Schriftenreihe für Vegetationskunde	H. 38	2002	75–91	Bundesamt für Naturschutz, Bonn

Phylogenie der Farn- und Blütenpflanzen Deutschlands

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Summary: Phylogeny of the ferns and flowering plants of Germany

A comprehensive phylogeny for the fern and flowering plant flora of Germany is presented representing the relationships among species and as a data basis for comparative analyses using phylogenetic independent contrasts. A supertree was constructed by assembling partial phylogenies mostly based on molecular DNA sequence data from more than 200 published sources. From these sources, the most parsimonious trees were used. The tree was constructed by manually pruning distal clades on basal clades. From the base to the family level, the tree is fully based on molecular studies. For intrafamilial relationships were no molecular studies are available, classical systematic taxa (subfamilies, genera, subgenera etc.) were used as if representing phylogenies. The resolution of the tree, i.e the percentage of dichotomies is 66 % based upon 3212 taxa (without *Rubus* Sect. *Rubus, Ranunculus auricomus* agg. and with only 57 *Hieracium* spp.). Using only 50 % randomly chosen taxa (n = 1606) the resolution increases to 76 %. At the familial level the tree is totally resolved in angiosperms and gymnosperms whereas there are some polytomies in the ferns. At the generic level, there are 88 polytomies (e.g.: Poaceae: 17; Caryophyllaceae: 12; Lamiaceae: 8; Apiaceae: 7; Brassicaceae: 7). Most polytomies are located at the species level (n = 993). A phylogenetic code as used in the program CAIC is given to each species in which at any node within the tree the branches are labelled A, B, C,… and for each taxon all labels are summed up.

1 Einleitung

Die Phylogenie, oder Stammesentwicklung, einer Organismengruppe ist die Darstellung der verwandtschaftlichen Vorläufer-Nachkommen-Beziehungen von einer gemeinsamen Wurzel aus bis hin zu den rezent vorhandenen Taxa. Im Idealfall wird ein rein dichotomer Stammbaum angestrebt, bei dem immer zwei Taxa genau einen gemeinsamen Vorfahren haben. Das pflanzensystematische taxonomische Klassifzierungssystem von Ordnungen, Familien, Triben, Gattungen, Arten, usw. verfolgt im Prinzip ebenfalls das Ziel, ein natürliches, die verwandtschaftlichen Beziehungen wiedergebendes System darzustellen. Die Taxonomie strebt dabei jedoch keine grundsätzlich dichotome Struktur an. Es ergeben sich deshalb auf allen hierarchischen Ebenen neben teilweiser Übereinstimmung auch große Unterschiede zwischen der Taxonomie und der molekular basierten Phylogenie. Deshalb wurde hier versucht, die in den letzten Jahren in großer Zahl durchgeführten phylogenetischen Analysen zusammenzufassen und einen gemeinsamen Stammbaum zu erstellen. Die phylogenetischen Analysen nutzen meist DNA-Sequenzen unterschiedlich stark konservierter Gene oder Intergenischer Bereiche (z. B.: *rbc*L, ITS-Region, *ndh*F, *trn*L, *trn*L/*trn*F-spacer) und Algorithmen, die einen Stammbaum (*most parsimonious tree*) suchen, der möglichst wenige Basen-Mutationen aufweist (PAGE & HOLMES 1998).

Die hier erstellte Phylogenie weicht an einigen Stellen von der in der Datenbank gleichzeitig verwendeten Struktur der Familien und Gattungen ab (z. B. Scrophulariales), da die taxonomische Fixierung den phylogenetischen Ergebnissen notwendigerweise zeitlich mit Verzug nachfolgt.

Die Kenntnis der Phylogenie ist für die Interpretation morphologischer und ökologischer Merkmale entscheidend (vgl. FELSENSTEIN 1985, HARVEY & PAGEL 1991, PRINZING et al. 2001, PRINZING 2002, PRINZING et al. 2002). Nah verwandte Arten sind wahrscheinlich morphologisch und ökologisch ähnlicher als weniger nah verwandte, sie sind nicht phylogenetisch unabhängig. Umgekehrt benutzen kladistische Methoden morphologische Merkmale wegen ihres phylogenetischen Konservatismus zur Analyse der Phylogenie.

