

IRYNA YATSIUK

Evolution, species delimitation
and diversity in myxomycetes:
Arcyria and allied genera



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Evolution, species delimitation and diversity
in myxomycetes: *Arcyria* and allied genera



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LIST OF ORIGINAL PUBLICATIONS

- I** Yatsiuk, I., Leontyev, D., Schnittler, M., Ehlers, T., Mikryukov V., Kõljalg U., 2024. *Arcyria* and allied genera: taxonomic backbone and characters evolution. *FUSE*, accepted.
- II** Yatsiuk, I., Leontyev, D., López-Villalba, Á., Schnittler, M., Kõljalg, U., 2023. A new nivicolous species of *Lamproderma* (Myxomycetes) from lowland and mountainous regions of Europe. *Nova Hedwigia* 116, 105–136. https://doi.org/10.1127/nova_hedwigia/2023/0807
- III** Leontyev, D., Yatsiuk, I., 2024. Dataset of barcoded Reticulariaceae: ten years of DNA sequencing. *Biodiversity Data Journal* 12, e115630. <https://doi.org/10.3897/BDJ.12.e115630>
- IV** Yatsiuk, I., Leshchenko Yu., Viunnyk V., Leontyev, D., 2024. The comprehensive checklist of myxomycetes of Ukraine based on extended occurrence and reference datasets. *Biodiversity data journal*, 12: e120891. <https://doi.org/10.3897/BDJ.12.e120891>
- V** Yatsiuk, I., Kastianje, V., Adamonyte, G., 2020. A comprehensive checklist of Estonian myxomycetes. *Karstenia* 58, 239–247. <https://doi.org/10.29203/ka.2020.497>

Papers are cited throughout the thesis with the corresponding Roman numerals.

The author’s contribution to the publications is shown below (* minor contribution; ** moderate contribution; *** major contribution/leading role).

	I	II	III	IV	V
Idea and study design	***	***	*	**	**
Fieldwork or other data sampling	***	***	–	**	**
Labwork and microscopy	***	***	–	–	***
Data management, analysis, visualisation	***	***	***	***	**
Manuscript writing	***	***	*	***	***

ABBREVIATIONS

16S, mitSSU	Mitochondrial ribosomal small subunit rDNA
18S, SSU	Nuclear ribosomal small subunit rDNA
BI	Bayesian Inference
bp	base pairs
DNA	Deoxyribonucleic acid
EF1- α	Translation elongation factor 1-alpha
FAIR (data, principles)	Findable, Accessible, Interoperable, Reusable
fam. nov.	new family
GBIF	Global Biodiversity Information Facility, www.gbif.org
gen. nov.	new genus
ITS	Internal transcribed spacer
LM	Light microscopy
ML	Maximum Likelihood
OTU	operational taxonomic unit
PCR	Polymerase chain reaction
rDNA	Nuclear ribosomal DNA (SSU, ITS, LSU)
SEM	Scanning electron microscopy
s. l.	sensu lato (Lat.), in a wide sense
s. str.	sensu stricto (Lat.), in a strict sense
sp. nov.	new species

INTRODUCTION

Myxomycetes, or Myxogastria, comprise approximately 1,050 species of macroscopic eukaryotes within the kingdom Amoebozoa (Adl et al., 2019). Unlike their amoeboid counterparts, myxomycetes have complex life cycle, which includes an amoeboid stage, a multinucleate mobile plasmodium, and the development of spore-bearing fruiting bodies (Fig. 1). In their amoeboid stage, myxomycetes are found in diverse substrates such as soil, decaying wood, living tree bark, leaf litter, and other plant debris. By some estimates based on transcriptome analyses, myxomycetes account for up to 50% of the biomass and 25% of the ribotypes among soil protozoans, playing crucial role as regulators of bacterial, algal, and protistean populations in terrestrial ecosystems (Urich et al., 2008). Many species of beetles, slugs and nematodes in their turn feed on myxomycetes obligately or accidentally (Keller and Everhart, 2010).

Despite their substantial ecological functions, myxomycetes have been systematically underrepresented in taxonomical and ecological research, including environmental DNA studies (Adl et al., 2014; Shchepin et al., 2019). The scarcity of taxonomical attention can be attributed to ongoing taxonomical impediment (Ebach et al., 2011). Since myxomycetes are not large charismatic organisms and due to their lack of direct economic importance, myxomycetes rarely attract significant research funding. However, the inadequate presence of myxomycetes in environmental DNA studies may be due to the enormous genetic variability, accumulated in this early-divergent group and difficult to discover with standard sets of primers, as well as because of the incompleteness of annotated reference libraries (Gao et al., 2019). This brings us back to the necessity of understanding (1) phylogenetic relations, (2) species boundaries, (3) developing of robust practices of species delimitation, description, and communication in myxomycetes.

Consequently, the first part of this thesis addresses phylogeny, evolution, and species delimitation practices in chosen groups of myxomycetes (**I, II**).

In the paper **I** I focus on the genus *Arcyria*, a large genus of the order Trichiales (García-Cunchillos et al., 2022), subclass *Lucisporomycetidae* or the “bright-spored” myxomycetes (Fig. 1). From the other genera it is traditionally distinguished by the combination of characters: sporocarpic, stalked fruiting bodies, early evanescent peridium leaving a basal cup, and hollow, typically branched in a net-like manner and ornamented with complex patterns capillitium (Fig. 2).

Arcyria includes 265 published species and infraspecific taxa, 55 of them are accepted according to the authoritative nomenclature database (Lado, 2005). The majority of them require revision, being taxonomic synonyms, taxa based on scarce descriptions or relying on doubtful morphological differences.

DARK-SPORED MYXOMYCETES (COLUMELLOMYCETIDAE)



Figure 1. Representatives of dark-spored vs. bright-spored myxomycetes (left) and a simplified myxomycete phylogeny (right, tree sources: Kang et al., 2017; Leontyev et al., 2019b).

Originally, *Arcyria* and several other genera were described in a “tribus” (Rostafinski, 1875) that later was validly published as the family *Arcyriaceae* (Cooke, 1877). Since then, there has been debate about taxonomic position of *Arcyria*. Some authors recognized the family *Arcyriaceae*, although the scope of the family varied depending on chosen sets of characteristics (Lister and Lister, 1911; Macbride, 1922; Nannenga-Bremekamp, 1982). Others argued for lumping *Arcyria* and allied genera and placing them in the family *Trichiaceae* (Martin and Alexopoulos, 1969).

The first phylogenetic studies of bright-spored myxomycetes revealed that most genera of *Trichiales* were polyphyletic, but found *Arcyria* and *Arcyodes* to form a monophyletic group (Fiore-Donno et al., 2013). However, the latest published phylogeny (García-Cunchillos et al., 2022), that included wider sampling of *Arcyria* species, recovered an additional *Arcyria* clade emerging as sister to *Hemitrichia* Rostaf. However, no morphological characteristics were identified to differentiate two branches of *Arcyria*, and the sampling of taxa was still limited. Therefore, no taxonomic decisions have been made regarding the genus and the family (García-Cunchillos et al. 2022).

To sum up, although general outlines of the classification of bright-spored myxomycetes are emerging, robust phylogeny with comprehensive sampling, particularly in *Arcyria* is yet to be constructed, and new combinations of traits are to be discovered.



Figure 2. Morphological characters used for delimitation and identification of *Arcyria* s. l. and some representatives of the genus (right). Modified figure from the paper I.

