

SPATIAL AND TEMPORAL FLOWER PRESENTATION IN APIACEAE-APIOIDEAE

DISSERTATION

zur Erlangung des Grades

„Doktor der Naturwissenschaften“

am Fachbereich Biologie

der Johannes Gutenberg-Universität Mainz

eingereicht von

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geb. am 15.03.1977 in Alzenau-Wasserlos

Mainz, März 2013

Dekan: [REDACTED]

1. Berichterstatterin: [REDACTED]

2. Berichterstatter: [REDACTED]

Tag der mündlichen Prüfung: [REDACTED]

The day is coming when a single carrot freshly observed will set off a revolution."

Paul Cezanne (1839-1906)

Kapitel 2 dieser Arbeit wurde veröffentlicht als: Reuther, K. & Claßen-Bockhoff, R. (2010) Diversity behind uniformity – inflorescence architecture and flowering sequence in Apioideae - *Plant Div. Evol.* 128/1-2: 181-220.

Kapitel 3 dieser Arbeit wurde veröffentlicht als: Reuther, K. & Claßen-Bockhoff, R. (2013) Andromonoecy and developmental plasticity in *Chaerophyllum bulbosum* (Apiaceae-Apioideae) - *Annals of Botany* [PART OF A SPECIAL ISSUE ON INFLORESCENCES; doi: 10.1093/aob/mct073; online verfügbar & im Druck].



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CONTENTS

SUMMARY OF THE THESIS.....	1
ZUSAMMENFASSUNG.....	3
1 GENERAL INTRODUCTION.....	5
2 DIVERSITY BEHIND UNIFORMITY – INFLORESCENCE ARCHITECTURE AND FLOWERING SEQUENCE IN APIACEAE-APIOIDEAE.....	9
2.1 ABSTRACT.....	9
2.2 INTRODUCTION.....	9
2.3 MATERIAL & METHODS.....	14
2.3.1 Species investigated.....	14
2.3.2 Plant architecture.....	14
2.3.3 Umbel organisation.....	17
2.3.4 Dichogamy.....	19
2.3.5 Flower types and sex distribution.....	20
2.3.6 Sex ratio.....	20
2.3.7 Flowering sequence.....	21
2.3.8 Photographical documentation.....	21
2.3.9 Symbols.....	21
2.4 RESULTS.....	22
2.4.1 <i>Xanthoselinum alsaticum</i>	23
2.4.2 <i>Anthriscus caucalis</i>	26
2.4.3 <i>Anthriscus sylvestris</i>	29
2.4.4 <i>Myrrhis odorata</i>	32
2.4.5 <i>Daucus carota</i>	34
2.4.6 <i>Oenanthe pimpinelloides</i>	37
2.4.7 <i>Echinophora spinosa</i>	39
2.4.8 <i>Trinia glauca</i>	42
2.4.9 <i>Zizia aurea</i>	44
2.5 DISCUSSION.....	47
2.5.1 The flower level.....	47
2.5.2 The umbellet and umbel level.....	48
2.5.3 The plant level.....	50
2.6 CONCLUSIONS.....	52

3	ANDROMONOECY AND DEVELOPMENTAL PLASTICITY IN <i>CHAEROPHYLLUM BULBOSUM</i> (APIACEAE-APIOIDEAE).....	53
3.1	ABSTRACT.....	53
3.2	INTRODUCTION.....	54
3.3	MATERIAL & METHODS.....	56
3.3.1	Study species and site	56
3.3.2	Experimental design.....	57
3.3.3	Data collection.....	59
3.3.4	Statistical analysis.....	61
3.4	RESULTS.....	61
3.4.1	Percentages of male flowers.....	61
3.4.2	Fruit production.....	62
3.5	DISCUSSION.....	65
3.5.1	Andromonoecy as an inherited character.....	66
3.5.2	Fruit set and self-pollination capacity	66
3.5.3	Developmental plasticity	67
3.6	CONCLUSIONS.....	68
4	‘AND YET THEY VARY’ - SPATIAL-TEMPORAL DIVERSIFICATION IN FLOWERING APIACEAE-APIOIDEAE & THEIR UNIFORMOUS FUNCTIONAL SYNDROME...69	
4.1	ABSTRACT.....	69
4.2	INTRODUCTION.....	70
4.3	MATERIAL & METHODS.....	74
4.3.1	Sampling and taxon origins.....	74
4.3.2	Taxonomy and geography of the selected species.....	75
4.3.3	Data collection.....	77
4.3.4	Data analysis and illustration.....	84
4.4	RESULTS.....	85
4.4.1	The model apioid – frequent character states in the Apioideae.....	85
4.4.2	Diversification.....	93
4.4.3	Summary.....	139
4.5	DISCUSSION.....	141
4.6	CONCLUSIONS.....	148
5	GENERAL CONCLUSIONS.....	149
6	REFERENCES.....	150
7	APPENDICES.....	174

SUMMARY OF THE THESIS

All members of the carrot family (Apiaceae), among them cosmopolitan subfamily Apioideae, resemble in inflorescence characters. The ‘compound’ umbels are formed by small, white or yellow flowers and visited by many unspecialized insects. The uniform impression, that is created, may be a reason that the underlying morphology has been barely analyzed to date. The purpose of the present dissertation is therefore, to demonstrate ‘cryptic diversity’ in the flowering shoots of the Apiaceae-Apioideae with the aim to identify the influence of the plants’ architecture on flower presentation in space and time and thereby on the reproductive system.

In the first chapter, a comparative analysis of nine selected species shows that in the self-fertile and unspecifically pollinated plants outcrossing is promoted by synchronized and rhythmic presentation of flowers. Thereby, the dichogamous plants either pass only one male and female flowering phase (*Xanthoselinum alsaticum*), or the modular construction of the plants entails a sequence of male and female phases (multicycle dichogamy). Dioecy in *Trinia glauca* may be regarded as a split of the flowering phases into separate individual. It is demonstrated that in the andromonoecious taxa the proportion of (functionally) male flowers increases inconsistently with umbel order. Thus, the plants, at different times and to different degrees, function rather as pollen acceptors or donors. It becomes clear that the uniform inflorescence pattern of the Apioideae including umbels of different order, dichogamous flowers and diverse sex forms represents a complex space-time-unit to optimize the breeding system.

The second chapter illustrates the results of manipulation experiments (hand-pollination, bagging, umbel removal) in *Chaerophyllum bulbosum* showing that, as a space-time-unit in flower presentation, the species is able to respond flexibly to environmental stress. Mechanical damage emerges to merely influence the degree of andromonoecy and percentage fruit set of the individuals. The basis requirement of the ability to respond to environmental influences is again the modular construction. This allows the plants, together with the andromonoecy-induced reservoir of – sexually flexible – male flowers, to compensate in the later-developing flowers for the lack of fruits in the early-flowering umbels.

In the third chapter, I provide data of a character analysis in 255 apioid taxa representing all major clades, life forms and distribution areas of the group. The aim of the study was the identification of character syndromes that were supposed to clarify the relationship of plant architecture and breeding system. Interestingly, the only traits that consistently accompany each other are protogyny and the gradual decrease in the number of male flowers with increasing umbel order. All other plant characters vary independently from each other and in many ways create a similar functional model that can be interpreted as the apioid 'breeding syndrome'.

This dissertation contributes towards the functional comprehension of Apiaceae inflorescences and to morphological variation in 'unspecialized' breeding systems. Obviously, in the Apiodeae selective pressure upholds the generalist pollination system and superimposes onto all morphological-phylogenetic character variations.

ZUSAMMENFASSUNG

Alle Doldengewächse (Apiaceae), darunter die größte, weltweit verbreitete Unterfamilie der Apioideen, weisen in ihren Blütenständen sehr einheitliche Merkmale auf. Die 'Doppeldolden' werden aus kleinen, weißen oder gelben Blüten gebildet und von vielen unspezialisierten Insekten besucht. Der uniforme Eindruck, der damit erweckt wird, ist unter Umständen ein Grund, dass die zugrundeliegende Morphologie bislang wenig untersucht wurde. Gegenstand der vorliegenden Dissertation ist es daher, die 'verborgene Diversität' im Blütenstandsbereich der Apiaceae -Apioideen mit dem Ziel darzustellen, den Einfluss der Architektur der Pflanzen auf die Art der Blütenpräsentation in Raum und Zeit und damit auf das Reproduktionssystem der Art zu ermitteln.

Im ersten Kapitel zeigt der Vergleich von neun ausgewählten Arten, dass in den selbstfertilen und unspezifisch bestäubten Pflanzen durch Synchronisation und Rhythmik in der Präsentation von Blüten Fremdbefruchtung gefördert wird. Entweder durchlaufen die Pflanzen dabei nur eine getrennte männliche und weibliche Blühphase (*Xanthoselinum alsaticum*) oder der moduläre Bau der Pflanzen führt zu einer Folge männlicher und weiblicher Blühphasen (multizyklische Dichogamie). Die Diözie in *Trinia glauca* kann in diesem Zusammenhang als eine Trennung der Blühphasen auf verschiedengeschlechtliche Individuen gesehen werden. Für die andromonözischen Arten wird gezeigt, dass der Anteil funktional männlicher Blüten mit steigender Doldenordnung nicht einheitlich zu- oder abnimmt. Dadurch fungieren die Pflanzen zu verschiedenen Zeiten und mit unterschiedlicher Stärke eher als Pollenrezeptoren oder Pollendonatoren. Es wird deutlich, dass das 'uniforme Muster' der Apioideen mit Dolden verschiedener Ordnungen, dichogamen Blüten und deren diversen Geschlechtsausbildungen ein komplexes Raum-Zeit-Gefüge zur Optimierung des Reproduktionssystems darstellt.

Das zweite Kapitel stellt die Ergebnisse von Manipulationsexperimenten (Handbestäubung, Bestäuberabschirmung, Entfernen von Dolden niedriger Ordnung) an *Chaerophyllum bulbosum* dar, die zeigen, dass das Raum-Zeit-Gefüge in der Präsentation der Blüten der Art erlaubt, flexibel auf Umwelteinflüsse zu reagieren. Es stellt sich heraus, dass mechanische Beschädigungen kaum Einfluss auf den Andromonöziegrad und prozentualen Fruchtansatz der Individuen nehmen. Grundvoraussetzung der Reaktionsfähigkeit ist wiederum deren modulärer Bau. Dieser erlaubt es den Pflanzen, zusammen mit dem andromonöziebedingten Reservoir an -

geschlechtlich flexiblen - männlichen Blüten,, in den später angelegten Dolden fehlenden Fruchtsatz der Blüten früh blühender Dolden zu kompensieren.

Im dritten Kapitel wird eine vergleichende Merkmalsanalyse an 255 Apioideen-Arten vorgelegt, die alle Verwandtschaftskreise, Wuchsformen und Verbreitungsgebiete der Gruppe repräsentieren. Ziel der Analyse war die Identifizierung von Merkmalssyndromen, die den Zusammenhang zwischen Architektur und Reproduktionssystem verdeutlichen sollten. Interessanterweise sind die einzigen Merkmale, die miteinander einhergehen, Protogynie und die graduelle Abnahme männlicher Blüten mit steigender Doldenordnung. Alle anderen Merkmale variieren unabhängig voneinander und erzeugen auf vielen verschiedenen Wegen immer wieder das gleiche Funktionsmuster, das als ‚breeding syndrome‘ der Apioideae gedeutet werden kann.

Die Arbeit leistet einen wichtigen Beitrag zum Verständnis der Blütenstände der Apiaceen und darüber hinaus zu morphologischer Variation in ‚unspezialisierten‘ Reproduktionssystemen. Offensichtlich liegt in den Apioideen der Selektionsdruck auf der Aufrechterhaltung der generalisistischen Bestäubung und überprägt alle morphologisch-phylogenetischen Merkmalsvarianten.

How do you lead a horse to water? With lots of carrots. (Old proverb)

1 GENERAL INTRODUCTION

Flowering species of the carrot family appear in diverse vegetation types or cultivation across the globe and throughout the seasons. The family is one of the largest taxonomic groups and probably the oldest recognized and systematically described (Daléchamps 1587; Bauhin et al. 1650-1651; Morison 1672; Sprengel 1813, 1818), its members sharing their similar, open-accessible, small flowers, aggregated into umbellets and umbels. More than 80% of today's 'Umbelliferae' species and genera belong to the cosmopolitan subfamily Apioideae (Fig. 1.1; contemporarily including most of former 'Saniculoideae'; Stevens 2001 onwards; Magee et al. 2010a) or to the small subfamilies Mackinlayoideae, Azorelloideae (plus *Hermas*) and *Platysace*. Inter- and intrageneric relationships are still not fully resolved in the approximately 380 apioid genera comprising 3200 species (Stevens 2001 onwards).



Figure 1.1 The geographic distribuion of the Apioideae (taken from Stevens 2001 onwards)

Apioideae encompass on the one hand plenty of economically important and widely cultivated species (e.g. *Daucus carota*, *Foeniculum vulgare*, *Coriandrum sativum*, *Carum carvi* or *Pastinaca sativa*) and on the other hand (locally) rare, e.g. *Angelica palustris* (Dittbrenner et al. 2005), *Monizia edulis* (Cannon 1994), *Rouya polygama* (Médail & Verlaque 1997; Pozzo Di Borgo & Paradis 2000; Bacchetta et al. 2007), or critically endangered taxa as *Cymopterus beckii*

(Tepedino & Messinger 2004), *Naufraga balearica* (Botey 2005; Cursach & Rita 2012) and *Ptilimnium nodosum* (Marcinko & Randall 2008). In order to optimize breeding conditions, cultivators as well as conservationists have studied the species' reproductive systems so that 'much of the published work on Apiaceae is concerned on effective pollination, seed set and quality' (Davila & Wardle 2002). Investigations on flowering phenologies and sequences revealed self-fertility (Foerste & Trelease 1882; Owens 1974; Keighery 1982; Schlessman 1982, 2010), an overall generalist pollination system (e.g. Ollerton et al. 2007), partly with *cryptic specialisation* (Bell 1971; Webb 1984; Lindsey & Bell 1985; Tollsten et al. 1994; Zych 2007) and flowering patterns, mainly discussed to prevent geitonogamy (Lindsey 1982; Schlessman 1982; Challe 1985; Schlessman & Graceffa 2002; Schlessman & Barrie 2004; Tepedino & Messinger 2004).

A well-established picture of Apioideae representatives shows herbaceous plants with white or yellow, rich-flowered umbels that terminate stems and branches of several orders. The uniform impression of the flowering shoots, created by the similar presentation of flowers, may be one reason why many morphologists were so far more interested in e.g. fruits and leaves, in apioid organs that show higher variation. However, even though many species may resemble in their outer appearance, they show varying forms of dichogamy – protandry and protogyny - in their flowers, and differ in their – andromonoecious, hermaphrodite or dioecious (e.g. Plunkett et al. in press.) sexual systems. Inconsistent with a once claimed constant floral sex ratio of one hermaphrodite per four male flowers (Doust 1980), many andromonoecious species vary slightly to enormously in their proportions of flower types, affecting possible fruit set per plant (e.g. Liehr 1927; Hendrix & Trapp 1981; Palevitch 1985; Koul et al. 1996; Pérez-Bañón et al. 2006; Reuther & Claßen-Bockhoff 2010). The architectural variation in the flowering shoots was investigated only occasionally, but revealed that branching does not follow a uniform, basic pattern in the largest Apiaceae subfamily (cp. Clos 1855; Clos 1874; Troll & Heidenhain 1951; Froebe 1971; Wiedmann & Weberling 1993). The studies on Apiaceae-Saniculoideae (Froebe 1964), meanwhile segregated into protoapioid tribes (Magee et al. 2010a), and Hydrocotyloideae (Froebe 1971, 1979), a former subfamily whose species are scattered today over Mackinlayoideae, Azorelloideae, Apioideae and Araliaceae (Stevens 2001 onwards) indicate that the apioid inflorescences are rather derived from paniculo-thyrsoid preforms than from a raceme (Froebe 1979), as Troll (1957) had first expected. Demonstrating their value in resolving relationships in Apiaceae, inflorescence characters, especially shape, the presence of bracts and

bracteoles, or number of umbellets and flowers plus proportions within, have been applied in cladistic analyses, repeatedly (Spalik 1996; Radford et al. 2001; Spalik & Downie 2001; Vessio 2001; Magee et al. 2010a; Sun & Downie 2010). The only typological approach on Apioideae that we are aware of (Bernardi 1979), in addition to the classification of a few species according to the presence or absence of a terminal flower within the umbellets (Froebe 1964), recognized and defined three inflorescence types. Flowering shoots in the genera *Ferula*, *Ferulago* and *Peucedanum*, differ mainly in the presence or absence of (i) a definite main axis and (ii) verticillated lateral umbels which (iii) constantly either set or lack fruits.

Unfortunately, whenever morphological information is available on Apioideae inflorescences, its access and further, comparative use is often restricted through the inappropriate application of morphological terms or terminological inconsistencies (see also Endress 2010). Only one of the numerous examples, which create much confusion, is the synonymous use of the terms monotelic, determinate and cymose, as well as polytelic, indeterminate and racemose. Another one is the differing method of numbering branch orders when referring to ordinal floral sex or fruit ratios (cp. Froebe 1979; Schlessman & Graceffa 2002; Endress 2010; especially studies on andromonoecy and floral sex ratios in Apiaceae). Additionally, many inflorescence morphological analyses, generating concepts to categorize inflorescence diversity (e.g. Čelakovský 1892; Parkin 1914; Pilger 1921; Bolle 1940; Rickett 1944, 1955; Troll 1964; Weberling 1965; Zimmermann 1965; Troll 1969; Maresquelle 1971; Sell 1976; Kusnetzova 1988; Sell & Cremers 1992; Weberling & Troll 1998; reviewed in Claßen-Bockhoff 2000) either omit inflorescences of ‘compound’ nature as the apioid’s completely or lack satisfactory solutions to a common terminology of ‘simple’ and ‘compound’ types. Therefore, the revision and extension of available terminological surveys on Apiaceae inflorescence morphology (e.g. Kljuykov et al. 2004) is badly needed for the comparability and comprehensibility of data in the future.

Today, the interest in inflorescences, that seems to replace a long-lived ‘floricentrism’ (Harder et al. 2004), is not driven by purely morphological-typological purposes. Recent studies rather address the question of their function, recognized as inseparable from their form (cp. Kaplan 2001), especially the functional significance of floral displays, plus their underlying inflorescence architecture, for pollination (e.g. Wyatt 1982; Ishii & Sakai 2001; Harder et al. 2004).

Regarding Apioideae, the question arises whether there are architectural features connected to certain sexual systems, which are andromonoecious, hermaphrodite and (gyno)dioecious (e.g. Plunkett et al in press). And if this interrelation exists, which traits mainly influence the reproductive system, and how. Comparative inflorescence morphological investigations, which are largely lacking in Apiaceae and their subfamilies (but see Troll & Heidenhain 1951), could establish a basis to functionally comprehend the relationship of morphological characters, or units, and their spatial and temporal synorganisation in the plants. This would help elucidating the impact of inflorescence morphology on the – here generalist - reproductive system of the group.

Therefore, in the present study, we analyse inflorescence architecture and flowering sequences comparatively in a large number of apioid species with a special focus on the functional consequences of morphological structures and on their clear terminology. To evaluate, thereby, the causes and consequences of andromonoecy, which is a common sexual system in apioids, we experimentally tested the hypothesis that the formation of morphologically male flowers in andromonoecious species is induced by resource limitations, in terms of developing fruits. At the same time, we intended to determine the influence of architectural effects on male flower formation. In view of the current attention to morphological research (see e.g. citations in Schönenberger & Balthazar 2012) and new, ontogenetic models on inflorescences (especially Claßen-Bockhoff & Bull-Hereñu 2013), our aim here, is to contribute to the comprehension of spatial and temporal flower presentation in Apiaceae-Apioideae.

2 DIVERSITY BEHIND UNIFORMITY – INFLORESCENCE ARCHITECTURE AND FLOWERING SEQUENCE IN APIACEAE-APIOIDEAE



Plant Div. Evol. Vol. 128/1–2, 181–220
Stuttgart, August 20, 2010

Diversity behind uniformity — inflorescence architecture and flowering sequence in Apiaceae-Apioideae

By Kerstin Reuther and Regine Claßen-Bockhoff

With 34 figures and 3 tables

Abstract

Reuther, K. & Claßen-Bockhoff, R: Diversity behind uniformity — inflorescence architecture and flowering sequence in Apiaceae-Apioideae. — Plant Div. Evol. 128: 181–220. 2010. — ISSN 1869-6155.

Plant architecture determines the degree to which a certain individual can respond to environmental factors. Inflorescences of the Apioideae are often regarded as being uniform, but species vary in spatial and temporal arrangement of their flowers and umbels expressed in different patterns of sex distribution, dichogamy and flowering sequence. We are interested in this subtle diversity, and we seek to elucidate how much apioideid architecture influences sex expression and the mating system and varies within the given constraints. To show the static and dynamic characters shaping inflorescence architecture nine species are illustrated in detail: *Anthriscus caucalis* Bieb., *Anthriscus sylvestris* (L.) Hoffm., *Daucus carota* L., *Echinophora spinosa* L., *Myrrhis odorata* (L.) Scop., *Oenanthe pimpinelloides* L., *Trinia glauca* (L.) Dum., *Xanthoselinum alsaticum* L. (Schur), *Zizia aurea* (L.) W.D.J. Koch). They differ in their monopodial or sympodial architecture, racemose and cymose branching pattern, determinate and indeterminate organisation of their umbellets, protandry or protogyny and hermaphroditic, andromonoecious or dioecious sexual system. However, they correspond in their modular construction and strong tendency to avoid geitonogamy and to promote outcrossing predominantly by synchronous and sequential flowering rhythms. We conclude that diversity in the umbel's architecture is less relevant for the mating system than the overall modular construction of the plant and the regulation of the flowering sequence.

Keywords: Apioideae, dichogamy, inflorescence architecture, modular construction, sex distribution.

Received March 3, 2009, in revised form May 4, 2009, accepted May 21, 2009

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DOI: 10.1127/1869-6155/2010/0128-0009 1869-6155/2010/0128-0001 \$ 10.00

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Figures 2.1-2.10 Plants investigated. – 1. *Daucus carota*, flowering plant; note the lacking inhibition zone. 2. *Anthriscus sylvestris*, tip of the plant showing the reduced and sessile terminal umbel (T). 3. *Oenanthe pimpinelloides*, flowering plants. 4. *Xanthoselinum alsaticum*, flowering plant. 5-6. *Trinia glauca*, flowering male (5) and female (6) plant; note the different attractiveness of the sexes. 7. *Myrrhis odorata*, top view of flowering shoots illustrating the close arrangements of different umbels. 8. *Echinophora spinosa*, view onto a lateral shoot showing its prostrate habit. 9. *Anthriscus caucalis*, flowering plant; note the small inconspicuous umbels. 10. *Zizia aurea*, plant with a flowering terminal umbel (T).

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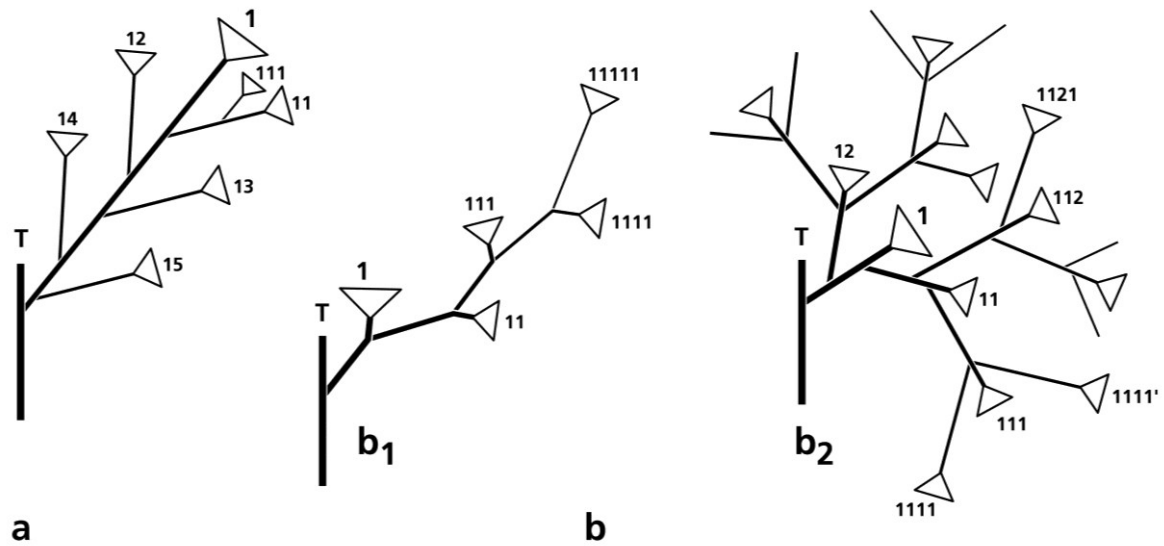


Figure 2.12 Branching patterns of lateral shoots. – a. racemose. – b. cymose with flower production (b_1) from only one prophyll (monochasial) and (b_2) from two prophylls (dichasial).

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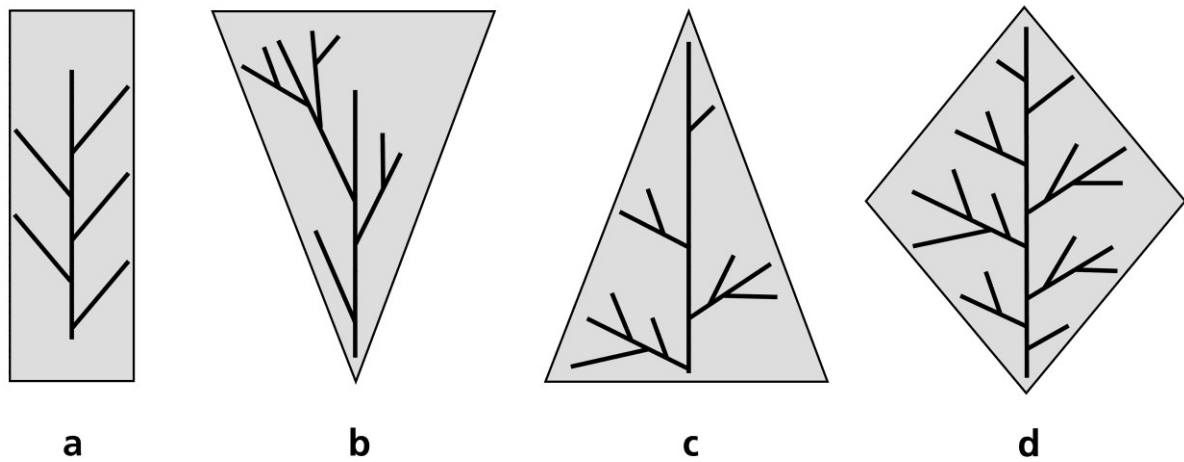
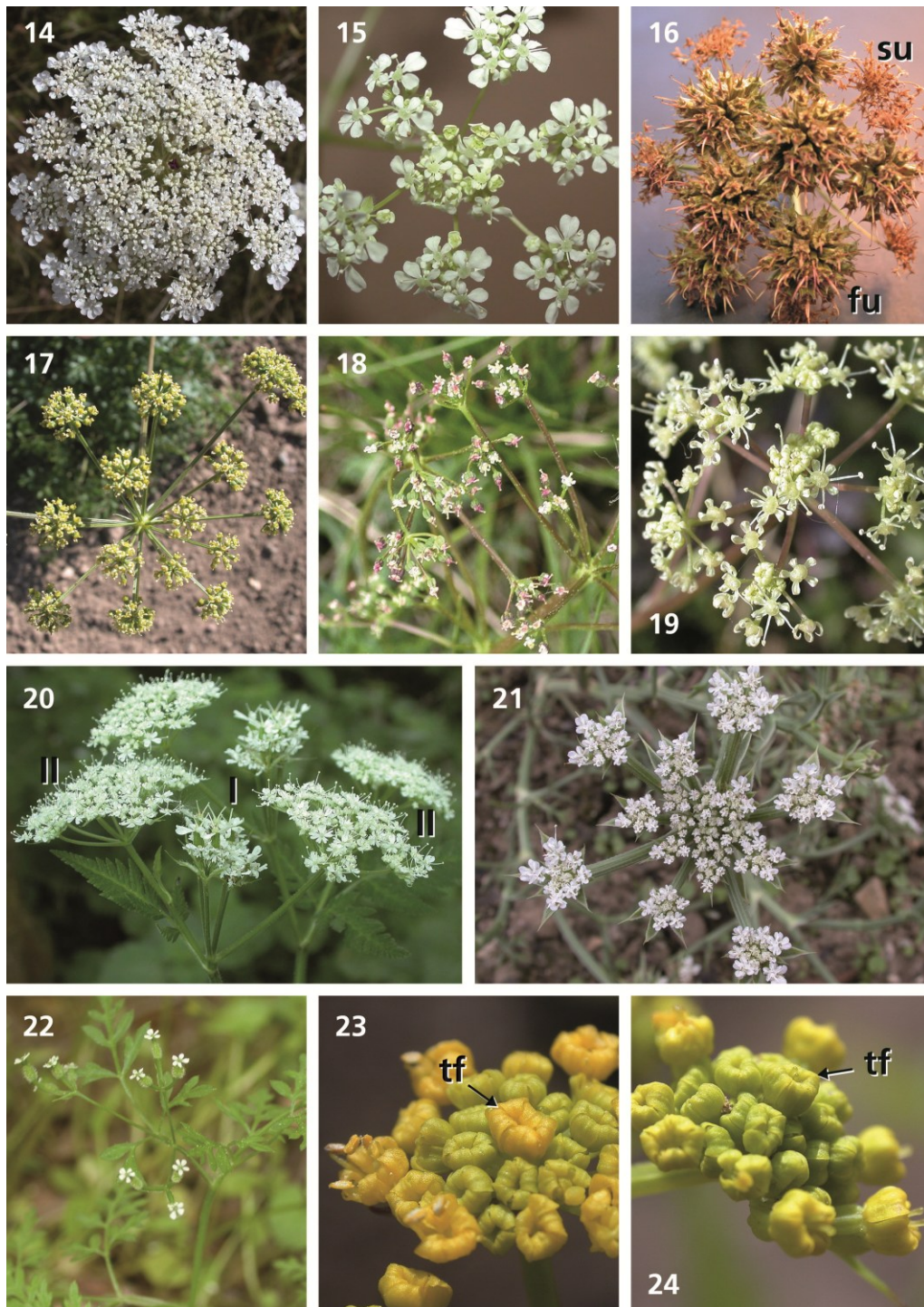


Figure 2.13 Promotion tendencies. – a, homogenous branching with no clear promotion. – b, acrotony (with lateral shoots overtopping the main shoot). – c, basitony. – d, mesotony. Note that the general appearance of a plant depends on its promotion tendencies.



Figs. 2.14-2.24 Flowers and inflorescences of the investigated plants. – 14. *Daucus carota*, flowering umbel with densely aggregated umbellets and slightly enlarged outer flowers. 15. *Anthriscus sylvestris*, flowering umbel in the male phase (note the stamens in the outer flowers). 16. *Oenanthe pimpinelloides*, umbel in the postfloral stage; note that the inner umbellets are fruiting (fu) while the outer ones are staminate (su). 17. *Xanthoselinum alsaticum*, flowering umbel. 18-19. *Trinia glauca*, female (18) and male (19) flowering umbel. 20. *Myrrhis odorata*, flowering unit of umbels of two different orders (I, II) in the female (I) and male (II) phase; note that the fruits' pedicels start to elongate. 21. *Echinophora spinosa*, flowering umbel with only one perfect flower in the centre of each umbellet. 22. *Anthriscus caucalis*, flowering umbel. 23-24. *Zizia aurea*, flowering umbellets; staminate umbellet in the early male phase (23) and andromonoecious umbellet in the early female phase (24); note the terminal flower (tf).

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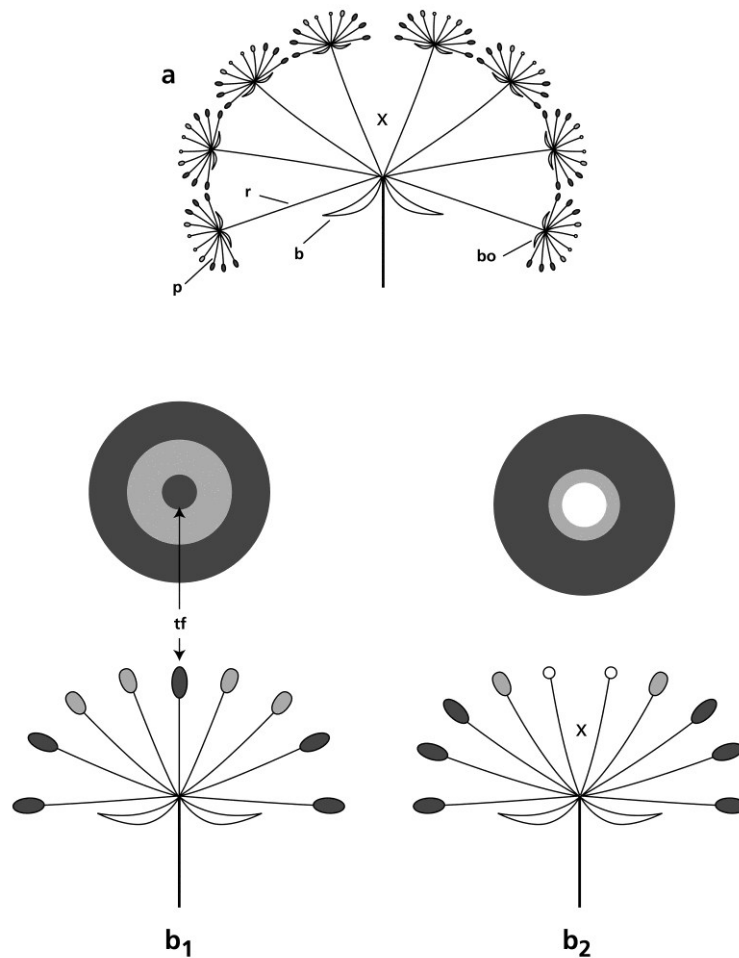


Figure 2.25 Umbel and umbellet organisation. – a., profile of an umbel with lateral umbellets; involucre bracts (b) below the rays (r) of the umbellets, involucellar bracteoles (bo) below the flower pedicels (p). – b., profiles and top views illustrating sex distribution (b₁) of an umbellet with terminal flower (tf) and (b₂) of an indeterminate umbellet ('x'); the different colors indicate bisexual flowers (dark grey), functionally male flowers (light grey) and female sterile/staminate flowers (white).

