygmaeus*—Withycombe, 1923; Killington, 1937; New, 1967b.

## Subfamily Psychobiellinae Oswald, new subfamily

Psychobiellinae Oswald, new subfamily (Type genus: *Psychobiella* Banks).

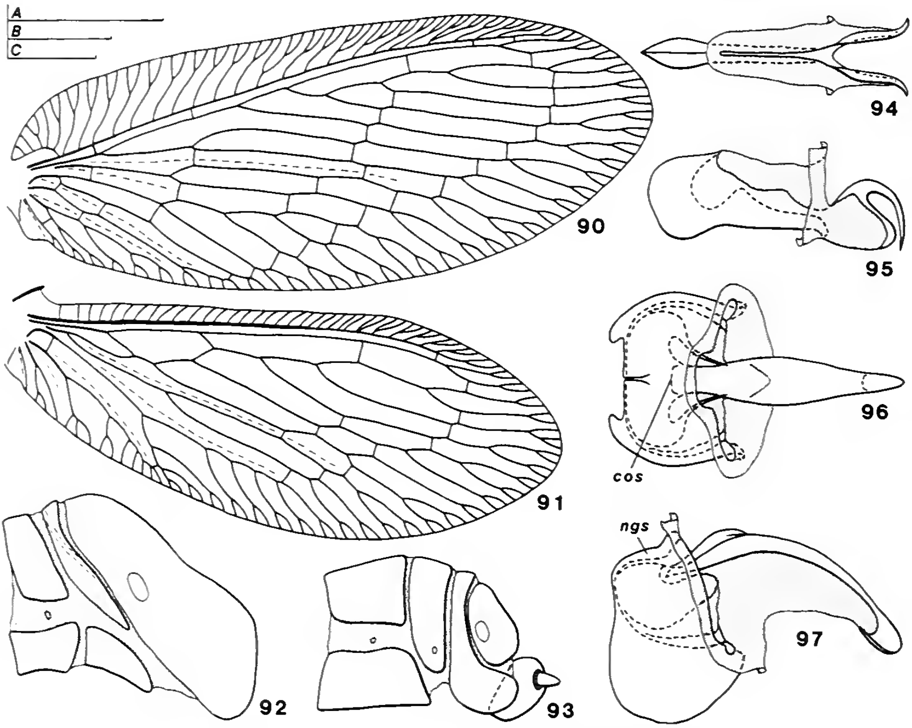
*Included Genera. Psychobiella.*

### Genus Psychobiella Banks
(Figs. 16, 90–97)

*Psychobiella* Banks, 1909:79 (Type species: *Psychobiella sordida* Banks, 1909:79, by monotypy. Etymology: Unexplained, probably Psycho- [from Greek *psyche*, breath, life or butterfly] + -bi- [from Greek *bios*, life] + -ella [from the Latin diminutive suffix *-ellus*]. Gender: Feminine.): Tillyard, 1916 (RD, A, Key, W*, Tax); New, 1988 (RD, A, Dst, Key, FT*, MT*, W*, Tax).

*Differential Diagnosis.* Distinguished from other Australian hemerobiids by the forewing character combination (Fig. 90): (1) crossvein 2sc-r present, (2) anterior radial trace bearing 3 (occasionally 4) prestigmal "radial sectors", (3) proximal humeral trace prominently recurrent and trichosores evident on humeral margin, and (4) forewing not falcate.

*Proposed Synapomorphies.* [12] Distal convexity of orad margin of right mandible strongly angulate; [17] ventromedial setae of clypeus lost; [31] forewing with 3 ORB's,



Figs. 90–97. *Psychobiella sordida.* 90, Forewing [Scale bar A]. 91, Hind wing [A]. 92, Male terminalia, lateral [B]. 93, Female terminalia, lateral [B]. 94, Parabaculum, dorsal [C]. 95, Parabaculum, lateral [C]. 96, Gonarcus, dorsal [C]. 97, Gonarcus, lateral [C]. Abbreviations: cos, costa; ngs, neogonarcus. Scale bars (mm): A = 2.0; B = 0.5; C = 0.2.

ORB1 deeply forked; [51] antecosta of male 9th tergite obliquely crossing tergite from anterior to posterior margin; [77] male mediuncus with a transverse ventral costa proximally; [82] male gonosaccal membrane with a scabriculous area below mediuncus; [87] terminal lobes of parabaculum each composed of a subapical spinose process superposed over a small ventral lobe.

*Species* (2). *occidentalis* New: South Australia; *sordida* Banks: Tasmania and eastern Australia.

*Distribution.* Australia and Tasmania.

*Preimaginal Stages.* Unknown.

## Subfamily Notiobiellinae Nakahara (revised)

Notiobiellinae Nakahara, 1960b:5 (Type genus: *Notiobiella* Banks).

*Differential Diagnosis.* Recognized by the forewing character combination: (1) anterior radial trace bearing 2 prestigmal "radial sectors" and (2) crossvein 2sc-r present, OR, if absent (secondarily lost), then trichosores lacking on humeral margin (some *Zachobiella*) or prestigmal subcostal space no wider than adjacent subcostal vein (many *Notiobiella*).

*Proposed Synapomorphies.* Notiobiellinae (Lineage 11): [40] Forewing radiomedial crossvein 4r-m lost; [42] forewing intramedial crossvein 4im lost; [45] forewing mediocubital crossvein 4m-cu lost.

Lineage 12 (*Psectra* + *Anapsectra* + *Zachobiella*): [7, 8] 5th maxillary and 3rd labial palpomeres simple, bisubsegmentation lost; [11] proximal convexity of orad margin of right mandible strongly angulate; [12] distal convexity of orad margin of right mandible strongly angulate; [36] forewing intraradial crossvein 4ir1 absent; [53] posteroventral angle of male 9th tergite produced as an elongate subectoproctal lobe, generally with a free distal process; [100] styli of female 9th gonocoxite lost; [103] female gonapophyses posteriores lost; [105] female 8th sternite (subgenitale) lost.

Lineage 13 (*Anapsectra* + *Zachobiella*): [24] Humeral veinlet recurrent and with only 1 or 2 rami (rami sometimes lost).

*Included Genera. Notiobiella*, *Psectra*, *Anapsectra*, and *Zachobiella.*

*Distribution.* One species is present in temperate North America (possibly introduced), Europe, and northern Asia. The remainder range through Central and South America, Africa, southeast Asia, India, Australia, and several islands of the southwestern Pacific.

### Genus Notiobiella Banks
(Figs. 4, 98–105)

*Notiobiella* Banks, 1909:80 (Type species: *Notiobiella unita* Banks, 1909:80, by original designation. Etymology: Unexplained, probably Notio- [from Greek *notios*, southern] + -bi- [from Greek *bios*, life] + -ella [from the Latin diminutive suffix *-ellus*]. Gender: Feminine.).

*Vaja* Navás, 1925a:192 (Type species: *Vaja tumida* Navás, 1925a:192, by monotypy. Etymology: See Navás, 1925a:192; An anagram of Java. Gender: Feminine.): Banks, 1932 (Syn).

*Buxtonia* Esben-Petersen, 1928:93 [not *Buxtonia* Thomas, 1914] (Type species: *Buxtonia fulva* Esben-Petersen, 1928:94, by original designation. Etymology: See Esben-Petersen, 1928:94; From the surname of British entomologist Patrick Alfred Buxton (1892–1955). Gender: Feminine.): Banks, 1932 (Syn).

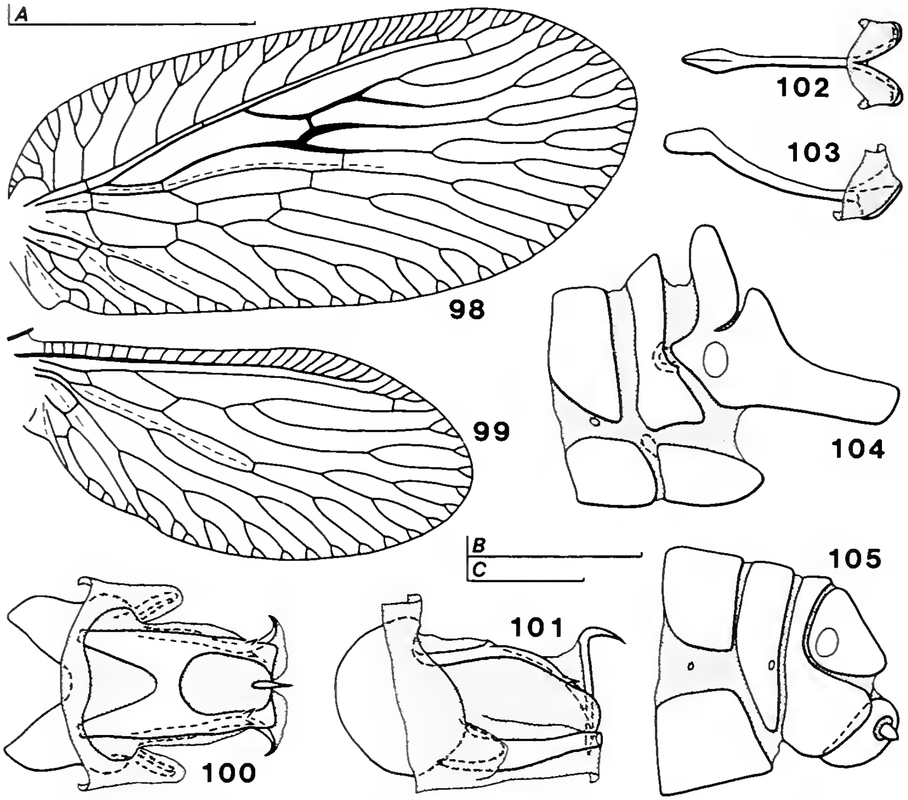
*Ganchetus* Navás, 1929a:21 (Type species: *Ganchetus africanus* Navás, 1929a:22, by monotypy. Etymology: Unknown. Gender: Masculine.): Banks, 1932 (Syn).

*Differential Diagnosis.* Recognized by the forewing character combination (Fig. 98): (1) anterior radial trace bearing 2 prestigmal "radial sectors", (2) CuP forked proximal to crossvein 2cua-cup, and (3) prestigmal subcostal space no wider than adjacent subcostal vein (sometimes slightly wider adjacent to crossvein 1sc-r). In the male, the eversible phallolingua of the gonarcus is diagnostic.

*Proposed Synapomorphies.* [15] Mesolateral setae of clypeus present; [19] mesal lobes of anterior tentorial arms closely adjacent or overlapping; [27] width of forewing subcostal space less than or equal to width of adjacent Sc; [34] most proximal fork of most proximal "radial sector" located in distal two-thirds of posterior sectoral trace; [48] forewing CuP deeply forked, most proximal fork located in proximal half of posterior CuP trace; [83] phallolingua present in male.

*Species* (ca. 35). No recent comprehensive listing is available.

*Distribution.* Widely distributed in Central and South America, Africa, southeast Asia, Australia and some southwestern Pacific islands.



Figs. 98–105. *Notiobiella multifurcata*, ex. New Caledonia (except as noted). 98, Forewing (sp. near multifurcata, ex. Queensland, Australia) [Scale bar A]. 99, Hind wing (sp. near *multifurcata*) [A]. 100, Gonarcus (phallolingua retracted, not shown), dorsal [C]. 101, Gonarcus (phallolingua retracted, not shown), lateral [C]. 102, Parabaculum, dorsal [C]. 103, Parabaculum, lateral [C]. 104, Male terminalia, lateral [B]. 105, Female terminalia (turneri, ex. South Africa), lateral [B]. Scale bars (mm): A = 2.0; B = 0.5; C = 0.2.

*Principle Revisions and Regional Faunas.* Alayo, 1968 [Cuba]; Kuwayama, 1962 [Japan]; Monserrat, 1980, 1984a [Africa]; Monserrat and Penny, 1983, Monserrat, 1984b [Neotropical]; New, 1988 [Australia]; New, 1988 [New Guinea]; Penny and Monserrat, [1985] 1983 [Amazon Basin]; Tjeder, 1961 [southern Africa].

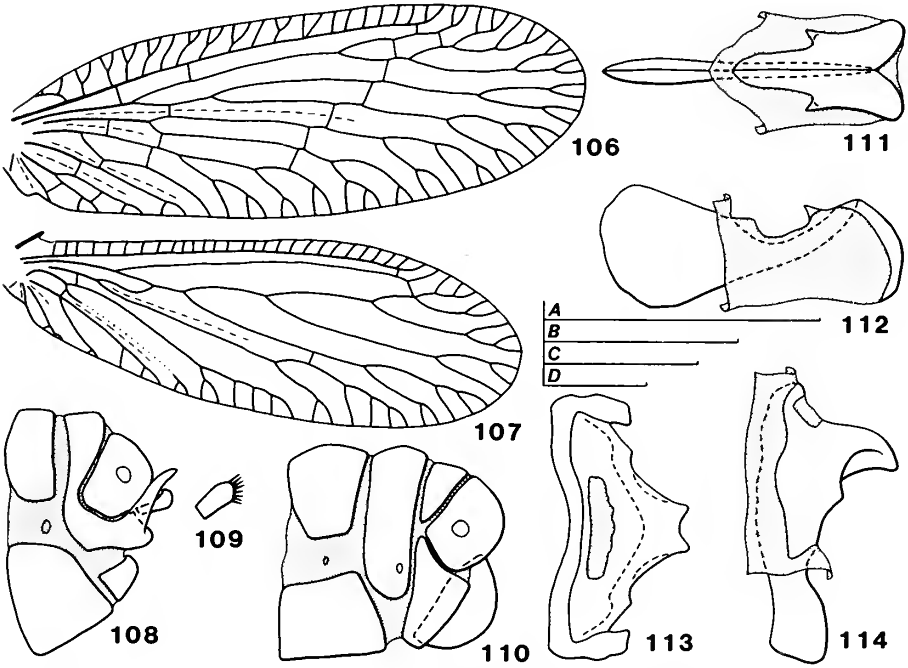
*Preimaginal Stages.* Unknown.

### Genus Psectra Hagen

(Figs. 15, 106–114)

*Psectra* Hagen, 1866:376, 458 (Type species: *Hemerobius diptera* Burmeister, 1839: 973, by monotypy. Etymology: Unexplained, probably from Greek *psektra* (feminine), scraper or currycomb. Gender: Feminine.).

*Annandalia* Needham, 1909:208 (Type species: *Annandalia curta* Needham, 1909:



Figs. 106–114. *Psectra diptera*. 106, Forewing [Scale bar A]. 107, Hind wing [A]. 108, Male terminalia, lateral [B]. 109, Male ectoproct lobe, posterolateral [B]. 110, Female terminalia, lateral [C]. 111, Parabaculum, dorsal [D]. 112, Parabaculum, lateral [D]. 113, Gonarcus, dorsal [D]. 114, Gonarcus, lateral [D]. Scale bars (mm): A = 2.0; B = 0.5; C = 0.5; D = 0.1.

208 [=*Hemerobius iniquus* Hagen, 1859:208], by monotypy. Etymology: Unexplained, probably from the surname of British zoologist Thomas Nelson Annandale (1876—1924)]. Gender: Feminine.): Nakahara, 1960b (ITSD); Tjeder, 1961 (Syn).

*Eucarobius* Esben-Petersen, 1928:95 (Type species: *Eucarobius fasciatus* Esben-Petersen, 1928:95, by original designation. Etymology: Unexplained, probably Eu- [from Greek *eu*, good or true] + *Carobius*. Gender: Masculine.): Tjeder, 1961 (Syn).

*Kimminsiella* Nakahara, 1960b:14. Type species: *Annandalia tillyardi* Kimmins, 1940:228, by original designation. Etymology: Unexplained, probably Kimmins- [from the surname of British entomologist Douglas Eric Kimmins (1905–1985)] + -iella [from the Latin diminutive suffix -ellus]. Gender: Feminine.): New, 1988 (Syn).

*Differential Diagnosis*. Not distinguishable from *Anapsectra* on the basis of venational traits. Together, *Psectra* and *Anapsectra* may be recognized by the forewing character combination (Fig. 106): (1) crossvein 2sc-r present, (2) anterior radial trace bearing 2 prestigmal "radial sectors", (3) CuP not forked proximal to crossvein 2cua-cup, and (4) some posthumeral costal veinlets branched OR trichosores evident in humeral area. The male ectoprocts of *Psectra* each possess a small articulated lobe bearing a row of terminal modified setae (Fig. 109). The male ectoprocts of *Anapsectra* each possess a lanceolate process (Fig. 117). The parabaculi of the two genera are also distinctive. In *Psectra* the parabacular apex possesses a pair (sometimes fused medially as a single structure) of broad, downturned, weakly sclerotized plates (Figs. 111–112), in *Anapsectra* the parabacular apex possesses a pair of erect lanceolate terminal lobes (Fig. 123).

*Proposed Synapomorphies.* [67] Male ectoproct with an articulating posteroventral lobe; [88] ventrodistal region of male parabaculum expanded as a pair of bulbously rounded lobes.

*Species* (ca. 25). No recent comprehensive listing is available.

*Distribution.* One species (*diptera*) is present in temperate eastern North America (possibly introduced) and broadly distributed across Europe and temperate Asia. The remaining species are distributed throughout sub-Saharan Africa, India, the primarily tropical areas of southeast Asia and eastern Australia, and several islands in the southwestern Pacific.

*Principle Revisions and Regional Faunas.* Aspöck et al., 1980 [Europe]; Tjeder, 1961 [southern Africa]; Makarkin, 1986 [USSR]; Kuwayama, 1962 [Japan]; New, 1988 [Australia]; New, 1988 [New Guinea]; Carpenter, 1961 [Micronesia]; Monserrat, 1980 [central Africa].

*Preimaginal Stages.* (1) *diptera*—Killington, 1946; New, 1966.

### Genus Anapsectra Tjeder
(Figs. 115–123)

*Anapsectra* Tjeder, 1975:115 (Type species: *Anapsectra medleri* Tjeder, 1975:117, by original designation. Etymology: Unexplained, probably Ana- [from Greek *ana*, up, back or again] + *Psectra*. Gender: Feminine.): Monserrat (in press).

*Differential Diagnosis.* See *Differential Diagnosis* for *Psectra.*

*Proposed Synapomorphies.* [78] Emargination of apex of male mediuncus lost; [96] female 7th sternite completely divided sagittally; [97] ventral margins of female 9th tergite with chalazate setae; [101] female 9th gonocoxites separated ventrally by a broad sclerotized sulcus; [102] female 9th gonocoxites each with a prominent ventral lobe.

*Species* (1). *medleri* Tjeder: Nigeria. The description of a second species by V. Monserrat is in press.

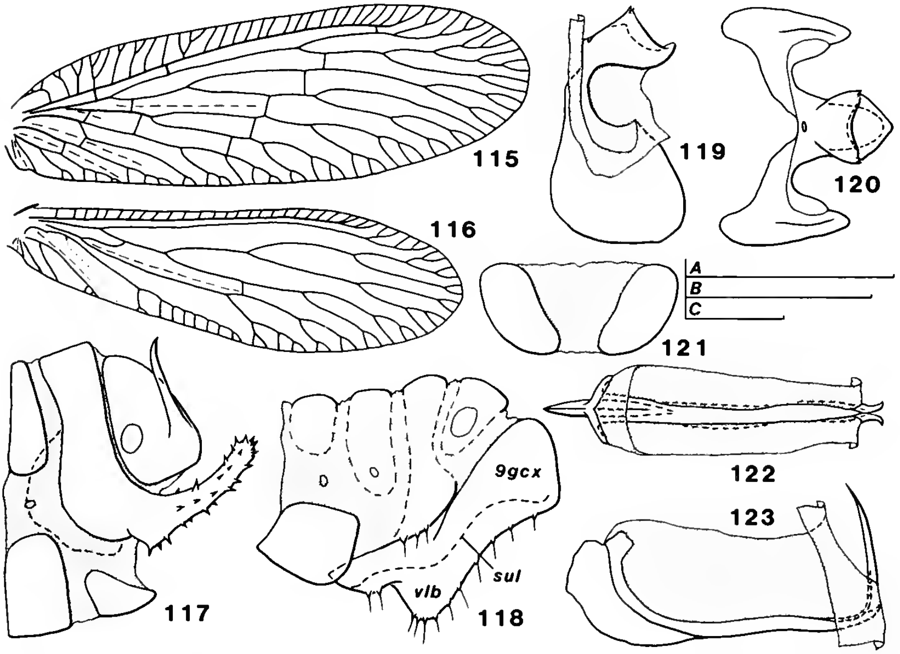
*Distribution.* West central Africa.

*Preimaginal Stages.* Unknown.

### Genus Zachobiella Banks
(Figs. 124–131)

*Zachobiella* Banks, 1920:335 (Type species: *Zachobiella punctata* Banks, 1920:335, by original designation. Etymology: Unexplained, probably Zacho- [origin unknown] + -bi- [from Greek *bios*, life] + -ella [from the Latin diminutive suffix *-ellus*]. Gender: Feminine.).

*Differential Diagnosis.* Recognized by the forewing character combination (Fig.



Figs. 115–123. *Anapsectra medleri*. 115, Forewing [Scale bar A]. 116, Hind wing [A]. 117, Male terminalia, lateral [B]. 118, Female terminalia, lateral [B]. 119, Gonarcus, lateral [C]. 120, Gonarcus, dorsal [C]. 121, Female 7th sternite, ventral [B]. 122, Parabaculum, dorsal [C]. 123, Parabaculum, lateral [C]. Abbreviations: 9gcx, 9th gonocoxite; sul, sulcus; vlb, ventral lobe of 9th gonocoxite. Scale bars (mm): A = 2.0; B = 0.5; C = 0.2.

124): (1) anterior radial trace bearing 2 prestigmal "radial sectors", (2) all posthumeral costal veinlets simple, and (3) trichosores not evident in humeral area.

*Proposed Synapomorphies*. [23] Trichosores lost proximally on anterior margin of forewing; [25] humeral silhouette not convex; [56] male 9th sternite lost (? fused to 8th sternite); [74] male gonofenestra lost; [86] terminal lobes of parabaculum fused into a single median lobe; [99] female 9th gonocoxites fused to adjacent margins of 9th tergite.