Moving from a deep phylogeny to the species level, it has been shown that barcoding and metabarcoding are powerful tools that bring benefits to taxonomical, ecological, and conservational studies. In species delimitation, the concept of barcoding gap is used, i.e. barcode sequences of the same species must be more similar to each other, than to any of the sequences of other species. In eDNA studies, barcoding is used to distribute sequences into proxy units (OTUs) by applying universal sequence similarity thresholds across sequences from environmental samples (Collins and Cruickshank, 2013). Both applications found their place in myxomycetology during last decades, with first part of 18S rRNA gene comprising ca 550 bp as the barcoding marker (Clissmann et al., 2015; Leontyev et al., 2015; Schnittler et al., 2017; Shchepin et al., 2019). However, in view of the unique biology and immense genetic diversity of the group, both must

be employed with caution. For example, the study based on short fragment of 18S as barcoding marker for dark-spored myxomycetes by Dahl et al. (2018) indicated the absence of a universal barcoding gap, suggesting that a single sequence similarity threshold might not suffice for accurate OTU-picking from environmental samples. Therefore, more research is needed to determine the best barcoding markers for both main groups of myxomycetes, their sequence lengths, and the optimal similarity thresholds. It is also important to test if UNITE Taxon Hypotheses paradigm is applicable to the myxomycetes (Köljalg et al., 2020, 2013) e. g. if other than ITS DNA barcoding genes can be used to calculate Species Hypotheses and mapped against morphological characters. Paper **II** deals with a genus *Lamproderma*, a comparatively lately radiated, species-rich genus of *Columellomycetidae* (Fig 1). Taxonomically, in the paper **II** I describe one species new for science, but what is more important, in this publication I address the application of the barcoding gap in myxomycetes.

In the yet unpublished part of this research I further studied the barcoding gap in bright-spored myxomycetes (conference abstract Yatsiuk, 2023) and applied automatized species delimitation methods (ASAP, STACEY) to our sequenced and morphologically examined specimens of *Arcyria* in order to disentangle species complexes revealed in the paper **I**.

It is widely recognized that morphospecies in myxomycetes often differ from genetic species. Rather by rule than by exception, closer analyses of morpho-species of myxomycetes reveal multiple genetic units, often understood as cryptic species or biospecies (García-Martín et al., 2023; Leontyev et al., 2023a; Ronikier et al., 2022; Shchepin et al., 2017, 2022). Thus, there is the problem of integration of morphospecies-based data obtained in the past with an increasing influx of sequence-based data. In this light, as much as it is important to move forward developing species delimitation methods and detecting species from environment, it is equally vital to gather and systematize the information accumulated in previous studies. To effectively integrate the data across different species concepts and make more informed decisions about biodiversity management (Fišer et al., 2018), it is essential that data coming from different sources are published in FAIR (Findable, Accessible, Interoperable, Reusable) way (Wilkinson et al., 2016). This principle is wholly applicable to species inventories (Reyserhove et al., 2020). Therefore, a part of this thesis summarizes the effort in collecting and publishing primary data about species diversity of myxomycetes, specifically papers **III**, **IV**, **V** that demonstrate how the data obtained from various sources, may be reported according to FAIR principles.

Aims for the present thesis were:

1. To establish a reliable taxonomical backbone for *Arcyria* and allied genera within the bright-spored myxomycetes (**I**)
2. To reconstruct the evolutionary pathway of morphological characters and evaluate their application in taxonomy of bright-spored myxomycetes (**I**). Specifically for this aim the following hypotheses were tested:
 - (i) a stalked sporocarp evolved independently in *Arcyriaceae*, *Hemitrichiaceae* and *Trichiaceae*
 - (ii) an abundant, net-like capillitium attached to the cup or to the stalk evolved independently in *Arcyriaceae* and *Hemitrichiaceae*
 - (iii) yellow pigments are plesiomorphic for *Arcyriaceae*, *Hemitrichiaceae*, and *Trichiaceae*, but red pigments evolved multiple times independently.
3. To assess the barcoding gap applicability in myxomycetes (**II**)
4. To investigate molecular vs. morphological species relationships in the genus *Arcyria* using exploratory and validation species delimitation techniques (unpublished but part of the results is shown in pages 15–16 and Fig. 6)
5. To consolidate different types of data about the species diversity in myxomycetes and establish good practices in reporting species, whether as taxonomic novelties or in biodiversity studies (**III, IV, V**)

MATERIALS AND METHODS

Morphological studies

In total, over 500 specimens of *Arcyria* spp. previously attributed to 34 morphospecies, and 71 specimens of *Lamproderma* spp. previously attributed to 14 morphospecies were studied morphologically (Fig. 3). The specimens were either collected in the field by the authors of paper **I** and **II** or obtained from herbaria of the University of Tartu, Estonia (TUF), Estonian University of Life Sciences (TAAM), University of Alcalá, Spain (AH), the University of Helsinki, Finland (H), the National Herbarium of Victoria, Australia (F), the Herbarium of the University of Greifswald, Germany (GFW, sc), University of Turku, Finland (TFU), V.N. Karazin Kharkiv National University, Ukraine (CWU), Geneva Botanical Gardens and Conservatory (G), Western Australian Herbarium (PERTH), the private collections of M. Meyer, France (MM), Teresa Van der Heul, Australia (TVDH), Anastasia Kochergina, Stanislav Sarzhevskiy, Yuliia Leshchenko, Petra Eimann, Bernard Woerly or Tyson Ehlers (Canada).

Specimens were visually studied, measured and photographed under a stereoscope or transmission microscope equipped with a camera. Slides for the light microscopy (LM) were mounted either in tap water, or Cotton Blue in lactic acid. Scanning electron microscopy (SEM) was performed on specimens spurred with platinum or gold ions. Details on equipment are provided in papers **I** and **II**.

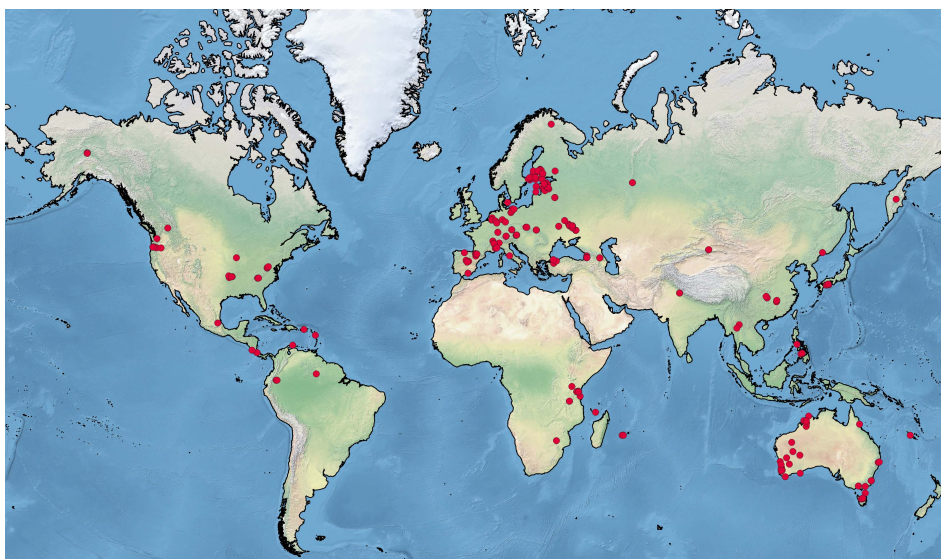


Figure 3. Map of collection localities of specimens studied for papers **I** and **II**.

Molecular and phylogenetic analyses

Genomic DNA was extracted from mature air-dried sporocarps without noticeable fungal contamination as described in detail in papers **II** and **I**. PCR was carried out using published or *de novo* designed sets of primers (**I**, **II**). Gene regions sequenced for the studies were partial 18S (ca 500–650 bp), partial or in separate cases full EF1- α (partial ca 700–850 bp, full ca 1150 bp), ITS (1000–2000 bp, for the paper **II**) and SSU–ITS–LSU region (paper **I**). Most of the sequences were obtained by Sanger method; SSU–ITS–LSU region was read by PacBio method, details are given in respective papers.

In total, 438 partial 18S, 300 EF1- α , 13 ITS and 21 SSU–ITS–LSU sequences were obtained *de novo*. Alignment of sequences was performed with different algorithms of MAFFT (Katoh et al., 2019), MACSE (Ranwez et al., 2018) or Bali-Phy (Suchard and Redelings, 2006), and manually adjusted. Phylogenetic analyses and tree reconstructions were carried out using Bayesian (Ronquist et al., 2012) and maximum likelihood: RaxML (Kozlov et al., 2019), and IQ-Tree (Nguyen et al., 2015) approaches. Phylogenetic trees were plotted in *ggtree* (Yu et al., 2017) or iTOL (Letunic and Bork, 2021).