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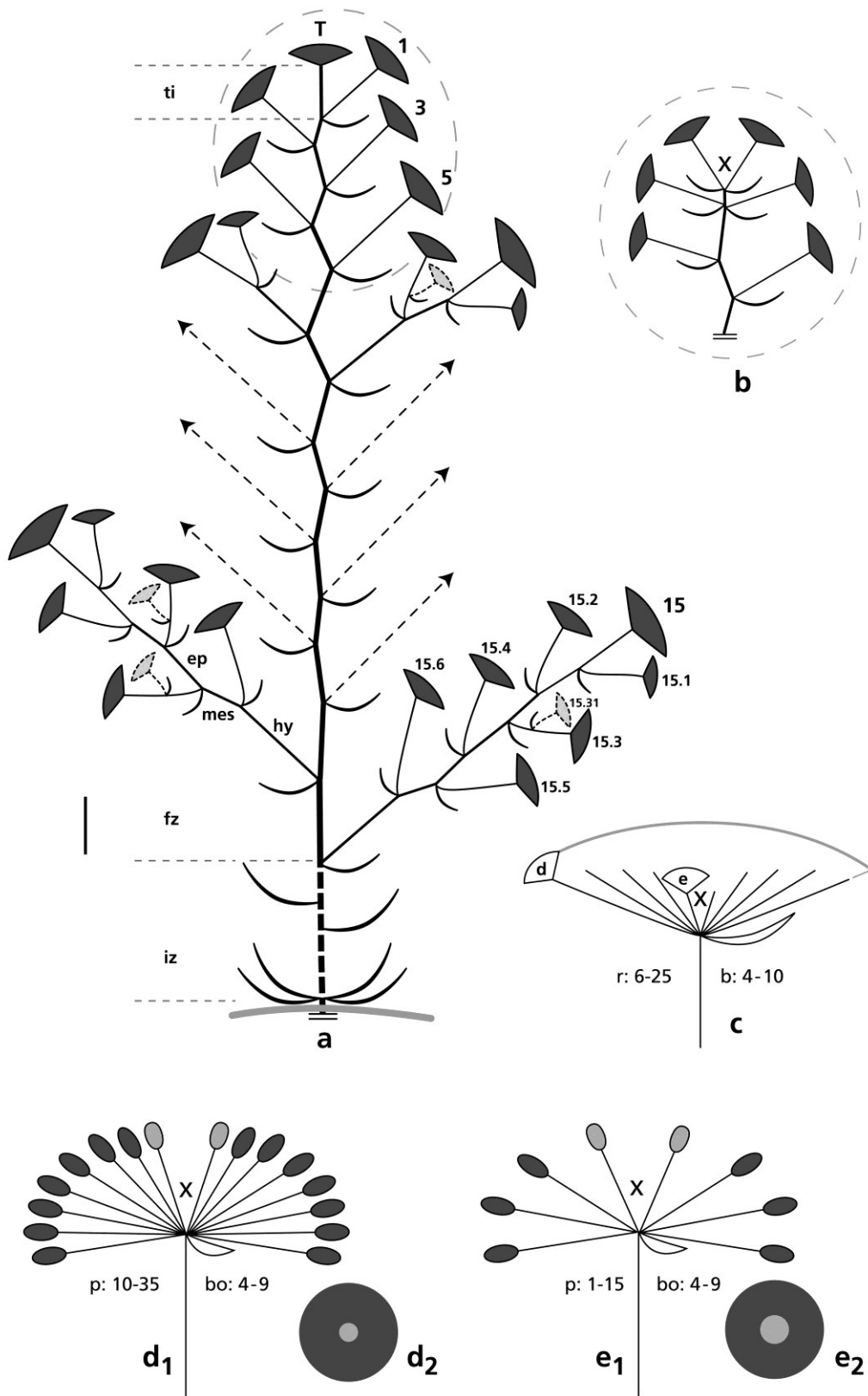


Figure 2.26 *Xanthoselinum alsaticum*, bar: 10cm. – a-b. plant profiles with (a) and without (b) terminal umbel; terminal flowering units encircled; note the counting in a. – c. schematic side view of an umbel, showing the number of rays (r) and bracts (b). – d-e. schematic side views (d₁, e₁) and top view (d₂, e₂) of a well-developed outer (d) and a weaker inner (e) umbellet.

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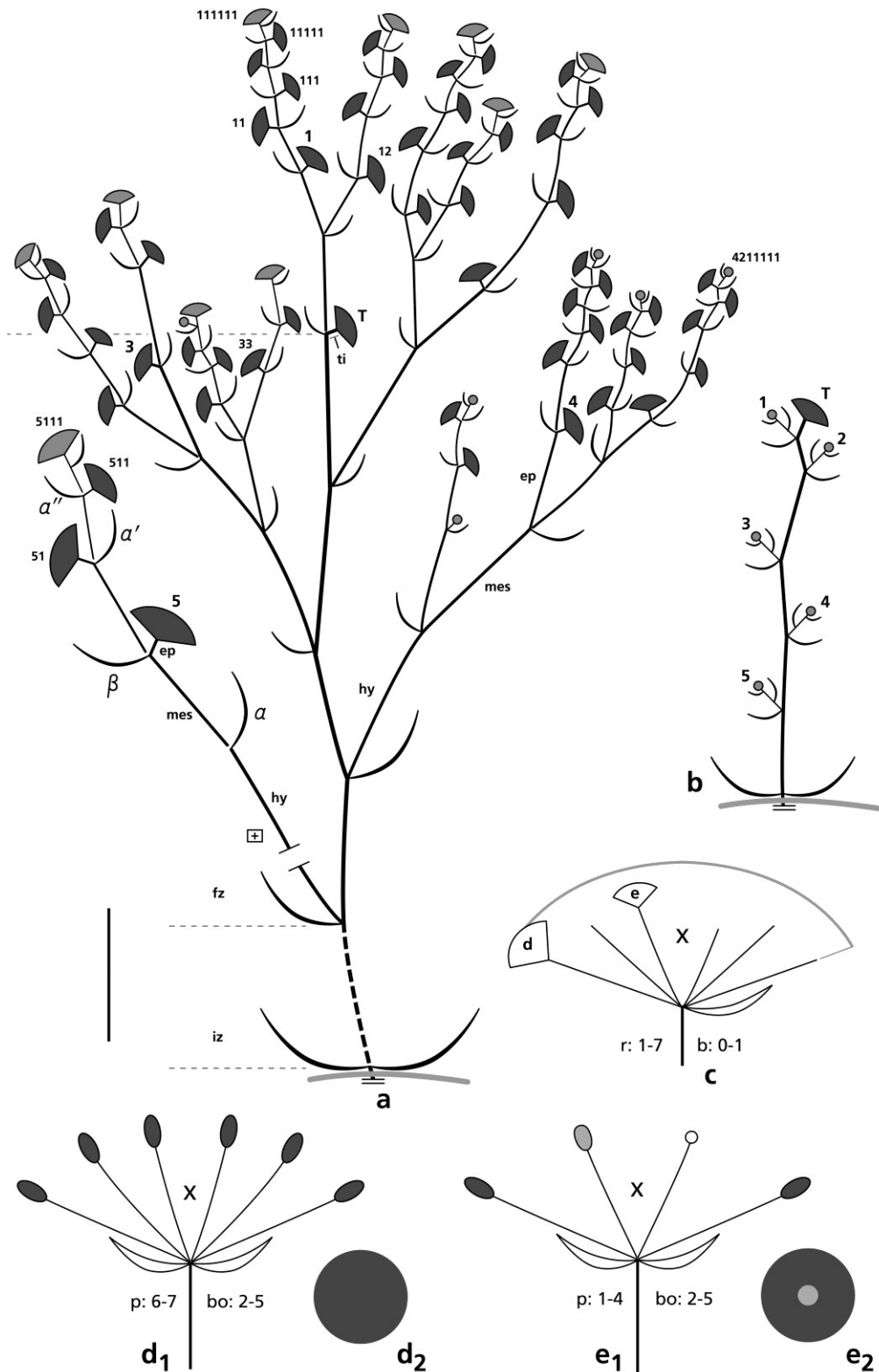


Figure 2.27 *Anthriscus caucalis*. – a-b. plant profiles of flowering plants (a) in full bloom and (b) at the beginning of anthesis (first-order umbels prefloral); branch 5 is enlarged to show the monochasial branching; note the mesotony in branch 4, the basitony in the branches 2 and 3, and the inhibited distal umbels in branch 4 remaining in bud stage (grey-shaded circles). – c. schematic side view of an umbel, showing the number of rays (r) and bracts (b). – d-e. schematic side views (d₁, e₁) and top view (d₂, e₂) of a well developed outer (d) and a weaker inner (e) umbellet with number of pedicels (p) and bracteoles (bo); note the high percentage of perfect flowers. Bars 10cm.

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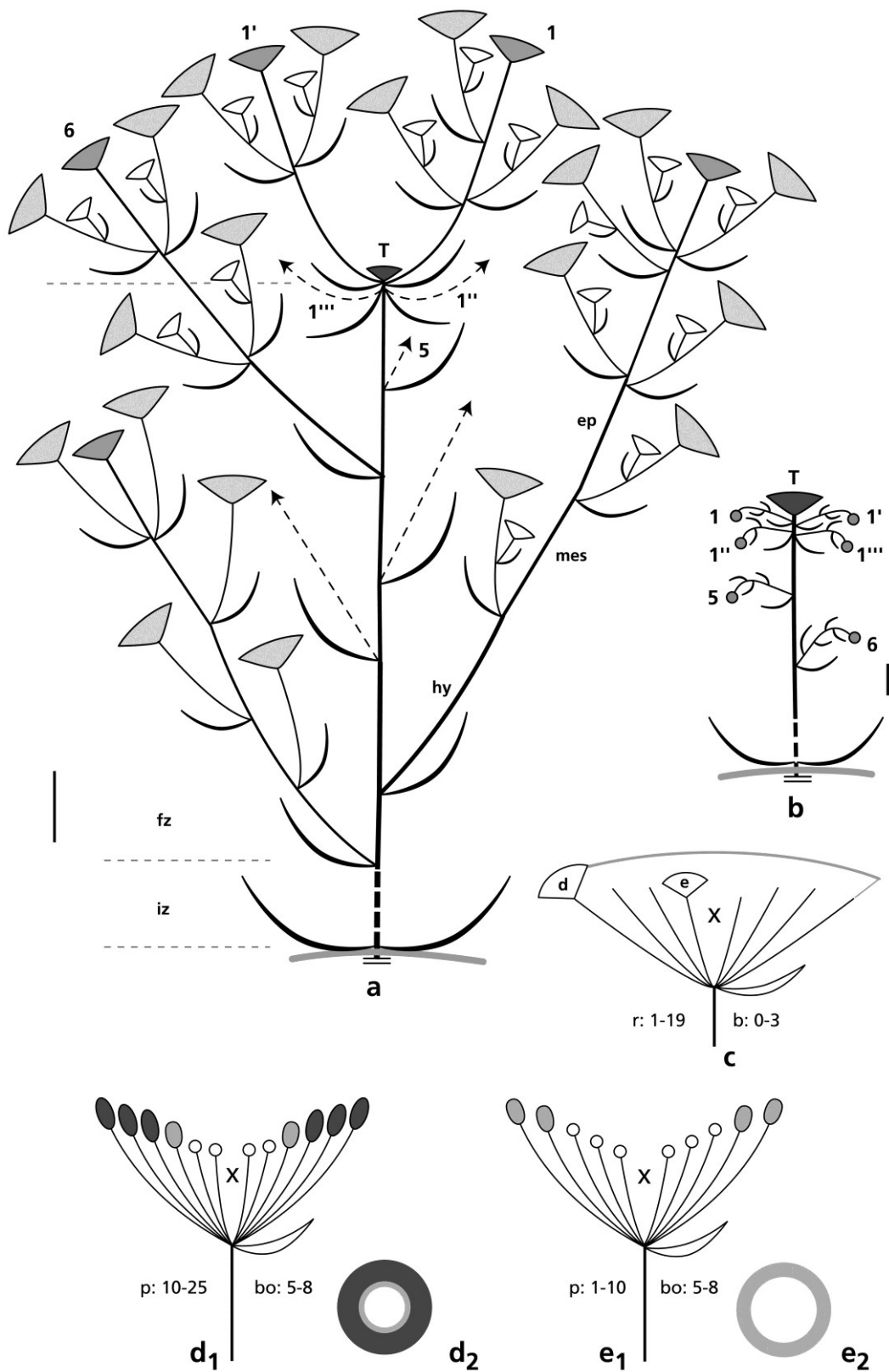


Figure 2.28 *Anthriscus sylvestris*. – a-b. plant profiles of flowering plants (a) in full bloom and (b) at the beginning of anthesis. – c. schematic side view of an umbel, showing the number of rays (r) and bracts (b). – d-e. schematic side views (d₁, e₁) and top view (d₂, e₂) of a well-developed outer (d) and a weaker inner (e) umbellet with number of pedicels (p) and bracteoles (bo); note the increase in male flowers. Bars 10cm.

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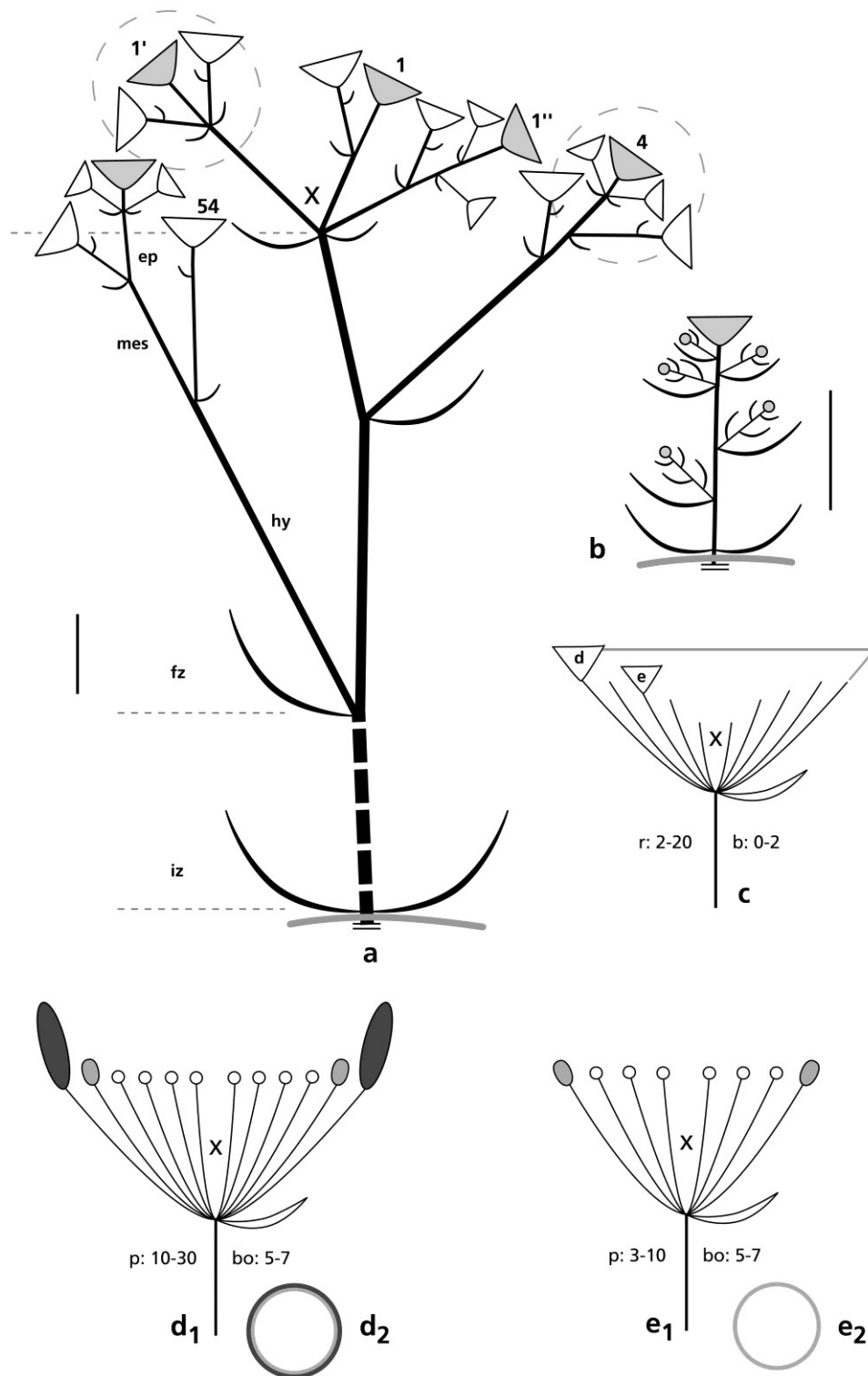


Figure 2.29 *Myrrhis odorata*. – a-b. plant profiles of (a) a flowering plant in full bloom and (b) a terminal umbel-bearing individual at the beginning of anthesis; note the floral aggregates of two umbel orders (encircled). – c. schematic side view of an umbel, showing the number of rays (r) and bracts (b). – d-e. schematic side views (d₁, e₁) and top view (d₂, e₂) of a well developed outer (d) and a weaker inner (e) umbellet with number of pedicels (p) and bracteoles (bo); note the few outer perfect flowers. Bars 10cm.

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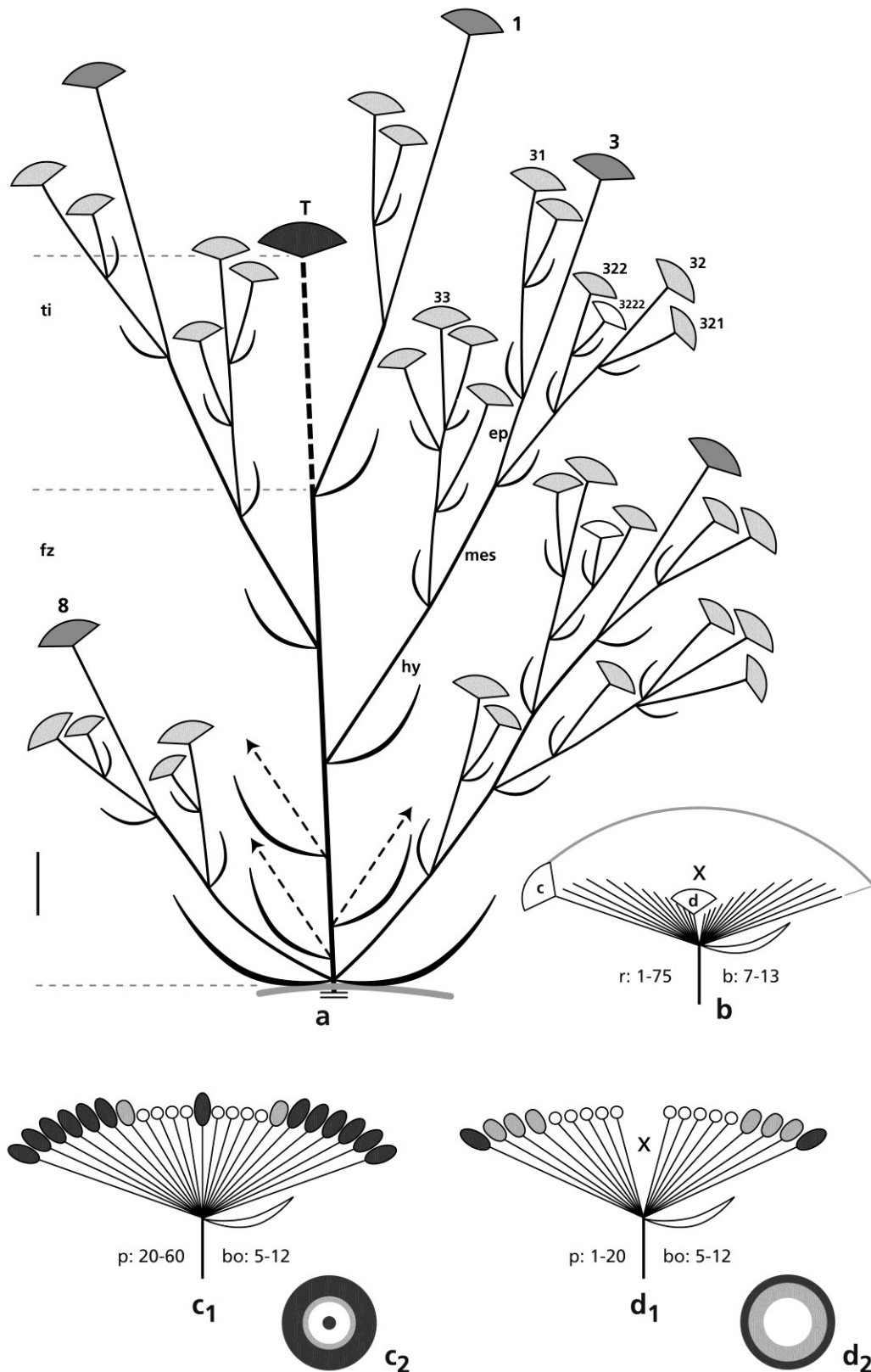


Figure 2.30 *Daucus carota*. – a. plant profile; note the weak lateral branches 1 and 8 indicating mesotony. – b. schematic side view of an umbel, showing the number of rays (r) and bracts (b). – c-d. schematic side views (c₁, d₁) and top view (c₂, d₂) of a well-developed outer (c) and a weaker inner (d) umbellet. with number of pedicels (p) and bracteoles (bo); note the facultative production of a terminal flower. Bar 10cm.

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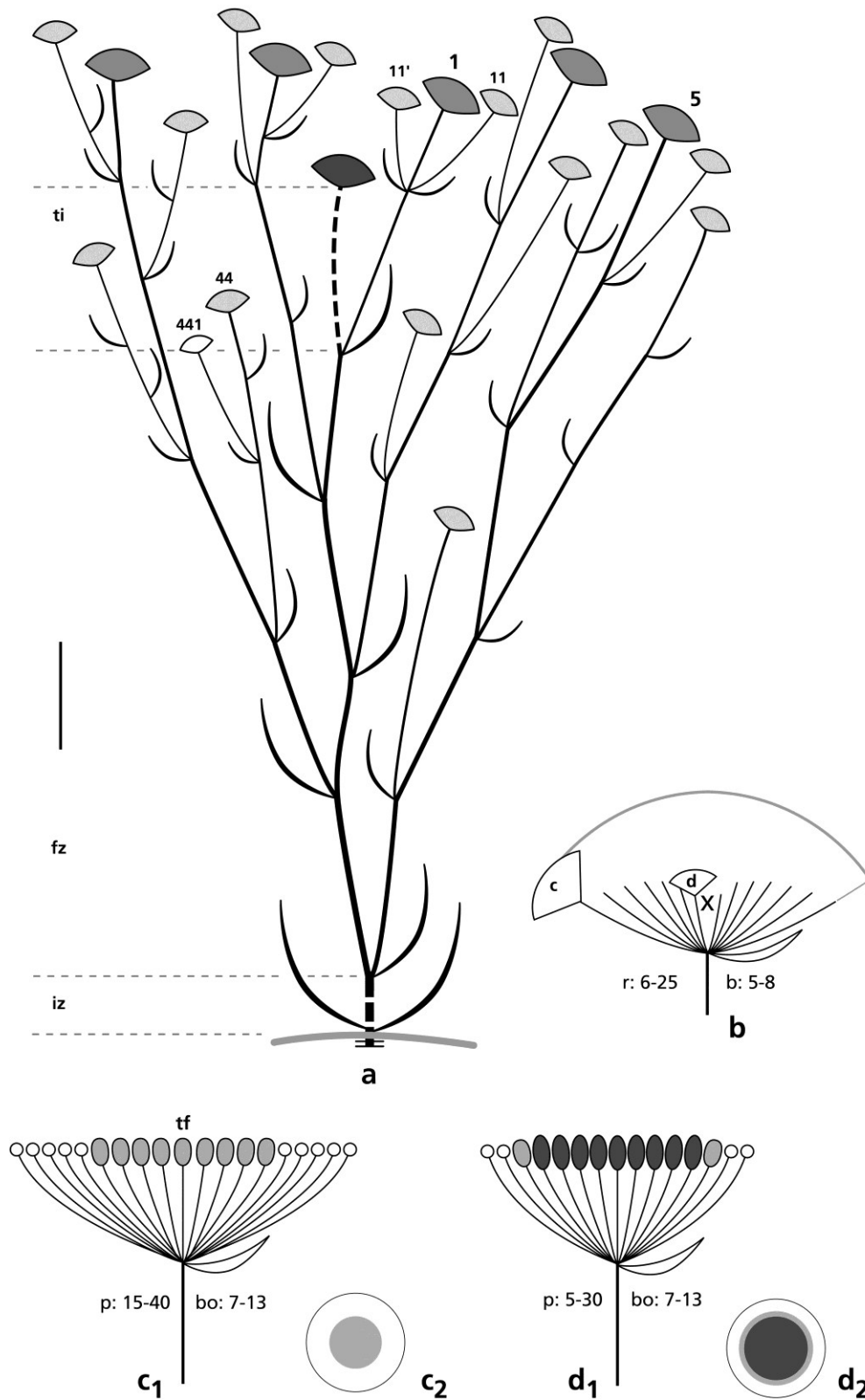


Figure 2.31 *Oenanthe pimpinelloides*. – a. plant profile. – b. schematic side view of an umbel, showing the number of rays (r) and bracts (b). – c-d. schematic side views (c₁, d₁) and top view (c₂, d₂) of a well-developed outer (c) and a weaker inner (d) umbellet with number of pedicels (p) and bracteoles (bo); note the unique sex distribution pattern with outer male and inner perfect flowers. Bar 10cm.

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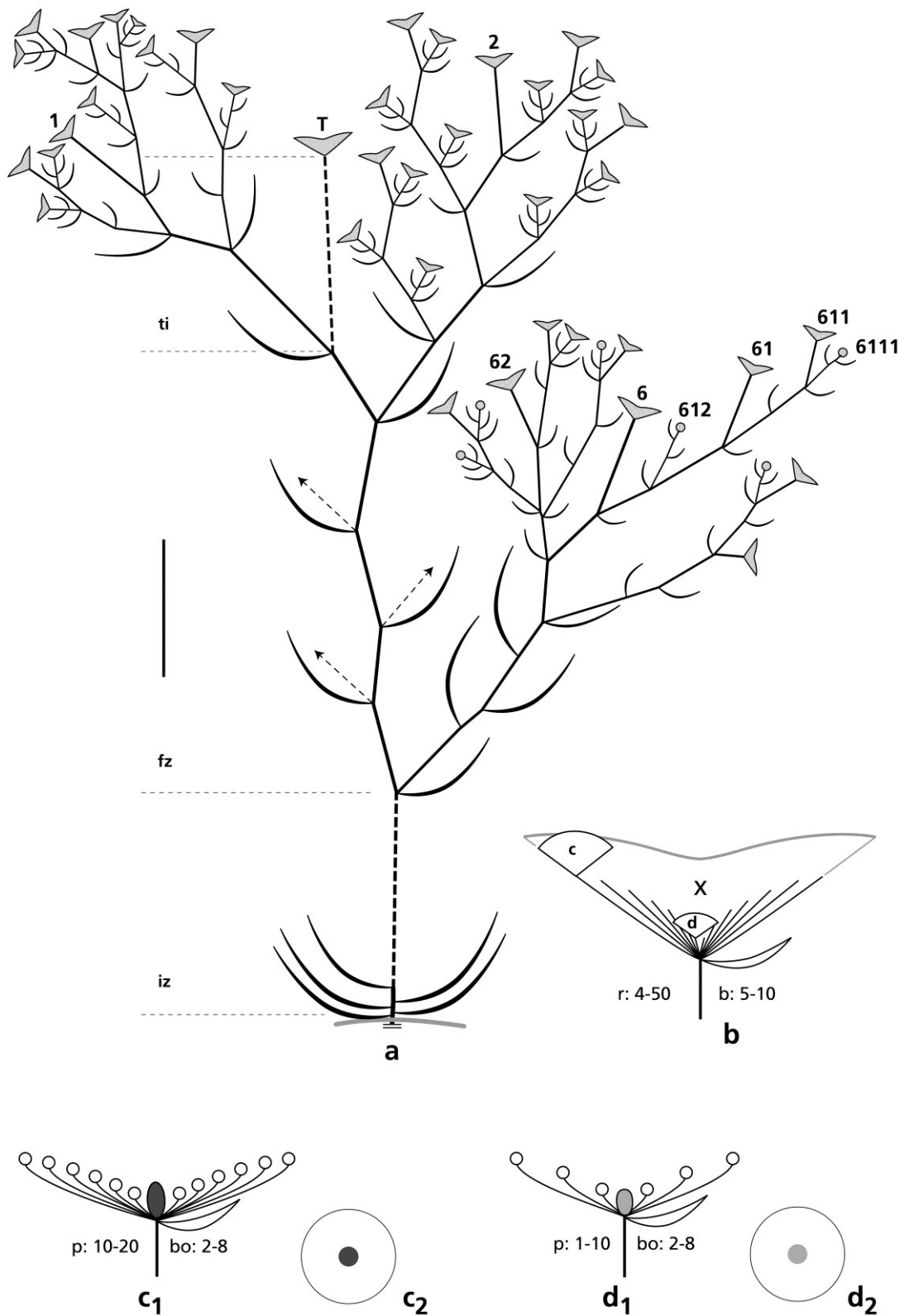


Figure 2.32 *Echinophora spinosa*. – a. plant profile. – b. schematic side view of an umbel, showing the number of rays (r) and bracts (b). – c-d. schematic side views (c_1 , d_1) and top view (c_2 , d_2) of a well-developed outer (c) and a weaker inner (d) umbellet with number of pedicels (p) and bracteoles (bo); note that only the terminal flower in each umbellet is perfect. Bar 10cm.

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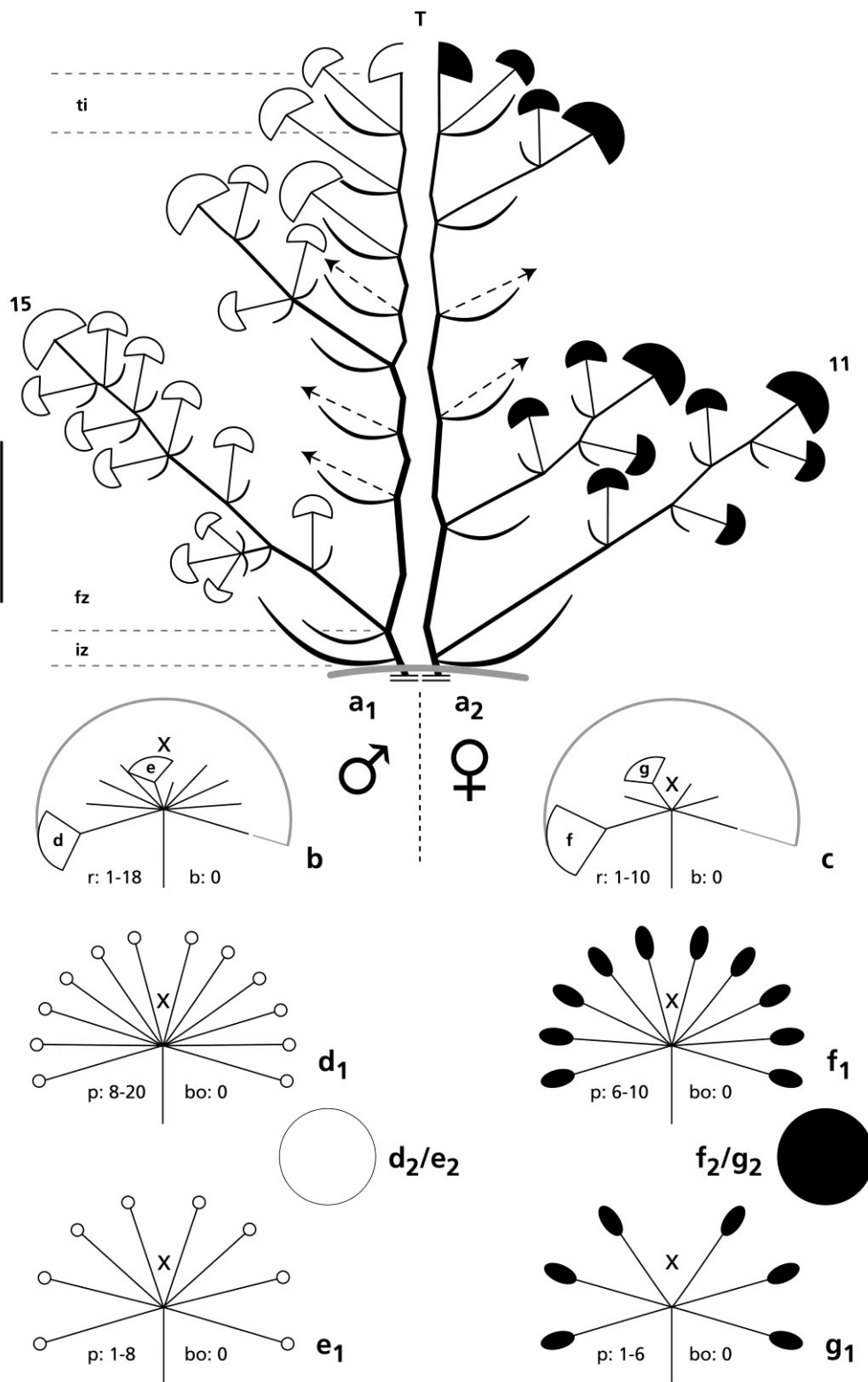


Figure 2.33 *Trinia glauca*. – a₁₋₂. combined plant profile of a male (a₁) and female (a₂) individual; note the different numbers of first-order branches. – b-c. schematic side view of a male (b) and female (c) umbel, showing the number of rays (r) and bracts (b). – d-g. schematic side views (d₁, e₁, f₁, g₁) and top view (d₂/e₂, f₂/g₂) of a well-developed outer (d, f) and a weaker inner (e, g) umbellet with number of pedicels (p) and bracteoles (bo); note the higher numbers of flowers and umbellets in the male plant. Bar 10cm.

