# Phylogeny of the Apochrysine Green Lacewings
# (Neuroptera: Chrysopidae: Apochrysinae)

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**ABSTRACT**    Phylogenetic relationships among the genera of Apochrysinae are examined. Exemplars from all 13 previously defined genera of the subfamily are compared with outgroups from the Nothochrysinae (*Nothochrysa* McLachlan) and Chrysopinae (*Italochrysa* Principi) in a parsimony analysis of 78 character states across 39 adult morphological characters. The analysis resulted in three most parsimonious trees with a length of 70 steps. The Apochrysinae are confirmed as monophyletic, with the enigmatic genus *Nothancyla* as the sister to the rest of the subfamily. The phylogenetic relationships among the genera of Apochrysinae are discussed, as are primitive and derived venational characters and wing vein reticulation in apochrysine wings. Six valid genera are recognized in light of the analysis: *Apochrysa* Schneider (*Anapochrysa* Kimmins, *Lauraya* Winterton, *Nacaura* Navás, *Oligochrysa* Esben-Petersen and *Synthochrysa* Needham, syns. nov.), *Domenechus* Navás, *Joguina* Navás (*Lainius* Navás syn. nov.), *Loyola* Navás (*Claverina* Navás syn. nov.), *Nobilinus* Navás and *Nothancyla* Navás. Valid genera are rediagnosed in a revised classification. A new key to genera and lists of included species are presented.

**KEY WORDS**    Neuroptera, green lacewings, Chrysopidae, phylogeny, systematics

THE SUBFAMILY APOCHRYSINAE Handlirsch is a taxonomically small group of slender, green lacewings with large, rounded wings, and often densely reticulated venation. The group was originally recognized as a distinct family of Neuroptera, Apochrysidae, by Handlirsch (1906–1908) and is included as a separate family sister to the Chrysopidae Schneider in the widely cited phylogeny of the order proposed by Withycombe (1925). Tillyard (1926) subsequently considered the group not sufficiently different from the rest of Chrysopidae to warrant status as a separate family and included it as a subfamily of Chrysopidae. The status of the group as a subfamily was questioned by Adams (1967), who suggested it might be the sister-tribe to Leucochrysini Adams (Chrysopinae). Subsequently, Brooks and Barnard (1990) identified several mutually exclusive synapomorphies diagnosing both Apochrysinae and Chrysopinae, clearly indicating that they are separate groups within Chrysopidae and warranting subfamilial ranking.

Apochrysinae are pantropical in distribution, but with each of the 13 previously described genera having rather limited biogeographical ranges. *Anapochrysa* Kimmins (monotypic) and *Apochrysa* Schneider (containing two species) were described from the Afrotropics (Brooks and Barnard 1990, Hölzel 1996). The monotypic genus *Nacaura* Navás was described

from Japan and Taiwan, with a possible second, undescribed species from India (Brooks and Barnard 1990). Four genera have been described from the Neotropics: *Lainius* Navás, *Domenechus* Navás and *Loyola* Navás, each with two species, and the monotypic *Claverina* Navás. The fauna of the Australasian-Oriental region is the most diverse with 16 described species in six genera. The monotypic genera *Oligochrysa* Esben-Petersen, *Nothancyla* Navás, and *Lauraya* Winterton were described from Australia, and *Synthochrysa* Needham (four species), *Joguina* Navás (three species), and *Nobilinus* Navás (six species and subspecies) are distributed from mainland south eastern Asia to the western Pacific islands (Kimmins 1952, Brooks and Barnard 1990, Winterton 1995).

The taxonomy and classification of Apochrysinae is considered unsatisfactory (Brooks and Barnard 1990, Brooks 1997). Most of the 13 constituent genera are currently defined based on wing venational characters and the high variability in venation across the subfamily has resulted in many monotypic genera (Brooks 1997). The structure of the male genitalia, useful or even critical for defining genera in many other chrysopid groups, are highly conserved in the subfamily Apochrysinae (Brooks and Barnard 1990). Brooks (1997) lamented that current generic definitions based on venational characters almost dictate that every new taxon be allocated to a new genus (e.g., *Anapochrysa* in Kimmins (1952), *Lauraya* in Winterton (1995). Consequently, the Apochrysinae are in need of revision in a phylogenetic context, with a

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Table 1.  List of exemplars and matrix of adult morphological characters for Apochrysinae (Chrysopidae)

| | |
|---|---|
| Nothochrysa fulviceps (Stephens, 1836) | 00000?00000010000000000000000000010010000 |
| Italochrysa facialis (Banks, 1910) | 00000100000000000000000000000000001100010 |
| Anapochrysa voeltzkowi (Weele, 1909) | 01111111100111111111010010001100001111 |
| Apochrysa wagneri (Hölzel, 1996) | 01101111101101111111010100011100?11101 |
| Claverina beata (Walker, 1858) | 01111111101111110100111111100??????1100 |
| Domenechus mirificus (Gerstaecker, 1888) | 0?0111111011111010011111111101100011101 |
| Joguina nicobarica (Brauer, 1864) | 01011??1111101110110111111?100100011101 |
| Lainius constellatus (Navás, 1913) | 0100111111111010111111?100100001101 |
| Lauraya retivenosa (Winterton, 1995) | 0111111101101111110101000010000011101 |
| Loyola croesus (Gerstaecker, 1894) | 010?11111011111010011111101??????1100 |
| Nacaura matsumurae (Okamoto, 1912) | 01111111011011111110111000011010011111 |
| Nobilinus albardae insignitus (Navás, 1913) | 0101111110110111010011111001000001011 |
| Nothancyla verreauxi (Navás, 1910) | 1?001001000001000000000000101010100010 |
| Oligochrysa lutea (Walker, 1853) | 01111111011011101010001100001111 |
| Synthochrysa montrouzieri (Girard, 1862) | 11011111101101110111010010001000001001 |

Combinations used are those prior to subsequent reclassification (see *Discussion*).

broadening of the current narrowly defined genus concepts.

The purpose of this phylogenetic study was to elucidate natural groupings of genera in the subfamily Apochrysinae, to determine primitive and derived character states (particularly for venational characters), and to identify probable synonyms. This revised hypothesis of relationships in a phylogenetic context will form a template for a future revision in which newly described taxa can be grouped by similarity rather than by dissimilarity, and avoid the continued proliferation of uninomials.

## Materials and Methods

**Exemplar Selection.** Exemplars from all previously described genera of Apochrysinae were compared in a cladistic analysis with representatives of the other two subfamilies of Chrysopidae: Chrysopinae and Nothochrysinae (Table 1). A member of the primitive subfamily Nothochrysinae, *Nothochrysa fulviceps* (Stephens), was chosen as the distant outgroup to root the tree. *Italochrysa* Principi is included in the tribe Belonopterygini Navás and was considered the most basal group of Chrysopinae by Brooks and Barnard (1990, figure 7). *Italochrysa facialis* (Banks) was chosen to represent the Chrysopinae in the analysis.

Ingroup selection consisted of exemplars from each of the previously described genera in the subfamily

Apochrysinae. Specimens of all species were examined (*Appendix 1*) except *Apochrysa wagneri* Hölzel, 1996, which was coded from the original description and figures given for this species. The phylogenetic position of *Nothancyla verreauxi* Navás within the Chrysopidae has been uncertain due to its possession of both chrysopine and apochrysine characteristics (New 1980, Brooks and Barnard 1990, Winterton 1995, Brooks 1997). New (1980) and Winterton (1995) supported its placement in Chrysopinae based on male genitalic characters, and Brooks and Barnard (1990) supported its inclusion in Apochrysinae based on wing venational and antennal characters. Brooks (1997), noting the uneasy placement of *N. verreauxi* in Apochrysinae, suggested that it may even belong in its own monotypic subfamily. In this study we accept the current hypothesis of *N. verreauxi* as a member of Apochrysinae, and have included it in the analysis to assess its position in the group.

**Character Descriptions.** Thirty-nine characters comprising 78 states were used in the analysis (Table 1). Taxon references refer to previous generic designations before any reclassifications proposed in the discussion. Wing venational terminology follows that used by Brooks and Barnard (1990). Males of *Claverina* and *Loyola* are unknown, and are coded as uncertain (?) for male character states.

1. *Vertex Shape.* (0) Flattened or only slightly rounded; (1) raised into a distinct ridge anteriorly. The vertex is flattened or only slightly rounded on most Chrysopidae and is clearly plesiomorphic for the group. A raised vertex is found in *Nothancyla* and *Synthochrysa*.

2. *Antennal Toruli Size.* (0) Small; (1) large. The size of the antennal toruli is highly variable within the Chrysopidae. Although large toruli are found in all members of the Apochrysinae (but not observed clearly in *Nothancyla*), the usefulness of the character appears limited.

3. *Antenna Length.* (0) Distinctly shorter than forewing; (1) distinctly longer than forewing. There is some intraspecific variability in this character. Across the specimens examined here, antennae longer than the forewing are found in *Claverina* and the *Apochrysa* clade (except *Synthochrysa*).