Barcoding gap between morphospecies of *Lamproderma* in the paper **II** and in conference abstract (Yatsiuk, 2023) was calculated based on pairwise sequence distances using functions of R package *ape* (Paradis and Schliep, 2019). Optimal sequence similarity threshold in datasets of dark-spored and bright-spored myxomycetes was searched by minimizing the cumulative error (wrong lumping + wrong splitting), using functions of the package *spider* (Brown et al., 2012). Species delimitation for the genera *Arcyria* and *Heterotruchia* was performed with ASAP (Puillandre et al., 2021) as exploratory tool and STACEY (Jones, 2017) as more robust method.

Ancestral state reconstruction

Morphological traits specific to *Arcyria* s. l. such as fruiting body habit; capillitium attachment to the cup; capillitium, spore and cup ornamentation were plotted on the phylogenetic tree (**I**, Fig. 1).

The character evolution inference (**I**) was performed for characters suitable for mapping across the order Trichiales (fruiting body type, capillitium arrangements, colouration, see Fig. 1). The reconstruction of morphological character states was performed by stochastic character mapping (Bollback, 2006) using R package *phytools* 1.5-1 (Revell, 2012).

R environment (R Core Team, 2022) was used for analyses and producing most graphs in all papers.

Data acquisition and management (papers III–V)

The selected literature sources encompassed only scientific literature, including monographs, peer-reviewed journal articles, conference abstracts, annual reports of protected areas, PhD and Master’s theses. Included herbarium specimens have either been identified or verified by professional myxomycetologists.

The paper V summarizes all available published data (24 sources) on myxomycetes of Estonia until 2020 and additionally includes revised unpublished material kept in herbaria TAAM, EAA, TUF (Pärtel et al., 2021a, 2021b). The occurrences were taxonomically assessed according to (Lado, 2005) and presented in classic checklist format “binomial+reference” (Fig. 4).

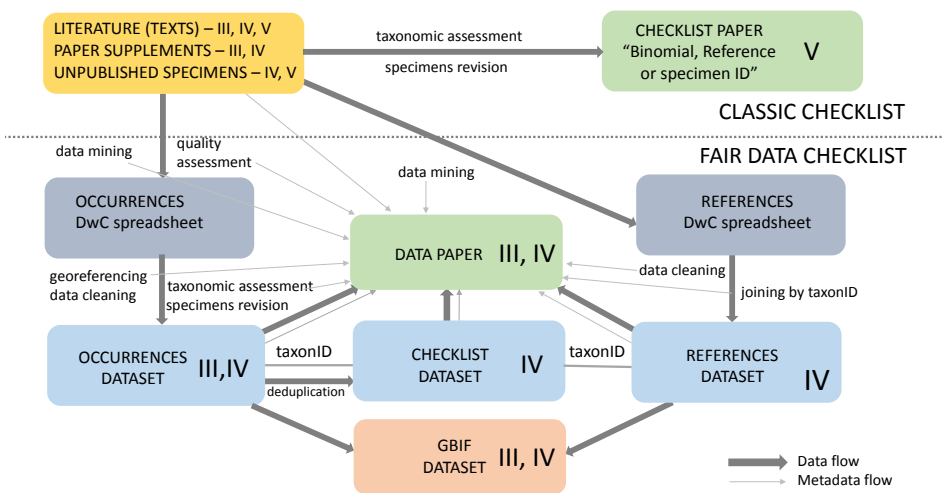


Figure 4. Schemes of data flow in the case of a classic checklist (V) and data papers III and IV.

The paper III encompasses collection data about myxomycete specimens, identified and barcoded within the project on critical revision of genera of Reticulariaceae in 2012–2022 (Leontyev et al., 2023a, 2015, 2019a). The paper IV summarizes all available published data (91 sources) on myxomycetes of Ukraine until 2023 with a minor supplement of unpublished specimens from the CWP herbarium. Occurrences in the papers III and IV, and also references in the paper IV were extracted into comma-separated spreadsheets containing columns named according to the Darwin Core standard (Wieczorek et al., 2012), followed by taxonomic assessment, georeferencing, and data cleaning procedures. After that the checklist (IV) was created automatically by extracting unique values from the scientificName column of the occurrence dataset (Fig. 4). Spreadsheets were checked and cleaned with Openrefine v. 3.2 (Ham, 2013). Taxa names were checked for misspelling by matching against the GBIF Species Matching tool (<https://www.gbif.org/tools/species-lookup>).

Data deposition, storage and publishing

DOI-cited datasets, containing specimens, alignments and sequences for the papers **I**, **II**, and **V** are available on PlutoF platform (<https://plutof.ut.ee>, Abarenkov et al., 2010). Links to the datasets: dx.doi.org/10.15156/BIO/807448, dx.doi.org/10.15156/BIO/2483934, dx.doi.org/10.15156/BIO/2483896, dx.doi.org/10.15156/BIO/2483892, dx.doi.org/10.15156/BIO/2959328, dx.doi.org/10.15156/BIO/2959329, dx.doi.org/10.15156/BIO/2959325.

Produced images of specimens and measurements of microstructures are available via PlutoF under CC BY 4.0 license. Datasets and original data for the papers **III** and **IV** are deposited in GBIF (<https://www.gbif.org/>) and Zenodo (<https://www.zenodo.org/>) platforms. New names and combinations were deposited in MycoBank (Robert et al., 2013).

RESULTS

Deep phylogeny of the genus *Arcyria*

Phylogenies inferred from 18S-EF1- α -mitSSU datasets demonstrate that the morphological genus *Arcyria* belongs to two evolutionary distant clades (A1 and A2 in Fig. 5), confirming the conclusion of García-Cunchillos *et al.* (2022) about the polyphyly of the genus. For taxonomic purposes we consider the robustly supported clade A1 as the family *Arcyriaceae* s. str., with one genus *Arcyria* s. str. The clade includes three subclades A1a, A1b and A1c that partially correspond to a visible morphological trait – colouration of spore masses.

The clade A2, although being partially supported by some methods of branch assessment in some of our phylogenies (I), was consistently recovered in the previous studies as well (Fiore-Donno *et al.*, 2013; García-Cunchillos *et al.*, 2022). Therefore, we classified the branch A2 + *Hemitrichia* as *Hemitrichiaceae* fam. nov., and re-erected the genus *Heterotrichia* Masee for the clade A2.

One taxon, showing a unique morphology is reconstructed as a sister to *Arcyriaceae* and described as a new genus *Spiromyxa* gen. nov. *incertae sedis* with one new species *S. sloacanensis*.

Character evolution and taxonomic value of morphological traits in *Arcyria*

Our analysis demonstrated that neither of traits traditionally used to delimit the genus *Arcyria* s. l., such as evanescent peridium, capillitium arrangement and ornamentation, spore ornamentation is consistent with the phylogeny, being instead scattered across the branches of *Arcyriaceae* s. str. and *Hemitrichiaceae* fam. nov (see Fig. 2 and pictograms on Fig. 5). Noticeably, in both families the cup ornamentation on the inner side was often similar to the ornamentation of capillitium.

Importantly, the colouration of spore masses in the fresh condition appeared to be partially consistent with the phylogeny. Among three subclades of *Arcyriaceae* s. str. (A1a, A1b and A1c on the Fig. 5) one contains species with spore mass coloured in shades of red (A1a, hereinafter also as “red *Arcyria*”), and the rest two mostly contain species with pale spore mass (A1b, A1c). Species of *Hemitrichiaceae* fam. nov. are predominantly yellow, but can have red colouration as well.

The character evolution analysis did not provide conclusive results about the origin of stalks in Trichiales. However, there is some evidence that the last common ancestor of *Arcyriaceae*, *Hemitrichiaceae* and *Trichiaceae* was stalked; the stalk filled with spore-like bodies perpetuates in *Arcyriaceae* and *Hemitrichiaceae*, but is lost in the common ancestor of *Trichiaceae* and evolves within this family *de novo* as the stalk filled with refuse matter. The capillitium at the same ancestral node was reconstructed as elastic net attached to the stalk, and spore colouration as yellow (I).