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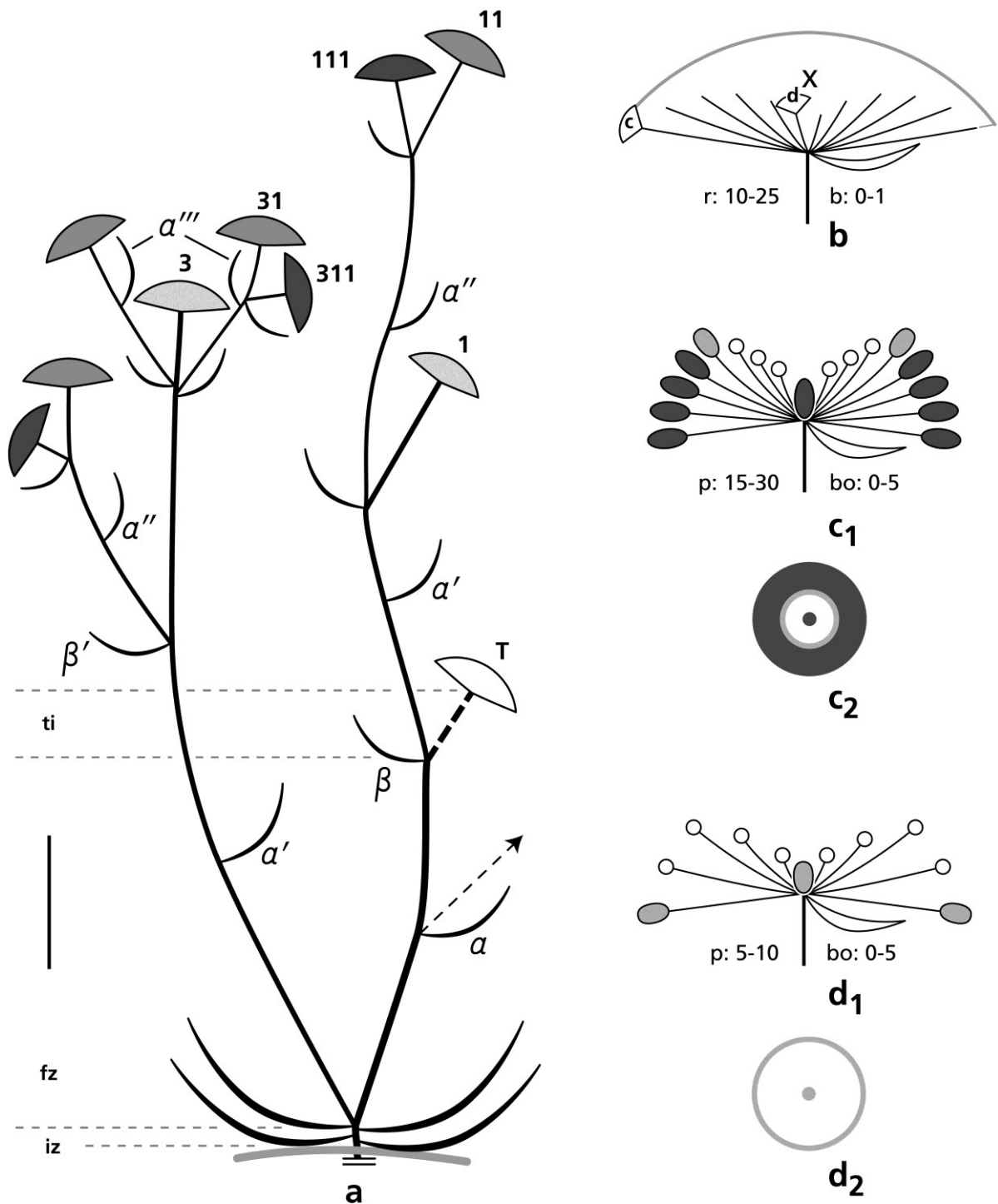


Figure 2.34 *Zizia aurea*. – a. plant profile; note the sterile proximal prophylls (α' , α'' , α''') and the unusual decreasing proportion of male flowers with umbel order. – b. schematic side view of an umbel, showing the number of rays (r) and bracts (b). – c-d. schematic side views (d_1 , d_1) and top view (c_2 , d_2) of a well developed outer (c) and a weaker inner (d) umbellet with number of pedicels (p) and bracteoles (bo); note the increase in (functionally) male flowers in d. Bar 10cm.

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3 ANDROMONOECY AND DEVELOPMENTAL PLASTICITY IN *CHAEROPHYLLUM BULBOSUM* (APIACEAE-APIOIDEAE)

Annals of Botany Page 1 of 9
doi:10.1093/aob/mct073, available online at www.aob.oxfordjournals.org

ANNALS OF
BOTANY
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PART OF A SPECIAL ISSUE ON INFLORESCENCES

Andromonoecy and developmental plasticity in *Chaerophyllum bulbosum* (Apiaceae – Apioideae)

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Received: 28 November 2012 · Returned for revision: 9 January 2013 · Accepted: 15 February 2013

- **Background and Aims** Andromonoecy, the presence of hermaphrodite and male flowers in the same individual, is genetically fixed or induced, e.g. by fruit set. Little is known about the forces triggering andromonoecy in the Apiaceae. In the present study, a natural population of the protandrous *Chaerophyllum bulbosum* was investigated to elucidate architectural constraints and effects of resource reallocation.
- **Methods** Three sets of plants (each $n = 15$) were treated by hand pollination, pollinator exclusion and removal of low-order inflorescences. Fifteen untreated plants were left as controls.
- **Key Results** Untreated plants produce umbels up to the third branch order, with increasing proportions of male flowers from 15 % (terminal umbel) to 100 % (third-order umbels). Fruit set correspondingly decreases from 70% (terminal umbel) to <10 % (second-order umbels). Insignificant differences from hand-pollinated plants do not reveal any sign of pollinator limitation at the study site. Bagged individuals show the same increase in male flowers with age as untreated plants, indicating that the presence of andromonoecy is not induced by fruit set. After umbel removal, individuals tend to present a higher number of hermaphrodite flowers and fruits in the umbels of second and third order. Three plants (25 %) produced an additional branch order composed of 100 % male umbels.
- **Conclusions** Inherited andromonoecy and the plastic response to environmental conditions are interpreted as a self-regulating system saving investment costs and optimizing fruit set at the same time.

Key words: Andromonoecy, Apiaceae, architecture, bagging experiments, *Chaerophyllum bulbosum*, developmental plasticity, fruit set effect, hand pollination, protandry, sex ratio, umbel removal.

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4 'AND YET THEY VARY' – SPATIAL-TEMPORAL DIVERSIFICATION IN FLOWERING APIACEAE-APIOIDEAE AND THEIR UNIFORMOUS FUNCTIONAL SYNDROME

4.1 ABSTRACT

Apioideae are easily recognized by well-established characteristic inflorescence features which are, however, known to vary within the group. To respond to the questions, what makes the species appearance so similar, and whether architectural and reproductive characters are linked, the flowering shoot systems of 255 species are analysed for character syndromes. Species were chosen both randomly and selectively to represent all major clades and habitat types. For each species, data were collected on plant habit, shoot architecture and sexual system, morphology of the umbels and umbellets, including sex ratios and distributions patterns of flower types, and lastly inflorescence development, including dichogamy and flowering sequences.

A lot of features occur frequently in the subfamily, probably accounting for the easy recognizability of many species. We designed a theoretical 'model apioid' from these 'characteristic' traits which, however, showed not to occur in this combination in any of the studied species. None of the species shares any other combination of characters, either. They all rather diversify in many ways. Only two of the observed traits, protogyny and the gradual increase in male flowers, consistently co-occur.

Because all species exhibit a generalist pollination system, it is concluded that the diverse character combinations in many ways create a similar functional pattern which is able to respond to the demands of promiscuous pollination, especially the avoidance of selfing and geitonogamy while setting high numbers of fruits. We can learn from this unspecialized, in terms of flower morphology, plant group that each species is able to create a unique character syndrome and at the same time a general 'functional syndrome', shared by all its members, which could be called the 'apioid breeding syndrome'.

4.2 INTRODUCTION

Recognizing a member of the Apioideae would probably be referred to as blindingly easy even by amateur or lay botanists. Also the overall picture, that those whoever have worked with species of this largest Apiaceae subfamily have in mind, might be very similar. The small and unspecialized flowers are aggregated into umbels, regarded as a characteristically apioid, uniform floral and 'reproductive unit' (Bell & Lindsey 1978). Each umbel is presented at the terminal end of an axis that the branched plants usually produce plenty of. With their open, nectar- and pollen-presenting flowers, they unspecificly attract flying and crawling insects (e.g. Vogel 1975; Baumann 1978; Lindsey 1984; Lindsey & Bell 1985; Sinha & Chakrabarti 1992; Pérez-Bañón et al. 2006; Ollerton et al. 2007; Zych 2007; Niemirski & Zych 2011) and, being self-fertile (Foerste & Trelease 1882; Owens 1974; Keighery 1982; Schlessman 1982, 2010), are likely to be promiscuously pollinated by most of the flower visitors. But is that already all it takes to make flowering apioids so similar to each other?

A closer look at the literature on Apiaceae and Apioideae species shows that inflorescences vary at least subtly (see citations in Davila & Wardle 2002; comparatively studied in Reuther & Claßen-Bockhoff 2010). Architectural analyses, retracing the branching patterns, revealed that umbels of e.g. *Trinia glauca* are borne in monopodial shoot systems (Clos 1874; Troll & Heidenhain 1951; Augier & Rubat du Mérac 1957; Reuther & Claßen-Bockhoff 2010) whereas umbel-bearing branches in *Coriandrum sativum* (Wydler 1860b), *Anthriscus caucalis* or *Zizia aurea* (Reuther & Claßen-Bockhoff 2010) like in woody *Myrridendron donnell-smithii* (Wiedmann & Weberling 1993) grow sympodially. In contrast to the verticillately arranged umbels formed in e.g. *Ferulago* (Bernardi 1979), *Seseli tortuosum* generates pseudowhorls of different-order branches (Hamann 1960). In addition, and most obviously, apioids vary in growth form and shoot orientation (cp. Fig. 4.1), from minute annuals (Fig. 4.1 A) via ground-covering (Fig. 4.1 B) or ascending (Fig. 4.1 C) perennial herbs to erect shrubs (Fig. 4.1 D, F), dendroid perennials (Fig. 4.1 E), and even trees (Fig. 4.1 G) back to very small (Fig. 4.1 H) or even creeping (Fig. 4.1 I) perennials. Unequal internode lengths and shoot sizes, being the result of differing intervals of branch and umbel production between plants and species, entail a great diversity of individual flower canopies. All of the structural elements of the plants, mainly branches and umbels, their architectural arrangement and the underlying meristem activities, are a more or less unexplored source of variation in the entire family.



Figure 4.1 Apioideae, diverse life and growth forms. A. *Hohenackeria exscapa*, minute annual plant (with closely aggregated, simple umbels!). B. *Falcaria vulgaris*, population of rather short, erect perennials presenting their umbels in a common, ground-covering plane. C. *Rouya polygama*, ascending perennial herb, note the post-floral, withered umbel (arrow) and the short-stalked to more or less sessile T (encircled), revealing sympodial growth of the shoots. D. *Bupleurum fruticosum*, evergreen shrub with single umbels terminating each flowering shoot. E. *Pimpinella anagodendron*, small subshrub with 3 umbel orders (encircled: T; I, II, smallest umbels, unmarked in the picture). F. *Anginon difforme*, rigid shrub with several flowering shoots, note the dead previous-year shoots (brown, arrow). G. *Heteromorpha arborescens*, seasonal shoot on the small tree, note T and the much younger I (arrow on bud). H. *Helosciadium repens*, creeping, sympodial shoot. I. *Heracleum pumilum*, small, erect perennial herb with few, coplanarly presented umbels; T = terminal umbel, I = 1st-order umbel.

Some traits, however, are known to frequently occur among species, rendering them 'typic' features in many descriptions of the group. These are e.g. the herbaceous habit (see any flora), protandry (e.g. Knuth 1898; Ponomarev 1960; Bell 1971; Bertin & Newman 1993), or andromonoecy (e.g. Liehr 1927; Webb 1981; Schlessman 2010), combined with gradients (mostly reductions) between early- and late-flowering umbels, including increasing numbers of male flowers and lowering seed set with declining germination rates of fruits deriving from respective umbels (e.g. Ullrich 1953; Braak & Kho 1958; Singh & Ramanujam 1973; Koul et al. 1984; Spalik & Woodell 1994). Dichogamous flowering phenologies and sequences often show similar patterns of alternating, more or less overlapping, male and female flowering phases (e.g. van Roon & Bleijenberg 1964; Koul et al. 1989a; Koul et al. 1989b; Koul et al. 1996; Németh et al. 1997; Németh & Székely 2000; Rovira et al. 2002; Reuther & Claßen-Bockhoff 2010).

A bulk of morphological and phenological data on Apioideae is assembled in the world's floras and taxonomic treatments. The search for comparative studies, revealing information on how commonly inflorescence architectural and developmental parameters are really distributed in the group, will, however, remain essentially unfruitful. For example, despite the long-known presence or lack of a terminal flower in the umbellets (Wydler 1860a, b; Warming 1876; Troll & Heidenhain 1951) which is a crucial feature of inflorescence typology (Weberling 1965, 1983), we completely lack quantitative information on the frequency of its occurrence in the subfamily. If not a clear taxonomic character as the sessile terminal flower in the genus *Zizia* (Mathias & Constance 1944), it has barely been taken into account in any, morphological, biological or cladistic, study of Apioideae (but see e.g. Froebe 1964 for examples of weak to strong 'central promotion' on the production of terminal flowers in the umbellets; Dihoru 1976 for discrimination of *Chaerophyllum* and *Anthriscus* species; Kumar 1977 for the presence of terminal flowers in coriander; Palevitch 1985 for delayed terminal flowering in *Coriandrum*).

A first aim here is to capture, illustrate and discuss the realized variation in flowering apioid shoots and to search for typic, i.e. frequently occurring traits, and for new, undescribed feature characteristics, e.g. floral sex patterns. A few basic parameters in the modularly constructed plants, e.g. *basic branching pattern*, *differential elongation* of internodes and *repetition* of patterns (see Endress 2010) are expected to provoke the diverse opportunities for umbel position, form and organisation, to produce "compound" (*double*, *triple*, *multiple*) structures,

and to allow modifications of the plants' overall flower canopy and branching structure ('scaffold'; see Harder & Prusinkiewicz 2012) during development. Particular attention is turned to these.

Furthermore, we are interested in character syndromes, shared by several or many species, e.g. phenological and architectural concurring with reproductive features, similar to the ones concurring with protogyny (e.g. yellow or purple flower colour or earlier flowering times, see Schlessman & Barrie 2004). Assuming that certain plant structures are linked to each other, to the sexual system or to specific flowering sequences, we expected other species to match or at least resemble the andromonoecious, hermaphrodite and dioecious 'types' already described (Reuther & Claßen-Bockhoff 2010). Additionally, we keep track of identifying basal and derived characters, and to determine inflorescence types (remember Bernardi 1979) and their derivation from each other by developmental pathways.

Therefore and with the intention of a first-time quantitative characterization of inflorescence morphological traits and the identification of character syndromes in Apioideae, we compare a large selection of 255 apioid species. Especially with view to the high diversity that only few species in comparison to each other can show (Reuther & Claßen-Bockhoff 2010), we try to illuminate the diversity in the whole group of Apioideae and the presence of characteristic, i.e. most frequently occurring features. If they really exist, we try to answer what they are and how they concur to create the image of a typical flowering apioid. The question is addressed if the common demands of a generalistic pollination system shape the entire group of Apiaceae-Apioideae.

4.3 MATERIAL AND METHODS

A comparative morphological survey was conducted on the flowering shoots and umbels of 255 flowering apioid species (Appendices 1, 2 and 4, attached on CD). First, they were picked at random, later on chosen selectively to represent all major (sub)clades, distribution areas, habitat types, growth forms and sexual systems, including dichogamy, of the subfamily. From living and herborized material, we collected, illustrated and analysed a set of 45 characters on the species, individual plants and inflorescences.

Nomenclature either follows IPNI, or the most recent find in publications (see sources of information on each species, Appendix 1). Because of the current, systematic research on Apiaceae, involving lively restructurings of the systematic groups, all species names were rechecked by REDURON, Mulhouse-France and DOWNIE, Urbana/Illinois-USA (pers. comm.). Please note that some common long-time names have become obsolete and are avoided here (see Appendix 1).

4.3.1 *Sampling and taxon origins*

The examined material comprises 146 wild and cultivated taxa, which had been clearly determined to the species-level, plus 108 herborized specimen, whose taxonomic status was personally re-checked. Additionally, pure literature data on *Myrrhidendron donnell-smithii*, also information taken from photographs and web pages, were included in the present study, as this species' growth form and architecture had already been analysed in detail (Wiedmann & Weberling 1993).

In the beginning, data were taken from living plants in their *wild* habitats (abbreviations are used in Appendix 1), i.e. from locally occurring taxa in the Rhine-Main area, Germany (**RM**; March 2004 – November 2012; 21 species) and from species found during field trips to France (Alps: **A**; Jura: **J**; Provence: **P**; July/August 2005, 8 + 1 + 2 species), Italy (the Gargano: **G**; June 2004; 6 species) and Russia (the Caucasus: **C**; July 2008; 2 species). Secondly, examinations in the Botanic Gardens at the Johannes Gutenberg-University Mainz (**MJG**, Germany. March 2004 – November 2012; 59 species), the J.W. Goethe-University Frankfurt (**F**; Germany. August 2011; 1 additional species), the Botanic Garden Berlin-Dahlem (**B**; Germany. November 2005 and July 2006; 18 species), Conservatoire Botanique de Mulhouse (**MCB**; France. April 2006; 20 species), the Botanic Garden of the Moscow

State University (*MWG*, Russia; June 2008; 7 species) and the Subtropical Botanical Garden and Arboretum of Kuban, Sochi (Russia, July 2008; no additional species) covered additional taxa in *cultivation* of a broader geographical range. The habitats comprise mainly grasslands, borders of woods and forests, river (mainly Rhine) banks and sand dunes (especially Mainzer Sand), ruderal and coastal places, dolines (Gargano) and mountains.

Based on current phylogenies and most recent systematic studies (e.g. Valiejo-Roman et al. 2006a; Valiejo-Roman et al. 2006b; Pimenov et al. 2007; Degtjareva et al. 2009; Magee et al. 2009; Nicolas & Plunkett 2009; Downie et al. 2010; Magee et al. 2010b; Sun & Downie 2010; Yu et al. 2011; Valiejo-Roman et al. 2012), *herborized* material from the personal collections of Jean-Pierre Reduron (*MCB*), Regine Claßen-Bockhoff and Hans A. Froebe (additionally, material stored in ehtnol; *MJG*) and the Botanical Museum Berlin-Dahlem (*B*) were adducted to cover a broader systematic range of the subfamily with as many major clades as possible (for guideline see Downie et al. 2010). Thereby, the geographical range of the species was extended to cover all five continents.

The digital herbarium on UMBELLIFERAE, available online at <http://ww2.bgbm.org/herbarium/>, provides high resolution specimen images, which are recommended viewing for some species (see Appendix 1: Roepert 2000 - [IMAGE ID]).

4.3.2 Taxonomy and geography of the selected species

Our species selection comprises species from the euapioids and protoapioids (Fig. 4.2). Altogether, 155 genera in 75% (32 of 43) of the recently described major tribes or (sub)clades (see Appendix 2) are studied. Besides 19% monotypics, 41% derive from small and 21% from large genera. Another 16% belong to the very large genera of more than 50 species. Neither on the genus *Helosciadium* which was repeatedly separated from *Apium*, nor on the three species *Balansaea fontanesii*, *Gasparrinia peucedanoides* and *Seseli webbii* any information concerning clade affiliation or species numbers is available.

Representatives of the most basal clades mainly originate from Africa (*Lichtensteinia*, *Itasina*, *Andriana*, *Steganotaenia*, *Heteromorpha* and *Anginon*), including the Canaries (*Astydamia latifolia*). The few representatives of very basal clades in Europe are the *Bupleurum* species plus Irano-turanian to Mediterranean *Hohenackeria exscapa* (forming a single clade with *Bupleurum*), and *Molopospermum peloponnesiacum* from the southern regions of Western

and Central Europe. Species of the most derived clades (Pyramidoptereae, Pimpinelleae, *Opopanax* Clade, Echinophoreae, Coriandreae, *Conium* Clade, Careae, *Cachrys* Clade and Apieae) appear all over the world. Likewise, small to large genera inhabit all global regions.

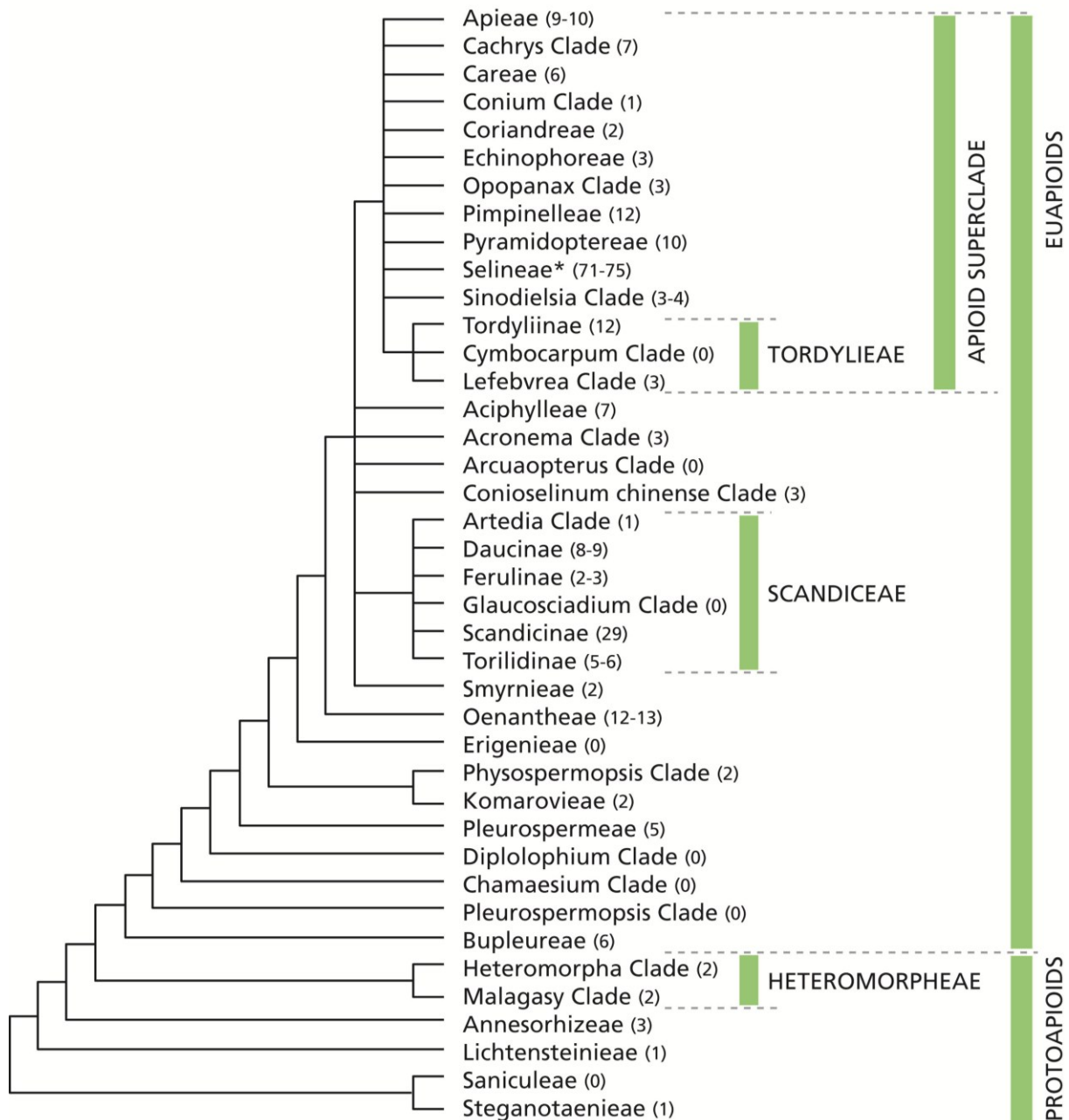


Figure 4.2 Study species in the major clades of Apioideae (in parentheses: exact number of species studied; further unidentified or possibly misplaced: 10-17 spp.); note that protoapioids (after Magee et al. 2010) additionally include Choritaenieae, Marlothiellae and Phlyctidocarpeae which are not regarded here. *(Selineae, see Apioid superclade): including *Arracacia* Clade, Perennial Endemic North American (PENA) Clade and smaller groups, e.g. *Johrenia* tribe (modified after Downie et al. 2010).

- **General geographical distribution** A major part of the investigated species mainly occurs in Europe (20%), the Mediterranean (16%), America (18%) and Asia (17%) species (for the geographical information on each single species, see Appendix 4). Corresponding to the relative pauperism of local genera, only seven species (four *Aciphylla* species, *Scandia rosifolia*, *Gingidia montana* and *Anisotome aromatica*), all of them belonging to the derived clade Aciphyllae, appear in Australia and New Zealand. The second least representatives are 15 species (6%) from Africa that also include the Canary Islands endemic herbaceous perennials *Athamanta montana*, *Pimpinella anagodendron*, *Seseli webbii* and *Todaroa aurea*. At least 16% (42 species) are widespread weeds and crops.
- **Distribution of life forms** About two thirds of our selected species are perennial herbs from all over the world. Only 4% of the study species are shrubs and (small) trees or woody perennials. The genera *Heteromorpha* (e.g. *H. arborescens*, Fig. 4.1 G), *Andriana* and *Anginon* (e.g. *A. difforme*, Fig. 4.1 F) grow only in Africa, *Myrrhoides* in Southern America, and the dendroid perennial *Pimpinella anagodendron* (Fig. 4.1 E) is endemic to the Canaries (Tenerife). *Scandia* is a New Zealand endemic genus, and *Bupleurum fruticosum* (Fig. 4.1 D), the only shrubby European Apioid - besides the Madeiran endemic, woody rosette plant *Monizia edulis* - is found in the Mediterranean area. Most of the remaining monocarps (28.5% of the species) derive from Asia or Europe and the Mediterranean, or they are widely distributed herbs. None of the studied annuals or biennials occurs in Australia or New Zealand, only two of them (*Ammodaucus leucotrichus*, *Astydamia latifolia*) in Africa and 5 (*Angelica hendersonii*, *Apiastrum angustifolium*, *Cyclospermum leptophyllum*, *Spermolepis divaricatus*, *Spermolepis echinatus*) in the Americas.

4.3.3 Data collection, terminology and symbols

For each species, 39 plant and umbel characters (Tab. 4.1 A-AM) are recorded (see Appendix 4) and six additional species characters (Tab. 4.1 AN-AS) included which are mainly taken from the literature. Special attention is paid to the zonation of the flowering shoots, the arrangement of lateral branches on the main axis and their architecture, the flowering units, numerical data as the number of branches and flowers or the specific degree of branching, and presence, absence or development of different organs and structures. Selected species are schematically drawn (for symbolism see Fig. 4.3).

Table 4.1 Variables of concern (= characters) in the data collection on Apioideae. They can be grouped into four subject areas: PLANT HABIT and FLOWERING SHOOT CONSTRUCTION (11 characters, *A-K*), UMBEL POSITION, FORM and ORGANISATION (22 characters, *L-AG*), FLOWERING and DEVELOPMENT (6 characters, *AH-AM*), GENERAL SPECIES INFORMATION (6 characters, *AN-AS*).

<u>A</u>	<u>B</u>	<u>C</u>	<u>D</u>	<u>E</u>	<u>F</u>	<u>G</u>	<u>H</u>	<u>I</u>
GROWTH FORM	HEIGHT OF THE PLANTS (CM)	SHOOT ARCHITECTURE	LATERAL AXES 1 ST ORDER (N)	BRANCHING EXTENT	INTERNODES FZ	BRANCH CLUSTERING	BRANCH CLUSTERS POSITION	LENGTHS PROMOTION
<u>J</u>	<u>K</u>	<u>L</u>	<u>M</u>	<u>N</u>	<u>O</u>	<u>P</u>	<u>Q</u>	<u>R</u>
INHIBITION ZONE	TERMINAL INTERNODE	TERMINAL UMBEL	UMBEL RAYS	FLOWERS PER UMBELLET	UMBELLET SIZE GRADIENT	TERMINAL FLOWERS	INVOLUCRUM	INVOLUCELLUM
<u>S</u>	<u>T</u>	<u>sex distribution</u>		<u>W</u>	<u>X</u>	<u>Y</u>	<u>Z</u>	<u>AA</u>
ATTRACTION FEATURES	PLANT SEX	<u>U</u>	<u>V</u>	ORDINAL SEX RATIO	DOMINANT FRUIT SET	UMBEL DIAMETER (CM)	DOMINANT UMBEL ORDER	UMBEL SIZE, GRADIENTS
		UMBELLET	UMBELS					
<u>AB</u>	<u>density</u>		<u>AE</u>	<u>AF</u>	<u>AG</u>	<u>AH</u>	<u>AI</u>	<u>AJ</u>
UMBEL SHAPE	<u>AC</u>	<u>AD</u>	UMBEL CLUSTERS	PETAL COLOR	PETAL CONSPICUITY	INDIVIDUAL GROWTH DYNAMICS	DICHOAMY	FLOWERING SEQUENCE UMBELLET
	UMBELLET	UMBELS						
<u>flowering sequence</u>			<u>AN</u>	<u>AO</u>	<u>AP</u>	<u>AQ</u>	<u>AR</u>	<u>AS</u>
<u>AK</u>	<u>AL</u>	<u>AM</u>	LIFE FORM	DISTRIBUTION AREA	HABITAT	FLOWERING PERIOD	CLADE (POSITION)	SPECIES WITHIN THE GENUS
UMBEL	UMBEL ORDER (I)	PLANT (FLOWERING CYCLES)						

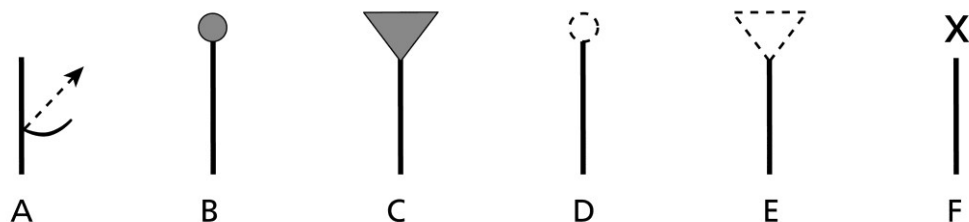


Figure 4.3 Symbols, used in the schematic drawings. A. Stem with leaf and indicated lateral axis (branch); B. Pedicelled (terminal) flower (here: hermaphrodite; with white filling: male, or SELDOM umbel bud). C. Peduncled umbellet or umbel (here: andromonoecious; with white filling: male; with black filling: female). D. Facultative flower. E. Facultative umbellet or umbel. F. Lacking (terminal) flower, umbel or umbellet (marked also in the photographs).

To account for natural variation, at least 2-3, mostly 5-10 or even more individuals were compared in the wild populations before we delimited the character state. Published literature, and a preliminary version of the family treatment in *THE FAMILIES AND GENERA OF VASCULAR PLANTS* (Plunkett et al., in press; provided by Plunkett, pers. comm.), was

always consulted to complement missing data on our data set, that were not evident from the plant material, or to reassess our observations. This was the case if we had only single individuals in cultivation or as herborized material, or umbels were only in very late (fruiting) or early (bud) stages, or if it was unclear which part of the plant – main axis or lateral axis - was on hand.

Collected characters are either more or less *constant* or *definite* variables (as shoot orientation, and architecture, color or dichogamy) or have a rather constant numerical *range* (especially repetitive features as numbers of umbellets and bracts per umbel or flowers and bracteoles per umbellet. Others describe within-plant *gradients* (e.g. in internode proportions, branch length promotion, comparative umbel and umbellet sizes, sex ratios or flowering sequences).

Terminology mainly follows Reuther & Claßen-Bockhoff (2010), but will be commented in the detailed context (see below). In view of recent inflorescence morphological studies and ontogeny-based inflorescence concepts (Tucker & Grimes 1999; Prenner et al. 2009), the umbel as a real 'inflorescence' in contrast to a more general flower aggregate is claimed to arise from a so-called floral unit meristem (Claßen-Bockhoff & Bull-Hereñu 2013). Regarding these current insights, the term '*compound umbel*', arising from a single meristem, becomes critical. Therefore, we follow the general use of the term *umbel* for the apioid umbels, made up of *umbellets*, and refer to the 'simple' umbels, made up of flowers, as umbellets. As the terms *determinate* and *indeterminate* refer to the nature of the meristems, and, as far as we know, all apioid umbels arise from determinate meristems, we prefer using the terms '*open*' for umbels (respectively umbellets) without and '*closed*' for umbels (respectively umbellets) with terminal umbellets (respectively flowers). We use the term 'inflorescence' in a general way, not exclusively for 'real' inflorescences, arising from a single inflorescence meristem. If so, this is specifically noted.

- **PLANT HABIT AND FLOWERING SHOOT CONSTRUCTION (SCAFFOLD)** By **growth form** (character *A*), we describe the orientation of the flowering shoots. Height, however, characterizes the size of the entire plant. We distinguish very small taxa, with inhibited stems (*dwarfs*), from small, medium and large (*giants*). For each species, the branching system of the main axis (or stem) and lateral axes (or branches) is examined for

monopodial or sympodial architecture, or transitional forms as pleiochasia (character **C**; Figs. 2.11-2.13, see Pilger 1921). The number of lateral branches is counted and a *ramification factor* established (following the branching extent, i.e. the number of umbel orders that the plants bear). We further characterize the flowering zone (also see Reuther & Claßen-Bockhoff 2010, Fig. 2.11) and evaluate enrichment patterns. Although internodes were observed to elongate in the course of plant development, certain species-specific proportions are usually maintained after all lateral branches have grown out. Because branches may develop highly ramified lateral systems during flowering, hindering the view of the main axis, relative internode lengths or gradients of the flowering zone (character **F**, if more than two lateral branches are produced) are assessed in the plants, shortly before or in the early flowering stage. The absence or presence of branch aggregations or clusters ('*whorls*' or '*rosettes*') through rhythmic internode inhibition is determined (character **G**) and located (character **H**) in the latter case.

As the *shape* of the inflorescences (flower *canopy*) is affected to a great extent by the '*longitudinal symmetry*' of the flowering shoot (see Barthélémy & Caraglio 2007; Reuther & Claßen-Bockhoff 2010, Fig. 2.13) *enrichment patterns* or rather *promotion tendencies* in the lengths of the lateral branches (character **I**) are further used to describe the plants.

