

European Science Foundation
Standing Committee for Life, Earth and Environmental Sciences (LESC)

ESF LESC EXPLORATORY WORKSHOP

**Lepidoptera Evolution, Taxonomy and
Systematics**

Scientific Report



Stockholm, Sweden, 26 - 29 April 2006

**Convened by:
Niklas Wahlberg**

1. Executive summary

The Lepidoptera (butterflies and moths) are the second most species rich order of insects, with about 170,000 recognised species and perhaps 300,000 still undescribed. They contain the charismatic day-flying butterflies (arguably the best known insects among both scientists and lay people), many serious pests of agriculture (both growing plants as well as grain stores) and stored animal products (such as wool). Yet their evolutionary history is still shrouded in mystery. We have little idea how, when and where any of the major groups within Lepidoptera have arisen. This lack of knowledge reflects the lack of robust phylogenetic hypotheses for the group. Without a robust phylogenetic hypothesis, we will not be able to understand the evolution of host plant use, the historical biogeography or other factors that have led to Lepidoptera being one of the most successful groups of insects on this planet. Large numbers of molecular markers suitable for systematic purposes can be identified from recent EST libraries, allowing researchers to arrive at robust phylogenetic hypotheses. DNA-level markers are also useful for identifying species using the DNA barcode idea.

This ESF Exploratory Workshop has brought together Europe's leading Lepidoptera systematists in order to formulate a common goal for research. Such a goal will require a research programme in which participants are willing to share biological material, unpublished results and methods. The research programme will investigate avenues of joint research funding from local as well as EU level sources. The workshop was successful in integrating, consolidating and rejuvenating the loose networks that have already been built up over time. The major aim of the workshop was to allow researchers working in taxonomy, systematics, molecular biology and evolutionary biology to interact and to familiarise ourselves with the needs and results of each others' fields' of research. European institutions have a particular advantage in the research area of this workshop. European museums are unanimously acknowledged as the best repositories of biological specimens in the world, and the taxonomic knowledge of the European fauna, especially Lepidoptera, is also very well-known compared to other regions of the world.

The workshop was attended by 27 scientists from 14 countries, including special invited guests from Russia and the United States. The workshop was held at the Tovetorp Research Station some 100 km south of Stockholm for a period of two intensive days of presentations and discussions. The workshop had two major themes, on Day 1 we concentrated on the higher level systematics of Lepidoptera, and on Day 2 we scrutinised the magnitude of work required to discover and describe all species of Lepidoptera. During both days, the mornings were dedicated to presentations on the state of the art of the subject by leading experts, and the afternoons were spent discussing future directions and concrete actions. Discussions were structured so that the participants were divided into 3 or 4 smaller groups to discuss specific topics, after which we regrouped to hear what had been discussed and to further discuss the topics. This strategy was very successful, and led to the identification of future research goals and several concrete action plans for the near future.

The foremost conclusion of the workshop was that there is an incredible knowledge and experience base on Lepidoptera in Europe, which far exceeds any other part of the world. This knowledge and experience is not limited to the political entity known as Europe (which has the best known fauna of the world), but is global in scale, due to the rich history of exploration of the natural world. European Lepidoptera systematists have not exploited this expertise to their advantage yet, and one of the main outcomes of this workshop was the founding of a Consortium for Lepidoptera Systematists in Europe. It is hoped that the consortium (to be known as LEPSYS.eu) will promote and facilitate broad collaborations among European systematists in areas such as phylogenetics, taxonomy, evolutionary biology and the integration of new and traditional methods.

One of the areas of expertise in Europe unsurpassed anywhere else is the detailed knowledge of morphology of Lepidoptera. This knowledge will help Lepidoptera systematists to standardise the terminology (quite disparate at the moment between people working on different groups within Lepidoptera), as well as define homologous characters that can be coded from all Lepidoptera. Such a standard set of morphological characters is being developed by participants of the workshop and will, as a consequence of the workshop, be quickly accepted and used by Lepidoptera systematists.

There are two funded projects at the moment working on the “backbone” phylogeny of Lepidoptera. To avoid overlap, the participants of the workshop agreed that the main focus of a European initiative on the phylogeny of Lepidoptera would concentrate on the relationships of taxa in the major lineages (ie. the superfamilies). The state of knowledge of superfamily phylogeny is abysmal, and thus the scope for a common project is great. The participants of the workshop agreed that there should be an agenda to target the superfamilies most in need of work, and to settle upon a common set of phylogenetic characters to sample. This common set would include the standard set of morphological characters discussed above, as well as a set of molecular markers. For the molecular markers, we agreed that there should be a list of priority that all Lepidoptera systematists starting on a project should follow.

