

FINAL REPORT

1 General Information

DFG reference number: LI 496/32-1

Project number: 437386703

Project title: A temperate radiation in a tropical plant family – factors underpinning evolution of the Eurasian *Vincetoxicum* (Apocynaceae) complex

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Reporting period (entire funding period): 01.10.2020 – 30.09.2025

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DOI: 10.15495/EPub_UBT_00009580

2 Summary

Vincetoxicum is the only genus of the otherwise predominantly tropical Apocynaceae-Asclepiadoideae subfamily that extends into Europe north of the Alps. Furthermore, some species are invasive in North America. To elucidate the reasons for this successful radiation, three independent lines of evidence were investigated: morphometry, molecular phylogeny, and the content of phenanthroindolizidine alkaloids (PIAs), chemical compounds unusual within the Asclepiadoideae. We (1) compiled a comprehensive morphological dataset that allowed for the delimitation of morphospecies; (2) generated a comprehensive phylogeny of *Vincetoxicum* s.str. based on numerous low-copy nuclear genes (targeted sequencing); (3) We developed a stable species concept for Eurasian *Vincetoxicum* based on various lines of evidence (morphospecies and coalescence-based species) – a much-needed base for further studies in the group; (4) we tested the hypothesis that the most successful species are those with the best chemical defenses, using the quantity and diversity of PIAs as an approximation of chemical defense strength.

The phylogenetic analysis contradicts the previous understanding that *Vincetoxicum* in Europe consists essentially of one widespread and variable species, *V. hirundinaria*. Most of the investigated “subspecies” of *V. hirundinaria* turned out to be distinct lineages, as did the Eastern European species often considered “doubtful.” In the core German distribution area of *V. hirundinaria*, two phylogenetically independent lineages of *V. hirundinaria* have been identified, although they cannot yet be distinguished morphologically. Furthermore, the investigations have established that *V. hirundinaria* is not invasive in North America. For the two invasive species, *V. nigrum* and *V. rossicum*, no correlation could be found between PIA content and geographic distribution.

Zusammenfassung

Vincetoxicum ist die einzige Gattung der sonst überwiegend tropischen Apocynaceae-Asclepiadoideae, die bis nach Europa nördlich der Alpen vorstößt. Darüber hinaus sind einige Arten invasiv in Nordamerika. Um die Hintergründe der Evolution dieser erfolgreichen Radiation zu beleuchten, wurden drei unabhängige Evidenzlinien untersucht: Morphometrie, molekulare Phylogenie und Gehalt an Phenanthroindolizidin-Alkaloiden (PIAs), eine innerhalb der Asclepiadoideae ungewöhnlichen chemischen Ausstattung. Wir haben (1) einen umfassenden morphologischen Datensatz zusammengestellt, der die Abgrenzung von Morphospezies erlaubt hat; (2) eine umfassende Phylogenie von *Vincetoxicum* s.str. erstellt, basierend auf zahlreichen in niedriger Kopienzahl vorliegenden Kerngenen (“targeted sequencing”); (3) ein stabiles Artkonzept für eurasische *Vincetoxicum* erarbeitet, beruhend auf verschiedenen Evidenzlinien (Morphospezies und koaleszenz-basierten Arten) – ein dringend

benötigtes Werkzeug für weitere Untersuchungen in diesem Komplex; (4) die Hypothese getestet, daß die erfolgreichsten Arten diejenigen mit der besten chemischen Verteidigung sind, wobei wir Menge und Diversität an PIAs als Annäherungsmaß für die Stärke der chemischen Verteidigung genutzt haben.

Die phylogenetische Analyse erteilt dem bisherigen Verständnis, dass *Vincetoxicum* in Europa im wesentlichen aus einer weitverbreiteten und variablen Art, *V. hirundinaria*, besteht, eine Absage. Die meisten untersuchten „Unterarten“ von *V. hirundinaria* haben sich als eigenständige Abstammungslinien erwiesen, ebenso wie die oft als „zweifelhaft“ geführten osteuropäischen Arten. Im deutschen Kerngebiet von *V. hirundinaria* lassen sich zwei phylogenetisch unabhängige Linien von *V. hirundinaria* nachweisen, die allerdings bislang morphologisch nicht unterschieden werden können. Im Rahmen der Untersuchungen konnte ferner geklärt werden, dass *V. hirundinaria* in Nordamerika nicht invasiv ist. Bei den beiden invasiven Arten, *V. nigrum* und *V. rossicum*, konnte kein Zusammenhang zwischen PIA-Gehalt und geographischer Verbreitung festgestellt werden.