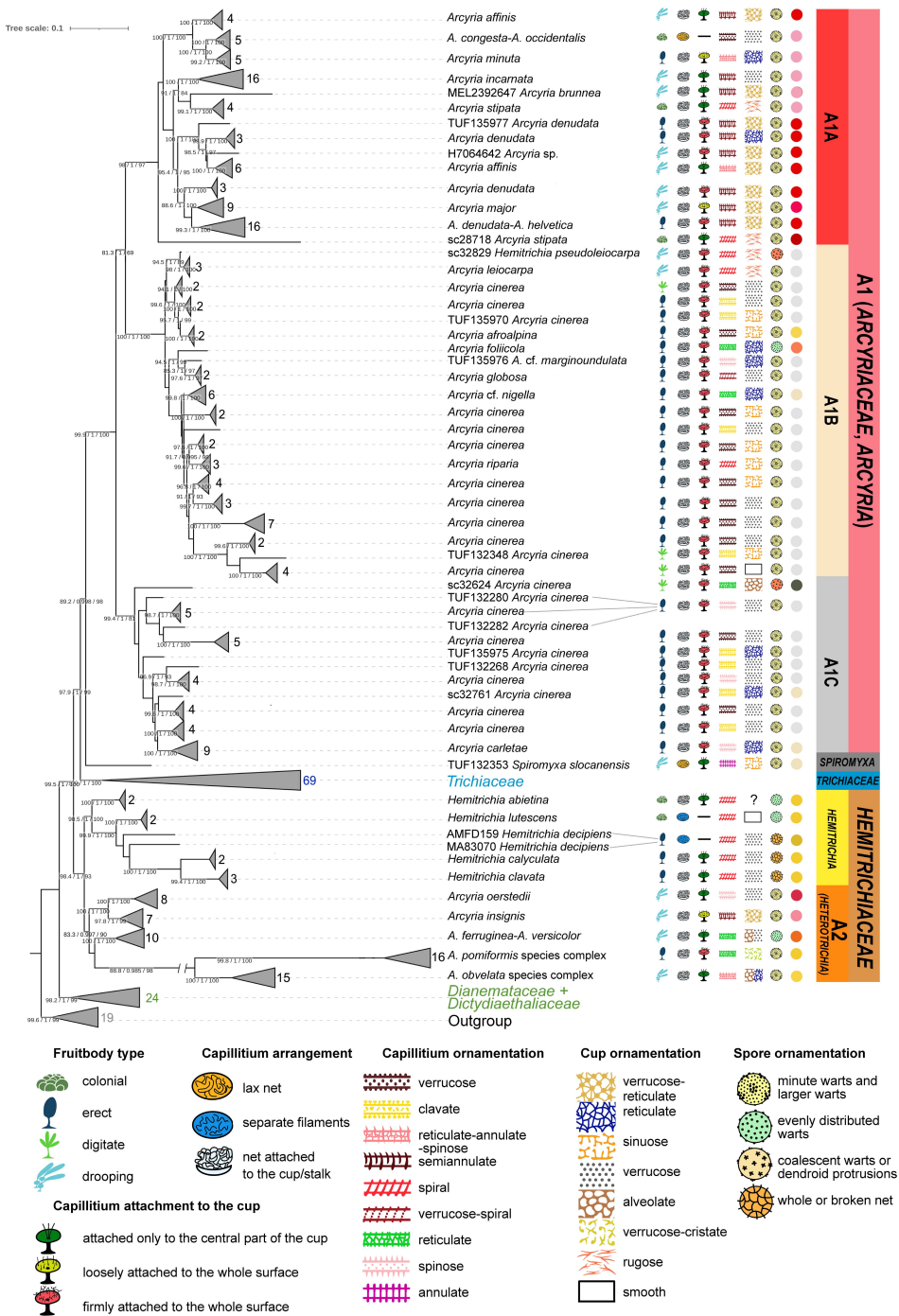


Figure 5. Phylogeny of *Trichiales* with the focus on the genus *Arcyria* (I), tree topology inferred from IQ-Tree analysis of the concatenated 18S–EF1– α –16S dataset. Numbers at nodes indicate SH-aLRT, aBayes and UFBoot support values. The length of triangles and numerals near collapsed branches indicate the number of specimens. The branches were collapsed if they formed a monophyletic clade and possessed the same combinations of traits according to the chosen classification (pictograms on the right). Pictograms denote the morphological traits (Fig 2), colored circles denote colouration.

Species complexes and species delimitation in myxomycetes

Based on the phylogeny of Trichiales with the focus on *Arcyria* we found that the majority of morphospecies of *Arcyria* including most common ones represents either species complexes, e. g. *A. obvelata* and *A. pomiformis*, or para- or polyphyletic taxa, with the extreme case of *A. cinerea* scattered over at least 23 branches, but as well *A. affinis*, *A. denudata*, and *A. stipata* (I, Fig. 5). Fifteen branches on three-gene tree are represented by singletons. Similarly, we found four lineages within a morphospecies *Lamproderma pulchellum* (II).

Different automated species delimitation approaches resulted in competing partition schemes that in some cases corresponded to species hypotheses relying on morphology, including 13 new provisional species names and excluding singletons, but in other cases were morphologically indistinguishable clusters (Fig. 6), hypothetically corresponding to complexes of cryptic species.

Distance-based, single-gene method ASAP applied to the 18S alignments suggested 49 partitions for red *Arcyria* (clade A1a, Fig. 5), and 23 partitions for *Heterotrichia* gen. nov. The same method based on EF1- α gene suggested 25 partitions for red *Arcyria* and 22 for *Heterotrichia*. The tree-based method that relies on the multispecies coalescent model (STACEY) suggested 37 or 31 partitions with ca. equal probability for red *Arcyria* (Fig. 6), and 24 for *Heterotrichia* (not shown here). Morphological examination allowed us to distinguish 17 species hypotheses in red *Arcyria* and 18 in *Heterotrichia*, excluding singletons. Thus, i. in all cases the number of morphological species hypotheses was lower than the number of units proposed by the automated species delimitation methods; ii. the automated methods were quite consistent in *Heterotrichia*, but highly inconsistent between each other and the used genes in red *Arcyria*.



Figure 6. Results of species delimitation for red *Arcyria* (clade A1a) based on different genes and methods (ASAP, STACEY, morphology). Black squares denote probabilities of sequences to belong to the same species from STACEY analysis. Names of new provisional species are written in red, existing species names are in black. Three colored stacks near the tree denote competing partition schemes: 18S (ASAP); EF1- α (ASAP); morphospecies.

Barcoding gap in myxomycetes

Most of the morphospecies of *Lamproderma* appeared to be separated from the nearest species by the local barcoding gap (II, results based on 18S marker are shown on Fig. 7, EF1- α not shown). Intraspecific pairwise distances calculated for 18S lied in a range 0–12.8%; EF1- α gene was more conservative (0–4%). In the analysed portion of *Arcyria* and *Heterotruchia* sequence data the local barcoding gap for both markers was also revealed in most cases (Yatsiuk, 2023). However, the distribution of intraspecific distances in both groups partly overlapped with the distribution of interspecific distances thus demonstrating no clear-cut groupwise threshold (II).

The analysis of 18S datasets of bright-spored vs. dark-spored myxomycetes showed that mean intra- and interspecific distances in the bright-spored clade were significantly higher than in the dark-spored clade.

