



## A revised checklist of Nepticulidae fossils (Lepidoptera) indicates an Early Cretaceous origin

CAMIEL DOORENWEERD<sup>1,2,6</sup>, ERIK J. VAN NIEUKERKEN<sup>1</sup>, JAE-CHEON SOHN<sup>3,4</sup>  
& CONRAD C. LABANDEIRA<sup>3-5</sup>

<sup>1</sup>Department of Terrestrial Zoology, Naturalis Biodiversity Center, Leiden, The Netherlands

<sup>2</sup>Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands

<sup>3</sup>Department of Paleobiology, Smithsonian Institution, National Museum of Natural History, Washington, DC, USA.

<sup>4</sup>Department of Entomology, University of Maryland, College Park, USA

<sup>5</sup>College of Life Sciences, Capital Normal University, Beijing 100048, China

<sup>6</sup>Corresponding author. E-mail: [camiel.doorenweerd@naturalis.nl](mailto:camiel.doorenweerd@naturalis.nl)

### Abstract

With phylogenetic knowledge of Lepidoptera rapidly increasing, catalysed by increasingly powerful molecular techniques, the demand for fossil calibration points to estimate an evolutionary timeframe for the order is becoming an increasingly pressing issue. The family Nepticulidae is a species rich, basal branch within the phylogeny of the Lepidoptera, characterized by larval leaf-mining habits, and thereby represents a potentially important lineage whose evolutionary history can be established more thoroughly with the potential use of fossil calibration points. Using our experience with extant global Nepticulidae, we discuss a list of characters that may be used to assign fossil leaf mines to Nepticulidae, and suggest useful methods for classifying relevant fossil material. We present a checklist of 79 records of Nepticulidae representing adult and leaf-mine fossils mentioned in literature, often with multiple exemplars constituting a single record. We provide our interpretation of these fossils. Two species now are included in the collective generic name *Stigmellites*: *Stigmellites resupinata* (Krassilov, 2008) comb. nov. (from *Ophiheliconoma*) and *Stigmellites almeidae* (Martins-Neto, 1989) comb. nov. (from *Nepticula*). Eleven records are for the first time attributed to Nepticulidae. After discarding several dubious records, including one possibly placing the family at a latest Jurassic position, we conclude that the oldest fossils likely attributable to Nepticulidae are several exemplars representing a variety of species from the Dakota Formation (USA). The relevant strata containing these earliest fossils are now dated at 102 Ma (million years ago) in age, corresponding to the latest Albian Stage of the Early Cretaceous. Integration of all records in the checklist shows that a continuous presence of nepticulid-like leaf mines preserved as compression–impression fossils and by amber entombment of adults have a fossil record extending to the latest Early Cretaceous.

**Key words:** Baltic Amber, Calibration points, Dakota Formation, Evolutionary history, Extinction, Fossil record, Larvae, Leaf mining, Plant hosts, *Stigmella*, *Stigmellites*

### Introduction

Numerous molecular phylogenetic studies spanning the entire megadiverse insect order Lepidoptera have been published during the past five years (Mutanen *et al.* 2010; Regier *et al.* 2009; Regier *et al.* 2013; Timmermans *et al.* 2014). Although there is as yet no complete consensus for all phylogenetic relationships, especially among superfamilies (Timmermans *et al.* 2014), the overall topology for the evolution of Lepidoptera presently is clearer than ever. This advancement offers opportunities to study the timeframe during which their evolution took place. One recent study used seven fossil calibration points across all Lepidoptera and has revealed several periods of increased diversification and a plausible, synchronous evolution with angiosperm hosts (Wahlberg *et al.* 2013). Their work became possible by combining the Mutanen *et al.* (2010) phylogenetic dataset with a LepTree project compilation of fossils (Sohn *et al.* 2012; Sohn & Lamas 2013). Molecular dating on phylogenetic trees has been a subject of considerable scientific debate, ranging from pointing out the pitfalls of using poorly supported