The use of DNA characters in species discovery and description was judged as necessary by the participants of the workshop. The use of DNA characters in taxonomy is still a hotly debated subject, and it is here that European expertise can help in deciding the best course of action. It was unanimously decided that the case for using only DNA or even mainly DNA in discovering and describing species was not compelling, and was based mainly on ignorance of morphology. Instead, a judicious use of both morphological and molecular features is necessary for species description. The almost complete knowledge of the European fauna will serve as an excellent test ground for molecular markers suitable for taxonomic work. The participants of the workshop were also of the opinion that any molecular markers used for taxonomic work, should be useful for phylogenetic work as well.

Our understanding of Lepidoptera systematics has come a long way in the past 250 years. Yet only now do we understand the magnitude of work still to be done. With up to 300,000 species still to be found and described, the task seems daunting. European expertise is poised to be at the forefront of any large international projects, and the major outcome of the workshop is a forum that will allow Europeans to lead the way in a coordinated fashion.

2. Scientific content of the event

Day 1. Systematics of Lepidoptera

On Day 1, the workshop concentrated on the phylogenetics of Lepidoptera, with several presentations giving the current status of our knowledge. The phylogenetic relationships of the so-called “primitive” Lepidoptera seem to be quite clear, although the time of divergence from its sister group Trichoptera (the caddisflies) is not. There is a succession of derived evolutionary features which describe inclusive clades in the primitive Lepidoptera, including phytophagy from clearly detritivorous ancestors, colonisation of angiosperms from conifer feeding ancestors, and the evolution of the proboscis (which apparently allowed a great radiation of diversity). Although the several of the first branches of the Lepidoptera phylogeny seem rather clear, it is obvious that the current hypotheses need to be tested with more data. Some relationships among primitive Lepidoptera are not clear and a molecular approach may well help to resolve the uncertainties.

The knowledge of relationships of major lineages in the more derived Lepidoptera (which comprise some 98% of all species) is in stark contrast to that of the primitive Lepidoptera. The only

consensus is that most superfamilies are monophyletic entities, although there are contentious issues here as well. The relationships of the superfamilies is unknown, as are the relationships of major lineages within the superfamilies. Several enigmatic lineages are difficult to place anywhere in the phylogenetic tree of Lepidoptera, based on current knowledge. The best known group of Lepidoptera are the butterflies and skippers (known as Rhopalocera), mainly due to the strong interest in the phylogenetic relationships of families in this group since the late 1950's. However, the Rhopalocera comprise only 7 out of the about 124 families, and the delimitation of these 7 families is relatively uncontroversial. In contrast, the delimitation of many families within the superfamilies of Lepidoptera are contentious and require careful phylogenetic work to resolve outstanding questions.

Two presentations on Day 1 focused on recent developments in molecular biology and their potential contributions to the systematics of Lepidoptera. Genomics is a rapidly rising field and several species of Lepidoptera are being studied using genomic methodology. In addition, the genome of the silk moth *Bombyx mori* has been sequenced and is available on public databases. Information from the *Bombyx* genome as well as information from Expressed Sequence Tag projects on various Lepidoptera will allow researchers to find new molecular markers for phylogenetic studies. These are desperately needed as at the moment there are only a few markers that are easily amplifiable across all of Lepidoptera, and researchers starting on new projects in previously unstudied groups often spend a lot of time trying to find markers that work. This has led to a "Tower of Babel" effect, where different researchers have generated sequence data for different markers, meaning that at the end of the day, it has not been possible to combine different datasets.

Generation of EST libraries is a relatively simple procedure and is a possible way to find suitable protein coding genes for phylogenetic work. Sequencing about 2000 ESTs from a selection of about 40 Lepidoptera would generate a large dataset with potentially tens or even hundreds of new protein coding genes from almost all superfamilies. The sequence from these new genes would allow the identification of conserved sites for primer design, and comparison with the *Bombyx mori* genome would allow the identification of suitably sized exons, which would then be possible to amplify from genomic DNA extracts under standard lab procedures. In this way, the number of routinely amplified genes could be increased to about 20, which should suffice for most phylogenetic problems in Lepidoptera.