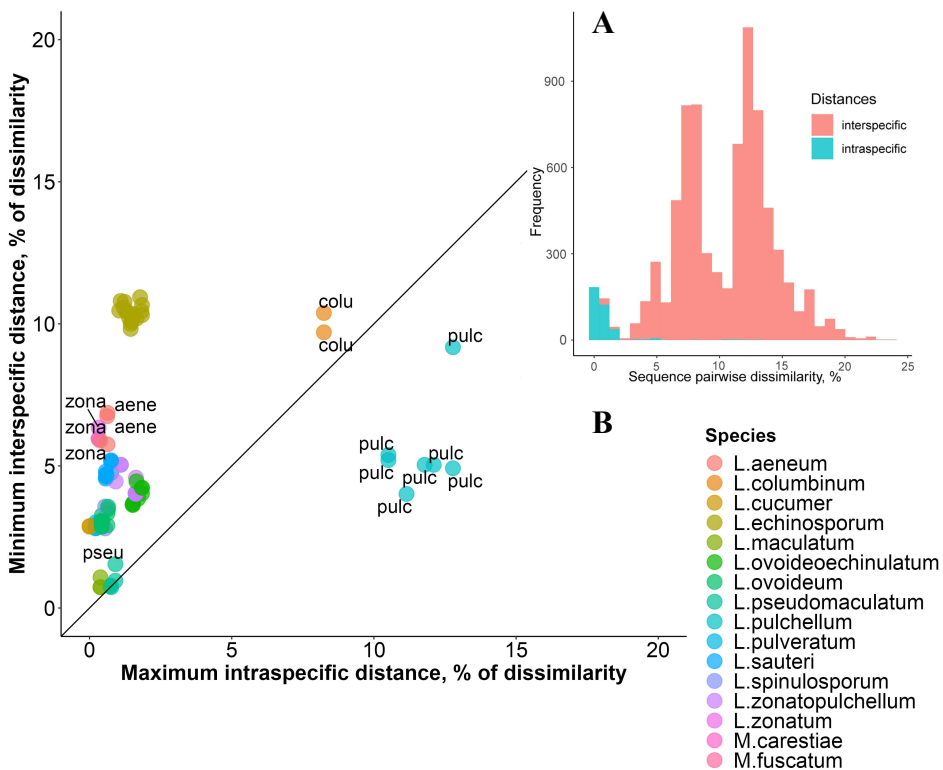


Figure 7. A – Histogram of inter- and intraspecific pairwise distances calculated for 18S alignment for species of *Lamproderma* and *Meriderma* from paper II (supplement 2). B – Maximal intraspecific distances vs with minimal interspecific distances. Points lying above the black line belong to species that show a local barcode gap and can be identified via the chosen marker.

Despite the presence of a local barcoding gap in most morphospecies within both evolutionary branches of myxomycetes, two types of exceptions were noted, where the maximal intraspecific distance surpassed the minimal interspecific distance. The first type of exception was loose clusters of ribotypes exhibiting high intra- and high interspecific distances, which may represent either extremely divergent species or the complexes of cryptic species, e. g. *L. pulchellum* (Fig. 7). The second exception involved closely related, but morphologically distinct species (both intra- and interspecific distances low). Examples of this were *Lamproderma maculatum*–*L. pseudomaculatum* (II) and *Heterotruchia ferruginea*–*H. versicolor* that differed from each other only by few species-specific substitutions (Yatsiuk, 2023).

The search for the optimal OTU-picking threshold revealed that the optimal range for dark-spored myxomycetes was 0.6–1.8 %, but in the bright-spored clade it was broader: 1.7–8.5%. Minimal cumulative errors were high in both groups and never reached zero.

Reporting the species diversity in myxomycetes

In papers III–V we present datasets that report species diversity of myxomycetes accordingly in Estonia, Ukraine, and barcoded specimens of Reticulariaceae worldwide.

The paper V encompasses 150 species representing 39 genera. The paper IV presents three datasets, Occurrences, Checklist and References published on GBIF. The datasets, including 5036 georeferenced occurrences, 339 taxa and 91 literature sources are formatted in DarwinCore terms and linked between each other through the taxonID field. Seventy-one of the used literature sources are uploaded to Zenodo repository in open access.

The paper III describes the occurrence dataset of 523 barcoded myxomycete specimens, gathered from five continents, published on GBIF, including 36 types. The dataset encompasses 43 distinct species and one subspecies of myxomycetes, including rare, endemic, and recently described taxa.

DISCUSSION

Taxonomy of myxomycetes has historically somewhat lagged compared to the state of the art in fungal taxonomy. However, works of the recent decades greatly improved the situation by developing more reliable phylogenetic frameworks for major groups (Fiore-Donno et al., 2013, 2012; García-Cunchillos et al., 2022; García-Martín et al., 2023; Leontyev et al., 2019b), and disentangling several species complexes (Dagamac et al., 2017; Feng and Schnittler, 2015; Janik et al., 2021; Leontyev et al., 2023a, 2015, 2019a; Shchepin et al., 2017, 2022).

Nonetheless, myxomycetes are taxonomically challenging due to their unique biology. In contrast to multicellular organisms, myxomycetes are scarce in features, which are mostly linked to their fruiting bodies. Fruiting bodies develop from plasmodia rapidly, therefore the environmental conditions during this period greatly influence the phenotype (Schnittler and Mitchell, 2000). Additionally, with the influx of sequence data it becomes evident that traits, earlier considered indicative for supraspecific taxa, instead evolved through complex pathways, including convergent evolution and reductive evolution (García-Cunchillos et al., 2021; Leontyev et al., 2019b).

This was clearly the case in my primary group of interest (**I**), polyphyletic *Arcyria* s. l. (Fiore-Donno et al., 2013; García-Cunchillos et al., 2022). Neither of the morphological traits such as habitus, stalk, capillitium, cup, that are traditionally used to delimit the genus or its subgenera were consistent with its phylogeny. However, I observed phylogenetically coherent patterns in colouration of spores *en masse*, a trait, previously given minor attention in *Arcyria* s. l. Given that, I proposed moderate adjustments to the system of *Trichiiales* as an attempt to harmonize it, compromising between upholding the principle of monophyly, accurately reflecting the evolutionary pathways, and facilitating phenotypical recognition.

The ancestral character state reconstruction showed that the ancestor of three families, *Arcyriaceae* s. str., *Hemitrichiaceae* fam. nov. and *Trichiaceae* s. str., might have had a secondary stalk filled with spore-like bodies, secondary net-like capillitium, and yellowish spore colouration. These traits mostly persisted in *Hemitrichiaceae* and are partially present in *Arcyriaceae* (**I**), but have undergone drastic changes in *Trichiaceae*, including multiple instances of stalk loss and capillitium transformation (García-Cunchillos et al., 2022, 2021).

After clarifying the higher-level phylogeny of *Arcyria*, I advanced to a fine-level examination of species complexes in this group. However, as not uncommonly happens, this work progressed slower than planned. Consequently, to avoid publishing nomina nuda, I choose not to list yet formally unpublished species names in this thesis. Instead, I will further discuss key conclusions derived from our analyses, presented in papers **I**, **II** as well as the conference abstracts (Yatsiuk, 2023, Yatsiuk and Leontyev, 2023).

Both distance-based and tree-based automated species delimitation methods expectedly revealed the landscape of much finer hypothetical taxonomic units

than morphology alone, supporting earlier findings of (Feng and Schnittler, 2017). Of 34 morphospecies studied only one, *A. oerstedii*, showed no considerable intraspecific variation and had no morphological “twins” elsewhere on the tree. Other than that, morphospecies were either polyphyletic or splitted onto several well-defined lineages or/and composed of sequences connected by long branches, in addition to high proportion of singleton sequences (**I**).

The existence of such multiple cryptic lineages, anywhere from three to 60 per morphospecies was convincingly demonstrated in previous single-species populational genetic studies (Dagamac et al., 2017; Feng and Schnittler, 2015; Janik et al., 2021; Leontyev et al., 2023a; Shchepin et al., 2017, 2022). Our study, being medium scale in terms of specimens per taxa sampling (average ca. 11 representatives per morphospecies), clearly demonstrates how widespread this phenomenon is across a wide range of taxa. It reveals a substantial amount of cryptic diversity to be described in *Arcyriaceae* and *Hemitricihaceae* and confirms the suggestion of Shchepin et al. (2022) that the actual number of species in myxomycetes may be several times higher than described.

The cryptic diversity in myxomycetes is usually explained by the existence of multiple, reproductively isolated biospecies that often co-occur on one research plot, but as well possess pronounced biogeographic structure worldwide (Janik et al., 2021; Leontyev et al., 2023a). To explain this phenomenon, the combination of sympatric and allopatric speciation has been suggested (Dagamac et al., 2017; Janik et al., 2020; Shchepin et al., 2022). However, since sequence-based methods alone usually do not strictly differentiate between the populational structure and established, reproductively isolated species (Carstens et al., 2013; Sukumaran and Knowles, 2017), other lines of evidence are being searched for. In some studies, thorough examination allowed to discover new traits that fully or partially distinguish biospecies (Dagamac et al., 2017; Janik et al., 2021; Leontyev et al., 2023b). However, other studies have not found such traits (Shchepin et al., 2022, 2017). In the research discussed here (**I**, **II**), I encountered both morphologically discernible and indiscernible lineages, even with the application of SEM. It should be mentioned, that regardless of whether these lineages are considered biospecies, cryptic species or other kinds of evolutionary units, there is still no community consensus about how to communicate them (Schnittler et al. 2024).

