

VILNIUS UNIVERSITY  
NATURE RESEARCH CENTRE

—— ANDRIUS REMEIKIS ——

FAUNA AND TROPHIC RELATIONSHIPS OF  
THE MIDDLE AND SOUTH AMERICAN NEPTICULOIDEA  
(LEPIDOPTERA: NEPTICULIDAE, OPOSTEGIDAE)

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Summary of doctoral dissertation

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Biomedical sciences, Ecology and Environmental science (03 B)

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**Research supervisor** Prof. Habil. Dr. Jonas Rimantas Stonis (Lithuanian University of Educational Sciences, Biomedical sciences, Ecology and Environmental science, 03 B)

The defence of the dissertation will be held at public meeting of dissertation defense Council:

**Chairman** Prof. Habil. Dr. Vincas Būda (Nature Research Centre, Biomedical sciences, Ecology and Environmental science, 03 B).

**Members:**

Prof. Dr. Algimantas Paulauskas (Vytautas Magnus University, Biomedical sciences, Ecology and Environmental science, 03 B);

Assoc. Prof. Dr. Jurga Turčinavičienė (Vilnius University, Biomedical sciences, Biology, 01 B);

Prof. Dr. Liliana Katinas (La Plata University, Biomedical sciences, Ecology and Environmental science, 03 B);

Dr. David C. Lees (Natural History Museum, London, Biomedical sciences, Ecology and Environmental science, 03 B).

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Address: Studentų St. 39, Vilnius LT-08106, Lithuania.

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VILNIAUS UNIVERSITETAS  
GAMTOS TYRIMŲ CENTRAS

—— ANDRIUS REMEIKIS ——

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FAUNA IR MITYBINIAI RYŠIAI

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Vilnius, 2017

Disertacija parengta 2013–2017 m. Gamtos tyrimų centre

**Mokslinis vadovas** – prof. habil. dr. Jonas Rimantas Stonis (Lietuvos edukologijos universitetas, biomedicinos mokslai, ekologija ir aplinkotyra – 03 B).

Disertacija ginama viešame disertacijos Gynimo tarybos posėdyje:

**Pirmininkas** – prof. habil. dr. Vincas Būda (Gamtos tyrimų centras, biomedicinos mokslai, ekologija ir aplinkotyra – 03 B).

**Nariai:**

Prof. dr. Algimantas Paulauskas (Vytauto Didžiojo universitetas, biomedicinos mokslai, ekologija ir aplinkotyra – 03 B);

Doc. dr. Jurga Turčinavičienė (Vilniaus universitetas, biomedicinos mokslai, biologija – 01 B);

Prof. dr. Liliana Katinas, La Platos universitetas, Argentina (biomedicinos mokslai, ekologija ir aplinkotyra – 03 B);

Dr. David C. Lees (Londono Gamtos muziejus, Jungtinė Karalystė, biomedicinos mokslai, ekologija ir aplinkotyra – 03 B).

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# 1. INTRODUCTION

## 1.1. RELEVANCE OF THE PROBLEM

Phylogenetically, the taxa under study (Nepticuloidea: Nepticulidae and Opostegidae) are among the most primitive Lepidoptera (Davis, 1989; Puplesis and Diškus, 2003). Being endobiotic, larvae of these insects feed within green (assimilative) tissues of plants and, therefore, Nepticuloidea are of exceptional practical and theoretical importance (Diškus and Stonis, 2012). They occur in almost all terrestrial biomes and continents except the Antartics. Because of species endemism and high degree of stenophagy, these insects can serve as convenient and reliable means for assessing the richness of natural regions and providing some light on the origin and evolutionary ties of various biodiversity centres (Puplesis and Diškus, 2003; Stonis, 2010). However, being very small and leading hidden lifestyle within plant tissues, these insects remain insufficiently investigated in many regions (Puplesis and Robinson, 2000; Davis and Stonis, 2007). Moreover, it is compounded by lack (and disturbing decline!) of qualified specialists (Stonis, 2014). All this motivated the author to carry out studies of Opostegidae and particularly Nepticulidae in Middle\* and South America, one of the Earth's richest but still poorly studied regions as regards leaf-mining insects. Prior to our research, the Nepticuloidea fauna and its trophic relationships had been very little known and needed to be assessed. Without such basic data on fauna and ecological characteristics (e.g. trophic relationships and seasonal cycles), it is impossible to efficiently solve problems of the protection of natural regions and continue any further research.

Nowadays, nature researchers are seriously concerned about the biodiversity crisis. The increasing concern by the international scientific com-

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\* In this dissertation, Middle America is defined as Central America with the tropical and subtropical areas of southern and southeastern Mexico + the Caribbean. From the biogeographical point of view, Middle and South America together represent two biogeographical regions or realms: the Neotropical (which is mostly tropical) and Ando-Patagonian (which is mostly temperate). The biogeographical regionalization follows Morrone 2014, 2015 except for the term "Ando-Patagonian", which in Morrone 2014, 2015 is "Andean".

munity over the issues of biodiversity stimulates to more actively inventory various biomes of the Earth. Unfortunately, biodiversity is undergoing very rapid decline due to human economic activity, severe destruction or fragmentation of habitats. In the tropical regions, this decline has gained even much greater rate (Stonis, 2010). Because of the ongoing climate change and with rather dramatic forecasts, this issue has been rapidly getting into the mainstream.

It should be also mentioned that the significance and urgency of biodiversity studies were declared by the Rio de Janeiro Convention on Biological Diversity, which has been ratified by the Seimas of the Republic of Lithuania.

As regards nature conservation, several strategies could be distinguished. Among them, protection of habitats, rather than specific organisms, seems the most correct approach. However, many habitats in Middle and South America have been insufficiently studied and their state has not been assessed.

Inventorying biodiversity is a huge long-lasting task: so far only a small portion of the world's biodiversity (12–14.5%) has been studied and described (Puplesis, 2002). Therefore, there is plenty work for researchers. Biotaxonomists are actually competing with time: many organism species may get extinct and will never be discovered. No wonder that there is a popular saying among biotaxonomists – “newly discovered species are the jewel of biodiversity” (Stonis, 2010).

## 1.2. THE GOAL AND OBJECTIVES OF THE RESEARCH

The **goal** of the dissertation is taxonomic and trophic assessment of the Nepticuloidea fauna (Lepidoptera: Nepticulidae, Opostegidae) of Middle and South America in the light of the latest taxonomic and trophic data.

The following **objectives** had to be accomplished in order to achieve this goal:

- 1) by studying the material collected in Costa Rica, Mexico and Ecuador, to identify Opostegidae species, revise data of the family distribution and to carry out chorological analysis of the Opostegidae species occurring in Middle and South America;

- 2) by investigating large unidentified material deposited at various research centres, to identify the composition of the Nepticulidae fauna of Middle and South America as well as describe newly discovered species;
- 3) on the basis of data from taxonomic analysis and newly identified diagnostic characters, to revise the taxonomic rank of some of Nepticulidae species; by investigating morphological structures and considering newly studied ecological peculiarities, to specify and designate species groups and their satellite taxa (i.e. similar species from the diagnostic point of view) as well as identify complexes of very closely related species characterized by low degree of differentiation;
- 4) to identify, describe and analyze the specific Nepticulidae fauna trophically associated with some plant groups, with special focus on the Fagaceae (*Quercus*), Asteraceae (*Baccharis*) and Rosaceae miners;
- 5) to analyze trophic relationships of the Nepticulidae of the Neotropical and Ando-Patagonian regions and compare them with those in the Holarctics;
- 6) to define trophic relationships of the Nepticulidae species occurring in various mountainous and lowland habitats as well as activity periods of adults and larvae, with the major focus on the high altitude fauna, including species trophically associated with the *Polylepis* forests;
- 7) to define groups of mining abundance of Nepticulidae, analyze species occurrence and identify Nepticulidae species which may be relevant as pests (or potential pests) of cultivated or otherwise economically significant plants.

### 1.3. SCIENTIFIC NOVELTY OF THE RESEARCH

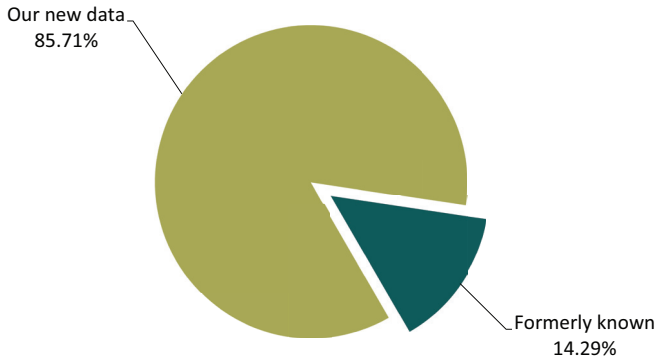
In spite of the previous attempts to investigate Nepticuloidea of Middle and South America (see “Literature review”), the current research and its outcome possess a high degree of novelty:

- 1) we were the first to do chorological analysis of the Opostegidae fauna based on newly collected material and recently described new species, and, as a result, defined diversity centres of Opostegidae;

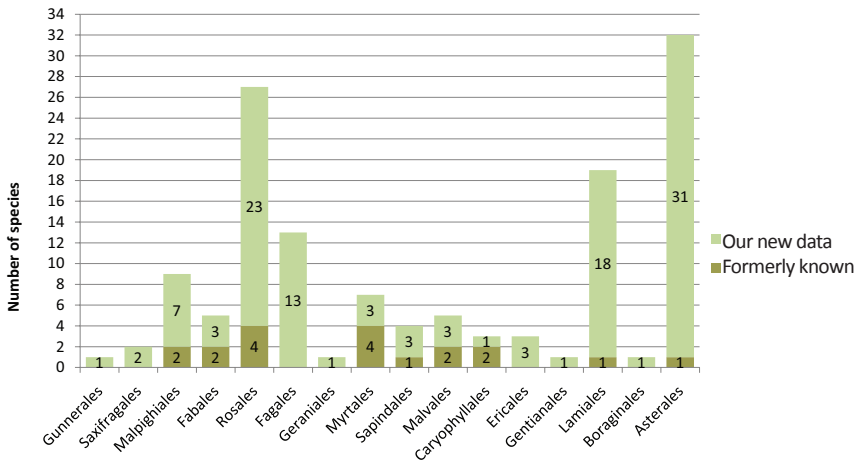
- 2) the dissertation deals with comprehensive taxonomic analysis of the Nepticulidae of Middle and South America which allowed us to designate many new species groups within the following genera: *Enteucha*, *Ectoedemia*, *Acalyptris* and *Stigmella*; we also designated new species complexes in *Acalyptris* (the *A. bicornutus* and *A. tenuijuxtus* species complexes) and *Stigmella* (the *S. sinuosa* species complex);
- 3) we were the first to provide diagnostic pictorial keys to species groups of *Stigmella* occurring in Middle and South America, including detailed analysis of the *Stigmella magnispinella* and *S. circinata* species groups, and the *S. sinuosa* complex within the *S. marmorea* group;
- 4) the dissertation deals with newly discovered morphological and ecological adaptations of Nepticulidae related to their lifestyle within plant tissues (including the formation of cocoons within leaf-mines and development of the ovipositor in some *Stigmella* species);
- 5) we were the first to describe and analyze Nepticulidae trophically associated with *Quercus* (Fagaceae) and discovered in Middle and South America; we also diagnosed the Neotropical *Stigmella saginella* group and the newly designated *S. nigriverticella* species complex as well as defined its association with various plants from the *Quercus* genus;
- 6) the dissertation deals with first-time analysis of all known species groups of the Nepticulidae fauna associated with host plants from the Fagaceae family resulting in the definition of the trophic spectrum of the *Stigmella quercipulchella* and *S. saginella* species groups occurring in America and associated with the *Lobatae* and *Quercus* sections of the *Quercus* genus and the *Castanaea* genus;
- 7) we were the first to publish data about the discovery of the Patagonian fauna of the presumably Gondwana origin (the *Stigmella purpurimaculae* species group comprising species which are assumed to be *Nothofagus* miners);
- 8) we were the first to reveal an entire Nepticulidae fauna trophically associated with Asteraceae in South America and were the first to



- report the *Baccharis*, *Liabum*, *Gynoxys* and some other Asteraceae genera which had never been known as host plants of Nepticulidae;
- 9) having discovered and documented new Nepticulidae taxa associated with Rosaceae plants in South America, we reviewed the specialized fauna for the first time;
  - 10) the dissertation deals with the first trophic analysis of the Nepticulidae from the Neotropical and Ando-Patagonian regions, where the predominating trophic associations with Asteridae and Rosidae were revealed and trophic relationships with 24 families and 16 plant clades were recorded;
  - 11) we were the first to define specific characteristics and tendencies of trophic relationships of Nepticulidae of Middle and South America by comparing them with those from the Holarctic region;
  - 12) the dissertation deals with the first provisional review of habitats occupied by Nepticulidae and preliminary assessment of trophic specialization and seasonal activity of Nepticulidae occurring in various habitats;
  - 13) we were the first to identify and describe the Nepticulidae fauna trophically associated with the high-Andean *Polylepis* forests, which are very significant from the ecological point of view, and were the first to identify the world's highest altitudinal Nepticulidae fauna and registered the altitude record of 4700 meters for *Stigmella nivea*;
  - 14) we prepared a new preliminary taxonomic catalogue of the Nepticuloidea of Middle and South America specifying the host plants for all the species that had been trophically investigated;
  - 15) the dissertation deals with the first attempt to analyze seasonal cycles, abundance and occurrence of Nepticulidae in Middle and South America and provides the first list of species trophically associated with cultivated, endemic or protected plants as well as plants of other economic significance;
  - 16) we identified new host-plant data for 114 Nepticulidae taxa (including undescribed species), i.e. the number of newly revealed trophic relationships of Nepticulidae of the region under research amounts to almost 86% (Figs. 1 and 2);



**Fig. 1.** Novelty of the data on trophic relationships of the Nepticulidae of Middle and South America.

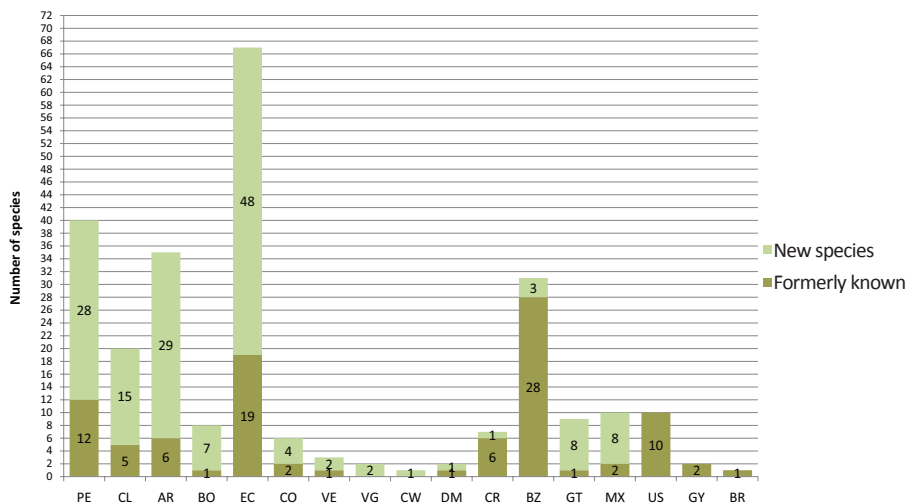


**Fig. 2.** Contribution to the knowledge of the subject: revealed trophic relationships of Nepticulidae by plant clades.

17) we discovered 146 previously unknown species (Figs. 3 and 4), considerable part of which were published (the remaining part is under preparation).



**Fig. 3.** Contribution to the knowledge of the subject: new data on the Nepticulidae fauna of Middle and South America.



**Fig. 4.** Contribution to the knowledge of the subject: relationships among the known Nepticulidae species and those discovered during the dissertation project in various countries of Middle and South America: AR – Argentina, BR – Brazil, BO – Bolivia, BZ – Belize, CL – Chile, CO – Colombia, CR – Costa Rica, CW – Curaçao, DM – Dominica, EC – Ecuador, GY – Guyana, GT – Guatemala, MX – tropical regions of Mexico, PE – Peru, US – Florida, VE – Venezuela, VG – British Virgin Islands.

#### 1.4. THEORETICAL AND PRACTICAL SIGNIFICANCE

From the scientific and theoretical points of view, Nepticuloidea are significant as being among the phylogenetically most primitive taxa. The adaptability of the organisms under research in the larval stage to feed within assimilative plant tissues is significant from the economical point of view as well. Some of the Nepticulidae have already been included into the lists of pests of cultivated plants (Kuznetsov and Puplesis, 1994). We suppose that today's global trade links and emergence of new touristic routes significantly increases the danger of the introduction of alien pests (Diškus and Stonis, 2012).

The new data revealed during our research (see in more detail in 4.5.3 of the Dissertation) about cultivated (or otherwise significant) plants of Middle and South America mined by the Nepticulidae taxa, their trophic specialization and activity cycles of larvae and adults could be used for preparing various means for the protection of plants from potential pests.