To characterize the length or rather proportion of the inhibition zone (character **J**) and terminal internode (character **K**) in each species, we assume a general subdivision of the annual shoot into three equal parts (cp. Reuther & Claßen-Bockhoff 2010) and record their relative proportions: '*short*' equates less than a third the length (cp. Fig. 2.11 **b₂**, **b₄**), '*present*' equates about a third, '*long*' or extended equates more than a third the length of the main axis.

- **UMBEL POSITION, FORM AND ORGANISATION** Each species is examined for the production (and if present: size) of a terminal umbel (character **L**, Fig. 4.3) *closing* the main stem. If the flowering shoot remains '*indeterminate*' (NOT sensu Prenner et al. 2009 who uses *indeterminate* synonymously to *racemose*), i.e. the terminal umbel is absent, the stem is referred to as *open*. As we have never observed a terminal umbellet within apioid umbels before, this feature is not considered a separate character, but kept in view during the observations. Umbels of different orders are viewed for size gradients of their

umbellets (character **O**). Several individuals and multiple umbels on a plant are checked for their *closed* in contrast to *open* nature, i.e. the presence or absence of **terminal flowers** (character **P**; Fig. 4.3; see Fig. 2.25) in their umbellets and of terminal umbellets in their umbels. **Bracts** (character **Q**) and **bracteoles** (character **R**; see e.g. Fig. 2.25) are **counted**, as described for umbellets and flowers.

Special attraction features (character **S**), e.g. enlarged floral or foliar organs, possibly shaping pseudanthia, or colorations of plant parts, are specially noted. Optimally twice – during flowering and in the fruiting stage - flowers were checked for their **sex** (character **T**), corresponding **distribution patterns** (characters **U-V**; cp. e.g. Figs. 2.25f) and **ordinal sex ratio** (character **W**), i.e. sex ratio or gradient between umbels of increasing order. We distinguish male, female and hermaphrodite flowers: Flowers producing only stamina are male, flowers exhibiting only styles and ovaries are female, and flowers showing both, are recorded as hermaphrodite (= bisexual). This means that morphologically bisexual, but male sterile flowers are possibly counted as hermaphrodites and flowers with male and female structures are determined hermaphrodite even if they do not develop viable seeds. As a consequence, the full spectrum of sex forms may not have been captured. Only non-fruiting flowers with clearly reduced or stunted female organs, already during flowering and definitely during the fruiting stage, are counted as (functionally) male flowers. In case of bearing multiple 'hermaphrodite' flowers with rudimentary organs in umbels of different orders, the plant was classified as andromonoecious (but put in parentheses, cp. 4.3.4 *Data analysis*, see Appendices 3-4). The *FLORAL SEX RATIO* is given as the gradient in the numbers of male flowers, i.e. the sex ratio of a species is de- or increasing if the numbers of male flowers de- or increase, and the sex ratio remains constant if a gradient is recorded to be lacking. The main reproductive output is described by means of the umbel order (or orders) bearing most **fruits** (character **X**) which is subjectively estimated without counting them.

The assessment of **umbel size** and **form** (character **AB**), within and between individuals, is based upon observations from the largest, mostly first-flowering umbels. Whenever a species shows extreme umbel size decreases with umbel order, such that only the terminal or few umbels reach the highest diameters, it is usually placed in the next-lower size category. The **diameter** (character **Y**) of the umbels was measured and umbel hierarchies

are diagnosed. The **dominat umbel order** (character *Z*) is defined by the largest umbel diameters. **Gradients in umbel sizes** (character *AA*) are subjectively assessed by the comparison of umbel diameters. Usually de- or increasing umbel diameters are the result of de- or increasing numbers of all flowers or umbellets. Thereby, however, the possible cases of increasing diameters, attended by decreasing flower numbers and vice versa, are not included. They can be provoked e.g. by changing sex ratios, if flower sizes vary dependent on their sex.

Whenever ***aggregates of umbels*** are displayed simultaneously as a unit to serve attraction (see Figs. 2.26 a-b, 2.29 a) they are recorded as **umbel clusters** (character *AE*). **Petal conspicuity** (character *AG*) is classified with reference to an average, 'normally present', relative petal size of the great majority of species, regarding umbellets as well as umbels as frame of reference.

- **FLOWERING AND DEVELOPMENT** Shoot systems with completed, differentiated inflorescence regions at the beginning of flowering are described by *low* or *lacking individual growth dynamics* (character *AH*). They remain mostly unchanged during the flowering season. Dynamics are assessed *high* if plenty of developmental changes in the shoots, as *internode elongations* and *branch overtoppings*, occurred during flowering. If additionally, augmenting and fading *colors* are exhibited in the floral organs or foliage during development, they are included in the **attraction features** (character *S*). To evaluate age and development of floral primordia, especially living plants are monitored during anthesis for **dichogamy** (character *AI*) and the order of their flowers opening (= *flowering sequence*) in the **umbellets** (character *AJ*), **umbels** (character *AK*) **and all 1st-order umbels** (character *AL*). Synchronous development of flowers, umbellets or umbels may indicate their joint meristematic origin which would bear a meaning in identifying a common floral unit meristem. Thus, we focused on *synchronisations* and *acropetal* (or *centripetal*, starting in the outermost flowers of the outermost umbellets and succeeding towards the center of the umbels), *basipetal* (or *centrifugal*, starting in the innermost flowers of the innermost umbellets and succeeding towards the periphery of the umbels) or other *flowering sequences*. Also for the herborized material and species screened only once data are collected by comparison of younger and older individuals and different umbels and flowers along the branches and within the plants. But because in

many-flowered and highly-branched species, flowering sequences cannot be easily and clearly reproduced, we pass on assessing them, from second umbel order onwards. As the last plant variable, the number of reproductive or **flowering cycles** (character *AM*) per flowering shoot (and usually season) is recorded. It is described as the number of repeating flowering sequences of synchronized flowers (or umbellets or umbels of different, i.e. usually successive umbel order).

- GENERAL SPECIES INFORMATION** In addition to these 39 characters, more *general data* (6 characters *AN-AS*) on each species are provided, gathered from the literature, mainly from regional floras, printed or online (see *references*, Appendix 1). Concerning **life forms** (character *AN*), we discriminate between 1. monocarpic (hapaxanthous), annuals or biennials (seldom perennials), 2. polycarpic (pollacanthous) herbaceous perennials and 3. shrubs or trees (woody plants), especially to interpret the reproductive cycles which are or are not repeated over years. To map the observed species, the anticipated **distribution area** (character *AO*) was split into the 5 continents. As a well-known center of distribution for many Apioideae species (cp. Fig. 1.1), and often comprising two or three continents for one species, the *Mediterranean* area was added separately. Species were either classified to be Mediterranean or temperate European, not both. To provide an idea of specific life circumstances, even though colonisation often stretches along diverse biotopes, we allocated each species to a certain **habitat type** (character *AP*). We therefor distinguish open vs. shaded, closed environments, lowland, coastal and mountainous habitats, and dry vs. humid locations and wetlands. Each species is characterized by the particular combination of locations of their occurrence, e.g. by an open, dry, lowland or a mountaineous, closed, humid habitat. Information on **flowering times** (character *AQ*) is given as the months of bloom, here irrespective of the effective season in the habitat. The **systematic positions** (character *AR*) were determined mainly by the recent work of Downie et al. (2010 and pers. comm.; assembled in Appendix 2), and more specific literature (see sources for each species, App.1). Species belonging to the clades 1-11 are subjectively assumed to form a basal group, and the clades 24-38 a more derived one. All other species (clades 12-23) are regarded as members of central clades. **Species numbers** (character *AS*) within the genus are used to distinguish monotypic, small (1-10 species) and large (11-50 species) from very large genera (> 50species).

Whenever a character must remain *undetermined* for now, a **question mark** is placed in the tables (see Appendices 3, 4). If it was seen in only one or few individuals, it remains *unconfirmed* and a **question mark is placed behind our observed or most presumed state**. All character states that are indistinct, or rather *weakly developed* are **put in parentheses**. Others (especially those with numerical ranges) that show to be largely *ambiguous*, i.e. to *vary* considerably, inter- or even intra-individually, are marked by an **asterisk ‘*’**. They are contributed to a species, only if the character occurred in the majority of plants.

4.3.4 *Data analysis and illustration*

Collected data are analysed for the most frequent character states (*peaks* in the distribution graphs), groupings and combinations or co-occurrence patterns of states to detect similar morphological types or models. Special attention is turned to parameters that are shared by many to most species and to exceptional or unique properties that only few or single species show. We manually matched up species against each other by shared character states, using the sorting function in MICROSOFT OFFICE EXCEL 2007, using different *sorting variables* (e.g. systematic position, geographical distribution, and parameters of obvious meaning for the breeding system, as dichogamy, sexual system, life form, petal conspicuity). Our purpose is to determine functional syndromes of umbel and plant or species characters, i.e. interacting morphological and ecological traits, especially in view of the pollination and breeding system; Features found in the majority of the most basal taxa are considered to be elements of the basic organisation of a characteristic Apioideae inflorescences.

Frequencies for each character state were calculated using SPSS 15.0 (SPSS Inc., IBM Chicago, Illinois, USA) and are given as percentaged bar charts (Figs. 4.5.1-4.5.3).

4.4 RESULTS

We found the 39 characters, collected from the plants and umbels (Tab. 4.2 *A-AM*) to each comprise 2-5(-7) character states. The morphological data set, and the general information on the species (Tab. 4.2 *AN-AS*), is recorded rather precisely with only few gaps for most of the study species (see attached Appendix 4, on CD).

4.4.1 *The model apioid - frequent character states in Apioideae*

Regarding each phenological and morphological character separately (cp. Fig. 4.5.1-3 and Appendix 3, containing summed-up information on each character and state), investigated species are most frequently polycarpic, herbaceous perennials (65.4%) of (15)20-200cm (84.0%; both characters combined in 135 species, 52.6%) with the following architectural and dynamic features (schematically drawn in Fig. 4.4):

PLANT HABIT and FLOWERING SHOOT CONSTRUCTION (SCAFFOLD)

- erect growth (93.8%) and monopodial shoot architecture [73.2%; e.g. Fig. 4.1 D, E, F, H];
- (2)3-10 lateral (1st order) axes [71.6%] branching out to the 2nd or 3rd order [53.7%];
- 1st order branches tending to be basitonously promoted [40.4 (-51.8)%; cp. Fig. 2.13 c];

UMBEL POSITION, FORM and ORGANISATION

- an obligate terminal umbel [90.3%] subtended by a short terminal internode [57.6%];
- mostly compact [45.5 (-52.1)%] and rather flat [55.3%] than globose umbels of diameters up to 10cm [49.4 (-57.3)%], producing or lacking [each about 43-44%] bracts, with 10-20(30) umbel rays [58.8%];
- umbellets of a more frequently compact structure [49.0 (-57.6)%] with 10-20(30) flowers per umbellet [59.1%], subtended by 5-12 bracteoles [39.3 (-60.3)%], lacking a terminal flower [58.8 (-66.9)%];
- white petals [63.4%] which were mostly spread and clearly visible [67.3%];
- umbels rather scattered than clustered [70.4%], their size decreasing ordinally [56.4%];
- an andromonoecious sexual system [64.0%] with a gradual in- or decrease in the proportion [45.1 (-49.4)%] of centered, (functionally) male flowers in the umbellets [72.3%] and umbels [72.0%];

FLOWERING and DEVELOPMENT

- centripetal flower opening [93.0% in umbellets, 86.4% in umbels], protandrous [79.4%] flowers;
- more or less synchronous flowering of the umbels in each umbel order [presumptively 62.3%];
- dynamic growth during bloom (with clear internode elongation) [50.2%], and
- 2-4 flowering cycles per flowering shoot [= *multicycle dichogamy*, 67.3 (-82.1)%].

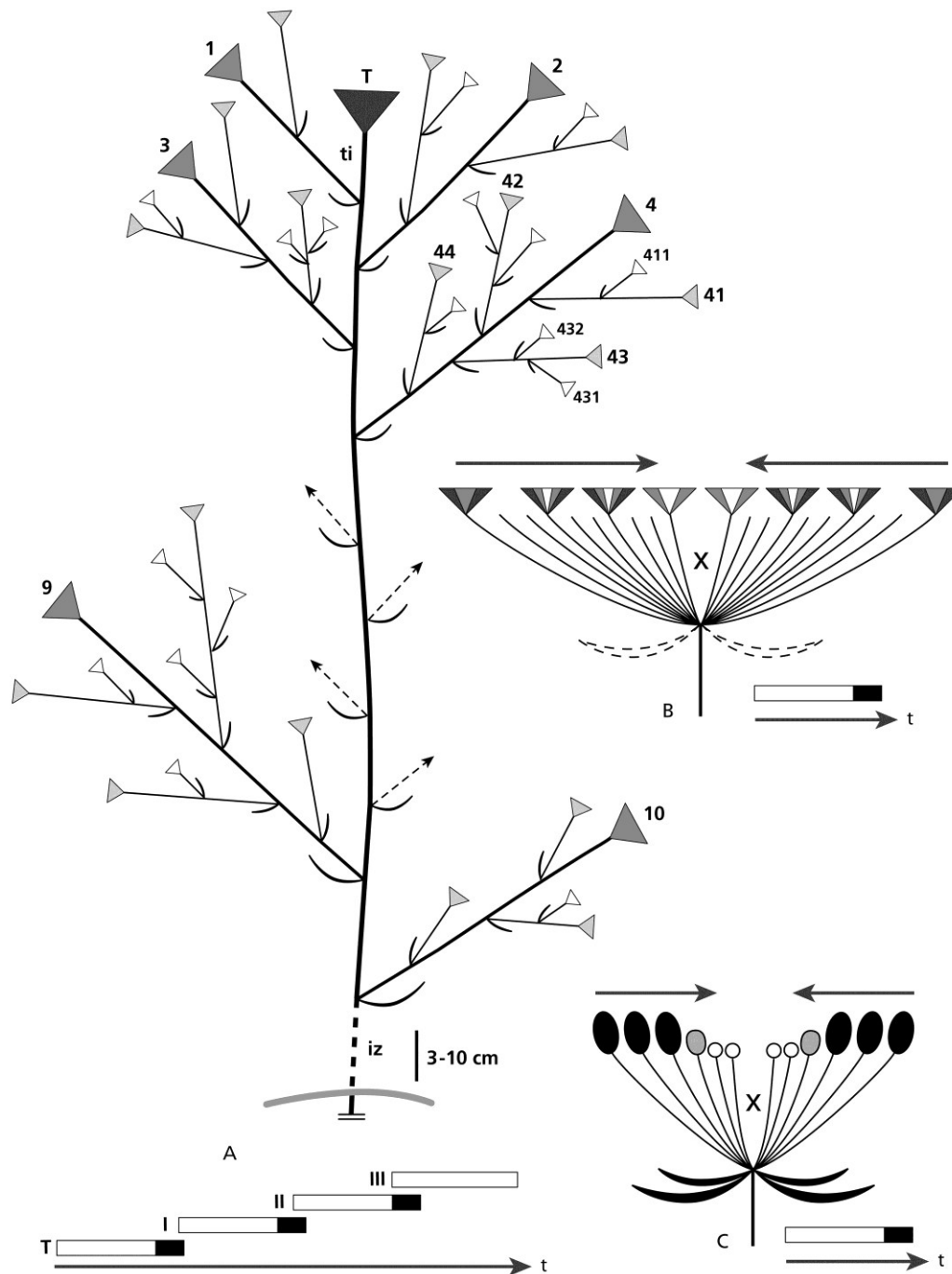


Figure 4.4 Scheme of the 'model apioid'; constructed of most of the frequently-occurring character states (data from the 255 study species). **A.** Plant architecture (above) and flowering sequence (below); above, numbers specify 1st- (1-10) to 3rd- (4-431) order umbels, and umbel color indicates umbel sex from \pm hermaphrodite, dark grey, via increasing percentages of male flowers, grey shadings from medium to light, to \pm male, white); below, bars represent synchronously flowering umbel orders T, I, II, III (= terminal umbel, 1st, 2nd and 3rd umbel order) being composed of protandrous flowers (white = male phase, black = female phase); **B.** Umbel (with facultative bracts), sex ratio (increasing proportions of male flowers towards the center of the umbel and umbellets, indicated by the color gradients from dark grey = \pm hermaphrodite to white = \pm (male), and flowering sequence (indicated by the arrows and bar, cp. **A**); **C.** Umbellet (with several bracteoles), sex distribution (peripheral fruiting = dark grey and non-fruiting = light grey, hermaphrodite and central male flowers) and flowering sequence (indicated by the arrows and bar, cp. **A**); t = time course.

Table 4.2 Characters and detected states, for further explanation see text.

<i>Character</i>	<i>Character states</i>
<i>A. Growth form, shoot orientation:</i>	0 , erect; 1 , creeping; 2 , ascending; 3 , inhibited; 4 , procumbent (Fig. 4.6).
<i>B. Plant (or stolon) height:</i>	0 , 0-10(15) cm (<i>dwarf</i>); 1 , (15)20-50(100) cm (small); 2 , 60-200 cm (medium); 3 , more than 200 cm (giant).
<i>C. Shoot architecture:</i> (based on the main axis; cp. Fig. 2.12).	0 , monopodial stem and branches; 1 , monopodial stem, overtopping (or reduced) to sympodial branches; 2 , sympodial stem and branches.
<i>D. Lateral, 1st-order axes (no.):</i>	0 , 0-1(-2); 1 , (2)3-10(13); 2 , >10.
<i>E. Branching extent:</i> (no. umbel orders).	0 , only T; 1 , T and I; 2 , T to III; 3 , T to many (usually ≥ IV).
<i>F. Flowering zone internodes:</i> (gradients, Fig. 4.10).	0 , equally dispersed; 1 , distally decreasing; 2 , divergent; 3 , distally increasing; 4 , irregular.
<i>G. Branch clusters/whorls:</i>	0 , absent; 1 , present; 2 , irregular between individuals.
<i>H. Position branch clusters:</i> (whorls; Fig. 4.12).	1 , basal; 2 , median or repeated; 3 , distal; 4 , irregular.
<i>I. Length promotion:</i> (1 st -order, cp. Fig. 2.11).	0 , homogenous; 1 , basitonous, 2 , mesotonous; 3 , acrotonous; 4 , irregular.
<i>J. Inhibition zone:</i>	0 , absent; 1 , short; 2 , present; 3 , long; 4 , irregular.
<i>K. Terminal internode:</i> (cp. Fig. 2.11).	0 , completely absent; 1 , short; 2 , present; 3 , long; 4 , irregular.

<i>Character</i>	<i>Character states</i>
<i>L. Terminal umbel:</i>	0 , present; 1 , absent; 2 , facultative (Fig. 4.3).
<i>M. Umbel rays (no.):</i>	0 , 1; 1 , 2-5(10); 2 , (3)6-15(20); 3 , (10-)16-30(-50); 4 , 31-∞.
<i>N. Flowers per umbellet (no.):</i>	0 , 1; 1 , 2-5(10); 2 , (3)6-20(30); 3 , (15)21-∞;
<i>O. Umbellet size (gradient):</i>	0 , constant size; 1 , horizontal decrease (Fig. 4.20)
<i>P. Terminal flowers:</i>	0 , present; 1 , absent; 2 , facultative within individuals; 3 , facultative between individuals.
<i>Q. Bracts (Involucrum):</i>	0 , 0(-3); 1 , (1)2-4(5) 2 , (4)5-10(12); 3 , >10.
<i>R. Bracteoles (Involucellum):</i>	0 , 0(-3); 1 , (1)2-4(5) 2 , (4)5-10(12); 3 , >10.
<i>S. Attraction feature:</i>	0 , umbel rays; 1 , umbellet rays; 2 , stamina; 3 , involucral rays; 4 , stylopodes; 5 , involucellar rays; 6 , leaves.
<i>T. Sex:</i>	0 , andromonoecious; 1 , hermaphrodite; 2 , (gyno-) dioecious.
<i>U. Sex distribution patterns</i> (umbellet):	0 , central staminate flowers (except terminal flowers); 1 , peripheral staminate flowers; 2 , <i>Echinophora</i> pattern.
<i>V. Umbel sex ratio:</i> (horizontal gradient).	0 , centripetal; 1 , centrifugal; 2 , constant;
<i>W. Ordinal sex ratio (gradient):</i>	0 , constant; 1 , gradual increase; 2 , gradual decrease; 3 , abrupt change; 4 , irregular.

Table 4.2 continued

Character	Character states	Character	Character states
<i>X. Predominating fruit set:</i> (no. seed)	0 , evenly spread; 1 , terminal umbel; 2 , 1 st (to 2 nd) order; 3 , higher orders (> 2 nd), 3 , irregular.	<i>AK. Flowering sequence umbels:</i>	0 , umbellets synchronously; 1 , centripetal; 2 , umbellets successively.
<i>Y. Umbel diameter (cm):</i>	0 , <2.5(3); 1 , (2)3-6(8); 2 , (4)6-20(25); 3 , (12)20-50(...); 4 , variable.	<i>AL. Serial flowering sequence:</i> (Fig. 4.35)	0 , umbels more or less synchronously; 1 , divergent; 2 , acropetal; 3 , basipetal; 4 , irregular, unclear pattern.
<i>Z. Predominating umbel order:</i>	0 , terminal; 1 , first; 2 , second; 3 , none; 4 , variable.	<i>AM. Flowering sequence plant</i> (<i>'cycles'</i>):	0 , 1; 1 , 2-4; 2 , normally at least 4-5.
<i>AA. Umbel size gradient:</i> (Fig. 4.28)	0 , ordinal decrease; 1 , rather constant; 2 , variable, without gradient; 3 , initial increase, then decrease.	<i>AN. Life form:</i>	0 , monocarpic; 1 , polycarpic, herbaceous; 2 , woody.
<i>AB. Umbel shape:</i> (Fig. 4.29)	0 , flat (to V-shaped); 1 , hemispheric to globose (convex); 2 , changing, irregular.	<i>AO. Distribution area:</i>	0 , temperate Europe; 1 , Mediterranean (Europe/Africa/Asia); 2 , Asia; 3 , New World, Americas; 4 , Africa; 5 , Australia, New Zealand, Australasia; 6 , widespread, across at least (2-)-3 continents.
<i>AC. Umbel density:</i> (Fig. 4.30)	0 , umbellets diffuse (A); 1 , loose (B); 2 , compact (C); 3 , condensed (D).	<i>AP. Habitat:</i>	0 , open, arid; 1 , open, semiarid to humid; 2 , open, wetlands, marshes, swamps; 3 , shaded (woodlands, shrubberies), dry; 4 , woodlands, shrubberies, moist to wet; 5 , mountains, gorges, cliffs (moist/wet); 6 , dry mountains, desert valleys.
<i>AD. Umbellet density:</i> (Fig. 4.30)	0 , flowers diffuse (A); 1 , loose (B); 2 , compact (C); 3 , condensed (D).	<i>AQ. Flowering:</i>	given as months
<i>AE. Umbel clusters:</i>	0 , absent; 1 , present.	<i>AR. Systematic affiliation:</i> (clade position)	0 , basal (clades 0-12); 1 , central (clades 13-23); 2 , derived (clades 24-38); 0 , unknown, unidentified.
<i>AF. Petal color:</i>	0 , white (-ish to reddish); 1 , yellow (-ish, to reddish-brownish); 2 , green (-ish to reddish); 3 , purplish.	<i>AS. Species number (within genus):</i>	0 , 1; 1 , <10; 2 , 11-50; 3 , >50.
<i>AG. Petal conspicuity:</i>	0 , reduced; 1 , normally present; 2 , enhanced.		
<i>AH. Dynamics (shoot system)</i>	0 , lacking or low; 1 , modifications; 2 , high.		
<i>AI. Dichogamy:</i>	0 , protogyny; 1 , protandry.		
<i>AJ. Flowering sequence umbellets:</i>	0 , flowers synchronously; 1 , centripetal (terminal flowers delayed); 2 , centripetal (terminal flowers first!); 3 , flowers successively.		

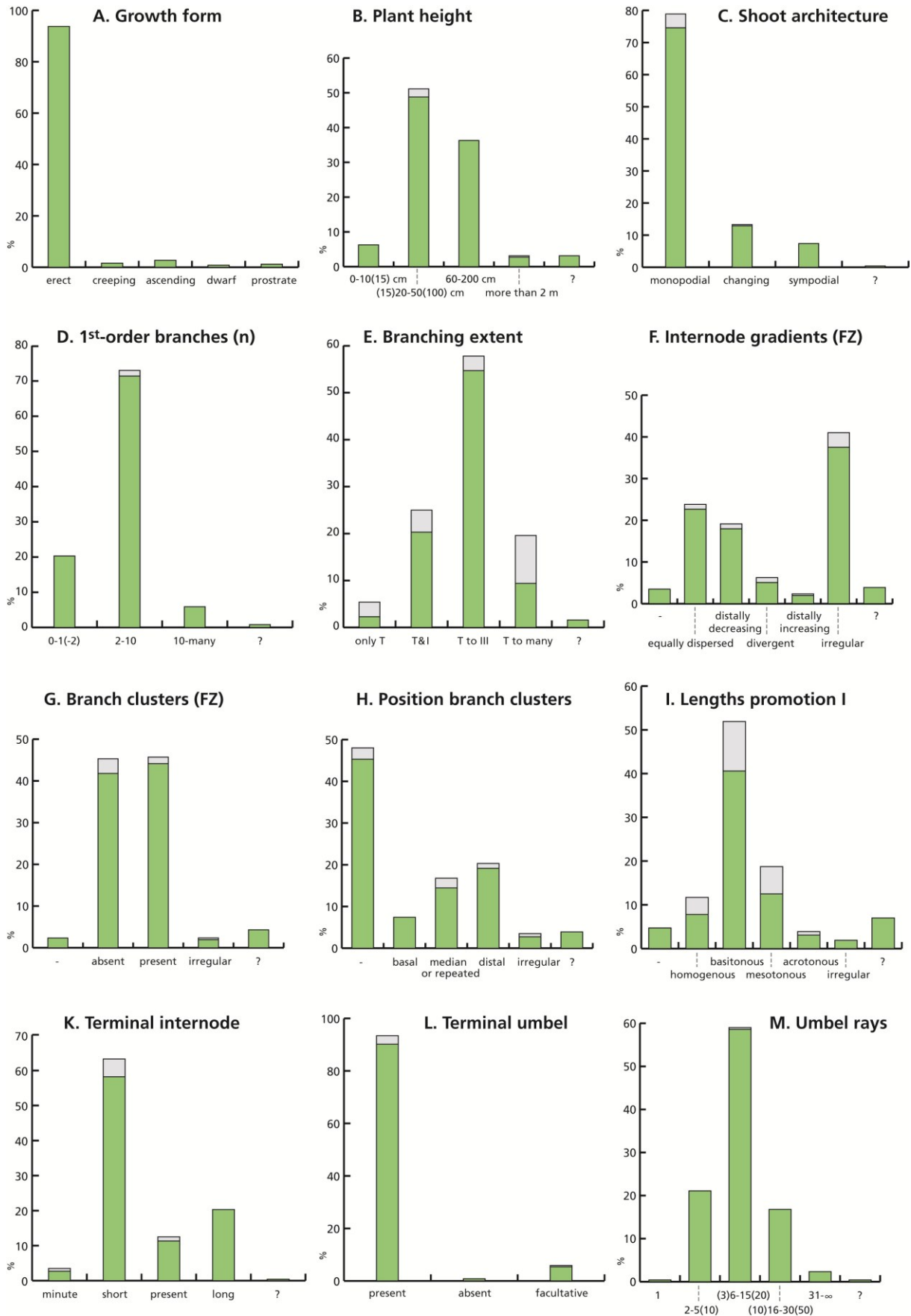


Figure 4.5.1

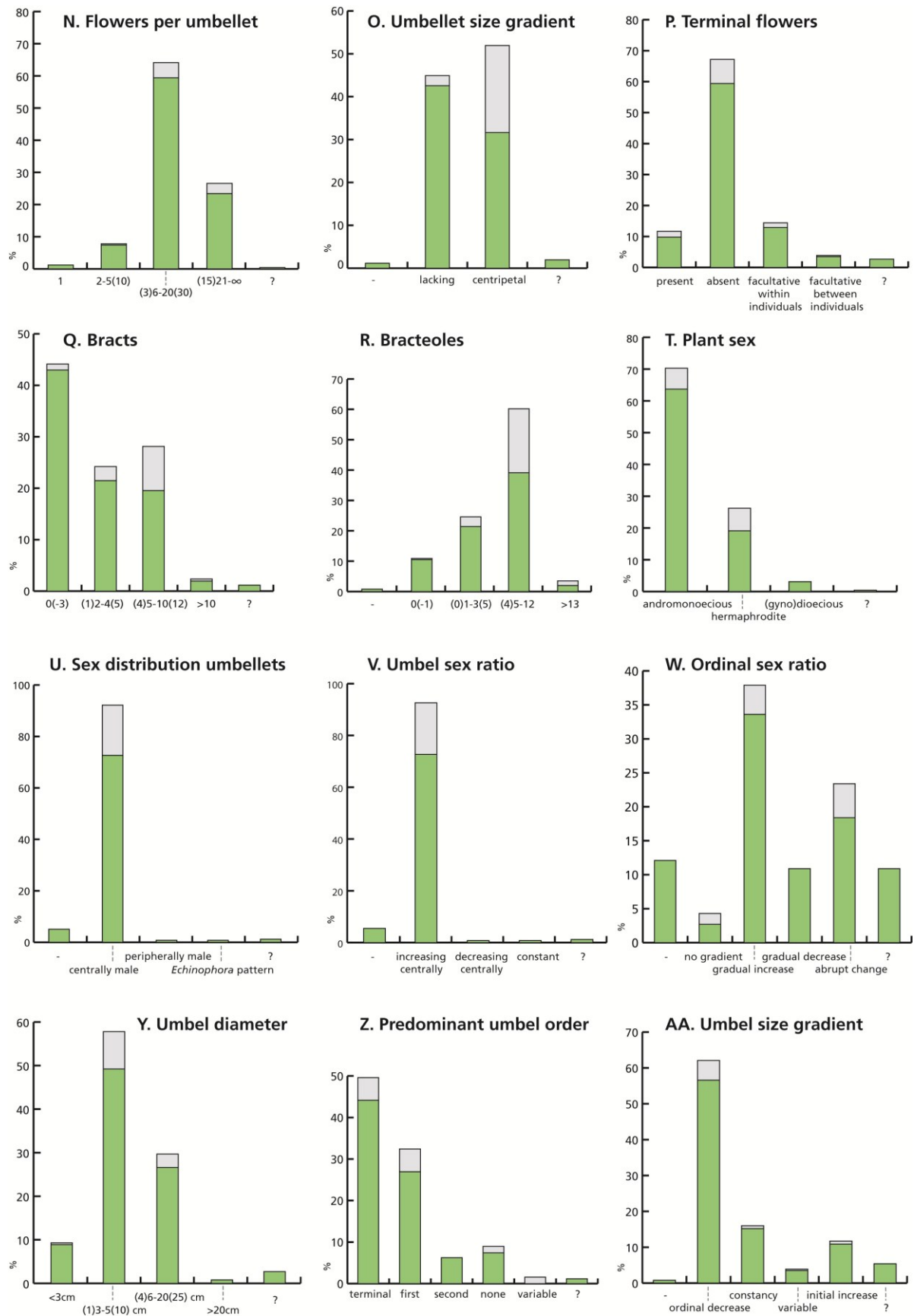


Figure 4.5.2

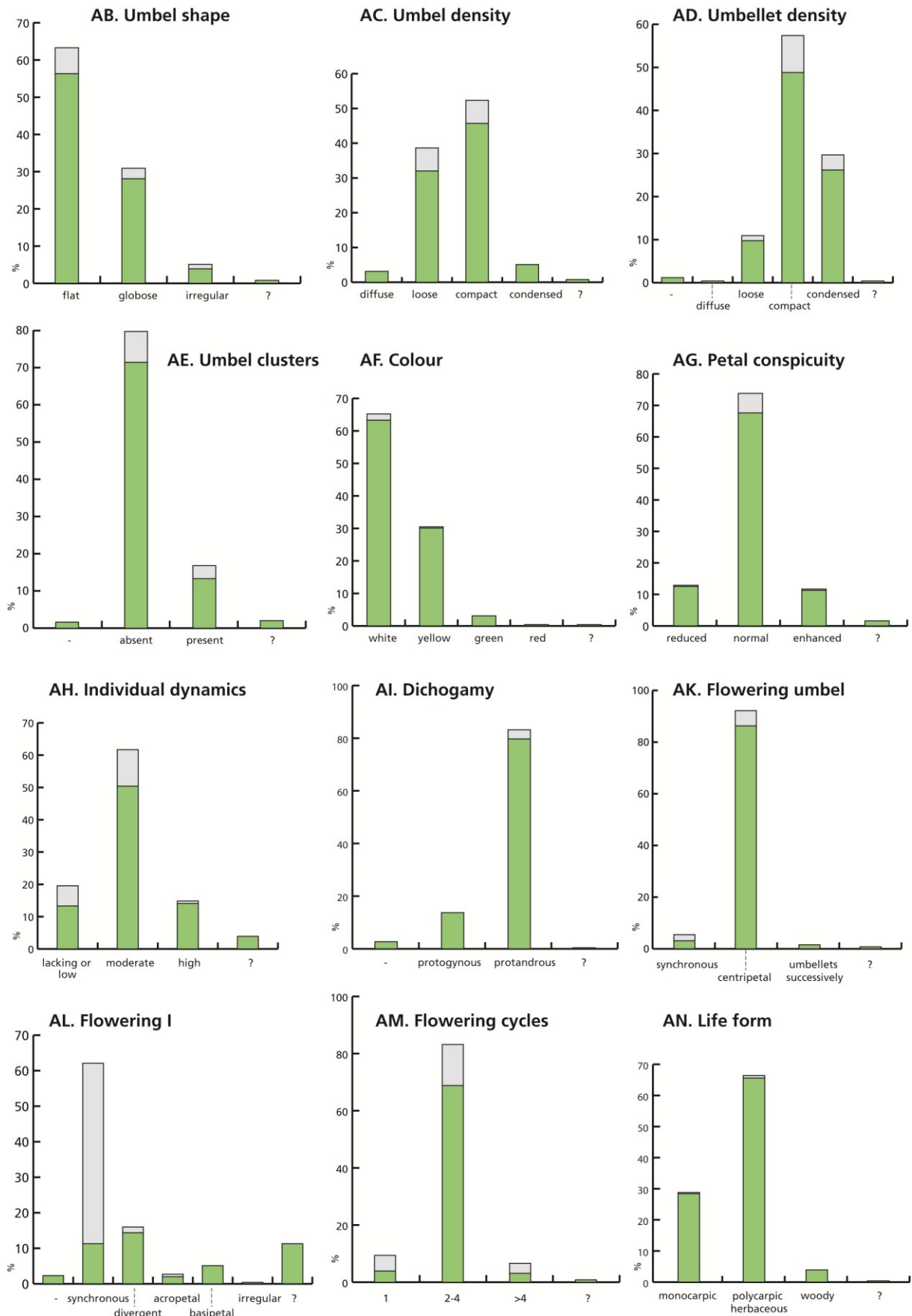


Figure 4.5.3

Figure 4.5.1-3 Frequency distributions of character states in the observed Apioideae species ($n = 255$; titles of subfigures adjusted to Tab. 4.2); bar charts are given as percentages of species showing each state, the single bar is composed of the percentage of species, definitely, varyingly or weakly showing the state of concern (green or lower part) plus the percentage of species presumably showing the characteristic feature (grey or upper part of the bar). Separate bars are given for the percentage of species that a character was not applicable to ('-'; very first bar, if present) or for which that character state could not be determined ('?'; last bar).