As mentioned earlier, the revolution in species definitions in myxomycetes poses another challenge: bridging the biodiversity data accumulated in the past with current species inventories. The first stage of this process involves gathering previously reported data on species diversity and publishing them according to FAIR principles. Adopting these principles for species inventories is a significant departure from traditional approach (Reyserhove et al., 2020). Initially, I used the traditional approach in the paper **V**, but later changed the mindset towards “data fairness”. Consequently, papers **III** and **IV** present data that are accompanied with rich metadata, employ persistent identifiers and are published not only in the journal itself but also in searchable resources GBIF and Zenodo (**Findable**); data are available for humans and machines from open data repositories (**Accessible**);

structured according to international data standard DwC (**Interoperable**) and are published under permissive Creative Commons licenses (**Reusable**).

Where this work should proceed?

Firstly, this work will be only considered complete when the identified species complexes within *Arcyria* and *Heterotrichia* are formally described.

More broadly, future myxomycete studies should include combining the multigene datasets from recent and upcoming myxomycete studies to create the reliable phylogeny of the whole group. The evolution of morphological traits should be traced accordingly, and taxonomy on supraspecific ranks harmonized. Equally important is to establish an annotated sequence database focused on myxomycetes barcode markers and helping to unequivocally communicate cryptic species. These goals would require a dedicated collaborative effort.

CONCLUSIONS

This thesis summarizes a series of studies on taxonomy, distribution, and genetic diversity of myxomycetes, with a particular focus on the genus *Arcyria* s. l. The main results and conclusions of this thesis are the following:

- The paper **I** provided a robust taxonomic backbone for *Arcyria* and allied genera with wide geographical and taxonomical sampling. This work has led to the emendment of the family *Arcyriaceae* s. str., establishment of a new family *Hemitrichiaceae*, a new genus *Spiromyxa*, and resurrection of the genus *Heterotrichia*.
- Practically all traits, traditionally used to delimit supraspecific taxa in *Arcyriaceae* appeared to be homoplastic or symplesiomorphic. However, colouration of the spore mass was identified to be more congruent with reconstructed trees; thus, it was used in delimitation of abovementioned genera and families.
- Most morphospecies of *Arcyria* sampled across the world and sequenced for the first time in this study appeared to be either species complexes, para- or polyphyletic entities (**I**). Similarly, at least four lineages were found that may represent cryptic species within a morphospecies *Lamproderma pulchellum* (**II**).
- Preliminary species delimitation analyses in *Arcyriaceae* s. str. demonstrated a tendency to oversplitting and high incongruence between used genes and methods of automated species delimitation as compared to morphology. However, in *Hemitrichiaceae* the delimitation schemes were much more congruent.
- Myxomycetes generally show a presence of a local barcoding gap between morphospecies, at least in thoroughly revised groups. However, there are exceptions representing i. morphologically indistinct lineages (cryptic species) and ii. morphologically distinct closely related species, where barcoding markers are very conservative. There is no universal OTU-picking threshold even at the genus level, presumably due to the difference in coalescent depth between species (**II**)
- The adherence to FAIR data principles is crucial for enhancing the reproducibility and utility of biodiversity data. Papers **III–V** demonstrate the evolution of views on importance of FAIR data publishing, and represent a pioneering effort in myxomycete studies.

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SUMMARY

Myxomycetes, or Myxogastria, comprise approximately 1,050 species within the kingdom Amoebozoa. Myxomycetes have complex life cycle, which includes an amoeboid stage, a multinucleate mobile plasmodium, and spore-bearing sporocarps. In their amoeboid stage, myxomycetes inhabit diverse substrates such as soil, bark of living trees, decaying wood, leaf litter, and other plant debris. There they feed on bacteria, algae and protists, and themselves are the source of food to beetles, slugs and nematodes, thus playing an important role in terrestrial ecosystems.

Despite their substantial ecological functions, myxomycetes have been systematically underrepresented in taxonomical and ecological research. Since myxomycetes were generally considered a cryptic and less economically significant group, their taxonomy historically lagged compared to the state of the art in fungal taxonomy. Consequently, there is still the need of understanding phylogenetic relations, species boundaries, and developing of robust practices of species delimitation, description, and communication in myxomycetes. The ongoing revolution in species definitions in myxomycetes poses another challenge: bridging the biodiversity data accumulated in the past with current species inventories. The first stage of this process involves gathering previously reported data on species diversity and publishing them according to FAIR principles.

Given these challenges, this study aims to fill the gaps in our understanding of myxomycetes. It is a multiaspect study, comprised of two major parts. The first part of this thesis addresses phylogeny, evolution, and species delimitation in chosen groups of myxomycetes (papers **I**, **II**).

In our taxonomical studies **I** and **II** we used morphological and molecular methods to (1) establish a reliable taxonomical backbone for *Arcyria* and allied genera within the bright-spored myxomycetes, (2) reconstruct the evolutionary pathway of morphological characters and evaluate their application in taxonomy of bright-spored myxomycetes; (3) assess the barcoding gap applicability in myxomycetes. Additionally, we used exploratory and validation species delimitation techniques to revise the genus *Arcyria* on the species level, however, this part of work is yet to be finished.

In the paper **I** we present phylogenies with wide taxonomical and geographical sampling across *Arcyria*, a genus of the order Trichiales that includes 265 published species and infraspecific taxa. The majority of species in this genus are problematic: representing taxonomic synonyms, taxa based on old and scarce descriptions, or relying on doubtful morphological differences. Phylogenies inferred from 18S–EF1– α –mitSSU datasets demonstrated that the genus *Arcyria* belongs to two evolutionary distant clades, confirming the conclusions of the previous studies about the polyphyly of the genus. In the paper **I** we emended the family *Arcyriaceae* s. str., established a new family *Hemitrichiaceae*, a new genus *Spiromyxa*, and resurrected the genus *Heterotrichia*.

The analyses of morphological traits demonstrated that neither of traits traditionally used to delimit the genus *Arcyria* s. l. is consistent with the phylogeny, being instead scattered across the branches of *Arcyriaceae* s. str. and

Hemitrichiaceae fam. nov. However, the colouration of spore masses in fresh condition, a trait, previously given minor attention in *Arcyria* s. l., appeared to be partially consistent with the phylogeny. The character evolution analysis did not provide conclusive results about the origin of stalks in Trichiales. However, there was some evidence that the last common ancestor of *Arcyriaceae*, *Hemitrichiaceae* and *Trichiaceae* was stalked; the stalk filled with spore-like bodies perpetuated in *Arcyriaceae* and *Hemitrichiaceae*, but was lost in the common ancestor of *Trichiaceae*. The capillitium at the same node was reconstructed as elastic net attached to the stalk, and spore mass colouration as yellow.

We found out that the majority of morphospecies of *Arcyria* including most common ones represent either species complexes or para- or polyphyletic taxa, with the extreme case of *A. cinerea* scattered over at least 23 branches. Different automated species delimitation approaches resulted in competing partition schemes that in some cases corresponded to species hypotheses relying on morphology (including 13 new provisional species names and excluding singletons), but in others were morphologically indistinguishable clusters, hypothetically corresponding to complexes of cryptic species.

Our paper II focuses on a genus *Lamproderma*, a comparatively lately-radiated, species-rich genus of *Columellomycetidae*. Apart from a taxonomical study and the description of a new species, in this publication and in a series of conference abstracts we address the application of the barcoding gap in myxomycetes. Most of the morphological species hypotheses of bright-spored and dark-spored myxomycetes included into the study appeared to be separated from the nearest neighbour by the local barcoding gap. However, in both groups there were exceptions representing i. morphologically indistinct lineages (cryptic species) and ii. morphologically distinct closely related species, where barcoding markers were extra conservative. The distribution of intraspecific distances in both groups partly overlapped with the distribution of interspecific distances thus demonstrating no clear-cut groupwise threshold, presumably due to the difference in coalescent depth between species.