#### 1.5. STATEMENTS TO DEFEND

1. From the taxonomic point of view, the Opostegidae fauna comprises at least 86 species in Middle and South America (or 40 species in Middle America alone); the richest fauna has been recorded from Costa Rica, but it is not uniform from the chorological point of view.
2. The Nepticulidae of Middle and South America comprise 11 genera and 222 species; most of them were newly discovered, identified and described.
3. Defining or interpreting new diagnostic characters allows to specify taxonomic status of some taxa, designate at least three species complexes within *Acalyptis* and *Stigmella* and designate new species groups within the following genera: *Enteucha*, *Ectoedemia*, *Acalyptis* and *Stigmella*, with the highest diversity of groups within *Stigmella* (including 18 newly designated).
4. Since America (especially Middle America) is one of the key global centres of diversity and endemism of the *Quercus* genus, in the region under research, we observe diverse Nepticulidae fauna trophically as-

sociated with plants of the *Quercus* genus; however, rich previously unknown but trophically specialized fauna is also associated with various host plant taxa from the families Asteraceae, Rosaceae, Lamiaceae, etc.

5. Asteridae and Rosidae predominate among the host plants occupied by the Nepticulidae of the Neotropical and Ando-Patagonian regions. The trophic specialization of the regions under study exhibits ecological exclusiveness and is characterized by features different from those of the earlier investigated Holarctic region.
6. The Nepticulidae of Middle and South America occur in various habitats, including the *Polylepis* forests or habitats above the forest line (páramo or puna); however, the most diverse trophic relationships are observed in the habitats of moist tropical montane forests.
7. The majority of Nepticulidae occurring in Middle and South America are characterized by moderately abundant and not abundant mining. Rare species prevail, however, there are pests or potential pests, i.e. species feeding on cultivated and otherwise significant plants.

## 1.6. APROBATION OF THE RESULTS

The key results that are the basis of the Dissertation were presented for discussion and were approbated at numerous national and international conferences, also seminars and meetings of research teams, including the following international conferences: „SmartBio“, Kaunas, Lithuania (2017); „The First North American Microlepidopterists Meeting“, Denver, USA (2016); „1st International Theoretical and Practical Conference, Fundamental and Applied Investigations on Priority Directions of Bioecology and Biotechnology“, Ulyanovsk, Russia (2014); „The First Baltic International Conference on Field Entomology and Faunistics“, Vilnius, Lithuania (2014); „V International Conference of Naturalists, From Biotechnology to Environment Protection“, Zielona Gora, Poland (2010) (for a complete list of conferences and seminars, see subchapter 1.6 of the Dissertation).

## 1.7. PUBLICATION OF RESEARCH RESULTS

The author published the results of the research in 57 co-authored publications. Sixteen of them were published in *Zootaxa*, the periodical *Impact Factor* journal included into the WoS list of publications (Q2); three, in *Acta Zoologica Lituanica* included into *Master Journal List*; one, in *Ecology and Zoology* included into *Master Journal List*; five, in *Biologija*, the peer-reviewed journal included into *Master Journal List*; and five, in materials of international conferences.

The author also co-authored one chapter of the monograph “Taxonomic, chorological, and trophic characterization of the Lithuanian Neptculidae fauna” (Diškus and Stonis, 2012), and 23 other, mostly science popular, articles describing the process of the research.

## 1.8. THE STRUCTURE AND VOLUME\* OF THE DISSERTATION

The dissertation consists of the following chapters: Introduction, Literature Review, Material and Methods of Research, Results of the Research (4 chapters and 37 subchapters), Summary of Results, Conclusions, References (190 sources), List of Publications by the Author (57 sources) and Annex. In total, there are 220 pages (178, of the Dissertation and 42, of the Annex), 66 figures and 4 tables. The dissertation is in Lithuanian and the Annex, in English. The Annex „Preliminary Catalogue of the fauna of Nepticuloidea of Middle and South America“ contains a taxonomic list of all the taxa discovered in the region under research (314 species) with their host-plants and geographical distribution.

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\* In the current Summary all taxa (genera and species) are provided without reference to authors and years of description; for these data, see the Annex to the dissertation „Preliminary Catalogue of the fauna of Nepticuloidea of Middle and South America“.

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## 2. LITERATURE REVIEW

The Literature review presented in the Dissertation consists of the following subchapters: 2.1. The history and region of the research (the history of the Opostegidae and Nepticulidae research, the region of the research (especially páramo and puna), biodiversity of the Andes and climate change and negative human impact on the environment); 2.2. The ecology of Nepticulidae (Nepticulidae trophically associated with plants of the *Quercus* genus, Nepticulidae trophically associated with plants of the Asteraceae and other families); 2.3. Applying molecular methods in the Nepticuloidea research.

## 3. MATERIAL AND METHODS OF THE RESEARCH

### 3.1. MATERIAL

In addition to some of the studied type-series deposited at ZMUC, Denmark and BMNH, U.K., we used sizeable unidentified material for the dissertation project. The major part of it was received from the following research centres: ZMUC, Denmark (648 Nepticulidae specimens), USMN, USA (88 specimens) and BMNH, U.K (5 specimens).

A significant part of the material was collected during the author's and his Lithuanian colleagues' fieldwork. In total, the author participated in seven research expeditions in various countries in cooperation with foreign research institutions (mostly from Middle and South America).

The number of the studied unidentified Nepticulidae specimens amounts to more than 1000, some 820 of which had been collected in Peru and the



southern Andes (Argentina and Chile) and some 200, in the equatorial Andes and Middle America. For taxonomic purposes, some 650 permanent microslides in Euparal were prepared. Since dissection of genital structures of Nepticuloidea is a very time-consuming task requiring much diligence, in average, the preparation of two permanent microslides took one working day.

## **3.2. STUDY METHODS**

### **3.2.1. Collection of adults in high montane habitats**

The dissertation presents detailed description of the method. It includes a methodological innovation, “the hood”, which approved itself because the majority of moths attracted by the light trap gathered at the top section of the screen (see Stonis and Remeikis, 2009).

In high montane habitats, collecting of Nepticulidae was possible only during favourable climatic conditions because these tiny moths are very sensitive to strong winds and low temperatures. Due to frequent fog and low temperatures at dusk, adults of Nepticulidae were being collected by brushing with a small entomological net over plants. The protocols for sampling and further description of the Nepticulidae material follow Puplesis, 1994; Puplesis and Diškus, 2003; and Puplesis and Robinson, 2000.

### **3.2.2. Rearing of mining adults**

The dissertation presents detailed description of the method. By rearing Nepticulidae adults from larvae, we were able not only to get premium quality collection material of Nepticulidae but also define new characteristics of the Nepticulidae ecology. Steps of this rather specific method draw on Puplesis, 1994; Puplesis and Diškus, 2003; and Diškus and Stonis, 2012.

### **3.2.3. Determining relative abundance and occurrence**

In line with the methodology for determining the mining abundance of Nepticulidae (Diškus and Stonis, 2012), we used five groups (categories) of the relative mining abundance (*spA*), which were determined by counting leaf-mines (empty and with larvae) found on 25x25 m sites. Our research

followed “Formula of Determining Abundance and Occurrence of Leaf-Miners” presented in the monograph by Diškus and Stonis (2012). Species occurrence (*Occ*) was determined by summing up spatial distribution of species (from very wide to very local, *spD*) and relative abundance (from very abundant to very scarce, *spA*) on the site (i.e.  $Occ = spA + spD$ ).

As a result, we determine three groups (common, not rare, and rare) or five groups (very common, common, not rare, rare, and very rare) of occurrence (*Occ*) of mining insects. If *Occ* equals 10–9, the species is determined as very common; 8, as common; 7–6, as not rare; 5–4, as rare; and 3–2, as very rare (see Diškus and Stonis, 2012).

#### 3.2.4. Laboratory protocols

In the Nepticulidae diagnostics, it is common practice to detect differences by comparing morphological characteristics of genital structures of males (sometimes females), which are characterized by high specificity (Puplesis and Robinson, 2000; Puplesis and Diškus, 2003; Stonis et al., 2016). Detailed description of the stages and steps of preparing temporary and permanent Nepticulidae slides (micro-mounts) are presented in the dissertation; they follow Diškus and Stonis (2012) and Stonis et al. (2014). The genital armature was stained in the alcohol solution of *Chlorazol Black* (*Direct Black 38/Azo Black*) and, occasionally, in mercurochrome.

#### 3.2.5. Taxonomic analysis

In the taxonomic analysis we applied morphological, chorological, and ecological data. The dissertation presents detailed description of chromatic and structural characteristics of the scaling of all tegmina; it also presents evaluation and description of the characters of genital structures. For determining phylogenetic affinity of taxa, only apomorphic characters were used.

Genital structures were thoroughly described, measured and digitally documented. For this purpose, we used a *Leica DM2500* microscope and *Leica DFC420* digital camera connected to the microscope and computer. For studying and illustrating the external morphology of adults, we used a *Leica S6D* microscope and *DFC290* digital camera connected to the microscope and computer.

The adults were measured by using a stereoscopic binocular microscope *MBS-10* or *Leica S6D* microscope and *DFC290* digital camera connected to the microscope and computer.

Names of new species were formed following the requirements of the International Code of Zoological Nomenclature (Kodeks, 2000).

### **3.2.6. Trophic analysis**

For analyzing phylogenetic clades of plants engaged by Nepticulidae, we followed one of the newest and most frequently used plant classification presented in Cole and Hilger (2016). We also documented and identified host-plants. The trophic analysis was done as a four-stage procedure, which is described in the dissertation.

### **3.2.7. Chorological analysis**

Though seldom applied in our dissertation and publications, the chorological analysis includes mapping and analyzing data of geographical distribution of species by drawing on published sources and our research results. Biogeographic regionalization mostly follows Morrone, 2014, 2015. The analyzed habitats were sometimes combined into groups of habitats (see 3.2.7 of the Dissertation).

### **3.2.8. Molecular research**

For molecular research of mitochondrial DNA, we used Nepticulidae adults fixed in the 96% ethanol solution (30%) and larvae (5%) as well as dry material (65%) (adult hindleg(s), thorax or the whole of a dry adult).

The dissertation presents the description of stages of extracting mitochondrial DNA, PGR amplification and sequencing of DNA fragments applied during the research. However, the data received from the molecular research have not been included into the dissertation; we intend to publish it after defending the dissertation.

## 4. RESULTS OF THE RESEARCH

### 4.1. TAXONOMIC ANALYSIS OF NEPTICULOIDEA MOSTLY BASED ON THE DATA OF RECENT RESEARCH

#### 4.1.1. The Opostegidae family

The description of three newly discovered Opostegidae species and analysis of geographical distribution of all the Opostegidae in Middle and South America revealed that many of the species were characterized by limited ranges; see Table 1 in 4.1 of the Dissertation and the publications by the author (Remeikis et al., 2009, 2010).

In total, we recognized two Opostegidae genera and 40 species in Middle America (19.8% of the world's Opostegidae fauna). More than half of these species (26 or 65%) occur only in Middle America; only a few taxa are more widely distributed. The species occurring in Costa Rica could be divided into four chorological groups.

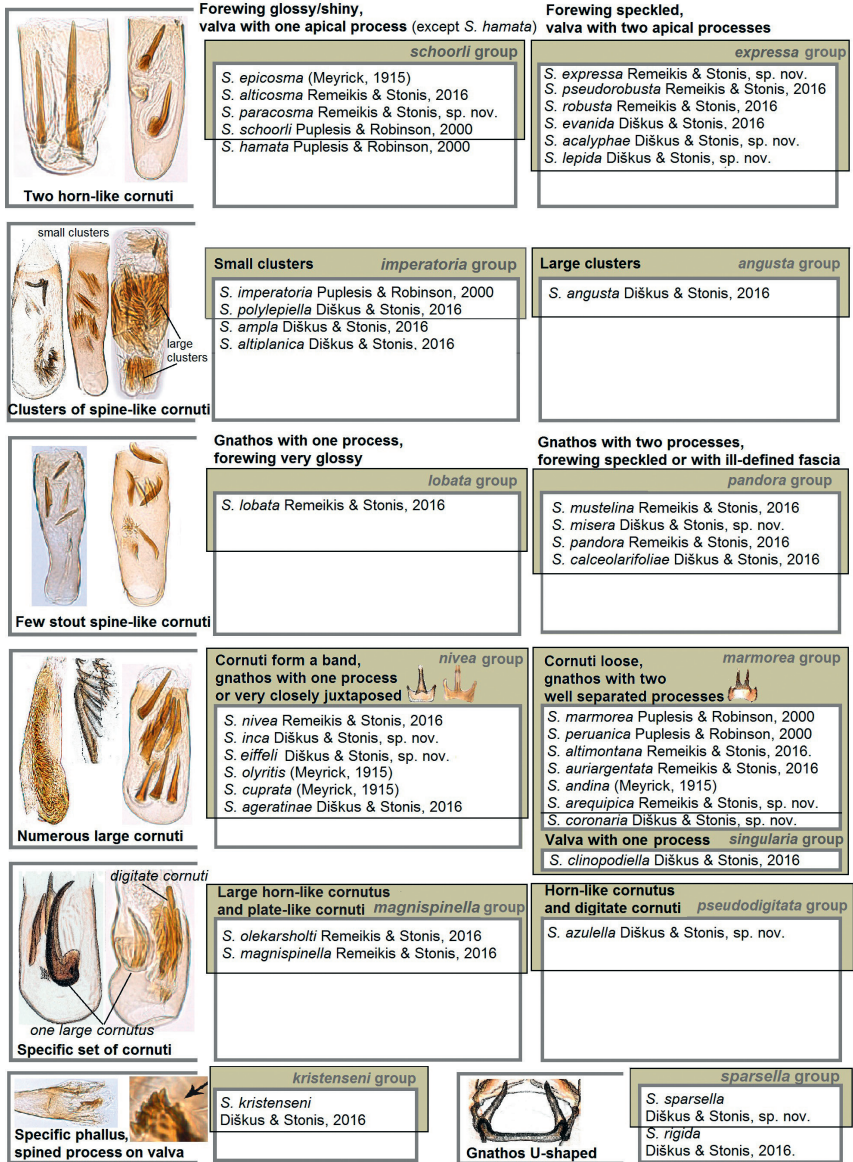
#### 4.1.2. The Nepticulidae family

##### 4.1.2.1. Results of the general taxonomic analysis

Our research revealed that the fauna of Middle and South America consisted of 222 species, 146 of which were discovered and described for the first time by the author of the dissertation; the majority of them were published in the following co-authored papers: Remeikis and Stonis, 2015; Stonis and Remeikis, 2015 and 2016; and Stonis et al., 2013a, 2013b, 2013c, 2013d, 2014b, 2015a, 2016c, 2016d, 2016e, 2016f, 2017a, 2017b, 2017c.

Within the studied fauna, we recognized 11 genera and designated new species groups and complexes of related species. The dissertation also newly estimates diagnostic characters of all taxa, including genera and species groups (see Chapter 3 of the Dissertation).

After studying the material obtained from Patagonia, we named the new species group *S. purpurimaculae*. From the morphological point of view, this group is very unusual: in the male genitalia, the copulation organ (phallus) is characterized by strong reduction of the phallus tube and dentate cornuti; until now, these characters have not been observed in Nepticulidae.



**Fig. 5.** Diagnostic characters of designated species groups (after the co-authored publication Stonis et al., 2017a).

	The <i>hemargyrella</i> group	The <i>circinata</i> group	The <i>sorbi</i> group
Phallus	[shared]**	Long phallus with apical sclerite*	[shared]**
	[shared]	Vesica with a band of large spine-like and minute scallop-like cornuti	Vesica with a band without scallop-like cornuti
	Phallus with manica	Phallus without manica	Phallus with manica
Male genital capsule	[shared]***	Uncus distinctly bilobed	Uncus with four small lobes
	[shared]	Vinculum short	Vinculum very long
	[shared]	Valva with one apical process	Valva with two apical processes
	Juxta absent	Juxta present, specific	Juxta absent
Female genitalia	[shared]****	Accessory sac very long, heavily folded	Accessory sac small or absent
	Bursa copulatrix with or without pectinations	Bursa copulatrix with indistinctive pectinations	Bursa copulatrix with or without pectinations
Bionomics and distribution	Leaf-mine as a slender gallery	Leaf-mine as a slender gallery abruptly widening to a blotch	[shared]
	Host-plants: Fagaceae, Sapindaceae, Caprifoliaceae	Host-plants: Rosaceae	[shared]
	Distribution: Europe and Asia	Distribution: South America	Distribution: Europe and Asia

**Fig. 6.** The newly designated *Stigmella circinata* group has common and presumably synapomorphic characters with the *S. hemargyrella* and *S. sorbi* groups distributed in Europe and Asia (after the co-authored publication Stonis et al., 2016b).

Whereas female genital structures exhibit some kind of perversion: corpus bursae is partially reduced and ductus spermathecae is extremely enlarged.

Contrary to other investigators (van Nieuwerkerken et al., 2016a, 2016b), our analysis of the *Stigmella salicis* species group revealed that this group was varied; therefore the dissertation presents new taxonomic evaluation. On the basis of the characters of the male genital apparatus, we designated 13–16 species groups (there had been only one such group before that) (Figs. 5 and 6).