Die hier vorliegende Phylogenie der mitteleuropäischen Flora soll 1. einen Überblick über den derzeitigen Kenntnisstand der verwandtschaftlichen Verhältnisse liefern und 2. Grundlage für die Berechnung phylogenetisch unabhängiger Kontraste bei der Auswertung pflanzlicher Merkmale sein (vgl. PRINZING 2002).

2 Aufbau der Phylogenie

Es wurde ein Baum aus verschiedenen Quellen zusammengestellt (*supertree*), indem von basalen zu distalen Taxa vorgehend distale Kladen auf basale Kladen aufgepfropft wurden (Abb. 1). Ausgehend von den klassischen pflanzensystematischen Einheiten der Familien, Unterfamilien, Triben, Subtriben, Gattungen, Untergattungen usw., wurden diese Einheiten und ihre Beziehungen, wo möglich, durch Phylogenien ersetzt, die auf molekularen oder kladistischen Analysen basierten. Aus diesen Arbeiten wurden in der Regel die *strict consensus trees* verwendet, die eine konservative Einschätzung der Verwandtschaftsbeziehungen bieten.

Da nur selten alle Kladen und Taxa unserer Phylogenie von den molekularen Studien vollständig erfasst waren, wurden die klassischen Taxa beibehalten, so lange dies angebracht schien. So wurden z. B. Arten als Repräsentanten ihrer bisher definierten Sektionen innerhalb der Gattung angesehen. Falls also aus einer artenreichen Sektion nur eine Art oder wenige Arten in einer molekularen Studie untersucht wurden, und diese eine monophyletische Gruppe bildeten, wurden auch die übrigen Arten der betreffenden Sektion als basale Polytomie zu diesen Arten gestellt. Wo bisher geltende Taxa sich als polyphyletisch herausstellten, wurde die molekular basierte Sichtweise übernommen. Polytomien resultieren aus nicht aufgelösten Kladen.

Da die verwendeten Phylogenien auf der Auswertung unterschiedlicher Gene beruhten, können in die Phylogenie nur die Topologien aufgenommen werden, nicht aber die Astlängen. Damit sind nur die Verzweigungsmuster des Stammbaumes, nicht jedoch die quantitativen Ähnlichkeiten der Kladen zueinander verfügbar. Die Astlängen geben somit keine Information über das Maß der Ähnlichkeit der Taxa. Einzig die Verzweigungsmuster enthalten die Information über relative Verwandtschaft der Taxa zueinander.

Es wurde nicht versucht, einen Baum mit automatischen Algorithmen aus den publizierte Teilbäumen zu erstellen (z. B. SANDERSON et al. 1998). Ein so großer Datensatz mit über 3000 Taxa lässt sich derzeit nicht mit *parsimony*-Methoden auswerten.

Für die Darstellung der phylogenetischen Beziehungen wurde ein Buchstabencode verwendet, der alle Kladen, die eine gemeinsame Wurzel haben, fortlaufend mit A, B, C... benennt. Für jede Art ergibt sich aus der Summe der Verzweigungspunkte, beginnend an der Wurzel ein Buchstabencode für die Position im Kladogramm (Abb. 1). Der hier verwendete Buchstabencode kann direkt für die Berechnung von phylogenetisch unabhängigen Kontrasten im Programm CAIC (ASKEW 1997, PURVIS & RAMBAUT 1995) verwendet werden.

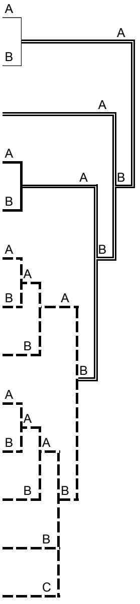
Art	**Unter -fam.**	**Gattung**	**Unter- gattung**	**Agg.**	**Phylogramm**	**Phylogenie code**
Macleaya cordata	Chel.	Macleaya				AA
Chelidonium majus	Chel.	Chelidonium				AB
Eschscholzia californica	Esch.	Eschscholzia				BA
Glaucium flavum	Chel.	Glaucium				BBAA
Glaucium corniculatum	Chel.	Glaucium				BBAB
Papaver hybridum	Papa.	Papaver	Argemonidium			BBBAAA
Papaver argemone	Papa.	Papaver	Argemonidium			BBBAAB
Papaver sendtneri	Papa.	Papaver	Meconella			BBBAB
Papaver dubium	Papa.	Papaver	Rhoeadium	dubium agg.		BBBBAAA
Papaver lecoqii	Papa.	Papaver	Rhoeadium	dubium agg.		BBBBAAB
Papaver rhoeas	Papa.	Papaver	Rhoeadium			BBBBAB
Papaver somniferum	Papa.	Papaver	Papaver			BBBBB
Papaver orientale	Papa.	Papaver	Macrantha			BBBBC