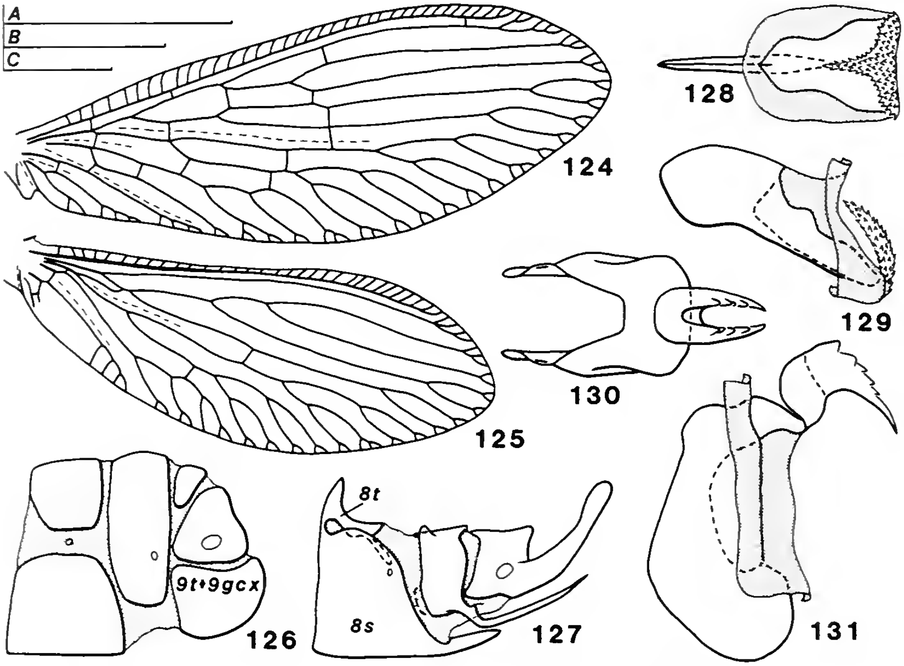
*Species* (8). *hainanensis* Banks: China; *jacobsoni* Esben-Petersen: Sumatra; *lobata* New: Australia; *marmorata* Navás: Sumatra; *pallida* Banks: Australia, New Guinea; *punctata* Banks: Philippines; *striata* Nakahara: Taiwan; *submarginata* Esben-Petersen: Australia.

*Distribution*. Southeast Asia and Australia.

*Principle Revisions and Regional Faunas*. New, 1988 [Australia]; New, 1988 [New Guinea].

*Preimaginal Stages*. Unknown.

*General Notes*. The only published information available on the male terminalia of *Zachobiella* is New's (1988) data on the Australian species *pallida*, *submarginata*



Figs. 124–131. *Zachobiella ? jacobsoni*, ex. Cameron Highlands, Malaysia [MCZ] (except as noted). 124, Forewing [Scale bar A]. 125, Hind wing [A]. 126, Female terminalia (*submarginata*), lateral [B]. 127, Male terminalia, lateral [B]. 128, Parabaculum, dorsal [C]. 129, Parabaculum, lateral [C]. 130, Gonarcus, dorsal [C]. 131, Gonarcus, lateral [C]. Abbreviations: 8s, 8th sternite; 8t, 8th tergite; 9t+9gcx, fused partial 9th tergite and 9th gonocoxite. Scale bars (mm): A = 2.0; B = 0.5; C = 0.1.

and *lobata*. The male terminalia of these species are abundantly apomorphic and provide good characters for species discrimination. The single male specimen used in this study (from peninsular Malaysia) has been tentatively identified as *jacobsoni* (described from Sumatra) based on wing characters. It is clearly not conspecific with any of the Australian species figured by New.

## Subfamily Drepanacrinae Oswald, new subfamily

Drepanacrinae Oswald, new subfamily (Type genus: *Drepanacra* Tillyard).

*Differential Diagnosis*. Not easily distinguished as a group on the basis of venational characters. Recognized by either the presence of a prominent gonofenestral plate of the gonarcus (*Conchopterella*, Fig. 134, gfp), or each gena bearing an elongate field of minute punctulae (*Austromegalomus* and *Drepanacra*, Fig. 5, gpt).

*Proposed Synapomorphies*. Drepanacrinae (Lineage 15): [49] Forewing A1 deeply forked, most proximal fork located in proximal half of posterior A1 trace; [82] male gonosaccal membrane with a scabriculous area below mediuncus.

Lineage 16 (*Austromegalomus* + *Drepanacra*): [21] Genae with fields of punctulae;

[51] antecosta of male 9th tergite obliquely crossing tergite from anterior to posterior margin.

*Included Genera. Conchopterella, Austromegalomus,* and *Drepanacra.*

*Distribution.* Southern South America, southeastern Asia, Australia, New Zealand, and islands of the South Pacific.

### Genus Conchopterella Handschin
(Figs. 132–139)

*Conchopterella* Handschin, 1955:9 (Type species: *Conchopterella kuscheli* Handschin, 1955:10, by original designation. Etymology: Unexplained, probably Concho- [from Greek *konchos*, shell] + -pter- [from Greek *pteryx*, wing] + -ella [from the Latin diminutive suffix *-ellus*]. Gender: Feminine.): Oswald, 1988a (Msc).

*Differential Diagnosis.* Recognized by the male terminalic character combination: (1) ectoprocts large and flap-like, with well-sclerotized medial surfaces (Fig. 136), (2) gonarcus with a large gonofenestral plate (Fig. 134, gfp), and (3) parabaculum narrow and distinctly arched just before terminal lobes (Fig. 139).

*Proposed Synapomorphies.* [1] Temporal costa lost or poorly developed; [64] mesal surfaces of male ectoprocts largely sclerotized; [75] gonarcus with a prominent gonofenestral plate; [89] apophyseal shaft of parabaculum prominently bowed before terminal lobes.

*Species* (3+). *kuscheli* Handschin: Juan Fernandez Islands; *maculata* Handschin: Juan Fernandez Islands; *stangei* Gonzalez-Olazo (New Combination): Chile and Argentina. One additional undescribed species from southern Chili (NMNH) has been examined.

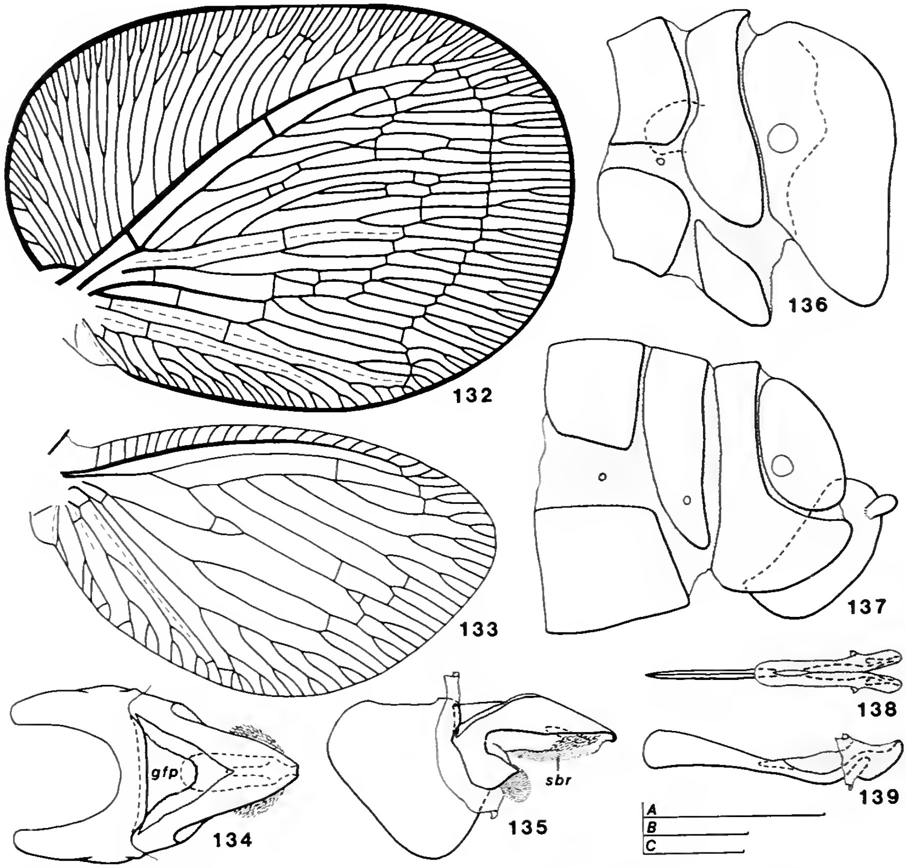
*Distribution.* Southern South America and the adjacent Juan Fernandez Is.

*Preimaginal Stages.* Unknown.

*General Notes.* The concept of *Conchopterella* is broadened here. *Conchopterella* was originally created for two Juan Fernandez Islands species in which the forewings are coriaceous, nearly circular, and somewhat irregularly veined. I have examined two species from mainland South America [*stangei* (Gonzalez-Olazo), and an undescribed species] which are clearly closely related to *kuscheli* and *maculata* on the basis of male terminalic characters (ectoprocts, gonarcus, and parabaculum). In the mainland species the forewings are falcate, membranous, and regularly veined. Since the venational characteristics of the Juan Fernandez Islands species are clearly derived, having probably evolved since their insular isolation, I regard forewing traits as variable within this genus. Based on the male terminalic characters noted in the cladistic analysis, the concept of *Conchopterella* is hereby extended to include the two mainland species.

### Genus Austromegalomus Esben-Petersen
(Figs. 140–148)

*Austromegalomus* Esben-Petersen, 1935b:139 (Type species: *Austromegalomus brunneus* Esben-Petersen, 1935b:140, by original designation. Etymology: Unexplained, probably Austro- [from Latin *austrinus*, southern] + *Megalomus*. Gender: Masculine.): Esben-Petersen, 1937 (Lst); Handschin, 1955 (Msc); Oswald, 1988a (RD, A, Dst, Key, FT*, MT*, W*, Tax).



Figs. 132–139. *Conchopterella kuscheli.* 132, Forewing [Scale bar A]. 133, Hind wing [A]. 134, Gonarcus, dorsal [B]. 135, Gonarcus, lateral [B]. 136, Male terminalia, lateral [C]. 137, Female terminalia, lateral [C]. 138, Parabaculum, dorsal [B]. 139, Parabaculum, lateral [B]. Abbreviations: gfp, gonofenestral plate; sbr, scabriculous region. Scale bars (mm): A = 2.0; B = 0.5; C = 0.5.

*Differential Diagnosis.* Recognized by the character combination: (1) each gena with a field of minute punctulae posteriorly (Fig. 5, gpt) and (2) gonosaccal membrane below mediuncus lacking a scabriculous region (Fig. 143).

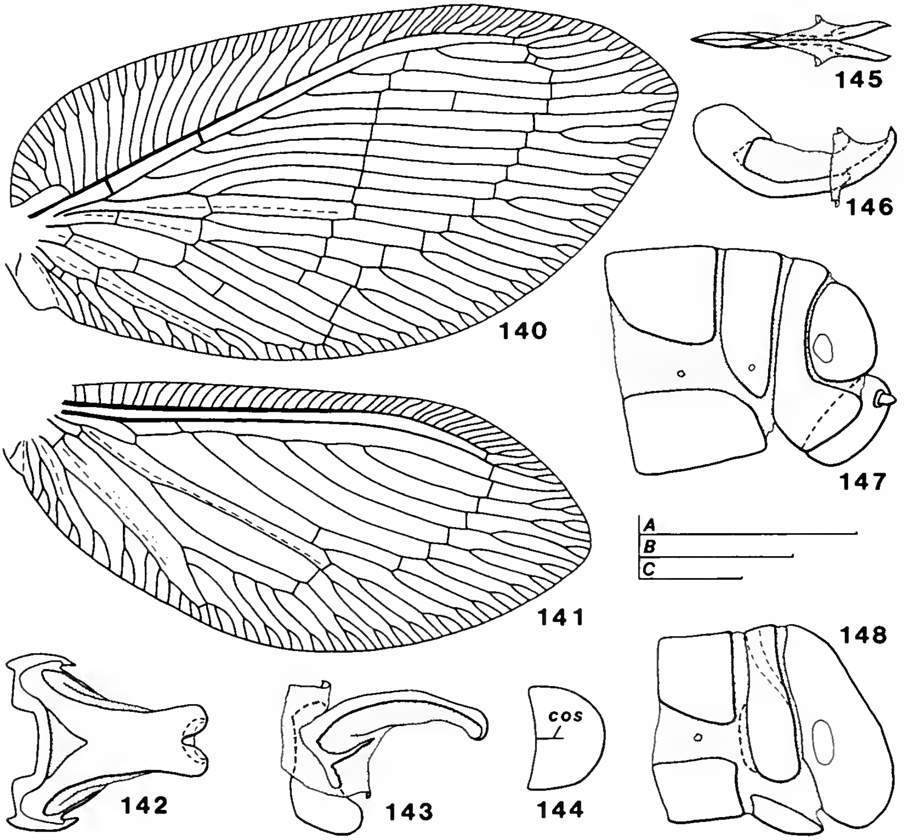
*Proposed Synapomorphies.* [57] Male 9th sternite with a small dorsosagittal costa; [82] scabriculous area of male gonosaccal membrane lost.

*Species* (2). *brunneus* Esben-Petersen: Tahiti Is.; *insulanus* Oswald: Rapa Is.

*Distribution.* French Polynesia (Tahiti and Rapa Islands).

*Preimaginal Stages.* Unknown.

*General Notes.* The presence of a sagittal costa on the dorsal surface of the male 9th sternite, proposed as a synapomorphy of *Austromegalomus*, requires confirmation in the type species *brunneus.*

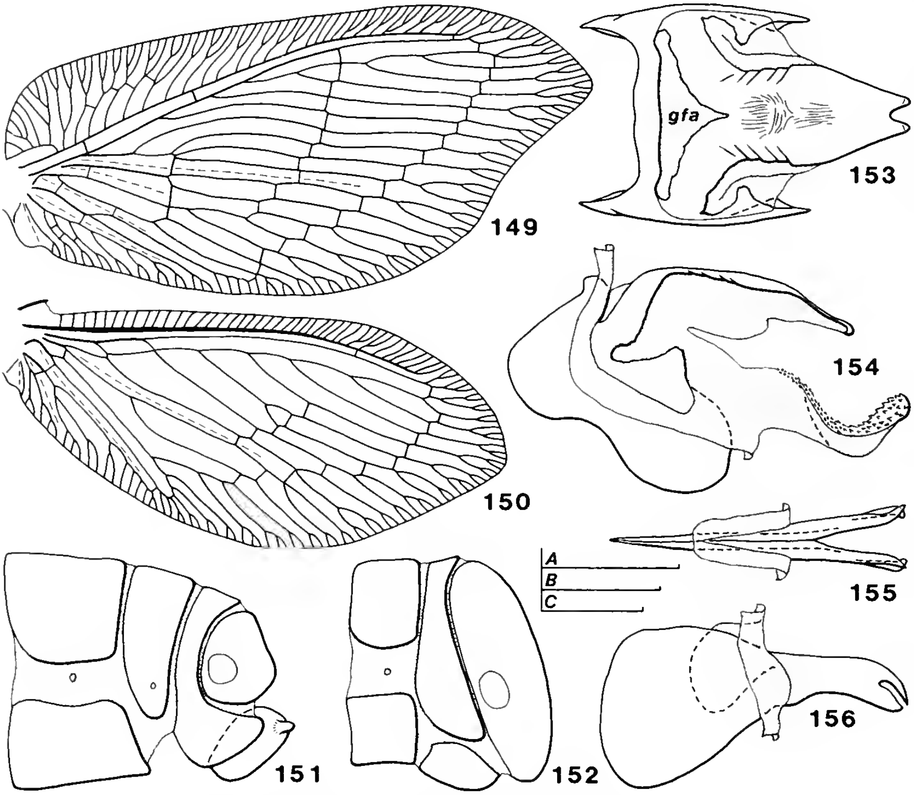


Figs. 140–148. *Austromegalomus insulanus.* 140, Forewing [Scale bar A]. 141, Hind wing [A]. 142, Gonarcus, dorsal [C]. 143, Gonarcus, lateral [C]. 144, Male 9th sternite, dorsal [B]. 145, Parabaculum, dorsal [C]. 146, Parabaculum, lateral [C]. 147, Female terminalia, lateral [B]. 148, Male terminalia, lateral [B]. Abbreviations: cos, costa. Scale bars (mm): A = 2.0; B = 0.5; C = 0.2.

## Genus Drepanacra Tillyard
## (Figs. 5, 149–156)

*Drepanacra* Tillyard, 1916:293 (Type species: *Drepanepteryx humilis* McLachlan, 1863:116 [=*Drepanepteryx binoculus* Newman, 1838:400], by original designation. Etymology: Unexplained, probably Drepan- [from Greek *drepane* or *drepanon*, sickle] + -acra [from Greek *akra* (feminine), highest or farthest point]. Gender: Feminine.): Esben-Petersen, 1937 (Lst); Nakahara, 1960b (RD, A, MT*, W*); New, 1988 (RD, A, Dst, FT*, MT*, W*, Tax); Oswald, 1988a (Msc).

*Menopteryx* Krüger, 1922:170 (Type species: *Megalomus lanceolatus* Gerstaecker, [1885] 1884:110 [=*Drepanepteryx binoculus* Newman, 1838:400], by original designation. Etymology: Unexplained, probably Meno- [from Greek *menos*, force,



Figs. 149–156. *Drepanacra binocula.* 149, Forewing [Scale bar A]. 150, Hind wing [A]. 151, Female terminalia, lateral [B]. 152, Male terminalia, lateral [B]. 153, Gonarcus, dorsal [C]. 154, Gonarcus, lateral [C]. 155, Parabaculum, dorsal [C]. 156, Parabaculum, lateral [C]. Abbreviations: gfa, gonofenestra. Scale bars (mm): A = 2.0; B = 0.5; C = 0.2.

courage or strength] + -pteryx [from Greek *pteryx* (feminine), wing]. Gender: Feminine.): Nakahara, 1960b (Syn).

*Monopteryx* [sic] Krüger, 1922:144 (an incorrect original spelling of *Menopteryx*; correct original spelling fixed by Oswald and Penny (1991), acting as first revisers).

*Drepanacrella* Kimmins, 1940:222 (Type species: *Drepanacrella khasiana* Kimmins, 1940:223, by original designation. Etymology: Unexplained, probably Drepan- [from Greek drepane or drepanon, sickle] + -acr- [from Greek akra, highest or farthest point] + -ella [from the Latin diminutive suffix -ellus]. Gender: Feminine.): Ghosh & Sen, 1977 (Lst). NEW SYNONYM

*Differential Diagnosis.* Recognized by the character combination: (1) each gena with a field of minute punctulae posteriorly (Fig. 5, gpt) and (2) forewing falcate (Fig. 149).

*Proposed Synapomorphies.* [37] Forewing falcate; [87] terminal lobes of parabaculum each composed of a subapical spinose process superposed over a small ventral lobe.

*Species* (4). *binocula* (Newman): Australia, Chatham Is., Kermadek Is., Lord Howe Is., New Caledonia (new record, BPBM), New Zealand, Norfolk Is., Tasmania; *khasiana* (Kimmins): China (new record, MCZ), India; *plaga* Banks: Formosa; *yunnanica* Yang: China.

*Distribution.* Southeastern Asia, Australia, New Zealand, and several smaller islands of the southwestern Pacific.

*Preimaginal Stages.* (1) *binocula*—New, 1975.

*Synonymical Notes. Drepanacrella.* Kimmins (1940:222—223) distinguished *Drepanacrella* from *Drepanacra* on the basis of (1) the configuration of its forewing cubital veins, (2) the highly autapomorphic male terminalia of *Drepanacrella khasiana*, and (3) the apparently disjunct ranges of the two genera. The first of these characters is based on a venational misinterpretation (see below); the second character is, in my view, not sufficient to justify its generic separation from *Drepanacra* (particularly since is removal may leave *Drepanacra* paraphyletic); and, the third character is discounted by new records of *khasiana* from mainland China, and the subsequent description of other *Drepanacra* species from Taiwan and mainland China.

Kimmins' misinterpretation of the cubital venation of *Drepanacrella* stems from his interpretation of "the basal cross-vein between Cu1 [CuA] and Cu2 [CuP]". In *Drepanacrella*, this apparent crossvein is actually the proximal segment of the anterior branch of the most proximal fork of the CuP (an interpretation supported by the presence of setae on this vein and the presence in most wings of a short, true 2cua-cup crossvein linking the anterior branch of the CuP to the CuA). However, Kimmins's interpretation is understandable, since the 2cua-cup crossvein in *khasiana* is often very short or even absent. In the latter case, the anterior branch of the CuP is fused directly to the CuA, and the proximal segment of the anterior branch of the CuA is extremely crossvein-like in appearance.

## Subfamily Megalominae Krüger (revised)

Megalominae Krüger, 1922:170 (Type genus: *Megalomus* Rambur).
Megalomini Navás, [1925b]:106.

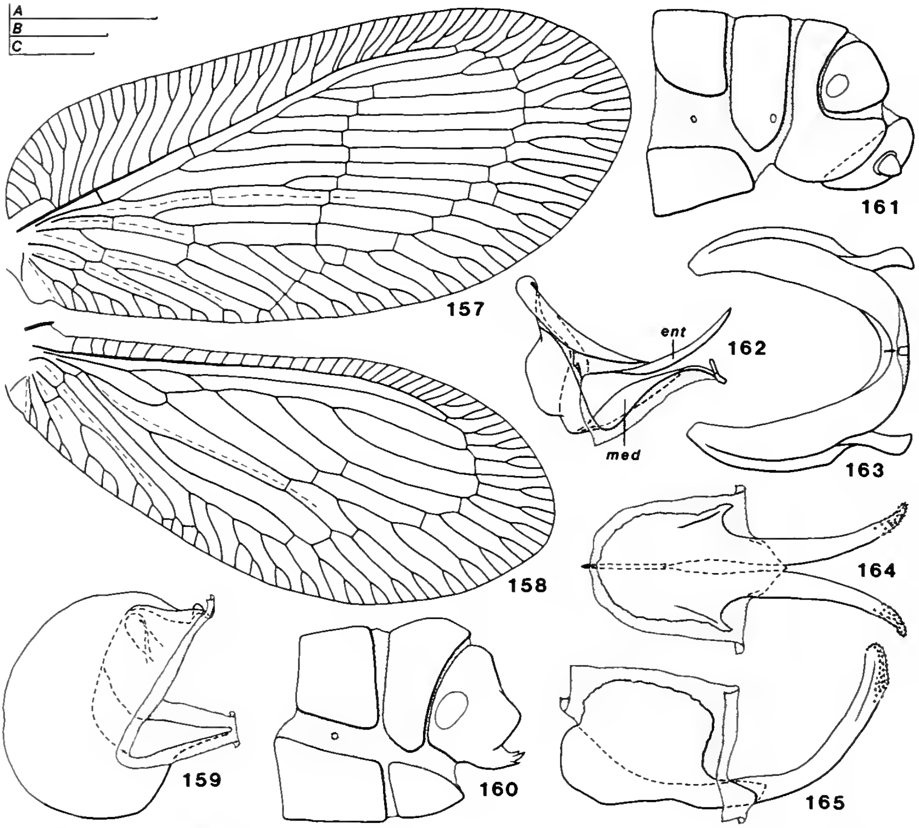
*Included Genera. Megalomus.*

### Genus Megalomus Rambur
(Figs. 3, 8–10, 157–165)

*Megalomus* Rambur, 1842:418 (Type species: *Megalomus tortricoides* Rambur, 1842: 419, by subsequent designation by Banks, 1905:43. Etymology: See Navás, [1924b] 1923:217; Megal- [from Greek megale, large] + -omus [from Greek omos (masculine), shoulder]. Gender: Masculine.): Krüger, 1922 (ITSD).

*Boriomyia* Banks, 1904:209 (Type species: *Hemerobius fidelis* Banks, 1897:27, by subsequent designation by Killington, 1937:256. Note: Killington's type designation was upheld by the International Commission on Zoological Nomenclature in Opinion 752 (1965:224). Etymology: Unexplained, probably Borio- [from Greek boreas, north] + -myia [from Greek myia (feminine), fly]. Gender: Feminine.): Banks, 1905 (ITSD). NEW SYNONYM

*Pleomegalomus* Krüger, 1922:170 (Type species: *Megalomus pictus* Hagen, 1861: 198, by original designation. Etymology: Unexplained, probably Pleo- [from Greek *pleo*, swim or sail] + *Megalomus*. Gender: Masculine.): Carpenter, 1940 (Syn).