#### 4.1.2.2. The problem of differentiating species of the *Stigmella sinuosa* complex

The problem of the differentiation and diagnosis of the newly designated complex of cryptic species (which is very difficult to differentiate) is very thoroughly described in the dissertation and the co-authored publication Stonis et al., 2016.

## 4.2. ECOLOGICAL CHARACTERISTICS OF NEPTICULIDAE AND NEWLY REVEALED TROPHIC RELATIONSHIPS (ECOLOGICAL NICHES)

### 4.2.1. Endobiotic lifestyle and revealed morphological and ecological adaptations

The dissertation presents data about unusual formation of cocoons of some *Stigmella* within the leaf-mine and the recorded various morphological types of leaf-mines, which include varied distribution of frass within the leaf-mine.

However, these data do not at all correlate with either host-plants, seasonality, the occupied habitat nor elevation. During our research, we were the first to identify species within the fauna of America, females of which have ovipositors (Remeikis et al., 2016a). All species with extended caudal segments were recorded exclusively from high-Andean habitats and presumably are related with very pilose host-plants growing in high Andes.

#### 4.2.2. Nepticulidae trophically related with plants of the *Quercus* genus

The research data revealed rather high diversity the *Quercus*-feeding Nepticulidae fauna in Central America. During the fieldwork in Guatemala, Belize and Honduras as well as Colombia, we identified larvae mining leaves of oaks (*Quercus* spp., including *Q. crassifolia* Humb. & Bonpl. and *Q. crispipilis* Trel., the section *Lobatae*); they were collected in habitats of mixed forests. We established that the *Quercus* miners occupied the elevation zone of approximately 1655–2500 m and belonged to nine species; all of these species are new to science (we described them in detail and published together with co-authors in 2013 and 2015 (see Stonis et al., 2013c; Remeikis and Stonis, 2015).

Though characters of genital structures within the *Stigmella* genus are known as reliable for the differentiation and diagnostics of species, the study of the species recorded in Colombia revealed that these characters of genital structures were not so universal as it had been considered before (especially in the case of the *Quercus* miners).

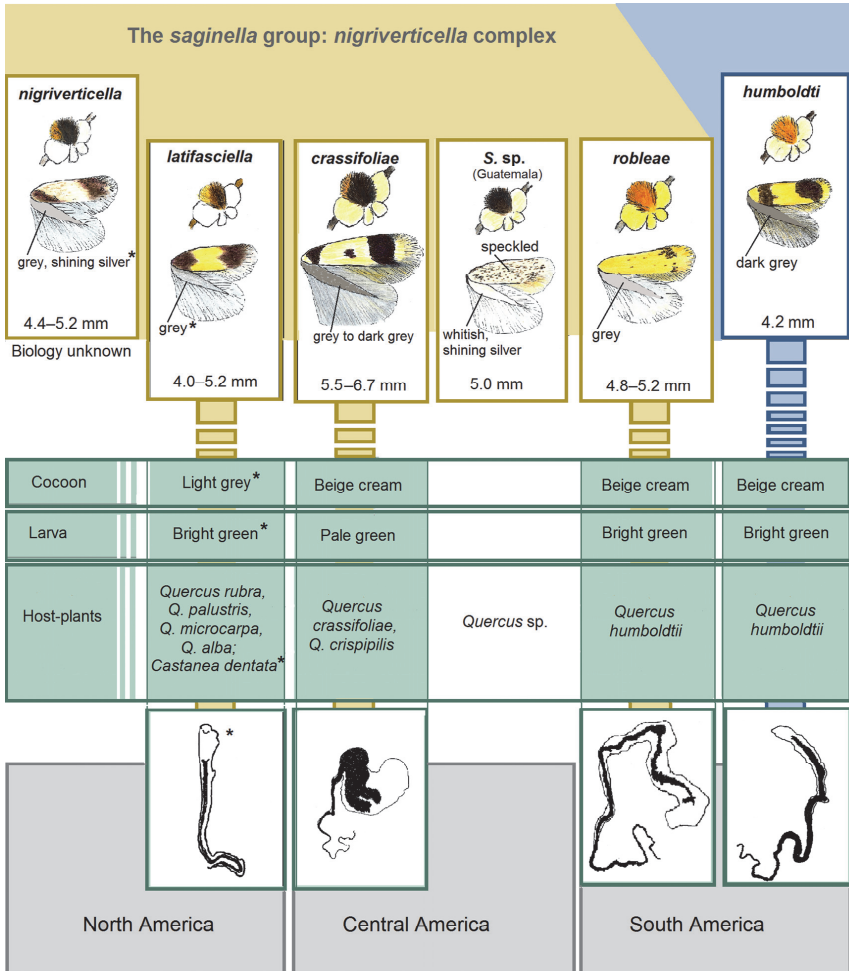
We established that within one of the groups (*S. saginella*), some species could be identified as a complex of very related, though distinct, species, which was named as a new *S. nigriverticella* species complex within the *S. saginella* group (Remeikis and Stonis, 2015) (Fig. 7).

The dissertation presents detailed characterization of diagnostic characters of the newly designated complex.

The *Quercus* miners that we were the first to record in South America (Colombia) significantly widen the knowledge about the geographical range of the distribution of Nepticulidae related with *Quercus* (Remeikis and Stonis, 2015). It should be noted that the *Quercus* genus is a new immigrant to northern regions of South America; according to palynological data from Pulido et al., 2006, the age of the oak pollen in Colombia is from 250 000 to 340 000 years.

Until now, Nepticulidae species trophically related with the *Quercus* plants, have been treated variously. Our detailed analysis of trophic relationships of these species revealed seven groups of the *Stigmella* species within the *Quercus* miners differing not only in their morphological characters but

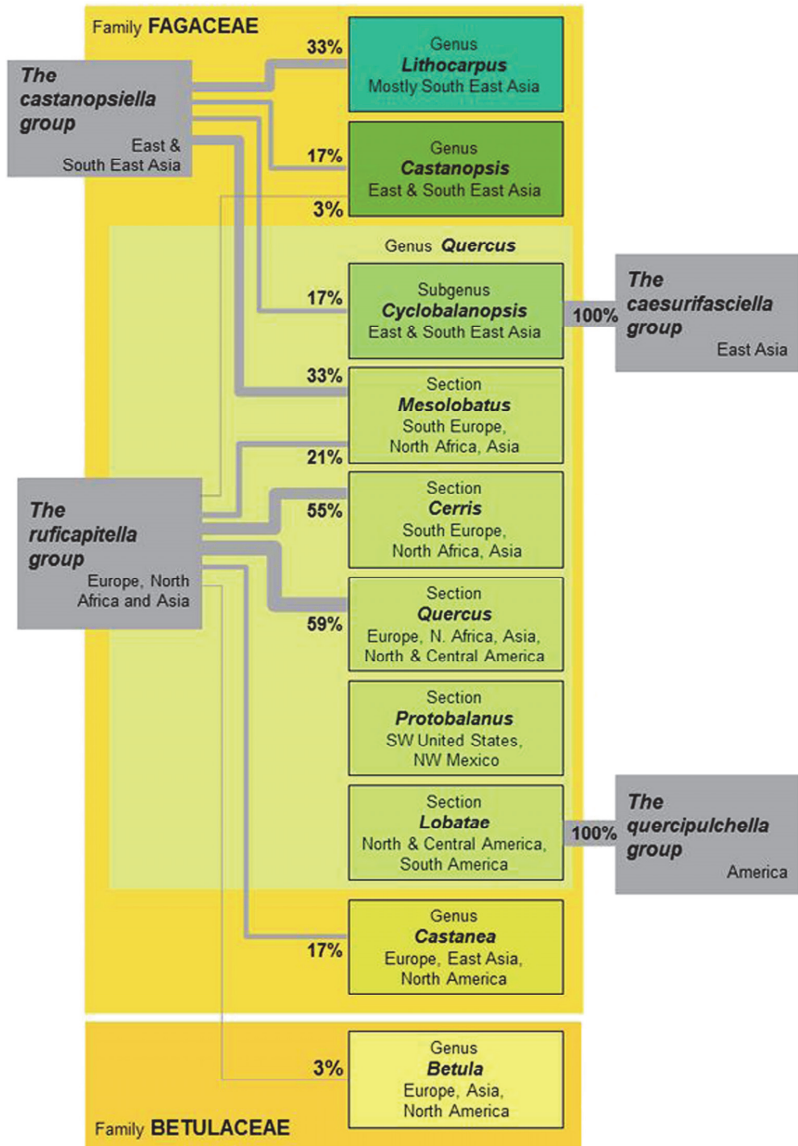




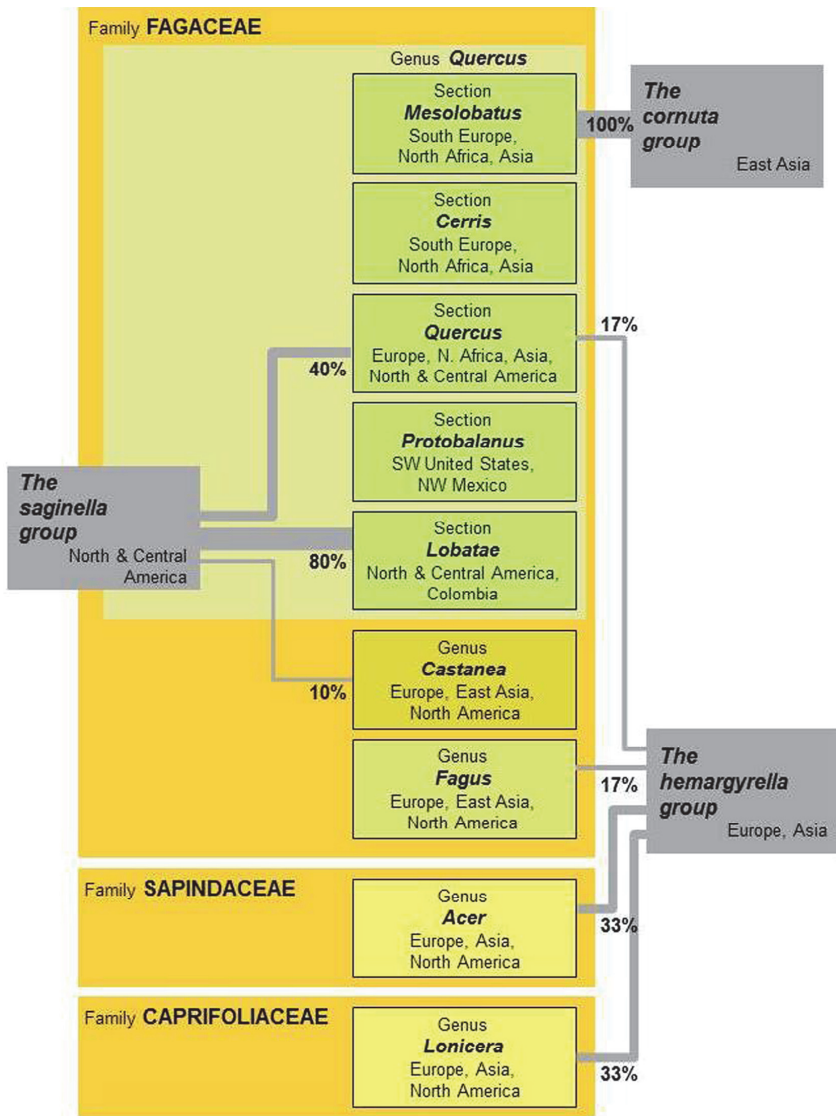
**Fig. 7.** Diagnostics of the *S. nigriverticella* species complex of the *Stigmella saginella* group (after Remeikis and Stonis, 2015).

also trophic preferences. The survey of the groups was published by the author together with co-authors in 2013 (Stonis et al., 2013a).

All the designated groups have unique features of their trophic preferences (Figs. 8 and 9). The dissertation presents detailed description of trophic relationships of these groups.



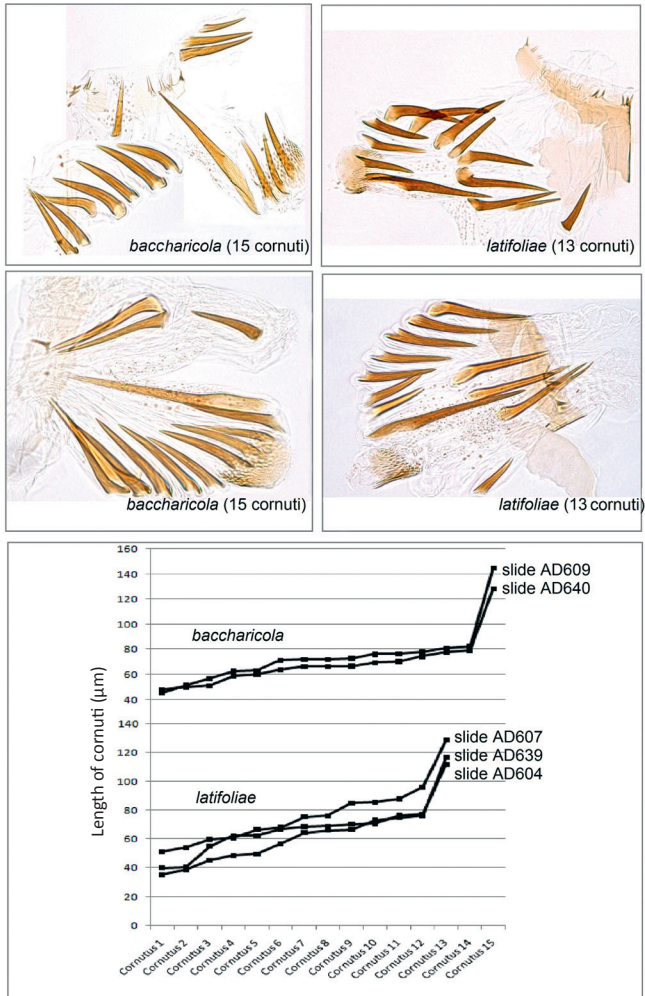
**Fig. 8.** Characteristics of trophic preferences of the *Stigmella castanopsiella*, *S. ruficapitella*, *S. caesurifasciella* and *S. quercipulchella* species groups (after the co-authored publication Stonis et al., 2013a).



**Fig. 9.** Characteristics of trophic preferences of the *Stigmella saginella*, *S. cornuta*, and *S. hemargyrella* species groups (after the co-authored publication Stonis et al., 2013a).

### 4.2.3. Nepticulidae trophically related with plants of the Asteraceae family

We were the first to record and describe the *Baccharis* L. genus as a genus of Nepticulidae host plants; eight *Baccharis*-mining species are analyzed in detail in a co-authored article (Stonis et al., 2016c).



**Fig. 10.** Comparison of *Stigmella baccharicola* and *S. latifoliae* (after the co-authored publication Stonis et al., 2016c).

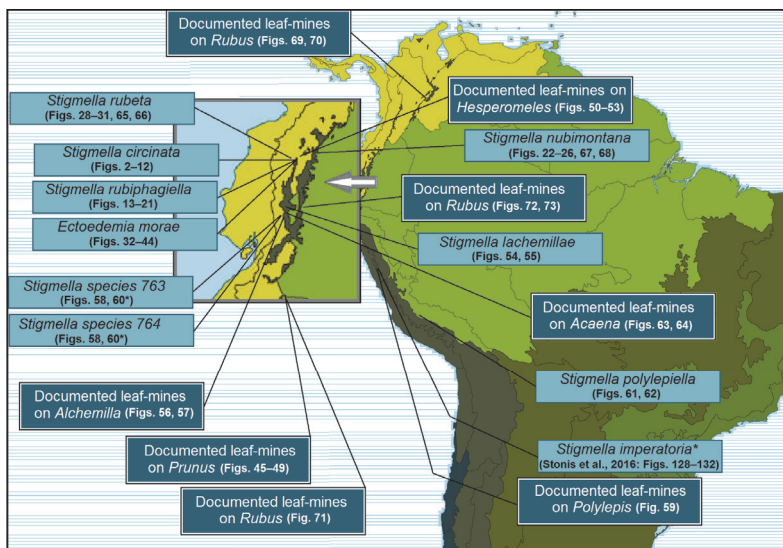
Though the majority of species trophically related with *Baccharis* exhibit exceptional morphological and mining characteristics and mine rather diverse plant species, the *Stigmella baccharicola* and *S. latifoliae* are very young species mining the same host plant *Baccharis latifolia* and only slightly differ in the colour of larvae and in some male genital structures, especially the set of cornuti (Fig. 10), as well as width of the mine.

The majority of *Baccharis*-miners occur in habitats of cloud forests (or habitats similar to cloud forests); only two *Baccharis*-mining Nepticulidae species (*Stigmella tripartita* and *S. confertae*) were recorded in páramo. We established that all the identified *Baccharis*-mining Nepticulidae species occupied the elevation zone of approximately 1800–3850 m.