3 Progress Report

Background and objectives of the project

- Starting from the recent recircumscription of *Vincetoxicum* (Liede-Schumann et al. 2012, 2016), an Apocynaceae-Asclepiadoideae genus presently comprising 271 species (WorldFloraOnline, <https://wfoplantlist.org/taxon/wfo-4000040301-2025-12>, accessed 2026-01-19), the European members had been identified as members of one of two temperate radiations in the genus, termed "*Vincetoxicum* s.str." clade, estimated at a crown age of 9.4 Ma. (the second temperate radiation is restricted to south-east Asia and not considered here). The "*Vincetoxicum* s.str." clade is distributed from Japan and China (first-branching members) via India and the Asian mountain chains to the Eastern Irano-Turanian Region, and from there to western central Asia, the Western Irano-Turanian Region, the Mediterranean, and Western Europe (excluding Great Britain), with the Western European members monophyletic in the top clade. Three members of the western European top clade have been reported as noxious weeds in north America.
- The present project was focussing on the western European top clade and the species neophytic in north America studying the underlying patterns of the obvious and successful expansion of this lineage. In order to reveal general causal mechanisms that make up temperate radiations, we have followed three lines of evidence: morphometric, molecular, and chemical. Synthetic analysis was carried out to elucidate

the phenotypic variation, the genetic basis, and the supposed chemical defence strategy (Phenanthroindolizidine alkaloids, PIAs) in this clade to test the hypothesis that the most successful lineages are the ones with the best chemical defence system. To trace the process of diversification in Eurasian *Vincetoxicum*, we created fully time-resolved structure of this clade allowing to obtain (1) a clear-cut concept of the taxonomic units involved and their spatial distribution; (2) a well-resolved and dated species phylogeny against which character distributions can be tested; (3) a suite of characters to test for their possible link to accelerated speciation.

The specific questions to be answered were:

- How many genetically and morphologically coherent species can be circumscribed, which can serve as basic taxonomic units to study species radiation ?
- In the same line, is the suspicion of the existence of several hybrid swarms in Eurasian *Vincetoxicum* supported by our data, and if so, which taxa are involved ?
- Are the taxa considered as subspecies of *V. hirundinaria* monophyletic or do they represent independent, morphologically similar lineages ?
- What are the exact phylogenetic positions of the invasive species ? That is, do they form one clade or is 'invasiveness' a polyphyletic feature in *Vincetoxicum*?
- Is the Caucasus indeed a biogeographic divide between a northern, temperate lineage of Eurasian *Vincetoxicum*, expanding into Russia and Central Europe, and a subtropical-temperate western lineage, expanding via Turkey into the Mediterranean, as inferred by Liede-Schumann et al. (2016) ?
- Which are the traits that offered the northern, temperate lineage successful diversification in freezing environments ?
- Is the occupied area of a species linked to the amount and diversity of PIAs it contains ?
- Similarly, do the invasive species contain a stronger and more diverse defence system than their immediate relatives ?
- Is speciation rate heterogeneity detectable in the group, and if so, is it linked to PIA heterogeneity patterns ?
- More generally, can we detect traits that explain evolutionary success of certain lineages within *Vincetoxicum* ?

- **Description of the project-specific results and findings.**

- The molecular dataset, processed by Seth Musker (today University of Cape Town), provided phylogenies revealing that the structure of *Vincetoxicum* in Europe was much more complex than hitherto thought. Our reconstruction suggests that the localized species described in particular from eastern and southeastern Europe generously subsumed under “*Vincetoxicum hirundinaria*” by earlier researchers (adopted by the Euro+Med PlantBase (Euro+Med 2006–) constitute genuine independent lineages and should be recognized as such. Of the characters thought to be important for *Vincetoxicum* (corolla colour, and indument, leaf shape, length of peduncles and pedicels, etc.) none exclusively characterizes a single clade, and few characterize groups of species. Very short peduncles are characteristic for two clades and highly fused corona lobes characterize most species of the *V. fuscatum* clade, but are neither exclusively found there, nor present in all species of the clade. There is some geographic structure in the data, in particular, the Western Mediterranean samples form a clade of their own, including the neophytic *V. nigrum*; and one clade is centered in the Eastern Mediterranean with some members extending to the Black Sea; however, a second clade has the same distribution, but is centered around the Black Sea with few species extending to the Eastern Mediterranean. The specimens identified morphologically as “*V. hirundinaria* s.str.” fall into two clades, one centered in central Europe, and the second one north, east and south of these samples. This is indicative of subsequent pushes of *V. hirundinaria*-like plants into Central Europe and thus cryptic speciation. These results are presently written up for publication in TAXON.
- From these results it became clear that a thorough revision of the available material of European *Vincetoxicum* would be indispensable for any future work in the genus. Based on his MSc thesis, Ludwig Seliger undertook the task of gathering the necessary information, such as protologues, types, distribution records and studying herbarium material from the larger central European herbaria. His study resulted in 44 European entities treated as species and is presently submitted to Systematic Botany Monographs. The work will include taxonomic information, descriptions, and a key to all species, as well as illustrations of almost all species. The first paper, a clarification of the name and typification of *V. fuscatum*, is published (Seliger & Meve, 2026). During this work it became clear that the assumption that there are three neophytic species in North America is incorrect. Of the few North American samples stored under “*Vincetoxicum hirundinaria*” the majority proved to be misidentified *Cornus* sp. (Cornaceae). The one specimen left turned out to be a white-flowered variant of *V. rossi-*