Figs. 157–165. *Megalomus tortricoides*. 157, Forewing [Scale bar A]. 158, Hind wing [A]. 159, Gonarcus, lateral (without mediuncus) [C]. 160, Male terminalia, lateral [B]. 161, Female terminalia, lateral [B]. 162, Mediuncus and entoprocessus, lateral [C]. 163, Gonarcus, dorsal (mediuncus not shown) [C]. 164, Parabaculum, dorsal [C]. 165, Parabaculum, lateral [C]. Abbreviations: ent, entoprocessus; med, mediuncus. Scale bars (mm): A = 2.0; B = 0.5; C = 0.2.

*Pirionus* Navás, [1929c] 1928:113 (Type species: *Pirionus nigratus* Navás, [1929c] 1928:114, by monotypy. Etymology: See Navás, [1929c] 1928:113; From the surname of R. P. Anastasio Pirion, S. J. Gender: Masculine.): Gonzalez-Olazo, 1981 (Tax). NEW STATUS

*Allotomyia* Banks, 1930:224 (Type species: *Hemerobius fidelis* Banks, 1897:27, by subsequent designation by Oswald and Penny (1991). Etymology: Unexplained, probably Alloto- [from Greek *allotrios*, of another kind] + -myia [from Greek *myia* (feminine), fly]. Gender: Feminine.). NEW SYNONYM

*Spinomegalomus* Nakahara, 1965:118 (Type species: *Spinomegalomus flinti* Nakahara, 1965:119, by original designation. Etymology: Unexplained, probably Spino- [from Latin *spina*, thorn] + *Megalomus*. Gender: Masculine.): Gonzalez-Olazo, 1981 (Syn).

*Differential Diagnosis.* Recognized by either: (1) epipharyngeal surface of labrum bearing two columns of transverse strigae (Fig. 3, str), or (2) male mediuncus terminating in a pair of long attenuate processes (Fig. 162).

*Proposed Synapomorphies.* [5] Epipharyngeal surface of labrum with two columns of transverse strigae; [78] mediuncus terminating in a pair slender, attenuate processes.

*Species* (ca. 40). No recent comprehensive listing is available.

*Distribution.* Widely distributed in North and South America, Europe, extreme northern Africa and much of Asia. Particularly speciose in Central and South America. Apparently absent from Australia and sub-Saharan Africa. This poorly studied genus may contain species belonging to other genera, particularly in southeastern Asia.

*Principle Revisions and Regional Faunas.* Alayo, 1968 [Cuba]; Aspöck et al., 1980 [Europe]; Carpenter, 1940 [Nearctic]; Gonzalez-Olazo, 1981 [southern South America]; Kimmins, 1935 [miscellaneous European and Neotropical species]; Makarkin, 1986 [USSR]; Penny and Monserrat, [1985] 1983 [Amazon Basin].

*Preimaginal Stages.* (1) *fidelis*—MacLeod, 1960; (2) *hirtus*—Killington, 1934, 1936, 1937.

*Synonymical Notes. Boriomyia* and *Allotomyia.* Most of the early confusion surrounding the interpretation of the genus *Boriomyia* stemmed from controversy over its type species. This nomenclatural question has been resolved by the International Commission on Zoological Nomenclature (ICZN, 1965). There is no question that *Boriomyia fidelis* and *speciosa* belong within the genus *Megalomus.* Such an association was suggested by Carpenter (1940) and MacLeod ([1961]) on the basis of both larval and adult characters, but was never formalized in synonymy. The present work fully corroborates this association.

Both *fidelis* and *speciosa* share the two synapomorphies of *Megalomus* proposed here [characters 5 and 78]. Furthermore, both species possess transverse ridges on the molar surfaces of the mandibles, a character elsewhere observed only in some (mostly New World) *Megalomus* species. On the basis of this last character, the removal of *fidelis* and *speciosa* from *Megalomus* to *Boriomyia* would appear to render *Megalomus* paraphyletic. The holophyly of *fidelis* + *speciosa* as a species group within *Megalomus* is supported by the apparently unique presence in these two species of a long, posteriorly directed, unpaired median lobe of the parabaculum. *Allotomyia* is a junior objective synonym of *Boriomyia.*

*Pirionus.* Gonzalez-Olazo (1981) revised the *Megalomus* species of southern South America and recognized two subgenera, *Megalomus* (*Megalomus*) and *M.* (*Pirionus*). *Megalomus* (*Pirionus*) was diagnosed principally on the basis of three characters: (1) posterior margin of male 7th tergite prominently produced, (2) male ectoprocts strongly narrowed, and (3) configuration of male gonarcus highly modified. While all three of these characters strongly support *M. nigratus* + *flinti* as a holophyletic species group within *Megalomus*, the corresponding characters in the subgenus (*Megalomus*)—(1) male 7th tergite not prolonged, (2) male ectoprocts not strongly narrowed, and (3) male gonarcus not highly modified—are plesiomorphic, and cannot justify the holophyly of *Megalomus* (*Megalomus*). Consequently, neither subgenus is recognized here.

## Subfamily Drepanepteryginae Krüger (revised)

Drepanepteryginae Krüger, 1922:170 (Type genus: *Drepanepteryx* Leach in Brewster).
Drepanopterygini Navás, 1933:224.

*Differential Diagnosis.* Large hemerobiids. See *Proposed Synapomorphies* below. The following character combination is characteristic of the Drepanepteryginae and Megalominae: (1) crossvein 2sc-r present (not uniquely identifiable in *Gayomyia*), (2) anterior radial trace bearing 4 or more (up to ca. 12) "radial sectors", (3) humeral area broad and with a well-branched humeral veinlet, and (4) 5th maxillary and 3rd labial palpomeres not subsegmented.

*Proposed Synapomorphies.* Drepanepteryginae (Lineage 19): [1] Temporal costae lost or poorly developed; [41] forewing intramedial crossvein 2im present; [47] forewing intercubital crossvein 1cua-cup present.

Lineage 20 (*Gayomyia* + *Drepanepteryx*): [18] Anteromesal process of tentorial bridge lost; [49] forewing A1 deeply forked, most proximal fork located in proximal half of posterior A1 trace; [74] gonofenestra of gonarcus lost.

*Included Genera. Neuronema, Gayomyia,* and *Drepanepteryx.*

*Distribution.* Southern South America and the Juan Fernandez Is., Europe, and Asia.

### Genus Neuronema McLachlan
(Figs. 166–173)

*Neuronema* McLachlan, 1869:27 (Type species: *Hemerobius decisus* Walker, 1860: 185, by monotypy. Etymology: Unexplained, probably Neuro- [from Greek *neuron*, nerve] + -nema [from Greek *nema* (neuter), thread]. Gender: Neuter.).

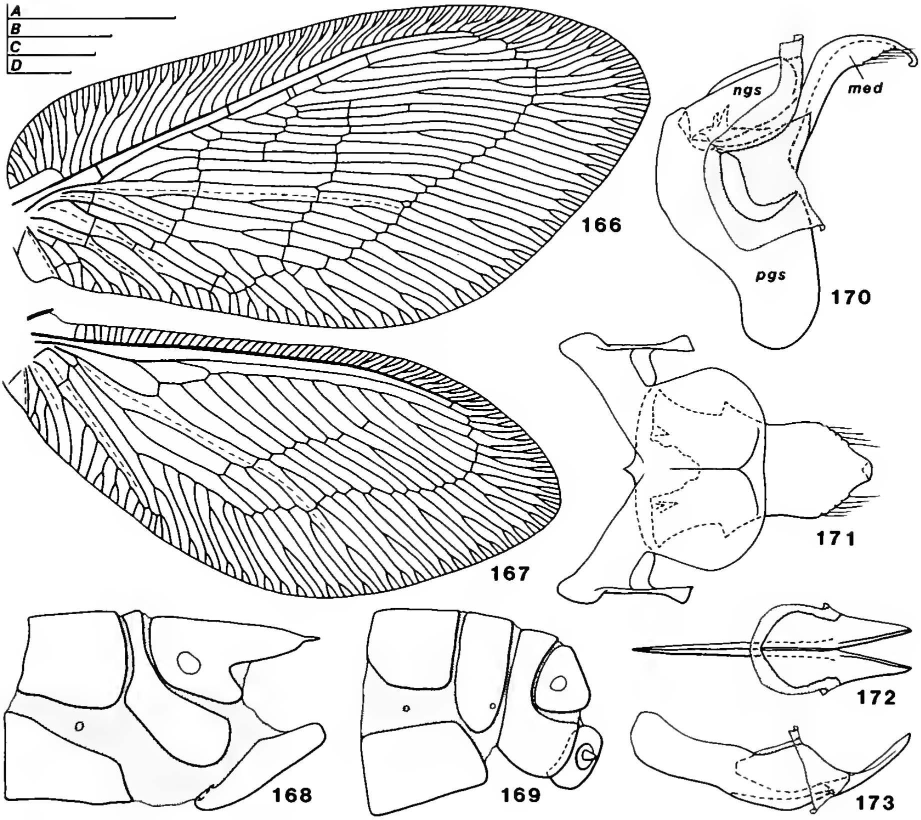
*Ninguta* Navás, 1912b:420 [not *Ninguta* Moore, 1892] (Type species: *Megalomus deltoides* Navás, [1910] 1909:396 [=*Hemerobius albostigmata* Matsumura, 1907: 171], by original designation. Etymology: Unknown. Gender: Feminine (implied from originally included species).): Kuwayama, 1962 (Syn).

*Ninga* Navás, 1913c:122 [a replacement name for *Ninguta* Navás, 1912b; not *Ninguta* Moore, 1892] (Type species: *Megalomus deltoides* Navás, [1910] 1909:396 [=*Hemerobius albostigmata* Matsumura, 1907:171], by original designation [for *Ninguta* Navás, 1912b]. Etymology: See Navás, 1913c:122; A contraction of *Ninguta*. Gender: Feminine.): Kuwayama, 1962 (Syn).

*Kulinga* Navás, 1936:49 (Type species: *Kulinga pielina* Navás, 1936:50, by monotypy. Etymology: See Navás, 1936:50; From Kuling, a locality in China. Gender: Feminine.): Yang, 1964 (Syn).

*Sineuronema* Yang, 1964:276, 280 (Type species: *Neuronema sinensis* Tjeder, 1936: 6, by original designation. Etymology: Unexplained, probably Si- [from Latin *Sina*, China] + *Neuronema*. Gender: Neuter.). NEW SYNONYM

*Differential Diagnosis.* A poorly characterized genus of large species restricted to eastern Asia. Distinguished from other east Asian hemerobiids by the presence of one or more forewing pre-3ir1 crossveins (Fig. 166), or the forewing character combination (Fig. 166): (1) crossvein 2sc-r present, (2) anterior radial trace bearing 4 to 6 prestigmal "radial sectors" (rarely more or fewer), (3) costal space with 4 or fewer



Figs. 166–173. *Neuronema decisum* (except as noted). 166, Forewing [Scale bar C]. 167, Hind wing [C]. 168, Male terminalia, lateral [D]. 169, Female terminalia (*kuwayamai*), lateral [D]. 170, Gonarcus, lateral [A]. 171, Gonarcus, dorsal [A]. 172, Parabaculum, dorsal [B]. 173, Parabaculum, lateral [B]. Abbreviations: med, mediuncus; ngs, neogonarcus; pgs, paleogonarcus. Scale bars (mm): A = 0.5; B = 0.5; C = 2.0; D = 0.5.

crossveins (not veinlets), (4) 2nd gradate series very well developed, and (5) forewing not falcate.

*Proposed Synapomorphies.* [35] Forewing pre-3ir1 intraradial crossveins present.

*Species* (ca. 30). No recent comprehensive listing is available.

*Distribution.* China (mainland and Taiwan) and the adjacent areas of the USSR to the north, to Japan in the east, and India and Nepal to the southwest.

*Principle Revisions and Regional Faunas.* Kimmins, 1943 [miscellaneous species]; Kuwayama, 1962 [Japan]; Makarkin, 1986 [USSR]; Yang, 1964, 1981 [China].

*Preimaginal Stages.* Unknown.

*Synonymical Notes. Sineuronema.* Yang (1964) diagnosed *Sineuronema* principally on the basis of four characters: (1) forewing M with only 2 primary branches, (2) intracubital reach of forewing 3rd (4th?) gradate series terminating on or near anterior cubital trace proximal to crossvein 3m-cu, (3) forewing 2nd gradate series not extending posteriorly into anal space, and (4) parabacular cleft at least three-eighths of total length of parabaculum. The corresponding characters in *Neuronema* are: (1) forewing M with at least 3 (usu. 4 or 5) primary branches, (2) intracubital reach of forewing 3rd (4th?) gradate series generally terminating on or near anterior cubital trace proximal between crossveins 3m-cu and 4m-cu, (3) forewing 2nd gradate series extending posteriorly into anal space, and (4) parabacular cleft less than three-eighths of total length of parabaculum. In the material of *Neuronema* and *Sineuronema* which I have examined, there is considerable variation in these venational characters; and I can find no strong support for maintaining these taxa as separate genera. Because the parabacular apophysis may increase in length with age, the ratio of the depth of the parabacular cleft to total parabacular length would seem to be a particularly unreliable character.

The *Neuronema/Sineuronema* complex is poorly supported by synapomorphic characters in the present cladistic analysis. However, one of the more striking terminalic characters within this complex—the presence of a pair of prominent supra-parabacular processes—is almost certain to be found to be synapomorphic at some level within *Neuronema* s. lat. The apparent presence of these structures in all *Sineuronema* species, and some but not all *Neuronema* species, suggests that the removal of *Sineuronema* from *Neuronema* s. lat. would leave *Neuronema* s. str. paraphyletic. Additional study of this complex of species is needed.

*General Notes.* A convenient diagnostic character for the differentiation of *Neuronema* species from other large eastern Asian hemerobiids (particularly *Drepanepteryx* and *Megalomus*) is the particularly long R1 space (Fig. 166), which results from the clustering of ORB's at the proximal end of the anterior radial trace.

### Genus Gayomyia Banks
(Figs. 174–181)

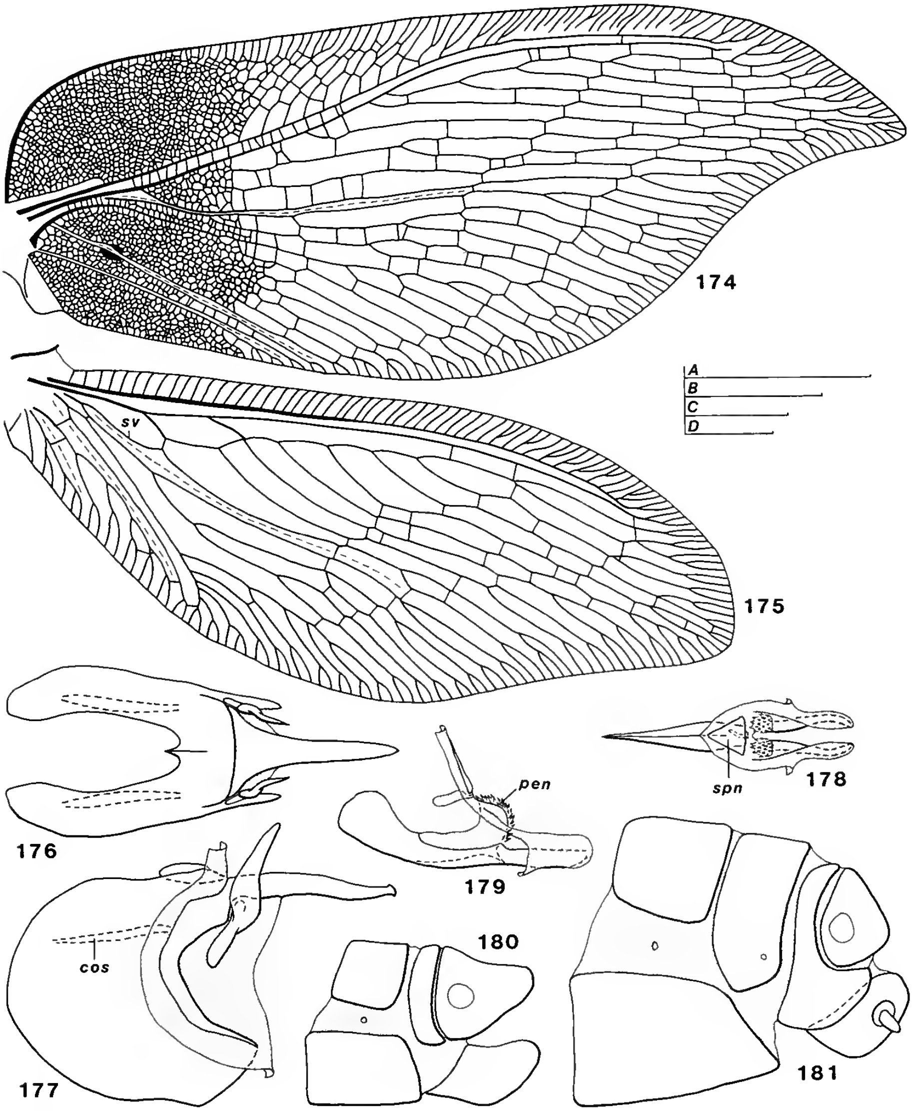
*Gayomyia* Banks, 1913:216 (Type species: *Megalomus falcatus* Blanchard in Gay, 1851:125, by original designation. Etymology: Unexplained, probably Gayo- [from the surname of Chilean natural historian Claudio Gay (1800-1873)] + -myia [from Greek *myia* (feminine), fly]. Gender: Feminine.): Stange, 1967 (Lst).

*Gayomia* [sic] Banks, 1913:217 (an incorrect original spelling of *Gayomyia*; correct original spelling fixed by Oswald and Penny (1991), acting as first revisers).

*Porter* Navás, 1924a:15 (Type species: *Porter discolor* Navás, 1924a:16 [=*Megalomus falcatus* Blanchard in Gay, 1851:125], by monotypy. Etymology: See Navás, 1924a: 16; From the surname of Chilean entomologist Carlos Emilio Porter (1868-1942). Gender: Masculine.): Handschin, 1955 (Syn).

*Differential Diagnosis.* Recognized by the finely reticulate forewing base and the forewing subcostal space containing 10 or more sc-r crossveins which divide the space basally into a single row of cells (Fig. 174).

*Proposed Synapomorphies.* [20] Cranium with numerous setal foveae; [26] costal space finely reticulate proximally; [34] most proximal fork of most proximal "radial sector" located in distal two-thirds of posterior sectoral trace; [35] forewing pre-3ir1 intraradial crossveins present; [37] forewing falcate; [46] forewing mediocubital flex-



Figs. 174–181. *Gayomyia falcata.* 174, Forewing [Scale bar A]. 175, Hind wing [A]. 176, Gonarcus, dorsal [D]. 177, Gonarcus, lateral [D]. 178, Parabaculum, dorsal [B]. 179, Parabaculum, lateral [B]. 180, Male terminally, lateral [C]. 181, Female terminally, lateral [C]. Abbreviations: cos, costa; pen, penniform sclerite; spn, suprapenniform sclerite; sv, sigmoid vein. Scale bars (mm): A = 2.0; B = 0.5; C = 0.5; D = 0.2.

ion line lost; [50] male 9th tergite sagittally divided; [71] inner surface of each intrahemigonarcus with a prominent horizontal costa; [90] parabaculum bearing a pair of penniform accessory sclerites; [91] gonosaccal membrane immediately dorsal to penniform sclerites containing a triangular, weakly sclerotized, area; [106] female bursa broadly, but weakly, sclerotized dorsally.

*Species* (3). *cinerea* Krüger: Chile (?); *falcata* (Blanchard in Gay): Argentina, Chile, Juan Fernandez Is., Peru; *stictica* (Blanchard in Gay): Chile. The taxonomic placement and validity of *cinerea* and *stictica* require confirmation.

*Distribution.* Southern South America and the Juan Fernandez Is.

*Preimaginal Stages.* Unknown.

### Genus Drepanepteryx Leach in Brewster
(Figs. 182–190)

*Drepanepteryx* Leach in Brewster, 1815:138 (Type species: *Hemerobius phalaenoides* Linnaeus, 1758:550, by monotypy. Etymology: See Navás, [1924b] 1923:221; Drepane- [from Greek *drepane* or *drepanon*, sickle] + -pteryx [from Greek *pteryx* (feminine), wing]. Gender: Feminine.): Tjeder, 1963b (RD, A, Dst, MT*, FT*, Tax); Kuwayama, 1962 (Dst, Tax); Aspöck et al., 1980 (Dst, MT*, FT*, Tax); Makarkin, 1986 (Dst, Tax).

*Drepanopteryx* [sic]: Burmeister, 1839:975 (an incorrect subsequent spelling of *Drepanepteryx*). Note: Burmeister's use of *Drepanopteryx* does not appear to be "demonstrably intentional" (ICZN, 1985, Art. 33b(i)). Under a strict interpretation of the rules of the Code, it should be considered an unavailable incorrect subsequent spelling, not an available emendation, of *Drepanepteryx*. See also *Drepanopteryx* Agassiz below.

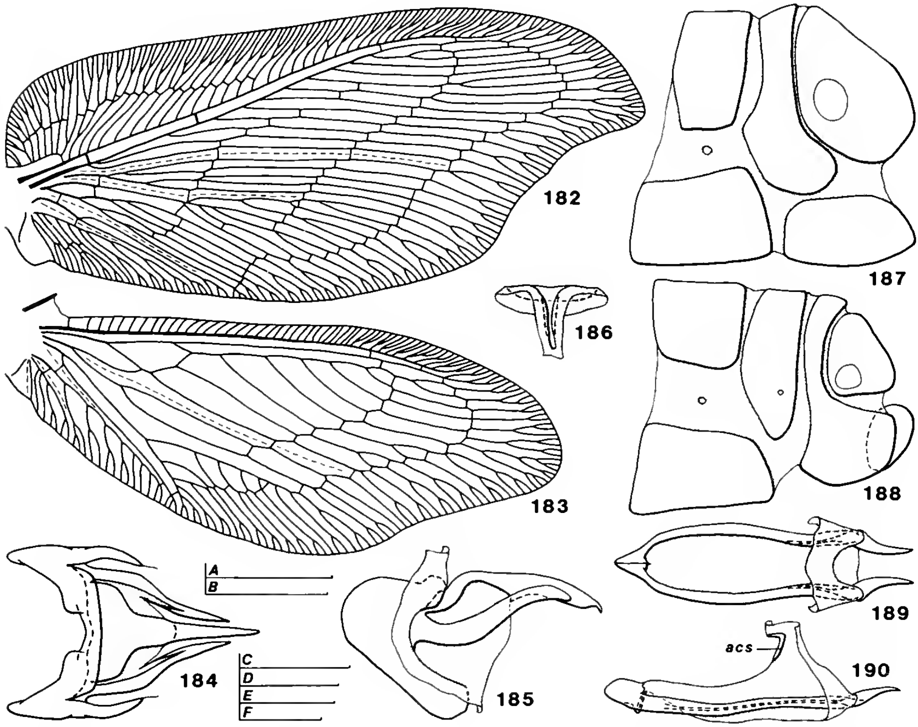
*Drepanopteryx* Agassiz, [1847] 1842–1846:130 (an unjustified emendation of *Drepanepteryx*). Note: Agassiz was apparently the first author to satisfy the "demonstrably intentional" criterion (ICZN, 1985, Art. 33b(i)), and therefore make the name *Drepanopteryx* available as an emendation. See also the *Drepanopteryx* of Burmeister above.