Abb. 1: Arten, klassische pflanzensystematische Kategorien, Phylogramm und Phylogeniecode der Papaveraceae. Beachte die Unterschiede zwischen molekular basierter Phylogenie und klassischer Systematik (Phylogenie der Unterfamilien nach HOOT et al. 1997, KADEREIT et al. 1995 [═══]; *Papaver* nach KADEREIT et al. 1997 [-----]; *Chelidonioideae* nach BLATTNER & KADEREIT 1999 [———]).

Species, classical plant systematic categories, phylogenetic code and phylogram of Papaveraceae. Note the differences between molecular phylogeny and classical systematics.

2.1 Auflösung

Die Auflösung, also der Anteil vorhandener Dichotomien bezogen auf einen vollständig aufgelösten dichotomen Stammbaum, beträgt 66 %, bezogen auf alle Taxa (3212 Arten; ohne *Rubus* sect. *Rubus, Ranunculus auricomus* agg. und mit nur 57 der häufigsten Hieracien). Wählt man zufällig 50 % der Taxa (1606) aus, so ergibt sich eine Auflösung von 76 %. Kleinere Datensätze werden fast vollständig dichotom aufgelöst (z. B. MAURER et al. 2002). Die Familienebene ist bei Angiospermen und Gymnospermen voll aufgelöst; lediglich bei den Farnen (Polypodiales) liegen einige Polytomien auf Familienebene vor (vgl. Abb. 2). Innerhalb der Familien, aber oberhalb der Gattungen liegen 88 Polytomien vor (z. B.: Poaceae: 17; Caryophyllaceae: 12; Lamiaceae: 8; Apiaceae: 7; Brassicaceae: 7). Der allergrößte Teil der Polytomien liegt auf Artebene innerhalb der Gattungen vor (n = 993 ohne apomiktische *Rubus, Ranunculus, Hieracium* teilweise). Zwischen den Familien schwankt die Auflösung sehr stark. Relativ gut bekannt sind z. B. Ranunculaceae, Rosaceae und auch artenärmere Familien, z. B. Ericaceae, Primulaceae oder Saxifragaceae. Weniger gut aufge-

Abb. 2: Phylogenetischer Baum der Familien der Gefäßpflanzenflora Deutschlands. In dieser Darstellung sind lediglich die Verzweigungsmuster von Bedeutung, die Astlängen haben keine Aussagekraft. Datengrundlage vgl. Text.

Unrooted phylogenetic tree of higher plant families of the German flora. In this type of tree, only the tree topology and not the branch lengths are meaningful. For data basis see text.

löst sind z. B. Poaceae und Brassicaceae oder artenreiche Gattungen wie *Carex* oder *Orobanche*. Kaum Information gibt es weiterhin zu den apomiktischen Sippen (*Rubus* sect. *Rubus*, *Hieracium*, *Ranunculus auricomus* agg.), bei denen wegen der häufig retikulaten Sippenentwicklung das hier verwendete dichotome Evolutionskonzept der Phylogenie ohnehin an seine Grenzen stößt.