4. *Scape Length.* (0) Short, broad; (1) elongate. Like character 3, the shape of the scape is also somewhat variable between individuals, and will require further assessment using a larger sample of specimens. An elongate scape is present in the ingroup, excluding *Nothancyla*. A secondarily reduced scape length is present in *Lainius* and *Apochrysa*.

5. *Length of Prothoracic Setae.* (0) Similar length or shorter than other body setae; (1) elongate, distinctly longer than other body setae. Elongate prothoracic setae, particularly along the lateral margins, is synapomorphic for the ingroup. Brooks and Barnard (1990) found elongate prothoracic setae to be present in a variety of genera from all subfamilies of Chrysopidae.

6. *Tarsal Claw Shape.* (0) Narrow (Brooks and Barnard 1990, figure 12); (1) basally dilated (Brooks and

Barnard 1990, figure 11). This character is based on the analysis by Brooks and Barnard (1990, character 18), examining the shape of the tarsal claw. A simple claw, without any basal dilation, is autapomorphic for *Nothancyla* in this analysis.

7. *Length of Setae on Femur and Tibia.* (0) Short; (1) relatively elongate. Relatively elongate leg setae is synapomorphic for Apochrysinae exclusive of *Nothancyla*.

8. *Length of Setae Along Costal Margin.* (0) Short; (1) long. Also based on a character used by Brooks and Barnard (1990; character 22), elongate costal setae are a synapomorphy for Apochrysinae, although it is also present in several chrysopine and nothochrysine genera.

9. *Forewing Costal Cells.* (0) Narrow near base of wing (Fig. 3); (1) broad near base of wing (Fig. 5). Although a broad costal space is synapomorphic for members of Apochrysinae, it is also present in some chrysopine genera (e.g., *Ankylopteryx* Brauer), and in other families of Neuroptera (e.g., Hemerobiidae, Psychopsidae).

10. *Forewing Costal Area.* (0) Costal veinlets not linked by crossveins (Fig. 3); (1) series of costal crossveins linking costal veinlets (Fig. 10). Crossveins linking costal veinlets is a synapomorphy for *Joguina* + *Lainius*.

11. *Costal Space Above Pterostigma.* (0) Narrowed (Fig. 3); (1) broad (Fig. 8). The costal space attenuates only slightly in all apochrysine lacewings except *Nothancyla* and *Anapochrysa*, resulting in the costal space adjacent to the pterostigma remaining relatively broad. Although the costal space is broad in several chrysopine genera, it is usually sharply attenuated near the wing apex (Brooks and Barnard 1990, figure 89).

12. *Posterior Margin of Forewing.* (0) Straight along at least basal ½ of wing (Fig. 16); (1) broadly rounded along entire margin (Fig. 14). Concurrent with the broad, rounded shape of the wings in apochrysine lacewings, the posterior margin of the forewing is rounded in all members (except *Nothancyla*). The plesiomorphic wing shape for Chrysopidae is with a distinct straight edge along the basal ½ of the wing.

13. *Pterostigma.* (0) Unmarked; (1) marked. A pterostigma suffused with pigment is present in *Nothochrysa, Anapochrysa, Loyola+ Claverina, Domenechus* and *Lainius*.

14. *Subcosta (Sc).* (0) Relatively widely separated from radius along length, clearly separate from radius near wing apex (Figs. 3 and 4); (1) close to radius along length, veins appearing to join near apex (Figs. 5 and 6). The subcostal and radius are closely associated toward the wing apex, with crossveins between the two hardly apparent. The apomorphic state is present in Apochrysinae (except *Nothancyla*).

15. *Basal Subcostal Crossvein (sc-r) in Both Wings.* (0) Present (Figs. 3 and 4); (1) absent (Figs. 8 and 9). The presence of *sc-r* is clearly plesiomorphic for Neuroptera, and the secondary loss is synapomorphic for Apochrysinae.

16. *Intramedial Cell (im) in Forewing.* (0) Present (Fig. 3); (1) absent (Fig. 5). Cell *im* is present in both subfamilies Nothochrysinae and Chrysopinae, but is secondarily lost in Apochrysinae (except *Nothancyla*). The loss of cell *im* is probably associated with migration of vein *Rs* basally along *R* toward the base of the wing.

17. *Posterior Marginal Veinlets in Both Wings with "End-Twigging" (i.e., Forked).* (0) Only in distal ⅓–½ of wing (Figs. 3 and 4); (1) present in distal ⅔–¾ of wing (Figs. 5 and 6). The apomorphic state, with extensive 'end-twigging' of posterior marginal veinlets, is present in the clade *Anapochrysa* + (*Lauraya* + *Nacaura* + *Apochrysa*).

18. *Origin of Rs Vein on R in Both Wings.* (0) Approximately ⅓ length from wing base (Fig. 3); (1) arises proximate to wing base, close to origin of *R* (Fig. 5). The plesiomorphic condition for all Neuroptera is *Rs* originating on *R* at ≈¼–½ wing length. The origin of *Rs* has clearly migrated basad along *R* in all apochrysine lacewings except *Nothancyla*, although the origin of *Rs* in *Nothancyla* is more basal than many other chrysopid genera.

19. *Forewing Rs Vein.* (0) Sinuous, broadly reflexed anteriorly toward radius (Fig. 5); (1) relatively straight along entire length (Fig. 3). A sinuous *Rs*, reflexed anteriorly is plesiomorphic for Chrysopidae, whereas a straight *Rs* is apomorphic for *Nobilinus, Joguina* and the *Apochrysa* clade. This character is variable at various levels across the family.

20. *Forewing Area Behind Pterostigma.* (0) With crossveins between *R* and *Rs* distally (Fig. 3); (1) without crossveins between *R* and *Rs* (Fig. 5). The lack of crossveins distally between *R* and *Rs* forms an elongate cell posterior and slightly distal to the pterostigma in *Lainius* and the *Apochrysa* clade. In the plesiomorphic condition, this cell is filled with crossveins.

21. *Forewing.* (0) With single row of cells between *R* and *Rs* veins (Fig. 3); (1) with two or more rows of cells between *R* and *Rs* veins (Fig. 8). Multiple rows of cells, sometimes reticulated, are present as an apomorphy between *R* and *Rs* in the *Joguina* clade exclusive of *Nobilinus*.

22. *Inner Gradate Series (ig).* (0) Not extending basally, usually joining *Psm* posteriorly (Fig. 3); (1) extending basally toward origin of *Rs*, not joining with *Psm* posteriorly (Figs. 8 and 14). The plesiomorphic state found in most Chrysopidae is for the inner gradate series to extend posteriorly where it may or may not join with *Psm* at ⅓–⅔ wing length. The apomorphic state, found in all Apochrysinae except *Nothancyla*, is for the inner gradate series to extend posteriorly and then basally, parallel with *Psm*, toward the base of the wing, often joining with *Rs* near its origin on *R*.

23. *Forewing Radial Area.* (0) With two or fewer rows of cells between *Rs* and *Psm* in basal ½ of wing (Fig. 16); (1) reticulated, with more than two rows of cells (often irregular) in basal ½ of wing (Fig. 5). Multiple, often reticulated, rows of cells are present in the basal ½ of the forewing of *Nacaura* + *Apochrysa* +

*Lauraya* and the *Joguina* clade. *Nobilinus* exhibits both states; *Nobilinus albardae insignitus* Navás (Fig. 14) has two rows of cells while *Nobilinus aurifera* (Walker) has multiple rows of cells in the basal ½ of the forewing.

24. *Hind Wing Radial Area.* (0) With two rows of cells or fewer between *Rs* and *Psm* (Fig. 17); (1) reticulated, with more than two rows of cells (often irregular) (Fig. 11). A reticulated radial area is apomorphic for *Nacaura* and the *Joguina* clade.

25. *Pseudocubital (Psc) and Pseudomedial (Psm) Veins.* (0) Relatively widely separated so that basally, *Psm* is closer to *Rs* or equidistant from *Rs* and *Psm* (Figs. 3 and 16); (1) closely associated along much of length (Figs. 5 and 8). Pseudomedial and *Psc* veins being closely associated along much of their length is a synapomorphy for Apochrysinae exclusive of *Nothancyla*. Composite veins *Psm* and *Psc* are closely associated along at least part of their length in some nonapochrysine genera such as *Tumeochrysa* Needham and *Cacarulla* Navás, but never to the extent found in apochrysine genera.

26. *Forewing Psc Vein Length.* (0) Not extending further than ¾ total wing length, rarely reaching level with pterostigma (Fig. 5); (1) extending well beyond ¾ wing length, past level of pterostigma (Fig. 8). A *Psc* veins extending beyond ¾ wing length, past the pterostigma is a synapomorphy for the *Joguina* clade.

27. *Forewing Cell $c_2$.* (0) Elongate (Fig. 5); (1) short, broad (Fig. 14). Homology statements for the forewing cell $c_2$ could not be defined with certainty for *Joguina* and *Lainius* (therefore coded as uncertain [?]) because of the dense basal reticulation of the forewing cells, making identification of posterior wing veins difficult.