*Canisius* Navás, 1913a:512 (Type species: *Hemerobius algidus* Erichson in Middendorff, 1851:69, by original designation. Etymology: See Navás, 1913a:513; From the surname of B. P. Pedro Canisio, S. J. Gender: Masculine.): Tjeder, 1963b (Syn).

*Oedobius* Nakahara, 1915:44 (Type species: *Oedobius infalcatus* Nakahara, 1915:44 [=*Megalomus punctatus* Okamoto, 1905:114], by original designation. Etymology: Unexplained, probably Oedo- [from Greek *oidos*, swelling or tumor] + -bius [from Greek *bios* (masculine), life]. Gender: Masculine.): Kuwayama, 1962 (ITSD); Tjeder, 1963b (Syn).

*Phlebonema* Krüger, 1922:170 (Type species: *Hemerobius algidus* Erichson in Middendorff, 1851:69, by original designation. Etymology: Unexplained, probably Phlebo- [from Greek *phlebos*, vein] + -nema [from Greek *nema* (neuter), thread]. Gender: Neuter.): Aspöck et al., 1980 (Syn).

*Bestreta* Navás, 1924c:222 (Type species: *Bestreta iaponica* Navás, 1924c:222 [=*Megalomus punctatus* Okamoto, 1905:114], by monotypy. Etymology: Unexplained, possibly from Catalonian *bestreta* (feminine), anticipation or advance. Gender: Feminine.): Kuwayama, 1962 (Syn).



Figs. 182–190. *Drepanepteryx phalaenoides.* 182, Forewing [Scale bar C]. 183, Hind wing [C]. 184, Gonarcus, dorsal [A]. 185, Gonarcus, lateral [A]. 186, Accessory sclerite, posterior [F]. 187, Male terminalia, lateral [E]. 188, Female terminalia, lateral [B]. 189, Parabaculum, dorsal [D]. 190, Parabaculum and accessory sclerite, lateral [D]. Abbreviations: acs, accessory sclerite. Scale bars (mm): A = 0.5; B = 1.0; C = 2.0; D = 0.5; E = 0.5; F = 0.2.

*Differential Diagnosis.* Recognized by the forewing character combination (Fig. 182): (1) crossvein 2sc-r present, (2) anterior radial trace bearing 8 or more (up to ca. 13) "radial sectors", and (3) costal space with a gradate series of 5 or more crossveins.

*Proposed Synapomorphies.* [26] Forewing costal space containing a gradate series with 5 or more crossveins; [93] gonosaccal accessory sclerite present; [100] styli of female 9th gonocoxite lost.

*Species* (6). *algida* (Walker): Europe, USSR; *falculoides* Walker: Hindostan; *fuscata* Nakahara: Japan; *phalaenoides* (Linnaeus): Canary Islands, China, Europe, Japan, USSR; *pleshanovi* Makarkin: eastern USSR; *punctata* (Okamoto): Japan, eastern USSR, Kuril Is.

*Distribution.* Widely distributed in Eurasia from western Europe east to eastern USSR and Japan.

*Preimaginal Stages.* (1) *phalaenoides*—Von Gleichen, 1770; Brauer, 1867; Morton, 1910; Killington, 1937; Fulmek, 1941.

### Subfamily Microminae Krüger (revised)

Microminae Krüger, 1922:171 (Type genus: *Micromus* Rambur).
Micromini Navás, [1925b]:104.
Micromidae Banks, 1939:466.

*Differential Diagnosis.* Recognized by the forewing character combination: (1) anterior radial trace bearing 4 or more (up to ca. 10, very rarely 3) prestigmal "radial sectors", (2) humeral margin lacking trichosores, its shape linear or shallowly concave (not distinctly convex). The majority of species (all except *Noius*) share the additional characters: (1) forewing crossvein 2m-cu absent, (2) forewing crossvein 1cua-cup present, and (3) 9th tergite dorsosagittally divided, each half more or less fused to adjacent margin of ipsilateral ectoproct.

*Proposed Synapomorphies.* Microminae (Lineage 21): [2] Transtorular costa well developed; [3] midfrontal costa well developed; [9] cervical margin of postmentum well defined and regularly parabolic; [23] trichosores lost proximally on anterior margin of forewing; [24] proximal humeral trace recurrent but with only 1 or 2 rami (rami and recurrency frequently secondarily lost); [25] humeral silhouette not convex; [34] most proximal fork of most proximal "radial sector" located in distal two-thirds of posterior sectoral trace; [100] styli of female 9th gonocoxite lost.

Lineage 22 (*Nusalala* + *Megalomina* + *Micromus*): [1] temporal costae lost or poorly developed; [28] forewing subcostal crossvein 2sc-r lost; [43] forewing mediocubital crossvein 2m-cu lost; [47] forewing intercubital crossvein 1cua-cup present; [48] forewing CuP simple or shallowly forked, most proximal fork located in distal half of posterior CuP trace; [50] male 9th tergite sagittally divided; [55] male 9th and 10th (ectoprocts) tergites fused.

Lineage 23 (*Megalomina* + *Micromus*): [74] gonofenestra of gonarcus lost; [107] female insemination-fertilization canal with a small distal constriction and lobe.

*Included Genera. Noius, Nusalala, Megalomina*, and *Micromus*.

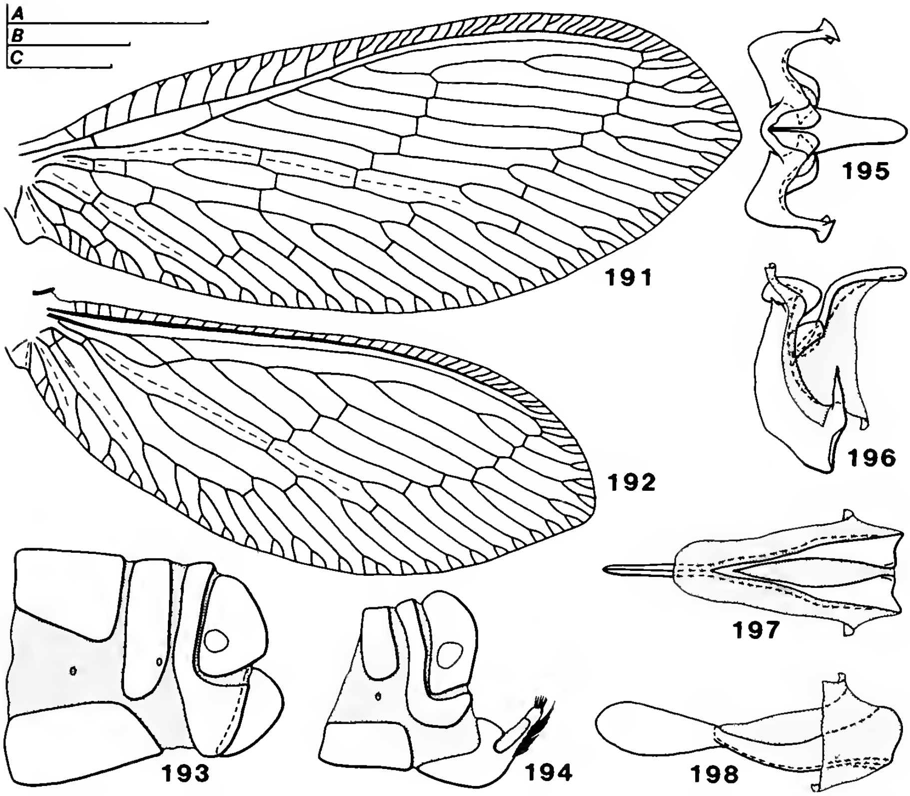
*Distribution.* Cosmopolitan. Widespread on all continents, except Antarctica. Well represented in the island faunas of the Atlantic, Indian, and Pacific oceans.

### Genus Noius Navás
(Figs. 191–198)

*Noius* Navás, 1929e:51 (Type species: *Noius oceanicus* Navás, 1929e:51, by monotypy. Etymology: Unexplained, possibly from Catalonian *noi*, (masculine or feminine), child or baby. Gender: Masculine.): Kimmins, 1958 (OD).

*Differential Diagnosis.* Recognized by the forewing character combination (Fig. 191): (1) crossvein 2sc-r present, but often weak, (2) anterior radial trace bearing 4 to 8 (rarely 9) prestigmal "radial sectors", and (3) crossveins 1m-cu and 2m-cu closely adjacent, separated only by approximately their combined lengths.

*Proposed Synapomorphies.* [4] Frontoclypeal costa strongly developed, transversely continuous across frontoclypeus; [11] proximal convexity of orad margin of right mandible strongly angulate; [18] anteromesal process of tentorial bridge lost; [60] apex of male 9th sternite produced as a digitiform process; [62] male 9th sternite bearing a pair of posterolateral lobes; [69] extragonopons sagittally emarginate; [103] female gonapophyses posteriores lost.



Figs. 191–198. *Noius oceanicus*. 191, Forewing [Scale bar A]. 192, Hind wing [A]. 193, Female terminalia, lateral [B]. 194, Male terminalia, lateral [B]. 195, Gonarcus, dorsal [C]. 196, Gonarcus, lateral [C]. 197, Parabaculum, dorsal [C]. 198, Parabaculum, lateral [C]. Scale bars (mm): A = 2.0; B = 0.5; C = 0.2.

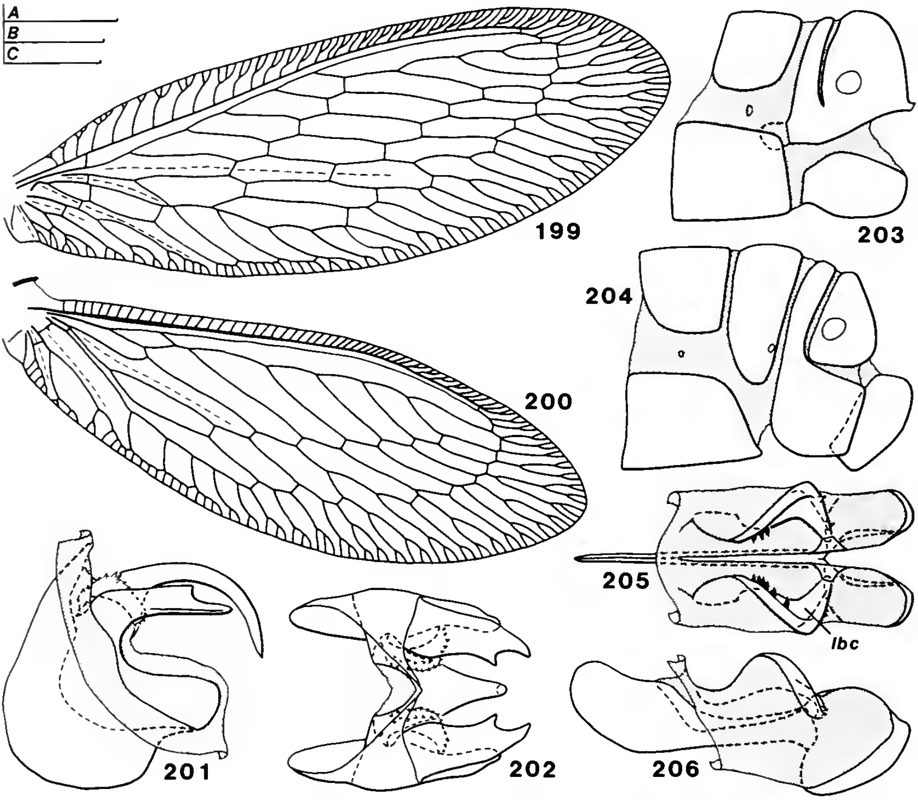
*Species* (2+). *noumeanus* Kimmins: New Caledonia, New Hebrides Is. (new record, ♂ & ♀, BPBM); *oceanicus* Navás: Fiji Is. (verified, ♂ & ♀, BPBM). I have also examined an undescribed species from Upolu Is., Western Samoa (BPBM).

*Distribution*. Islands of the southwestern Pacific, including: Fiji Is., New Caledonia, New Guinea (new record, ♀ only, BPBM), New Hebrides Is., Solomon Is. (new record, ♀ only, BPBM), Western Samoa (new record, ♂ & ♀, BPBM), and American Samoa (new record, ♀ only, BPBM).

*Preimaginal Stages*. Unknown.

## Genus Nusalala Navás
## (Figs. 199–206)

*Nusalala* Navás, 1913b:74 (Type species: *Nusalala erecta* Navás, 1913b:75, by monotypy. Etymology: Unknown. Gender: Feminine (implied from originally included species).).



Figs. 199–206. *Nusalala dispar* (except as noted). 199, Forewing [Scale bar B]. 200, Hind wing [B]. 201, Gonarcus, lateral [C]. 202, Gonarcus, dorsal [C]. 203, Male terminalia, lateral [A]. 204, Female terminalia (*championi*), lateral [A]. 205, Parabaculum, dorsal [C]. 206, Parabaculum, lateral [C]. Abbreviations: lbc, laterobaculum. Scale bars (mm): A = 0.5; B = 2.0; C = 0.2.

*Haarupiella* Esben-Petersen, 1914:263 (Type species: *Haarupiella neotropica* Esben-Petersen, 1914:264, by original designation. Etymology: See Esben-Petersen, 1914: 263; Haarup- [from the surname of Danish entomologist Anders Christian Jensen-Haarup (1863–1934)] + -iella [from the Latin diminutive suffix -ellus]. Gender: Feminine.): Kimmins, 1936a (Syn).

*Palaeomicromus* Krüger, 1922:171 (Type species: *Palaeomicromus schmidti* Krüger, 1922:171, by original designation. Etymology: Unexplained, probably Palaeo- [from Greek *palaios*, ancient or old] + *Micromus*. Gender: Masculine.): Nakahara, 1965 (Syn).

*Nesbe* Navás, 1929d:320 (Type species: *Nesbe irrebita* Navás, 1929d:321, by monotypy. Note: Navás (1935:58) emended *irrebita* to *irretita*. However, since there is no clear evidence within the original publication itself of an unintentional error (the etymology of the specific name was not originally stated), under a strict interpretation of the Code (ICZN, 1985, Arts. 32 and 33), the latter spelling should be considered an unjustified emendation, regardless of Navás's (1935) statement that *irretita* was the intended spelling. Etymology: See Navás, 1929d:320; An anagram of "Esben", from the surname of Danish entomologist Peter Esben-Petersen (1869—1942). Gender: Feminine.): Navás, 1935:58 (Nom). NEW SYNONYM

*Differential Diagnosis*. Distinguished from other South and Central American hemerobiids by the forewing character combination (Fig. 199): (1) base of M3+4 forming a short, oblique, vein proximal to its fusion with CuA and (2) CuA simple proximal to its fusion with M3+4. In sympatric *Micromus* species, vein CuA is either forked proximal to its fusion with M3+4, or not fused to M3+4. The presence of a pair of laterobacula associated with the parabaculum (Fig. 205, lbc) is also diagnostic.

*Proposed Synapomorphies*. [44] Forewing mediocubital crossvein 3m-cu lost; [92] male laterobaculum present; [106] female bursa with prominently sclerotized lateral walls.

*Species* (ca. 20). For a recent world listing see Penny, [1978].

*Distribution*. Central and South America and the Antilles.

*Principle Revisions and Regional Faunas*. Alayo, 1968 [Cuba]; Kimmins, 1936a [miscellaneous Neotropical species]; Penny and Monserrat, [1985] 1983 [Amazon Basin]; Stange, 1967 [Argentina and Uruguay].

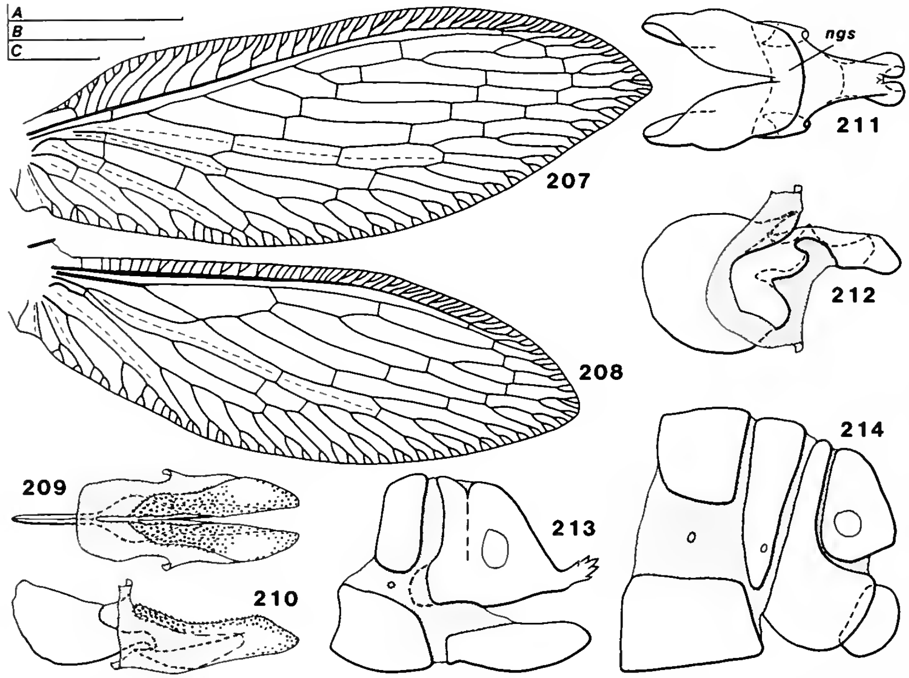
*Preimaginal Stages*. Unknown.

*Synonymical Notes*. *Nesbe*. Navás apparently described *Nesbe* and its type species, *irrebita*, from a single specimen formerly in the Hamburg Museum (now presumed destroyed; see Weidner, 1972). The original descriptions of these taxa clearly support their placement in the Microminae, almost certainly in the genus *Nusalala*. The following passages concerning forewing characters support placement in the Microminae [free translations in brackets]: (1) "Ala anterior area costali basi angusta" [forewing costal space narrow basally]; (2) "sine ramo recurrente" [no recurrent vein, i.e., proximal humeral trace not recurrent]; (3) "radio fere 5 sectoribus" [anterior radial trace with five "radial sectors"]; (4) "area cubitali elongata, 2 venulis divisa" [intercubital space elongate, with 2 intercubital crossveins]. Three additional forewing characters support the synonymy of *Nesbe* with *Nusalala*: (1) "venulis gradatis in tres series" [three post-subcostal gradate series], (2) "procubito. . .ramo posteriore brevi, cum cubito fuso" [posterior branch of media (i.e., M3+4) short and fused to cubitus], and (3) "venulis plerisque ad costam furcatis aut ramosis; medio biareolata, venulis pluribus serie venularum gradatarum connexis" [subcostal veinlets numerous and forked or branched, intervening spaces medially biareolate due to interconnecting crossveins of a costal gradate series]. The type locality of *irrebita* (San José, Costa Rica) is also consistent with its placement in *Nusalala*; and *irrebita* may be synonymous with *Nusalala kruegeri* Nakahara (1965; Type Locality: Córdoba, Mexico), which also possesses a costal gradate series.

## Genus Megalomina Banks
(Figs. 207–214)

*Megalomina* Banks, 1909:78 (Type species: *Megalomina acuminata* Banks, 1909: 78, by original designation. Etymology: Unexplained, probably Megal- [from Greek *megale*, large] + -om- [from Greek *omos*, shoulder] + -ina [from the Latin diminutive suffix *-ina*]. Gender: Feminine.): New, 1988; New, 1988.

*Drepanomina* Tillyard, 1916:302 (Type species: *Drepanomina gibbosa* Tillyard, 1916:



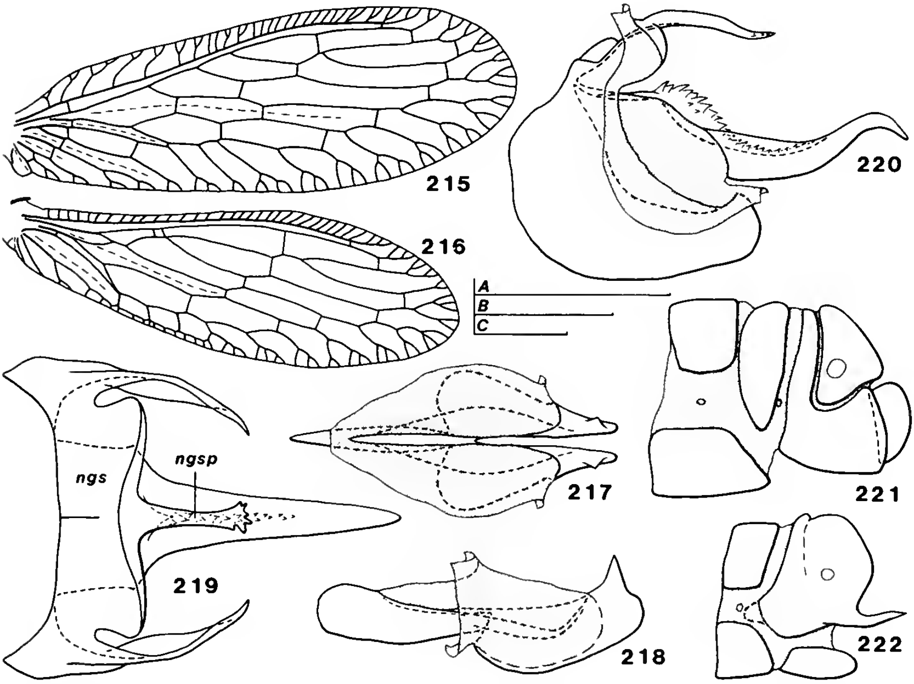
Figs. 207–214. *Megalomina berothoides* (except as noted). 207, Forewing (*bridwelli*) [Scale bar A]. 208, Hind wing (*bridwelli*) [A]. 209, Parabaculum, dorsal [C]. 210, Parabaculum, lateral [C]. 211, Gonarcus, dorsal [C]. 212, Gonarcus, lateral [C]. 213, Male terminalia, lateral [B]. 214, Female terminalia (*bridwelli*), lateral [B]. Abbreviations: ngs, neogonarcus. Scale bars (mm): A = 2.0; B = 0.5; C = 0.2.

303 [=*Drepanepteryx berothoides* McLachlan, 1869:22], by original designation. Etymology: Unexplained, probably Drepan- [from Greek *drepane* or *drepanon*, sickle] + -om- [from Greek *omos*, shoulder] + -ina [from the Latin diminutive suffix -ina]. Gender: Feminine.): New, 1988 (Syn).

*Oxybiella* Tillyard, 1916:305 (Type species: *Oxybiella bridwelli* Tillyard, 1916:305, by original designation. Etymology: Unexplained, probably Oxy- [from Greek *oxys*, sharp] + -bi- [from Greek *bios*, life] + -ella [from the Latin diminutive suffix -*ellus*]. Gender: Feminine.): New, 1988 (Syn).