Once a relatively large number of gene sequences are available, the information can be used to investigate the rates and tempo of molecular evolution, as well as to estimate times of divergence of major lineages. The age of Lepidoptera and of the major lineages within Lepidoptera are not well-known. Current estimates are entirely based on fossils, which are few and far between for Lepidoptera, and represent minimum ages for clades. Preliminary results using a large molecular dataset from very few Lepidoptera samples suggest that Lepidoptera and Trichoptera diverged a longer time ago than the fossil evidence suggests. Clearly a larger sample of Lepidoptera is needed to refine age estimates using molecular data. Almost all Lepidoptera species are dependent on angiosperm plants as larval food plants. This association has long been known to be evolutionarily conserved, but fossil based age estimates suggest that Lepidoptera diversified long after their host plants diversified. Age estimates derived from molecular data may be able to help us understand the co-evolution of insects and their host plants better.

The afternoon of Day 1 was reserved for discussions. The participants were divided into four groups with specific topics to discuss. The topics were "Molecular strategy", "Sampling strategy", "European focus" and "Morphological data in the molecular era". Approximately equal numbers of participants made up the individual discussion groups and a chairperson was appointed for each group.

The “Molecular strategy” group pointed out that systematists need a standard set of genes to sequence in any molecular systematic project, much like the botanists have. So far only two gene regions have primers that are universal in Lepidoptera. The two gene regions are *cytochrome oxidase subunit I* in the mitochondrial genome and *elongation factor-1 alpha* in the nuclear genome. These two gene regions have been sequenced for the most species of Lepidoptera (2400 and 1100 species, respectively). Any project working on the molecular systematics of Lepidoptera should sequence at least these two genes. Universal primers for more genes need to be developed to get the number of routinely sequenced genes up to at least 20. The possibility of generating an EST library for about 40 key species of Lepidoptera was deemed feasible if funding could be found.

The “Sampling strategy” group discussed the necessity of an information platform with which it would be possible to get information about what taxa are needed for which project to the right people. It is necessary to find out what has been collected already for possible molecular work, where it can be found and who to contact if one wants to access such material. Once that is known, it is possible to target specific groups of Lepidoptera for which samples are lacking, especially taking into account the opinions of practicing taxonomists, who often have a good feeling for what taxa are interesting in a phylogenetic perspective. Standard methods of collecting and preserving specimens in the field are also necessary so that one is able to get good quality DNA extracted from specimens. Also, collecting immature stages requires care and proper storage.

The “European focus” group discussed the areas of Lepidoptera systematics that could and should be the focus of European joint projects. Since there are already two groups working on the backbone phylogeny of Lepidoptera, it was unanimously agreed that the most fruitful angle of attack would be to focus on within superfamily relationships. The main targets should be the 11 species rich superfamilies, which comprise a large proportion of all Lepidoptera species. The delimitations of families within these superfamilies is in many cases contentious and requires decisive treatment to arrive at a stable classification. Stabilising the classification of Lepidoptera is seen as one of the endeavours that could be led by a European initiative.

Morphological data is seen as an essential part of phylogenetic work, as discussed by the “Morphological data in the molecular era” group. One of the main points raised by this group was the loss of morphological expertise currently, as the generation of molecular data is seen as less demanding. Indeed the misperception that morphological data are somehow “old-fashioned” needs to be addressed. It is clear that without knowledge of variation in morphological and behavioural features, we would have no idea of how evolutionary forces have acted on the diversification of a group of species. The widespread discord in naming morphological features of different groups was seen as one reason behind the loss of interest in morphological data, even within Lepidoptera the names of homologous features are different in different superfamilies. The necessity of standardising names cannot be overstated. Also, as with molecular data, it would be necessary to develop a standard set of morphological characters that should be coded in any new work being done on morphological systematics of Lepidoptera. Such a standard set could be developed from Lauri Kaila’s already published character set, initially built up for the superfamily Gelechioidea.

Day 2. Lepidoptera taxonomy and the use of DNA characters

On Day 2, the workshop concentrated on the diversity of Lepidoptera at the species level, with experts giving estimates of described and undescribed species numbers for all the major groups of Lepidoptera. It became clear that only a few groups with just a few species (less than 1000) are relatively well-known, although some of these may have a few hundred undescribed species. For the larger groups with several to tens of thousands of described species, the estimated number of undescribed species is almost double the number of described species. The least known group is

Gelechioidea, for which only the European region is relatively well-known, all other regions are either poorly known, or not known at all.