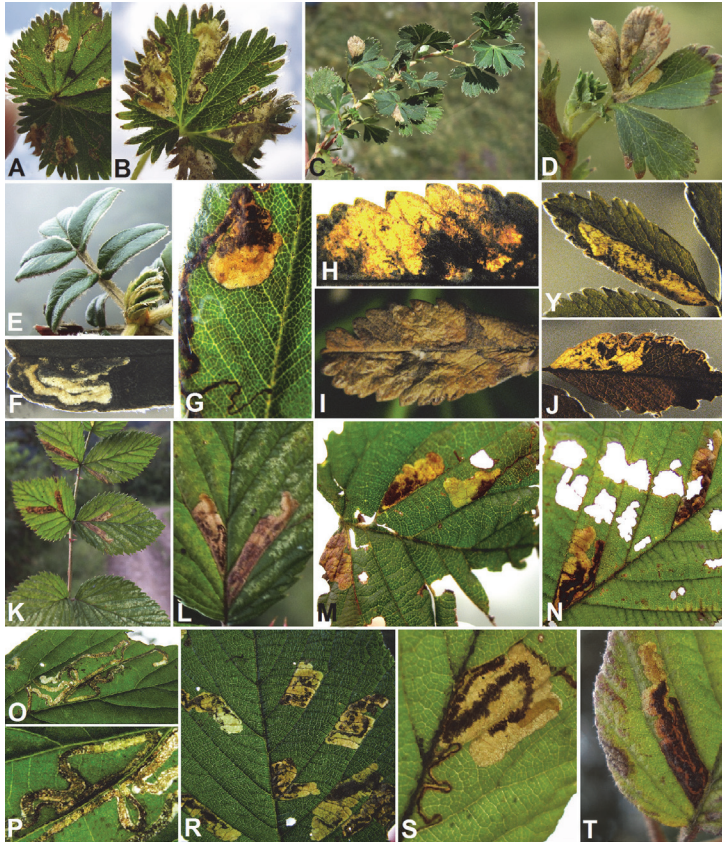
Other Asteraceae-mining species were described in the co-authored article Stonis et al., 2015a.

#### 4.2.4. Other trophic data

In the Palearctic region, the Rosaceae miners predominate. Therefore it was logical for us to identify trophic relationships of Nepticulidae regarding



**Fig. 11.** Nepticulidae taxa trophically related with Rosaceae (after the co-authored publication Stonis et al., 2016b).



**Fig. 12.** Samples of leaf-miners on Rosaceae from South America: A, B – *Stigmella lachemillae*, host plant *Lachemilla orbiculata* (Ruiz & Pav.) Rydb., Ecuador, 25 km NW Riobamba, 1°31'20"S, 78°50'27"W, 3980 m; C, D – host plant *Alchemilla procumbescens*, Ecuador, 30 km NE Pallatanga, 1°52'41"S, 78°54'11"W, 3025 m; E – host plant *Polylepsis pauta* Hieron.; F – host plant *Polylepsis racemosa* Ruiz & Pav., Peru, Junin Province, Ondores, 4100 m; G – leaf-mine of *Stigmella* species 763 (see Stonis et al., 2016); H, I – *Stigmella polylepiella*, host plant *Polylepsis racemosa* Ruiz & Pav., Peru, NW of Cuzco, 13°15'31"S, 72°15'54"W, 2850 m; Y, J – host plant *Acaena elongata* L., Ecuador, NW Riobamba, 1°31'20"S, 78°50'27"W, 3900 m; K, L – leaf-mine of *Stigmella nubimontana* (*Rubus* sp.), Ecuador, 11 km NW Alóag, 0°26'44"S, 78°37'36"W, 3085 m; M, N – leaf-mine of *Stigmella rubeta* (*Rubus* sp.), Ecuador, Tandapi, 0°25'26"S, 78°47'44"W, 1550 m; O, P – host plant *Rubus* sp., Colombia, Parque Chicaque, 4°36'21"N, 74°18'24"W, 2550 m; R – host plant *Rubus* sp., Ecuador, SE Loja, 4°04'53"S, 79°09'55"W, 2200 m; S, T – host plant *Rubus niveus* Thunb., Ecuador, Baños, 1°23'44"S, 78°26'14"W, 1855–2200 m.

the Rosaceae family in the region under research. In total, we registered 18 Nepticulidae taxa trophically related with various Rosaceae plants (Figs. 11 and 12). Trophic relationships with other plant taxa that we revealed and described are summarized in 4.3 of the Dissertation.

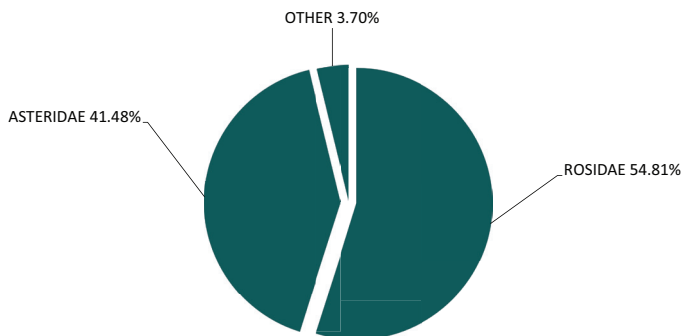
### 4.3. TROPHIC SPECIALIZATION OF NEPTICULIDAE

#### 4.3.1. New data about trophic relationships

Until our research, 88 Nepticulidae species had been known and only 10–15% of their host plants had been discovered in the Neotropical and Ando-Patagonian regions. During our research, we recognized 234 Nepticulidae species and documented leaf-mines belonging to 31 other unnamed taxa (in total, 265 Nepticulidae taxa). For half of these taxa, we established trophic relationships. See in more detail in the Dissertation.

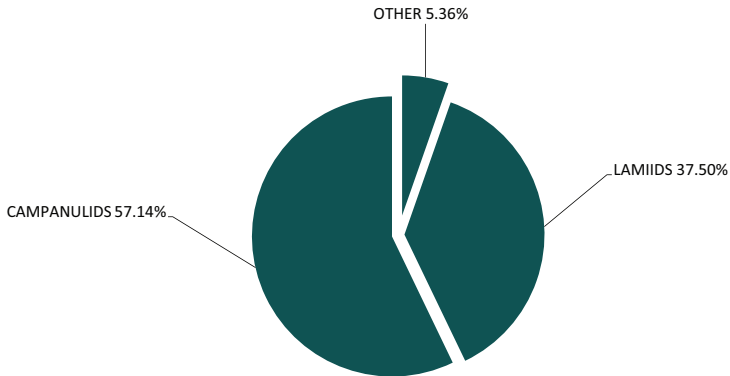
#### 4.3.2. Results of the trophic analysis

Preliminary analysis of tropical relationships of Nepticulidae occurring in Middle and South America revealed strong predominance of some host plants: most of the species are trophically associated with either Asterids (Asteridae, 41.5%) or Rosids (Rosidae, 54.8%); only a small fraction (3.7%) is trophically associated with host plants from other subclasses (Fig. 13).



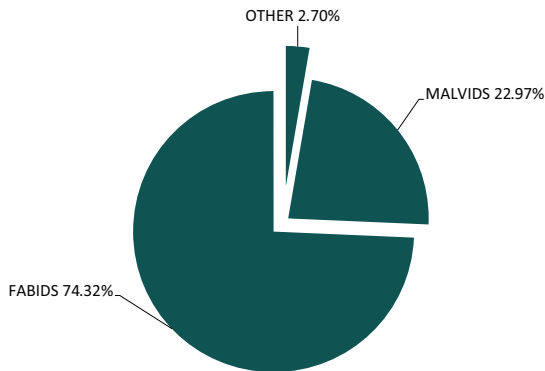
**Fig. 13.** Strong predominance of Asteridae and Rosidae miners in the Nepticulidae fauna of Middle and South America.

Among the Asteridae-feeders, species tropically associated with Campanulids account for 57.1% and species feeding on Lamiids, for 37.5%; only a minor percentage (5.4%) was detected as feeding on other Asterids (Fig. 14).



**Fig. 14.** Among the Asteridae-feeders, species tropically associated with Campanulids and Lamiids prevail.

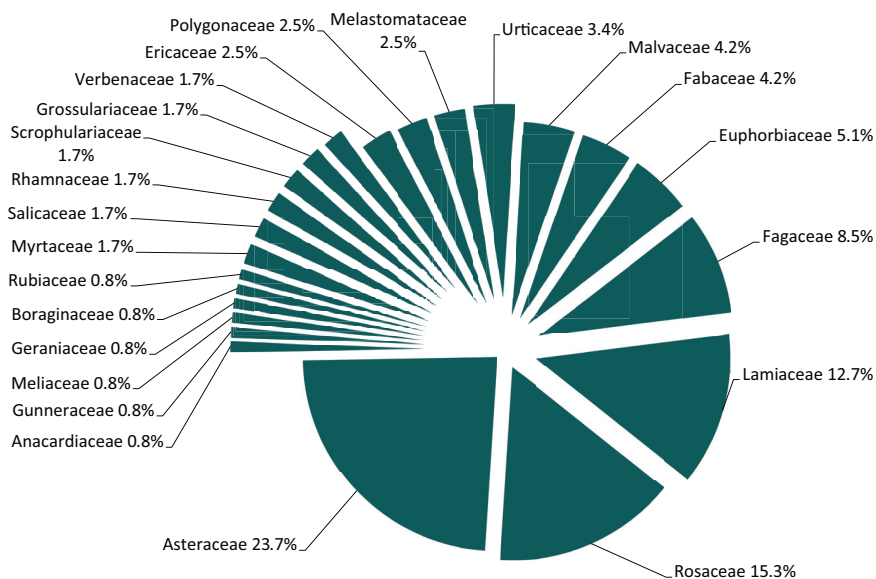
Among Rosidae-feeders, species tropically associated with Fabids account for 74.3% and species feeding on Malvids, for 22.9%; only a minor percentage (2.8%) was detected as feeding on other Rosids (Fig. 15) (Remeikis et al., 2016a).



**Fig. 15.** Among the Rosidae-feeders, species tropically associated with Fabids and Malvids prevail.



In the fauna of the Neotropical region, host plants from some families are very pronounced: feeding on Asteraceae plants was recorded for 23.7% of Nepticulidae taxa; on Rosaceae, for 15.3%; on Lamiaceae, 12.7%; on Fagaceae, 8.5%; on Euphorbiaceae, 5.1%; on Fabaceae and Malvaceae, 4.2% (each); on Urticaceae, 3.4% (each) ; on Polygonaceae, Melostomataceae, and Ericaceae, 2.5% (each); and on Grossulariaceae, Salicaceae, Rhamnaceae, Myrtaceae, Scrophulariaceae, and Verbenaceae, 1.7% (each) (Fig. 16). Some Nepticulidae were also detected on Gunneraceae, Geraniaceae, Anacardiaceae, Meliaceae, Rubiaceae, and Boraginaceae (0.8% each) (Remeikis et al., 2016a).



**Fig. 16.** Trophic relationships of Nepticulidae of the Neotropical region.

In the fauna of the Ando-Patagonian region, host plants from Asteraceae are the most pronounced, too: Nepticulidae taxa with host-plant records on Asteraceae account for 33.3%; there are also host plants detected from Myrtaceae, Anacardiaceae, and Salicaceae and some Nepticulidae are expected to be miners of Nothofagaceae (see Stonis et al., 2015).

In total, 24 plant families and 16 plant orders (Fig. 17) are currently revealed as host-plant clades for the Nepticulidae occurring in America, south of Neartic Mexico (Remeikis et al., 2016a).

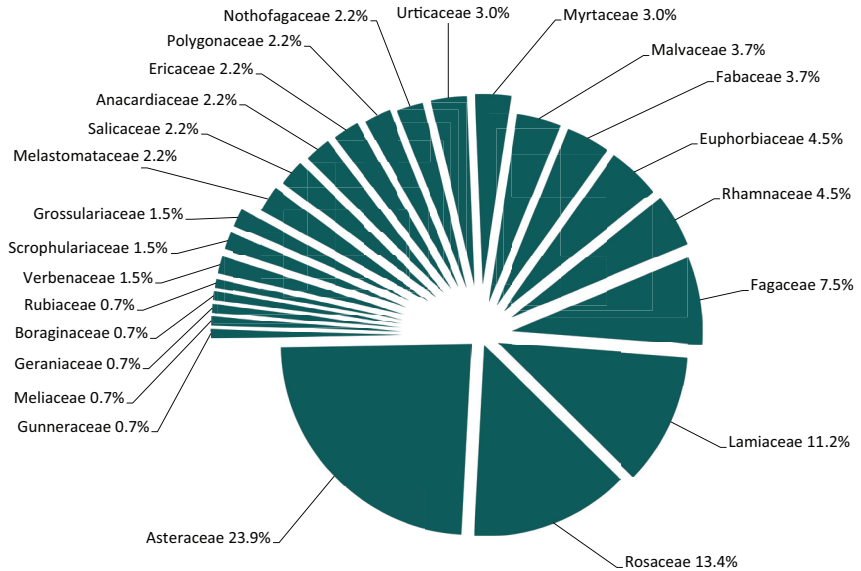


Fig. 17. Trophic relationships of Nepticulidae from Middle and South America (the Neotropical and Ando-Patagonian regions).

Preliminary analysis showed some unexpected but pronounced feeding tendencies of Nepticulidae occurring in the Neotropics and the Ando-Patagonian region (Fig. 18). In contrast to the Holarctic fauna, where only 0.2% of Nepticulidae species are associated with the Asterales order, in the region under study, 24% of the species are Asterales-feeders. A less pronounced but still striking difference between faunas of the Holarctic and Neotropical + Ando-Patagonian (formerly Neotropical, *sensu lato*) was detected among the Lamiales-feeders: they are very abundant (accounting for about 14.3% of all tropically investigated non-Nearctic American species); however, in contrast to the Holarctics, almost all of them belong to a single genus (*Stigmella* Schrank) (Remeikis et al., 2016a). On the other hand, the Rosales-feeders, the largest group of Nepticulidae in the Holarctics, are still less pronounced

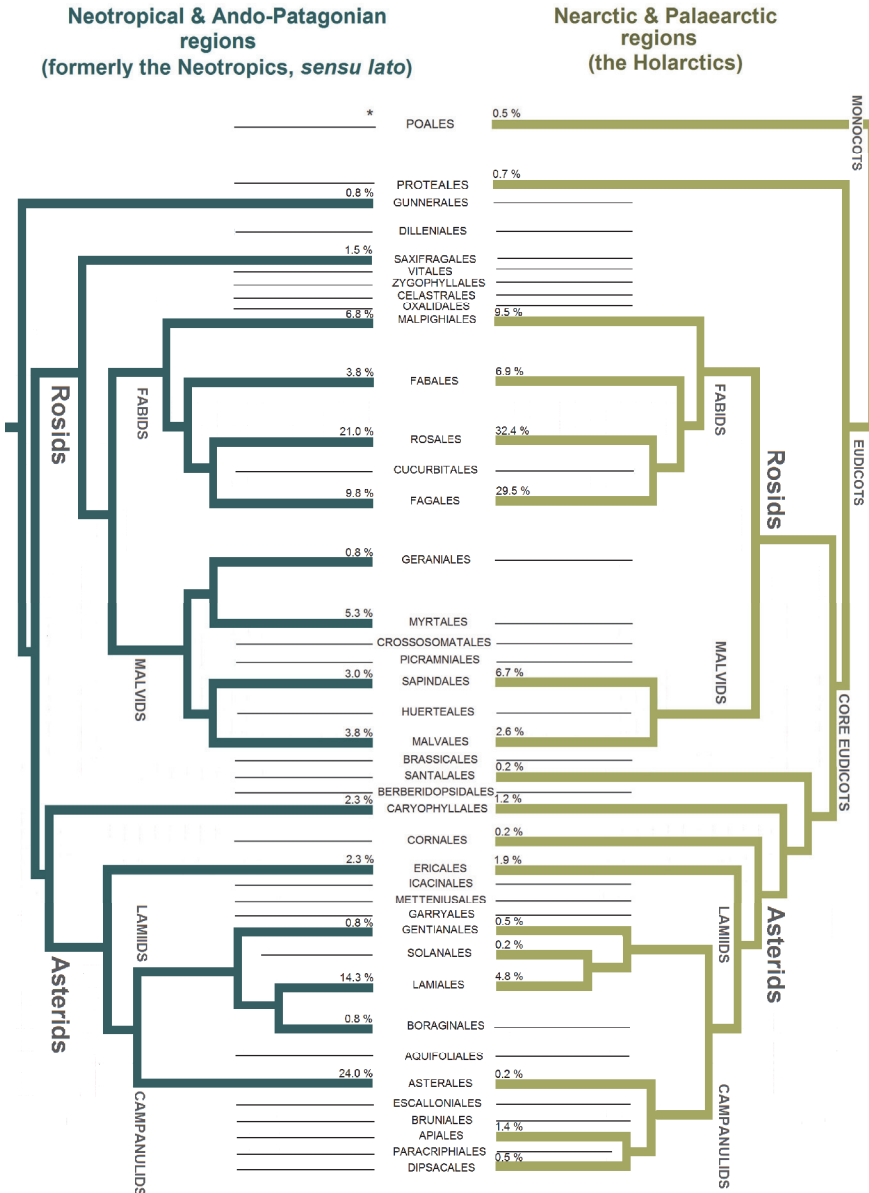


Fig. 18. The plant clades engaged by Nepticulidae in the Neotropical and Ando-Patagonian regions, and the Holarctics (\* – van Nieukerken, pers. comm.).

in non-Nearctic America (species on Rosales account for 21% in comparison with 32.4% in the Holarctics) (Remeikis et al., 2016a). Another interesting particularity of the American (Neotropical and Ando-Patagonian) fauna is the presence of leaf-miners on Myrtales, Geraniales, Boraginales, and even on Poales (van Nieuwerkerken, pers. comm.) which are still unknown in the Holarctic fauna with about 250-years of study history.