*Differential Diagnosis.* Distinguished from other Australian and New Guinean hemerobiids by the forewing character combination (Fig. 207): (1) crossveins 2sc-r and 2m-cu absent, (2) crossveins 1cua-cup and 2cua-cup present, and (3) proximal humeral trace prominently recurrent and multiply branched. In sympatric *Micromus* species the humeral veinlet is simple, or at most possesses a short inconspicuous recurrent branch.

*Proposed Synapomorphies.* [2] Transtorular costa lost or poorly developed; [3] midfrontal costa lost or poorly developed; [9] cervical margin of postmentum poorly defined and not regularly parabolic; [24] proximal humeral trace recurrent and usually with 3 or more rami; [78] apex of male mediuncus emarginate.



Figs. 215–222. *Micromus variegatus*. 215, Forewing [Scale bar A]. 216, Hind wing [A]. 217, Parabaculum, dorsal [C]. 218, Parabaculum, lateral [C]. 219, Gonarcus, dorsal [C]. 220, Gonarcus, lateral [C]. 221, Female terminalia, lateral [B]. 222, Male terminalia, lateral [B]. Abbreviations: ngs, neogonarcus; ngsp, neogonarcal process. Scale bars (mm): A = 2.0; B = 0.5; C = 0.1.

*Species* (3). *acuminata* Banks: eastern Australia, New Guinea; *berothoides* (McLachlan): southeastern Australia; *bridwelli* (Tillyard): Australia, New Guinea (new record, ♀, BPBM).

*Distribution*. Australia and New Guinea.

*Preimaginal Stages*. Unknown.

## Genus Micromus Rambur
(Figs. 11, 215–222)

*Micromus* Rambur, 1842:416 (Type species: *Hemerobius variegatus* Fabricius, 1793: 85, by subsequent designation by Banks, 1905:44. Etymology: See Navás, [1924b] 1923:212; Micro- [from Greek *mikros*, small] + -mus [from Greek *omos* (masculine), shoulder]. Gender: Masculine.).

*Micromerus* [sic] Hagen, 1858:483 (an incorrect subsequent spelling of *Micromus*).

*Nesomicromus* Perkins, 1899:37 (Type species: *Nesomicromus vagus* Perkins, 1899: 37, by subsequent designation by Zimmerman, 1940:505. Etymology: Unexplained, probably Neso- [from Greek *nesos*, island] + *Micromus*. Gender: Masculine.): Tjeder, 1961 (Tax); Klimaszewski and Kevan, 1988 (Tax, Syn). NEW STATUS

*Pseudopsectra* Perkins, 1899:46 (Type species: *Pseudopsectra lobipennis* Perkins, 1899: 46, by monotypy. Etymology: Unexplained, probably Pseudo- [from Greek *pseudos*, lie] + *Psectra*. Gender: Feminine.): Tjeder, 1961 (Syn).

*Nesothauma* Perkins, 1899:46 (Type species: *Nesothauma haleakalae* Perkins, 1899: 47 [currently a secondary homonym of *Nesomicromus haleakalae* Perkins, 1899: 42], by monotypy. Etymology: Unexplained, probably Neso- [from Greek *nesos*, island] + -thauma [from Greek *thauma*, wonder or marvel]. Gender: Feminine.): Tjeder, 1961 (Syn).

*Nenus* Navás, 1912a:199 (Type species: *Nenus longulus* Navás, 1912a:200 [=*Micromus multipunctatus* Matsumura, 1907:171], by monotypy. Etymology: See Navás, 1912a:199; From Catalonian *nen* (masculine or feminine), infant or baby. Gender: Masculine.): Nakahara, 1960b (Syn); Monserrat (in press) (Tax).

*Nemis* [sic] Banks, 1913:217 (an incorrect subsequent spelling of *Nenus*).

*Eumicromus* Nakahara, 1915:36 (Type species: *Micromus numerosus* Navás, [1910] 1909:396, by original designation. Etymology: Unexplained, probably Eu- [from Greek *eu*, good or true] + *Micromus*. Gender: Masculine.): Carpenter, 1940 (Syn).

*Eumicronus* [sic] Nakahara, 1915:37, 39 (an incorrect original spelling of *Eumicromus*; correct original spelling fixed by Oswald and Penny (1991), acting as first revisers).

*Paramicromus* Nakahara, 1919:137 [not *Paramicromus* Krüger, 1922] (Type species: *Eumicromus dissimilis* Nakahara, 1915:43, by original designation. Etymology: Unexplained, probably Para- [from Greek *para*, beside or near] + *Micromus*. Gender: Masculine.): Tjeder, 1961 (Syn).

*Archaeomicromus* Krüger, 1922:171. Type species: *Micromus timidus* Hagen, 1853: 481, by original designation. Etymology: Unexplained, probably Archaeo- [from Greek *archaios*, old or primitive] + *Micromus*. Gender: Masculine.): Kimmins, 1936b (Syn).

*Indomicromus* Krüger, 1922:171 (Type species: *Micromus australis* Hagen, 1858: 483 [in *Micromerus* (sic)], by original designation. Etymology: Unexplained, probably Indo- [from Latin *Indicus*, of India] + *Micromus*. Gender: Masculine.): Tjeder, 1961 (Syn).

*Stenomicromus* Krüger, 1922:171 (Type species: *Hemerobius paganus* Linnaeus, 1767:912, by original designation. Etymology: Unexplained, probably Steno- [from Greek *stenos*, narrow] + *Micromus*. Gender: Masculine.): Tjeder, 1961 (Syn).

*Heteromicromus* Krüger, 1922:171 (Type species: *Heteromicromus audax* Krüger, 1922:171, by original designation. Etymology: Unexplained, probably Hetero- [from Greek *heteros*, different] + *Micromus*. Gender: Masculine.): Tjeder, 1961 (Syn).

*Neomicromus* Krüger, 1922:154 (Type species: *Micromus tessellatus* Gerstaecker, [1888] 1887:129, by original designation. Etymology: Unexplained, probably Neo- [from Greek *neos*, new] + *Micromus*. Gender: Masculine.): Tjeder, 1961 (Syn [as *Meomicromus* (sic)]).

*Meomicromus* [sic] Krüger, 1922:172 (an incorrect original spelling of *Neomicromus*; correct original spelling fixed by Oswald and Penny (1991), acting as first revisers).

*Pseudomicromus* Krüger, 1922:172 (Type species: *Hemerobius angulatus* Stephens, 1836:106, by original designation. Etymology: Unexplained, probably Pseudo- [from Greek *pseudos*, lie] + *Micromus*. Gender: Masculine.): Imperial Bureau of Entomology, [1924] 1922 (ITSD); Tjeder, 1961 (Syn).

*Paramicromus* Krüger, 1922:172 [not *Paramicromus* Nakahara, 1919] (Type species: *Micromus insipidus* Hagen, 1861:199 [=*Micromus posticus* Walker, 1853:283], by original designation. Etymology: Unexplained, probably Para- [from Greek *para*, beside or near] + Micromus. Gender: Masculine.): Carpenter, 1940 (Syn).

*Stenomus* Navás, 1922:55 [not *Stenomus* Rafinesque, 1815] (Type species: *Stenomus nesaeus* Navás, 1922:55 [=*Micromus africanus* Van der Weele, 1910c:17, NEW SYNONYM (holotype female examined, MNHP), by monotypy. Etymology: Unexplained, probably Steno- [from Greek *stenos*, narrow] + -mus [from Greek *omos* (masculine), shoulder]. Gender: Masculine.). NEW SYNONYM

*Phlebiomus* Navás, [1923] 1922:24 (Type species: *Phlebiomus yunnanus* Navás, [1923] 1922:25, by monotypy. Etymology: See Navás, [1923] 1922:24; Phlebio- [from Greek *phlebion*, veinlet] + -mus [from Greek *omos* (masculine), shoulder]. Gender: Masculine.): Nakahara, 1960b (Syn).

*Tanca* Navás, 1929b:373 (Type species: *Tanca loriana* Navás, 1929b:374, by monotypy. Etymology: Unexplained, probably from Catalonian *tanca* (feminine), fence. Gender: Feminine.): Tjeder, 1961 (Syn).

*Menutus* Navás, 1932:35 (Type species: *Micromus haitiensis* Smith, 1931:800, by original designation. Etymology: Unexplained, probably from the Catalonian adjective *menut*, little or small. Gender: Masculine.): Alayo, 1968:22 (Msc). NEW SYNONYM

*Idiomicromus* Nakahara, 1955:8 (Type species: *Idiomicromus kanoi* Nakahara, 1955: 8, by original designation. Etymology: Unexplained, probably Idio- [from Greek *idios*, one's own or personal] + *Micromus*. Gender: Masculine.): Nakahara, 1960b: 37 (Tax); Yang, 1981:303, 316 (NS, Tax); Monserrat (in press) (Syn).

*Spilomicromus* Nakahara, 1960b:26 (Type species: *Eumicromus maculatipes* Nakahara, 1915:39 [in *Eumicronus* (sic)], by original designation. Etymology: Unexplained, probably Spilo- [from Greek *spilos*, spot] + *Micromus*. Gender: Masculine.): Tjeder, 1961 (Syn).

*Anomicromus* Nakahara, 1960b:30. (Type species: *Nesomicromus paradoxus* Perkins, 1899:39, by original designation. Etymology: Unexplained, probably Ano- [from Greek *ano*-, up] + *Micromus*. Gender: Masculine.): Tjeder, 1961 (Syn).

*Ameromicromus* Nakahara, 1960b:33 [an objective replacement name for *Paramicromus* Krüger, 1922; not *Paramicromus* Nakahara, 1919] (Type species: *Micromus insipidus* Hagen, 1861:199 [=*Micromus posticus* Walker, 1853:283], by original designation (for *Paramicromus* Krüger, 1922. Note: The type species originally named by Nakahara, *Micromus posticus*, is nomenclaturally incorrect. A replacement genus-group name automatically assumes the type species of the name it replaces (ICZN, Article 67h). Etymology: Unexplained, probably Amero- [from America] + *Micromus*. Gender: Masculine.): Carpenter, 1940 (Syn).

*Afromicromus* Nakahara, 1960b:34 (Type species: *Micromus capensis* Esben-Petersen, 1920:508, by original designation. Etymology: Unexplained, probably Afro- [from Africa] + *Micromus*. Gender: Masculine.): Tjeder, 1961 (Syn).

*Austromicromus* Nakahara, 1960b:35. (Type species: *Hemerobius tasmaniae* Walker, 1860:186, by original designation. Etymology: Unexplained, probably Austro- [from Latin *austrinus*, southern] + *Micromus*. Gender: Masculine.): Tjeder, 1961 (Syn).

*Mixomicromus* Ghosh, 1977:235 (Type species: *Mixomicromus lampus* Ghosh, 1977: 235, by original designation. Etymology: Unexplained, probably Mixo- [from Greek *mixis* or Latin *mixtus*, to mix or mingle] + *Micromus*. Gender: Masculine.). NEW SYNONYM

*Differential Diagnosis*. The forewing characters (1) crossveins 2sc-r and 2m-cu absent, (2) crossveins 1cua-cup and 2cua-cup present, and (3) humeral area narrow, its margin lacking trichosores, will distinguish *Micromus* from all genera except *Nusalala* and *Megalomina*. The diagnoses of these genera should be consulted for characters to differentiate them from species placed in *Micromus*. See also *General Notes* below.

*Proposed Synapomorphies*. None.

*Species* (ca. 95). No recent comprehensive listing is available.

*Distribution*. Nearly cosmopolitan. Widespread in North and Central America, Europe, Africa, Asia, and Australia. Present also on numerous islands in the Atlantic, Indian and Pacific oceans. A notably diverse endemic fauna exists in the Hawaiian Islands. The taxonomic placement of the few species reported from South America requires confirmation; they may belong to *Nusalala*.

*Principle Revisions and Regional Faunas*. Alayo, 1968 [Cuba]; Aspöck et al., 1980 [Europe]; Klimaszewski and Kevan, 1988 [Nearctic]; Kuwayama, 1962 [Japan]; Makarkin, 1985 [USSR]; New, 1988 [Australia]; New, 1988 [New Guinea]; Tjeder, 1961 [southern Africa]; Zimmerman, 1957 [Hawaiian Islands].

*Preimaginal Stages*. (1) *angulatus*—Aubrook, 1935 (as *aphidivorus*); Killington, 1936; Miermont and Canard, 1975; (2) *numerosus*—Nakahara, 1954; Kawashima, 1958; (3) *paganus*—-Withycombe, 1923; Killington, 1936 (in *Eumicromus*); (4) *posticus*—Cutright, 1923; Smith, 1923; Miller and Cave, 1987; (5) *tasmaniae*—New and Boros, 1983; (6) *vagus*—Terry, 1908 (in *Nesomicromus*); (7) *variegatus*—Brauer, 1871; Withycombe, 1924; Killington, 1936; Kimmins, 1939; Dunn, 1954.

*Synonymical Notes*. *Stenomus*. Navás' (1922) description of the genus *Stenomus* contains no characters which would exclude it from the broad concept of the genus *Micromus* adopted here. I have examined the female holotype of *S. nesaeus* in the Paris Museum, and I propose it here as a new junior subjective synonym of *Micromus africanus* Van der Weele (1910c).

*Menutus*. Smith's (1931: fig. 10) illustration of the forewing of *haitiensis* clearly shows it to be a small micromine species. Alayo (1968) reported the common North American species *Micromus subanticus* from the Greater Antilles [Cuba], and cited "*Micromus haitiensis*" as a possible synonym. I have seen the holotype and single paratype of *haitiensis* in the MCZ and they clearly fall within the broad *Micromus* concept adopted here. However, since the holotype of *haitiensis* is a female, and the paratype is missing its abdomen, additional males from Haiti are needed before the synonymical status of *subanticus* and *haitiensis* can be determined.

*Mixomicromus*. In distinguishing *Mixomicromus* from *Micromus* Ghosh (1977: 236) states: the "Rs with 4 branches; two regularly arranged [series of] gradate crossveins, absence of recurrent humeral veinlets in the forewings, elongated anal plate with long ventral process, very elongated, tubular 9th sternite produced beyond the apex of the anal plate and the genitalia of the male are some unique features to distinguish it [*Mixomicromus*] as a distinct genus". Having examined more than 30 distinct species of *Micromus* from all regions of the globe (including specimens of *lampus* from India), the only character cited by Ghosh which is unusual within *Micromus* is the narrowly produced 9th sternite. In all other respects, *lampus* falls well within the broad concept of *Micromus* adopted here, and given the terminalic variability within *Micromus*, the modified 9th sternite is not sufficient to justify its ranking as a separate genus.

*General Notes*. Characterization and subdivision of the large and widespread genus *Micromus* has long been a problem (see discussions in Tjeder, 1961, and Klimaszewski and Kevan, 1988), and is reflected in its extensive list of generic synonyms. The fact that no synapomorphies are known for the genus further attests to its intractability. A worldwide revision of this genus will be necessary before any stable intrageneric groupings can be established. Such a revision should also include the closely related genera *Nusalala* and *Megalomina*, which represent potential outgroups (or, possibly, ingroups). Until such a revision has been completed, it is strongly recommended that interim intrageneric groupings be expressed in the literature as "species-groups", not as formal genera or subgenera.

## Unplaced Genera

### Genus Notherobius New

*Notherobius* New, 1988:358 (Type species: *Notherobius nothofagi* New, 1988:359, by original designation. Etymology: Unexplained, probably Noth- [from Greek *nothos*, spurious] + -erobius [from *(Hem)erobius*]. Gender: Masculine.).

*Status*. Apparently valid.

*Species* (3). *hastatus* New: southeastern Australia; *nebulosus* New: southeastern Australia; *nothofagi* New: southeastern Australia, Tasmania.

*Distribution*. Australia.

*General Notes*. New (1988) proposed this genus for three newly described species from Australia. Unfortunately, none of these have been available for examination during the present study. *Notherobius* species are clearly distinct from other Australian hemerobiids on the basis of forewing and male terminalic characters, and the proposal of a new genus for them appears justified. The placement of this genus in the Hemerobiidae is confirmed by the presence of a small, but distinct, parabaculum in the male, and the presence of two ORB's branching from the anterior radial trace.

A preliminary assessment of the cladistic position of *Notherobius* suggests that it would join the preferred cladogram as a fourth lineage arising from the trichotomy formed by lineages 4, 7, and 9 (see Fig. 23). This position is inferred from the absence in *Notherobius* of those synapomorphies of lineages 4, 7, 9, and 10 interpretable from New's treatment (9 of 12 applicable characters), and the presence of two synapomorphies of lineage 3 ([29] forewing anterior radial trace bearing two prestigmal ORB's, the most proximal deeply forked, and [95] male 9th gonocoxites lost).

On the basis of the two characters: (1) forewing anterior radial trace with two prestigmal ORB's, and (2) presence of styli on the female 9th gonocoxites, *Notherobius* superficially resembles sympherobiine genera more than hemerobiine genera. However, these characters are plesiomorphic "above" lineage 3, and thus cannot justify a sister-group relationship between *Notherobius* and the Sympherobiinae.

## Nomina Dubia

### Genus Subboriomyia Steinmann

*Subboriomyia* Steinmann, 1967:159 (Type species: *Subboriomyia fusca* Steinmann, 1967:160, by original designation. Etymology: Unexplained, probably Sub- [from Latin *sub*, under or from] + *Boriomyia*. Gender: Feminine.): Aspöck et al., 1980: 409 (Tax).

*Status.* Treated here as a *nomen dubium*, following Aspöck et al. (1980).

*Species* (1). *fusca* Steinmann: Hungary.

*Distribution.* Reported from Hungary.

*General Notes.* Horst Aspöck (pers. comm.), who has personally questioned Dr. Steinmann regarding the identity of *Subboriomyia*, has informed me that *Subboriomyia* and its type species, *S. fusca*, were described by Dr. Steinmann from memory, and that no type material exists for *fusca*. Aspöck et al. (1980:411) were unable to identify any species in the European Neuroptera fauna possessing the character combination attributed to *fusca* by Steinmann. Having been described from memory, it seems probable these "taxa" represent fanciful combinations of characters.

## NEUROPTERIDA INCERTAE SEDIS

### Genus Ormiscocerus Blanchard in Gay

*Ormiscocerus* Blanchard in Gay, 1851:128 (Type species: *Ormiscocerus nitidipennis* Blanchard in Gay, 1851:129, by monotypy. Note: Blanchard's work contains two specific names for the type species of *Ormiscocerus*—*nitidipennis*, in the text, and *sticticopterus*, in the legend to plate 2. Brauer (1866:989), acting as first reviser (ICZN, Article 24), fixed the correct original spelling as *nitidipennis*. Etymology: Unexplained, probably Ormisco- [from Greek *ormiskos*, a small necklace] + -cerus [from Greek *keras* or *keros*, horn or antenna]. Gender: Masculine.): Brauer, 1866: 986, 989 (Tax); Banks, 1913:211 (Key).

*Ormismocerus* [sic]: Hagen, 1866:375, 454 (Lst).

*Status.* Treated here as Neuropterida *incertae sedis*. The ordinal affinities of this taxon are here considered to be unknown.

*Species* (1). *nitidipennis* Blanchard in Gay: Chile.

*Distribution.* Reported from Chile.

*General Notes.* Blanchard based the description of *O. nitidipennis* on an unrecorded number of specimens then contained in Claudio Gay's collection of Chilean insects. Although Gay's collection is known to reside in the Paris Museum (Papavero, 1971), the whereabouts of the type of *nitidipennis* is unknown. A search of the Paris Museum Neuroptera collection (personal visit, 1989) failed to turn up its type, though other specimens described by Blanchard from Gay's collection were found. The possibility that the type is present in another part of the Paris Museum collection cannot be ruled out.

The unavailability of type material together with Blanchard's enigmatic figure render the identity and phylogenetic position of *Ormiscocerus* highly uncertain. The subsequent literature citations to this taxon also note uncertainty about its placement. Hagen (1866) listed *nitidipennis* under the generic name *Ormismocerus* [sic] and tentatively retained it in his restricted concept of the family "Hemerobidae". Brauer (1866), after noting similarities between Blanchard's figure of *Ormiscocerus* and taxa now placed in the orders Raphidioptera, Megaloptera and Neuroptera, tentatively suggested that it might be most closely related to *Raphidia*. Banks (1913) keyed *Ormiscocerus* to his tribe Polystoechotini; however, some characters used in his key (e.g., "wings plainly falcate at tips") clearly contradict the original figure and description. None of the preceding references appear to have been based on a reexamination of Blanchard's type material or new specimens. Based on the little available evidence, *Ormiscocerus* is regarded here as Neuropterida *incertae sedis*.

The following characters (based on Blanchard, 1851, pl. 2, fig. 11), justify removal of *Ormiscocerus* from the modern concept of the family Hemerobiidae: (1) profemora expanded [not cylindrical], (2) prothorax elongate [not transverse], (3) head apparently prognathous [not hypognathous], and (4) antennae inserted well before [not between] eyes.

### FOSSIL HEMEROBIIDAE

*General.* Fossils confidently assignable to the Hemerobiidae are known from the Paleogene Tertiary of British Columbia and western Europe, and the Upper Jurassic of Kazakhstan, USSR; a questionable record from the Lower Cretaceous of China also exists (see *Catalog* below). Several Tertiary hemerobiid fossils have been referred to extant genera on the basis of venational similarities. However, until corroborating evidence from terminalic structures becomes available, such placements must be regarded as speculative. The scarcity of hemerobiid fossils and their uncertain phylogenetic affinities limit their usefulness for drawing evolutionary and biogeographic conclusions about the family.

*Identification.* Apart from specimens embedded in fossil resins (e.g., amber), fossil hemerobiids, like most other neuropterous fossils, are principally diagnosed and identified on the basis of venational traits. The single most important diagnostic character for fossil hemerobiids is the presence of two or more ORB's diverging from the forewing anterior radial trace. The following additional forewing traits are ubiquitous or widespread, but apparently plesiomorphic, within the family; although these traits cannot definitively substantiate the placement of a specimen in the Hemerobiidae, the presence of alternative states may suggest the exclusion of a specimen from the family: (1) some trichosores always present, (2) most longitudinal veins prominently twigged near wing margin, (3) proximal humeral trace usually distinctly recurrent [occasionally simple], (4) subcostal veinlets numerous, frequently branched, particularly proximally, (5) pterostigma absent or very poorly developed, (6) Sc and anterior radial trace connected distally by a crossvein [rarely fused], and (7) one or two prestigmal sc-r crossveins present [rarely more].