2.2 Verwendete Literaturquellen

Die Beziehungen unter den niederen Gruppen der Gefäßpflanzen wurden aus DOYLE (1998) entnommen. Die familiäre Ebene (Abb. 2) basiert auf PRYER et al. 1995 (Farne), CHASE et al. 1993 (Gymnospermen), GRAHAM & OLMSTEAD 2000 (basale Angiospermen), SAVOLAINEN et al. 2000 (Dikotyle), KUBITZKI 1998 (Monokotyle excl. Potamogetonales) und HAYNES et al. 1998 (Potamogetonales), OLMSTEAD & REEVES 1995, OLMSTEAD et al. 2001, OXELMAN et al. 1999, WOLFE & DEPAMPHILIS 1998 (Scrophulariales).
Innerhalb der Familien wurden molekulare Phylogenien zusammengestellt aus:

- ***Aceraceae*** (SUH et al. 2000)
- ***Adoxaceae*** (vgl. Dipsacales)
- ***Alismataceae*** (TRIEST & ROELANDT 1991 [*Alisma*])
- ***Alliaceae*** (HANELT et al. 1992, LINNE VON BERG et al. 1996, VAN RAAMSDONK et al. 2000 [Untergattung *Rhizirideum*])
- ***Amaranthaceae*** (vgl. Chenopodiaceae)
- ***Antirrhinaceae = Veronicaceae*** (***Scrophulariceae*** p.p., ***Plantaginaceae, Globulariaceae, Hippuridaceae, Callitrichaceae***)*:* GHEBREHIWET et al. 2000, NEUBAUER et al. 2000, OLMSTEAD et al. 2001 [Antirrhinaceae]; PHILBRICK & LES 2000 [*Callitriche*]; ALBACH & CHASE 2001 [*Veronica*]; RAHN 1996 [Plantagineae])
- ***Apiaceae***, ***Araliaceae*** (DOWNIE et al. 1998, 2000a, 2000b, 2000c, 2002, LEE & DOWNIE 2000, PLUNKETT & DOWNIE 2000; VALIEJO-ROMAN et al. 2002 [Saniculoideae])
- ***Asteraceae****:* (JANSEN et al. 1990 [Triben]; BREMER 1994 [Subtriben/Gattungen]; OBERPRIELER & VOGT 2000, WATSON et al. 2000 [Anthemideae Gattungen]; OBERPRIELER 2001 [*Anthemis, Tripleurospermum*]; PELSER et al. 2002 [*Senecio*]; NOYES & RIESEBERG 1999 [Astereae Gattungen]; HUBER & NILSSON 1995, NOYES 2000 [*Erigeron*]; ANDERBERG 1991 [Inuleae] WHITTON et al. 1995 [Lactuceae]; KOOPMAN et al. 1998, KOOPMAN et al. 2001 [Lactucinae]; CERBAH et al. 1998 [*Hypochoeris*]; PARK et al. 2001 [*Tolpis*]; KIM et al. 1999 [*Sonchus*]; ALVAREZ FERNANDEZ et al. 2001 [*Doronicum*]; HÄFFNER & HELLWIG 1999 [Carduinae]; GARCIA-JACAS et al. 2000, 2001, SUSANNA et al. 1995 [Centaureinae]; KARIS 1995 [Ambrosiinae]; GANDERS et al. 2000 [*Bidens*])
- ***Boraginaceae*** (LUQUE 1995, WINKWORTH et al. 2002 [Boragineae Gattungen])
- ***Brassicaceae*** (KOCH et al. 2001 [Triben]; MARTIN & SANCHEZ-YELAMO 2000, WARWICK & BLACK 1997 [Brassiceae]; BOWMAN et al. 1999, ZUNK et al. 1999 [Lepidieae]; KOCH & MUMMENHOFF 2001, MUMMENHOFF et al. 1997, ZUNK et al. 1996 [*Thlaspi*]; KOCH et al. 1998, 1999 b [*Cochlearia*]; BLEEKER et al. 2002, NEUFFER et al. 2001, SWEENEY & PRICE 2000 [Cardamininae]; FRANZKE et al. 1998, KOCH et al. 1999 a [*Arabis, Arabidopsis*])
- ***Dipsacales*** (***Caprifoliaceae, Adoxaceae, Linnaeaceae, Dipsacaceae***): BACKLUND & BREMER 1997, BACKLUND & PYCK 1998, DONOGHUE et al. 1992, PYCK et al. 1999 [Gattungen])
- ***Caryophyllaceae*** (BITTRICH 1993 [Subtriben]; OXELMAN et al. 1997, 2000, OXELMAN & LIDEN 1995 [Sileneae Gattungen, Sektionen]; BRYSTING & BORGEN 2000 [*Cerastium*])