Though host-plant data were available only for half of the Neotropical and Ando-Patagonian taxa, our trophic analysis shows pronounced feeding strategies, though it has to be confirmed by further sampling.

#### 4.4. NEPTICULIDAE IN VARIOUS HABITATS

##### 4.4.1. Occupied habitats

While analyzing trophic relationships of Nepticulidae found in páramo, we established that the majority of mining species (about 50%) were related with the Asteraceae family: about 25% of species were trophically related with host plants of the *Baccharis* genus; 12.5%, with *Gynoxys*; and 12.5%, with *Pentacalia*. In total, we registered four families of host plants in páramo: Asteraceae (about 50%), Grossulariaceae (25%, trophically related with plants of the *Ribes* genus), Scrophulariaceae (12.5%, trophically related with plants of the *Calceolaria* genus) and Rosaceae (12.5%, trophically related with plants of the *Lachemilla* genus).

The study of the activity of Nepticulidae larvae in páramo revealed one activity peak starting in January and ending at the beginning of March. Similar data were received during the study of the activity of adults, which was observed in February–March.

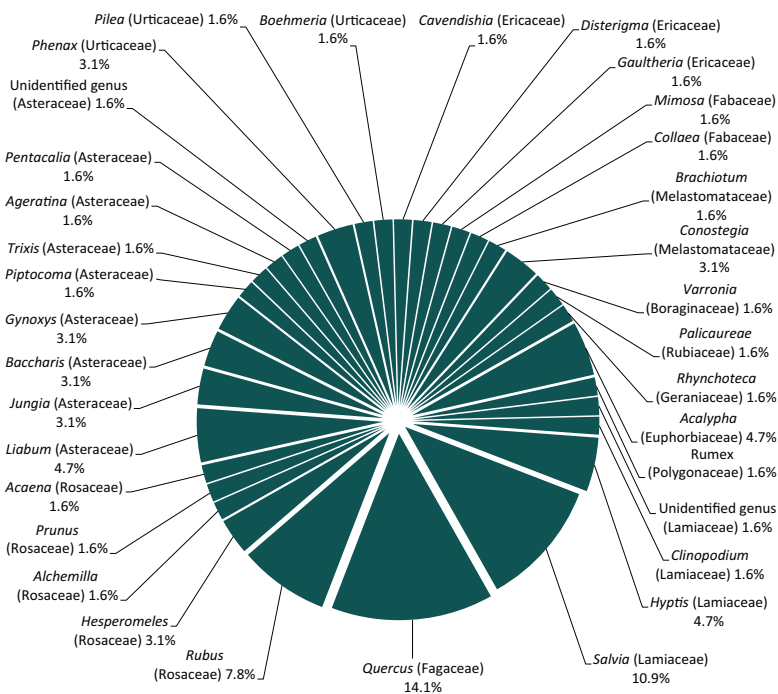
Nepticulidae of puna do not exhibit explicit trophic regularities; however, we could state that a large part of miners are related with Asteraceae and Euphorbiaceae (in total, about 57% taxa are trophically related with *Ageratina*, *Acalypha* and other genera of Asteraceae and Euphorbiaceae).

The seasonal cycles of Nepticulidae in puna (especially regarding those of adults) were more thoroughly studied than those of páramo; however, the data on puna should be treated only as preliminary (for more detail see 4.4.1 of the Dissertation).

After evaluating trophic relationships in cloud forest habitats, we revealed trophic relationships with 11 plant genera; the majority of miners (by assessing the percentage of Nepticulidae species) feed on plants of *Baccharis* (20%), *Liabum* (16%) and *Rubus* (20%). It must be noted that in cloud forests, the majority of Nepticulidae are related with the Asteraceae (about 44%) and Rosaceae (28%) families. In cloud forest habitats, we registered the following three more families of host plants: Lamiaceae (12% of Nepticulidae taxa), Urticaceae (8%) and Fagaceae (4%).

In cloud forests, we registered one activity peak in January–February. Similar data were received from estimating the activity of adults: the activity peak was registered in February–March.

In our dissertation, we treated diverse tropical montane moist forest habitats as one habitat (*sensu lato*). Our study revealed very high diversity of host-plants in tropical montane moist forests (Fig. 19).



**Fig. 19.** Trophic specialization of Nepticulidae occurring in habitats of tropical montane moist forests.

We are of an opinion that such diversity is determined not only by variety and abundance of habitats but presumably also more favourable climatic conditions. The Nepticulidae species are trophically related with 34 plant genera, which make up 13 plant families, among which most mined (by assessing the percentage of Nepticulidae species) are the following host-plant groups: Asteraceae (22% of recorded Nepticulidae taxa), Lamiaceae (about 19%), Rosaceae (about 16%) and Fagaceae (14%).

The activity of Nepticulidae in habitats of tropical moist forests was recorded as starting in December and achieving its peak in February (larvae) and March (adults).

In tropical montane dry forest habitats, Nepticulidae are related with the following three host plant families: Asteraceae, Lamiaceae and Myrtaceae, though this fact has not been sufficiently investigated.

We recorded one activity peak starting in January and ending at the beginning of March. Similar data we received while studying the activity of Nepticulidae registered in February–March.

Our estimation of trophic relationships of tropical lowland forest habitats revealed that host plants from Malvaceae, Fabaceae and Salicaceae mined by Nepticulidae larvae slightly predominated and made up about half of the host-plants in the tropical lowland forests (46%). It should be noted that in tropical lowland forest habitats, we also recorded the following Nepticulidae host plants: Anacardiaceae, Salicaceae, Rhamnaceae, Gunneraceae and Meliaceae.

In tropical lowland forests, the following two activity peaks could be distinguished: one starting in January and ending in March and another, which is shorter (but more pronounced), in April. During these periods, we did not register significant increase of mining activity except somewhat more active mining in January–February.

It appeared that in the tropical coastal zone, rather a large part of miners trophically relate with the Malvaceae and Verbenaceae families (about 45%): 11.1% of Nepticulidae feed on *Guazuma* (Malvaceae); 11.1%, on *Gossypium* (Malvaceae); and 22.2%, on *Lantana* (Verbenaceae).

In tropical coastal habitats, activity cycles of adults were more thoroughly studied than mining cycles; the following three activity peaks could be

distinguished: the first (somewhat longer) starting in February and continuing until May; the second, in July–August; and the third, which is the shortest but most pronounced, in September.

Our estimation of trophic relationships of the Nepticulidae occurring in habitats of temperate south Andean forests revealed that trophically, Nepticulidae species were mostly related with Asteraceae (25%), Rhamnaceae (25%) and presumably Nothofagaceae\* (about 19%).

The analysis of the activity of Nepticulidae adults occurring in temperate south Andean forests showed one activity peak starting in September and ending in March; however, we did not register any pronounced activity peaks while estimating the mining of Nepticulidae.

Trophic relationships of Nepticulidae occurring in various habitats and their registered activity peaks are analyzed in more detail and illustrated in 4.4.1 of the Dissertation.

#### **4.4.2. Nepticulidae trophically related with the ecologically very significant Andean *Polylepis* forests**

After the glacial period the highlands of the Andes were open to colonization by *Polylepis* trees, and *Polylepis* forests constituted the natural vegetation in much of the high Andes (Hooghiemstra, Cleef, 1995; Fjeldså, Kessler, 1996).

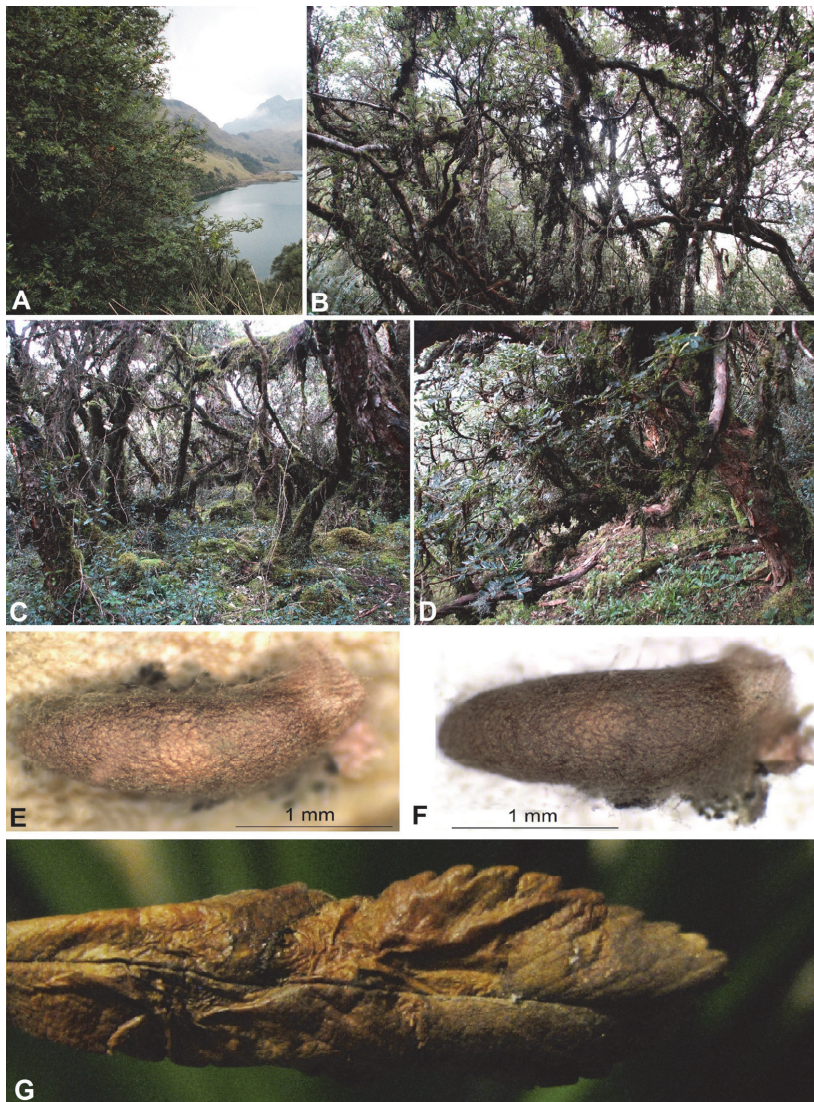
However, nowadays, mainly because of heavy deforestation, remnants of the high Andean forests, which have been conserved to present time, mostly either inhabit inaccessible steep slopes, deep canyons and ravines, places among rocks or the remaining patches of *Polylepis* forests are spread out in an open landscape but separated by huge areas of grass páramo (Ridbäck, 2008).

The forests of *Polylepis* have a unique biological diversity and no leaf-mining Nepticulidae associated with *Polylepis* have been recorded previous-

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\* *Nothofagus* (Nothofagaceae) is assumed to be a host plant of some *Stigmella* species (Nepticulidae); though no leaf-mines have been discovered, adults have been observed flying around *Nothofagus pumilio* trees (see our co-authored publication Stonis et al., 2014b).

ly. In the dissertation we reported on the first discoveries of *Polylepis*-feeding Nepticulidae species in the high Andes of Ecuador and Peru (Fig. 20).



**Fig. 20.** *Polylepis* forest (A–D), cocoons (E, F) and leaf-mine (G) of *Stigmella polylepiella*, Peru (after the co-authored publication Stonis et al., 2016e).



Leaf-mining Nepticulidae species are associated with at least two species of *Polylepis* as a host plant (including *Polylepis racemosa* and *P. pautai*) occurring in the high Andes of Peru and Ecuador and belong to the genus *Stigmella* Schrank. All discovered Nepticulidae taxa were new, but only *Stigmella polylepiella* sp. nov. was described and named; other taxa were documented but left unnamed pending additional material (currently, only dissected pupae, not adults, are available).

In contradiction to expectations, the first discoveries of leaf-mining Nepticulidae on *Polylepis* revealed that species feeding on *Polylepis* are not closely related but indicate unexpectedly great morphological diversity (more than usual in comparison to species feeding on the most of other host-plant genera in South America) and represent highly distinctive taxa among all known *Stigmella* worldwide. Apriori we can assume that these species (particularly *Stigmella* species 764) are rather a result of older evolutionary events than the recent speciation so commonly known in the Andean fauna (see our co-authored paper Stonis et al., 2016e)

#### **4.4.3. The world's highest altitudinal Nepticulidae fauna (at the elevation of 3700–4700 m)**

One of the most unexpected results of the present study was the discovery of a species-rich fauna occurring in the High Andes (Fig. 21): twenty-nine species of leaf-mining pygmy moths are recorded as occurring in the Andes in elevations above 3700 m (see our co-authored paper Stonis et al., 2016d). The described fauna represents the world's highest altitude Nepticulidae fauna. The absolute height record belongs to the Peruvian *Stigmella nivea* sp. nov. collected at elevation of 4700 m.

In the Andes, the high-altitude Nepticulidae fauna engages various habitats from northern shrub and grass páramo in Ecuador to moist puna in southeastern Peru and western Bolivia. All currently known high-Andean species are described from two biogeographical provinces: the Páramo and Puna belonging to the South American transition zone.

Host plants of some twenty species are still unknown; however, some tendencies of trophic relationships can be preliminary predicted based on ten species whose host-plants are known. The species associated with

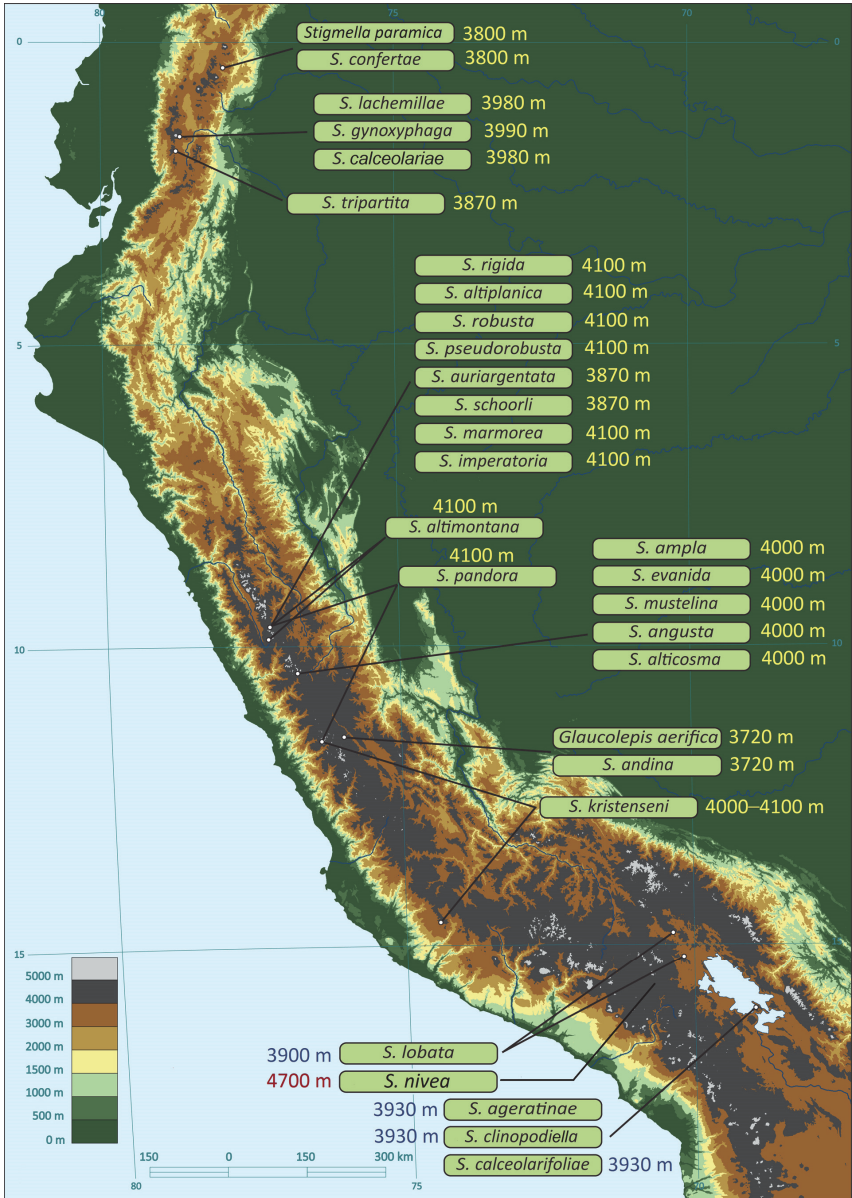


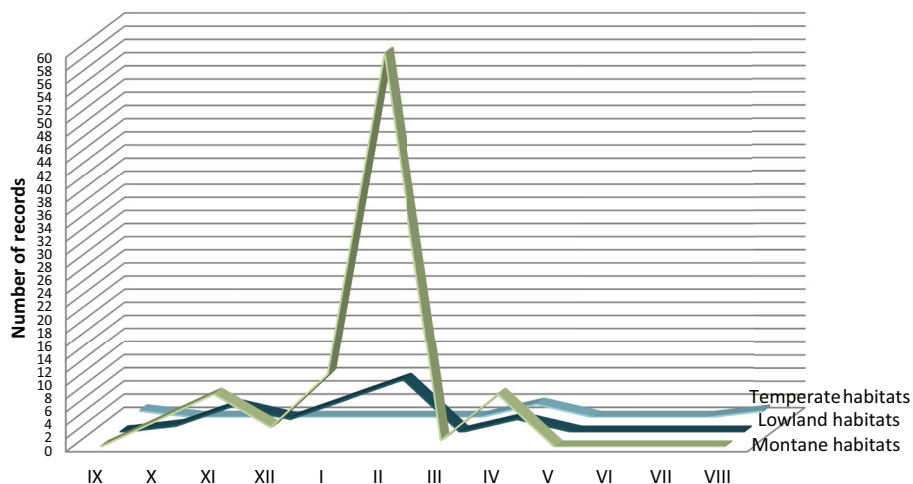
Fig. 21. The world's highest altitudinal fauna recorded for the first time (after the co-authored monograph Stonis et al., 2016d).