*Catalog.* Existing literature records of fossil 'hemerobiids' can be divided into three categories:

(1) Unsubstantiated Records: Records of fossil 'hemerobiid' taxa which cannot be substantiated because they lack adequate descriptions or figures, or references to them. These records are excluded from the catalog below. Most such records date from the 19th century (see listings in Handlirsch, 1906—1908 and Scudder, 1891), when the prevailing concepts of the family Hemerobiidae and the genus "*Hemero-*

Table 5. Synopsis of stratigraphic and geographic distributions of fossil hemerobiids.

| Era | Period or epoch | Local | Taxon | Citation |
|---|---|---|---|---|
| Cenozoic | Eoc. Olig. | England | *Hemerobius tinctus* | Jarzembowski, 1980 |
| Cenozoic | Eoc. Olig. | England | *Neuronema* spp. | Jarzembowski, 1980 |
| Cenozoic | Eoc. Olig. | England | Hemerobiidae spp. | Jarzembowski, 1980 |
| Cenozoic | Eocene | Denmark | Hemerobiidae sp. | Larsson, 1975 |
| Cenozoic | Eocene | Denmark | *Megalomus densistriatus* | Henriksen, 1922 |
| Cenozoic | Eocene | Denmark | *Megalomus* sp. | Henriksen, 1922 |
| Cenozoic | Pal. Eoc. | Germany | *Megalomus* sp. | Illies, 1941 |
| Cenozoic | Tertiary | British Columbia | *Bothromicromus lachlani* | Scudder, [1878] |
| Cenozoic | —?— | Baltic amber | *Prolachlanius resinatus* | (Hagen, 1856) |
| Cenozoic | —?— | Baltic amber | *Prophlebonema resinatum* | Krüger, 1922 |
| Cenozoic | —?— | Baltic amber | *Prospadobius moestus* | (Hagen, 1856) |
| Cretaceous | Lower | China | *Mesohemerobius jeholensis* | Ping, 1928 |
| Jurassic | Upper | Kazakhstan, USSR | *Promegalomus anomalus* | Panfilov, 1980 |

*bius*" were much broader than at present. Many of these records almost certainly pertain to taxa properly assigned to other neuropterous families, or other related orders.

(2) Invalid Records: Records of fossil taxa originally described in, or once placed in, the Hemerobiidae, but currently placed elsewhere. These taxa are excluded from the catalog below. The taxonomic histories of most such taxa are recorded by Handlirsch (1906–1908).

(3) Apparently Valid Records: Records of fossil taxa which appear to fall within the modern concept of the Hemerobiidae. New taxa diagnosed in these records may be unnamed, undescribed, or unfigured, but not all three. The catalog below gives all hemerobiid taxa of which I am aware which fit these requirements. The stratigraphic and geographic distributions of these taxa are summarized in Table 5. Remarks contained under the *Comments* headings in the catalog are given based on information available in published figures and descriptions. Because the fossils themselves have not been examined, and because few relevant characters are diagnosable from published descriptions and illustrations, I have refrained from assigning fossil taxa to extant subfamilies. The only taxonomic change formally suggested here is treatment of the Panfilov's family Promegalomidae as a junior synonym of the Hemerobiidae.

## Family Hemerobiidae Latreille
(Extant, Tertiary, Cretaceous, Jurassic)

Hemerobiidae Latreille, 1802:288 (as Hemerobini). Type genus: *Hemerobius* Linnaeus.

Promegalomidae Panfilov in Dolin et al., 1980:87. Type genus: *Promegalomus* Panfilov in Dolin et al. NEW SYNONYM (see comments under *Promegalomus*).

### Genus *Hemerobius* Linnaeus (Extant, Tertiary)

*Hemerobius* Linnaeus, 1758:549. Type species: *Hemerobius humulinus* Linnaeus, 1758:550. See treatment of extant genus above for complete synonymy.

*tinctus* Jarzembowski

*Hemerobius tinctus* Jarzembowski, 1980:257 (OD, FW*). Etymology: Unexplained, probably from the Latin noun or adjective *tinctus*. Provenance: Late Eocene or early Oligocene, Bembridge Marls of the Isle of Wight, England.

Comments: The forewing venation of *tinctus* (see Jarzembowski, 1980:254, fig. 31) resembles that of the genus *Psychobiella* (currently restricted to Australia, see Fig. 90) more than that of *Hemerobius*. The following similarities between *tinctus* and *Psychobiella* are particularly striking: (1) the anterior radial trace bears 3 ORB's, the most proximal of which is forked in the basal third of the posterior sectoral trace [in extant Hemerobiinae the most proximal ORB is never this deeply forked (derived)], (2) crossvein 2sc-r is present (derived) [absent in extant Hemerobiinae], (3) four m-cu crossveins are present [three in almost all *Hemerobius* (derived)]. This combination of traits strongly suggests that *tinctus* is not a *Hemerobius*. Its possible relationship with *Psychobiella* should be investigated further. *Hemerobius tinctus* appears distinguishable from both genera by its deeply forked CuP.

### Genus *Neuronema* McLachlan (Recent, Tertiary)

*Neuronema* McLachlan, 1869:27. Type species: *Hemerobius decisus* Walker, 1860: 185. See treatment of extant genus above for complete synonymy.

? Species A

"? *Neuronema* Sp. A" Jarzembowski, 1980:259 (OD, FW*). Provenance: Late Eocene or early Oligocene, Bembridge Marls of the Isle of Wight, England.

Comments: The wing fragment illustrated by Jarzembowski (1980:258, fig. 39) appears consistent with this generic determination.

? Species B

"? *Neuronema* Sp. B" Jarzembowski, 1980:259 (OD, FW*). Provenance: Late Eocene or early Oligocene, Bembridge Marls of the Isle of Wight, England.

Comments: The wing fragments illustrated by Jarzembowski (1980:258, fig. 40) appear consistent with this generic determination, although costal crossveins are not as numerous in recent *Neuronema* species.

### Genus Megalomus Rambur (Extant, Tertiary)

*Megalomus* Rambur, 1842:418. Type species: *Megalomus tortricoides* Rambur, 1842: 419. See treatment of extant genus above for complete synonymy.

*densistriatus* Henriksen

*Megalomus densistriatus* Henriksen, 1922:14 (OD, FW*). Etymology: After the dense venation. Provenance: Lower Eocene, Mo-clay of Denmark.

Comments: Placement of *densistriatus* in *Megalomus* is speculative since terminalic characters are lacking. The vein interpreted by Henriksen as the "M" is herein regarded as the most proximal branch of the R. Henriksen's second specimen ("*Megalomus* ? *densistriatus*" Henriksen, 1922: fig. 5), is certainly a forewing, not a hind wing. Based on the different configuration of its distal ORB's, it is probably not conspecific with *densistriatus*. See also *Comments* below under *Promegalomus anomalus*.

Species A

*Megalomus* sp. Henriksen, 1922:17 (Bdy*, W*). Provenance: Lower Eocene, Mo-clay of Denmark.

Comments: Judging from Henriksen's figure, this specimen is a poorly preserved body and wing with the general habitus of a hemerobiid.

Species B

*Megalomus* sp. Illies, 1941:21, fig. 4 (FW*). Provenance: Upper Paleocene or Lower Eocene of Havighorst (near Hamburg) Germany.

Comments: Forewing figure only. Venation similar to wings figured by Henriksen (1922), Larsson (1975), and Panfilov in Dolin et al. (1980). See Illies ([1943]) for a treatment of the stratigraphy of the collection area.

Genus *Bothromicromus* Scudder (Tertiary)

*Bothromicromus* Scudder, [1878]:462. Type species: *Bothromicromus lachlani* Scudder, [1878], by monotypy. Etymology: Unexplained, probably Bothro- [from Greek *bothros*, hole or trench] + *Micromus*. Gender: Masculine.
*Bothriomicromus* [sic]: Zoological Record, Literature year 1877:202 (an incorrect subsequent spelling of *Bothromicromus*).

*lachlani* Scudder

*Bothromicromus lachlani* Scudder, [1878]:462 (OD). Etymology: From the surname of British entomologist Robert McLachlan (1837–1904). Provenance: Tertiary of Quesnel, British Columbia, Canada.: Scudder, 1890:163-165 (RD, Bdy*, W*); Handlirsch, [1907]:909 (Tax).

Comments: From Scudder's description, this species appears to be closely related to the extant genus *Drepanepteryx*, particularly in the broad costal area, presence of a costal gradate series, and the large number of ORB's. However, the specimen apparently lacks a recurrent proximal humeral trace (a preservational artifact?).

### Genus *Prolachlanius* Krüger (Tertiary)

*Prolachlanius* Krüger, 1923:88. Type species: *Hemerobius resinatus* Hagen in Pictet and Hagen, 1856, by original designation. Etymology: Unexplained, probably Pro- [from Latin *pro*, before] + *Lachlanius*. Gender: Masculine.

*resinatus* (Hagen in Pictet and Hagen)

*Hemerobius resinatus* Hagen in Pictet and Hagen, 1856:88 (OD, FW*). Etymology: From the Latin adjective *resinatus*, resined. Provenance: Baltic Amber.: Hagen, 1854:228 (nom. nud., no description or indication, Art. 12a).
*Mucropalpus elegans* Berendt in Pictet and Hagen, 1856:88 (*nom. nud.*, invalid when first proposed and not subsequently made available, Art. 11d & e): Handlirsch, [1907]:909 (Tax).
*Prolachlanius resinatus*: Krüger, 1923:88 (RD).

### Genus *Prophlebonema* Krüger (Tertiary)

*Prophlebonema* Krüger, 1923:85. Type species: *Prophlebonema resinata* [sic] Krüger, 1923, by original designation. Etymology: Unexplained, probably Pro- [from Latin *pro*, before] + *Phlebonema*. Gender: Neuter.

*resinatum* Krüger

*Phlebonema resinata* [sic] Krüger, 1922 (OD). Etymology: From the Latin adjective *resinatus*, resined. Provenance: Baltic Amber.
*Prophlebonema resinata* [sic]: Krüger, 1923:85 (RD).

### Genus *Prospadobius* Krüger (Tertiary)

*Prospadobius* Krüger, 1923:90. Type species: *Hemerobius moestus* Hagen in Pictet and Hagen, 1856, by original designation. Etymology: Unexplained, probably Pro- [from Latin *pro*, before] + *Spadobius*. Gender: Masculine.

*moestus* (Hagen in Pictet and Hagen)

*Hemerobius moestus* Hagen in Pictet and Hagen, 1856:88 (OD, FW*). Etymology: From the Latin adjective *moestus* [var. of *maestus*], sad or melancholy. Provenance: Baltic Amber.: Hagen, 1854:228 (nom. nud., no description or indication, Art. 12a); Handlirsch, [1907]:908 (Tax).
*Prospadobius moestus*: Krüger, 1923:90 (RD).

### Genus *Mesohemerobius* Ping (Lower Cretaceous)

*Mesohemerobius* Ping, 1928:42. Type species: *Mesohemerobius jeholensis* Ping, 1928: 42, by original designation. Etymology: Unexplained, probably Meso- [from Meso(zoic)] + *Hemerobius*. Gender: Masculine.

*jeholensis* Ping

*Mesohemerobius jeholensis* Ping, 1928:42 (OD, FW*). Etymology: After Jehol, a region in China. Provenance: Lower Cretaceous, Upper Volcanic series of Pei-piao [=Beipiao], Jehol, China.

Comments: *Mesohemerobius jeholensis* is known only from the distal two-thirds of one forewing. If Ping's (1928:42, fig. 21) illustration and venational interpretation are accurate, this specimen possesses multiple ORB's along the anterior radial trace and would appear to be a hemerobiid. However, several aspects of Ping's figure are in potential conflict with this interpretation. First, absolutely no crossveins are shown (a drawing or fossil artifact?). No extant (or fossil?) neuropteran entirely lacks forewing crossveins. Second, the subcostal veinlets in the figure lack any proximal associations with a longitudinal vein. This calls into question Ping's venational homologies. If the subcosta of this specimen was inadvertently removed during its preparation (a possibility which would explain the lack of subcostal veinlet connections), Ping's veins "Sc" (simple) and "R" (pectinately branched) would actually represent the R1 and Rs respectively. If this is the case, the sole basis for considering this fossil a hemerobiid (the presence of a pectinately branched forewing anterior radial trace) would be eliminated. A critical reexamination of the type of *jeholensis* is needed to eliminate this possibility.

### Genus *Promegalomus* Panfilov in Dolin et al.
(Upper Jurassic)

*Promegalomus* Panfilov in Dolin et al., 1980:87. Type species: *Promegalomus anomalus* Panfilov in Dolin et al., 1980, by original designation. Etymology: Unexplained, probably Pro- [from Latin *pro*, before] + *Megalomus*. Gender: Masculine.

*anomalus* Panfilov in Dolin et al.

*Promegalomus anomalus* Panfilov in Dolin et al., 1980, 87 (OD, FW*). Etymology: From the Greek (or Latin) adjective *anomalos* (*-us*), anomalous. Provenance: Upper Jurassic of Kazakhstan, USSR.

Comments: This species is known only from the complete forewing holotype, for which Panfilov created the new family Promegalomidae. However, as justified below, I consider *Promegalomus* a hemerobiid, and the Promegalomidae a junior synonym of the Hemerobiidae.

Of the eight putative synapomorphies of the Hemerobiidae identified in the cladistic analysis of recent genera, only Character 35 is a forewing character. Panfilov's figure (1980, fig. 91) of *anomalus* shows the derived state of this character, i.e., absence of pre-3ir1 crossveins. In addition, the figure shows the anterior radial trace of *anomalus* with two oblique radial branches, a further derived characteristic found in all extant hemerobiids. Finally, the prominently and pectinately branched posterior sectoral trace is very similar to the configuration found in some extant (e.g., some Drepanacrinae and Drepanepteryginae) and fossil hemerobiids (e.g., the Lower Eocene specimens illustrated by Henriksen, 1922; Larsson, 1975:203; and Illies, 1941).

### Genus Unknown

Hemerobiidae "Species A" Jarzembowski, 1980:260 (OD, W*). Provenance: Late Eocene or early Oligocene, Bembridge Marls of the Isle of Wight, England.

Comments: Based on two small wing fragments. Genus undeterminable.

Hemerobiidae "Species B" Jarzembowski, 1980:260 (OD, Bdy*, W*). Provenance: Late Eocene or early Oligocene, Bembridge Marls of the Isle of Wight, England.

Comments: Based on a body impression and several small wing fragments. Genus undeterminable.

Hemerobiidae "Species C" Jarzembowski, 1980:260 (OD, W*). Provenance: Late Eocene or early Oligocene, Bembridge Marls of the Isle of Wight, England.

Comments: Based on one small wing fragment. Genus undeterminable.

Hemerobiidae sp. Larsson, 1975:203, fig. 6. Provenance: Lower Eocene, Mo-clay of Jutland, Denmark.

Comments: The specimen illustrated by Larsson may be related to *Promegalomus*. Larsson mentions that hemerobiids are rather common in the Mo-clay of Denmark, but that the material collected to date remains largely undescribed.

## BIOGEOGRAPHY

### Age of the Clade Hemerobiidae

Only limited data are available relevant to estimation of the absolute age of the Hemerobiidae. A minimum age may be inferred from the age of the oldest known hemerobiid fossil. If assignment of the genus *Promegalomus* to this family is correct, see *Fossil Hemerobiidae* above, the clade Hemerobiidae dates at least from the late Jurassic. The only other putative hemerobiid reported from Mesozoic strata is *Mesohemerobius jeholensis* Ping, from the Lower Cretaceous of China; however, the assignment of this fossil to the Hemerobiidae requires confirmation, see *Fossil Hemerobiidae* above.

The existence of several genera with species occupying land areas in both the New and Old Worlds (i.e., *Hemerobius*, *Wesmaelius*, *Sympherobius*, *Notiobiella*, *Megalomus*, and *Micromus*), particularly those represented in the faunas of the southern continents of both hemispheres (*Hemerobius*, *Sympherobius*, *Notiobiella*, and *Micromus*), offers additional potential support for a Mesozoic origin for the family. If the broad distributions of these genera have resulted principally from the broad distributions of their respective common ancestors, species or groups of species within these genera found to be endemic to individual continents might be attributed to late Mesozoic vicariance events associated with the fragmentation of Gondwanaland, and support a somewhat earlier Mesozoic origin of the family. All of the preceding genera contain species restricted to single continents; however, estimates of phylogenetic relationships among species within these genera, which will be necessary to critically interpret their biogeographic histories, are not currently available.

Table 6. Distribution of hemerobiid genera by faunistic realm.

| Subfamily genus | No. spp. | Distribution[1] | | | | | |
|---|---|---|---|---|---|---|---|
| | | New World | | Old World | | | |
| | | NEA | NEO | PAL | ETH | ORI | AUS |
| Carobiinae | | | | | | | |
| *Carobius* | 9 | — | — | — | — | — | X* |
| Hemerobiinae | | | | | | | |
| *Hemerobius* | 125 | X | X | X | X | X | X |
| *Nesobiella* | 1[3] | — | — | — | — | — | — |
| *Wesmaelius* | 70 | X | X | X | X | X | [2] |
| *Hemerobiella* | 1 | — | X* | — | — | — | — |
| Sympherobiinae | | | | | | | |
| *Nomerobius* | 4 | — | X* | — | — | — | — |
| *Neosympherobius* | 1 | — | X* | — | — | — | — |
| *Sympherobius* | 55 | X | X | X | X | ? | — |
| Psychobiellinae | | | | | | | |
| *Psychobiella* | 2 | — | — | — | — | — | X* |
| Notiobiellinae | | | | | | | |
| *Notiobiella* | 35 | — | X | X | X | X | X |
| *Psectra* | 25 | [2] | — | X | X | X | X |
| *Anapsectra* | 1 | — | — | — | X* | — | — |
| *Zachobiella* | 8 | — | — | — | — | X | X |
| Drepanacrinae | | | | | | | |
| *Conchopterella* | 4 | — | X* | — | — | — | — |
| *Austromegalomus* | 2[4] | — | — | — | — | — | — |
| *Drepanacra* | 4 | — | — | — | — | X | X |
| Megalominae | | | | | | | |
| *Megalomus* | 40 | X | X | X | — | X | — |
| Drepanepteryginae | | | | | | | |
| *Neuronema* | 30 | — | — | X | — | X | — |
| *Gayomyia* | 1 | — | X* | — | — | — | — |
| *Drepanepteryx* | 6 | — | — | X* | — | — | — |
| Microminae | | | | | | | |
| *Noius* | 3 | — | — | — | — | — | X* |
| *Nusalala* | 20 | — | X* | — | — | — | — |
| *Megalomina* | 3 | — | — | — | — | — | X* |
| *Micromus* | 95 | X | ? | X | X | X | X |
| Unplaced genera | | | | | | | |
| *Notherobius* | 3 | — | — | — | — | — | X* |
| Endemic genera[5] | — | 0 | 6 | 1 | 1 | 0 | 5 |
| Total genera[5] | — | 5 | 11? | 9 | 7 | 9? | 11 |
| % genera endemic | — | 0 | 54 | 11 | 14 | 0 | 45 |

## Overview of Generic Distributions

The distributions of hemerobiid genera are summarized by biogeographic realm in Table 6, and by continent in Table 7. No hemerobiids are known from Antarctica.

The two most speciose hemerobiid genera, *Hemerobius* and *Micromus*, are nearly cosmopolitan in distribution. *Hemerobius* is broadly distributed in all temperate and tropical land areas except Australia (1 sp. in Queensland; 3 spp. in New Guinea), where it may be a relatively recent immigrant (? a member of the "Younger Northern Element" of Mackerras, 1970). *Micromus* is also broadly distributed throughout the temperate and tropical areas of all continents, with the possible exception of South America. Several *Micromus* species earlier reported from South America have proved to belong to *Nusalala*, and the remaining South American species currently assigned to *Micromus* require reexamination.

Five other genera possess broad intercontinental distributions: *Sympherobius* (North and South America, Eurasia, and Africa), *Megalomus* (North and South America, Eurasia, and northern Africa), *Wesmaelius* (North America, Eurasia, and Africa), *Psectra* (North America [1 sp.], Europe [1 sp.], Africa, India, SE Asia, and Australia), and *Notiobiella* (South and Central America, Africa, SE Asia, and Australia).

The remaining genera are restricted to (1) a single continent: *Carobius*, *Psychobiella*, *Notherobius*, *Noius*, and *Megalomina* [Australia]; *Conchopterella*, *Hemerobiella*, *Nomerobius*, *Neosympherobius*, and *Gayomyia* [South America]; *Anapsectra* [Africa]; *Neuronema* and *Drepanepteryx* [Eurasia], (2) the neighboring portions of two adjacent continents: *Zachobiella* and *Drepanacra* [SE Asia and Australia], and *Nusalala* [South and Central America], or (3) isolated oceanic islands: *Nesobiella* [Hawaiian Islands] and *Austromegalomus* [Society Islands].

## Overview of Subfamily Distributions

Of the nine hemerobiid subfamilies recognized herein, three are monogeneric (Carobiinae, Psychobiellinae, and Megalominae), and, consequently, show no intergeneric distribution patterns. Five of the six remaining subfamilies (Hemerobiinae, Sympherobiinae, Notiobiellinae, Drepanacrinae, and Microminae) consist of one or two genera with broad intercontinental distributions, and one or two genera endemic to a single continent. The only subfamily containing multiple genera, each of which is endemic to a single continent, is the Drepanepteryginae, which contains two genera in Eurasia (*Drepanepteryx* and *Neuronema*) and one in southern South America (*Gayomyia*). The extreme biogeographic disjunction exhibited by this subfamily

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* Genus endemic to a single faunistic realm.

? Presence uncertain.

[1] NEA, Nearctic; NEO, Neotropical; PAL, Palearctic; ETH, Ethiopian; ORI, Oriental; AUS, Australian.

[2] One or more species present, but presumed introduced.

[3] Hawaiian Islands

[4] Society Islands (Tahiti and Rapa).

[5] Presumed introductions omitted.

Table 7. Distribution of hemerobiid genera by continent.

| Subfamily genus | No. spp. | Distribution[1] | | | | |
|---|---|---|---|---|---|---|
| | | New World | | Old World | | |
| | | NA | SA | EUR | AFR | AUS |
| Carobiinae | | | | | | |
| *Carobius* | 9 | – | – | – | – | X* |
| Hemerobiinae | | | | | | |
| *Hemerobius* | 125 | X | X | X | X | X |
| *Nesobiella* | 1[3] | – | – | – | – | – |
| *Wesmaelius* | 70 | X | – | X | X | [2] |
| *Hemerobiella* | 1 | – | X* | – | – | – |
| Sympherobiinae | | | | | | |
| *Nomerobius* | 4 | – | X* | – | – | – |
| *Neosympherobius* | 1 | – | X* | – | – | – |
| *Sympherobius* | 55 | X | X | X | X | – |
| Psychobiellinae | | | | | | |
| *Psychobiella* | 2 | – | – | – | – | X* |
| Notiobiellinae | | | | | | |
| *Notiobiella* | 35 | X | X | X | X | X |
| *Psectra* | 25 | [2] | – | X | X | X |
| *Anapsectra* | 1 | – | – | – | X* | – |
| *Zachobiella* | 8 | – | – | X | – | X |
| Drepanacrinae | | | | | | |
| *Conchopterella* | 4 | – | X* | – | – | – |
| *Austromegalomus* | 2[4] | – | – | – | – | – |
| *Drepanacra* | 4 | – | – | X | – | X |
| Megalominae | | | | | | |
| *Megalomus* | 40 | X | X | X | X | – |
| Drepanepteryginae | | | | | | |
| *Neuronema* | 30 | – | – | X* | – | – |
| *Gayomyia* | 1 | – | X* | – | – | – |
| *Drepanepteryx* | 6 | – | – | X* | – | – |
| Microminae | | | | | | |
| *Noius* | 3 | – | – | – | – | X* |
| *Nusalala* | 20 | X | X | – | – | – |
| *Megalomina* | 3 | – | – | – | – | X* |
| *Micromus* | 95 | X | ? | X | X | X |
| Unplaced genera | | | | | | |
| *Notherobius* | 3 | – | – | – | – | X* |
| Endemic genera[5] | – | 0 | 5 | 2 | 1 | 5 |
| Total genera[5] | – | 7 | 10? | 11 | 8 | 11 |
| % genera endemic | – | 0 | 50 | 18 | 12 | 45 |

seems best interpreted as relictual. No clear, repeated, patterns of intergeneric distributions are evident among the multigeneric subfamilies.