The second part of this thesis summarizes our effort in collecting and publishing primary data about species diversity of myxomycetes. In papers (III–V) we demonstrate how the data obtained from various sources, may be reported according to FAIR (Findable, Accessible, Interoperable, Reusable) principles. The paper V reports 150 species representing 39 genera of myxomycetes of Estonia. The paper IV presents the occurrence-based checklist of myxomycetes of Ukraine and includes three datasets: Occurrences (5036 georeferenced occurrences), Checklist (339 taxa) and References (91 sources). The datasets, published on GBIF, are formatted in DarwinCore terms and linked between each other through the taxonID field. Seventy-one of the used literature sources were uploaded to Zenodo repository in open access. The paper III describes the worldwide occurrence dataset of 523 barcoded myxomycete specimens, including 36 types, gathered from five continents. The dataset encompassed 43 species and one subspecies of myxomycetes, including rare, endemic, and recently described taxa.

SUMMARY IN ESTONIAN

Limakute evolutsioon, liikide piiritlemine ning mitmekesisus *Arcyria* ja seotud perekondade näitel

Myxogastria (ehk limakud) sisaldab ligikaudu 1500 liiki, mis kuuluvad protistide riiki *Amoebozoa*. Limakutel on mitmeetapiline elutsükkel, mis hõlmab amöboidset staadiumi, mitmetuumalist liikuvat plasmoodiumi ja eoseid kandvaid struktuure. Limakud elavad amöboidses staadiumis substraatidel nagu muld, eluspuude koor, kõdupuit ja muu taimne varis. Seal toituvad nad bakteritest, vetikatest ja teistest protistidest ning on ise mardikate, nälkjate ja nematoodide toiduallikaks, omades maismaaökosüsteemide toitumisahela olulist rolli.

Vaatamata toitumisahela olulisele rollile on limakud taksonoomilistes ja ökoloogilistes uuringutes alaesindatud. Traditsiooniliselt on limakuuid uurinud mükoloogid. Kuna neid peeti üldiselt vähem oluliseks taksoniks, jäi nende taksonoomia seentega võrreldes väheuurituks. Seetõttu on jätkuvalt oluline selle taksoni fülogeneesi ja liikide eristamise uurimine ning ökoloogilised uuringud. Limakute uurimine esitab veel ühe väljakutse: minevikus kogutud mitmekesisuse andmete ühendamise kaasaegsete liigi nimedega. Selle protsessi esimene etapp hõlmab liikide varem avaldatud andmete digitaliseerimist ja avaandmetena avaldamist FAIR (Findable=leitav, Accessible=ligipääsetav, Interoperable=koostalitlusvõimeline, Reusable=korduvkasutatav) põhimõtete kohaselt.

Neid väljakutseid arvestades on käesoleva doktoritöö eesmärk täiendada teadmisi limakute taksonoomiast ja evolutsioonist ning korrastada ja digitaliseerida limakute varasemaid uurimisandmeid. Doktoritöö koosneb peamiselt kahest osast: 1) valitud limaku taksonite fülogeneesi, evolutsiooni ja liikide piiritlemisega seotud uuringud (artiklid I, II); 2) limakute liikide varasemate andmete korrastamine, digitaliseerimine ja avaandmetena avaldamine (artiklid III–V).

Doktoritöö esimeses osas kasutame morfoloogilisi ja molekulaarseid meetodeid (I, II), et (1) luua perekond *Arcyria* ja teiste heledaeoseliste sõsarperekondade uus taksonoomiline süsteem, (2) luua evolutsiooniline morfoloogiliste tunnuste ontoloogia ja hinnata nende rakendamist heledaeoseliste limaku liikide eristamisel, (3) hinnata limakutel DNA triipkoodi geenmarkerite rakendatavust.

Artiklis I esitame fülogeneesi uurimistöö, mis hõlmab perekonna *Arcyria* laia taksonoomilise ja geograafilise valimi. Selles perekonnas on teadusele kirjeldatud 265 liiki ja liigisisest taksonit. Suur osa *Arcyria* liikidest vajab täiendavaid uuringuid: siin esineb palju taksonoomilisi sünonüüme, liigid põhinevad puudulikel kirjeldustel või tuginevad väikestele morfoloogilistele erinevustele. Kolme geenimarkeri (18S SSU, EF1- α ja mitSSU) põhine fülogenees näitas, et perekond *Arcyria* liigid kuuluvad kahte evolutsiooniliselt kaugesse taksonisse. Käesoleva töö tulemused kinnitasid varasemat hüpoteesi *Arcyria* polüfüleetilisusest. Artiklis I täiendasime sugukonna *Arcyriaceae* s. str. varasemat klassifikatsiooni, kirjeldasime uue sugukonna *Hemitrichiaceae*, uue perekonna *Spiromyxa* ja võtsime uuesti kasutusele perekonna *Heterotrichia*.

Morfoloogiliste tunnuste analüüs näitas, et kumbki perekonna *Arcyria* s. l. piiritlemiseks enim kasutatud tunnusest pole molekulaarse fülogeneesi tulemustega kooskõlas. Enamik kasutatud morfoloogilistest tunnustest esinevad sugukondade *Arcyriaceae* s. str. ja *Hemitrichiaceae* fam. nov. liikidel hajutatult. Kuid värskete eksemplaride eosmassi värvus (tunnus, millele on varem *Arcyria* s. l. vähe tähelepanu pööratud), on fülogeneesiga osaliselt kooskõlas. Seltsi *Trichiales* tunnuste evolutsiooni analüüs ei andnud lõplikke tulemusi eosla jala päritolu kohta. Siiski leidsime tõendeid selle kohta, et sugukondade *Arcyriaceae*, *Hemitrichiaceae* ja *Trichiaceae* ühisel esivanemal esines eosla jalg. Käesoleva uuringu põhjal on nimetatud jalg püsinud sugukondades *Arcyriaceae* ja *Hemitrichiaceae* tänapäevani, kuid on evolutsioonis kaduma läinud sugukonnas *Trichiaceae*. Seltsis *Trichiales* esinev kapilliitium kirjeldati kui eosla jala külge kinnitunud elastne võrk ja eosmassi värvus kollasena.

Selgitasime välja, et enamik perekonna *Arcyria* morfoloogilistel tunnustel põhinevad liigid on para- või polüfüleetilised liigikompleksid. Meie andmetel on näiteks liigi *Arcyria cinerea* eksemplarid molekulaarsete tunnuste põhjal fülogeneesi puu 23 erinevas harus. Erinevad statistilised meetodid nagu automatiseeritud liikide eristamise meetodid (STACEY, ASAP) andsid mõnel juhul tulemuse, mida toetasid ka morfoloogilised tunnused. Selle meetodi abil võib eristada 13 potentsiaalset uut liiki. Samas saadi selle meetodiga ka mitmeid krüptilisi liike, mis on morfoloogiliselt eristamata.

Doktoritöö II artikkel keskendub fülogeneetilisel suhteliselt hiljuti eristunud liigirikkale perekonnale *Lamproderma*, mis kuulub sugukonda *Columellomycetidae*. Lisaks taksonoomilisele uuringule ja uue liigi kirjeldusele käsitleme DNA triipkoodi vahemiku rakendamist limakutel (II). Enamikel uuringusse kaasatud heleda- ja tumedaoselistel morfoloogilistel tunnustel eristatud sõsarliikidel esineb DNA triipkoodi vahemik. Siiski oli mõlemas rühmas erandeid: (i) morfoloogiliselt ebaselged liinid (tõenäoliselt krüptilised liigid) ja (ii) morfoloogiliselt erinevad liigid, kus DNA triipkoodi markerid osutusid konservatiivseks. Liigisisese varieeruvuse suurus kattus osaliselt liikidevaheliste kauguste jaotusega, mis ei võimaldanud valida selget liikide eristamise läviväärtust.