Asteraceae may possibly prevail (five species have been detected on *Pentacalia*, *Baccharis*, *Gynoxys* and *Ageratina* plants); only a few are associated with Calceolariaceae (*Calceolaria*), Lamiaceae (*Clinopodium*), and Rosaceae (*Lachemilla* and *Polylepis*; see our co-authored paper Remeikis et al., 2016a).

#### 4.5. SEASONALITY AND OCCURRENCE IN MIDDLE AND SOUTH AMERICA IN GENERAL

##### 4.5.1. Seasonality of Nepticulidae

On the basis of our field research, we could provide data about the seasonality of Nepticulidae in Middle and South America regarding the following groups of habitats: tropical lowland, tropical montane and temperate (Figs. 22 and 23). Detailed description of the Nepticulidae seasonality is provided in 4.5.1 of the Dissertation.



**Fig. 22.** Seasonality of Nepticulidae larvae in Middle and South America (see our co-authored paper Remeikis et al., 2016a).

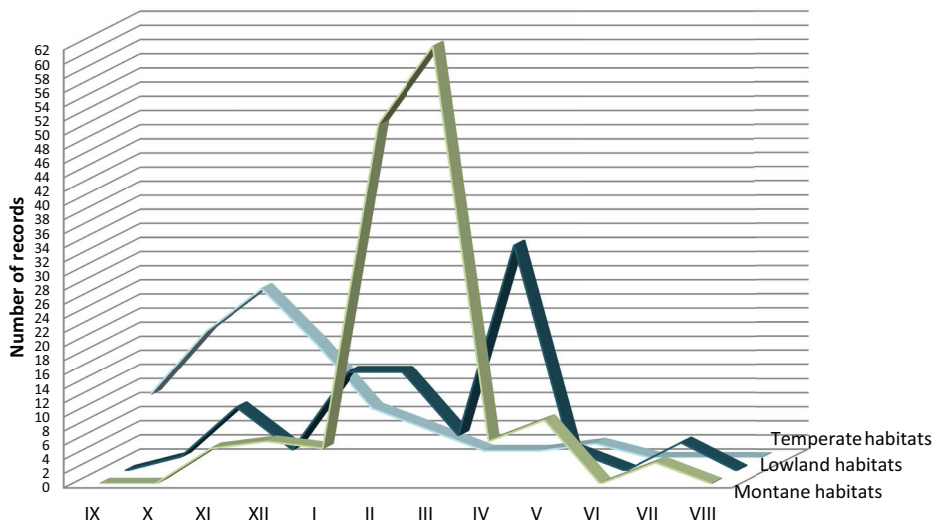


Fig. 23. Seasonality of Nepticulidae adults in Middle and South America (see our co-authored paper Remeikis et al., 2016a).

#### 4.5.2. Abundance and occurrence

By incorporating our research data and all data published by other researchers (see “Research history”), we revealed groups of relative mining abundance of Nepticulidae in Middle and South America (in line with the methodology presented in 3.2.3 of the Dissertation and this Summary).

After analyzing occurrence of Nepticulidae species in Middle and South America, we designated the common and rare species. After summing up relative mining abundance (*spA*) and spatial (geographical) distribution (*spD*), we were able to designate the species occurrence (*Occ*) groups (in line with the methodology presented in 3.2.3 of the Dissertation). It appeared that the rare species predominated; however, this occurrence group is not homogeneous. The majority of the species of this occurrence category are characterized by limited distribution and moderately abundant mining; in total, we attributed 59 species to this group. Detailed analysis of species occurrence is analyzed in 4.5.2 of the Dissertation.

#### 4.5.3. Nepticulidae trophically related with cultivated and otherwise significant as well as endemic and protected plants

Part of Nepticulidae taxa in the regions under research were designated as pests (or potential pests) of cultivated and otherwise significant as well as endemic and protected plants. Only four of these species (*Stigmella rubeta*, *S. nubimontana*, *S. gossypii* and *Ozadelpha guajavae*) had already been considered pests; the remaining species were considered as such for the first time.

The dissertation presents a survey of pests (or potential pests) according to groups of their host plants: 1) miners of berry plants, 2) miners of pharmaceutically significant and aromatic plants, 3) miners of cultivated plants, 4) miners of plants having other economic significance, 5) miners of endemic and protected plants.

## 5. SUMMARY OF THE RESULTS

### 5.1. FAUNAL DATA

After studying the material collected in Costa Rica, Mexico and Ecuador, we identified 40 Opostegidae species (19.8% of the world's fauna) including the following three species: *Pseudopostega robusta*, *P. mexicana* and *P. latiplana*, which were described as new species during the dissertation project. In total, we identified 86 Opostegidae species, which comprise 43% of the world's currently known Opostegidae fauna;

After reviewing the distribution data of Opostegidae, we established that the majority of Opostegidae species were from Costa Rica; chorological analysis of this abundant fauna showed that the Opostegidae species occurring in Costa Rica could be divided into four chorological groups. At present, half of all the Opostegidae species (13 or 50%) occur exclusively in Costa Rica and only several Opostegidae taxa occur in other territories. One Opostegidae species occurs in Costa Rica and Panama; two species (7.7%), only in Middle America (Costa Rica) and the Caribbean region; seven Opostegidae species (27%), in Middle and South America (but not in the Carib-

bean region); and only three Opostegidae species (11.5%) are characterized by transneotropical distribution.

The data from the taxonomic analysis, during which we studied unidentified collection material deposited at various research centres as well as research material of the author, show that the Nepticulidae fauna of Middle and South America now comprises 11 genera and 222 species (among them, 146 species were newly identified during the dissertation project and the first authorship of 67 Nepticulidae species belongs to the author of the dissertation). During the dissertation project the richest Nepticulidae fauna was observed in Ecuador (67 species), Peru (40 species), Argentina (35 species) and Belize (31 species).

Drawing on newly established diagnostic characters, we restored the generic status to *Manoneura* (in contrast to the statements of some other authors); we treat *Neotrifurcula* van Nieukerken as part of *Glaucolepis*.

The study of morphological structures (taking into account the newly studied ecological peculiarities) allowed us to designate species groups within all the genera of the Nepticulidae of Middle and South America. Diagnostic characters of these groups are analyzed in the dissertation. Species which were not attributed to groups but were diagnostically similar were listed as satellite taxa.

Though many Nepticulidae taxa have high morphological differentiation, among the four species groups designated within *Acalyptis*, we named two complexes of very closely related species (*A. bicornutus* and *A. tenuijustus*). The highest diversity of groups was found within *Stigmella*. Among the 18 newly designated species groups, we also found cryptic taxa characterized by very low morphological differentiation. These taxa occurring in the Ando-Patagonian region were attributed to the new *Stigmella sinuosa* species complex.

## 5.2. ECOLOGICAL DATA

Miners of the *Quercus* genus (Fagaceae), which we were the first to discover in the Neotropical region, occupy the elevation zone of 1655–2500 m and are distributed in various habitats (mostly in mixed oak and pine forests as well as cloud forests). From the taxonomic (species) point of view, the Nep-

ticulidae fauna of Middle and South America is very diverse. It comprises ten taxa trophically related with various species of the genus and includes the miners discovered at the southern border of the *Quercus* range, in Colombia (*Stigmella robleae* and *S. humboldtii*). The host-plant, *Quercus humboldtii*, is the endangered tree of the Pliocene origin.

Analysis of the *Quercus* mining Nepticulidae showed that the specialized Nepticulidae fauna was not homogeneous from the taxonomic point of view and was of polyphyletic origin.

Detailed study of trophic relationships of Nepticulidae allowed us to indicate seven groups of the *Quercus* miners within *Stigmella*. They differ not only in their morphological characters but also in their trophic preferences as well as their trophic preferences for various *Quercus* subgenera or sections. The study revealed that the most specific are species belonging to the *S. quercipulchella* species group, which mine plants exclusively belonging to the section of red oaks (*Lobotae*). It exhibits strong tendencies for strict oligophagy of this group. Other *Stigmella* species groups are not homogeneous.

We designated a species group (*Stigmella purpurimaculae*) presumably related to *Nothofagus*. This group may be one of the new examples of the Gondwana fauna.

We were the first to discover and describe the Nepticulidae fauna trophically associated with *Baccharis* (Asteraceae). It is distributed in habitats of cloud forests (or habitats resembling moist forests including páramo) and occurs in the elevation zone of 1800–3850 m. The eight species that we described from *Baccharis* are characterized by abundant or very abundant mining; however, the mortality of larvae is unusually high (the reasons unknown).

Though in other regions (Palearctic as well as Nearctic), Rosaceae-miners predominate, we recorded 18 taxa in Middle and South America (mostly belonging to the *Stigmella* genus) trophically related with various Rosaceae plants; the trophic spectrum comprises the following plant genera: *Rubus* (4 taxa), *Lachemilla* (1 taxon), *Alchemilla* (1 taxon), *Acaena* (1 taxon), *Hesperomeles* (2 taxa), *Prunus* (1 taxon) and *Polylepis* (4 or 5 taxa of miners).

After analyzing trophic relationships, we found that 96% of Nepticulidae of the Neotropical and Ando-Patagonian regions were trophically related with Asteridae (41.5%) and Rosidae (54.8%). Among the specialized Aste-

ridae miners, about 57% taxa are related with Campanulids and 38%, with Lamiids, whereas among the Rosidae miners, the majority of taxa (74%) are related with Fabids and 23%, with Malvids. In total, the Nepticulidae taxa of the Neotropical and Ando-Patagonian regions are trophically related with 24 families of host-plants belonging to 16 plant clades.

Trophic specialization of the Nepticulidae of Middle and South America (the Neotropical and Ando-Patagonian regions) exhibits ecological exclusiveness and characteristics different from the earlier investigated Nearctic and especially Palaearctic regions. In the Palaearctics the miners of some host-plants are not abundant (e.g. Asteraceae miners make up 0.3% and Lamiaceae, 4%); whereas in the Neotropical and Ando-Patagonian regions, Asteraceae and Lamiaceae are the most engaged host-plant families: 24% of miners are trophically related with plants of the Asteraceae family and 11%, with Lamiaceae.

In páramo habitats, we registered four host-plant families utilized by Nepticulidae; about 50% of species are trophically related with exclusively Asteraceae plants (among them, 25% of species, with *Baccharis*; 12.5%, *Gynoxys*; and 12.5%, with *Pentacalia*).

Cloud forest habitats are particularly significant for their humidity, support of the hydrological cycle, plant diversity and endemism of fauna. After analyzing trophic relationships of Nepticulidae of cloud forest habitats, we established that Nepticulidae species were trophically related with 11 plant genera, among which *Baccharis*, *Rubus* and *Liabum* prevailed.

Among all the eight habitat groups analyzed in the dissertation, moist tropical montane forests exhibit the highest diversity of host-plants; the Nepticulidae species are trophically related with 33 plant genera belonging to 13 plant families, among which the following families of host-plants are most utilized (by assessing the percentage of Nepticulidae species): Asteraceae (about 22%), Lamiaceae (about 18%), Rosaceae (about 16%) and Fagaceae (about 15%).

The Andean *Polylepsis* forests are particularly significant from the ecological point of view. After identifying and describing for the first time their Nepticulidae fauna, we established that the Nepticulidae species feeding on *Polylepsis* were not closely related but were characterized by a wide range of



morphological characters; it could be assumed that these species are rather a result of old evolutionary events than “products” of the recent speciation commonly characteristic of the Andean fauna.

Twenty-nine Nepticulidae species (among them, 22 species are presented as new to the science in the dissertation) were recorded at the elevation of more than 3700 m and represent the world’s highest altitudinal Nepticulidae fauna (the highest elevation record belongs to *Stigmella nivea*, which was collected in Peru at the elevation of 4700 m). Though the fauna of the high Andes is rich in species, from the taxonomic point of view, this fauna is rather homogeneous (almost all species belong exclusively to *Stigmella*).

Investigation of the activity of Nepticulidae adults in montane habitats reveals one peak which starts in January and ends at the beginning of April. At the lowland habitats we observed two pronounced activity cycles of adults: the first starts in January and ends in March and the second peak, which is shorter, starts in April and ends at the beginning of May. The activity of Nepticulidae adults in temperate habitats is observed at other times: the majority of adults fly from September to January.

In both montane and lowland habitats, active mining of Nepticulidae larvae starts in December and ends in March. We also observed mining during later months but its activity does not reach parallel the January–February peak.

Among the identified five groups of relative mining abundance of Nepticulidae in Middle and South America, about 46% of known species are characterized by moderately abundant mining and 34%, not abundant mining. The analysis of species occurrence revealed that rare species prevail; however, this group is not homogeneous: most species are characterized by limited distribution and not abundant mining.

Some of the identified Nepticulidae species of Middle and South America are relevant from the economical point of view as potential pests: *Stigmella rubeta*, *S. nubimontana*, *S. species 4852*, *S. sp.*, *S. sp.*, *Ectoedemia morae* (miners of berry plants); *Stigmella sp.*, *S. sp.*, *S. sp.* (miners of pharmaceutically significant and aromatic plants); *Acalyptis cedrelus*, *Ozadelpha guajavae*, *Stigmella gossypii*, *Fomoria miranda* (miners of cultivated plants); and *Stigmella humboldti*, *S. podantheae*, *S. sp.* (miners of endemic or protected plants).

## CONCLUSIONS

1. The Opostegidae fauna now counts three genera and 86 species from Middle and South America (which comprise 43% of the world's currently known Opostegidae) or 40 species from Middle America alone (i.e. 19.8% of the world's fauna), including the following newly discovered species: *Pseudopostega robusta*, *P. mexicana* and *P. latiplana*. The majority of Opostegidae species are known from Costa Rica, and, from the chorological point of view, could be divided into four chorological groups, from which only one group is characterized by wider transneotropical distribution, while three other groups (comprising 88.5% of the species) have various but limited distribution within Middle America.
2. The Nepticulidae fauna of Middle and South America now counts 11 genera and 222 species, including 146 species which were newly introduced, i.e. discovered, identified and most of them described.
3. Drawing on the newly reviewed diagnostic characters, the generic status was restored to *Manoneura* Davis; however, *Neotrifurcula* van Nieukerken was recognized as part of *Glaucolepis* Braun. Though many Nepticulidae taxa have high morphological differentiation, among species groups newly designated within *Acalyptis*, there are at least two complexes of very closely related species (*A. bicornutus* and *A. tenuijuxtus*). The highest diversity of groups can be found within *Stigmella*; among the 18 newly designated species groups, some cryptic taxa characterized by very low morphological differentiation were found (e.g. the Ando-Patagonian *S. sinuosa* species complex).
4. In Middle and South America, diverse trophically specialized *Quercus*-feeding Nepticulidae fauna occupies the elevation zone of 1655–2500 m (including at the southern border of the host-plant range). Rich, previously unknown but trophically specialized fauna was also found associated with many Rosaceae, Lamiaceae and Asteraceae host-plants, particularly plants from the *Baccharis* genus occupying the elevation zone of 1800–3850 m mostly in cloud forest habitats.

5. Though Nepticulidae of the Neotropical and Ando-Patagonian regions are trophically related with 24 plant families belonging to 16 plant clades, about 96% of the Nepticulidae in these regions are trophically related with Asteridae (41.5%) and Rosidae (54.8%). In the Palearctics the miners of some host-plants are not abundant (e.g. Asteraceae miners make up 0.3% and Lamiaceae, 4%); however, in the Neotropical and Ando-Patagonian regions, Asteraceae and Lamiaceae are the most engaged host-plant families: 24% of miners are trophically related with plants of the Asteraceae family and 11%, with Lamiaceae.
6. Despite the extraordinary wide range of habitats occupied by Nepticulidae in the Neotropical and Ando-Patagonian regions, tropical montane moist forests could be characterized by the highest diversity of utilized host plants (34 genera and 13 families). The world's highest altitudinal Nepticulidae fauna with the record of 4700 m belonging to *Stigmella nivea*, is rich in species but, from the taxonomic point of view, this fauna is rather homogeneous and trophically related with Asteraceae (which presumably prevail), Calceolariaceae, Lamiaceae and Rosaceae. The Nepticulidae species feeding on *Polylepis* do not represent a monophyletic entity (they are not closely related but can be characterized by a wide range of morphological characters).
7. The majority of the studied species are characterized by either moderately abundant (46% of known species) or not abundant mining (34%). According to the current data, the most of the Nepticulidae species occurring in Middle and South America are rare species and the majority of them are characterized by limited distribution and not abundant mining. The recorded pests (or potential pests) of cultivated or otherwise significant plants are *Stigmella rubeta*, *S. nubimontana*, *S. gossypii*, *Ectoedemia morae*, *Acalyptris cedrelus*, *Ozadelpha guajavae*, *Fomoria miranda* and several other investigated species.



