



OXFORD  
BIOLOGY



*the* **TIMETREE** *of* **LIFE**

*edited by* **S. BLAIR HEDGES** *and* **SUDHIR KUMAR**  
*foreword by* James D. Watson

# Lacewings (Neuroptera)

Shaun L. Winterton<sup>a,\*</sup> and Brian M. Wiegmann<sup>b</sup>

<sup>a</sup>Entomology, Queensland Department of Primary Industries & Fisheries, 80 Meiers Road, Indooroopilly, Queensland, Australia 4068; <sup>b</sup>Department of Entomology, North Carolina State University, Raleigh, NC 27695, USA

\*To whom correspondence should be addressed (wintertonshaun@gmail.com)

## Abstract

Lacewings (~5700 species) are divided into 17 families distributed on all continents. This group of insects is well defined by complex larval characteristics such as modified sucking jaws, incomplete gut, and modified Malpighian tubules used for spinning a silken cocoon in which the immature pupates. Recent molecular evidence supports a Permian (299–251 million years ago, Ma) origin of the order with Coniopterygidae as the closest relative of all other neuropterans. The only well-defined group of families is Myrmeleontiformia. This group of five families diverged from the rest of the order ~184 Ma and has become the most species-rich lineage of Neuroptera.

The lacewings comprise a moderately sized group of insects whose adults are characterized by delicate wings, often large in size, with highly reticulate or lacelike venation (Fig. 1). The order is presently divided into 17, mostly well defined, families with ~5700 species worldwide. Lacewings, together with Megaloptera and Raphidioptera, constitute the Superorder Neuropterida, which is assumed to be the closest relative of Coleoptera. Three unique larval characters distinguish Neuroptera from other insects: modified jaws for sucking, incomplete gut, and modified Malpighian tubules for spinning a silken cocoon in which the immature pupates (1). Here, we review the relationships and divergence times of the families of lacewings (Fig. 2).

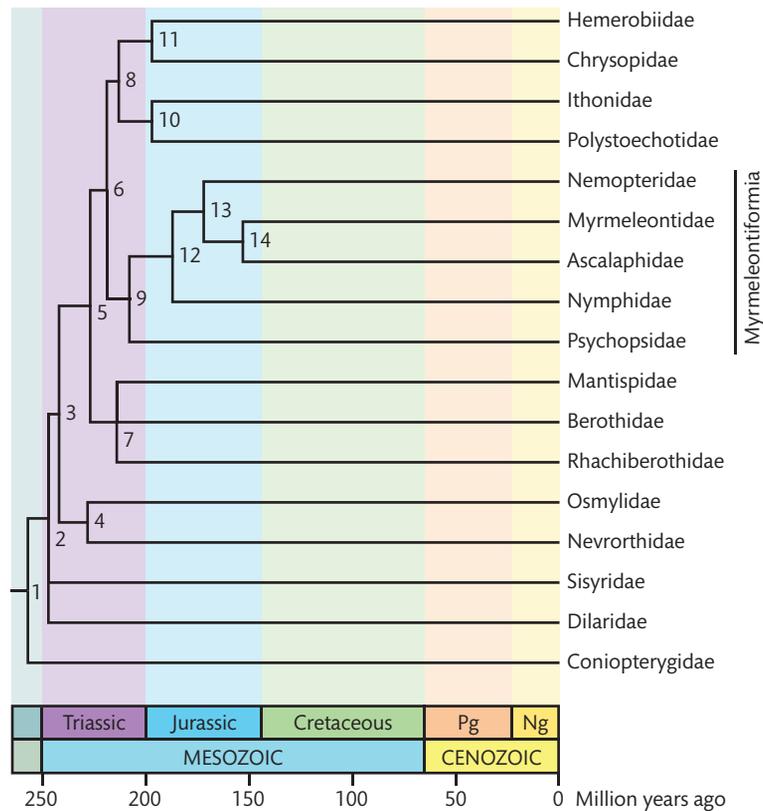
Elucidating the evolutionary history of lacewings has proven to be highly problematic. Neuroptera classification has traditionally been founded largely on the intuitive phylogenies by Handlirsch (2) for fossils and by Withycombe (3) for larval anatomy and morphology. From these works a number of higher-level groups have

