Phylogeny of the *Yponomeuta* species (Lepidoptera, Yponomeutidae) and the history of their host plant associations

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This study presents the results of cladistic analyses of the morphology of 1) the subfamilies of the Yponomeutidae, 2) the genera of the Yponomeutinae, and 3) the species of *Yponomeuta* Latreille, 1796. The sequential steps in the evolution of the host plant associations, the presumed key factor in the processes of speciation within *Yponomeuta*, as extrapolated from the cladograms are discussed. The hypothesis that the present-day host plant associations evolved from an ancestral relation with Celastraceae through speciation in allopatry mostly on *Euonymus* is supported by the underlying study. The biogeographical patterns suggest speciation through dispersion from Australia, the Oriental region, Africa to western Europe. Sandrine A. Ulenberg, Zoological Museum, University of Amsterdam, Plantage Middenlaan 64, 1018 DH Amsterdam, The Netherlands. s.a.ulenberg@uva.nl

Introduction

The study of speciation mechanisms as a means to gain a better understanding of the origins of biological diversity has always been a key area in biological research. Recently, the role of ecological specialisation has received considerable attention. Good theoretical (Dieckmann & Doebeli 1999; Doebeli & Dieckmann 2000; Janz & Nylin 2008; Percy et al. 2004; Via 2001) as well as empirical progress is being made, in particular in our understanding of the evolution of insect–plant relations and speciation in phytophagous insects (Kölsch & Pedersen 2008; Via 2002; Via & Hawthorne 2002).

One of the model systems developed for this purpose is the genus *Yponomeuta* Latreille, 1796 and its host relations. Since the 1970s many multidisciplinary studies have been dedicated to the associations between *Yponomeuta* species and their host plants. The main objectives of studying this model were to obtain insights into the evolution of the host relations, and the speciation processes that have led to the present-day associations (Bakker et al. 2008; Hora & Roessingh 1999; Menken 1996; Menken et al. 1992; Menken & Roessingh 1998; Rajmann & Menken 2000). According to Menken & Roessingh (1998) “These studies were based on the working hypothesis that the present-day host plant associations evolved from an ancestral relation with Celastraceae through speciation in allopatry mostly on *Euonymus* and through host shifts in sympathy or allopatry to mainly Rosaceae, following the scenario of host race formation (Bush 1975)”. In the present paper the validity of this working hypothesis is tested by analysing the most probable sequence of the evolutionary changes in the host plant associations of *Yponomeuta* based on their species phylogeny.

*Yponomeuta*’s distribution and host plant associations

The species of the genus *Yponomeuta* are phytophagous and have a wide, mainly palaearctic, distribution. The genus is represented in all major eco regions except South America and Antarctica. Host-associations are known for 39 of the 76 species. Of the 39 *Yponomeuta* species with a known host-association, 32 are mono- or oligophagous within one genus of trees or shrubs. Of those 32, 27 species feed on Celastraceae genera, of which 22 exclusively feed on species of the genus *Euonymus*. The *Yponomeuta* species that do not use Celastraceae as their host plant...
feed on Crassulaceae, Rosaceae, Rhamnaceae, or Salicaceae (see Gershenson & Ulenberg 1998).

**Classification of the Yponomeutidae**
The systematic position of the (sub)families within the superfamily Yponomeutoidea was open to discussion until recently and differently treated by systematists, according to the historical review in Gershenson & Ulenberg’s (1998) book on the Yponomeutinae.

No general consensus exists regarding the ranks of the higher taxa in Yponomeutidae. Some authors (Kyrki 1990; Moriuti 1977) lowered the position of what was formerly regarded as a well-defined family, the Yponomeutidae, to the level of subfamily. Kyrki (1984) discussed the different classifications of earlier authors and in his paper published in 1990 tentatively reclassified the Holarctic Yponomeutoidea, its families and subfamilies based on what he regarded as apomorphies. Kyrki’s reclassification was followed by Scoble (1992) and Dugdale et al. (1998) in their treatment of the Yponomeutoidea. Heppner (1998), in his general classification of Lepidoptera, summarized the characters defining Yponomeutoidea. However, though he recognized three subfamilies (viz. Yponomeutinae, Saridoscelinae and Cedestinae), he did not treat these in detail. Neither of them published on the phylogeny of the groups within the Yponomeutidae.

**Material and Methods**
The subfamilies of the Yponomeutidae and the genera of the Yponomeutinae were analysed cladistically to determine the sister group of *Yponomeuta* and the history of the host plant associations within the Yponomeutinae leading to those in *Yponomeuta*.

**The subfamilies of the Yponomeutidae**
The relationship between the subfamilies of the Yponomeutidae has been investigated largely based on the characters given by Kyrki (1990). One character state was changed, viz., the number of segments of the maxillary palp in the Yponomeutinae. Kyrki gives the number as four. According to the observations of Gershenson & Ulenberg (1998) the number of segments in this subfamily is less than four, as they did not count the protuberance of the stipes as basal maxillary segment (see also Moriuti 1977; Dugdale et al. 1998). Heppner (1998: 51) mentioned 1–2 for the family Yponomeutidae (Yponomeutinae, Saridoscelinae, Cedestinae). For a description of the characters and the matrix, see Table 1.

In the analysis an all-zero outgroup, with zero as plesiomorphic state, was incorporated based on Kyrki’s opinion on plesio- and apomorphies of the subfamilies. This hypothetical ancestor is chosen as outgroup because the group most related to the Yponomeutidae is unknown. In this and the following analyses, PAUP* 4.0b10 (Swofford 2003) was used, all characters were unordered and of equal weight. An exhaustive search was made for the most parsimonious tree.

**The genera of the Yponomeutinae**
The phylogenetic relationships of the yponomeutine genera was examined utilizing a maximum parsimony analysis of the type species of the genera in the subfamily. The search was heuristic.


As the literature did not give sufficient insight in their characters, neither of other species classified in these four genera, they were not incorporated in the analysis.

*Saridoscelis sphenias* Meyrick, 1894, the type species of the only genus classified in the Saridoscelinae, the Yponomeutinae’s presumed sister group, served as outgroup.

For a description of the characters and the matrix, see Table 2a and 2b.

A heuristic search for the most parsimonious tree was performed with PAUP* 4.0b10 (Swofford 2003), all characters were unordered and of equal weight. Starting trees were obtained via stepwise addition with random sequence. The number of replicates was one million. The branch-swapping algorithm was tree-bisection-reconnection (TBR).

**The species of Yponomeuta**
The phylogeny of the *Yponomeuta* species treated in Gershenson & Ulenberg (1998) was investigated, viz., the *Yponomeuta* species of the world exclusive of the Americas. One of the six Nearctic *Yponomeuta* species, *Y. multipunctellus* Clemens, has been incorporated in the cladistic analyses. The other five species have been left out because of the author’s insufficient insight in the American fauna.