Doktoritöö teises osas võetakse kokku uurimistöö limakute liigilise mitmekesisuse esmaste andmete kogumisel ja avaldamisel. Kolm käesoleva doktoritöö artiklit (III–V) käsitlevad kuidas saab erinevate allikate digitaliseeritud andmeid esitada vastavalt FAIR põhimõtetele. Artikkel III käsitleb 150 liiki, mis kuuluvad 39 eri limaku perekonda ja esinevad Eestis. IV artiklis esitatakse Ukraina limakute sageduspõhine nimekiri ja avaldatakse kolm andmekogumit: taksoni esinemised (5036 georefereeritud taksoni esinemist), liikide nimestik (339 taksonit) ja seotud kirjanduse viited (91 allikat). Globaalses elurikkuse portaali (GBIF) limakute avaldatud andmestikud on vormindatud vastavalt DarwinCore standardile ja omavahel seotud takson ID välja kaudu. Seitsekümmend üks kasutatud kirjandusallikat laeti avatud juurdepääsuga Zenodo digiarhiivi. Artiklis V kirjeldatakse viielt eri kontinendilt kogutud 523 DNA triipkoodiga limaku eksemplari (sealhulgas 36 tüüpeksemplari) põhjal nende liikide levikut. Andmekogum sisaldab 43 limaku liiki ja ühte alamliiki, sealhulgas ka haruldasi, endeemseid ja viimastel aastatel kirjeldatud taksonideid.

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- Yatsiuk, I.** Leontyev, D. *Arcyria* and allied genera: taxonomic backbone, diversity and characters evolution. 11th International Congress on the Systematics and Ecology of Myxomycetes (ICSEM11), 28–31 August 2023, Tartu, Estonia.
- Yatsiuk, I.** Barcoding in species delimitation and otu-picking for dark-spored vs. bright-spored myxomycetes. 11th International Congress on the Systematics and Ecology of Myxomycetes (ICSEM11), 28–31 August 2023, Tartu, Estonia.
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- Yatsiuk, I.**, Shyriaeva, D., Prylutskyi, O. GBIF and open biodiversity data in Ukraine. BioDATA Final Conference, 13 November 2022, Oslo, Norway.
- Yatsiuk, I.**, Prikhodko, I., Leontyev, D. Barcoding in bright-spored and dark-spored myxomycetes: no universal threshold. Poster. International Conference on DNA Barcoding and Biodiversity (ICDBB). 25–27 May, 2022, Sofia, Bulgaria.
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- Yatsiuk, I.** Molecular species definition in myxomycetes – where are we now? PhD Student Conference of the Department of Botany, 2020, UT.

Other publications: datasets, educational materials:

- Prylutskyi, O., **Yatsiuk, I.**, Yatsiuk, Y., 2022. Records of *Sarcoscypha austriaca* and *Urnula craterium* from the territory of Eastern Ukraine. Version 1.5. V. N. Karazin Kharkiv National University. Occurrence dataset.
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- Mikryukov, V, Savchenko, A, **Yatsiuk, I.**, 2021. Phylogenetic reconstruction workshop. <https://mycology-microbiology-center.github.io/Phylo2021/>
- Savchenko, A., Ordynets, A., Prylutskyi, O., **Yatsiuk, I.**, Akulov, O., Usichenko, A., 2017. V.N. Karazin Kharkiv National University herbarium, Department of Mycology and Plant Resistance. Occurrence dataset.
<https://doi.org/10.15468/kuspj6>

Teaching, management:

- 2023** 11th International Congress on the Systematics and Ecology of Myxomycetes (ICSEM11), 28–31 August 2023, Tartu, Estonia – president, organizer.
- 2021** Phylogenetic reconstruction workshop, Tartu – organizer, teacher
- 2019–2022** BioData, biodiversity data management skills for students, Norway–Ukraine, mentor
- 2018** Ukrainian Rufford Small Grants Conference “From monitoring to implementation”. Kharkiv, Ukraine, 23–25 April 2018 – conference organizer.

Grants and scholarships:

- 2024** Mobility grant of Estonian Doctoral School grant for the participation in the International Mycological congress, oral talk
- 2024** BiCIKL infrastructure, a grant for free of charge publication in the dedicated topical collection in the Biodiversity Data Journal within the project “Linking FAIR biodiversity data through publications: The BiCIKL approach”
- 2022** University of Oslo, BioDATA grant for data mobilization including digitization, data quality assurance, data preparation, and publication of collection specimen and other species data from Ukraine to GBIF, project “Deciphering Cyrillic: the checklist from invisible sources”
- 2021** Archimedes DORA Plus short-term mobility grant for attending the XXV Nordic Mycological Congress in Scania, Sweden – the event was cancelled due to COVID19 pandemic and grant declined by me.
- 2020** Kristjan Jaak National Scholarship for short study visits, attending 10th International Congress on the Systematics and Ecology of Myxomycetes, Costa-Rica.
- 2016** The Rufford Foundation, small grant for the project “Conservation of rare fungus *Pleurotus calypttratus* in aspen stands of Ukrainian Forest-Steppe”.

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Yatsiuk, I. Leontyev, D. *Arcyria* and allied genera: taxonomic backbone, diversity and characters evolution. 11th International Congress on the Systematics and Ecology of Myxomycetes (ICSEM11), 28–31 August 2023, Tartu, Estonia.

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Yatsiuk, I., Prikhodko, I., Leontyev, D. Barcoding in bright-spored and dark-spored myxomycetes: no universal threshold. Poster. International Conference on DNA Barcoding and Biodiversity (ICDBB). 25–27 May, 2022, Sofia, Bulgaria.

Yatsiuk, I. Do “lowland nivicolous” myxomycetes fruitify more regularly than we think? 10th International Congress on the Systematics and Ecology of Myxomycetes (ICSEM10). 25–28 February 2020, Turrialba, Costa-Rica.

Yatsiuk, I. Molecular species definition in myxomycetes – where are we now? PhD Student Conference of the Department of Botany, 2020, UT.

Muud publikatsioonid:

Prylutskyi, O., **Yatsiuk, I.**, Yatsiuk, Y., 2022. Records of *Sarcoscypha austriaca* and *Urnula craterium* from the territory of Eastern Ukraine. Version 1.5. V. N. Karazin Kharkiv National University. Occurrence dataset.

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Savchenko, A., Ordynets, A., Prylutskyi, O., **Yatsiuk, I.**, Akulov, O., Usichenko, A., 2017. V.N. Karazin Kharkiv National University herbarium, Department of Mycology and Plant Resistance. Occurrence dataset.

<https://doi.org/10.15468/kuspj6>

Õpetamine, juhtimine:

- 2023** 11th International Congress on the Systematics and Ecology of Myxomycetes (ICSEM11), 28–31 August 2023, Tartu, Estonia – president, korraldaja.
- 2021** Phylogenetic reconstruction workshop, Tartu – korraldaja, mentor
- 2019–2022** BioData projekt– õpilaste bioloogilise mitmekesisuse andmehaldus-
oskused, mentor
- 2018** Ukraina Ruffordi sihtasutuse konverents “From monitoring to implementation”. Harkiv, Ukraina, 23–25 April 2018 – konverentsi korraldaja.

Uurimistoetused ja stipendiumid:

- 2024** BiCIKL infrastruktuur, Toetus artikli avaldamiseks ajakirjas projekti “Linking FAIR biodiversity data through publications: the BiCIKL approach” raames
- 2022** Oslo Ülikool, BioDATA toetus andmete koondamiseks, projekt „Kirillitsa dešifreerimine: nähtamatute allikate kontrollnimekiri“
- 2021** Archimedes DORA Plus lühiajalise liikuvustoetus XXV Põhja-
maade mükoloogiakongressil Scania, Rootsis osalemiseks. Üritus
tühistati COVID19 pandeemia tõttu ning toetuse andmisest loobuti.
- 2020** Kristjan Jaagu nimelise õpirände stipendium, 10. rahvusvahelisel
limakute süstemaatika ja ökoloogia konverentsil osalemine,
toimumiskoht: Costa Rica
- 2016** Väike toetus Rufford sihtasutuselt projekti “Haruldase seene *Pleurotus calypratus* kaitse Ukraina metsastepi haavametsades”

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