The sister-group relationship between the hemerobiine genera *Hemerobius* and *Nesobiella* is biogeographically intriguing. *Nesobiella* is monobasic and restricted to the Hawaiian Islands, while *Hemerobius* is speciose, nearly cosmopolitan, and absent from these islands except for the apparently recent introduction of *H. pacificus* from western North America. Zimmerman (1957) speculated that *Nesobiella* might have been recently introduced into the Hawaiian Islands from an unknown source area. To date however, *Nesobiella* has never been reported from outside the Hawaiian Islands, nor have any congeners been described from elsewhere in the world. Given the volcanic origin of the Hawaiian Islands, the ancestors of *Nesobiella* must have reached them by long-distance dispersal; and, given the absence of known close relatives, the present distribution of *Nesobiella* appears relictual.

## Faunal Similarities and Differences between Adjacent Continental Landmasses

North America and Eurasia share seven genera: *Hemerobius*, *Wesmaelius*, *Sympherobius*, *Notiobiella*, *Psectra*, *Megalomus*, and *Micromus*. Of these, *Hemerobius*, *Wesmaelius*, *Sympherobius*, *Megalomus*, and *Micromus* are broadly distributed on both continents. *Notiobiella* (pantropical) is primarily restricted to the tropical regions of both continents. *Psectra* is most diverse in southeastern Asia, but a single species, *P. diptera*, is distributed across temperate Eurasia from Japan to Europe, and is present (probably introduced) in eastern North America. Four Eurasian genera are lacking in North America: *Neuronema*, an east Asian endemic; *Drepanepteryx*, a Palearctic endemic; and *Zachobiella* and *Drepanacra*, a pair of southeast Asian taxa shared with Australia. The genera comprising the North American and European faunas are identical, except for the additional presence of *Drepanepteryx* in Europe.

North and South America share five genera: *Hemerobius*, *Sympherobius*, *Notiobiella*, *Megalomus*, and *Nusalala*. Of these, *Hemerobius*, *Sympherobius*, and *Megalomus* are broadly distributed on both continents. The genera *Notiobiella* (pantropical) and *Nusalala* (Neotropical), reach North America only in the tropical portions of Central America and the Antilles. The principal faunal differences between these regions are the apparent absence of *Micromus* species from South America (present in the Antilles) and the presence in the South American fauna of five additional, small, endemic genera: *Hemerobiella*, *Nomerobius*, *Neosympherobius*, *Conchopterella*, and *Gayomyia*. North America has no endemic genera.

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←

* Genus endemic to a single continent.

? Presence uncertain.

[1] NA, North America; SA, South America; EUR, Eurasia; AFR, Africa; AUS, Australia (including New Guinea and New Zealand).

[2] One or more species present, but presumed introduced.

[3] Hawaiian Islands.

[4] Society Islands (Tahiti and Rapa).

[5] Presumed introductions omitted.

Table 8. Hemerobiid genera endemic to northern and southern continents.

| No. genera[3] | Continents | |
|---|---|---|
| | Northern[1] | Southern[2] |
| Endemic | 2 | 11 |
| Total | 12 | 21 |
| Percent endemic | 17 | 52 |

[1] North America, Europe, Asia.
[2] South America, Africa, Australia.
[3] Presumed introductions omitted.

Europe and Africa share six genera: *Hemerobius*, *Wesmaelius*, *Sympherobius*, *Psectra*. *Megalomus*, and *Micromus*. The genera *Hemerobius*, *Wesmaelius*, *Sympherobius*, *Psectra* and *Micromus* are broadly distributed in both regions. *Megalomus* has been reported from extreme northwestern Africa (? a recent immigrant from Europe), but is otherwise absent. The only generic-level faunal differences between these continents are the additional presence of *Drepanepteryx* (a Palearctic endemic) in Europe, and of *Anapsectra* (an Ethiopian endemic) and *Notiobiella* (pantropical) in Africa.

Australia/New Guinea and southeast Asia share six genera: *Hemerobius*, *Notiobiella*, *Psectra*, *Zachobiella*. *Drepanacra*, and *Micromus*. *Psectra*, *Drepanacra* and *Micromus* are broadly distributed within both regions. In Australia, *Hemerobius*, *Notiobiella*, and *Zachobiella* appear largely confined to the north, principally Queensland, but are more widely distributed in southeast Asia. The Australian fauna is especially distinctive because of five endemic genera: *Carobius*, *Psychobiella*, *Noius*, *Megalomina*, and *Notherobius*. There are no genera endemic to the adjacent areas of southeastern Asia.

## Continental Generic Endemism

Southern landmasses possess a percentage of endemic genera triple that of northern land areas (Table 8). The percentage of generic endemics is particularly high for South America and Australia. This is apparent both when genera are tabulated by biogeographic realms and by continental boundaries (Tables 6 and 7).

This pattern is consistent with the markedly different tectonic histories of the northern and southern continents. Since the division of Pangea into Laurasia and Gondwanaland in the late Mesozoic, east-west routes between North America and Eurasia (i.e., Beringia and northern trans-Atlantic routes [Matthews, 1980]) continued, at least intermittently, to facilitate faunal exchange between the northern continents. Faunal exchange via these routes may account for, in a general way, the low percentage of generic endemism (17%) and high percentage of common genera (33%) of the northern continents, relative to the same percentages (52% and 9% respectively, see Tables 8 and 9) for the southern continents, which were isolated by oceanic barriers subsequent to the fragmentation of Gondwanaland.

The subfamily Drepanacrinae, which contains three genera (*Conchopterella*, *Austromegalomus*, and *Drepanacra*) distributed entirely or principally in the southern hemisphere, exhibits the hemerobiid subfamily distribution which most closely resembles a classic southern Gondwanian distribution.

Table 9. Hemerobiid genera common to northern and southern continents.

| No. genera[3] | Continents | |
|---|---|---|
| | Northern[1] | Southern[2] |
| In common | 4 | 2 |
| Total | 12 | 21 |
| Percent endemic | 33 | 9 |

[1] North America, Europe, Asia.
[2] South America, Africa, Australia.
[3] Presumed introductions omitted.

## Island Endemism

Hemerobiids are present on numerous oceanic islands and island groups (Table 10), many of which are not of continental origin. The widespread presence of hemerobiids on non-continental islands supports the contention that hemerobiids, although relatively weak fliers, are good long-distance aerial dispersers. Most near-shore insular species, however, are conspecific with or appear to be closely related to species found on adjacent continental areas. Only three genera, *Austromegalomus*, *Nesobiella*, and *Noius*, are completely endemic to oceanic islands.

Although intentional introductions of hemerobiids into island faunas have been documented for a few species (e.g., *Micromus timidus* [as *M. vinaceus*], introduced into the Hawaiian Islands, see Williams, 1931), the extent to which man has augmented insular distributions through inadvertent introductions has not been well studied. Certainly, some such introductions have been made, e.g., the introduction of the western North American species *Hemerobius pacificus* into Hawaii (MacLeod, 1964) and the introduction of the Holarctic species *Wesmaelius subnebulosus* into New Zealand (Wise, 1973), and some other records are highly suspect, e.g., the presence of the Palearctic species *variegatus* on Galiano Is., British Columbia, Canada.

A few insular species exhibit remarkable secondary morphological modifications. These alterations are particularly apparent in the shape and extent of development of the wings. The most striking of these modifications are found in the complex of 20+ *Micromus* species endemic to the Hawaiian Islands (Zimmerman, 1957), and in the two species of *Conchopterella* endemic to the Juan Fernandez Islands (Handschin, 1955).

## Discussion

As indicated above, no clear repeated patterns of intergeneric distributions are evident among the subfamilies of the Hemerobiidae. Thus, there is presently no good evidence to support the idea that a common vicariant history has significantly shaped its subfamily distributions. However, given the certain occurrence of vicariant events, the list of factors which can be invoked to explain the absence of a repeated, vicariantly induced, pattern in a taxon the age of the Hemerobiidae is lengthy. Patterns may be obscured by: (1) dispersal, particularly in association with changing environments, or extinction subsequent to a vicariant event, (2) the presence of ancestral taxa which were regionally, not catholically, distributed, (3) comparison of taxa [even if de-

Table 10. Summary of principal literature on insular hemerobiid faunas (for additional titles see works cited in the papers given below).

Ocean area
  Island or group: Reference

Atlantic: Eastern
  Azores: Aspöck et al., 1980: 378–379;
  Canaries: Aspöck et al., 1980: 378–379;
  Cape Verde: Ohm and Hölzel, 1982;
  General: Aspöck et al., 1980;
  Iceland: Fristrup, 1942; Tjeder, 1964;
  Madeira: Aspöck et al., 1980: 378–379;
  Mediterranean Islands: Aspöck et al., 1980;
  St. Helena: Tjeder, 1976;

Atlantic: Western
  Bermuda: Hilburn, 1990;
  Cuba: Alayo, 1968;
  Greenland: Nielsen, 1909; Richard and Harmston, 1972;
  Hispanola: Banks, 1941; Navás, 1932; Smith, 1931;
  Puerto Rico: Wolcott, [1950];

Indian: Eastern
  General: Van der Weele, 1909; Handschin, 1935;
  Java: Van der Weele, 1910a;
  Sri Lanka (Ceylon): Hagen, 1858: Hagen, 1859;

Indian: Western
  Madagascar: Fraser, 1951;
  Reunion: Fraser, 1957;
  Seychelles: Kimmins, 1933; Enderlein, 1910;

Pacific: Eastern
  Galapagos: Klimaszewski et al., [1988];
  Isla del Coco: Oswald, unpublished data;
  Juan Fernandez: Handschin, 1955;
  Revillagigedo: Oswald, 1988b;

Pacific: Western and Central
  Borneo: Banks, 1931; Banks, 1934;
  General: Carpenter, 1961; Esben-Petersen, 1937; Van der Weele, 1909;
  Hawaiian: MacLeod, 1964; Perkins, 1899; Zimmerman, 1957;
  Japan: Kuwayama, 1962;
  Kuril: Kuwayama, 1956;
  Marquesas: Esben-Petersen, [1935a];
  New Caledonia: Kimmins, 1958; Nakahara, 1960a;
  New Guinea: New, [1989];
  New Hebrides: Kimmins, 1958;
  New Zealand (and adjacent islands): Wise, 1977; Wise, 1983;
  Philippines: Banks, 1937;
  Rapa: Oswald, 1988a;
  Ryukyu: Kuwayama, 1964; Nakahara, 1966;
  Samoa: Esben-Petersen, 1928;
  Tahiti: Esben-Peterson, [1935b]; Oswald, 1988a;
  Taiwan (Formosa): Nakahara, 1966

monstrably holophyletic and of equal rank] of incongruent age, or (4) comparison of inappropriate [i.e., nonholophyletic] taxa. A further alternative is the true absence of a repetitive, vicariantly induced, pattern. This implies that factors such as dispersal, extinction, lack of speciation at vicariant events, and ancestral regionalism, may reduce the ability of sequential vicariant events to produce detectable, repeated, patterns of distribution in some kinds of organisms. This does not deny the existence of vicariant events, only their ability to universally produce repeated patterns of distribution. Clearly, our ability to detect common biogeographic patterns attributable to vicariant events depends upon the relative magnitude and frequency of both the pattern-producing vicariant events themselves and the diverse kinds of events which tend to obscure such patterns.

In the case of the Hemerobiidae, little unambiguous information is currently available regarding dispersal, extinction, and the ancestral distributions and absolute (or, at least, minimum) ages of its genera and subfamilies. Consequently, there are insufficient data from which to infer the principal causal agents which have resulted in the apparent lack of common distribution patterns among the genera comprising hemerobiid subfamilies. This said, a few general comments and preliminary speculations regarding hemerobiid biogeography are given below.

The high levels of generic endemism in South America and Australia are almost certainly attributable to their long isolation from other continental landmasses. The fact that these endemic genera did not aggregate in the cladistic analysis into subfamilies exhibiting common area-cladogram elements, may be attributable to subsequent extinction of related taxa in other areas or restricted distributions of their ancestors.

Distributions associated with the most widespread genera are probably due to a combination of vicariant and dispersive events. The balance between these two general processes, however, cannot be understood without more detailed investigations of the phylogenies of these genera. The existence of several widespread Holarctic species in the genera *Hemerobius*, *Wesmaelius*, and *Micromus*, and the presence of few widespread species common to adjacent northern and southern continents, suggests that dispersal between North America and Eurasia may be less difficult than movement between the northern and southern continents. Such a phenomenon may be primarily due to ecological preferences of the taxa in question.

The lack of concordance of intergeneric distribution patterns among subfamilies may be due to an attempt to compare taxa of substantially different ages. Although the relative (and implied absolute) ages of hemerobiid subfamilies increase toward the base of the preferred cladogram (Fig. 23), a basic cladistic inference, this does not necessarily imply that the immediate common ancestors of the collected extant genera of each subfamily are of increasing or even similar age, since older subfamily sister-groups may have become extinct and not be represented in the analysis. Since clades of differing ages experience at least partially different vicariant histories, there is no a priori reason to expect fully concordant distribution patterns among such clades. Thus, it may be generally inappropriate to limit the search for congruent distribution patterns strictly to holophyletic groups of identical rank. In the case of the Hemerobiidae, congruent patterns may yet be identified by comparisons of, for example, subfamilies and widely distributed genera. This underscores the need for additional phylogenetic and biogeographic studies of individual widespread genera to facilitate such comparisons.

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Appendix 1. Sequenced classification of world Hemerobiid genera. This classification incorporates the conventions recommended by Wiley (1981: 205–213) for annotated Linnaean classifications. See also the discussion under the heading *Phylogenetic Analysis: Results: Classification.*

Classification of world Hemerobiidae

Family Hemerobiidae Latreille
- Subfamily Carobiinae Oswald, new subfamily
    - Genus *Carobius* Banks
- Subfamily Hemerobiinae Latreille, *sedis mutabilis*
    - *Hemerobius* Genus-group
        - Genus *Hemerobius* Linnaeus
        - Genus *Nesobiella* Kimmins
    - *Wesmaelius* Genus-group
        - Genus *Wesmaelius* Krüger
        - Genus *Hemerobiella* Kimmins
- Subfamily Sympherobiinae Comstock, *sedis mutabilis*
    - Genus *Nomerobius* Navás
    - Genus *Neosympherobius* Kimmins
    - Genus *Sympherobius* Banks
- Subfamily Psychobiellinae Oswald, new subfamily
    - Genus *Psychobiella* Banks
- Subfamily Notiobiellinae Nakahara
    - Genus *Notiobiella* Banks
    - Genus *Psectra* Hagen
    - Genus *Anapsectra* Tjeder
    - Genus *Zachobiella* Banks
- Subfamily Drepanacrinae Oswald, new subfamily
    - Genus *Conchopterella* Handschin
    - Genus *Austromegalomus* Esben-Petersen
    - Genus *Drepanacra* Tillyard
- Subfamily Megalominae Krüger
    - Genus *Megalomus* Rambur
- Subfamily Drepanepteryginae Krüger
    - Genus *Neuronema* McLachlan
    - Genus *Gayomyia* Banks
    - Genus *Drepanepteryx* Leach in Brewster
- Subfamily Microminae Krüger
    - Genus *Noius* Navás
    - Genus *Nusalala* Navás
    - Genus *Megalomina* Banks
    - Genus *Micromus* Rambur

Unplaced Genera
- Genus *Notherobius* New

Nomina Dubia
- Genus *Subboriomyia* Steinmann

Neuropterida Incertae Sedis
- Genus *Ormiscocerus* Blanchard in Gay

Appendix 2. Hemerobiid species richness and species examined. This appendix summarizes the known species richness of all higher hemerobiid taxa, and lists the species examined for this work. Some examined species could not be identified to species level; such species are collectively recorded under the appropriate genus as "unknown spp."

Symbols: *, Includes one or more unidentified or undescribed species; +, Species selected for comprehensive examination (see discussion under the heading *Phylogenetic Analysis: Methods and Data: Data*); −, Includes species-group names of particularly doubtful validity; ?, Uncertain identification; M, Male; F, Female.

| Family-group taxon (no. spp., no. spp. examined) | | |
|---|---|---|
| Genus | Total no. spp. | No. spp. examined |
| Species examined (sex[s] examined) | | |
| **Family Hemerobiidae** (ca. 550, ca. 185) | | |
| **Subfamily Carobiinae** (9, 2*) | | |
| *Carobius* | 9 | 2* |
| +**pulchellus** (MF), unknown sp. [1] (F). | | |
| **Subfamily Hemerobiinae** (ca. 200, 56) | | |
| *Hemerobius* | ca. 125 | 37 |
| *adelgivorus* (M), *alpestris* (M), +**aper** (M), +**australis** (M), *chilensis* (M), *conjunctus* (M), +**costalis** (MF), *domingensis* (M), *dorsatus* (M), +**falciger** (MF), *flaveolus* (M), *hageni* (MF), +**harmandinus** (MF), +**humulinus** (MF), *jamaciensis* (M), +**japonicus** (MF), *kokaneeanus* (M), +**lutescens** (MF), +**marginatus** (MF), *micans* (M), *montanus* (M), +**nairobicus** (MF), *neadelphus* (M), +**nigrans** (M), *nigrocornis* (M), *nitidulus* (M), *ovalis* (M), +**pacificus** (M), +**pini** (MF), *pinidumus* (M), *reconditus* (M), *simulans* (M), +**stigma** (M), +**subacutus** (MF), *tolimensis* (M), +**tristriatus** (MF), +**withycombei** (MF). | | |
| *Nesobiella* | 1 | 1 |
| +**hospes** (MF). | | |
| *Wesmaelius* | ca. 70 | 17* |
| +**coloradensis** (MF), +**concinnus** (MF), *fassnidgei* (F), +**furcatus** (M), *involutus* (MF), *longifrons* (MF), *longipennis* (MF), *fassnidgei* (F), +**navasi** (MF), +**nervosus** (MF), +**nubilus** (MF), *pretiosus* (MF), *quadrifasciatus* (MF), *reisseri* (F), +**subnebulosus** (MF), unknown spp. [2] (M). | | |
| *Hemerobiella* | 1 | 2* |
| +**sinuata** (M), unknown sp. [1] (F). | | |
| **Subfamily Sympherobiinae** (ca. 60, 17) | | |
| *Nomerobius* | 4 | 4 |
| +**cuspidatus** (MF), +**psychodoides** (MF), *signatus* (MF), *spinosus* (MF). | | |
| *Neosympherobius* | 1 | 1 |
| +**cinereus** (MF). | | |
| *Sympherobius* | ca. 55 | 12 |
| +**amiculus** (MF), *angustus* (M), *barberi* (M), +**bifasciatus** (M), +**domesticus** (MF), +**fallax** (MF), *fuscescens* (F), *maculipennis* (M), +**marginatus** (M), *nigricornis* (MF), *pygmaeus* (M), *tessellatus* (MF). | | |
| **Subfamily Psychobiellinae** (2, 1) | | |
| *Psychobiella* | 2 | 1 |
| +**sordida** (M), unknown sp. [1, *sordida*?] (F). | | |

Appendix 2. Continued.

| **Family-group taxon** (no. spp., no. spp. examined) | | |
|---|---|---|
| Genus | Total no. spp. | No. spp. examined |
| Species examined (sex[s] examined) | | |
| **Subfamily Notiobiellinae** (ca. 70, 24) | | |
| *Notiobiella* | ca. 35 | 10* |
| *costalis* (MF), *multifurcata* (M), *rosea* (MF), +**turneri** (MF), *valida* (MF), *viridis* (F), unknown spp. [4] (M). | | |
| *Psectra* | ca. 25 | 8* |
| +**diptera** (MF), *franzeni* (M), *iniqua* (F), +*oblongus* (M), *pretiosa* (F), +**tillyardi** (MF), unknown spp. [2] (M). | | |
| *Anapsectra* | 1 | 1 |
| +**medleri** (MF). | | |
| *Zachobiella* | 8 | 4* |
| +**?jacobsoni** (M), +**pallida** (F), *submarginata* (F), unknown sp. [1] (F). | | |
| **Subfamily Drepanacrinae** (ca. 10, 7) | | |
| *Conchopterella* | 4* | 4* |
| +**kuscheli** (MF), +**maculata** (MF), *stangei* (MF), unknown sp. [1] (MF). | | |
| *Austromegalomus* | 2 | 1 |
| +**insulanus** (MF). | | |
| *Drepanacra* | 4 | 2 |
| +**binocula** (MF), +**khasiana** (MF). | | |
| **Subfamily Megalominae** (ca. 40, 18) | | |
| *Megalomus* | ca. 40 | 18* |
| *angulatus* (M), *fidelis* (MF), *hirtus* (M), +**moestus** (MF), +**parvulus** (MF), +**nigratus** (MF), *pyraloides* (F), +**setosulus** (MF), *speciosus* (M), *tineoides* (F), +**tortricoides** (M), unknown spp. [7] (M). | | |
| **Subfamily Drepanepteryginae** (ca. 40, 16) | | |
| *Neuronema* | ca. 30 | 12* |
| +**albostigam** (MF), *decisum* (M), nr. *gyironganum* (M), +**kuwayamai** (MF), *kwanshiensis* (M), +**laminatum** (MF), +**omeishanum** (MF), *shensiensis* (M), *zhamanumn* (M), unknown spp. [3] (M). | | |
| *Gayomyia* | 3– | 1 |
| +**falcata** (MF). | | |
| *Drepanepteryx* | 6 | 3 |
| *algida* (F), *falculoides* (MF), +**phalaenoides** (MF). | | |
| **Subfamily Microminae** (ca. 120, 45) | | |
| *Noius* | 3* | 3* |
| +**noumeanus** (M), +**oceanicus** (MF), unknown sp. [1] (M). | | |
| *Nusalala* | ca. 20 | 9* |
| +**dispar** (M), +**krugeri** (M), +**rhegmatica** (M), unknown spp. [6] (M). | | |

Appendix 2. Continued.

| **Family-group taxon** (no. spp., no. spp. examined) | | |
|---|---|---|
| Genus | Total no. spp. | No. spp. examined |
| Species examined (sex[s] examined) | | |
| *Megalomina* | 3 | 3 |
| +**berothoides** (MF), +**acuminata** (F), +**bridwelli** (F). | | |
| *Micromus* | ca. 95 | 30* |
| +**africanus (MF),** +**angulatus** (MF), *bifasciatus* (F), *brandti* (M), *dissimilis* (MF), *drepanoides* (F), +**gradatus** (MF), +*lampus* (MF), +**maculatipes** (MF), +**marquesanus** (MF), *montanus* (M), +**multipunctatus** (MF), +**numerosus** (M), +**oblongus** (MF), +**paganus** (MF), +**posticus** (MF), *rubrinervis* (F), +**sjostedti** (MF), +**subanticus** (MF), +**tasmaniae** (MF), +**timidus** (MF), +**vagus** (MF), +**variegatus** (MF), +**variolosus** (MF), unknown spp. [6] (M). | | |
| **Unplaced genera** | | |
| *Notherobius* | 3 | 0 |