Nine characters (of 45, taken from each species) **not illustrated** (plus comment on the reason, →):

J. Inhibition zone: very variable → peak lacking

S. Attraction features: instead of definite character state, there are state combinations → $n \neq 255$

X. Predominant fruit set: hard to determine without counting fruits → states very unsure

AJ. Flowering umbellet: similar to flowering umbel → peak: centripetal flowering [93.7(-95.7)%]

AO-AS. General species information → peaks of no concern

The distribution graphs of only few characters lack a clear *peak state* (e.g. Fig. 4.5.1 **B**, **G**; 4.5.2 **O**). Two, almost equally large groups of species, differ in their production or lack of branch clusters or whorls, a consequence of repeated internode inhibition. The group without whorls varies further in their internode gradients (cp. Fig. 4.5.1 **F**). These two examples are only a first step towards the diversification of species that can be seen if species are directly compared for shared traits. Regarding the most frequently occurring 'typical attributes', partly shown in the schematic model apioid (Fig. 4.4), effectively not a single species seems to combine these into a characters syndrome. For the only species featuring all characteristic states, *Palimbia salsa*, the data set is very fragmentary, because available plant material had been scarce, so that many collected traits remain questionable or unconfirmed (because they are based mainly on the published literature). Our model apioid therefore exists only virtually, so far. All other apioids diversify in multiple ways generating various character combinations.

4.4.2 Diversification

The 3-4 further character states beyond each 'peak', that are usually determined at least for each character, provide a rich basis for the diversification of the flowering shoots. Not two species, even of the same genus, share exactly the same traits. All differ in at least one character state, such as their overall branching structures or only in details, as the formation of whorls, or production of a long terminal internode, or terminal umbel (chapter 4.4.2.1); in features of their umbels which are usually structural, repetitive elements (chapter 4.4.2.2); as well as in heterogeneous developmental processes, mainly flowering phenologies (chapter 4.4.2.3). The specific character combinations lead to specific floral displays, i.e. 'architectural snapshots', and additionally generate specific patterns of flower presentation in time.

In view of the phenomenon, that apioid species are generally perceived as being uniformous, a closer look at the found variation is required.

4.4.2.1 Plant habit and flowering shoot construction

Growth form (Tab. 4.2 A). Besides the erect, vertically arising (Fig. 4.6 A, e.g. Figs. 4.1 E, F; 4.8 A, C, G; 4.11 A-E; 4.13 A, ...) growth form, resembling the apioid model, four other orientations of the shoots (Fig. 4.6 B-E, for frequency distribution see Fig. 4.5.1 A) occur, mainly in the herbaceous perennials, but also in annuals, as in the cushion plant *Hohenackeria exscapa* or *Torilis nodosa*.

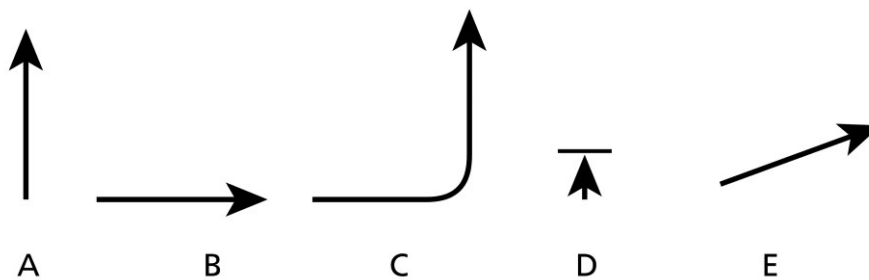


Figure. 4.6 Growth forms of flowering Apioideae shoots. A. erect (orthotropic); B. creeping (plagiotropic); C. ascending; D. inhibited; E. procumbent.

The few observed creeping shoots (Fig. 4.6 **B**; in *Apium fernandezianum*, Fig. 4.9; *Helosciadium bermejoi*, Fig. 4.18 **A**; *Helosciadium repens*, Fig. 4.1 **I**; and *Naufraga balearica*, Figs. 4.8 **E**, 4.19) grow horizontally with at most only the umbels presented upright. The seven species with ascending shoots (Fig. 4.6 **C**, cp. Fig. 4.1 **C**) have vertical inflorescences, but are able to grow horizontally before flowering (e.g. *Rouya polygama*, cp. Fig. 4.1 **C**). The inhibited shoots (Fig. 4.6 **D**, observed only in *Hohenackeria exscapa*, cp. Figs. 4.1 **A**, 4.32 **B**, and in *Chamaesciadium acaule*) remain very short, not exceeding a height of 1-2 cm. The last type of prostrate or procumbent shoots (Fig. 4.6 **E**, in *Echinophora spinosa*, cp. Fig. 2.8; *Dasispermum suffruticosum* and *Torilis nodosa*, cp. Fig. 4.8 **F**) lies down because of lacking mechanical support tissue.

Heights of the plants (Tab. 4.2 **B**). In contrast to most of the Apioideae (growing up to 2m high), shoot lengths vary between species from not much exceeding 1 cm to several meters (cp. Fig. 4.5.1 **B**). The *dwarf* species, for example (Tab. 4.3) comprise mainly erect, monocarpic and polycarpic herbs, but also the two species with inhibited shoots. They are rare but occur on all continents except Australia or New Zealand and in different clades, from basal Bupleureae to the rather derived Perennial Endemic North American Clade (in the following, abbreviated as **PENA Clade**) and Apieae. Their architectural construction is similar to much taller species; their branching extent varies from 0, i.e. completely lacking lateral axes and producing only a terminal umbel, to ~4th-order umbels in a few 1st-order branches. The dominant umbels are mostly the terminal ones, rarely the 1st-order umbels and repeatedly none, i.e. they are all about the same size. Terminal flowers are found only in *Anisosciadium*, but are also presumed in the little available herborized material of *Synclinostyles denisjordanii*. These dwarfs are andromonoecious or hermaphrodite, protandrous or protogynous, with mostly flat umbels (except *Hohenackeria exscapa* and *Naufraga balearica*), and their petals are white, yellow or green.

Table 4.3 Diversity of characters in the observed apioid dwarf species, with heights < 15cm.

Species	Tribe, clade	Distribution area	Life form, growth form	Dominant umbel (order)
<i>Ammodaucus leucotrichus</i>	Daucinae	Africa	erect monocarp	terminal (T)
<i>Anisosciadium orientale</i>	Echinophoreae	Asia (Syria, Iraq, Iran, Afghanistan)	erect monocarp	T
<i>Aphanopleura capillifolia</i>	Pimpinelleae	Asia	erect monocarp	1 ^s order (I, weakly)
<i>Bunium alpinum</i> subsp. <i>montanum</i> ¹	Pyramidoptereae	(temperate Europe)	erect polycarp	none
<i>Caropsis verticillato-inundata</i>	Oenantheae?	(temperate Europe)	erect polycarp	I?
<i>Chamaesciadium acaule</i>	Careae	Asia (NE Turkey, N Iran, Caucasus)	inhibited polyocarp	T
<i>Cymopterus anisatus</i> ¹	PENA Clade	Northern America	erect polycarp	T (weakly)
<i>Cymopterus duchesnensis</i> ¹	PENA Clade	Northern America	erect polycarp	none?
<i>Cymopterus ibapensis</i> ¹	PENA Clade	Northern America	erect polycarp	T
<i>Helosciadium bermejoi</i> ¹	Oenantheae	Mediterranean	creeping polycarp	none
<i>Helosciadium repens</i>	Oenantheae	Worldwide	creeping polycarp	none
<i>Heracleum pumilum</i> ¹	Tordyliinae	(temperate Europe)	erect polycarp	T (weakly)?
<i>Hohenackeria exscapa</i>	Bupleureae	Mediterranean (NW Africa, S Spain, SW & C Turkey, S Iran, Transcaucasus)	inhibited monocarp	T
<i>Musineon tenuifolium</i> ¹	PENA Clade	Northern America	erect polycarp	T
<i>Naufraga balearica</i>	Apieae	Mediterranean	creeping polycarp	T (weakly)
<i>Oreoxis humilis</i>	PENA Clade	Northern America	erect polycarp	T (weakly)
<i>Ormosolenia alpina</i>	Johrenia Clade	Mediterranean	ascending polycarp	T (weakly)
<i>Orogenia fusiformis</i>	PENA Clade	Northern America	erect polycarp	T (weakly)
<i>Orogenia linearifolia</i>	PENA Clade	Northern America	erect polycarp	T
<i>Synclinostyles denisjordanii</i>	Acronema Clade?	Asia	erect polycarp	T (weakly)
<i>Tauschia filiformis</i>	PENA Clade	Northern America	erect polycarp	none
<i>Tauschia nudicaulis</i> .	PENA Clade	Northern America	erect polycarp	none

¹ 'dwarfed' individuals observed, but according to literature, species may grow taller

Eight species reach **heights** of more than 2-3m ('giants'; Tab. 4.4). They also occur in diverse clades and habitats, but are all more or less andromonoecious (unsure only for *Hausknechtia elymaitica* which is more likely to be hermaphrodite) and, except protogynous *Myrrhidendron*, protandrous. They do not necessarily produce more 1st-order branches or branch out further than the the 'dwarfs'. However, they more frequently feature repeated or distal branch clusters. Their umbel sizes show higher variation than the dwarfs', from rather small (5-15 rays, $\emptyset \leq 3\text{cm}$; e.g. in *Hausknechtia elymaitica*) to large (≥ 30 rays, $\emptyset \geq 20\text{cm}$; e.g. in *Heracleum mantegazzianum*). Furthermore, their form and conspicuity are far from being uniform: we found flat or globose umbels and, comparable to the dwarf species, weakly conspicuous ones to highly attractive ones enhanced by petal rays or colored stamina or stylopodes.

Table 4.4 Diversity of giant species in the observed Apioideae, with heights > 200cm.

species	clade	distribution	Terminal flowers	Umbel form	Petal conspicuity	Attraction features
<i>Andriana tsaratananensis</i>	Malagasy Clade	Southern Africa	lacking	flat	?	?
<i>Ferula communis</i>	Ferulinae	worldwide	lacking	globose	weak	stamina and stylopodes
<i>Hausknechtia elymaitica</i> (cp. Fig. 4.32 A)	Pimpinelleae	Iran	lacking	globose	normal?	-?
<i>Heracleum mantegazzianum</i>	Tordyliinae	worldwide	intraindividually facultative	flat	enhanced	enlarged petals
<i>Heteromorpha arborescens</i> (Figs. 4.1 G, 4.34 J)	<i>Heteromorpha</i> Clade	Southern Africa	interindividually facultative	globose	inconspicuous	-?
<i>Myrrhidendron donnellsmithii</i>	<i>Arracacia</i> Clade	South America	lacking	flat	normal	-
<i>Steganotaenia araliacea</i>	Steganotaenieae	Southern Africa	lacking?	globose	inconspicuous?	-
<i>Tommasinia altissima</i>	Selineae	Europe	lacking	flat	inconspicuous	-
<i>Xanthogalum purpurascens</i> (Figs. 4.13 A, 4.25 A)	Selineae	Eurasia	lacking	changing	inconspicuous	stamina and stylopodes

Shoot architecture (Tab. 4.2 C). The prevailing strictly monopodial scaffold is not limited to herbaceous perennials but is shown also in shrubs as *Anginon difforme* (Fig. 4.7) which resembles the model apioid but has dominating 1st-order umbels, a facultative terminal

umbellet, hermaphrodite flowers, more bracts and inconspicuous petals. Two other ramification types occur (Fig. 4.5.1 C) though not generally differing in other model features as the number of 1st-order branches or branching extent:

- In 18 species, e.g. *Zizia aurea* (Fig. 4.8 A), a clear main stem fails to develop or remains very short so that the lateral branches build the sympodial, mono- to pleiochasial flowering shoot from the beginning. In e.g. *Anisosciadium lanatum*, the main stem with the terminal umbel serves only as the erect base point of the overtopping, but procumbent lateral systems. Mainly creeping, monochasia are found in e.g. *Apium fernandezianum* (Figs. 4.8 B, 4.9), *Helosciadium repens* (Fig. 4.1 I) or *H. bermejoi* (Fig. 4.18 A), and *Torilis nodosa* (Fig. 4.8 F). Strictly erect, dichasial branching has been observed in *Kruberia peregrina* (Fig. 4.8 D) or *Apiastrum angustifolium*. In *Naufraga balearica* (Fig. 4.8 E, schematic in Fig. 4.19) a kind of growth from the beginning happens without spatial overtopping of the previous-order umbels during further ramification but results in a close proximity of presented flowers. Among the taxa featuring sympodial branches, are mainly small species inhabiting open and ruderal grasslands (7 species, 39 %) or sandy to desert places (3 species, 17 %), but also coastal or wet sites (5 species, 28 %).
- In e.g. polycarpic *Rouya polygama* (Fig. 4.1 C) and monocarpic *Lagoecia cuminoides* (Figs. 4.8 C) or *Anthriscus caucalis* (Figs. 4.8 G, H), the branching system forms a pleiochasium. This can be observed tendentiously also in the minute *Hohenackeria exscapa*, procumbent *Echinophora spinosa* and more than two dozen other species. The branches thereby either tend to grow sympodially with overtopping as in *Anthriscus caucalis* (Fig. 4.8 H, schematic also in Fig. 2.27) or without overtopping of the previous-order umbels during further ramification as in *Cryptotaenia canadensis* (cp. Fig. 4.15). Other examples of pleichasia appear in: *Berula erecta*, *Chaerophyllum nodosum*, *Coriandrum sativum*, *Helosciadium nodiflorum*, *Lomatium utriculatum*, *Myrrhidendron donnellsmithii*, *Pastinaca sativa*, *Spermolepis echinatus* or *Tordylium syriacum*, which otherwise also have little in common.



Figure 4.7 *Anginon difforme*. A. Apiooid model-like, flowering shoot system with dispersed lateral axes; but note the small T and hermaphrodite sex. B. Terminal end of the flowering shoot with the reduced T (encircled). C. Umbel, schematic; a terminal umbellet in form of several, prematuring flowers was observed in only one individual.



Figure 4.8 Sympodial architectures in Apiioideae. A. *Zizia aurea* (see also Fig. 2.34), fruiting flowering shoots with overtopping branches; note the terminal umbel on the short main stem close to ground level. B. *Apium fernandezianum*, flowering plant (schematic in Fig. 4.9). C. *Lagoecia cuminoides*, flowering pleiochasium. D. *Krubera peregrina*, fruiting plant with clearly dichasial branches. E. *Naufraga balearica*, flowering shoot (schematic in Fig. 4.19). F. *Torilis nodosa*, fruiting plant, not the terminal umbel on the short main stem. G-H. *Anthriscus caucalis*., adolescent, just starting ramification (G) and in full bloom, branched to the 3rd order (H). T, I-IV: terminal umbel, umbels of 1st-4th order.

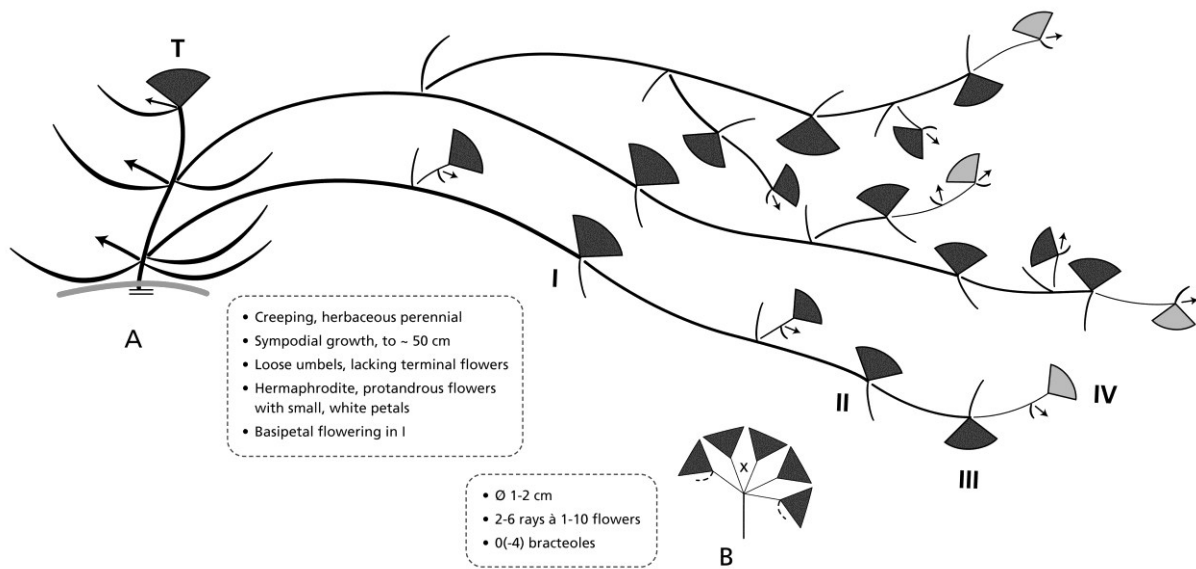


Figure 4.9 *Apium fernandezianum* A. plant, schematic; showing monochasial branching; B. Umbel, schematic, in more detail (5 umbellets), showing e.g. the lack of bracts and a terminal umbellet, and the presence of few bracteoles (facultative, not in each umbellet). T, I-IV: terminal umbel, umbels of 1st-4th order.

As their umbels flower synchronously (see below), the branching pattern in several *Aciphylla* species is not yet confirmed to be pleiochasial. Their lateral axial systems, however, repeatedly show sessile 1st-order umbels, and few, long-stalked, presumably overtopping 2nd-order ones.

In contrast to the creeping herbs which all grow *sympodially*, ascending *Seseli webbi* and *Aegopodium podagraria*, inhibited *Chamaesciadium acaule* and procumbent *Dasispermum suffruticosum* show *monopodial* architectures. The other species with these growth forms tend to overtopping and sympodial growth.

Lateral axes of 1st order (Tab. 4.2 **D**). Besides the frequent range between 2-10 lateral axes, the variation in numbers of branches per flowering shoot splits into two further categories (Fig. 4.5.1 **D**):

- About 20% of the species produce less than two branches. Those are not the smallest taxa, because even dwarf species (*Anisosciadium orientale*, *Aphanopleura capillifolia*, *Chamaesciadium acaule*, some individuals of *Hohenackeria exscapa*) bear more than 2-3 1st-order branches. The terminal umbel represents the only umbel (viz. order) per shoot in *Bupleurum fruticosum* (Fig. 4.1 **D**) and few other, most of them protogynous, species. As

all of them are polycarpic species or woody scrubs, they produce more than only one flowering shoot and umbel per plant during one season or lifetime.

- Only 15 species, and none of the African and American taxa, have usually more than 10 lateral branches: 20% of them are dioecious (*Aciphylla squarrosa*, *Aciphylla horrida*, *Trinia glauca*). Except *Bupleurum falcatum*, they all have repeatedly (e.g. *Cachrys cristata*, *Ferula glauca*, *Libanotis pyrnaica*) or distally whorled (e.g. *Conium maculatum*, *Opopanax chironium* *Pastinaca sativa*, *Xanthoselinum alsaticum*) branches.

Branching extent (Tab. 4.2 *E*). Denominating their *ramification factor*, 50 species are branched only to the 1st order (Fig. 4.5.1 *E*). About two thirds of them have, apioid model-like, up to ten 1st-order branches whereas one third has only up to three. The few taxa that have at least four umbel orders, never have more than 10 1st-order branches. More than three-fourths of them are annuals.

Internodes (flowering zone) (Tab. 4.2 *F*). The main stem is quite variable not only due to differing numbers of branches and e.g. angles between them, but also due to differing lengths of the stem internodes (Fig. 4.5.1 *F*) leading to variable distances (close *approximation* vs. far *dislodgement*) between branches and their umbels. In only about a fourth of the observed species, internodes follow characteristic gradients – decreasing, increasing or divergent - within the shoots (Fig. 4.10 **B-D**). This is in contrast to the more or less equally long (Fig. 4.10 **A₁**) or irregularly dispersed (Fig. 4.10 **A₂**) internodes of the model-majority of species. In e.g. *Smyrniium perfoliatum*, *Levisticum officinale* or *Silaum tenuifolium*, (Fig. 4.11 **A, B, C**) beneath about another 50 species, internodes are very regularly distally decreasing, in *Anthriscus sylvestris* or *Carum carvi* (Fig. 4.11 **D**) mostly divergent. Internodes increase distally only in monocarpic (e.g. *Daucus carota* or *Tordylium apulum*) and/or very small species (e.g. *Bupleurum baldense*, Fig. 4.11 **E**).

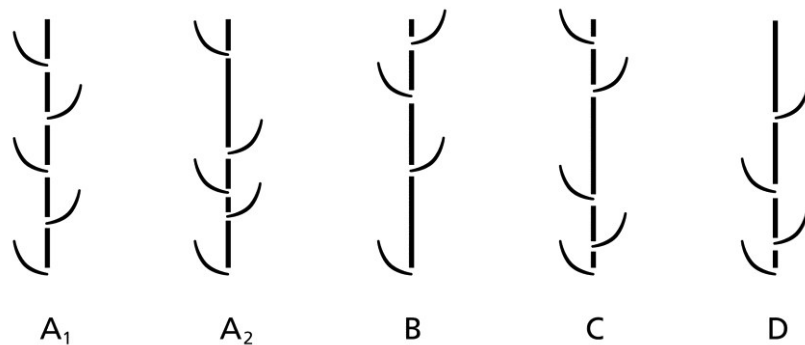


Figure 4.10 Internode gradients of the main stem. A. Regularly, equally (A₁) or irregularly (A₂) dispersed. B. Distally decreasing. C. Divergent. D. Distally increasing.



Figure 4.11 Internode gradients in the stems of flowering Apiioideae. A-C. Distally decreasing. *Smyrnium perfoliatum* (A), *Levisticum officinale* (B), *Silaum tenuifolium* (C). D. Divergent. *Carum carvi*. E. Distally increasing. *Bupleurum baldense*.

Irregular internodes (Fig. 4.10 A₂) are on the one hand observed to entail substantial variation between plants, on the other they lead to the formation of branch whorls which were unvarying in most of the respective species.

Branch clustering (Tab. 4.2 G). Branch clusters or whorls (Tab. 4.2 G; Fig. 4.5.1 G) are usually either always present or absent in a certain species, only sometimes, the pattern irregularly varies between individuals as in *Levisticum officinale* or *Zizia aurea*. The group with dispersed ramification, lacking whorls, comprise the species which produce branches more or less continuously and successively throughout (e.g. Figs. 4.1 F, 4.8 C) or follow any of the described internode gradient (see above). The almost equally large group forming branch clusters, whorls or rosettes, through rhythmical growth patterns further splits unequally into a basal, repeated and distal form (Fig. 4.12).

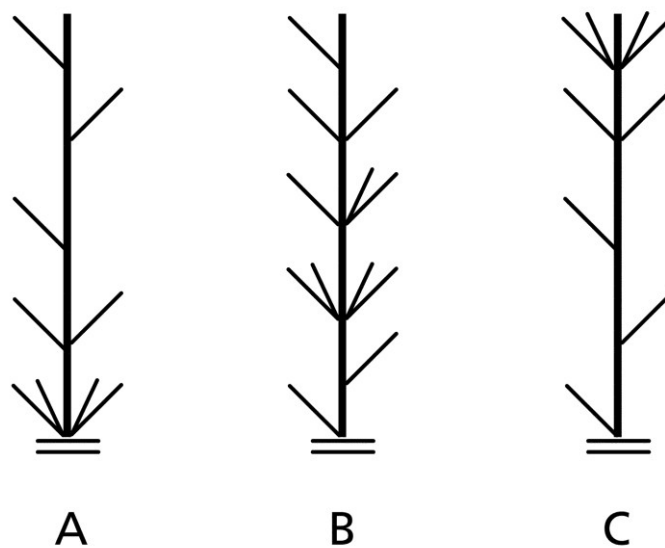


Figure 4.12 Whorl formation along the main stem of the FZ. A. 'Basal whorl' (*rosette*) formation; B. Repeated whorl (and pair) formation. C. distal whorl formation.

Branch clusters position (Tab. 4.2 *H*). Basally clustered branches (*rosettes*), entailing a lacking inhibition zone (Figs. 4.12 *A*, 4.13 *H*, 4.14 *A*), are the least frequent compared to repeatedly (Figs. 4.5.1 *H*, 4.12 *B*, 4.13 *F-G*), or distally (Figs. 4.12 *C*, 4.13 *A-E*), whorled branches. They are found only in species of few clades. These are especially the PENA clade (e.g. *Cymopterus ibapensis*), Scandiceae (e.g. *Athamanta cretensis*; Figs. 4.13 *H*, 4.14 *A*, and *Scandix pecten-veneris*), Torilidinae, Daucinae (*Daucus carota*, cp. Fig. 2.1), Selineae (*Xatartia scabra*), and derived Careae and Pyramidopterae. The species usually additionally share a small size and a habitat in dry regions or montane plains.

Species with repeated whorls have otherwise little in common. They are annuals (e.g. *Pimpinella peregrina*) or polycarpic perennials (e.g. *Trochiscanthes nodiflorus*, Fig. 4.13 *F*), with different growth (cp. *Echinophora spinosa*, *Pimpinella anagodendron*, Fig. 4.1 *E*, *Ferula glauca* Fig. 4.13 *G*, *Apium fernandezianum*, Fig. 4.9 *A*) and umbel forms (cp. *Komarovia anisosperma*, Fig. Fig. 4.23 *B*, *Laser trilobum*, Fig. 4.16 *A*), and also petal color. They additionally differ in their sexual systems (cp. dioecious *Trinia glauca* and *Aciphylla* species, hermaphrodite *Seseli gummiferum*, and andromonoecious *Tommasinia altissima*) and derive from basal (e.g. *Molopospermum peloponnesiacum*, *Physospermum verticillatum*, *Pleurospermum austriacum*) to very derived clades (e.g. *Anisosciadium* species, *Cachrys cristata*, *Prangos trifida*). However, none of the protogynous species was found to bear repeated branch whorls along the main stem.

Also the species that regularly form distal whorls, are a rather inhomogenous group, though never with creeping or procumbent flowering shoots. Again, they derive from most basal (e.g. *Steganothaenia araliacea*, *Heteromorpha arborescens*) to more derived clades (e.g. *Aegopodium podagraria*, *Angelica archangelica*, *Conium maculatum*, *Falcaria vulgaris*, *Silaum tenuifolium*, *Ferulago sylvatica*, *Opopanax chironium*, *Pastinaca sativa*, *Xanthogalum purpurascens*).

In very basal species, the internode patterns occur intermingled: In andromonoecious *Heteromorpha* species, branch arrangement is either dispersed (Fig. 4.1 *G*) or pairwise with a tendency to form distal whorls. In hermaphrodite *Anginon difforme* (Fig. 4.7), 1st-order branches are dispersed regularly, but 2nd-order umbels consistently throughout produce paired, opposite prophylls without branching further, though.



Figure 4.13. Whorl formation (encircled) in the observed Apioideae. A-E. Distal whorls or pairs. A. *Xanthogalum purpurascens*, flowering plants. B. *Conium maculatum*, flowering shoot. C. *Angelica archangelica*, fruiting plants (distal whorl of one shoot encircled). D. *Silaum tenuifolium*, flowering shoot, shortly before anthesis (distal pair encircled). E. *Ferulago sylvatica*, flowering shoot (distal whorl encircled). F-G. Repeated whorls (encircled). F. *Trochiscanthes nodiflorus*, flowering shoot, fruiting. G. *Ferula glauca*, flowering shoot. H. Basal rosette (encircled). *Athamanta cretensis*, flowering plant.

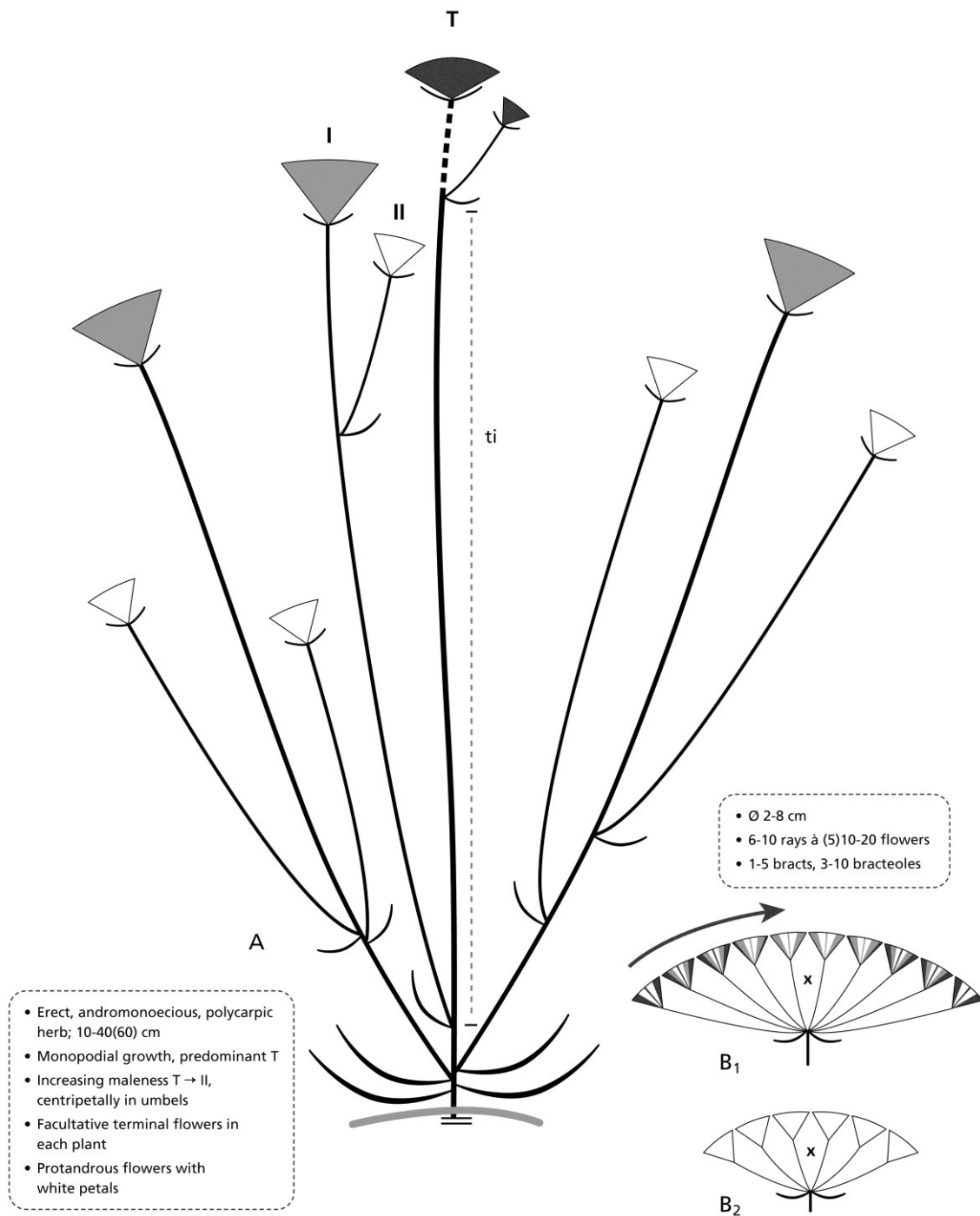


Figure 4.14 *Athamanta cretensis*. A. Plant, schematic, note the basally whorled branches, elongated terminal internode (the umbellet preceding the terminal umbel is facultative) and umbel colors indicating umbel sex. B. Umbels, schematic. B₁. Andromonoecious umbel/umbellets, note the grey shadings indicating terminal flowers and centripetally increasing sex ratio: decrease in functionally hermaphrodite (fading grey) and resulting increase in (functionally) male flowers (see floral sex and distribution patterns, chapter 4.3.2.2); arrow indicates flowering sequence. B₂, Male umbel with male umbellets.

Length promotion (Tab. 4.2 *I*). Assessment of the *promotion tendencies* in the lengths of the lateral branches, forming inflorescence shapes, turn out to be difficult because they partly change a lot during development, or transitions between basitony, mesotony and acrotony are smooth. Therefore, a definite character state is determined for only 179 species and about a fourth of the study taxa remains unsure or completely questionable concerning this property (cp. Fig. 4.5.1 *I*).

Branches are not always basitonously promoted in length as in the species, similar to the model (e.g. *Daucus carota*, *Xanthoselinum alsaticum* or *Trinia glauca*, see Figs. 2.1, 2.4-2.6, schematic in e.g. *Cryptotaenia japonica*, Fig. 4.15). And the basitonous promotion is not restricted to species with dispersed branches, either. Repeatedly, these are mesotonously promoted (e.g. in *Anginon difforme*, schematic in Fig. 4.7 *A*, or *Anthriscus caucalis*, schematic in Fig. 2.29 *a*) or equally long throughout the entire flowering shoot (e.g. in *Athamanta cretensis* or *Hausknechtia elymaitica*, schematic in Figs. 4.14 *A* and 4.32 *A*). Only rarely, the longest branches are the distal ones (in 3% of the observed species, e.g. *Tordylium syriacum*, Fig. 4.16 *B*) and even more rarely, branches are very irregular in length between plants of one species. Although we could not find any exclusive, other features shared by species showing a certain promotion pattern, the acrotonously promoted branches are never arranged into whorls.

Going along with the lengths of the branches, the production of umbels, *enriching* the flowering zone, is mainly basitonously promoted, i.e. the basalmost branches produce the highest relative number of umbels (as in *Cryptotaenia japonica*, schematic in Fig. 4.15). Mostly, the *floral canopy* thereby became more or less pyramidal, even if single basalmost branches are developed weakly, suggesting a mesotonous promotion.