28. *Forewing Cell dcc.* (0) Open (Fig. 3); (1) closed (Fig. 16). The forewing distal cubital cell (*dcc*) is formed adjacent and distal to cell $c_2$ and is open in the plesiomorphic state. The apomorphic state, where vein $Cu_1$ joins to the anterior branch of $Cu_2$ instead to joining to the posterior wing margin, is present in *Nothancyla* and *Domenechus* + (*Joguina* + *Lainius*).

29. *Forewing Vein 1A.* (0) Forked; (1) unforked. A forked vein *1A* is present in *Loyola* and the *Apochrysa* clade (except *Lauraya* and *Nacaura*).

30. *Male Ectoprocts.* (0) Separated dorsally; (1) fused dorsally. The male ectoprocts are typically joined dorsally in Apochrysinae, but are separate in *Joguina* + *Lainius*.

31. *Male Ectoproct and Tergite 9.* (0) Fused; (1) separate. This character is based on the character coding by Brooks and Barnard (1990, character 58) and will be subject to further evaluation across all species in the subfamily. In this analysis the ectoprocts are separate from tergite 9 in *Nacaura*, *Apochrysa* and *Domenechus* + *Joguina* + *Lainius*. Males are unknown for *Loyola* and *Claverina* and are coded as uncertain (?).

32. *Entoprocesses.* (0) Present; (1) absent. Entoprocesses are present in many genera of Chrysopidae, but are absent in all apochrysine genera except *Nothancyla*, which has well defined entoprocesses.

33. *Gonarcus.* (0) Arcuate; (1) transverse. The gonarcus is plesiomorphically arcuate for Chrysopidae, but is straightened transversely in *Italochrysa* and *Nacaura*.

34. *Arcessus Shape.* (0) Short, broad; (1) elongate, narrow. In Chrysopidae, the arcessus is typically relatively short, broad at the base and tapered to an apex. It is elongate in *Nothancyla* and *Italochrysa*.

35. *Gonosetae on Arcessus.* (0) Absent; (1) present. Sensory gonosetae are present on the arcessus of *Nothancyla*, *Lauraya* + *Nacaura* + *Apochrysa*, *Joguina* and *Domenechus*.

36. *Depth of Ventral Impression of Spermatheca.* (0) Shallow; (1) deep. The ventral impression of the spermatheca, which is a conical, pit-like invagination on the ventral surface of the spermatheca is barely evident in some chrysopid taxa, including *Nothancyla*. The rest of the apochrysine lacewings have a deep ventral impression often extending into the inner portion of the vela (see Brooks and Barnard 1990, figures 4 and 63).

37. *Shape of Spermathecal Duct.* (0) Relatively short and slightly coiled; (1) very long and tightly coiled. A long, highly coiled spermathecal duct is found in most Apochrysinae except *Nothancyla*, *Nobilinus* and *Synthochrysa*.

38. *Female Ectoproct and Lateral Gonopophyses.* (0) Separate; (1) partially joined. A highly variable character which may require reassessment; the lateral gonopophyses are partially joined to the ectoproct in *Italochrysa*, *Nothancyla*, *Oligochrysa*, *Anapochrysa*, *Nacaura* and *Nobilinus*.

39. *Spermatheca.* (0) Smooth; (1) with lateral striations. Lateral striations on the spermatheca is a synapomorphy for Apochrysinae, excluding *Nothancyla*. The lateral striations are also absent in *Claverina* and *Loyola*.

**Data Analysis.** Cladistic analyses were conducted using the parsimony function in PAUP*4.0b2a (Swofford 1998) with the "branch and bound" tree finding algorithm. Successive weighting (SACW) (Farris 1969) was applied in PAUP*4.0b2a using the rescaled consistency index from the initial parsimony analysis. Branch support values were calculated using Autodecay version 3.0 (Eriksson and Wikstrom 1996) and PAUP 3.1 (Swofford 1993). Branch support (BS) is defined as the extra tree length required for a branch to be lost in the strict consensus of near-most parsimonious trees. The greater the length of additional trees included in the consensus before a branch is lost, the greater the support for that branch by the data (Bremer 1988, 1994).

## Results

Cladistic analysis of the equally weighted matrix in Table 1 produced three most parsimonious trees 70 steps in length (consistency index [CI] = 0.56; retention index [RI] = 0.73). The only topological differences between the most parsimonious trees was in alternating arrangements of *Lauraya* + *Apochrysa* + *Nacaura*. Application of successive weighting to the
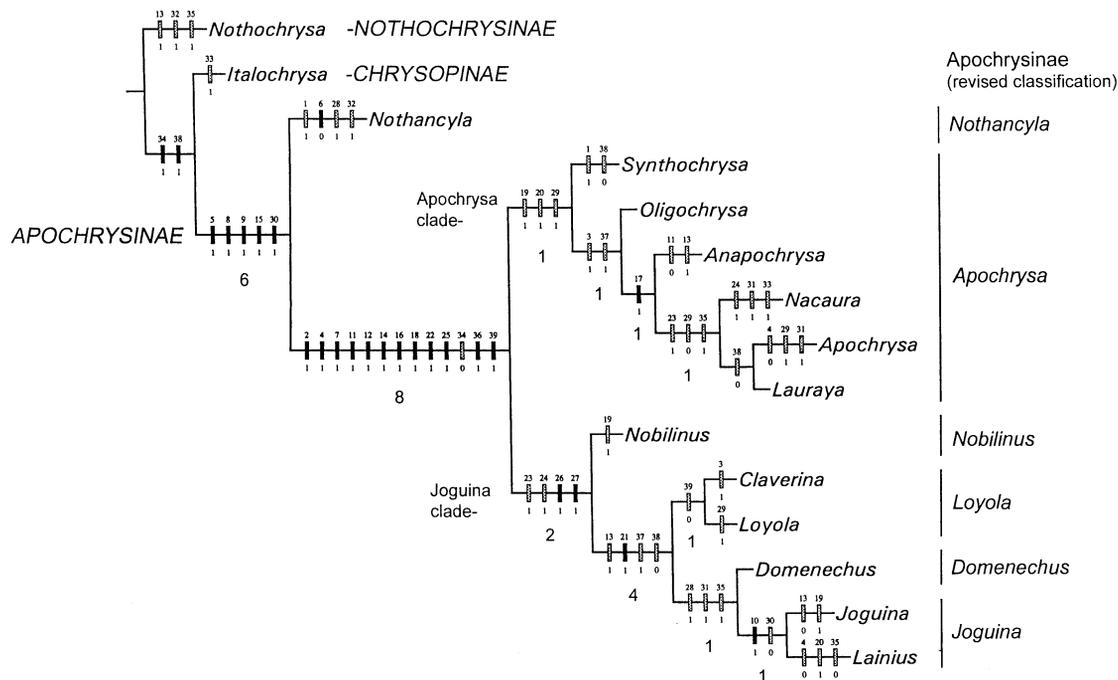
**Fig. 1.** Phylogenetic relationships of *Apochrysinae* (Chrysopidae) based on previously defined genera. Preferred tree of three most parsimonious trees (length = 70 steps) corresponding to the successively weighted tree. Character changes are marked on branches with character number above, and state number below each hash. Black hashes = forward nonhomoplasious changes; gray hashes = forward homoplasious changes. Branch support values are presented below unambiguous nodes found on consensus tree. Revised classification summarizing generic synonymies is presented along on right side of figure.

original data set resulted in a single most parsimonious tree, with the only change in tree topology being the sister grouping of *Lauraya* with *Apochrysa*+ *Nacaura*. This successively weighted tree was identical to one of the three most parsimonious trees and was therefore selected as the preferred tree. This tree is presented in Fig. 1 with branch support values beneath unambiguous nodes.

Apochrysinae are monophyletic in this analysis relative to *Nothochrysa* and *Italochrysa*, with relatively high branch support (BS = 6). *Nothancyla* is found to be the most basal member of the subfamily; sister to the more 'typical' apochrysines. Synapomorphies supporting the monophyly of Apochrysinae inclusive of *Nothancyla* include: elongate prothoracic and costal vein setae (characters 5 and 8), costal area broad basally (character 9) (Fig. 5) (also found in various Chrysopinae genera, e.g., *Ankylopteryx*) and basal subcostal crossvein absent [secondarily lost] (character 15) (Fig. 5, cf. 3).

The rest of Apochrysinae, exclusive of *Nothancyla*, is also well supported (BS = 8) with numerous synapomorphies defining the group in this analysis. The most diagnostic of these synapomorphies include: elongate setae on the femur and tibia (character 7), costal space above pterostigma broad (reversed in *Anapochrysa*) (character 11), *Sc* closely associated with *R* along length (character 14), cell *im* lost (character 16), vein *Rs* arising close to base of wing (char-

acter 18), inner gradate (*ig*) series extended basally toward base of wing (character 22), pseudocubital (*Psc*) and pseudomedial (*Psm*) veins closely associated over entire length (character 25) and ventral impression of spermatheca deep (character 36). This clade is divided basally into two groups of genera, the *Joguina* clade and the *Apochrysa* clade, each comprising six genera (Fig. 1).