been identified, but they usually differ greatly between subsequent authors with regard to membership of families in each (1). Recent quantitative analyses of morphological characters and phylogeny by Aspöck *et al.* (4) led to consolidation of this classification into only three Suborders Nevrorthiformia (containing Nevrorthidae only), Myrmeleontiformia (containing five families: Nemopteridae, Psychopsidae, Nymphidae, Ascalaphidae, and Myrmeleontidae), and Hemerobiiformia (containing 11 families: Ithonidae, Polystoechotidae, Chrysopidae, Hemerobiidae, Mantispidae, Rhachiberothidae, Berothidae, Coniopterygidae, Dilaridae, Sisyridae, and Osmylidae). The most significant aspects of this work were (a) placement of Ithonidae (moth lacewings) not as the closest relative of remaining neuropterans but rather in a more derived position closer to Myrmeleontiformia and (b) the placement of Nevrorthidae, instead, as the earliest-branching family.

A monophyletic Hemerobiiformia as circumscribed by Aspöck *et al.* (4) has never been recovered as a natural group in any molecular analysis (5, 6). Myrmeleontiformia



Fig. 1 A split-footed lacewing (*Norfolius howensis*) from Australia. Credit: S. L. Winterton.



**Fig. 2** A timetree of lacewings (Neuroptera). Divergences are shown in Table 1. *Abbreviations:* Ng (Neogene) and Pg (Paleogene).

is a strongly supported group in all published phylogenies based on morphological (3, 4, 7–9) and molecular data (Winterton and Wiegmann, submitted; 5, 6). A suite of adult and larval morphological characters define this group.

Relative to morphological data, very few molecular phylogenies of Neuroptera have been published. Haring and Aspöck (5) published the first attempt at elucidating lacewing phylogeny using molecular data by sequencing representatives of most neuropteran families for amino acid sequences of *cytochrome c oxidase* subunit III. The results of this study recovered monophyletic Myrmeleontiformia and Nevrothiformia, but a polyphyletic Hemerobiiformia, with considerable discord between molecular and morphological data regarding the placement of the families Osmylidae and Dilaridae. Using 18S rDNA sequences Winterton (6) also showed strong support for Myrmeleontiformia, but did not recover a monophyletic Hemerobiiformia. In this analysis Dilaridae were also placed as a basal group rather than being closely related to Mantispidae, Rhachiberothidae, and Berothidae.

The most recent analysis of lacewing phylogeny is by Winterton and Wiegmann (submitted), using both molecular and morphological data with much greater taxon sampling than in previous studies of the group. They produced the most comprehensive phylogeny of the order to date, by using DNA sequences for *16S*, *18S* ribosomal genes, *COI* and *CAD*, combined with morphological data for representatives of all families of Neuroptera. Results from this study show that Coniopterygidae rather than Nevrothidae is the earliest-branching family in the order, and that Hemerobiiformia is a paraphyletic group having a ladder topology leading to a monophyletic Myrmeleontiformia. Dilaridae is again supported as a basal group closely related to Sisyridae and Coniopterygidae.

Neuropterans have a rich fossil record with definitive neuropteridan ancestors dating back to the Permian (1, 10). Only Winterton and Wiegmann (submitted), using the aforementioned gene sequences, have estimated divergence times among lacewing families based on genetic data. Coniopterygidae diverged from the rest of the order during the late Permian (~257 Ma) followed by

**Table 1.** Divergence times (Ma) and confidence/credibility intervals (CI) among lacewings (Neuroptera) based on Winterton and Wiegmann (submitted).