- ***Chenopodiaceae*** incl. ***Amaranthaceae*** (CLAUSING et al. 2001, DOWNIE et al. 1997 [Triben]; CHAN & SUN 1997 [*Amaranthus*])
- ***Convolvulaceae*** (NEYLAND 2001)
- ***Cornaceae*** (FAN & XIANG 2001)
- ***Crassulaceae*** (MORT et al. 2001, T´HART 1991, VAN HAM & T´HART 1998 [Arten])
- ***Cucurbitaceae*** (JOBST et al. 1998 [Gattungen])
- ***Cyperaceae*** (MUASYA et al. 1998 [Triben]; BRUEDERLE & JENSEN 1991, ROALSON et al. 2001, YEN & OLMSTEAD 2000 [*Carex, Kobresia*]; MUASYA et al. 2001 [*Isolepis*]; ROALSON & FRIAR 2000 [*Eleocharis*])
- ***Ericaceae*** (KRON 1997, 1999b, KRON et al. 1999a, [Gattungen]; FREUDENSTEIN 1999 [Pyroloideae-Gattungen])
- ***Equisetaceae*** (BENDICH & ANDERSON 1983)
- ***Fabaceae*** (DOYLE et al. 1997 [Triben]; KÄSS & WINK 1997b, WINK & WATERMAN 1999 [Gattungen]; LISTON & WHEELER 1994 [Galegeae]; BADR et al. 1994 [Genisteae]; KÄSS & WINK 1997a [*Lupinus*]; ALLAN & PORTER 2000 [Loteae]; VALIZADEH et al. 1996 [*Medicago*]; IVIMEY-COOK 1968 [*Ononis*])
- ***Fagaceae*** (MANOS et al. 1999 [*Quercus*])
- ***Fumariaceae*** (FUKUHARA 1999, LIDEN et al. 1997 [Gattungen])
- ***Gentianaceae*** (GIELLY & TABERLET 1996, HUNGERER & KADEREIT 1998 [*Gentiana*]; VON HAGEN & KADEREIT 2001 [*Gentianella* s.l.]; VAN DER SLUIS 1985 [*Centaurium*])
- ***Grossulariaceae*** (MESSINGER et al. 1999 [*Ribes*])
- ***Iridaceae*** (REEVES et al. 2001, SOUZA-CHIES et al. 1997 [Gattungen])
- ***Lamiaceae*** (WAGSTAFF et al. 1998 [Unterfam.]; KAUFMANN & WINK 1994, WAGSTAFF et al. 1995 [Nepetoideae]; WINK & KAUFMANN 1996 [Lamioideae])
- ***Lemnaceae*** (LES et al. 1997)
- ***Lycopodiaceae*** (WIKSTRÖM & KENRICK 2000, 2001)
- ***Malvaceae*** (LA DUKE & DOEBLEY 1995)
- ***Oleaceae*** (WALLANDER & ALBERT 2000 [Gattungen])
- ***Onagraceae*** (CONTI et al. 1993 [Gattungen]; BAUM et al. 1994 [*Epilobium*])
- ***Orchidaceae*** (CAMERON et al. 1999 [Triben]; ACETO et al. 1999, BATEMAN et al. 1997, BATEMAN 2001, PRIDGEON et al. 1997 [Orchidinae]), SOLIVA et al. 2001 [*Ophrys*]; HEDRÉN et al. 2001 [*Dactylorhiza*])
- ***Orobanchaceae*** (incl. ***Scrophulariceae*** p.p.) (DEPAMPHILIS et al. 1997, OLMSTEAD & REEVES 1995, OXELMAN et al. 1999, WOLFE & DEPAMPHILIS 1998; SCHÜTZE 2000, VITEK 1986 [*Euphrasia*])
- ***Papaveraceae*** (BLATTNER & KADEREIT 1999, HOOT et al. 1997, KADEREIT et al. 1995, 1997)
- ***Pinaceae*** (CHASE et al. 1993 [Gattungen]; BERGMANN & GILLET 1997, LEWANDOWSKI et al. 2000)
- ***Poaceae*** (CATALAN et al. 1997, DUVALL & MORTON 1996 [Triben]; GIUSSANI et al. 2001 [Panicoideae]; CATALAN & OLMSTEAD 2000 [*Brachypodium*-Arten]; SORENG & DAVIS 1998 [Poeae s.str., Agrostidinae]; AINOUCHE et al. 1999, OJA 1998, OJA & JAASKA 1998, PILLAY & HILU 1995 [*Bromus*]; LI et al. 2000 [*Avena*]; BULINSKA-RADOMSKA & LESTER 1988 [*Vulpia*]; HILU & ALICE 2001 [Chloridoideae]; AYELE & NGUYEN 2000 [*Eragrostis*]; HSIAO et al. 1995, PETERSEN & SEBERG 1997 [Triticeae]; GREBENSTEIN et al. 1998 [Aveneae]; BULINSKA-RADOMSKA & LESTER 2002, GAUT et al. 2000 [*Festuca*])
- ***Polemoniaceae*** (PRATHER et al. 2000)
- ***Potamogetonaceae*** (HETTIARACHCHI & TRIEST 1991)