## REZIUMĖ

### TYRIMŲ TIKSLAS IR UŽDAVINIAI

Disertacinio darbo tikslas – Vidurio ir Pietų Amerikos Nepticuloidea faunos (Lepidoptera: Nepticulidae, Opostegidae) taksonominis ir trofinis įvertinimas, daugiausiai remiantis duomenimis apie naujai atrastų taksonų mitybinius ryšius.

Šiam tikslui pasiekti reikėjo įgyvendinti šiuos uždavinius:

- 1) ištyrus kolekcinę medžiagą, naujai surinktą Kosta Rikoje, Meksikoje ir Ekvadore, išaiškinti Vidurio ir Pietų Amerikoje aptinkamas baltųjų gaubtagalvių rūšis, patikslinti jų paplitimo duomenis bei atlikti Vidurio Amerikos Opostegidae chorologinę analizę;
- 2) ištyrus įvairiuose užsienio mokslo centruose saugomą neidentifikuotą kolekcinę medžiagą, o taip pat disertacijos metu surinktus mokslinius rinkinius ir atlikus taksonominę analizę, nustatyti Vidurio ir Pietų Amerikos Nepticulidae faunos sudėtį, išaiškinti ir aprašyti naujas mokslui rūšis;
- 3) remiantis taksonominės analizės duomenimis ir naujai išaiškintais diagnostiniais požymiais, patikslinti kai kurių Nepticulidae taksonų sistematinį rangą, o atlikus morfologinių struktūrų tyrimus (bei atsižvelgiant į naujai ištyrtas taksonų ekologijos ypatybes) išskirti ir įvardyti rūšių grupes, o taip pat satelitinius (grupėms nepriskirtus, tačiau diagnostiniu požiūriu artimus) taksonus, įvardyti itin artimų rūšių kompleksus, pasižyminčius menka morfologine diferenciacija;
- 4) išaiškinti, aprašyti ir analizuoti specifinę, mitybos požiūriu su tam tikromis augalų grupėmis susijusių minuotojų fauną, ypatingą dėmesį skiriant rūšims, trofiniais ryšiais susietomis su Fagaceae (*Quercus*), Asteraceae (*Baccharis*) ir Rosaceae augalais;
- 5) atlikti Neotropinio ir Andų-Patagonijos regionų Nepticulidae trofinių ryšių analizę, išaiškinti ir analizuoti tiriamų regionų mažųjų gaubtagalvių trofinius ryšius;
- 6) atskleisti ir analizuoti įvairiose kalnų ir žemumų buveinėse aptinkamų Nepticulidae rūšių trofinių ryšių ypatybes bei sezoninius suau-

gėlių ir vikšrų aktyvumo ciklus, didžiausią dėmesį skiriant aukštųjų kalnų faunai, įskaitant rūšis, trofiškai susijusias su ekologijos požiūriu itin svarbiais *Polylepis* miškais;

- 7) nustatyti Vidurio ir Pietų Amerikos mažųjų gaubtagalvių minavimo gausumo grupes, atlikti rūšių aptinkamumo analizę ir išaiškinti Nepticulidae rūšis, kurios svarbios kaip potencialūs kultūrinių ar kitą ekonominę reikšmę turinčių augalų kenkėjai.

## MOKSLINIS NAUJUMAS

Nors Vidurio ir Pietų Amerikos Nepticulidoidea jau buvo tyrinėta ir iki šios parengtos disertacijos (žr. Literatūros apžvalgą), mūsų atliktų tyrimų ir rezultatų naujumas yra didelis:

- 1) išanalizavus naujai surinktą medžiagą ir aprašius tris naujas mokslui rūšis, pirmą kartą buvo atlikta Opostegidae faunos taksonominė analizė, kurios metu nustatyti baltųjų gaubtagalvių įvairovės centrai;
- 2) pirmą kartą atlikta išsami Vidurio ir Pietų Amerikos Nepticulidae taksonominė analizė, kurios metu pirmą kartą *Enteucha* gentyje įvardytos rūšių grupės; naujos rūšių grupės taip pat išskirtos *Ectoedemia*, *Acalyptris* ir *Stigmella* gentyse; pirmą kartą aprašyti *Acalyptris bicornutus*, *A. tenuijuxtus*, *Stigmella sinuosa* rūšių kompleksai, o taip pat parengtos taksonominės charakteristikos, leidžiančios įvardyti 1–2 naujas mokslui Nepticulidae gentis;
- 3) pirmą kartą sudarytos diagnostinės schemas, padedančios identifikuoti Vidurio ir Pietų Amerikoje aptinkamas *Stigmella* genties rūšių grupes, detaliai diagnozuojant *Stigmella magnispinella*, *S. circinata* ir kai kurias *Stigmella* genties kriptines rūšis;
- 4) pirmą kartą išaiškintos kai kurios Nepticulidae morfologinės bei ekologinės adaptacijos, susijusios su endobiontiniu gyvenimo būdu (įskaitant kokonų susidarymą minose, gyvatiškų minų dominavimą, kai kurių *Stigmella* rūšių uodeginių pilvelių segmentų transformaciją į kiaušdėtį ir kt.);
- 5) pirmą kartą Vidurio ir Pietų Amerikoje aptikti, aprašyti ir analizuoti mažieji gaubtagalviai, trofiniais ryšiais susiję su *Quercus* genties augalais; atskleisti naujai aptiktos ir aprašytos faunos trofinių ryšių ypa-

- tumai, pateikiant naujai išskirto *Stigmella nigriverticella* rūšių komplekso diagnostines schemas ir prieraišumą skirtingiems *Quercus* genties augalams;
- 6) pirmą kartą atlikus visų šiuo metu žinomų pasaulio Nepticulidae faunos rūšių grupių, prieraišių Fagaceae šeimos augalams analizę, nustatytas Amerikoje aptinkamų *Stigmella quercipulchella* ir *S. saginella* rūšių grupių trofinis spektras, susietas su *Quercus* – sekcija *Quercus*, *Quercus* – sekcija *Protobalanus*, *Quercus* – sekcija *Lobatae* ir *Castanea* gentimi;
  - 7) pirmą kartą publikuoti duomenys apie galimai gondvaninės faunos aptikimą Patagonijoje (*Stigmella purpurimaculae* grupė, kurios rūšys galimai minuoja *Nothofagus* augalus);
  - 8) pirmą kartą Vidurio ir Pietų Amerikoje išaiškintos ir aprašytos mažųjų gaubtagalvių rūšys, kurios trofiškai susijusios su Asteraceae augalais, pirmą kartą įvardinant *Baccharis*, *Liabum*, *Gynoxys* ir daugelį kitų Asteraceae genčių, iki šiol nežinomų Nepticulidae mitybinių ryšių analizėse;
  - 9) aptikus naujų, su Rosaceae augalais susijusių taksonų ir dokumentavus iki šiol nežinomas Rosaceae augalų lapų minas, pirmą kartą apžvelgta specializuota, išskirtinai su Rosaceae susijusių Nepticulidae fauna Pietų Amerikoje;
  - 10) analizuojant Neotropinio ir Andų-Patagonijos regionų bendrąją trofinę specializaciją, pirmą kartą išaiškinta, kad 96 proc. visų šiuo metu trofiškai ištirtų taksonų yra susieti išskirtinai su Asteridae ir Rosidae. Pirmą kartą nustatyta, kad Neotropinio ir Andų-Patagonijos regionų Nepticulidae taksonai trofiškai yra susiję su 24 šeimomis, priklausančiomis 16 augalų eilių;
  - 11) palyginus naujai išaiškintas Vidurio ir Pietų Amerikos Nepticulidae trofinių ryšių ypatybes su Nepticulidae trofiniais ryšiais Holarkties regione, pirmą kartą nustatytos aiškios mūsų tiriamo regiono mažųjų gaubtagalvių specifinės ypatybės ir trofinių ryšių tendencijos;
  - 12) pirmą kartą atlikus Nepticulidae užimamų buveinių apžvalgą ir jose aptinkamos faunos ekologinę analizę, įvertinta įvairiose buveinėse aptinkamų Nepticulidae trofinė specializacija ir aktyvumo laikotarpiai;

- 13) pirmą kartą išaiškinta ir aprašyta Nepticulidae fauna, trofiškai susijusi su ekologijos požiūriu itin svarbiais Andų kalnų *Polylepis* miškais bei pirmą kartą nustatyta aukščiausiai pasaulyje aptinkama mažųjų gaubtagalvių fauna bei *Stigmella nivea* rūšiai registruotas 4700 m aukščio rekordas;
- 14) rengiant disertacinį darbą sudarytas naujas ir išsamus Vidurio bei Pietų Amerikos Nepticuloidea taksonominis katalogas, nurodantis visų šiuo metu ištirtų rūšių trofinį prieraišumą;
- 15) pirmą kartą analizuoti Vidurio ir Pietų Amerikos Nepticulidae sezoniniai ciklai, gausumas ir aptinkamumas bei pirmą kartą įvardyti tiriamo regiono Nepticulidae, kurie trofiniais ryšiais susiję su kultūriniais, kitais ekonominę reikšmę turinčiais bei endeminiais ir saugojamais augalais;
- 16) šio darbo metu išaiškinti nauji trofinių ryšių duomenys 114 rūšių (t. y. tiriamo regiono Nepticulidae trofinių ryšių naujumas yra apie 86 proc. (1 ir 2 pav.);
- 17) atlikus ekspedicinius lauko tyrimus Vidurio ir Pietų Amerikos šalyse bei ištyrus iki šiol neidentifikuotą kolekcinę medžiagą, surinktą kitų tyrėjų ir deponuotą Danijos, JAV ir D. Britanijos mokslo institucijose, šio darbo metu iš viso aptikta 146 naujos mokslui rūšys (3–4 pav.), iš kurių didelė dalis publikuota (kita dalis – spaudoje arba rengiama spaudai).

## DISERTACIJOS SANDARA

Disertacija sudaryta iš įvado, literatūros apžvalgos, tyrimų metodų ir medžiagos, tyrimų rezultatų (5 skyriai ir 45 poskyriai), išvadų (7), literatūros sąrašo (190 šaltinių), autoriaus disertacijos tema skelbtų darbų sąrašo (57 pozicija), angliškos santraukos ir priedo. Iš viso: 220 puslapiai (177 - disertacijos, 42 - priedo), 66 paveikslai, 4 lentelės. Disertacija parašyta lietuvių kalba, o priedas – anglų kalba. Priede „Preliminary Catalogue of the Fauna of Nepticuloidea of Middle and South America“ yra sistematine tvarka išvardijami visi tyrimų regione aptikti taksonai (314 rūšių), pateikiant jų mišybinius augalus ir geografinį paplitimą.



## TYRIMŲ REZULTATŲ PUBLIKAVIMAS

Autorius disertacinio darbo tyrimų rezultatus ir apie atliktų tyrimų eigą paskelbė 57 publikacijose kartu su bendraautoriais. Iš jų 16 buvo paskelbti *Zootaxa* žurnale, užsienio periodiniame mokslo leidinyje su svorio koeficientu (*Impact factor*), įtrauktame į WoS leidinių sąrašą (Q2), 3 – *Acta Zoologica Lituanica* žurnale, Lietuvoje recenzuotame leidinyje, įtrauktame į ISI (*Master Journal List*) sąrašą, 1 – *Ecology and Zoology* žurnale, užsienyje recenzuojamame leidinyje, įtrauktame į ISI (*Master Journal List*) sąrašą, 4 – *Biologija* žurnale, Lietuvoje recenzuojamame leidinyje, įtrauktame į ISI (*Master Journal List*) sąrašą, 5 straipsniai – tarptautinių konferencijų leidiniuose. Šiose publikacijose aprašomos naujos mokslui rūšys, pateikiami naujai išaiškinti mitybiniai augalai, analizuojamos taksonominių grupių trofinių ryšių ypatybės).

Taip pat publikuoti 3 metodiniai leidiniai, 1 skyrius monografijoje „Lietuvos Nepticulidae faunos taksonominė, chorologinė ir trofinė charakteristika“ (Diškus, Stonis, 2012) ir 23 kiti (daugiausia mokslo sklaidos) straipsniai, aprašantys atliktų tyrimų eigą.

Iš viso 25 darbai yra publikuoti anglų kalba (visi mokslinių tyrimų straipsniai), o 27 darbai – lietuvių kalba (daugiausiai monografijų / knygų skyriai ar mokslo sklaidos publikacijos).

## TYRIMŲ REZULTATŲ APŽVALGA

### Faunos duomenys

Ištyrus kolekcinę medžiagą, naujai surinktą Kosta Rikoje, Meksikoje ir Ekvadore, Vidurio Amerikoje išaiškinta 40 Opostegidae rūšių (19,8 proc. pasaulio faunos), įskaitant 3 rūšis: *Pseudopostega robusta*, *P. mexicana* ir *P. latiplana*, kurios darbo metu buvo aprašytos kaip naujos mokslui rūšys. Iš viso Vidurio ir Pietų Amerikoje išaiškintos 86 baltųjų gaubtagalvių rūšys, kurios sudaro apie 43 proc. šiuo metu žinomos pasaulio Opostegidae faunos.

Patikslinus Opostegidae rūšių paplitimo duomenis, nustatyta, kad daugiausia Opostegidae taksonų (26 rūšys) yra paplitę Kosta Rikoje; tokios nepaprastai gausios faunos chorologinė analizė parodė, kad Kosta Rikoje ap-

tinkamos Opostegidae rūšys gali būti suskirstytos į keturias chorologines grupes. Pusė visų baltųjų gaubtagalvių rūšių (13 arba 50 proc.) šiuo metu aptinkamos tik Kosta Rikoje ir tik keli Opostegidae taksonai yra paplitę kituose kraštuose. Viena Opostegidae rūšis aptinkama Kosta Rikoje ir Panamoje, dvi rūšys (7,7 proc.) žinomos tik Vidurio Amerikoje (Kosta Rikoje) ir Karibų regione, septynios Opostegidae rūšys (27 proc.) aptinkamos Vidurio ir Pietų Amerikoje (bet ne Karibų regione) ir tik trims baltųjų gaubtagalvių rūšims (11,5 proc.) būdingas transneotropinis paplitimas.

Taksonominės analizės duomenimis, ištyrus įvairiuose užsienio mokslo centruose saugomą neidentifikuotą kolekcinę medžiagą, o taip pat disertacijos autoriaus mokslinius rinkinius, nustatyta, kad Vidurio ir Pietų Amerikos Nepticulidae fauną šiuo metu sudaro 11 genčių ir 222 rūšys (iš jų 146 rūšys buvo naujai išaiškintos disertacijos rengimo metu, o 67 Nepticulidae rūšių pirmoji autorystė priklauso disertacijos autoriui). Didžiausia rūšių gausa nustatyta Ekvadore (67 rūšys), Peru (40 rūšių), Argentinoje (35 rūšys) ir Belize (31 rūšis).

Remiantis naujai išaiškintais diagnostiniais požymiais *Manoneura* taksonui (skirtingai nei teigia kiti autoriai) pripažintas genties rango statusas, tuo tarpu *Neotrifurcula* van Nieukerken traktuojama kaip *Glaucolepis* dalis (sinonimas).

Atlikti morfologinių struktūrų tyrimai (atsižvelgiant ir į naujai ištirtas taksonų ekologijos ypatybes) parodė, kad visose Vidurio ir Pietų Amerikos Nepticulidae gentyse gali būti išskirtos ir įvardytos rūšių grupės (kurių diagnostiniai požymiai pateikti disertacijoje), o taip pat satelitiniai, grupėms nepriskirti, tačiau diagnostiniu požiūriu artimi, taksonai.

Nors daugeliui Nepticulidae taksonų būdinga didelė morfologinė diferenciacija, tarp keturių *Acalyptris* gentyje išskirtų rūšių grupių įvardyti du itin artimų rūšių kompleksai (*A. bicornutus* ir *A. tenuijustus*). Didžiausia rūšių grupių įvairovė pasižyminčioje *Stigmella* gentyje, tarp 18 naujai išskirtų rūšių grupių, aptikti ir kriptiniai taksonai, kurie paplitę Andų-Patagonijos regione, pasižymi labai menka morfologine diferenciacija ir priskirtini naujam *Stigmella sinuosa* rūšių kompleksui.