The application of molecular data to species discovery and description is potentially of high utility, especially as a relatively quick way to roughly group unidentified specimens. Recently a fragment of the mitochondrial genome has been advocated as the standard for molecular identification, the so-called “DNA barcode”. This fragment consists of only 658 base pairs of the gene *cytochrome oxidase subunit I*, the same gene already mentioned previously, for which there are a large number of sequences available on public databases. Although this standard fragment appears to work quite well in many cases, it is known to fail in crucial cases where there is no consensus about whether a group of taxa comprise one or more species. It is also known to fail in some cases where species are readily identifiable externally, but not genetically. Clearly the concept needs to be developed by increasing the number of markers. Markers on the sex chromosomes may well be worth testing in a “barcode” sense.

Another concern with the “DNA barcode” idea is that if a database is not fully populated with sequences of all described species, it is of no use for identifying species. This is easily demonstrated by attempting to identify test specimens of Lepidoptera from Europe on the Barcode of Life Data Systems web page (www.barcodinglife.org). None of the test specimens (*Hepialus lupulinus*, *Scopula immorata*, *Hipparchia semele*) were identified correctly, simply because these common species are not in the database. Indeed most European species have not been “DNA barcoded” yet. The almost complete knowledge of the Lepidoptera fauna in Europe (compared to the rest of the world) will allow researchers to investigate the utility of DNA based identification, if there are sufficient funds to “barcode” all species.

The number of described species is known with accuracy only for very few groups of Lepidoptera (and indeed any insects), and only for groups containing less than a thousand species. This is because the number of described taxa far exceeds the number of actual species, due to duplications, lack of revisions and local rather than global perspectives. The only way to keep track of what has been described and what the taxonomic status of each name is, is to catalogue all names. This has been done for several groups, but usually at a regional level and in the form of books, which means that published data are often out-dated when made available. Current internet technology would allow catalogues to be up-datable in real-time and made available to everybody, rather than just those who can afford to buy the usually expensive catalogues. An example of such a catalogue is the database of names of taxa in Pyraloidea (www.pyraloidea.org). Most taxonomists maintain their own name databases in various formats. Clearly a common platform for internet catalogues would benefit the world in many ways.

As with Day 1, the afternoon was reserved for discussion of key topics. The topics were “Molecular strategy”, “European focus” and “DNA taxonomy and traditional taxonomy”. The “Molecular strategy” group pointed out that the standard “barcoding” gene fragment, the COI, is also one of the most sequenced genes in Lepidoptera and one of the recommended gene regions for phylogenetic work (based on discussions during Day 1). This idea that DNA data used for identification and species delimitation can also be used for phylogenetic work was considered important. One should strive to sequence more than just the 658 bp of “barcode” sequence, preferably the full 1560 bp of the COI gene, and preferably also another nuclear gene to allow identification of higher taxa. Once again the EF-1 α gene was considered useful in this respect. The generation of DNA data purely for identification purposes was considered to be a waste of resources, when at the same time one can generate useful data for other purposes. New nuclear markers were considered to be crucial for the development of the idea of DNA taxonomy.

The “European focus” group were convinced that there was much scope for European collaboration in Lepidoptera taxonomy. At the level of the European fauna, it was concluded that a

project to barcode all species should be implemented as soon as possible and would require funding of its own. At the level of the global fauna, it was suggested that Europeans could initiate the building of web-based catalogues that are editable by experts. By setting a standard, it would be possible to unite different catalogues into one large database. The discovery and description of new species will heavily rest on European collections, and thus it is clear that Europe will have a central role in the determination of the world fauna. It was decided that to facilitate the collaboration of European scientists among themselves as well as internationally, a consortium should be founded.

The “DNA taxonomy and traditional taxonomy” group stressed that traditional taxonomic procedures are still a vital part of the description of new species. New molecular methods are a welcome addition to these methods, and should be integrated in a way that enhances species discovery and description. It was unanimously decided that a single, short piece of DNA is not enough to delimit species, but would be a useful addition to the “toolbox” being used for species description. If more genes can be easily sequenced, these should be included in species descriptions. The main concern is the loss of expertise in morphological methodology, due to the misconceived perception that it is somehow “old fashioned”. More effort needs to be made to educate a new generation of taxonomists that are comfortable working both with morphology and with molecular data.