The *Joguina* clade is made up mostly of broadly rounded-winged lacewings with densely reticulated wing venation (Figs. 10 and 11) (except *Nobilinus*). Synapomorphies defining this clade include forewing *Psc* vein extended >¾ of total wing length toward the wing apex (character 26), and forewing cell $c_2$ rather short and broad (character 27). *Nobilinus* is the most basal member of the *Joguina* clade, with rather open venation similar to members of the *Apochrysa* clade (Figs. 14 and 15). This genus is the largest in the subfamily, containing six species and subspecies. Kimmins (1952) divided *Nobilinus* into two species groups, the 'albardae' group (represented in this analysis) and the 'aurifera' group. The 'aurifera' group differs from the 'albardae' group by more reticulated wing venation, a derived characteristic. The rest of the *Joguina* clade forms a clade (BS = 4) that can be divided into two groups: *Claverina* + *Loyola* and *Domenechus* + (*Joguina* + *Lainius*). The spermatheca of *Claverina* and *Loyola* secondarily lack lateral striations, a feature

also lacking in *Nothancyla* and all other chrysopid subfamilies.

The *Apochrysa* clade is poorly supported with no clearly diagnostic synapomorphies useful for defining the clade taxonomically. This is reflected in the poor branch supports for all nodes and the lack of hierarchal resolution in the terminal clade (*Lauraya* + *Nacaura* + *Apochrysa*) in the strict consensus of the three most parsimonious trees. *Synthochrysa* is the most basal member of the clade, with the rest of the clade represented in a laddered relationship on the preferred tree.

## Discussion

The definition of a genus is basically a well delimited, yet arbitrary collection of similar taxa (Mayr 1982). The first function of a genus is to express similarity, and not difference, therefore (monophyletic) groups of similar taxa should be grouped together rather than split into a series of uninomials (Mayr 1943, Dubois 1988). Monotypic genera (typically based solely on autapomorphic characters) undermine the basic premise and utility of the genus concept. Most monotypic taxa contain all the characteristics to easily place them into existing genera by grouping them based on similarity, rather than placing them in new genera based on a few autapomorphic characters. Because five of the six genera (i.e., all except *Synthochrysa*) in the *Apochrysa* clade were originally described as monotypic, it would be pertinent to base future comparisons of members of this clade on inclusion with broader genus concepts, rather than exclusion using autapomorphies leading to the proliferation of monotypic genera.

Various workers on Apochrysinae (Kimmins 1952, Brooks and Barnard 1990, Brooks 1997, Winterton 1995) have commented on the unsatisfactory nature of the classification of this group based solely on venational characteristics. This is partly due to the fact that character suites useful in other groups of Chrysopidae (e.g., male and female genitalia) are unusually uniform across Apochrysinae and wing venational characters appear to be the only characters with adequate variation. These workers have indicated the need to redefine the limits of many genera and thus reduce the number of genera in this subfamily by realigning generic definitions in a phylogenetic context. To date, this requirement has not been realized, and the number of monotypic genera has actually increased (Kimmins 1952, Winterton 1995).

A phylogenetic framework for the subfamily Apochrysinae is proposed in light of the analysis presented here (Figs. 1 and 2). The subfamilial placement of *Nothancyla* could not be tested fully in this study and requires phylogenetic analysis of the greater Chrysopidae using a broader selection of exemplars from all subfamilies to fully assess its position in the family. Including *Nothancyla* as a tentative member of Apochrysinae, our analysis found it to be clearly placed as the most basal member of the subfamily. The inclusion of this monotypic genus in Apochrysinae has been
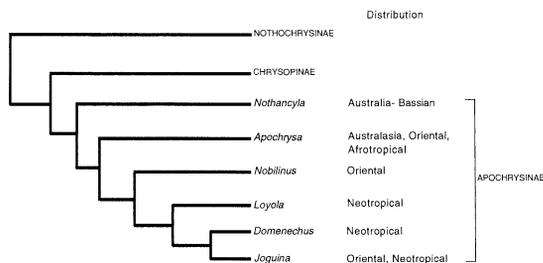


Fig. 2. Summary phylogenetic tree of redefined genus concepts showing biogeographical distributions.

debated without firm resolution (New 1980, Brooks and Barnard 1990, Winterton 1995, Brooks 1997), although Brooks (1997) suggested that it could be placed in a separate monotypic subfamily. *Nothancyla* exhibits a combination of characters from both Apochrysinae and Chrysopinae. Characters supporting inclusion in Chrysopinae (or exclusion from Apochrysinae) include intramedial (*im*) cell present (character 16) (Fig. 16), *Psm* relatively widely separated from *Psc* (character 25), vein *Rs* originating distal to wing base (character 18), tignum present (New 1980, Winterton 1995), entoprocesses present, arcessus narrow and spermathecal ventral impression shallow (Brooks and Barnard 1990). Conversely, characters supporting inclusion in Apochrysinae include loss of the basal *sc-r* crossvein (character 15), and flagellomeres with five rows of setae (the latter character is also found in Nothochrysinae [Brooks and Barnard 1990]).

Division of Apochrysinae (exclusive of *Nothancyla*) into two groups was previously suggested by Brooks and Barnard (1990), who proposed that the Afrotropical and Australasian genera with more open wing venation (=*Apochrysa* clade) were the more primitive members, whereas the Oriental and Neotropical genera with highly reticulated venation (= *Joguina* clade) were more derived members of the group. The results of this study support the basal division of the subfamily (excluding *Nothancyla*) into two groups, and show that increasingly reticulated wing venation is the derived condition in both groups (e.g., *Joguina*, *Lainius*, *Domenechus* and *Nacaura*). The most basal taxa in both clades, *Nobilinus* and *Synthochrysa*, respectively, each have distinctly open venation in many or all of their constituent species. In the *Apochrysa* clade, an increase in reticulation has occurred in the discal area in *Lauraya*, *Apochrysa* (Fig. 5) and *Nacaura*. In the *Joguina* clade the increase in reticulation is more pronounced and typically involves increased reticulation in the discal area, including extra secondary crossveins between the veins *R* and *Rs* (all genera except *Nobilinus*), and numerous secondary crossveins in the costal and postpseudocubital areas (*Joguina* and *Lainius*) (Fig. 10).

Two synonyms are proposed in the *Joguina* clade, based on sister-groupings of very similar taxa (Fig. 1). *Claverina* is the sister of *Loyola*, and based on the very similar wing venation of both genera we conclude that *Claverina* is likely a synonym of *Loyola*. The males of

both genera are unknown (Brooks and Barnard 1990). *Lainius* is considered a synonym of *Joguina*, with both genera characterized by highly reticulated venation and secondary crossveins in the costal area. *Lainius* is known only from females, whereas both sexes are known for *Joguina*.

The *Apochrysa* clade is based mostly on homoplasious characters and is reflected in the analysis by little terminal resolution and low branch supports (BSs = 1). On the most parsimonious trees only one step longer (length = 71) than the most parsimonious tree, the *Apochrysa* clade displays no internal resolution at all. Unlike the *Joguina* clade, the venation of the *Apochrysa* clade is open and relatively conserved, with only minor differences between most genera. The close similarity and absence of diagnosable synapomorphies is the most likely reason for the lack of resolution and branch support throughout this clade. Based on the high degree of similarity between all members of the *Apochrysa* clade, we see no support for maintaining the generic limits within this group and synonymize *Synthochrysa, Oligochrysa, Lauraya, Anapochrysa,* and *Nacaura* with *Apochrysa* (see taxonomic treatment). Brooks and Barnard (1990) showed that only *Apochrysa leptalea* (Rambur) differed from the apochrysine genitalic ground-plan with a distinctively shaped gonarcus complex. This is proven to be autapomorphic for *A. leptalea* because *Apochrysa wagneri* Hölzel has a gonarcus complex that is similarly shaped to other members of the subfamily (Hölzel 1996).

A revised genus classification generic is presented on the right side of Fig. 1, and is summarized in Fig. 2 with biogeographical distributions mapped onto the revised tree. As stated above, the monotypic genus *Nothancyla* from southern Australia is the sister taxon to the rest of the apochrysine lacewings. There is a clear progression from more basal 'Old-World' genera (*Nothancyla, Apochrysa,* and *Nobilinus*) with relatively open wing venation, to more derived 'New-World' genera (*Loyola, Joguina,* and *Domenechus*) with densely reticulate wing venation. *Joguina* transcends this trend by having members represented in both regions.