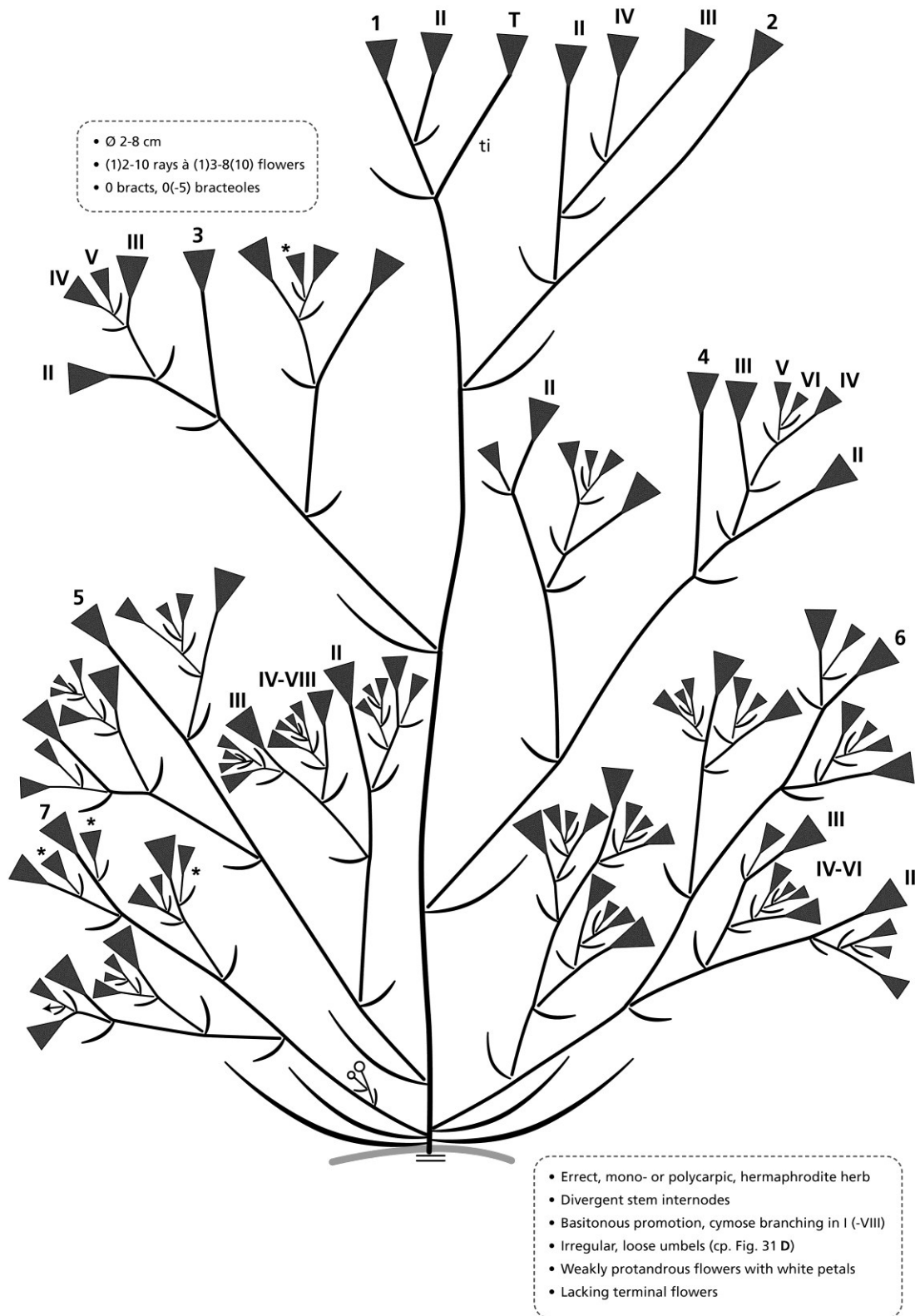


Figure 4.15 *Cryptotaenia canadensis*, schematic. Showing basal promotion in the flowering shoot. Note the consistently rising numbers of umbels and increasing branch lengths, the highest branching order (VIII) is reached in branch 5 (producing umbel 53221111; for umbel numeration see chapter 2 or 3); also note the divergent internode pattern in the FZ and the inhibited umbel buds (circles) in the lowermost branch 7; *: single umbellets

Inhibition zone (Tab. 4.2 **J**) and **terminal internode** (Tab. 4.2 **K**). Neither the inhibition zone, nor the terminal internode, is usually integrated into the internode gradients of the flowering zone as in *Bupleurum baldense* (cp. Fig. 4.11 **E**). The length of the **inhibition zone** varies highly throughout the observed species. It is completely absent in only few species (as *Athamanta montana*) and, each in about a third of our taxa selection, either short (as in *Oenanthe pimpinelloides*, schematic in Fig. 2.32) or considerably elongated (as in *Anginon difforme*, Fig. 4.7). Less frequently, as in *Laser trilobum* (cp. Fig. 4.16 **A**) or several *Angelica* species, it accounts regularly for about a third the length of the main stem.

Compared to its short length in the model majority of species (Fig. 4.4), the **terminal internode** was further observed to be even much shorter or longer (cp. Fig. 4.5.1 **K**). It is definitely highly reduced or completely lacking, rendering the terminal umbel \pm sessile, in only seven protandrous species, that all also lack terminal flowers in their umbellets but otherwise have little in common (Tab. 4.5). Usually this reduction is attended by overtopping branches resulting in sympodial growth (see above). However, the branching system can still remain monopodial as in e.g. *Ferula jaeschkeana*.

Table 4.5 Diversity of apioid species with sessile terminal umbels, lacking terminal internodes.

Species	clade	Life and growth form	Branch clusters	Flowers per umbellet	Plant sex
<i>Apiastrum angustifolium</i>	Selineae	erect monocarp	distal	<10	hermaphrodite
<i>Apium graveolens</i>	Apiaceae	more or less erect, mostly monocarpic perennial	distal	<20	hermaphrodite
<i>Astomaea seselifolia</i>	Pyramidoptereae	erect polycarpic perennial	lacking	<20	hermaphrodite
<i>Cyclospermum leptophyllum</i>	Pyramidoptereae	erect monocarp	lacking	<20	andromonoecious
<i>Ferula jaeschkeana</i>	Ferulinae	erect monocarp	repeated	>20	hermaphrodite
<i>Helosciadium nodiflorum</i>	Oenantheae	ascending polycarpic perennial	lacking	<20	andromonoecious
<i>Naufraga balearica</i> (Figs. 4.8 E , 4.19)	Apiaceae	creeping polycarpic perennial	lacking	<10	hermaphrodite

In e.g. the andromonoecious and protandrous *Laser trilobum* (Fig. 4.16 **A**) or *Tordylium syriacum* (Fig. 4.16 **B**) the terminal internode is highly elongated, accounting for the greatest

section of the stem length. This is also true for other Daucinae and Tordyliinae and mostly more derived species (as many Selineae), but also for basal *Physospermopsis* species. The terminal umbel is thereby separated from the enriching 1st-order branches to a considerable extent with respect to shoot size (see also Fig. 4.11 E). Neither creeping, sympodially branched nor woody nor dioecious species, nor any of the observed African and Australian/New Zealand taxa, show this feature. And none of the species with elongated terminal internodes has more than 10 1st-order branches or usually (tendentially in *Xatartia scabra* and unsure for *Osmorhiza chilensis*) forms any umbel clusters.

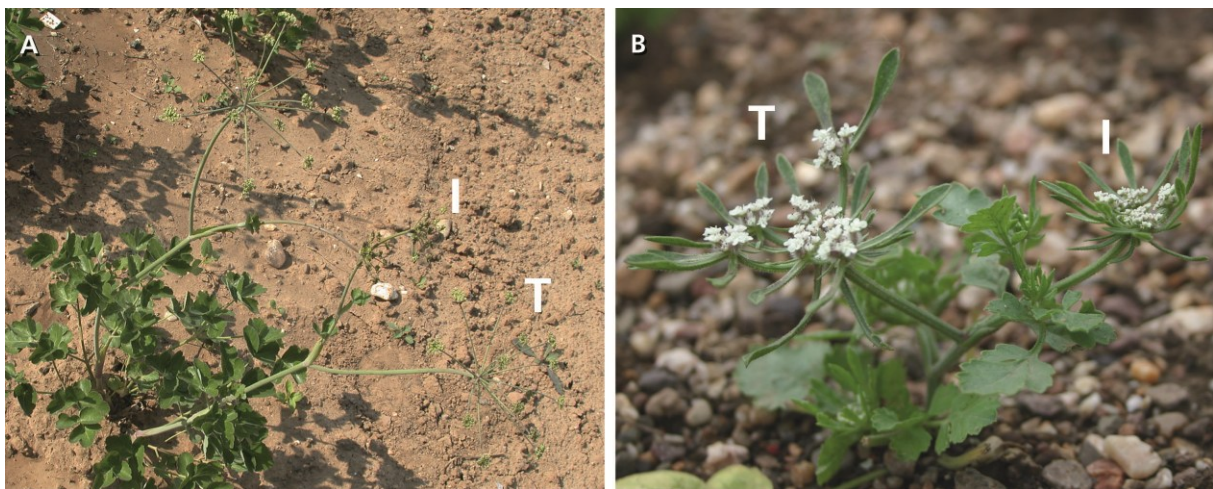


Figure 4.16 Long terminal internodes in Apiioideae, causing widely segregated umbels: A. *Laser trilobum*, flowering plant. B. *Tordylium syriacum*, flowering plant.

4.4.2.2 Umbel production, forms and organisations

As in the model apioid, each axis of apioid flowering shoots is usually terminated by an umbel, appearing as a more or less definite, floral aggregate in all species. Similar to their overall habits, many taxa on the one hand share characteristic, qualitative (form, density) or quantitative (numbers of elements as flowers or bracts) umbel features and on the other hand specifically differ from each other in these.

Terminal umbel (Tab. 4.2 L). In contrast to its presence in the great majority of species (see 'T' in e.g. 4.1 C-E, G-I; 4.4 A; 4.8 A, C-G, 4.11, ...), the terminal umbel was occasionally observed to be facultative or always lacking (Tab. 4.2 L; Fig. 4.5.1 L). The main stem remains facultatively open in a dozen of erect, herbaceous taxa (Figs. 4.13 G, 4.17 A-E, 4.25 D, Tab.

4.6; see also Fig. 2.26), four of them belonging to the genus *Anthriscus*. Except for *Bupleurum ranunculoides*, the only very basal species among them, and *Pimpinella major*, they share distal or repeated whorl formation. In *Pimpinella major* (Fig. 4.17 A-C), the distalmost branches are only whorled when the terminal umbel is not produced, otherwise dispersed. All species, except *Bupleurum ranunculoides* and *Xanthoselinum alsaticum*, are andromonoecious. Except their common, facultative lack of the terminal umbel, the species differ in most of their other characters.

Only in the two herbaceous perennials *Ferula communis* and *Opopanax chironium* (Fig. 4.17 F), the terminal umbel was always found to be lacking being replaced by a whorl of 1st-order branches. Both species are usually branched further to the 2nd or 3rd order (Fig. 4.17 G). And they share the yellow petal color, andromonoecious sexual system and several other features, but differ slightly in their shoot architectures and number of bracts and bracteoles. Besides, they are not closely related. Umbels terminating the branches from 1st order onwards, are always formed in each of the observed species.

More than 50 % of the species produce a terminal umbel but lack terminal flowers within their umbellets (136 species; plus presumably at least another 20, where either one of the traits had not been clearly observable). Terminal flowers are produced – facultatively or more or less constantly - in 65 species with terminal umbels (and assumed in 10-15 species more). The only species with facultative terminal flowers that also produces its terminal umbel facultatively is *Bupleurum ranunculoides*. Nowhere else did we find terminal flowers in the species with lacking or facultative terminal umbels, i.e. they all have open umbellets (Tab. 4.6).

Table 4.6 Diversity of the apioid species facultatively producing terminal umbels, but lacking terminal flowers.

Species	Clade * (no. acc. to App. 2)	Distribution	Life form	Umbel rays	Ordinal ratio	Petal color
<i>Anthriscus kotschyi</i>	Scandicinae (16)	Asia	polycarpic perennial	<10 (2-7)	gradual increase	white
<i>Anthriscus lamprocarpa</i>	Scandicinae (16)	Mediterranean	mostly mono-carpic perennial	<10* (4-15)	gradual increase	white
<i>Anthriscus nemorosa</i>	Scandicinae (16)	Europe	polycarpic perennial	<20*(5-22)	gradual increase	white
<i>Anthriscus sylvestris</i>	Scandicinae (16)	Worldwide	mostly poly-carpic perennial	<20* (1-25)	gradual increase	white
<i>Falcaria vulgaris</i>	Careae (36)	Worldwide	polycarpic perennial	≤20 (2-15)	abrupt change	white
<i>Ferula glauca</i>	Ferulinae? (18)	Europe	polycarpic perennial	≤50 (20-40)	abrupt change	yellow
<i>Myrrhis odorata</i>	Scandicinae (16)	Europe	polycarpic perennial	≤20 (1-13)	abrupt change	white
<i>Pimpinella major</i>	Pimpinelleae (31)	Worldwide	polycarpic perennial	≤20 (2-20)	gradual increase	white
<i>Prangos trifida</i>	<i>Cachrys</i> Clade (37)	Mediterranean	polycarpic perennial	≤20 (4-15)	abrupt change	yellow
<i>Ptychotis saxifraga</i>	?	Europe	monocarpic perennial	≤20 (5-15)	gradual increase?	white
<i>Trochiscanthes nodiflorus</i>	<i>Conioselinum chinense</i> Clade (21)	Europe	polycarpic perennial	≤10 (4-8)	gradual increase	greenish
<i>Xanthoselinum alsaticum</i>	Selineae (29)	Europe	polycarpic perennial	≤20 (10-15)*	constant	greenish

* Number according to Appendix 2

In contrast to the frequent rich-flowered, many-umbelled individuals, about 10% of our species (e.g. *Heracleum pumilum*, *Helosciadium repens*) have only single to few lateral branches and umbels per flowering shoot. Plants with seldomly more than 4-5 umbels either due to little ramification (~30-35 species) and/or only single 1st-order umbels (~10 species), are still able to reach heights of >1m and produce many-rayed and –flowered umbels (e.g. *Laserpitium halleri* or *Pyramidoptera cabulica*). Others, especially annuals, remain very small or minute as *Hohenackeria exscapa* (Figs. 4.1 **A**, 4.32 **B**). About 50% of the seasonally poorly ramified species belong to the protogynous PENA and *Arracacia* clade. The annual shoots of the woody species are mostly reduced to only few umbels, too. Hermaphrodite *Bupleurum fruticosum* e.g., forms unbranched stems with only single, terminal umbels (Fig. 4.1 **D**), but in the entire plant, produces many of such shoots. Also one of the eight dioecious species, *Anisotome aromatica*, joins the group of species producing only a fairly small number of umbels.



Figure 4.17 Facultative umbel formation in flowering shoots of Apioideae. A-C. *Pimpinella major*, individuals with dominant (A), lacking (B) and reduced (C) T note the whorled 1st-order branches in B. D-E. *Prangos trifida*, individuals with (D) and without (E) terminal umbel. F-G. *Opopanax chironium*, flowering shoots. F. main stem with distally whorled 1st-order branches, lacking a terminal umbel. G. 1st-order branch, with overtopping lateral axes, ramified to III. T, I-III: terminal umbel, umbels of 1st-3rd order.

In addition to the differing numbers of umbels in a plant, **umbels** are organized differently and vary in their forms and sizes, which further increases the observed variation in Apioideae.

Umbel rays (Tab. 4.2 *M*) and **flowers per umbellet** (Tab. 4.2 *N*). Numbers of umbellets (Fig. 4.5.1 *M*) and flowers (Fig. 4.5.2 *N*) vary in diverse combinations. We found umbels consisting of few few-flowered umbellets (17 species), of few many-flowered umbellets (1 species: *Oenanthe fistulosa*) or of many many-flowered umbellets (always more than 20 flowers and umbellets, 45 species), but none with many few-flowered umbellets.

Usually, as illustrated in the model apioid (Fig. 4.4 *B, C*), umbels consist of more than a few umbellets, but single umbellets are found in *Helosciadium bermejoi* (Fig. 4.18 *A*), and the annuals *Hohenackeria exscapa* (Figs. 4.1 *A*) and *Lagoecia cuminoides* (Fig. 4.18 *B*). These three species derive from very distant clades (very basal Bupleureae, rather central Oenantheae and very derived Pyramidopterae), but however, all share their Mediterranean distribution area and approximate flowering period, the lack of terminal flowers, the presence of few to many bracts, a hermaphrodite sexual system and inconspicuous petals. Even their numbers of rays falls into the joint category of 6-20. The umbels of *Helosciadium bermejoi* have mostly less than 5-10 flowers (Fig. 4.18 *A*). *Lagoecia cuminoides* and *Hohenackeria exscapa* usually exceed 10(-20) flowers.



Figure 4.18 Simple umbels in Apioideae. A. *Helosciadium bermejoi*, flowering. B. *Lagoecia cuminoides*, flowering. x: lacking terminal flower.

Generally only one, few-flowered umbellet, but sometimes two umbellets, were observed to develop in the minute andromonoecious perennial herb, *Naufraga balearica*, (schematic in Fig. 4.19, cp. Fig. 4.8 E). Other small umbels with very few rays are characteristic for *Aciphylla horrida*, *Anisosciadium orientale*, *Aphanopleura capillifolia*, *Bifora radians*, *Bunium (alpinum subsp.) petraeum*, *Bupleurum baldense*, *Cryptotaenia japonica*, *Kruberia peregrina*, *Orogenia fusiformis* and *Scandix pecten-veneris*. Although their umbels belong to the smallest observed, the number of rays is relatively high (about 10 or more) in *Aciphylla squarrosa*, *Haussknechtia elymaitica*, *Orogenia fusiformis*, *Aletes acaulis* and *Cymopterus ibapensis*.

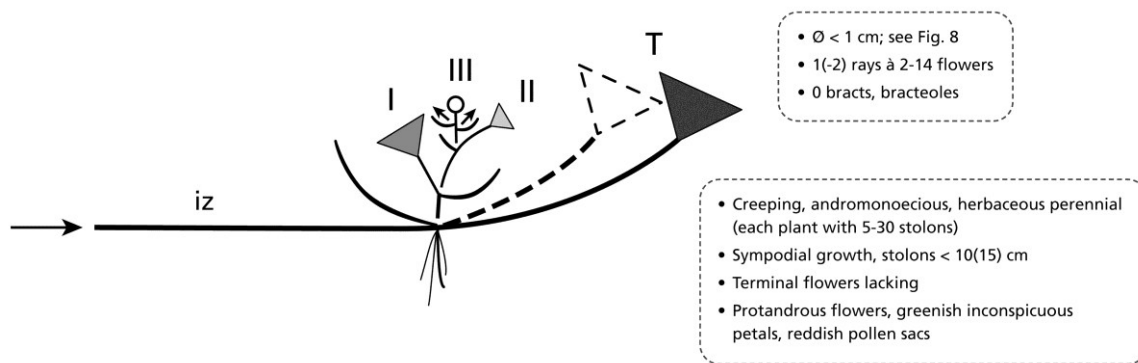


Figure 4.19 Flowering shoot of *Naufraga balearica*, schematic, showing the sympodial branching pattern and formation of umbellets.

Rays and pedicels exceed a number of 100 in the largest umbels of *Heracleum mantegazzianum* and *Visnaga daucoides*, and an upper bound of about 50 rays and pedicels, is often reached in e.g. *Angelica*, *Peucedanum/Oreoselinum* (cp. Fig. 4.27 C), *Laserpitium* or *Daucus* species.

Umbellet size gradient (Tab. 4.2 O). Within the umbels, horizontal changes in umbellet size (Fig. 4.5.2 O) are unremarkable (Fig. 4.20 A) in about every second observed species (e.g. *Anginon difforme*, Fig. 4.7 B, *Bupleurum* species, Figs. 4.1 D, 4.11 E, *Pimpinella anagodendron*, Fig. 4.1 E, or *Tordylium syriacum*, Fig. 4.16 B). But countings of flowers have shown in the past that the number of flowers within the umbellets often decreases centripetally (Fig. 4.20 B). This can be observed as a clear decrease in umbellet size in the other half of the species, e.g. *Conium maculatum* (Fig. 4.13 B), *Laser trilobum* (Fig. 4.16 A) and *Zizia aurea* (Fig 4.8 A).

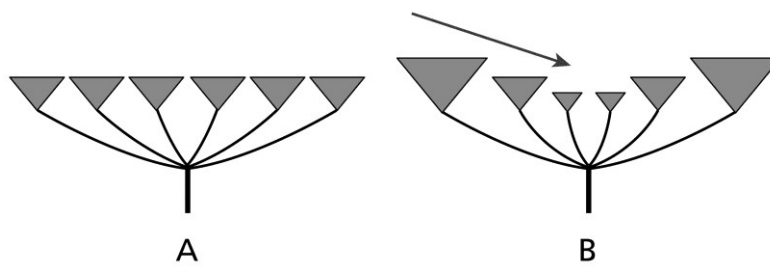


Figure 4.20 Umbellet size gradients;, cp. Tab. 4.2 *O*. A. absent. B. centripetal.

Terminal flowers (Tab. 4.2 *P*). Less than a third of the observed species has terminal flowers (Fig. 4.5.2 *P*) in their umbellets (Fig. 4.21 *A-H*), either overall or facultative. This contrasts with the vast majority of chosen study species, generally lacking a terminal flower within their centre (Fig. 4.21 *I-M*), i.e. producing open umbellets. Terminal flowers occur in diverse clades from very basal to derived and are found in species from all continents except Australia/New Zealand. This goes along with their lack of occurrence in the dioecious species. Other limitations have not been found: We noticed them in hermaphrodite as well as andromonoecious species, white-flowered as well as yellow-flowered taxa, protandrous as well as protogynous, annuals and trees, basal and derived clades and monopodial as well as sympodial systems.

In *Aegopodium podagraria*, *Aethusa cynapium*, *Coriandrum sativum*, *Daucus carota*, *Heracleum sphondylium*, *Heteromorpha arborescens*, and another 3-4 species, a facultative development of terminal flowers between individuals can be observed, i.e. they completely lack in some plants, although they are usually produced in the majority of the umbellets and umbels within one plant. If they are facultatively lacking within a plant, which is the case in about half of the species exhibiting terminal flowers, it is always in the distal, central umbellets and higher-order umbels.



Figure 4.21 Terminal flowers in flowering Apioideae umbels. **A-H:** Terminal flower **formation** in the umbellets (**arrows!**). **I-M:** Terminal flowers **lacking** in the umbellets. A. *Astydamia latifolia*, note the premature terminal flower of a reduced central umbellet (yellow arrow). B. *Todaroa aurea*, note the delayed anthesis of the terminal flowers. C. *Orlaya grandiflora*. D. *Chaerophyllum aureum*. E. *Athamanta cretensis*. F. *Heracleum* spec. G. *Seseli webbii*. H. *Ammi majus*. I. *Angelica archangelica*. J. *Scaligeria tripartita*. K. *Oreoselinum nigrum*. L. *Apium nodiflorum*. M. *Silaum tenuifolium*.

Involucrum (Tab. 4.2 **Q**). While *bracts* are completely lacking in a only a relative majority of species (as in *Bupleurum rotundifolium*, Fig. 4.22 **A**), which produces, however, at least single, mostly several, bracteoles, about half of the taxa splits into producing 1 to 5 or 5-10 bracts (Fig. 4.5.2 **Q**). Members of each group vary alot in their other character states, in their distribution areas, growth forms, architecture and further umbel features. But consistently, all species with more than 5 bracts, produce more than 5 flowers in their umbellets, which do not (except *Helosciadium bermejoi*) lack bracteoles either. Woody species usually produce several bracts (except *Myrrhidendron donnell-smithii* and *Pimpinella anagodendron*) and bracteoles. Up to about 10 bracts are also borne in species of very different systematic position, e.g. basal *Astydamia latifolia*, *Echinophora spinosa*, *Rouya polygama* or very derived *Seseli webbii* (Fig. 4.22 **B-F**). More than 10 bracts are rare, occurring only in a handful of our study species (e.g. *Ammi majus*).

Involucellum (Tab. 4.2 **R**). The involucellum is rarely absent (Fig. 4.5.2 **R**), independent of umbel size, the production of terminal flowers or plant sex. But mostly, *bracteoles* are lacking when also bracts are not produced. This occurs in species of very different systematical status (e.g. *Carum carvi*, *Komarovia anisosperma*, *Smyrniium perfoliatum*, Fig. 23). Consistently however, all of our observed species of the most basal clades below Komarovieae, all woody species, and the African and Australian species, always have at least 2-3 bracteoles. In contrast to the other dioecious species, *Trinia glauca* usually lacks bracteoles completely and only rarely has a single- to few-leaved involucellum. The frequently produced, consistent number of ~5 bracteoles can still vary in form and size (Fig. 4.22 **A-E**). In at least 5 species (*Angelica pachycarpa*, *Libanotis pyrenaica*, *Myrrhidendron glaucescens*, *Oenanthe pimpinelloides*, *Seseli gummiferum*) more than 10 bracteoles are produced. They do not necessarily share the same number of bracts, but all subordinate to the pattern that the number of bracteoles is at least as high as the number of bracts, often higher, rarely lower..

Attraction features (Tab. 4.2 **S**). Showy, rayed bracts and/or bracteoles (*semaphylls*) additionally to other floral or extrafloral features, enhance visual *attraction*, in only about a dozen species. *Oenanthe pimpinelloides* (and *Anisosciadium lanatum*?) form enlarged involucral bracts which merely contribute, however, additionally to the visual impact of the dense umbels with slightly rayed outer flowers. Pseudanthial-like floral units, surrounded by involucellar bracts are borne in several more species of a diverse group of annuals and perennials, monopodial to sympodial, protandrous and protogynous, hermaphrodite and

andromonoecious, basal *Bupleurum* and many derived species, form them by rays. Further, they, except *Echinophora spinosa*, share only the erect herbaceous growth form.



Figure 4.22 Bracts and bracteoles in Apiioideae. A. *Bupleurum rotundifolium*, showy bracteoles (arrow), bracts lacking. B. *Seseli webbii*, up to 10 bracts (white arrow) and bracteoles (yellow arrow). C. *Echinophora spinosa*, spiny, up to 10 bracts (white arrow) and bracteoles (yellow arrow). D. *Rouya polygama*, up to 10 bracts and bracteoles (white arrow). E-F. *Astydamia latifolia*, umbellets with up to 10 bracteoles (E; arrow), umbels with up to 10 bracts (F; arrow).

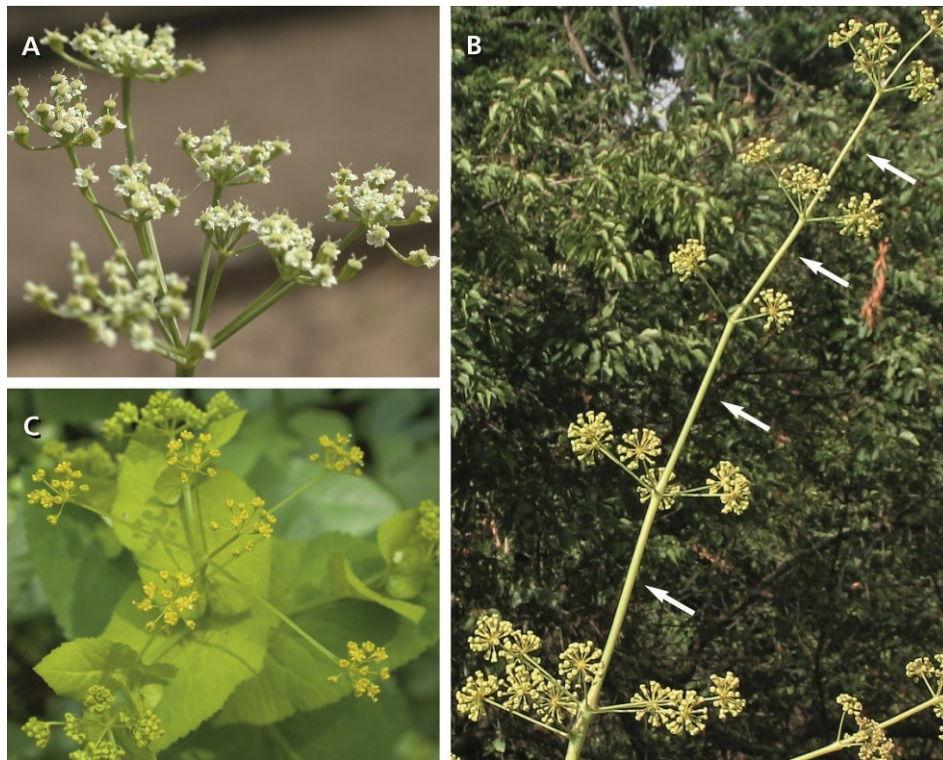


Figure 4.23 Lacking bracts and bracteoles in Apioidae. A. *Carum carvi*, flowering umbel. B. *Komarovia anisosperma*, flowering umbels on a shoot; note the elongated internodes between the whorled umbellets (arrows!). C. *Smyrniium perfoliatum*, flowering umbel.

Plant sex (Tab. 4.2 *T*). Besides the andromonoecious species, our study group of species comprises two more *sexual types*: A much smaller group of hermaphrodites and very few dioecious species (Fig. 4.5.2 *T*). Just as the andromonoecious taxa, our hermaphrodites occur in all continents and many different clades, as herbs and trees, erect and creeping species with small or large umbels, forming or lacking terminal flowers. They still produce perfect flowers, or at least flowers with rudimentary male and female organs, in the last umbels orders which are, however, usually aborting.

The eight dioecious (sometimes reported to be gynodioecious) species are mainly restricted to Australia and New Zealand - only *Trinia glauca* occurs in Europe – and are members of derived clades (Aciphyllae, Selineae). Most of them resemble each other, in forming repeated whorls along their stems, and in many of their umbel characters. In *Trinia glauca*, the male plants usually produce female rudiments, especially rudimentary styles which is also known from the New Zealand taxa.

Sex distribution umbellet (Tab. 4.2 *U*). In different andromonoecious Apioideae, the positions of male and hermaphrodite flowers and their quantitative relations vary. The model apioid pattern (Fig. 4.4 *C*), with centrally located male and lacking terminal flowers (cp. Figs. 4.24 *A*, 4.25 *A-B*), is only one of seven umbellet types we found. Beyond umbellets (and umbels) composed entirely of male or hermaphrodite flowers, there are three general sex distribution patterns within the umbellets (Figs. 4.5.2 *U*, 4.24) which are 1) centrally located male flowers, 2) centrally located hermaphrodite flowers and 3) single, central (= terminal) hermaphrodite flowers surrounded by male flowers.

The first two (Fig. 4.24 *A, B*) split further into a *open* or *closed* type, i.e. in umbellets with (see Fig. 2.25 *b*₁) or without terminal flowers. Wherever a terminal flower is produced, it is usually hermaphroditic. Exceptions, i.e. male terminal flowers, occur only sporadically, in *Daucus carota* and *Monizia edulis* (Fig. 4.25 *C*). In *Daucus*, they are more likely to be found in the higher-order umbels, in *Monizia* they have been observed in the terminal or first-order umbels.

The latter two patterns (Fig. 4.24 *B, C*) occur in only three genera from three different clades. In the observed *Oenanthe* species, which both usually have terminal flowers, male flowers fill the outer positions of the umbellet (and umbel, see Fig. 2.31 *c, d*, and below). In *Echinophora* (see also Fig. 2.32 *c, d*) and *Exoacantha* only the terminal flower of the umbellets, surrounded by male flowers, is hermaphrodite, but tendentially aborted, i.e. becomes male (cp. *Monizia edulis*, Fig. 25 *C*), or sterile, towards the center of the umbels.

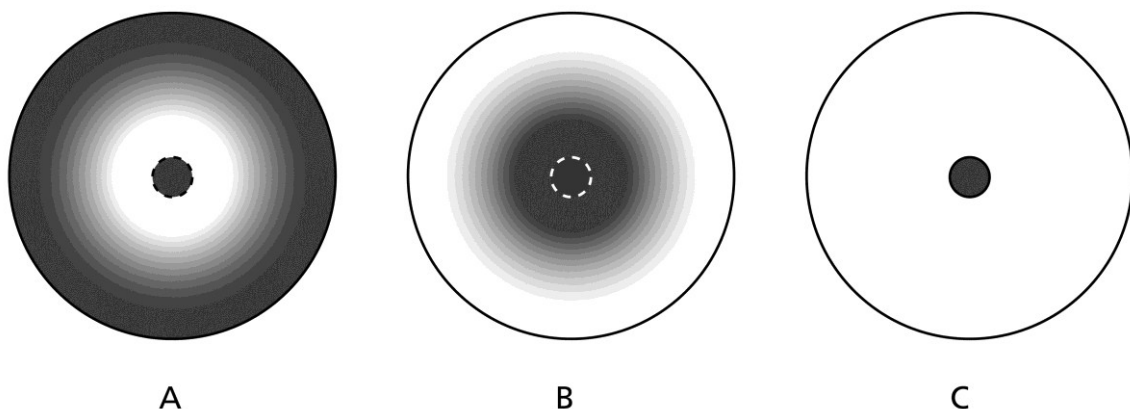


Figure 4.24 Sex distribution patterns in apioid umbellets (illustrating 5 of the 7 types, see text); A. Central male flowers, with or without, usually hermaphrodite, terminal flower. B. *Oenanthe* pattern, Peripheral male flowers, with or without, usually hermaphrodite, terminal flower. C. *Echinophora* pattern, single, terminal hermaphrodite flower surrounded by male flowers. Grey shades indicate gradients from fully hermaphrodite flowers (dark grey) via rudimentary types (light grey) towards male flowers (white).

Sex distribution umbel (Tab. 4.2 *V*). Concomitant to the numerical gradients of rays (umbellets) and pedicels (flowers), the **sex ratio** in the andromonoecious species often changes with umbel order and umbellet position. At the level of the umbel, only five species differ from the general pattern of increasing proportions of male flowers, proceeding centripetally, from the outer towards the inner umbellets (cp. Fig. 4.5.2 *V*). In the *Oenanthe* umbels, the proportion of male flowers gradually decreases towards the center of the umbels (see Fig. 2.16). Sex ratio remains rather constant in *Echinophora spinosa* in all umbels of a plant (unfortunately undeterminable in the *Exoacantha* material), increasing only when the centrally located hermaphrodite flowers aborted. In *Heptaptera triquetra* (Fig. 4.25 **F, G**) and *Scandix pecten-veneris* (Fig. 4.25 **E**), the proportions of male flowers in the umbellets changes only little within the umbels, but changes clearly with the umbels' position and order.