3. Assessment of the results, contribution to the future direction of the field

The main outcome of the workshop was the founding of the Consortium of Lepidoptera Systematists in Europe (LEPSYS.eu), which will aim to:

- Provide a complete catalogue and systematic framework for the Lepidoptera of the world
- Promote collaboration between European Lepidoptera systematists and coordinate applications for joint funding
- Promote and coordinate collaboration between European and non-European Lepidoptera systematists
- Facilitate the integration of traditional morphological methods with new molecular methods
- Catalogue the diversity of Lepidoptera by exploring new methods for species discovery and databasing nomenclature

The consortium LEPSYS.eu will, through its website (www.lepsys.eu), act as a catalyst for collaborations. It will have a recommended set of standard molecular markers with a priority ordering and information about primers and laboratory protocols. LEPSYS.eu will also have a recommended set of morphological characters that should be coded for all Lepidoptera. Members of LEPSYS.eu will develop molecular markers that are suitable for routine genomic DNA extracts, often from old specimens with degraded DNA. LEPSYS.eu will help to develop a standard for online catalogues of names that will be searchable and editable. LEPSYS.eu will also investigate new ways of integrating traditional morphological methods with new molecular methods in both systematics and taxonomy.

This ESF Exploratory Workshop has laid the foundation for a strong collaboration between European Lepidoptera systematists. The future direction of the field is clear; LEPSYS.eu will help make the European Lepidoptera fauna the best known insect fauna on the planet (using both traditional and new methods). The role of Europe in elucidating the global diversity of Lepidoptera will also be substantial, and LEPSYS.eu will facilitate the collaboration between researchers around the world and in different subdisciplines of evolutionary biology.

4. Final programme

PROGRAMME

Wednesday 26 April 2006

Late afternoon *Arrival to Stockholm and transport to Tovetorp Research Station from Department of Zoology, Stockholm University. Buffet dinner at Tovetorp.*

Thursday 27 April 2006

09:00 **Presentation of the European Science Foundation (ESF), Z. Kucan and Z. Varga**
(Standing Committee for Life, Earth and Environmental Sciences)

09:30 **N. Kristensen** - The state of Lepidoptera phylogeny, with an emphasis on the "primitive" Lepidoptera

10:00 **C. Mitter** - LepTree.net, a genomics-inspired community collaboration

10:30 **C. Jiggins** - Expressed sequence tags: a shortcut to the transcriptome and a source of phylogenetic characters

11:00 **C. Wheat** - Phylogenomics and functional genomics

11:30 **L. Kaila** and **N. Wahlberg** - The state of Ditrysia phylogeny

12:00 *Lunch*

14:00 **Summary of morning talks, introduction of discussion groups**

14:30 Divide into 4 groups
1) Molecular strategy
2) Sampling strategy
3) European focus
4) Morphological data in the molecular era

15:30 Coffee break

15:50 **Common discussion**

18:00 *Dinner*
Evening - free conversation, refreshments will be available at own cost

Friday 28 April 2006

09:00 **N. Wahlberg** - DNA based taxonomy in Europe, strategy and need

09:40 **J. Baixeras-Almela** - State of tortricoid taxonomy

10:00 **L. Kaila** - State of gelechioid taxonomy

10:20 **E. van Nieukerken** - State of the taxonomy of Non Ditrysia and lower Ditrysia

10:40 **M. Nuss** - State of pyraloid taxonomy

11:00 **A. Hausmann** - State of geometroid taxonomy

11:20 **L. Ronkay** - State of noctuid taxonomy

11:40 **V. Lukhtanov** - Problems of butterfly taxonomy and their solution by using molecular methods and information technology: a call for cooperation

12:00 *Lunch*

14:00	Summary of morning talks, introduction of discussion groups
14:30	Divide into 3 groups 1) Molecular strategy 2) European focus 3) DNA taxonomy and traditional taxonomy
15:30	Coffee break
15:50	Common discussion
17:30	<i>Closing of the workshop</i>
18:00	<i>Dinner</i> <i>Evening - free conversation, refreshments will be available at own cost</i>

Saturday 29 April 2006

Morning *Transport to airports*

5. Statistical information on participants

Geographical distribution

Country	Number of participants
Belgium	1
Denmark	1
Finland	4
Germany	3
Hungary	2
Italy	1
Netherlands	3
Poland	2
Russia	1
Spain	1
Sweden	4
Switzerland	1
United Kingdom	2
United States	1

Career stage

Career stage	Number
Established academic	16
Early career academic	7
PhD student	4

Gender distribution

Male	Female
26	1

6. Final List of Participants

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