## Key to Genera of Apochrysinae

1. Forewing with intramedial cell (*im*) present
     . . . . . . . . . . . . . . . . . . *Nothancyla*
     Forewing lacking intramedial cell (*im*)   . . . . 2
2.(1) Two or more rows of cells between *R* and *Rs* in basal half of forewing . . . . . . . . . . 3
     One row of cells between *R* and *Rs* in basal half of forewing . . . . . . . . . . . . . . . 5
3.(2) Forewing costal and posterior marginal areas densely reticulated . . . . . . . . . *Joguina*
     Forewing costal and posterior marginal areas with single row of cells . . . . . . . . . . . 4
4.(3) Cells in posterior marginal area irregularly subdivided with cross veins; forewing veins *1A* and *2A* forked; spermatheca with lateral striations . . . . . . . . . . . . . . *Domenechus*
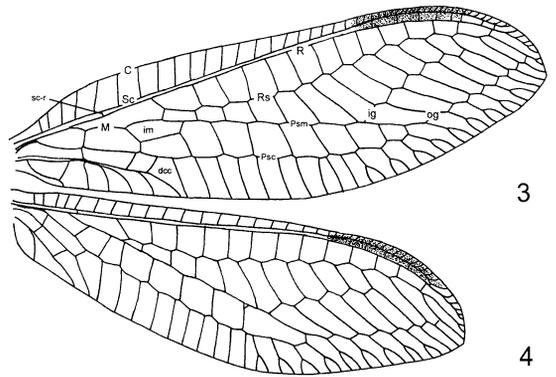


Figs. 3–4. *Italochrysa facialis* (Banks) (Chrysopinae): 3, forewing; 4, hind wing. Forewing length = 16 mm. Abbreviations: *sc-r* = basal sc-r crossvein; *dcc* = discal cubital cell; *C* = costa; *Sc* = subcostal; *R* = radius; *Rs* = radial sector; *M* = medius; *Psm* = pseudomedial vein; *Psc* = pseudocubital vein; *im* = intramedial cell; *ig* = inner gradate series; *og* = outer gradate series.

     Cells in posterior marginal area simple; forewing vein *1A* sometimes forked, *2A* simple; spermatheca without lateral striations . . . . . . . . . . . . . . . . . . . *Loyola*
5.(2) Pseudocubital vein (*Psc*) extending to ¾ total wing length; forewing veins *1A* and *2A* forked . . . . . . . . . . . . . . . . *Nobilinus*
     Pseudocubital vein (*Psc*) not extending >⅔ of total wing length; forewing vein *1A* usually forked, *2A* simple . . . . . . *Apochrysa*

## Genus *Apochrysa* Schneider
(Figs. 5–7)

*Apochrysa* Schneider, 1851: 157. Type species: *Hemerobius leptaleus* Rambur.
*Synthochrysa* Needham, 1909: 202. Type species: *Hemerobius stigma* Girard. syn. nov.
*Nacaura* Navás, 1913c: 280. Type species: *Apochrysa matsumurae* Okamoto. syn. nov.
*Oligochrysa* Esben-Petersen, 1914: 639. Type species: *Oligochrysa gracilis* Esben-Petersen. syn. nov.
*Anapochrysa* Kimmins, 1952: 932. Type species: *Anapochrysa africana* Kimmins. syn. nov.
*Lauraya* Winterton, 1995: 139. Type species: *Lauraya retivenosa* Winterton. syn. nov.

**Diagnosis.** Costal cells simple; forewing *Psc* extending no >⅔ of total wing length toward apex; forewing without crossveins between *R* and *Rs* distally.

**Description.** Antennal pedicel constricted; forewing costal cells simple; single row of cells between *R* and *Rs*; *Rs* relatively straight; *Sc* closely associated with *R* along length; cell *im* absent; *Rs* arises close to base of wing; forewing without crossveins between *R* and *Rs* distally (i.e., behind pterostigma) (Figs. 5 and 6); inner gradate (*ig*) series extended basally toward base of wing; forewing *Psc* extending no >⅔ of total wing length toward apex; forewing cell $c_2$ elongate; elongate setae on the femur and tibia, costal space above
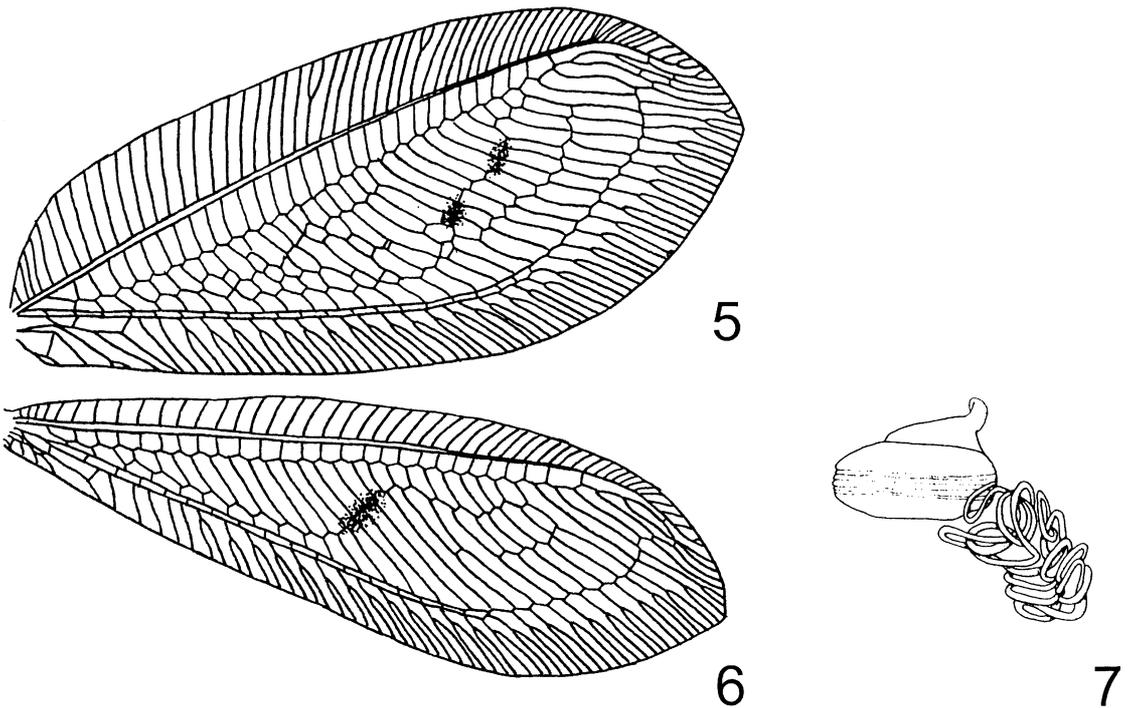
**Figs. 5–7.** *Apochrysa leptalea* (Rambur): 5, forewing; 6, hind wing (from Kimmins 1952); 7, spermatheca (from Brooks and Barnard 1990). Forewing length = 21 mm.

pterostigma broad or slightly narrowed apically; *Psc* and *Psm* veins closely associated over entire length; *1A* usually forked; *2A* simple; ventral impression of spermatheca deep, spermathecal duct short or long; spermatheca with lateral striations; gonarcus arcuate, narrow; arcessus usually triangular.

**Distribution.** Southern and eastern Africa, Madagascar, Japan, Taiwan, eastern Australia, Norfolk Island, Indonesia, western Pacific.

**Comments.** Banks (1931) suggested that *Oligochrysa* be synonymized with *Synthochrysa,* and *Synthochrysa evanida* Gerstaecker was previously placed in *Apochrysa.* In describing *Anapochrysa,* Kimmins (1952) mentions the close similarity of his new genus to *Apochrysa* and *Oligochrysa,* and Winterton (1995) suggested a close relationship of *Lauraya* to *Oligochrysa* and *Anapochrysa.* Based on the absence of clear apomorphic character suites defining most of the genera and the obvious similarities of all taxa to each other, *Anapochrysa* Kimmins, *Lauraya* Winterton, *Nacaura* Navás, *Oligochrysa* Esben-Petersen, and *Synthochrysa* Needham are synonymized with *Apochrysa* Schneider.

There is considerable variation in wing venation in the revised concept of *Apochrysa,* but several characteristics unite the members of this genus. The most significant character is the *Psc* not extending beyond ⅔ of the total wing length toward the apex. The wings are generally narrower and venation is relatively open compared with other apochrysine genera, although

the basal discal area may be reticulated. There are usually no cross veins between *R* and *Rs* behind the pterostigma.

**Included Species.** *A. cognata* (Kimmins 1953) comb. nov., *A. evanida* (Gerstaecker, 1894) comb. nov., *A. leptalea* (Rambur, 1842), *A. lutea* (Walker, 1853) comb. nov., *A. matsumurae* Okamoto, 1912 comb. nov., *A. montrouzieri* (Girard, 1862) comb. nov., *A. retivenosa* (Winterton 1995) comb. nov., *A. salomonis* (Kimmins 1951) comb. nov., *A. voeltzkowi* (Weele 1909) comb. nov., *A. wagneri* Hölzel, 1996.

### Genus *Domenechus* Navás
(Figs. 8 and 9)

*Domenechus* Navás, 1913a: 298. Type species: *Domenechus sigillatus* Navás.