Ordinal sex ratio (Tab. 4.2 *W*). In sum, four sex distribution patterns can be described between umbels of successive order (Fig. 4.5.2 *W*) in the andromonoecious taxa. These are attended by three types of *sex gradients* (Fig. 4.26).

- As shown in the model apioid, most frequently the sex ratio gradually increases, i.e. the terminal umbel mainly produces hermaphrodite flowers with only few male flowers, or none at all, while umbels of higher order produce increasingly higher proportions of (in part functionally) male flowers (Fig. 4.26 **A**). Some of the hermaphrodite species, e.g. *Anginon difforme*, *Levisticum officinale* or *Silaum tenuifolium*, show this pattern, too, by increases in their proportions of non-fruiting, functionally male flowers which, however, still bear female organs.
- The opposite phenomenon, that produced terminal umbels are mainly composed of male flowers or bear only low proportions of fruits and show gradually decreasing proportions of male flowers with increasing umbel order (Fig. 4.26 **B**), is always attended by protogyny.
- Instead of gradually increasing, the sex ratio can change abruptly from one umbel order to the succeeding one (Fig. 4.25 **D-F**, see also Fig. 2.29) or from distal to basal branches (Fig. 4.26 **C**, observed only in *Heptaptera triquetra*, Fig. 4.25 **G**). The rather large proportion of species showing this type of ordinal sex ratio, also comprises hermaphrodites, which, abruptly develop only few **fruit**, or not any at all, in their last-produced umbel order. This

is especially true for the entirely, functionally male umbel orders of e.g. many *Angelicas* and other Selineae.

- Seldomly, as in: *Echinophora spinosa*, the sex ratio found in the terminal umbel remains constant throughout all later-produced umbels.



Figure 4.25 Sex distribution patterns within andromonoecious apioid umbels and flowering shoots. A. *Xanthogalum purpurascens*. B. *Laser trilobum*. C. *Monizia edulis*, male terminal flower (within a terminal umbel). D. *Ferula glauca*. E. *Scandix pecten-veneris*. F-G. *Heptaptera triquetra*, abrupt sex change from I to II (F), and male basal (proximal) umbels (G). T, I-II: terminal umbel, umbels of 1st – 2nd order.

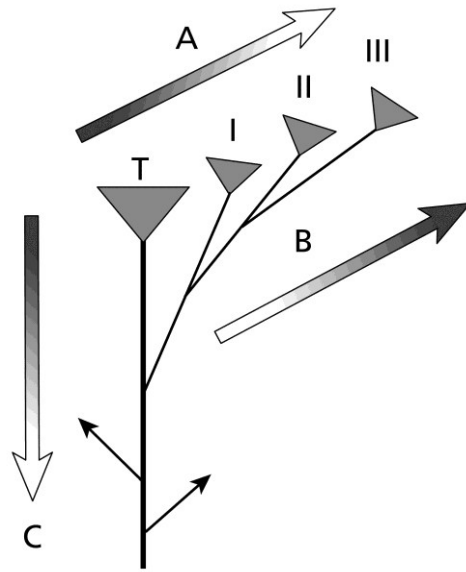


Figure 4.26 Ordinal sex gradients. A. Increasing numbers of male flowers (sex ratio) with umbel order. B. Increasing numbers of hermaphrodite flowers (decreasing sex ratio) with umbel order. C. Increasing sex ratio with umbel position along the stem (here: basitonous gradient). Grey shades indicate gradients from \pm fully hermaphrodite umbels (dark grey) via decreasing proportions of hermaphrodite flowers and increasing numbers of male flowers (light grey) towards \pm male umbels (white).

Dominant fruit set (Tab. 4.2 X). The umbel order accounting for most fruit in a flowering shoot is hard to determine and remains unsure whenever one order has less umbels but higher proportions of fruit and another more umbels but higher proportions of male flowers. Besides, in many species, major fruit set fluctuates between terminal and 3rd-order umbels depending on plant size. Mostly, the predominant fruit set originates from the 1st- or 2nd umbel order.

Umbel diameter, dominant umbel order (Tab. 4.2 Y-Z). The umbel order, bearing most fruit (see above), is not necessarily the order with the largest umbels. Umbel sizes in relation to plant size, as well as between species, vary considerably, more often exceeding the model-like **diameter** of $\sim 5\text{cm}$ than falling below this size (Fig. 4.5.2 Y). The smallest umbels, from a diameter of less than two centimetres, were found in the species forming simple umbels (Fig. 4.18), in short monocarps as *Bupleurum baldense* (Fig. 4.11 E), *Aphanopleura capillifolia* and *Torilis nodosa* (Fig. 4.8 F), or even perennial herbs as *Apium fernandezianum* (Fig. 4.8 B), *Caropsis verticillato-inundata*, *Oreoxis humilis* and other species of the PENA clade.

The largest umbels observed, even exceeding the measure of 20-25 centimeters, were found in the andromonoecious *Heracleum mantegazzianum* with its closed umbellets (which is known to reach diameters of more than 50cm; cp. *H. pubescens*, Fig. 4.27 A). Many other *Heracleum* species reach the widest diameters of umbels, as well as *Angelicas* (cp. Fig. 4.13 C) which, however, show extreme umbel size decreases with increasing umbel order.

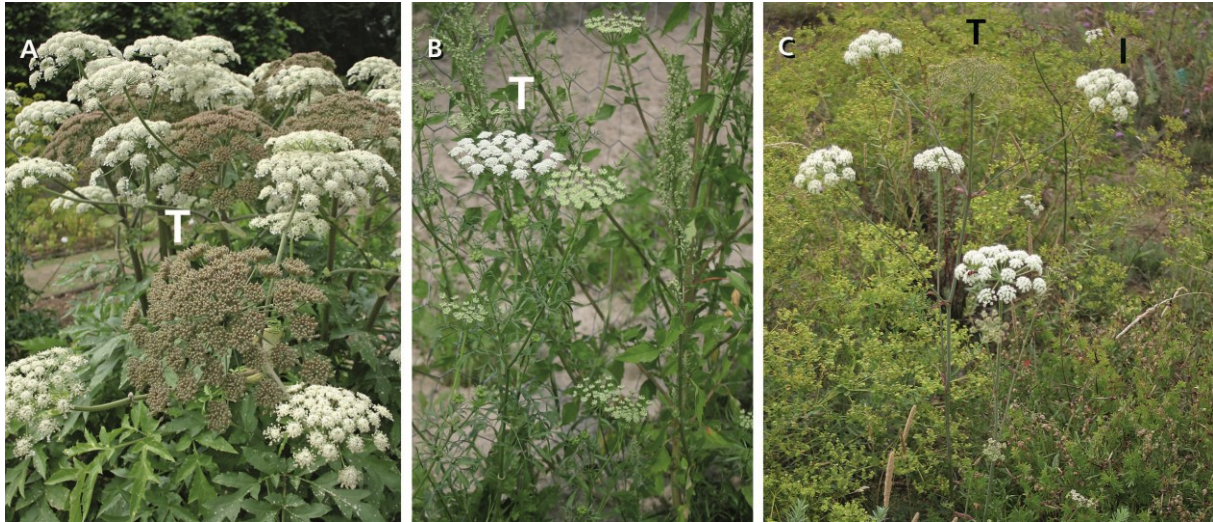


Figure 4.27 Dominant umbels in flowering Apioidae. A. *Heracleum pubescens*, dominant T. B. *Ammi majus*, dominant T. C. *Oreoselinum nigrum*, dominating 1st-order umbels. T, terminal umbel; I, 1st-order umbels.

Most frequently, independent of the size of the flowering shoots, the first-produced, terminal umbel is the **dominant umbel** of the shoot (Fig. 4.5.2 Z). Quite a few of the species with dominant terminal umbels, e.g. andromonoecious *Heracleum pubescens* (Fig. 4.27 A), however, set most fruits in the 1st-order umbels. Hermaphrodite *Ammi majus* (Fig. 4.27 B), produces fruits rather equally in all orders of umbels. On the other hand, species with dominant 1st-order umbels as *Oreoselinum nigrum* (Fig. 4.27 C), which, however, bear a high proportion of male flowers in this order, still have their highest fruit set in the terminal umbel because 1st-order umbels are almost completely composed of (functionally) male flowers. Most of the few species that do not produce their largest umbels before the 2nd branch order belong to clade Scandicinae, e.g. *Anthriscus sylvestris* (cp. Figs. 2.2, 2.28 a), whose terminal umbel is largely reduced to single umbellets and few flowers, or rarely even completely absent. None of the observed African species, but several dioecious taxa bear umbels of similar size throughout (cp. Fig. 4.28 D), as well as some of the rare creeping, ascending and procumbent

species. A clearly assessable dominating umbel order is also lacking in e.g. *Scandix pecten-veneris*, but here because of interindividual variation, i.e. different individuals produce their largest umbels in different orders.

Umbel size gradients (Tab. 4.2 AA). Usually, the dominance of of a certain umbel order goes along with gradients in umbel size. Whenever the first two umbel orders are of rather similar size, however, and the 1st-order umbels have been determined the dominant ones, the gradients afterwards is still a decreasing, without having been largely increasing in the beginning. Therefore, the most frequent, ordinal decrease in umbel size (mostly combined with a decrease in flower numbers; cp. Fig. 4.28 A), is observed in more species than species exhibiting dominant terminal umbels (Fig. 4.5.2 AA). The second-large group, of species with constant umbel size, comprises none of the African, i.e. also none of the woody, species and none of the species with >20 umbel rays. A clear gradient lacks e.g. in two species exhibiting facultative terminal umbels, *Prangos trifida* and *Xanthoselinum alsaticum*. None of basal species shows initially increasing umbel sizes. In several Scandicinae (*Myrrhis odorata*, *Chaerophyllum* and *Anthriscus* species,) the initial increase in umbel sizes is a common character and goes along with increasing numbers of male flowers.

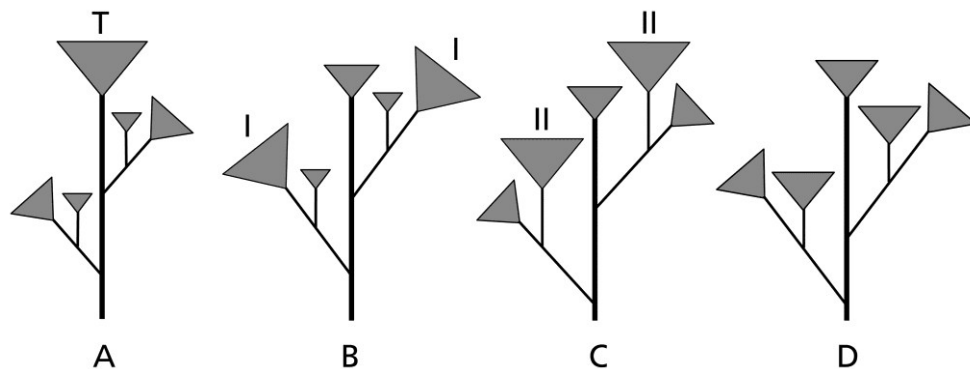


Figure 4.28 Dominant umbel orders. A. Dominant T (cp. model apioid, Fig. 4.4 A; *Daucus carota*, diverse *Heracleum* and *Angelica* species). B. Dominant I (cp. *Oreoselinum nigrum*, *Anginon difforme*, *Athamanta cretensis*, *Opopanax chironium*). C. Dominant II (cp. *Anthriscus sylvestris*, diverse *Chaerophyllum* species). D. Dominance lacking (cp. *Trinia glauca*, *Apium fernandezianum*, *Torilis nodosa*). T, I-II: terminal umbel, umbels of 1st – 2nd order.

Umbel shape (Tab. 4.2 *AB*). In contrast to the model apioid umbel shape which is flat to v-shaped (Fig. 4.29 *A-C*) only half as many species have roundish umbels (Figs. 4.5.3 *AB*, 4.29 *D-E*). Very few species have irregularly shaped umbels either because of unequal lengths of their rays (cp. Fig. 4.31 *B*) or because their umbel shape changes largely during development. None of the hemispheric to globose umbels has diffusely arranged flowers or umbellets. But all of the dioecious species have this umbel shape in common.

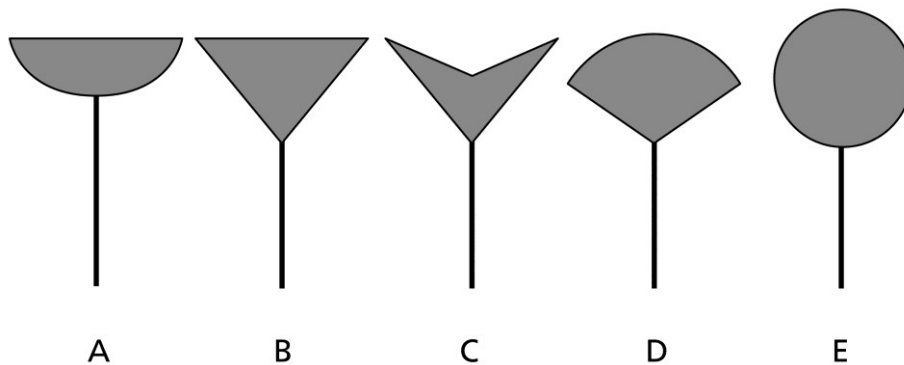


Figure 4.29 Umbel shapes. A-C. Flat to v-shaped. D-E. Hemispheric to globose.

Density umbellet (Tab. 4.2 *AC*) and **density umbel** (Tab. 4.2 *AD*). Regarding umbel surface, i.e. the compactness or density of the structures, umbels and flowers are widely segregated (cp. Fig. 4.30 *A*) only rarely. Distances are created by very unequally long umbel rays, as in *Laser trilobum* (Fig. 4.31 *A*), or by elongated internodes between whorls of umbellets, as in *Komarovia anisosperma* (Figs. 4.23 *B*, 4.31 *C*). These and the other species with distances between their umbellets clearly larger than the umbellets' diameters belong to very different clades (among them also very basal *Bupleurum ranunculoides* and rather derived *Chamaescidium acaule*). All of them are perennials, with yellow to greenish petals, and disproportionally often, they have only single 1st-order branches and umbels. None of them occurs on the African or Australian continent. But they differ a lot in shoot and umbel sizes and most of the remaining characters, e.g. having their umbels composed of either loose, compact or condensed umbellets. Only a single species, *Cryptotaenia japonica* (Fig. 4.31 *B*) has umbellets that can be characterized as diffuse, because its pedicels are highly unequal in length.

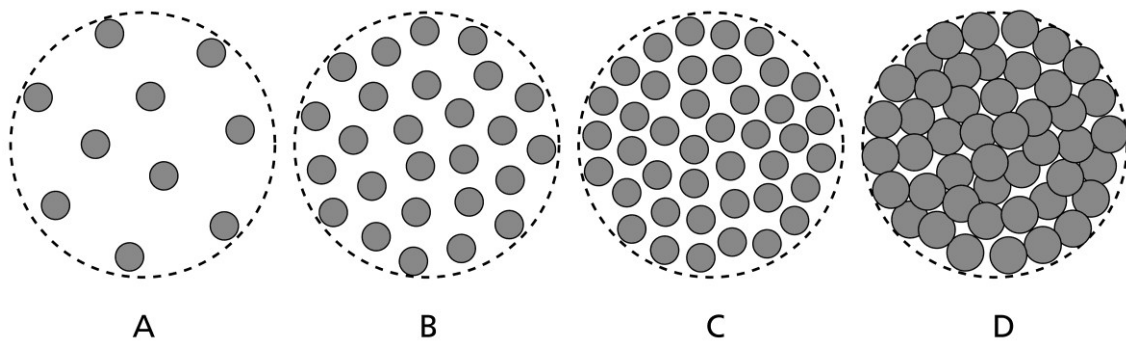


Figure 4.30 Densities in the umbels and umbellets. A. Diffuse arrangement (of flowers or umbellets); flower (umbellet) diameter \ll distances between flowers (umbellets). B. Loose arrangement (of flowers or umbellets); flower (umbellet) diameter \sim distances between flowers (umbellets). C. Compact arrangement (of flowers or umbellets); flower (umbellet) diameter $>$ distances between flowers (umbellets). C. D. Condensed arrangement (of flowers or umbellets); no gaps at all between flowers (umbellets).

While in the observed Apioideae, the compact arrangement (cp. Fig. 4.30 C) is apioid model-like for both, umbel and umbellet density (as in *Carum carvi*, Fig. 4.31 D), both of these floral or umbellet aggregation can also be more loose or even more compact. However, concerning the **density of the umbel** (Fig. 4.5.3 AC) the loose arrangements (of umbellets; cp. Fig. 4.30 B, shown in *Cryptotaenia canadensis* or *Anthriscus caucalis*, Fig. 4.31 E, F) occurs more frequently than the condensed arrangement (cp. Fig. 4.30 D). The small, though diverse, group of species exhibiting umbellets very condensedly in their umbels also comprises *Hohenackeria exscapa* (Fig. 4.32 B₂) and *Lagoecia cuminoides* (Fig. 4.18 B) which are in fact producing single umbellets with densely arranged flowers. Whereas four other species in this group (*Hausknechtia elymaitica* and three species of the PENA clade) have furthermore very dense umbellets, the umbellets in the remaining seven species, e.g. *Daucus carota* (cp. Fig. 4.33 B; see also Fig. 2.14) and *Myrrhis odorata* (see Fig. 2.20) are more compact.

In *Aciphylla squarrosa*, we relativized our first impression of very dense umbels. A detailed analysis showed that at least one of their umbellets is sessile, and therefore rather distant from the other umbellets, because we found single flowers in the centres.

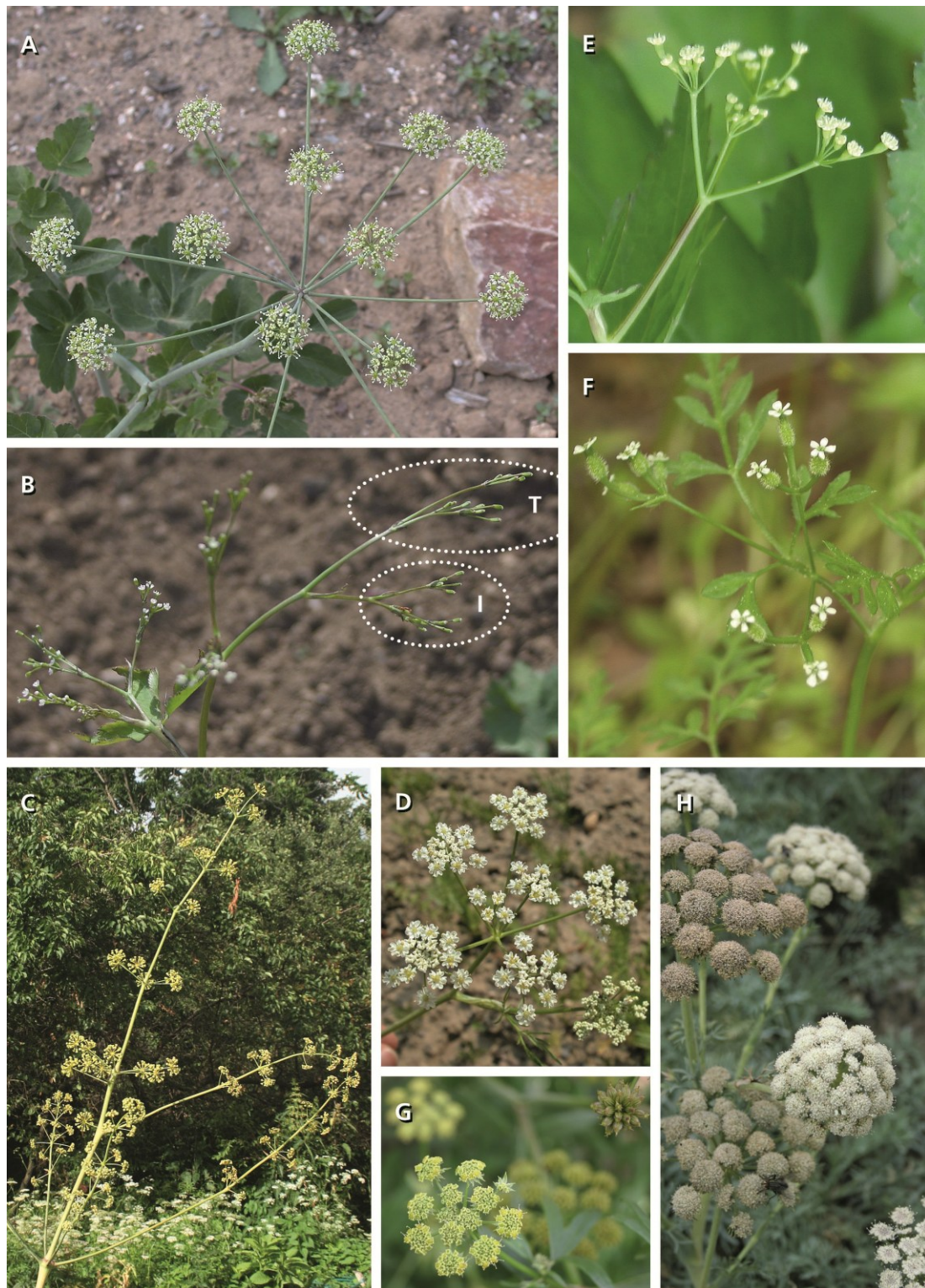


Figure 4.31 Densities in flowering Apioideae umbels. A. *Laser trilobum*, diffuse umbel with compact umbellets. B. *Cryptotaenia japonica*, loose umbel with diffuse umbellets. C. *Komarovia anisosperma*, diffuse umbels with rather loose umbellets, note the whorls of umbellets separated by elongated internodes. D. *Carum carvi*, more or less compact umbels with compact umbellets. E. *Cryptotaenia canadensis*, loose umbel and umbellets. F. *Anthriscus caucalis*, 3-rayed, loose umbel with usually more compact umbellets. G. *Levisticum officinale*, compact umbel with condensed umbellets. H. *Seseli gummiferum*, more or less compact umbels with condensed umbellets.

Regarding the **density of the umbellets** (Fig. 4.5.3 **AD**) alone, flowers are more often condensed (as shown in *Levisticum officinale* or *Seseli gummiferum*, Fig. 4.31 **G, H**) than loosely arranged (cp. Fig. 4.31 **E**). Among the species with condensed umbels, only *Daucus carota* has very facultative terminal flowers. In about half of the species with condensed umbellets, however, a terminal flower is produced. The species bearing umbellets with loosely arranged flowers (see above; amongst others also comprising *Aegopodium podagraria*, *Falcaria vulgaris*, *Ferula glauca*, *Opopanax chironium*, *Rouya polygama*, *Smyrniium perfoliatum*, *Trochiscanthes nodiflorus*) form a diverse group, e.g. also producing or lacking terminal flowers.

Umbel clusters (Tab. 4.2 **AE**). *Myrrhis odorata* (cp. Fig. 2.7) and *Hausknechtia elymaitica* (see plant images, e.g. Roepert 2000-), both exhibiting the rare umbel type with densely arranged umbellets, further have their umbels densely arranged into *clusters* (Fig. 4.5.3 **AE**) of two different umbel orders (for *Hausknechtia* illustrated in Fig. 32 **A**). Although most species present their umbels more or less individually, scattered over the flowering shoots (cp. Fig. 4.4 **A**), erect species on all continents, e.g. *Scandix pecten-veneris* (see Fig. 4.34 **H**), *Conium maculatum* (cp. Fig. 4.13 **B**), *Prangos trifida* (cp. Fig. 4.17 **E**) or basal *Steganotaenia araliacea*, *Molopospermum peloponnesiacum* and *Astydamia latifolia* (cp. Fig. 4.22 **F**), show the tendency to approach their umbels and present them in groups (Fig. 4.32 **B**). Either are umbels of the same order, mostly originating from branch whorls which are usually equally long, aggregated into '**tertiary umbels**' or umbels of different-order form superior floral units - at one or different levels in space. Besides (highly) andromonoecious *Myrrhis* and *Hausknechtia*, very dense and clear umbel clusters are found in the dioecious *Scandia rosifolia*. In the 'inhibited' dwarf *Hohenackeria exscapa* even the entire minute plant (Fig. 4.32 **B₂**) is built from several, highly condensed umbels (schematic in Fig. 4.32 **B₁**). Vague umbel clusters are even observed in species without whorled branches, whereas in many species forming branch whorls umbel clusters are lacking at all. They never occur in protogynous species or strictly sympodially branched shoots.

Another form of umbel clustering is shown by *Falcaria vulgaris* individuals (Fig. 4.1 **B**) without dense aggregations of flowers. The single flowering shoots are spreading and mesotonously promoted, bearing successively flowering, more or less compact umbels with loosely arranged flowers in up to three orders. All umbels, however, are presented at a same

level (similarly observed in *Saposhnikovia divaricata*), creating a more or less platform-like *floral canopy*, usually within large populations of adjacent individuals. The entire shoot thereby forms a homogenous unit although single flowers are relatively distant from each other. The same homogenous appearance is also often created by species with synchronized flowers in all umbels and umbel orders of each, possibly widely-branched flowering shoot (see below).

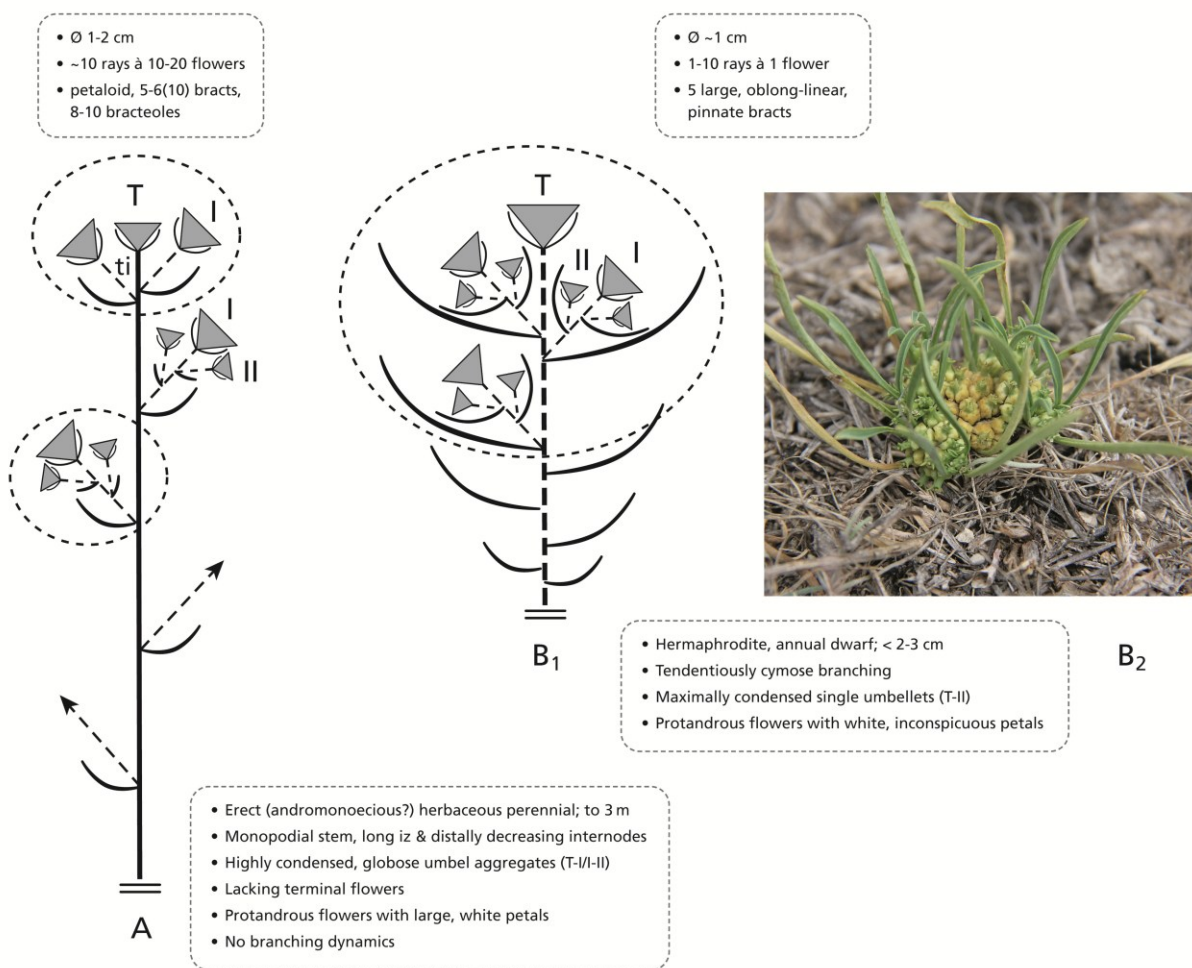


Figure 4.32 Apioideae species with highly condensed umbel units of different-order umbels. A. *Haussknechtia elymaitica*, schematic; in reality, encircled umbels form small, highly-condensed, globose floral units; the terminal internode (ti) therefore remains minute. B₁₋₂. *Hohenackeria exscapa*, schematic (B₁) and at a natural site (B₂). T, I-II: terminal umbel, umbels of 1st - 2nd order.



Figure 4.33 Umbel and umbellet rays in Apioidae umbels: A. *Scandix pecten-veneris*, radiant umbellets (and umbellets). B. *Daucus carota*, radiant umbel. C. *Heracleum* spec., radiant umbellet. D. *Coriandrum sativum*, radiant umbellets. E. *Orlaya grandiflora*, radiant umbellets and umbel.

Petal color (Tab. 4.2 *AF*) and **conspicuity** (Tab. 4.2 *AG*). Attractivity of the flowering Apioidae shoots varies a lot between species and seems to be influenced only in part by petal color (Fig. 4.5.3 *AF*). Only eight, more derived mono- and polycarpic herbaceous species have flowers with greenish petals which are more or less inconspicuous. Seven of them occur mainly in Europe and the Mediterranean, the eighth, *Angelica archangelica*, is widely cultivated and distributed. But we also found inconspicuous flowers with small, white or

yellow petals. In the species with inconspicuous flowers, other attraction features as colored stamina or stylopodes occur relatively more frequently than in the more conspicuous ones but not even in a half of them. Amongst the yellow-flowered taxa, the proportion of protogynous species is slightly higher (~ 30%) than amongst all selected Apioideae (< 20%). Only white-flowered, erect plants were found to enhance their *conspicuity* (cp. Fig. 4.5.3 **AG**) and bear eye-catching pseudanthial flower aggregates by petal rays (Fig. 4.33). These affect either mostly the entire umbel (as in *Daucus carota*, Fig. 4.33 **B**), mainly umbellets (as in many *Heracleum* species, Fig. 4.33 **C** or *Coriandrum sativum*, Fig. 4.33 **D**) or both, to different degrees (as in *Scandix pecten-veneris*, Fig. 4.33 **A** or *Orlaya grandiflora*, Fig. 4.33 **E**).

4.4.2.3 Flowering and development

The observed Apioideae are in bloom throughout the whole year, dependent on their geographic distribution. Their common peak flowering season stretches over several months from May to August when more than half of the species flower. Almost 100 species are also in bloom during April and September. But from October until March only 15-40 species, mainly African species are.

Individual growth dynamics (Tab. 4.2 **AH**). The model apioid illustrates that flowering in apioids usually comes along with internode elongations and branch development. This is especially true of the modularly organized shoot systems, with umbels of several branch orders flowering successively. Quite often, the later-developing lateral shoots overtop their mother shoots, thereby presenting the umbels at the outer periphery of the whole plant. However, not all species develop in the same manner (Fig. 4.5.3 **AH**). A single flowering cycle in andromonoecious and hermaphrodite species (see below), or dioecy, always concurs with low dynamical changes in the shoots, indicating a connection of these characters. Plants exhibiting lacking or low dynamics during bloom, have more frequently an elongated inhibition zone ($\geq 50\%$) than all species of our sampling ($\leq 1/3$). They are often few-branched which in part explains the lacking dynamics of the shoot system. Those with many 1st-order axes never branched higher than to the 3rd order. Beyond these qualities, they share no further characters, but are either protandrous or protogynous, world-widely distributed and not closely related to each other.

Plants with highly dynamic changes in their flowering shoots, i.e. internode elongations and branch overtoppings, belong especially to the species usually not growing higher than 50cm. *Thaspium barbinode* is the only among them reaching heights of > 1m. None of them is a member of the basal clades, is distributed in Africa (cp. Tab. 4.7) or Australia/NewZealand or shows clearly monopodial growth.

Dichogamy (Tab. 4.2 *AI*). Flowering of bisexual flowers in the study plants appears to be always strictly dichogamous, because male and female flowering phases can be clearly defined separately, by pollen presentation and stigmatic exsudates. Protandry is prevalent in the maturation of flowers, whereas protogyny occurs in at least 35 species (Fig. 4.5.3 *AI*). These are all Northern American, andromonoecious perennials. Quite a few species have yellow or reddish colored stylopodia or stamens and pollen sacs, by which nice color contrasts are evoked during anthesis. The overall visual impact of the umbels is, however, merely enhanced. It is much higher in species that show colorations in their foliage, accentuating the male and female flowering phase, as *Smyrnum perfoliatum* or *Myrrhis odorata*. In *Smyrnum*, the uppermost leaves turn bright yellow during the very early male phase of the terminal umbel and only back to green after all umbel orders have started fruit maturation. In *Myrrhis odorata*, many of the pinnate leaves look white-speckled at their bases before the very beginning of anthesis, which, though, disappears mostly during the first male flowering phase.

Flowering sequence umbellets (Tab. 4.2 *AJ*). Flowers in the umbellets usually flower in a, clearly or weakly, centripetal sequence (Fig. 4.34 *A-F*). However, in the few-flowered umbellets of the American, hermaphrodite annual *Apiastrum angustifolium*, centripetal flowering appears to be very slow. This rather results in a slightly successive flowering sequence of the flowers, before they simultaneously pass male and female phases. In contrast, another American annual, *Spermolepis divaricatus*, two species of the woody, African genus *Andriana* and the Asian perennial *Komarovia anisosperma*, show highly synchronous flowering in their umbellets. Terminal flowers, if present, tend to start flowering synchronously to the outer flowers (or slightly later) and earlier than other innermost flowers. In the Canarian endemic *Astydamia latifolia* (Fig. 4.21 *A*) and European *Athamanta turbith* which possess closed umbellets, the flowering sequence is changed in the way that the terminal flowers are always the first to start anthesis, followed by the outer flowers of the

outer umbellets. Terminal flowers of all other species (e.g. *Coriandrum sativum*, Fig. 4.34 F) always open before their surrounding, centrally located flowers. But compared to the outermost flowers, they flower delayed, without considerably changing the centripetal flowering sequence.