cum.

- The chemical dataset was collected in two tranches, first the assumed neophytic species *V. hirundinaria*, *V. nigrum* and *V. rossicum* originating from their home range as well as from their neophytic range in Canada and the US, then the total dataset. Leaf samples were sent to the lab of Kevin Minbiole and analyzed by his students Quaadir Bryant and Alice Wu. While the results from the first tranche have been analysed, the ones from the second tranche are presently under evaluation. The neophytic dataset, however, was still analysed under the assumption that there were three neophytic species and that *V. hirundinaria* was a monophyletic species in Europe. Both assumptions have meanwhile been contradicted, neither is *V. hirundinaria* neophytic in North America, nor is it a monophyletic species in Europe. In addition, for *V. rossicum*, only one European wild collected sample was available, and more was inaccessible due to the Russian-Ukrainian war. Therefore the only species suitable to test our hypothesis that the neophytic samples contain more PIAs than the samples from the native region, is *V. nigrum*. However, there is no difference in the PIA content of native and invasive individuals tested. The same was true for all single components analyzed. The results of the chemical analyses will be written up in the near future.
- **3.3 Description of the handling of research data generated during the project and measures for science communication**
 - The molecular dataset was checked for paralogy and hybridization and doubtful samples were removed from analysis.
 - For the PIA dataset, the respective substance standards were included in the runs.
 - Results of this study have been presented roundtable meeting on reticulate evolution organised by the *Christoph Oberprieler* at Regensburg University in October 2024 on behalf of the Priority Programme 'TaxonOmics—New approaches to discovering and naming biodiversity' (SPP 1991) of the DFG.
- **3.4 Bibliography**
 - **Liede-Schumann, S.**, Khanum, R., Mumtaz, A.S., Gherghel, I. & Pahlevani, A. 2016. Going west – A subtropical lineage (*Vincetoxicum*, Apocynaceae: Asclepiadoideae) expanding into Europe. *Molecular Phylogenetics and Evolution* 94: 436–46. <http://dx.doi.org/10.1016/j.ympev.2015.09.021>

- **Liede-Schumann, S.**, Kong, H.-H., Meve, U. & Thiv, M. 2012. *Vincetoxicum* and *Tylophora* (Apocynaceae–Asclepiadoideae: Asclepiadeae) – two sides of the same medal: Independent shifts from tropical to temperate habitats. *Taxon* 61: 803–825. <https://doi.org/10.1002/tax.614007> <https://doi.org/10.1002/tax.614007>

4 Published Project Results

4.1 Publications with scientific quality control

- Seliger, L. W. & Meve, U. (2026). (3166) Proposal to conserve the name *Asclepias fuscata* (*Vincetoxicum fuscatum*) (Apocynaceae, Asclepiadoideae) with a conserved type. *Taxon* 75(3): e70185. <https://doi.org/10.1002/tax.70185>
- Seliger, L. W.; Liede-Schumann, S. & Meve, U. (submitted) Taxonomic Revision of Western Eurasian *Vincetoxicum* (Apocynaceae, Asclepiadoideae). *Syst. Bot. Monogr.*

4.2 Further publications and published results

- The molecular data produced for the project have been submitted to Genbank (BioProject PRJNA1445693: <https://dataview.ncbi.nlm.nih.gov/object/PRJNA1445693?reviewer=tt1d3raq49t6gsi1dai81b2dki>) and will be made public upon publication of the phylogeny.