**Diagnosis.** Costal cells simple; forewing with two rows of cells between *R* and *R;* forewing with crossveins between *R* and *Rs* distally; *Psc* extending >¾ of total wing length toward apex.

**Description.** Antennal pedicel constricted; forewing costal cells simple; costal space above pterostigma broad; *Sc* closely associated with *R* along length, fused apically; two rows of cells between *R* and *Rs; Rs* slightly sigmoid; forewing with crossveins between *R* and *Rs* distally (i.e., behind pterostigma); *Rs* arises close to base of wing; *C* and *Sc* in hind wing equidistant along length; two conspicuous pustules in
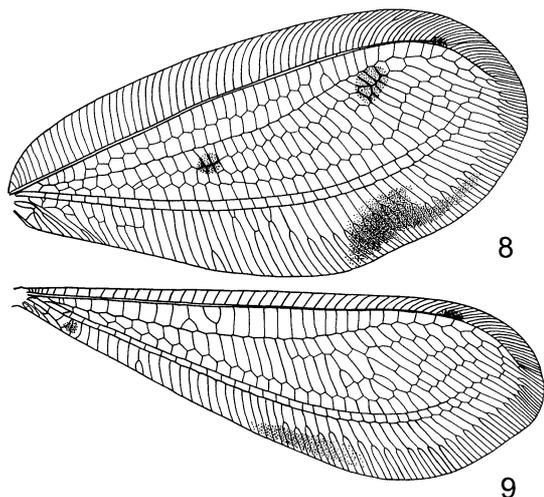
Figs. 8–9. *Domenechus mirificus* (Gerstaecker): 8, forewing; 9, hind wing (from Kimmins 1952). Forewing length = 28–29 mm.
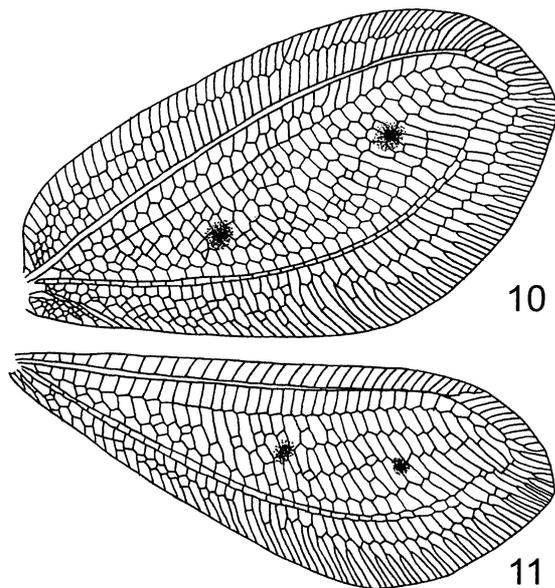


Figs. 10–11. *Joguina nicobarica* (Brauer): 10, forewing; 11, hind wing. Forewing length = 26–27 mm (from Kimmins 1952).

forewing discal area; several semiregular gradate series; inner gradate series extended basally toward base of wing; cell *im* absent; *Psc* and *Psm* veins closely associated along entire length; *Psc* extending >¾ of total wing length toward apex; forewing cell $c_2$ short and broad; *1A* and *2A* forked; posterior marginal area of wing partially divided; elongate setae on the femur and tibia; spermatheca with lateral striations, ventral impression deep; spermathecal duct long, tightly coiled; gonarcus arcuate, narrow; arcessus triangular.

**Distribution.** South America.

**Comments.** *Domenechus* is intermediate between *Joguina* and *Loyola*. The wing venation of this genus is very similar to *Loyola*, but the lateral striations on the spermatheca in *Joguina* and *Domenechus* (apomorphic for the subfamily) are secondarily lost in *Loyola*.

**Included Species.** *D. marianellus* (Guérin-Méneville, 1853), *D. mirificus* (Gerstaecker, 1888).

### Genus *Joguina* Navás
### (Figs. 10 and 11)

*Joguina* Navás, 1912: 98. Type species: *Apochrysa nicobarica* Brauer.

*Lainius* Navás, 1913a: 300. Type species: *Lainius constellatus* Navás. syn. nov.

**Diagnosis.** Forewing costal cells reticulate basally; forewing with multiple rows of cells between *R* and *Rs*; *Psc* extending >¾ of total wing length toward apex.

**Description.** Antennal pedicel constricted; forewing costal cells reticulate basally, gradually forming two rows of cells distally (Fig. 10); costal space above pterostigma broad; *Sc* closely associated with *R* along length, separate apically; two rows of cells or reticulate between *R* and *Rs*; *Rs* straight or slightly sigmoid; forewing usually with crossveins between *R* and *Rs* distally; *Rs* arises close to base of wing; *C* and *Sc* in hind

wing equidistant along length; 2–8 conspicuous pustules in discal area; numerous irregular gradate series; inner gradate series extended basally toward base of wing; cell *im* absent; *Psc* and *Psm* veins closely associated along entire length; *Psc* extending >¾ of total wing length toward apex; forewing cell $c_2$ short and broad, poorly defined due to numerous cross veins; *1A* and *2A* forked; posterior marginal area of wing reticulate basally, gradually forming two rows of cells distally (excluding end-twigging in apical ½); elongate setae on the femur and tibia; spermatheca with lateral striations, ventral impression deep; spermathecal duct long, tightly coiled; gonarcus arcuate, narrow; arcessus triangular.

**Distribution.** Central and South America, India (Assam), Myanmar, Malaysia, Borneo.

**Comments.** *Joguina*, with three species from the Orient, and two species from South America, is the most derived genus in the subfamily Apochrysinae. The highly reticulated venation, particularly in the costal and posterior marginal areas, is distinctive for the genus. The two Neotropical species of *Joguina*, described originally in *Lainius*, have slightly more reticulate venation than the Oriental species, with smaller wings. *Lainius* is synonymized here with *Joguina* based on the results of the analysis, evidenced by the distinct similarity in venational characters such multiple rows of cells on costal and posterior marginal areas of the forewing.

**Included Species.** *J. constellata* (Navás, 1913a) comb. nov., *J. borneensis* Kimmins, 1952, *J. decorata* (Navás, 1930) comb. nov., *J. malayana* Banks, 1931, *J. nicobarica* (Brauer, 1864).
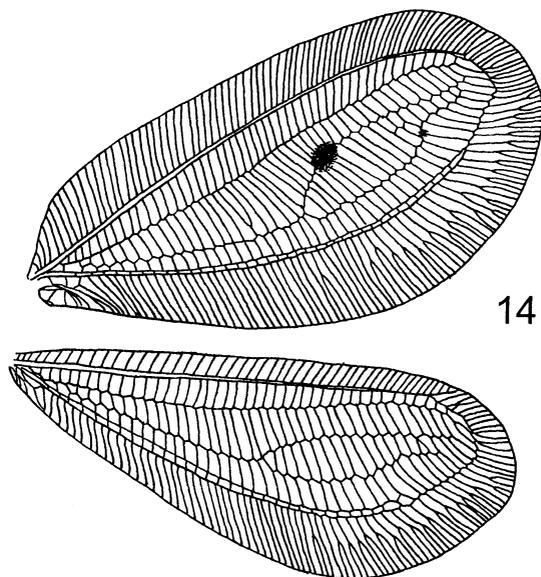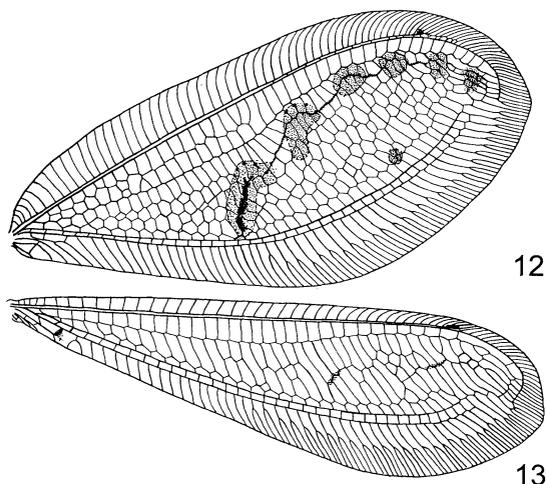
**Figs. 12–13.** *Loyola croseus* (Gerstaecker): 12, forewing; 13, hind wing. Forewing length = 33–34 mm (from Kimmins 1952).



**Figs. 14–15.** *Nobilinus albardae insignitus* Navás: 14, forewing, 15, hind wing. Forewing length = 25 mm.

### Genus *Loyola* Navás
### (Figs. 12 and 13)

*Loyola* Navás, 1913a: 297. Type species: *Apochrysa croesus* Gerstaecker.
*Claverina* Navás, 1913b: 164. Type species: *Apochrysa beata* Walker. syn. nov.

**Diagnosis.** Costal cells simple; forewing with two rows of cells between *R* and *Rs* basally; posterior marginal cross-veins simple in basal half of both wings.