Node	Timetree	
	Time	CI
1	257	268–244
2	247	259–235
3	242	254–229
4	228	242–212
5	227	239–214
6	219	231–207
7	214	230–199
8	213	226–200
9	208	221–195
10	197	211–184
11	197	214–177
12	187	200–176
13	172	183–167
14	153	162–150

Note: Two protein-encoding genes and two ribosomal genes were used to estimate divergence times in Winterton and Wiegmann (submitted).

all major family-level divergences occurring during the Jurassic (>145 Ma). This is reflected in the fossil record, with fossil taxa of most extant families present in Jurassic or early Cretaceous aged deposits (1, 2, 10). The estimated age of the divergence of Myrmeleontiformia from its closest relative is ~216 Ma. The most recent family-level divergence is that of Ascalaphidae from Myrmeleontidae (~153 Ma).

Based on these data, interesting questions may be posed regarding the origins of certain families. One example is that of the origins of freshwater sponges and spongilla flies (Sisyridae). Freshwater sponges are classified in the Suborder Spongillina and likely colonized freshwaters from marine ancestors during the early Jurassic (210–141 Ma) (11). Considering that the origin of Sisyridae is estimated at ~247 Ma (Winterton and Wiegmann, submitted), and that this group are specialist predators on freshwater sponges and bryozoans, ancestral sisyrids possibly fed on freshwater bryozoans during the Triassic before expanding to freshwater sponges during the Jurassic.

Neuroptera is a relatively ancient group of insects with a rich fossil record. This, along with tremendous morphological disparity between families and highly disjunct biogeographical patterns across related taxa, indicate that the golden age of lacewings has long since past (4). Divergence estimates support this view with all major divergences occurring during the Mesozoic (251–66 Ma) (Winterton and Wiegmann, submitted). Our understanding of the evolutionary history of this group is still developing, with morphology providing only fragmentary insights. Further studies using molecular data (e.g., more molecular markers) and intermediate fossil material are needed to fully elucidate the evolutionary history of Neuroptera.

### Acknowledgment

Support was provided by the U.S. National Science Foundation to the authors.

### References

1. T. R. New, *Handbook of Zoology. Planipennia: Lacewings*, Vol. IV. Part 30 (Walter de Gruyter, Berlin, 1989).
2. A. Handlirsch, *Die fossilen Insekten Und Die Phylogenie Der Rezenten Formen: Ein Handbuch Für Paläontologen Und Zoologen* (Engelmann, Leipzig, Germany, 1906–1908).
3. C. L. Withycombe, *Trans. Entom. Soc. Lond.* **72**, 303 (1925).
4. U. Aspöck, J. D. Plant, H. L. Nemeschkal, *Syst. Entom.* **26**, 73 (2001).
5. E. Haring, U. Aspöck, *Syst. Entom.* **29**, 415 (2004).
6. S. L. Winterton, *Entomol. Abhand.* **61**, 158 (2003).
7. E. G. MacLeod, *A Comparative Morphological Study of the Head Capsule and Cervix of Larval Neuroptera (Insecta)*, Ph.D. Thesis (Harvard University, Cambridge, Massachusetts, 1964).
8. C. S. Henry, *Psyche* **85**, 265 (1978).
9. M. W. Mansell, in *Current Research in Neuropterology. Proc. Fourth Int. Symp. on Neuropterology*, M. Canard, H. Aspöck, M. W. Mansell, Eds. (Privately printed, Toulouse, France, 1992), pp. 233–241.
10. D. Grimaldi, M. S. Engel, *Evolution of The Insects* (Cambridge University Press, Cambridge, UK, 2005).
11. R. Manconi, R. Pronzato, in *Systema Porifera: A guide to the classification of sponges*, J. N. A. Hooper, R. W. M. Van Soest, Eds. (Kluwer Academic/Plenum Publishers, New York, 2002), pp. 921–1021.