Appendix 3. Character fits to the preferred cladogram (aggregated by character). This appendix summarizes the "fit" of each character used in the cladistic analysis to the preferred cladogram (Fig. 23). Three "fit" characteristics are given: (1) character length, (2) all equally most parsimonious optimizations [if more than 1 exists, the optimization plotted on the preferred cladogram is given in boldface type], and (3) the cladogram placement of each character state transformation. Terminal lineages are identified by generic names; nonterminal lineages are identifed by the reference numbers given on the preferred cladogram.

| Char. no. | Length | Opt. no. | Lineage (state transformation) |
|---|---|---|---|
| 1 | 4 | 1 | 2(0→1), 18(1→0), *Conchopterella* (1→0), *Noius* (0→1). |
| | | **2**[1] | **2(0→1), 19(1→0), 22(1→0), Conchopterella (1→0).** |
| 2 | 2 | 1 | 21(0→1), *Megalomina* (1→0). |
| 3 | 2 | 1 | 21(0→1), *Megalomina* (1→0). |
| 4 | 1 | 1 | *Noius* (0→1). |
| 5 | 1 | 1 | *Megalomus* (0→1). |
| 6 | 1 | 1 | 2(0→1). |
| 7 | 3 | 1 | 3(0→1), 12(1→0), 17(1→0). |
| 8 | 3 | 1 | 3(0→1), 12(1→0), 17(1→0). |
| 9 | 2 | 1 | 21(0→1), *Megalomina* (1→0). |
| 10 | 3 | **1**[2] | **3(1→0), Psychopsis (1→0), Polystoechotes (1→2).** |
| | | 2 | *Nothochrysa* (0→1), *Polystoechotes* (0→2), *Carobius* (0→1). |
| | | 3 | 1(0→1), *Polystoechotes* (1→2), *Carobius* (0→1). |
| | | 4 | 1(0→2), *Polystoechotes* (2→1), *Carobius* (0→1). |
| 11 | 3 | 1 | 4(0→1), 12(0→1), *Noius* (0→1). |
| 12 | 3 | 1 | 7(0→1), 12(0→2 [+1]), *Psychobiella* (0→2 [+1]). |
| 13 | 1 | 1 | 2(0→1). |
| 14 | 1 | 1 | *Hemerobius* (0→1). |
| 15 | 1 | 1 | *Notiobiella* (0→1). |
| 16 | 1 | 1 | 2(0→1). |
| 17 | 2 | 1 | 2(0→1), *Psychobiella* (1→0). |
| 18 | 3 | 1 | 1(0→1), 20(0→1), *Noius* (0→1). |
| 19 | 1 | 1 | *Notiobiella* (0→1). |
| 20 | 1 | 1 | *Gayomyia* (0→1). |
| 21 | 1 | 1 | 16(0→1). |
| 22 | 1 | 1 | *Neosympherobius* (0→1). |
| 23 | 4 | 1 | 21(0→1), *Nothochrysa* (0→2 [+2]), *Zachobiella* (0→1). |
| 24 | 5 | 1 | 13(0→1), 21(0→1), *Nothochrysa* (0→2 [+2]), *Megalomina* (1→0). |
| 25 | 3 | 1 | 21(0→1), *Nothochrysa* (0→1), *Zachobiella* (0→1). |
| 26 | 2 | 1 | *Gayomyia* (1→2), *Drepanepteryx* (1→0). |
| 27 | 1 | 1 | *Notiobiella* (0→1). |
| 28 | 2 | 1 | 9(0→1), 22(1→0). |
| 29 | 1 | 1 | 3(0→1). |
| 30 | 1 | 1 | *Carobius* (0→1). |
| 31 | 2 | 1 | 9(0→1), 11(1→0). |
| | | **2**[3] | **14(0→1), Psychobiella (0→1).** |
| 32 | 1 | 1 | 4(0→1). |
| 33 | 1 | 1 | 14(0→1). |
| 34 | 5 | **1**[4] | **4(0→1), 21(0→1), Carobius (0→1), Notiobiella (0→1), Gayomyia (0→1).** |
| | | 2 | 2(0→1), 7+9(1→0), 21(0→1), *Notiobiella* (0→1), *Gayomyia* (0→1). |
| 35 | 3 | **1**[5] | **2(0→1), Neuronema (1→0), Gayomyia (1→0).** |
| | | 2 | 2(0→1), 19(1→0), *Drepanepteryx* (0→1). |

Appendix 3. Continued.

| Char. no. | Length | Opt. no. | Lineage (state transformation) |
|---|---|---|---|
| 36 | 2 | 1 | 12(0→1), *Neosympherobius* (0→1). |
| 37 | 2 | 1 | *Drepanacra* (0→1), *Gayomyia* (0→1). |
| 38 | 2 | 1 | *Psychopsis* (0→1), *Hemerobius* (0→1). |
| 39 | 2 | 1 | *Nothochrysa* (0→1), *Carobius* (0→1). |
| 40 | 3 | 1 | 7(0→1), 11(0→1), *Nothochrysa* (0→1). |
| 41 | 2 | 1 | 19(0→1), *Nothochrysa* (0→1). |
| 42 | 3 | 1 | 11(0→1), *Nothochrysa* (0→1), *Sympherobius* (0→1). |
| 43 | 1 | 1 | 22(0→1). |
| 44 | 4 | 1 | 6(0→1), *Nothochrysa* (0→1), *Carobius* (0→1), *Nusalala* (0→1). |
| 45 | 3 | 1 | 11(0→1), *Nothochrysa* (0→1), *Sympherobius* (0→1). |
| 46 | 2 | 1 | *Nothochrysa* (0→1), *Gayomyia* (0→1). |
| 47 | 2 | **1**[6] | **19(0→1), 22(0→1).** |
|  |  | 2 | 18(0→1), *Noius* (1→0). |
| 48 | 4 | 1 | 10(0→1), 12(1→0), 22(1→0), *Polystoechotes* (0→1). |
|  |  | **2**[7] | **14(0→1), 22(1→0), Polystoechotes (0→1), Notiobiella (0→1).** |
| 49 | 3 | 1 | 15(0→1), 20(0→1), *Psychopsis* (0→1). |
| 50 | 2 | 1 | 22(0→1), *Gayomyia* (0→1). |
| 51 | 2 | 1 | 16(0→1), *Psychobiella* (0→1). |
| 52 | 1 | 1 | *Nomerobius* (0→1). |
| 53 | 2 | 1 | 7(1→0), 12(1→2). |
| 54 | 1 | 1 | *Hemerobiella* (0→1). |
| 55 | 2 | 1 | 22(0→1), *Nothochrysa* (0→1). |
| 56 | 2 | 1 | *Nothochrysa* (1→2), *Zachobiella* (1→0). |
| 57 | 1 | 1 | *Austromegalomus* (0→1). |
| 58 | 1 | 1 | *Nesobiella* (0→1). |
| 59 | 2 | 1 | *Polystoechotes* (0→1), *Nomerobius* (0→1). |
| 60 | 1 | 1 | *Noius* (0→1). |
| 61 | 1 | 1 | *Wesmaelius* (0→1). |
| 62 | 1 | 1 | *Noius* (0→1). |
| 63 | 1 | 1 | *Nomerobius* (0→1). |
| 64 | 1 | 1 | *Conchopterella* (0→1). |
| 65 | 1 | 1 | *Nesobiella* (0→1). |
| 66 | 1 | 1 | *Wesmaelius* (0→1). |
| 67 | 1 | 1 | *Psectra* (0→1). |
| 68 | 1 | 1 | *Nomerobius* (0→1). |
| 69 | 1 | 1 | *Noius* (0→1). |
| 70 | 1 | 1 | *Neosympherobius* (0→1). |
| 71 | 1 | 1 | *Gayomyia* (0→1). |
| 72 | 1 | 1 | *Neosympherobius* (0→1). |
| 73 | 1 | 1 | *Nomerobius* (0→1). |
| 74 | 4 | 1 | 10(0→1), 20(1→0), 23(1→0), *Zachobiella* (1→0). |
| 75 | 1 | 1 | *Conchopterella* (0→1). |
| 76 | 1 | 1 | *Nomerobius* (0→1). |
| 77 | 1 | 1 | *Psychobiella* (0→21). |
| 78 | 7 | 1 | 8(1→0), 10(1→2), 18(2→1), *Psychopsis* (1→2), *Anapsectra* (2→1), *Megalomus* (2→3), *Megalomina* (1→2). |
| 79 | 1 | 1 | 7(0→1) |
| 80 | 1 | 1 | *Sympherobius* (0→1). |
| 81 | 1 | 1 | *Sympherobius* (0→1). |

Appendix 3. Continued.

| Char. no. | Length | Opt. no. | Lineage (state transformation) |
|---|---|---|---|
| 82 | 3 | 1 | *Psychobiella* (0→1), *Conchopterella* (0→1), *Drepanacra* (0→1). |
| | | **2**[8] | **15(0→1), Psychobiella (0→1), Austromegalomus (1→0).** |
| 83 | 1 | 1 | *Notiobiella* (0→1). |
| 84 | 1 | 1 | 2(0→1). |
| 85 | 1 | 1 | 5(0→1). |
| 86 | 2 | 1 | *Hemerobius* (1→0), *Zachobiella* (1→2). |
| 87 | 2 | 1 | *Psychobiella* (0→1), *Drepanacra* (0→1). |
| 88 | 1 | 1 | *Psectra* (0→1). |
| 89 | 1 | 1 | *Conchopterella* (0→1). |
| 90 | 1 | 1 | *Gayomyia* (0→1). |
| 91 | 1 | 1 | *Gayomyia* (0→1). |
| 92 | 1 | 1 | *Nusalala* (0→1). |
| 93 | 1 | 1 | *Drepanepteryx* (0→1). |
| 94 | 1 | 1 | 4(0→1). |
| 95 | 1 | 1 | 3(0→1). |
| 96 | 2 | 1 | *Psychopsis* (1→0), *Anapsectra* (1→2). |
| 97 | 1 | 1 | *Anapsectra* (0→1). |
| 98 | 1 | 1 | *Hemerobiella* (0→1). |
| 99 | 1 | 1 | *Zachobiella* (0→1). |
| 100 | 5 | 1 | 4(0→1), 12(0→1), 21(0→1), *Nothochrysa* (0→1), *Drepanepteryx* (0→1). |
| 101 | 1 | 1 | *Anapsectra* (0→1). |
| 102 | 1 | 1 | *Anapsectra* (0→1). |
| 103 | 5 | 1 | 5(0→1), 12(0→1), *Carobius* (0→1), *Nomerobius* (0→1), *Noius* (0→1). |
| 104 | 1 | 1 | 2(0→1) |
| 105 | 2 | 1 | 5(0→1), 12(0→1). |
| 106 | 3 | 1 | *Polystoechotes* (0→3 [+1]), *Gayomyia* (0→1), *Nusalala* (0→2) [+1]). |
| 107 | 1 | 1 | 23(0→1). |
| | 196 | | |

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[1] Optimization 2 is preferred. Optimization 1 would require a rereversal transformation series 0→1→0→1 between lineages 2 and *Noius*.

[2] Optimization 1 is arbitrarily plotted on the preferred cladogram. The three states of character 10 were analyzed as nonadditive. Since the two states (0 and 1), found basally within the Hemerobiidae are also found in the outgroups, the polarity of this character is ambiguous at the base of the cladogram.

[3] Parallel increase in the number of "radial sectors" along the anterior radial trace (optimization 2) is preferred over reversal in this character (optimization 1).

[4] Optimization 1 is preferred, see discussion in text under the heading *Phylogenetic Analysis, Results, Cladograms.*

[5] The occurrence of forewing pre-3irl crossveins in *Gayomyia* and *Neuronema* is interpreted as convergent (optimization 1). In *Gayomyia* these crossveins are associated with a general increase in the number of forewing crossveins, in *Neuronema* they are not.

[6] The occurrence of a 1cua-cup crossvein in the forewings of most Drepanepteryginae, and in the clade *Nusalala* + *Megalomina* + *Micromus* is interpreted as a convergence (optimization 1).

[7] Optimization 2, which maximizes parallelism in this character, is preferred.

[8] Optimization 2, which interprets the well-developed submediuncal scabriculous patches in *Conchopterella* and *Drepanacra* as homologs, is preferred.

Appendix 4. Character fits to the preferred cladogram (aggregated by lineage). This appendix summarizes the "fit" of each character used in the cladistic analysis to the preferred cladogram (Fig. 23). This appendix is similar to Appendix 3, except that character transformations are aggregated by lineage, rather than by character. For characters 1, 10, 31, 34, 35, 47, 48, and 82, the character transformations specified by the preferred optimizations identified in Appendix 3 are used. Terminal lineages are identified by generic names; nonterminal lineages are identified by the reference numbers given on the preferred cladogram.

| Lineage | Length | Character transformations |
|---|---|---|
| | | **Outgroups** |
| 1 | 1 | 18(0→1). |
| *Psychopsis* | 5 | 10(1→0), 38(0→1), 49(0→1), 78(1→2), 96(1→0). |
| *Nothochrysa* | 15 | 23(0→2 [+2]), 24(0→2 [+2]), 25(0→1), 39(0→1), 40(0→1), 41(0→1), 42(0→1), 44(0→1), 45(0→1), 46(0→1), 55(0→1), 56(1→2), 100(0→1). |
| *Polystoechotes* | 4 | 10(1→2), 48(0→1), 59(0→1), 106(0→3 [+1]). |
| | | **Ingroups** |
| 2 | 8 | 1(0→1), 6(0→1), 13(0→1), 16(0→1), 17(0→1), 35(0→1), 84(0→1), 104(0→1). |
| 3 | 5 | 7(0→1), 8(0→1), 10(1→0), 29(0→1), 95(0→1). |
| 4 | 5 | 11(0→1), 32(0→1), 34(0→1), 94(0→1), 100(0→1). |
| 5 | 3 | 85(0→1), 103(0→1), 105(0→1). |
| 6 | 1 | 44(0→1). |
| 7 | 4 | 12(0→1), 40(0→1), 53(1→0), 79(0→1). |
| 8 | 1 | 78(1→0). |
| 9 | 1 | 28(0→1). |
| 10 | 2 | 74(0→1), 78(1→2). |
| 11 | 3 | 40(0→1), 42(0→1), 45(0→1). |
| 12 | 9 | 7(1→0), 8(1→0), 11(0→1), 12(0→2 [+1]), 36(0→1), 53(1→2), 100(0→1), 103(0→1), 105(0→1). |
| 13 | 1 | 24(0→1). |
| 14 | 3 | 31(0→1), 33(0→1), 48(0→1). |
| 15 | 2 | 49(0→1), 82(0→1). |
| 16 | 2 | 21(0→1), 51(0→1). |
| 17 | 2 | 7(1→0), 8(1→0). |
| 18 | 1 | 78(2→1). |
| 19 | 3 | 1(1→0), 41(0→1), 47(0→1). |
| 20 | 3 | 18(0→1), 49(0→1), 74(1→0). |
| 21 | 8 | 2(0→1), 3(0→1), 9(0→1), 23(0→1), 24(0→1), 25(0→1), 34(0→1), 100(0→1). |
| 22 | 7 | 1(1→0), 28(1→0), 43(0→1), 47(0→1), 48(1→0), 50(0→1), 55(0→1). |
| 23 | 2 | 74(1→0), 107(0→1). |
| *Carobius* | 5 | 30(0→1), 34(0→1), 39(0→1), 44(0→2), 103(0→1). |
| *Hemerobius* | 3 | 14(0→1), 38(0→1), 86(1→0). |
| *Nesobiella* | 2 | 58(0→1), 65(0→1). |
| *Wesmaelius* | 2 | 61(0→1), 66(0→1). |
| *Hemerobiella* | 2 | 54(0→1), 98(0→1). |
| *Nomerobius* | 7 | 52(0→1), 59(0→1), 63(0→1), 68(0→1), 73(0→1), 76(0→1), 103(0→1). |
| *Neosympherobius* | 4 | 22(0→1), 36(0→1), 70(0→1), 72(0→1). |

Appendix 4. Continued.

| Lineage | Length | Character transformations |
|---|---|---|
| *Sympherobius* | 4 | 42(0→1), 45(0→1), 80(0→1), 81(0→1). |
| *Psychobiella* | 7 | 12(0→2 [+1]), 17(1→0), 31(0→1), 51(0→1), 77(0→1), 82(0→1), 87(0→1). |
| *Notiobiella* | 6 | 15(0→1), 19(0→1), 27(0→1), 34(0→1), 48(0→1), 83(0→1). |
| *Psectra* | 2 | 67(0→1), 88(0→1). |
| *Anapsectra* | 5 | 78(2→1), 96(1→2), 97(0→1), 101(0→1), 102(0→1). |
| *Zachobiella* | 6 | 23(0→1), 25(0→1), 56(1→0), 74(1→0), 86(1→2), 99(0→1). |
| *Conchopterella* | 4 | 1(1→0), 64(0→1), 75(0→1), 89(0→1). |
| *Austromegalomus* | 2 | 57(0→1), 82(1→0). |
| *Drepanacra* | 2 | 37(0→1), 87(0→1). |
| *Megalomus* | 2 | 5(0→1), 78(2→3) |
| *Neuronema* | 1 | 35(1→0). |
| *Gayomyia* | 11 | 20(0→1), 26(1→2), 34(0→1), 35(1→0), 37(0→1), 46(0→1), 50(0→1), 71(0→1), 90(0→1), 91(0→1), 106(0→1). |
| *Drepanepteryx* | 3 | 26(1→0), 93(0→1), 100(0→1). |
| *Noius* | 7 | 4(0→1), 11(0→1), 18(0→1), 60(0→1), 62(0→1), 69(0→1), 103(0→1). |
| *Nusalala* | 3 | 44(0→1), 92(0→1), 106(0→2 [+1]). |
| *Megalomina* | 5 | 2(1→0), 3(1→0), 9(1→0), 24(1→0), 78(1→2). |
| *Micromus* | 0 | |
| | 196 | |

Appendix 5. Cladistically coded data. This appendix presents the data matrix of 27 taxa (24 ingroup, 3 outgroup) and 107 characters used in the cladistic analysis. Bold values in the matrix indicate the presence of intrageneric variation for the possible characer states at these positions (see discussion in text under the heading *Phylogenetic Analysis: Methods and Data: Data*). Question marks (?) indicate unobtainable or uncertain character states.

| | Character Number |
|---|---|
| | 00000000000000000000000000000000000000000 |
| | 00000000011111111112222222222333333333344 |
| Taxon | 12345678901234567890123456789012345678901 |
| *Anapsectra* | 10000100001210011000000101011000001100010 |
| *Austromegalomus* | 10000111000010011000100001011010101000000 |
| *Carobius* | 10000100010010011000000001000100011000100 |
| *Conchopterella* | 0000011100001001100000000**1**01101010**100**000**0** |
| *Drepanacra* | 10000111000010011000100001011010101010000 |
| *Drepanepteryx* | 000001000000100111000000000110101010**0**0001 |
| *Gayomyia* | 000001000000100111010000020?1010110010001 |
| *Hemerobiella* | 10000111001010011000000001001001011000000 |
| *Hemerobius* | **1**00001110010110110000000010010010110**0**1000 |
| *Megalomina* | 000001000000100110000010110010101110**0**000**0** |
| *Megalomus* | 100011000000100110000000010110101**0**1000000 |
| *Micromus* | 0**110**0100100010011000001**1**1**1**001010111**00**0**0**0**0** |
| *Neosympherobius* | 10000111000110011000010001001000001100010 |
| *Nesobiella* | 10000111001010011000000001001001011000000 |
| *Neuronema* | 00000100000010**0**1100000000101101010**0**0000001 |
| *Noius* | 11110100101010011100001**1**11011010111000000 |
| *Nomerobius* | 10000111000110011000000001001000001000010 |
| *Notiobiella* | 100001110000101110100000011**1**100001100**0**0**1**0 |
| *Nusalala* | 01100100**1**00010011000001111001010111000000 |
| *Psectra* | **1**0000100001210011000000**0**01011000001**1**00010 |
| *Psychobiella* | 10000111000210010000000001011010001000000 |
| *Sympherobius* | 10000111000110011000000**0**010010000**0**10**0**0010 |
| *Wesmaelius* | 10000111001010011000000001001001011000000 |
| *Zachobiella* | **1**0000100001210011000001**1**110**1**1000001100010 |
| *Nothochrysa* | 000000000100000001000022110000000?0?00111 |
| *Polystoechotes* | 00000000020000000100000001000000000?00000 |
| *Psychopsis* | 000000000000000000000000010?0000000?01000 |

Appendix 5. Extended.

| Character Number |
|---|
| 000000000000000000000000000000000000000000000000000000000001111111 |
| 444444445555555555666666666677777777778888888888999999999900000000 |
| 234567890123456789012345678901234567890123456789012345678901234567 |
| 100100000002001000000000000000001000100000101000000001210011111100 |
| 000000110101001100000000000000001000200000101000000011000000001000 |
| 001000000001001000000000000000000000100000101000000000100000011000 |
| 000000**11**0001001000000010000000001100200010101001000001100000001000 |
| 000000110101001000000000000000001000200010101100000001100000001000 |
| 000001110001001000000000000000000000100000101000000101100010001000 |
| 00001?111001001000000000000001000000100000101000110001100000001010 |
| 001000000000110100000000000000000000100000101000000011101010001000 |
| 00**0**0000000010010000**0**0000000000000000100000110000000011100010**0**11100 |
| 010001001001011000000000000000000000200000101000000001100010001001 |
| 00**0**0001**0**00010010000000000000000010003000001010000000110000000**00**1**0**00 |
| 01**00**010010010110000000000000000000001000001010000000011**0**0010**00**1**00**1 |
| 000000000000001000000000000010100000010000101000000001100000001000 |
| 000000000001001010000001000000000000100000111000000011100010011100 |
| 00000**1**1**0**00010010000000000000000010001000001010000000110000**0**0010**0**0 |
| 0000001000010010001010000001000010001000001010000000110001**0**011000 |
| 000000000010001001000100001000010010110000101000000001100000011000 |
| 1001001000010010000000000000000010002000011010000000110000**0**0**0**10**0**0 |
| 011001001001011000000000000000001000100000101000001001100010001020 |
| 100100000002001000000000010000001000200000101010000001**1**0001**0**011100 |
| 000000000101001000000000000000000001100010101100000001100000001000 |
| 1001000000000010000000000000000000000111001010000000011000000**0**1000 |
| 0010000000001001000010001000000000001000001010000000**1**1100010001000 |
| 100100000002000000000000000000000000200000102000000001100110011100 |
| 10111?000001012000000000000000000000100000001000000000100010000000 |
| 000000100001001001000000000000000000100000001000000000100000000030 |
| 000000010001001000000000000000000000200000001000000000000000000000 |

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