## Ekologijos duomenų analizė

Pirmą kartą Neotropiniame regione išaiškinti ir aprašyti *Quercus* (Fagaceae) genties augalų minuotojai užima aukščio zoną nuo 1655 m iki 2500 m virš jūros lygio ir paplitę įvairiose buveinėse (daugiausiai ažuolų-pušų miškuose bei rūkų miškuose). Taksonominiu (rūšių) požiūriu Vidurio ir Pietų Amerikos Nepticulidae fauna yra labai įvairi (jungianti 10 taksonų, trofiškai susijusių su įvairiomis *Quercus* genties rūšimis), įskaitant ir pietiniame *Quercus* arealo pakraštyje, Kolumbijoje, aptiktus minuotojus (*Stigmella robleae* ir *S. humboldti*, trofiškai susijusius su nykstančiu Plioceno kilmės mitybinio augalu *Quercus humboldtii*).

*Quercus* augalus minuojančių Nepticulidae rūšių diferenciacijos požymiai rodo, kad specializuota Nepticulidae fauna taksonominiu požiūriu nėra vienalytė, o yra polifiletinės kilmės.

Mūsų atliktų tyrimų metu detaliau analizavus įvairių Nepticulidae rūšių trofinį prierašumą, tarp *Quercus* minuotojų nustatytos septynios *Stigmella* rūšių grupės, besiskiriančios ne tik morfologiniais požymiais, bet ir trofinėmis ypatybėmis, priklausomybe skirtingoms *Quercus* pogentėms arba sekcijoms. Tyrimai parodė, kad specifiškiausios yra *S. quercipulchella* rūšių grupei priklausančios rūšys, kurios 100 proc. minuoja augalus, priklausančius tik raudonųjų ažuolų (*Lobatae*) sekcijai. Tai rodo stiprias šios rūšių grupės vienalytės oligofagijos tendencijas. Kitos *Stigmella* rūšių grupės mitybos požiūriu nėra vienodos.

Išaiškinta ir galimai su *Nothofagus* susijusi rūšių grupė (*Stigmella purpurimaculatae*) galimai yra vienas iš naujų gondvaninės faunos pavyzdžių.

Tyrimų metu pirmą kartą išaiškinta ir aprašyta Nepticulidae fauna, trofiškai susijusi su *Baccharis* (Asteraceae) genties augalais yra paplitusi rūkų miškų buveinėse (arba buveinėse artimose rūkų miškams, įskaitant paramus) ir užima aukščio zoną nuo 1800 m iki 3850 m virš jūros lygio. Visoms aštuonioms *Baccharis* augalus pažeidžiančioms rūšims yra būdingas gausus arba itin gausus mitybinio augalo minavimas, tačiau neįprastai didelis vikšrų mirtingumas (prižastys nežinomos).

Nors kituose regionuose (Palearktyje, taip pat Nearktyje) Rosaceae minuotojai yra vyraujantys, Vidurio ir Pietų Amerikoje registruota 18 taksonų (daugiausiai priklausančių *Stigmella* genčiai), kurie trofiškai yra susiję su

įvairiais erškėtiniais augalais; mitybinis spektras apima šias augalų gentis: *Rubus* (4 minuotojų taksonai), *Lachemilla* (1 minuotojų taksonas), *Alchemilla* (1 taksonas), *Acaena* (1 taksonas), *Hesperomeles* (2 taksonai), *Prunus* (1 taksonas) ir *Polylepis* (4 arba 5 minuotojų taksonai).

Atlikus trofinių ryšių analizę, išaiškinta, kad apie 96 proc. Neotropinio ir Andų-Patagonijos regionų Nepticulidae trofiškai yra susieti su Asteriidae (41,5 proc.) ir Rosidae (54,8 proc.). Tarp specializuotų asteridų minuotojų apie 57 proc. taksonų yra susiję su kampanulidais, 38 proc. su lamiidais, tuo tarpu tarp rosidų minuotojų daugumą taksonų (74 proc.) susieti su fabidais, 23 proc. su malvidais. Iš viso Neotropinio ir Andų-Patagonijos regionų Nepticulidae taksonai yra trofiškai susiję su 24 mitybinių augalų šeimomis, priklausančiomis 16 augalų eilių.

Vidurio ir Pietų Amerikos (Neotropinio ir Andų Patagonijos regionų) Nepticulidae trofinė specializacija demonstruoja ekologinį išskirtinumą ir pasižymi ypatingomis, besiskiriančiomis nuo ankščiau ištirtų Nearkties ir ypač Palearkties regionų. Palearktyje kai kurių mitybinių augalų šeimų minuotojai menkai aptinka (pvz., Asteraceae minuotojai sudaro 0,3 proc., o Lamiaceae – 4 proc.). Tuo tarpu Neotropiniame ir Andų Patagonijos regionuose Asteraceae ir Lamiaceae yra daugiausiai įsisavintos mitybinių augalų šeimos: su Asteraceae šeimos augalais trofiniais ryšiais siejasi apie 24 proc. minuotojų, o su Lamiaceae – 11 proc. minuotojų.

Remiantis tyrimų duomenimis paramų buveinėse registruotos keturios Nepticulidae mitybinių augalų šeimos, tačiau apie 50 proc. rūšių yra trofiškai susiję vien tik su Asteraceae augalais (iš jų 25 proc. rūšių su *Baccharis*, 12,5 proc. su *Gynoxys* ir 12,5 proc. su *Pentacalia* genčių augalais).

Įvertinus Nepticulidae mitybinius ryšius rūkų miškų buveinėse, kurios ypatingai svarbios dėl drėgmės, hidrologinio ciklo palaikymo, augalijos įvairovės ir gyvūnų endemizmo, nustatyta, kad Nepticulidae rūšys trofiškai susijusios su 11 augalų genčių, tarp kurių vyrauja *Baccharis*, *Rubus* ir *Liabum* augalai.

Tarp visų aštuonių analizuotų Nepticulidae užimamų buveinių grupių didžiausia mitybinių augalų įvairove pasižymi atogrąžų kalnų drėgnieji miškai; mažųjų gaubtagalvių rūšys trofiškai susietos su 33 augalų gentimis, priklausančioms 13 augalų šeimoms, iš kurių gausiausiai minuojamos (vertinant Nepticulidae rūšių procentinę dalį) yra šios mitybinių augalų šeimos:

Asteraceae (apie 22 proc.), Lamiaceae (apie 18 proc.), Rosaceae (apie 16 proc.) ir Fagaceae (apie 15 proc.).

Pirmą kartą išaiškinus ir aprašius ekologijos požiūriu itin svarbių Andų kalnų *Polylepis* miškų Nepticulidae fauną nustatyta, kad mažųjų gaubtagalvių rūšys, minuojančios *Polylepis* nėra artimai giminiškos, o pasižymi išskirtine morfologinių požymių įvairove, kas daugiau byloja apie anksčiau vykusius evoliucinius procesus nei nesenos evoliucijos „produktus“.

Iš viso 29 mažųjų gaubtagalvių rūšys (iš jų 22 disertacijoje pateiktos kaip naujos mokslui) buvo aptiktos aukščiau nei 3700 m virš jūros lygio ir atstovauja pasaulyje aukščiausiai aptinkamą Nepticulidae fauną (aukščio rekordas priklauso *Stigmella nivea* rūšiai, kuri buvo surinkta Peru 4700 m aukštyje virš jūros lygio). Nors aukštųjų Andų fauna yra gausi rūšimis, tačiau taksonominiu požiūriu ši fauna yra gana vienalytė (beveik visos rūšys priklauso vienintelei *Stigmella* genčiai).

Tiriant Nepticulidae suaugėlių aktyvumą kalnų buveinėse galima išskirti vieną aktyvumo piką, kuris prasideda sausio mėn. ir užsibaigia balandžio mėn. pradžioje. Tuo tarpu žemumų buveinėse buvo nustatyti du ryškesni suaugėlių aktyvumo ciklai: pirmasis prasideda sausio mėn. ir užsibaigia kovo mėn., o antrasis aktyvumo pikas (trumpesnis) prasideda balandžio mėn. ir baigiasi gegužės mėn. pradžioje. Vidutinių platumų buveinėse Nepticulidae suaugėlių aktyvumas vyksta kitu laiku: didžioji dauguma suaugėlių pradeda skraidyti rugsėjo mėn., o baigia sausio mėn.

Ženklesnis mažųjų gaubtagalvių vikšrų minavimas tiek tirtose kalnų buveinėse, tiek ir žemumų buveinėse prasideda gruodžio mėn. ir baigiasi kovo mėn. (vėlesniais mėnesiais minavimas taip pat registruotas, tačiau jo aktyvumas neprilygsta sausio – vasario mėn. pikui).

Nors Vidurio ir Pietų Amerikoje nustatytos 5 mažųjų gaubtagalvių minavimo santykinio gausumo grupės, apie 46 proc. aptiktų rūšių pasižymi vidutiniškai gausiu minavimu, o 34 proc. negausiu minavimu. Atlikus rūšių aptinkamumo analizę nustatyta, kad retosios rūšys vyrauja, tačiau pastaroji rūšių aptinkamumo grupė nėra vienalytė: daugiausia aptinkama rūšių, kurioms būdingas ribotas paplitimas ir negausus minavimas.

Kai kurios išaiškintos Vidurio ir Pietų Amerikos Nepticulidae rūšys yra svarbios ūkiniu požiūriu kaip potencialūs kenkėjai: *Stigmella rubeta*, *S. nu-*

*bimontana*, *S. species 4852*, *S. sp.*, *Ectoedemia morae* (uoginių augalų, turinčių svarbią maistinę reikšmę, minuotojai); *Acalyptris cedrelus*, *Ozadelpha guajavae*, *Stigmella gossypii*, *Fomoria miranda* (kultūrinių augalų, turinčių svarbią ekonominę reikšmę, minuotojai); *Stigmella humboldti*, *S. cana*, *S. podanthae*, *S. sp.* (endeminių ir saugojamų augalų minuotojai).

## IŠVADOS

1. Šiuo metu Opostegidae fauną sudaro trys gentys ir 86 rūšys Vidurio ir Pietų Amerikoje (t.y. apie 43 proc. šiuo metu žinomos pasaulio Opostegidae faunos) arba 40 rūšių vien tik Vidurio Amerikoje, kas sudaro 19,8 proc. pasaulio faunos, įskaitant šias neseniai Vidurio Amerikoje atrastas naujas rūšis: *Pseudopostega robusta*, *P. mexicana* ir *P. latiplana*. Dauguma Opostegidae rūšių yra žinomos iš Kosta Rikos ir priklauso keturioms chorologinėms grupėms, iš kurių tik vienai grupei būdingas platus transneotropinis paplitimas; tuo tarpu likusių trijų grupių rūšys (sudarancios 88,5 proc.) pasižymi ribotu paplitimu Vidurio Amerikoje.
2. Šiuo metu Nepticulidae fauną Vidurio ir Pietų Amerikoje sudaro 11 genčių ir 222 rūšys, įskaitant 146 naujai išaiškintas rūšis, kurių dauguma aprašytos.
3. Remiantis naujai išaiškintais ir įvertintais diagnostiniais požymiais, atstatomas *Manoneura* Davis genties statusas; tuo tarpu *Neotrifurcula* van Nieukerken pripažįstama kaip *Glaucolepis* Braun sinonimas. Nors daugelis Nepticulidae taksonų pasižymi morfologine diferenciacija, tarp naujai išskirtų *Acalyptris* genties grupių aptikti mažiausiai du itin artimų kriptinių rūšių kompleksai (*A. bicornutus* ir *A. tenuijustus*). Didžiausia rūšių grupių įvairovė pasižymi *Stigmella* gentis; tarp 18 naujai nustatytų rūšių grupių išskirti kriptiniai taksonai, pasižymintys itin menka morfologine diferenciacija (t.y. Andų-Patagonijos *S. sinuosa* rūšių kompleksas).
4. Įvairi ir trofiškai susijusi su *Quercus* Nepticulidae fauna Vidurio ir Pietų Amerikoje užima 1655–2500 m aukščio zoną (įskaitant *Quercus* arealo pietinį pakraštį). Tyrimų regione žinomos ir kitos trofiškai specializuotos faunos, susijusios su Rosaceae, Lamiaceae ir Astera-

ceae mitybiniais augalais (ir ypač su pastarosios šeimos *Baccharis* genties augalais daugiausiai rūkų miškų buveinėse 1800–3850 m aukščio zonoje.

5. Nors Neotropiniame ir Andų-Patagonijos regionuose Nepticulidae yra trofiškai susiję su 24 augalų šeimomis, priklausančioms 16 augalų eilių, apie 96 proc. Nepticulidae rūšių yra trofiškai susiję vien tik su Asteridae (41,5 proc.) ir Rosidae (54,8 proc.). Jeigu Palearktyje kai kurie mitybiniai augalai yra menkai minuojami (pvz., Asteraceae minuotojai sudaro iki 0,3 proc., o Lamiaceae iki 4 proc.), tai Neotropiniame ir Andų-Patagonijos regionuose Asteraceae ir Lamiaceae yra daugiausiai įsisavintos mitybinių augalų šeimos: Asteraceae minuotojai sudaro apie 24 proc., o Lamiaceae minuotojai sudaro apie 11 proc. visų žinomų Vidurio ir Pietų Amerikos Nepticulidae rūšių.
6. Vertinant pagal įsisavintus mitybinius augalus, pačia didžiausia įvairove tarp visų Nepticulidae apgyvendintų buveinių, pasižymi drėgnieji atogrąžų kalnų miškai (34 Nepticulidae mitybinių augalų gentys priklausančios 13 augalų šeimų). Aprašyta pasaulio aukščiausia Nepticulidae fauna (4700 m aukščio rekordas priklauso *Stigmella nivea*) yra gausi rūšimis, tačiau taksonominiu požiūriu yra gana homogeniška bei mitybiniais ryšiais susijusi su Asteraceae, Calceolariaceae, Lamiaceae ir Rosaceae. Aptiktos Nepticulidae rūšys, susijusios su *Polylepis* nėra monofiletinė grupė (jos nėra artimai giminiškos, o jų morfologiniai požymiai pasižymi didele įvairove).
7. Daugumai tyrimų regione aptiktų rūšių būdingas arba vidutiniškai gausus (46 proc. rūšių), arba negausus minavimas (34 proc.). Remiantis šiuo metu turimais duomenimis, dauguma Vidurio ir Pietų Amerikoje aptinkamų rūšių yra retos ir pasižymi ribotu paplitimu ir negausiu minavimu. Kai kurios rūšys yra kultūrinių ar kitaip svarbių augalų kenkėjai (arba potencialūs kenkėjai): *Stigmella rubeta*, *S. nubimontana*, *S. gossypii*, *Ectoedemia morae*, *Acalyptris cedrelus*, *Ozadelpha guajavae*, *Fomoria miranda* ir kai kurios kitos rūšys.

## LIST OF AUTHOR'S PUBLICATIONS

In total, 57 co-authored publications: 25 papers in scientific periodical journals, 28 mainly science popular publications, 3 study books, one chapter in monograph.

### Papers in Impact Factor journals (Web of Science)

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56. Stonis J. R., **Remeikis A.**, Diškus A., Megoran N. 2017. New species of leaf-mining Nepticulidae (Lepidoptera) from the Neotropics and Ando-Patagonian region, with new data on host-plants. *Zootaxa*, 4272 (1): 1–39. ISSN 1175-5326

55. Stonis J. R., **Remeikis A.**, Diškus A., Gerulaitis V. 2016. The Ando-Patagonian *Stigmella magnispinella* group (Lepidoptera, Nepticulidae) with description of new species from Ecuador, Peru and Argentina. *Zootaxa*, 4200 (4): 561–579. ISSN 1392-0146. DOI: <http://doi.org/10.11646/zootaxa.4200.4.7>

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23. Stonis, J. R., **Remeikis, A.**, Diškus, A. 2012. Gvatemalos dienoraštis. Šalies gamta nepakartojama, bet dar mažai ištirta *Mokslas ir gyvenimas*, 11/12: 42–48. ISSN 0134-3084

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**For the full of conferences and seminars participated, see subchapter 1.6 of the Dissertation.**

# CURRICULUM VITAE

## PERSONAL DETAILS

Name : Andrius Remeikis  
Date and Place of Birth : 11<sup>th</sup> August 1987, Lithuania, Ukmergė  
Nationality : Lithuanian  
Languages : Lithuanian (native), English, Russian  
Address : Švitrigailos St. 4-120, LT-03222,  
Vilnius, Lithuania  
Phone : +370 602 05030  
E-mail : andrius4research@googlegmail.com  
andrius.remeikis@gamtostyrimai.lt

## EDUCATION

2013-2017 PhD fellow in Ecology & Environmental Science (03 B),  
Nature Research Centre.  
2013 Master's Diploma in Biology with Honors (Lithuanian  
University of Educational Sciences).  
2011 Bachelor Diploma, degree of Bachelor of Biology  
(Vilnius Pedagogical University).

## PROFESSIONAL EXPERIENCE

2015 - to date Appointed member of the Baltic-American Biotaxonomy  
Institute ([www.balticamerican.org](http://www.balticamerican.org)).  
2009 - to date Assisting the following study courses at the Lithuanian  
University of Educational Sciences: Invertebrate Zoology,  
Lithuanian Fauna, Exotic Entomology, Global Biodiver-  
sity, Evolutionary Systems.

## AWARDS AND OTHER RECOGNITION

Award from the Lithuanian Academy of Sciences (2012).  
Grants from the Lithuanian Science Council (2014, 2016, 2017).