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Molecular relationships of the Australian Ennominae (Lepidoptera: Geometridae) and implications for the phylogeny of the Geometridae from molecular and morphological data

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#### Abstract

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Molecular data from the 28S D2 ribosomal nuclear gene fragment were utilised to construct a phylogeny for the Australian Ennominae. Sequences were obtained from 68 geometrid and 5 outgroup species. Sequences from a smaller subset of 17 species also were analysed using the nuclear protein-coding gene EF-1α. Species were sampled from all major subfamilies of the Geometridae as no *a priori* assumptions could be made confidently about possible sister groups to the Australian Ennominae.

The major findings from these analyses were as follows:

- (a) Drepanidae are a sister group to Geometridae;
- (b) Larentiinae are derived basally within the Geometridae; the Sterrhinae are the penultimate basally derived group;
  - (c) Oenochrominae s. str. are closely related to the Geometrinae.
  - (d) Ennominae are not monophyletic;
- (e) Tasmanian Archiearinae are misplaced in the Archiearinae and have close affinities to Australian Nacophorini (Ennominae);
  - (f) Australian Nacophorini are not monophyletic.

These results are at odds with traditionally held beliefs on the origins of Geometridae but are in broad agreement with and elaborate on the findings of Abraham *et al.* (2001). The implications of these findings in relation to key morphological characters are discussed using the proposed phylogenetic framework.

**Key words:** 28S D2, Archiearinae, Australia, EF-1α, Ennominae, Geometridae, Gondwana, Lepidoptera, molecular phylogeny, morphology, Nacophorini

#### Introduction

The monophyly of the family Geometridae is well supported by the possession and unique structure of an abdominal tympanum in the adult (Kennel & Eggers 1933; Cook & Scoble 1992; Scoble 1995; Minet & Scoble 1999). The larvae also are distinguished from other families by the presence of an extra L seta, L4, on the abdominal segments (Dugdale 1961) and usually a reduction in the number of anterior prolegs resulting in a looping gait in the caterpillars. More recently the presence of saccular dorsal sex pheromone glands in the adult female has been proposed as another geometrid synapomorphy (Bendib 2001). However, despite the universally accepted monophyly of the family, relationships among geometrid subfamilies and lower taxonomic groupings are generally very unclear (Minet & Scoble 1999).

The Ennominae are the largest of the six subfamilies of Geometridae with 9,700 described species in approximately 1,100 genera, representing just under half of all geometrids (Scoble 1999). The Australian fauna is comprised of a large number of endemic species that are well adapted to the characteristic Australian flora. The ancestors of these species possibly existed as part of the Gondwanan fauna or evolved after the separation of Australia from Antarctica 45 million years ago (Common 1993). The