**Description.** Antennal pedicel constricted; forewing costal cells simple; costal space above pterostigma broad; *Sc* closely associated with *R* along length, separate apically; two rows of cells between *R* and *Rs* basally, single row distally; *Rs* sigmoid; forewing with cross veins between *R* and *Rs* behind pterostigma; *Rs* arises close to base of wing; *C* and *Sc* in hind wing equidistant along length; 2–6 conspicuous pustules in forewing discal area; numerous irregular gradate series; inner gradate series extended basally toward base of wing; cell *im* absent; *Psc* and *Psm* veins closely associated along entire length; *Psc* extending >¾ of total wing length toward apex; forewing cell $c_2$ long and broad; *1A* forked or unforked; *2A* unforked; discal area of hind wing reticulate; posterior marginal cross-veins simple in basal half of both wings; elongate setae on the femur and tibia; spermatheca smooth, without lateral striations, ventral impression deep; spermathecal duct long, tightly coiled.

**Distribution.** South and Central America.

**Comments.** Kimmins (1952) noted that Banks compared *C. tripunctata* with *L. beata* (Walker), wondering whether this was a typographical error, or that Banks actually considered *Claverina* to be a synonym of *Loyola.* Based on the similarity of the two genera and results of this study, the latter is probably true. The male is unknown for this genus.

**Included Species.** *L. beata* (Walker, 1858) comb. nov., *L. croesus* (Gerstaecker, 1894), *L. tripunctata* Banks, 1924.

### Genus *Nobilinus* Navás
### (Figs. 14 and 15)

*Nobilinus* Navás, 1913a: 295. Type species: *Nobilinus insignitus* Navás.

**Diagnosis.** Costal cells simple; single row of cells between *R* and *Rs; Psc* extending >¾ of total wing length toward apex; posterior marginal cross-veins simple in basal half of both wings.

**Description.** Antennal pedicel constricted; forewing costal cells simple; costal space above pterostigma broad; *Sc* closely associated with *R* along length, separate apically; single row of cells between *R* and *Rs; Rs* sigmoid (almost straight in *N. a. insignitus);* forewing with cross veins between *R* and *Rs* behind pterostigma; *Rs* arises close to base of wing; *C* and *Sc* in hind wing equidistant along length; 1–2 conspicuous pustules in forewing discal area; typically three regular gradate series to irregular; inner gradate series extended basally toward base of wing; cell *im* absent; *Psc* and *Psm* veins closely associated along entire length; *Psc* extending >¾ of total wing length toward apex; forewing cell $c_2$ short and broad; *1A* and *2A* forked; posterior marginal area of wing simple; discal area of hind wing reticulate; posterior marginal cross-veins simple in basal half of both wings; elongate setae on the femur and tibia; spermatheca with lateral striations, ventral impression deep; spermathecal duct long, tightly coiled; gonarcus arcuate, narrow; arcessus triangular.
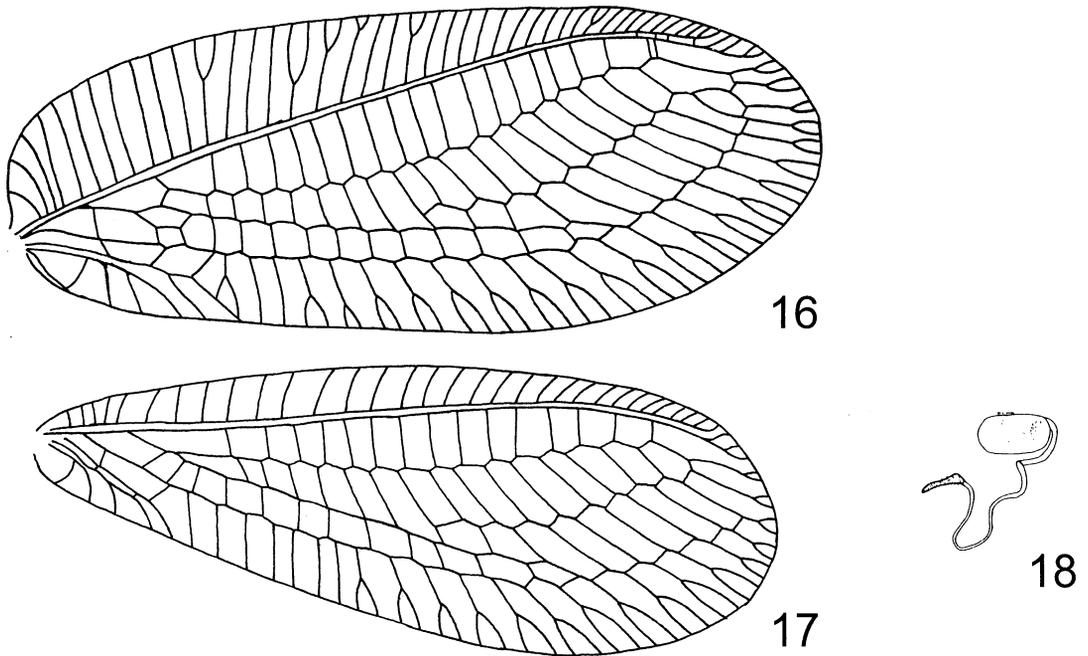
**Figs. 16–17.** *Nothancyla verreauxi* Navás: 16, forewing; 17, hind wing; 18, spermatheca (from Brooks and Barnard 1990). Forewing length = 18 mm.

**Distribution.** Oriental.

**Comments.** The record of *Nobilinus* from northern Australia was shown to be erroneous, and based on a misidentification of *Apochrysa retivenosa* (Winterton) comb. nov. (see discussion in Winterton 1995). Two undescribed species are represented in the Natural History Museum (London) collection (Brooks and Barnard 1990).

**Included Species.** *N. albardae albardae* (McLachlan, 1875), *N. albardae insignitus* Navás, 1913, *N. albardae phantomus* (Gerstaecker, 1894), *N. auriferus* (Walker, 1853), *N. bellulus* (Banks 1914), *N. coccineus* (Brauer, 1864).

### Genus *Nothancyla* Navás
### (Figs. 16–18)

*Nothancyla* Navás, 1910: 51. Type species: *Nothancyla verreauxi* Navás.

**Diagnosis.** Intramedial cell present; *Rs* originating distal to wing base; inner gradate series not extended basally toward base of wing; *Psc* extending no >⅔ of total wing length toward apex; entoprocesses present.

**Description.** Antennal pedicel not constricted; forewing costal cells simple, some veinlets irregularly forked; costal space basally very broad, narrowed distally; single row of cells between *R* and *Rs*; *Rs* sigmoid; forewing with several cross veins between *R* and *Rs* behind pterostigma; vein *Rs* originating distal to wing base; costal area narrowed distally in hind wing; two gradate series; inner gradate series not extended basally toward base of wing; intramedial (*im*) cell quadrangular; *Psm* relatively widely separated

from *Psc*; *Psc* extending no >2/3 of total wing length toward apex; forewing cell $c_2$ short and broad; posterior marginal area of forewing forked close to base of wing; short setae on the femur and tibia; ectoprocts greatly elongate posteriorly; tignum usually present, entoprocesses present, arcessus narrow; spermatheca smooth, without lateral striations, ventral impression shallow; spermathecal duct short (Fig. 18).

**Distribution.** Southern Australia (Bassian distribution).

**Comments.** The presence of both chrysopine and apochrysine characters makes *Nothancyla* easily diagnosed from the rest of the apochrysine genera. As such, this combination of characters from both subfamilies, clearly suggests that *Nothancyla* is an intermediate between the two. Brooks and Barnard (1990) presented a tentative phylogeny of the Chrysopidae, and found Chrysopinae as a paraphyletic, and consequently artificial grouping. Until a revised phylogeny of Chrysopidae using quantitative cladistic data can be determined, the placement of *Nothancyla* will be problematic. Brooks (1997) suggested that *Nothancyla* could be placed in a separate, monotypic tribe, but we prefer to retain it in Apochrysinae, although uneasily, rather than erecting another uninomial.

**Included Species.** *Nothancyla verreauxi* Navás, 1910.

### Acknowledgments

## References Cited

Adams, P. A. 1967. A review of the Mesochrysinae and Nothochrysinae (Neuroptera: Chrysopidae). Bull. Mus. Comp. Zool. 135: 215–238.

Banks, N. 1914. New neuropteroid insects, native and exotic. Proc. Acad. Nat. Sci. Phila. 66: 608–632 (issued 1915).

Banks, N. 1924. Descriptions of new neuropteroid insects. Bull. Mus. Comp. Zool. 65: 419–455.

Banks, N. 1931. XVIII—Some neuropteroid insects from the Malay peninsula. J. Fed. Malay. States Mus. 16: 377–409.

Brauer, F. 1864. Entomologische Beitrage. Verh. Kaiserlich-Koniglichen Zool.-Bot. Ges. Wien 14: 891–902.

Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. Evolution 42: 795–803.

Bremer, K. 1994. Branch support and tree stability. Cladistics 6: 369–372.