- ***Portulacaceae*** (HERSHKOVITZ 1993)
- ***Primulaceae*** s.l. (ANDERBERG et al. 1998 [Triben]; KÄLLERSJÖ et al. 2000 [Gattungen]; CONTI et al. 2000, MAST et al. 2001 [*Primula*]; ZHANG et al. 2001 [*Soldanella*])
- ***Ranunculaceae*** (HOOT 1995B, JOHANSSON 1995, RO et al. 1997 [Gattungen]; JOHANSSON 1998 [*Ranunculus*]; JOHANSSON 1999 [*Adonis*]; WERNER & EBEL 1994 [*Helleborus*]; CONSTANTINIDIS et al. 2001 [*Consolida*]; HOOT 1995A [Anemoneae])
- ***Rosaceae*** (MORGAN et al. 1994 [Triben]; CAMPBELL et al. 1995 [Maloideae-Gattungen]; ALICE & CAMPBELL 1999 [*Rubus*-subgenera]; SMEDMARK & ERIKSSON 2002 [*Geum*]; ERIKSSON et al. 1998, ONTIVERO et al. 2000, POTTER et al. 2000 [Potentilleae, Alchemilleae]; LEE & WEN 2001, SHIMADA et al. 2001 [*Prunus* s.l.]; TAKEUCHI et al. 2000 [*Rosa*])
- ***Rubiaceae*** (NATALI et al. 1995 [Arten])
- ***Saxifragaceae*** (CONTI et al. 1999, VARGAS 2000 [Arten]; SOLTIS et al. 1996 [Gattungen])
- ***Scrophulariceae s.str.*** u. ***s.l.*** (OLMSTEAD & REEVES 1995, OLMSTEAD et al. 2001, SAVOLAINEN et al. 2000) vgl. auch ***Antirrhinaceae, Orobanchaceae***
- ***Solanaceae*** (OLMSTEAD & SWEERE 1994 [Triben/Gattungen]; BOHS & OLMSTEAD 1997, [*Solanum* s.l.])
- ***Violaceae*** (BALLARD et al. 1998 [Sektionen, Subsektionen]; MARCUSSEN & BORGEN 2000 [Subsektion *Viola*])

In den Fällen, in denen innerhalb der Familien keine oder unvollständige molekulare Phylogenien verfügbar waren, wurden die traditionellen pflanzensystematischen Taxa der Triben, Subtriben, Gattungen, Untergattungen, Sektionen, Subsektionen, Serien und Aggregate verwendet, die als phylogenetische Kladen interpretiert wurden. Prinzipielle Quellen waren „Flora Europaea“ (TUTIN & et al. 1964), „Illustrierte Flora von Mitteleuropa“ (HEGI 1939 ff.) und WISSKIRCHEN & HAEUPLER 1998. *Trifolium* wurde aus ZOHARY & HELLER 1984, *Geranium* aus AEDO et al. 1998, *Orchidaceae* aus DRESSLER 1993 und REINHARD et al. 1991, *Poaceae* aus WATSON & DALLWITZ 1992, *Carduus* aus KAZMI 1963, KAZMI 1964, *Dipsacus* aus EHRENDORFER 1962 entnommen.

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