Brooks, S. J. 1997. An overview of the current status of Chrysopidae (Neuroptera) systematics. Dtsch. Entomol. Zeit. 44(2): 267–275.

Brooks, S. J., and Barnard, P. C. 1990. The green lacewings of the world: a generic review (Neuroptera: Chrysopidae). Bull. Br. Mus. (Nat. Hist.) 59(2): 117–286.

Dubois, A. 1988. The genus in Zoology: a contribution to the theory of evolutionary systematics. Mem. Mus. Nat. Hist. Nat. Ser. A Zool. 140: 1–123.

Eriksson, T., and Wikstrom, N. 1996. Autodecay, version 3.0. Stockholms Universitet, Stockholm, Sweden.

Esben-Petersen, P. 1914. Australian Neuroptera. Part I. Proc. Linn. Soc. NSW 39: 635–645.

Farris, J. S. 1969. A successive approximations approach to character weighting. Syst. Zool. 18: 374–385.

Gerstaecker, A. 1887. Weitere Beiträge zur artenkenntniss der Neuroptera Megaloptera. Mitt. Naturwissenschft. Ver. Neu-Vorpommern Rugen Greifswald 19: 89–130 (issued 1888?).

Gerstaecker, A. 1893. Ueber neue und weniger gekannte Neuropteren aus der familie Megaloptera Burm. Mitt. Naturwissenschft. Ver. Neu-Vorpommern Rugen Greifswald 25: 93–173 (issued 1894).

Girard, M.J.A. 1862. Indication et discussion d'un nouveau caractère générique du genre Hemerobius, tribu des Myrméléoniens, ordre des Névroptères et description de deux espèces nouvelles de ce genre recucillies par le R. P. Montrouzier et désignées par Lui sons les noms de Chloromelas et stigma. Ann. Soc. Entomol. Fr. 2: 597–614.

Guérin-Méneville, F. É. 1853. Description d'une nouvelle espèce de Névroptères. Rev. Mag. Zool. Pure Appl. 5: 261–263.

Handlirsch, A. 1906–1908. Die fossilen Insekten und die Phylogenie der rezenten Formen. W. Engelmann, Leipzig, Germany.

Hölzel, H. 1996. Neue Chrysopidae-Spezies aus Afrika 1. Apochrysa wagneri n. sp. (Neuroptera: Chrysopidae). Entomol. Zeit. 106(3): 117–120.

Kimmins, D. E. 1951. New species of Neuroptera from the Solomon Islands. Ann. Mag. Nat. Hist. 4: 780–785.

Kimmins, D. E. 1952. A revision of the Apochrysinae (Fam. Chrysopidae). Ann. Mag. Nat. Hist. 12(5): 929–944.

Kimmins, D. E. 1953. Miss L. E. Cheesman's expedition to New Caledonia, 1949—Orders Odonata, Ephemeroptera, Neuroptera and Trichoptera. Ann. Mag. Nat. Hist. 12(6): 241–257.

Mayr, E. 1943. Criteria of subspecies, species and genera in ornithology. Ann. N.Y. Acad. Sci. 44: 133–139.

Mayr, E. 1982. The growth of biological thought. Diversity, evolution, and inheritance. Belknap Press of Harvard University Press, Cambridge, MA.

McLachlan, R. 1875. Neuroptera s. str, Planipennia, pp. 1–24. In Reise in Turkestan von Alexis Fedtschenko: auf veranlassung des General-Gouverneurs von Turkestan, General von Kaufmann, hrsg. von der Gesellschaft der Freunde der Naturwissenschaften, Moskau.

Navás, L. 1910. Crisópidos nuevos. Broteria 9: 38–59.

Navás, L. 1912. Crisópidos y hemerobidos (Ins. Neur.) nuevos ó críticos. Broteria 10: 98–113.

Navás, L. 1913a. Les Chrysopides (Ins. Névr.) du Musée de Londres. Ann. Soc. Sci. Bruxelles 37: 292–330 (prior to June 1913).

Navás, L. 1913b. Crisópidos Sudamericanos. Broteria (Zool.) 11: 73–104, 149–168 (October 1913).

Navás, L. 1913c. Neuroptera Asiatica. I Ser. Rev. Russe Entomol. 13: 271–284.

Needham, J. G. 1909. Notes on the Neuroptera in the collection of the Indian Museum. Rec. Indian Mus. Calcutta 3: 185–210.

New, T. R. 1980. A revision of the Australian Chrysopidae (Insecta: Neuroptera). Aust. J. Zool. 77(suppl.): 1–143.

Rambur, M. P. 1842. Histoire Naturelle des Insectes, Névroptères. Librairie encyclopédique de Roret. Fain et Thunot, Paris.

Schneider, G. 1851. Symbolae ad monographiam generis Chrysopae, Leach. Hirt, Vratislaviae.

Swofford, D. L. 1993. PAUP: phylogenetic analysis using parsimony, version 3.1. Illinois Natural History Survey, Champaign, IL.

Swofford, D. L. 1998. PAUP*: phylogenetic analysis using parsimony (*and other methods), version 4.0. Sinauer, Sunderland, MA.

Tillyard, R. J. 1926. The insects of Australia and New Zealand. Angus and Robertson, Sydney.

Walker, F. 1858. Characters of undescribed Neuroptera in the collection of W. W. Saunders. Trans. Entomol. Soc. Lond. 5: 176–199 (issued 1860).

Weele, H. W. Van der. 1909. Mecoptera and Planipennia of Insulinde. Notes Leyden Mus. 31: 1–100.

Winterton, S. L. 1995. A new genus and species of Apochrysinae (Neuroptera: Chrysopidae) from Australia, with a checklist of Australian species. J. Aust. Entomol. Soc. 34: 139–145.

Withycombe, C. L. 1925. Some aspects of the biology and morphology of the Neuroptera. With special reference to the immature stages and their possible phylogenetic significance. Trans. Entomol. Soc. Lond. 1924: 303–411.

## Appendix 1.

Exemplars examined during this study: number of specimens examined given in parentheses following collection location. Collection acronyms: Natural History Museum, London (NHM); United States National Museum, Smithsonian Institution (USNM); University of Queensland Insect Collection (UQIC); Queensland Museum (QM); Australian National Insect Collection, Commonwealth Scientific and Industrial Research Organization Entomology (ANIC).

### Nothochrysinae

*Nothochrysa fulviceps* (Stephens): Germany (2) (USNM).

### Chrysopinae

*Italochrysa fascialis* (Banks): Australia: Queensland (7), New South Wales (2) (UQIC, QM).

### Apochrysinae

*Anapochrysa africana* Kimmins: Africa: São Thomé (3); Kenya, Nairobi (1); Tanzania (1); Pondoland (1) (Holotype and five Paratypes) (synonym of *A. voeltzkowi* (Weele)) (NHM).
*Apochrysa leptalea* Rambur: South Africa (3) (NHM).
*Claverina beata* (Walker): South America: 'Amazonia' (Holotype) (NHM).
*Domenechus mirifica* (Gerstaecker): Costa Rica (1); Panama (2) (Holotype) (USNM, NHM).
*Domenechus marianella* (Guérin-Méneville): South America: 'Amazonia' (2); Guyana (1); Brazil (Holotype) (NHM).

*Joguina nicobarica* (Brauer): India: Assam (3); Nicobars (3) (NHM).
*Joguina malayana* Banks: Malaysia (1) (NHM).
*Joguina borneensis* Kimmins: Indonesia: Borneo (Holotype) (NHM).
*Lainius constellatus* Navás: Guatemala (Lectotype and two paralectotypes) (NHM).
*Lauraya retivenosa* Winterton: Australia: Queensland (Holotype and two paratypes) (QM).
*Loyola croesus* (Gerstaecker): Mexico (1); Brazil (1); Costa Rica (2); Venezuela (1); Panama (1); Nicaragua (1); (NHM, USNM).
*Nacaura matsumurae* (Okamoto): Japan: Osaka Prefecture (6) (NHM).
*Nobilinus albardae albardae* (McLachlan): Indonesia: Sulawesi (1) (NHM).
*Nobilinus albardae phantoma* (Gerstaecker): Papua New Guinea (6) (NHM).
*Nobilinus albardae insignitus* Navás: Malaysia (2) (Holotype) (NHM).
*Nobilinus aurifera* (Walker): Sri Lanka (4) (Lectotype and paralectotype) (NHM).
*Nothancyla verreauxi* Navás: Australia: Western Australia (1), Australian Capital Territory (2), Tasmania (2), New South Wales (3) (NHM, ANIC).
*Oligochrysa lutea* (Walker): Australia: Norfolk Island (5); New South Wales (3); Queensland (5) (Holotype) (NHM, UQIC, QM).
*Synthochrysa montrouzieri* (Girard): Lifu (3) (NHM).
*Synthochrysa cognata* Kimmins: New Hebrides (3) (Holotype and two paratypes) (NHM).
*Synthochrysa salomonis* (Kimmins): Guadalcanal (1); Solomon Islands (Holotype and three paratypes) (NHM).

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