Flowering sequence umbels (Tab. 4.2 AK). Concerning the flowering sequences within the umbels (Tab. 4.2 AK), others than the centripetal sequence, starting in the outermost flowers of the outermost umbellets (cp. Fig. 4.34 A-B), are rare, as within the umbellets (Fig. 4.5.3 AK). Umbels with very few-umbellets (as in *Scandix* species, *Bifora radians*, *Chaerophyllum nodosum*, *Turgenia latifolia*, *Cyclospermum leptophyllum*, *Anthriscus caucalis*, *Apiastrum angustifolium*), similar to few-flowered umbellets, create the impression of umbellets opening rather successively, one after the other, or, by contrast, synchronously (cp. *Oenanthe fistulosa*, Fig. 4.34 C). In the protandrous species, five (*Cryptotaenia canadensis*, *Cryptotaenia japonica*, *Tordylium syriacum*, *Torilis nodosa*, *Turgenia latifolia*) differ from all others in showing a weaker dichogamy. At the level of the umbel, their male and female flowering phases are generally not clearly separated any more and may overlap (as shown also in *Pimpinella anagodendron*, Fig. 4.34 I: T). Only once, in one individual of *Anginon difforme*, flowering started in a centrally located umbellet (Fig. 4.34 D), but afterwards followed the general centripetal pattern. This unusual sequence indicates the presence of a terminal umbellet, but is not confirmed, yet, by further observations. Mainly, the sexual phases in the umbellets of a given umbel are synchronized, so that each umbel, if protandrous and bearing hermaphrodite flowers, passes a male phase first and a female phase later on.

Serial flowering sequence (Tab. 4.2 AL). Next-order umbels usually start flowering when the previous order starts fruiting (cp. Fig. 4.34 G). As all umbels of 1st order are in about the same stage of development in almost all observed species, they most probably start their anthesis rather simultaneously (Fig. 4.35 A), even if we have not observed this exact moment in more than 50% of the study species (cp. Fig. 4.5.3 AL). Repeatedly, but never in protogynous or sympodially branched species, flowering in the 1st-order starts in umbels of a median position and follows a more or less divergent sequence, with flowers in the most basal and most distal umbels opening delayed (Fig. 4.35 B). Only in four erect herbs with monopodial architecture, i.e. dioecious *Trinia glauca* (see chapter 2.4.8), the two andromonoecious *Laserpitium* species and hermaphrodite *Kundmannia sicula*, the first flowers were clearly observed to open in the basalmost 1st-order branches (Fig. 4.35 C).



Figure 4.34 Flowering sequences in Apioideae. A. *Todaroa aurea*, centripetally, protandrously flowering umbel, lacking terminal flowers in the umbellets. B. *Athamanta cretensis*, abnormal umbel with centripetal, protandrous flowering; note the single umbellet (arrow) which corresponds to the other outer umbellets but is separated by irregular internode elongation. C. *Oenanthe fistulosa*, umbel showing weak centripetal flowering sequence; note the central flower buds (weakly pink) that umbellets tend to flower rather synchronously. D. *Anginon difforme*, umbel starting to flower in the most central flowers (terminal umbellet? Arrow). E. *Todaroa aurea*, centripetally flowering umbellets with premature terminal flowers; note the flower buds surrounding them. F. *Coriandrum sativum*, protandrously flowering umbellet with premature terminal flowers (arrow). G-J. Flowering shoots showing the ordinal flowering sequence. G. *Todaroa aurea*, well separated flowering phases; note T in the late female stage, with petals already lost, and I still in bud stage. H. *Scandix pecten-veneris*, flowering shoot apex showing T (2 umbellets, arrows) in female (receptive or fruiting) phase, distal I (3 umbellets, arrows pointing to 2 of them) in male-phase and basal I in bud (basitpetal flowering in I). I. *Pimpinella anagodendron*, showing the tendency to phase overlaps; note T similarly presenting stamens, styles and petals, and I mainly in bud stage, but the umbel on the very right already presenting its first stamen; note also that this umbel is produced by the most basal 1st-order branch and flowering therefore follows an acropetal sequence. J. *Heteromorpha arborescens*, umbels showing the ordinal flowering sequence; note that fruiting in T is already advanced while I is still in bud stage. T, I-II: terminal umbel, umbels of 1st–2nd order.

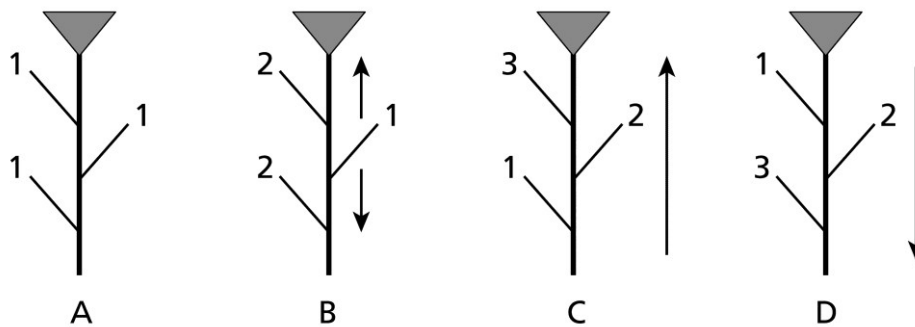


Figure 4.35 Flowering sequences in the 1st-order umbels. A. Synchronous. B. Divergent, starting in median position. C. Acropetal, starting in basal position. D. Basipetal, starting in distal position. Numbers indicate the sequence of flowering; 1: First, 2: Second, 3: Third (opening umbel).

A diverse group of species, among them *Scandix pecten-veneris* (cp. Fig. 4.34 H), *Apium fernandezianum* with its creeping shoots, basal *Astydamia latifolia* or scarcely-branched *Crithmum maritimum*, starts flowering in their distalmost 1st-order umbels (Fig. 4.35 D). In *Scandix*, their close proximity to the terminal umbel facilitates geitonogamy, if male and female phases overlap. Irregular flowering patterns, as in *Berula erecta*, are likely to be found when regarding the plants just as they start flowering, within one day, though, all flowers of the same branch order appear mostly synchronized.

If next-order umbels follow successively, multicycle dichogamy results, with several alternating male and female flowering phases (cp. *Todaroa aurea*, Fig. 4.34 G). Exceptions from this frequent pattern especially occur in the weakly protandrous species (see above). Male-female phase overlaps that rarely occur within the umbels because phases are not strictly separated, become more frequent between successively flowering umbels of increasing order, while flowering proceeds (cp. *Pimpinella anagodendron*, Fig. 4.34 I). The very reverse, the elongated separation of flowering phases, occurs in woody *Heteromorpha trifoliata* shoots (Fig. 4.34 J). Here, 1st-order umbels are only initiated when the terminal umbel already flower. Their protandrous flowers do not open, until long after fruits have started ripening in the terminal umbel.

Plant flowering sequence (*flowering cycles*; Tab. 4.2 *AM*). Over the entire flowering shoots, the number of flowering cycles of synchronized umbel orders is not always in accordance with the branching extent, which is mostly up to III (cp. Figs. 4.5.1 *E* and 4.5.3 *AM*). It is one cycle in the species producing only one umbel or umbel order, e.g. *Bupleurum fruticosum* (cp. Fig. 4.1 *D*), or in several species of the PENA clade. In addition, especially all dioecious Aciphyllae, the Selineae *Xanthoselinum alsaticum* and (also dioecious) *Trinia glauca* (and presumably *Komarovia anisosperma*) have all of their bisexual (or unisexual in the dioecious species) flowers synchronized. They pass only one male first and (or, in dioecious species) female flowering phase afterwards, although their branching system produces several orders of umbels.

Because higher umbel orders are usually aborted before or during anthesis, several species, e.g. *Daucus carota* or *Echinophora spinosa*, never have more than four flowering cycles (T-III). Even though they are sometimes branched to IV. More than four flowering cycles occur in a group of species that have either at least sympodially growing branches (as *Anthriscus caucalis* or the *Cryptotaenia*.species, or that produce sympodial stems (as *Helosciadium repens* or *Torilis nodosa*). They were neither found in monopodially growing shoots, nor in species with yellow flowers, nor in basal, Australian or the diverse group of African taxa (cp. Tab. 4.7).

4.4.3 *Summary*

Our data show that in the Apioideae, many features, regarded individually, are shared by a majority of species, rendering them characteristic traits of the group.

As to plant height, however, species equally split into small- and medium-sized, so that either their combination into a single size category of 20-200 cm, or the setting of more categories, to classify species in more detail, should be reasoned in future. Also in the zonation of the plants (see inhibition zone, internode gradients or branch clusters), or concerning predominant fruit set, not one most frequent character state emerged, but two or more, with about equal distribution among the study species. These characters represent sources of high variation in the flowering shoots. A great variety of different inflorescence patterns are additionally created by modifications of the produced umbels and their arrangement. Their varying components are the absolute number of flowers and umbels or bracts and bracteoles. Many forms of variation in the flowering shoots are not easily distinguishable without a detailed morphological analysis. They appear rather cryptic in the highly-ramified plants, with their similar flower canopies, displaying umbels at few to many different planes.

Less than 2% of all species show interesting peculiarities, e.g. creeping or procumbent growth or dwarfism, heights of more than 2m, apically increasing internode lengths, lacking terminal or simple umbels, umbel diameters of more than 25cm, diffuse umbellets, more than 10 bracts or bracteoles, red petals, or sex distribution patterns as in *Oenanthe*, *Echinophora* or the newly discovered pattern in *Heptaptera triquetra*. Only about a third of the taxa has additional, structural attraction features or enhances their visual impact by colors.

Despite the wide distribution of characteristic features in the subfamily, the typical apioid as a species, combining all most frequent features of Apioideae inflorescences, does not exist in our species selection and can only be created in a model. The combination of only five of the most frequent character states leaves only 50% of the species sharing them; combining 10-11 'peak states' leaves only 10% of taxa with these characters in common. Only few or many deviations from the characteristic features between single species lead to a tremendous multitude of character combinations. Not even two species share the very same combination of properties.

Certain characters occur more frequently within certain groups, e.g. basal or derived, andromonoecious or hermaphrodite, protandrous or protogynous, or sympodially branched,

than in our entire selection of Apioideae, as yellow petals in the protogynous species. Furthermore, hermaphroditism is much more common (~ 50%) in species not exhibiting erect growth, than in all observed species ($\leq 26\%$). However, the only unique pair of concurring traits that we could find, and that was already known, is protogyny and the gradual decrease in the proportion of male flowers, with increasing umbel order.

Geographical data have shown that, in any continent, diversity of the species is rather high. Maybe it is highest in Africa (Tab. 4.7) where also the rather extraordinary woody habit is common. In New Zealand, dioecious species are numerous that otherwise only occur, in form of a single species, *Trinia glauca*, in Europe. Because of the complexity of seasonal influences (depending on geography) and effects of habitats (because they stretch widely for many species), they are not evaluated in detail, yet. Apparent correlations did not show up during the analysis of our data, but information is kept in the data collection and in mind for further work.

Table 4.7. Diversity of African species, with regard to systematics, life form and habitat.

<i>species</i>	<i>clade</i>	<i>life form</i>	<i>habitat</i>
<i>Ammodaucus leucotrichus</i>	19. Daucinae	annual	sandy desert soil
<i>Andriana marojejensis</i>	3. Heteromorpheae Malagasy clade	woody	montane heathers, stony, gneissic ground
<i>Andriana tsaratananensis</i>	3. Heteromorpheae Malagasy clade	woody	montane heathers, stony, trachytic ground
<i>Anginon difforme</i> (Figs. 4.1 F, 4.7)	4. Heteromorpheae Heteromorpha clade	woody	in sandstone and quartzite areas on rocky slopes
<i>Astydamia latifolia</i>	2. Annesorhizeae	monocarpic	coastal rocks (splash water zone), sandy and salty places
<i>Athamanta montana</i>	16. Scandicinae	herbaceous perennial	rock slopes of the forests
<i>Athamanta sicula</i>	16. Scandicinae	herbaceous perennial	dry, calcareous rocks
<i>Dasispermum suffruticosum</i>	25. <i>Lefebvrea</i> Clade	herbaceous perennial	coastal sands
<i>Heteromorpha arborescens</i> (Fig. 4.1 G)	4. Heteromorpheae Heteromorpha clade	woody	forest margins and rocky woodland
<i>Itasina filifolia</i>	2. Annesorhizeae	herbaceous perennial	sandstone and limestone flats
<i>Lichtensteinia interrupta</i>	1. Lichtensteinieae	herbaceous perennial	grassland and bush
<i>Pimpinella anagodendron</i>	31. Pimpinelleae	dendroid perennial	rocks, laurel forests
<i>Todaroa aurea</i>	16. Scandicinae	herbaceous perennial	crevices (lower levels)

4.5 DISCUSSION

Our search for combined, characteristic features in the inflorescences of Apioideae has resulted in the discovery of highly diversifying species, each one of them dealing with a promiscuous pollination system in its own specific manner. Obviously, the function of their entire flowering shoot systems is retained to meet the requirements of belonging to a generalist plant group, although the underlying characters in part vary enormously.

4.5.1 *Structural diversity and the requirements of a promiscuous pollination system – the apioid breeding syndrome*

Special attraction features in Apioideae as pseudanthia, formed by petal or involucral and involucellar rays, colorations of the stamina or stylopodes or even upper leaves, are mostly absent in a subfamily whose flowers are openly presented and visited by many insects, beneath feeding for mating and romping. Investigations on pollinators, preferring visually enhanced male or female flower phases, gave differing results, so far (Schlessman et al. 2004; Davila & Wardle 2007; Zych 2007; Niemirski & Zych 2011). Even investigations on the attractivity of *Daucus carota* umbels with their characteristic dark flowers, are very dissenting (Kronfeld 1891; Westmoreland & Muntan 1996; Lamborn & Ollerton 2000; Goulson et al. 2009; Polte & Reinhold 2013). This is in accord with our expectation that boosted visual attraction plays a minor role in the Apioideae breeding system. Umbels rather need to serve as landing platforms, which gives the species much room for variation to find their optimal size and form (cp. Harder & Johnson 2005). This is also confirmed by experiments, testing the effects of umbel and umbellet density on pollinator attraction, again giving differing results (Bell 1976, 1977; Bell & Lindsey 1978; Koul et al. 1989a), indicating that umbel form plays a minor role, too. In all species, certain compactness is maintained, either within the umbels or rather the umbellets, facilitating the visitors' access to more than one flower after landing. Changes in umbel density, partly accompanied by the rounding of umbellets, are known to be noticeably during anthesis in individuals of some species, e.g. *Zizia trifoliata* or *Coriandrum sativum*. But it is likely that their meaning is rather found in e.g. the avoidance of sexual interference of male and female function (cp. Barrett 2002; Dai & Galloway 2011) within and between the flowers of andromonoecious and hermaphrodite species, by separating flowers spatially.

The risk of sexual interference within apioid flowers is completely excluded by their strict dichogamy. The open-pollinated, self-fertile plants with large floral displays (see Harder et al. 2001; Harder & Johnson 2005), however, need to deal with the risks of geitonogamous pollination (e.g. de Jong et al. 1993; Harder & Barrett 1995; Snow et al. 1996, and most studies on flowering sequences in Apiaceae). Most effectively, geitonogamy in our study species is prevented by synchronous and rhythmic flowering sequences of the protandrous or protogynous flowers. The almost exclusively centripetal flowering sequence of flowers and umbellets, with separately synchronized male and female flowering phases, renders geitonogamy within the umbels unlikely, especially when pollen is removed by insects shortly after its presentation. The centripetal flowering additionally entails an elongated male phase with pollen-portioning, mostly over several days, whereas the female phase is highly synchronized (Reuther & Claßen-Bockhoff 2010). Phase overlaps between umbels, rendered possible by the modular construction of the sequentially flowering plants, mostly allow geitonogamy only after a certain period of female receptivity (tested in *Daucus carota*, Reuther 2009). This, because pollinating insects usually are not a limiting factor, promotes outcrossing in the first place. However, even a generalist pollination system may be limited by pollinators, especially early in the season. Therefore, phase overlaps ensure fruit set even if only few pollen vectors are around. *Scandix pecten-veneris*, an early-flowering monocarp, forms a floral unit of terminal and 1st-order umbels to provide pollen (of the 1st-order umbels) in close proximity to hermaphrodite flowers (of the terminal umbel), shortly after their stigmata become receptive. In case of immediate pollination with foreign pollen, selfing is excluded. Otherwise, the available pollen from the next-order umbel is likely to guarantee fruit set. Another strategy, to deal with early flowering times, is, amongst others, seen in the development of protogyny (Schlessman & Barrie 2004) whereby pollen is provided for the first receptive stigmata.

Interestingly, the synchronisation of flowers in the umbels renders different sex distribution patterns (remember *Oenanthe* and *Echinophora*) merely unnoticeable, i.e. the sequence of male and female phases remains unchanged (cp. Reuther & Claßen-Bockhoff 2010). The reproductive system is therefore not directly influenced. However, the male peripheral flowers, especially in *Oenanthe* species, where they are frequently slightly radiating, remind of the sterile ray flowers in many Asteraceae and are one of the few presumed features targeting pollinator attraction.

Compared to the multicycle dichogamous taxa sequentially producing and displaying single or few umbels, enhanced visual impact on insects is given by the few species that present all of their umbels at the same time. The result differs mainly quantitatively, as e.g. *Xanthoselinum alsaticum* or many dioecious species achieve highest possible fruit set during one flowering cycle, and *Coriandrum sativum* or *Anthriscus caucalis* profit from investment in higher branch orders, and the extension of their flowering period.

Concerning investment costs and optimizing resources, this is most likely where the functional significance of andromonoecy in Apioideae may be sought for (e.g. Spalik 1991; Reuther & Claßen-Bockhoff in press), rather than in serving pollinator attraction by excess flowers (cp. Burd & Callahan 2000). This means for species with abruptly changing sex ratios that they usually achieve their optimal fruit by a certain umbel order, and further invest 'only' in the male function, which then mainly serves pollen export. The functioning of the male flowers in combination with the basitonus sex gradient of *Heptaptera triquetra* probably also lies in resource economies, if flowers in lower positions are unlikely to set fruit. This sex distribution pattern has not been described before, but a similar pattern in *Dorema aucheri* is investigated at present (Ajani & Classen Bockhoff 2012). Another indication that male flowers are unlikely to enhance attraction and serve only pollen donation in many apioids, is that they are usually not specially exposed in distal positions of the plants (but remember *Oenanthe*).

It is noteworthy that part of the species produces their largest umbels with the highest proportions of hermaphrodite flowers, others, especially the species with the largest umbels in the 1st or 2nd branch order, increase their umbel diameters by rising numbers of male flowers. The differing promotion of umbel sizes, independent from a certain order, indicates that they specifically depend on the direct environment of each single species or plant, rather than on one certain selective pressure in the subfamily. This is also true for the formation of a large terminal umbel, which probably conforms to the picture that most botanists would draw of a characteristic species. Variability of the terminal umbel as in *Pimpinella major*, which has also been described for *Peucedanum* (= *Tommasinia*) *altissimum* (Troll & Heidenhain 1951), suggests that selective pressures are lacking on this structure even within one species. It loses its importance if its reproductive output is naturally low. In *Myrrhis odorata* and *Anthriscus sylvestris*, terminal umbels may get lost because of functional constraints combined with the early flowering time of the species, when pollination is not guaranteed. In other species it

could, however, be the result of a developmental abbreviation, indicating developmental potential, which leads over to possible morphological classifications of the apioid inflorescences.

4.5.2 *Morphological approaches to apioid inflorescences*

Classifications into smaller groups of species, sharing certain features, and characterizing them separately, are especially useful to illustrate and comprehend diversity. In the flowering shoots of the Apioideae, though, many different architectural forms can be identified, e.g. in combining monopodial or sympodial growth with racemose or cymose branching and dispersed or whorled branches. Additionally including only the diverse acro-, basi- and mesotonous promotion and enrichment patterns, would render a simple classification highly voluminously, as species show a great diversity of combinations.

Our first idea was, to describe Apioideae inflorescences after their developmental pathway, starting in the very basal clades. The majority of the characteristic, most frequent character states concurs with 'basic' features in Apioideae that can already be found in the most basal clades (Lichtensteinieae, Annesorhizeae, Heteromorpheae, Bupleureae), indicating that variation is based on these. Noticeable discrepancies appear, however, in the presence of *bracts* - which in general are produced numerously in the basal clades – and *terminal flowers* – which occur relatively more frequently in the basal species. Furthermore, many of the observed basal species' umbels are *rather globose than flat*, and their petal colour is often *yellowish*. Even if terminal flowers do not occur exclusively, but frequently in most of the basal species, we presume them to be an ancestral character state in Apioideae, in contrast to families whose closed 'florescences' are due to reversal (see Bayer 1998 and citations therein). In view of the recent findings that spatial constraints in the meristems determine the production or lack of terminal flowers (Bull-Hereñu & Claßen-Bockhoff 2010, 2011a, b), their meaningfulness in tracing relationships becomes, however, questionable.

Another approach would have been to identify pathways within related groups, to understand floral aggregation and accumulation of flowers and branches, or towards loosening and segregation of structures. This could help to explain e.g. the dense umbel clusters of *Haussknechtia* or *Hohenackeria*. Internode gradients e.g., could turn out to be pre-stages to

whorl formations, or few-flowered umbellets within an umbel, a link to umbels with 1-flowered umbellets (which resemble to single umbellets but are expected not to be homologous).

Mostly because of the quantity of forms in the Apioideae, we were not yet able to identify particular directions of morphological changes and modifications of the inflorescences in the entire group. Maybe, species diversity in so many ways and directions, that we will not be able to trace them in future. But the idea remains, to also confirm known phylogenetic pathways of transformation processes in Apioideae in future, as are (Stauffer 1963): apical dominance - loss of terminal structures - proliferation, the gradual reduction of basal inflorescence sections, the de- or increase in the numbers of elements (flowers, umbellets, bracts, bracteoles, ...) or the elongation or inhibition of internodes. Especially when phylogenetic relationships within the subfamily are better resolved, mapped characters would most likely help to find transformation processes. But we already expect them to be manifold.

What should have become clear by regarding the complex flowering shoots, is that the established 'synflorescence' system is not applicable on apioids. Traditionally, in the sense of Troll (1964, 1969) or Weberling (1965, 1989; Weberling & Troll 1998) 'the complete flowering branch system produced by an apical bud of the embryonal axis or an innovation bud during a growth season is called synflorescence' (citation by Acosta et al. 2009). Therefore, regardless of foliation, all of the described apioid flowering shoots could be termed *synflorescences*, bearing umbels as their *inflorescences*. Then, we would, however, have to extend the term 'truncate synflorescence' to different levels, starting at least at level 3 (leaving out levels 1 and 2: 1, truncated terminal flower within the terminal umbellet, and 2, truncated terminal umbellet) because terminal umbellets usually do not occur in the subfamily. The only sign of a terminal umbellet, which has to our knowledge never been reported for the Apioideae hitherto, we found in the basal *Anginon difforme*. This could indicate that this feature got reduced and lost in the apioids, but maybe spatial constraints – as on the formation of terminal flowers (Bull-Hereñu & Claßen-Bockhoff 2011b) - have always inhibited its formation in the apioid umbels. It is interesting, however, that also in *Anginon difforme* single umbellets instead of umbels were found repeatedly in the flowering shoots (Burt 1991). We can, however, not confirm this by our greenhouse study individuals. The observations suggest further investigation of this species' characters, in view of intermediate or link states between basal and 'more evolved' Apioideae.

Another problematic question, remaining in the system of Troll, is the one after the vegetative or generative nature of leaves and bracts as Troll accepts foliar leaves to be elements of the inflorescence. Leaf sizes in apioid flowering shoots generally pass through metamorphosis gradually, unremarkably decreasing apically and distally (e.g. Reuther & Claßen-Bockhoff 2010). The great reduction of leaves in the one-cycle-flowering plants (*Trinia glauca*, *Xanthoselinum alsaticum*) indicates their loss of vegetative function, so that the respective flowering shoots would be real generative units, i.e. inflorescences, and arising from a single meristem. Similar units are usually the umbels and umbellets, indicated by the formation of bracts and bracteoles. With maybe few exceptions, i.e. species with very numerous and leafy bracts (*Daucus carota?* *Ammi visnaga?*), bracts and bracteoles seem to be formed as parts of the floral unit meristem, forming the umbels (see Claßen-Bockhoff & Bull-Hereñu 2013)

In our view, a promising approach to regard apioid inflorescences in future, would be to follow a new ontogenetic concept (Claßen-Bockhoff & Bull-Hereñu 2013) specifying flowering shoot systems, flowering units and real inflorescences based on their meristematic origin and developmental processes. They give further information that the flowering shoots of *Xanthoselinum* and *Trinia*, maybe also in other dioecious species, represent real inflorescences, producing flowers in umbels, instead of vegetative flowering shoots, producing floral unit meristems that form the umbels. The flowering sequence within inflorescences is defined to be acropetal and leaves are expected to be reduced to bracts, suggesting a developmental disruption in meristem activity.

In this model, the apioid umbels are interpreted to derive from fractionating floral unit meristems, usually borne in vegetative flowering shoot systems. The umbels' origin from floral unit meristems is indicated amongst others by the centripetal flowering sequence of their umbellets and flowers. Our observations, showing that not all apioid species meet these expected assumptions, indicate that neither all 'umbels' nor all of the 'flowering shoots' have the same ontogenetic basis. Especially basipetal flowering sequences, as in *Scandix pecten-veneris* or *Helosciadium repens*, will need further investigation. Different mechanisms regulating the time of floral or rather inflorescence meristem transition, from vegetative to reproductive stage, are expected. This model would help to define umbels, as homologous or analogous structures, and very likely different types of umbel-forming inflorescences in the group. Therefore in future studies, more attention will be needed to be turned to clearly visible reduction of leaves to bracts in the species, or their complete lack, to identify inflorescence

and floral unit meristems. Future developmental studies will be necessary toward understanding inflorescence morphology and diversification in Apioideae.

In view of the new inflorescence morphological concepts, terminology in the Apioideae should be thoroughly reconsidered at large, especially the use of the term 'inflorescence'. For further work on Apiales, we for example encourage the use of the terms 'terminal' (umbel) and 'main' (axis) instead of 'primary' or '1st-order' (umbel). To emphasize the difference between the main axis (stem) and the lateral axes, the laterals (branches) should be named after their degree of branching, i.e. '1st order' (referring to the contrasting use of terms by e.g. Schlessman & Graceffa 2002; Endress 2010 and many others).

It will also take careful observation in the future to clear differing results, as some of ours differ from the information given by other authors (e.g. the presence of terminal flowers in *Naufraga balearica*, Froebe 1979; or the presumed monopodial growth in *Apium repens*, Burt 1991; p. 144). We eagerly anticipate future studies, testing the practicability of our chosen characters in different, systematical, ecological or developmental, contexts and hope that others will follow our applied terminology to create a common basis for inflorescence morphological data on the Apioideae and their relatives.

4.6 CONCLUSIONS

We conclude from the observation that there are more morphological opportunities of variation and diversification than functional constraints in the flowering shoots of Apioideae. Variation in the subfamily is much higher than observed before in a comparative study of few selected, highly variable species.

We could show that apioids have many frequently-occurring features, that may be called characteristic for the subfamily. But morphological and phenological characters are combined in many ways and form a huge variety of individual morphological character syndromes. All studied species in this species-rich subfamily have found their specific solution, to the demands of attracting pollinators while reducing the risk of geitonogamous pollination, in varying sexual and flowering patterns, instead of floral specialisation. This indicates that flowering shoots of the Apioideae are made up of mostly independently varying 'modules' making the subfamily so characteristically successful in diverse habitats all over the world (see Mathias 1965).

The nature of these modules, mainly the umbels, will need to be investigated in future ontogenetic and developmental studies, as there are signs that they are not homologous structures. This may also help to identify developmental pathways in the diversification processes and possibly to define inflorescence types within the subfamily.

Despite varying morphologies, a common functional syndrome, serving generalist mating, is maintained: This includes: self-fertility, open-accessible, clustered flowers (umbels), an extended male phase, pollen-portioning, (multicycle) dichogamy with separate, synchronous (and rhythmically alternating), male and female flowering phases, which may, however, be delayed to overlap on certain conditions (or dioecy). We call it the apioid breeding syndrome.

5 GENERAL CONCLUSIONS

Our purpose, to provide criteria for applicable, apiooid inflorescence morphological characters and their clear definitions, has been achieved so far. A large data set is now provided to further work with. It needs to be, however, evaluated in future, especially with regard to the current morphological and developmental treatments of inflorescences. With respect to recent advances towards an understanding of plant architecture and branching patterns (Turnbull 2005), investigations of the highly variable shoot systems in the Apioideae reaching from inhibited to extremely elongate internodes, from monopodial to sympodial growth, and dispersed to whorled branches, are a promising approach to be continued in future.

The assumption, that morphological and reproductive characters are correlated, is confirmed only within narrow confines, applying only to protogyny and the gradual decrease in the number of male flowers with increasing umbel order. The modular construction of the plants allows them to diversify in many features and mainly independent from each other. Most surprisingly, however, not even all characteristic apiooid traits are combined in any of the study species.

The results of this large-scale comparative analysis illuminate the enormous morphological, spatial and temporal, variation in the flowering shoots and inflorescences of a generalist plant group, the Apioideae. The question remains after the causes of this variation. Is variation related to the species-richness of the family? Does the variation just exist because it is facilitated by the modular plant construction of apiooids? Or is each species highly specialized to its surroundings, by its specifically combined features? There are many more possible questions to be addressed in future.

As the functional ‘apiooid breeding syndrome’ seems to be a very effective reproductive strategy in the Apioideae, indicated by the fact that the subfamily is so successfully distributed all over the world, it deserves closer attention of a *specific* in contrast to a *generalistic* mating pattern.

In conclusion, this thesis has especially raised the question whether somewhere, among the about 4000 species that have not been investigated, yet, there exists a characteristic apiooid, combining all typical traits. The search for it has just begun ...

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7 APPENDICES

Appendix 1. List of plant species and sources used for the investigation. Living material observed in full bloom is marked in **bold**. Vouchers of the cultivated species are available at the Botanical Gardens of Berlin, Germany (B), Frankfurt, Germany (F), Mainz, Germany (MJG, mainly private collections of Regine Claßen-Bockhoff), Moscow, Russia (MWG) and the Conservatoire Botanique de Mulhouse, France (MCB, mainly private collections of Jean-Pierre Reduron).

- Nomenclature follows IPNI or - if deviating - the most recent literature on Apiaceae (see respective citations). If only the alternative, obsolete name can be found in any of the citations, this name is additionally given at the end of the sources.
- Species names are complemented by the number (n) of individuals examined/investigated (^{superior}: 1 = only one specimen, 2 = 2-5(-10) specimen, 3 = more than 10 specimen).
- For systematic classification, the name of the major clade is given (UPPER CASE, mainly after Downie et al. 2010 and Magee et al. 2010a), followed by the total number of species in the genus (in brackets).
- Continuing, origins and sources of the material are listed following the order, separated by semicolons: i) living plants in their natural location ('wild', see *MATERIAL AND METHODS*), botanical gardens and conservatories ('cult. '); ii) herborized specimens (for the Herbarium of Berlin-Dahlem the image online index *B 10...* is added in square brackets) and iii) websites and (in parentheses) consulted literature. If a look at the digital herbarium of Berlin (Roepert 2000 -) is especially recommended, where each of the herbarium sheets is additionally stored, the respective image ID is given.
- Whenever our applied species name deviates from the one used in the sources, the alternative name is given in curly brackets

Example

Species^{number of individuals observed} – CLADE (species within genus) provenance [= natural location and/or other origin and references (herbarium; optionally digital herbarium imageID; online information)] (printed literature) {alternative name}

A

Aciphylla glacialis (F. Muell.) Benth.² – ACIPHYLLEAE (42) Strid 22007 [*B 10 0184246*], Walter 1617 [*B 10 0184247*] (Webb 1986; Pickering 2000; Radford et al. 2001).

Aciphylla horrida W. R. B. Oliv.² - ACIPHYLLEAE (42) Degener 35,194 [*B 10 0184245*], (Cheeseman 1915; Oliver 1956; Radford et al. 2001).

- Aciphylla simplicifolia* (F. Muell.) Benth.² – ACIPHYLLEAE (42) Strid 22127 [B 10 0184243], Walter 3283 [B 10 0184244] (Cheeseman 1915; Oliver 1956; Webb 1986; Radford et al. 2001; Pickering & Hill 2002).
- Aciphylla squarrosa* J. R. Forst. & G. Forst.¹ – ACIPHYLLEAE (42) Froebe 2540 (MJG), Robbins s.n. (1949-05) [B 10 0184242] (Hooker 1864; Cheeseman 1915; Oliver 1956; Webb & Druce 1984; Webb 1986; Brookes & Jesson 2007).
- Aegokeras caespitosa* (Sibth. & Sm.) Raf.² – CAREAE (1) cult. (B); (Davis 1972; Reduron 2008).
- Aegopodium podagraria* L.³ – CAREAE (7) wild (RM), cult. (MJG); (Thellung 1926; Troll & Heidenhain 1951; Burton 2002; Reduron 2008).
- Aethusa cynapium* L.² - ANGELICA clade (1) wild (A), cult. (MJG); (Thellung 1926; Burton 2002; Reduron 2008).
- Agasyllis latifolia* Boiss.¹ - ANGELICA clade? (1) Gagnidze, Ivanishvili, Nakhutsrishvili & Eristavi 767 [B 10 0184238]; www.plantarium.ru [accessed: 2013-3-27] (Shishkin 1974).
- Aletes acaulis* (Torr.) J.M. Coult. & Rose² - ANGELICA clade (20-40?) Arsène 16572 [B 100184235] (Coulter & Rose 1900b; Coulter & Rose 1900a; Mathias & Constance 1944; Theobald et al. 1964; Kartesz 1994; Snow 2009).
- Alocarum erianthum* (DC.) Riedl & Kuber² – SMYRNIAEAE? (1) Gauba 21.2a [B 10 0184395] Gauba s.n. (1933-08-10 & 1933-09-22) [B 10 0184396] (Hedge et al. 1987; Ajani et al. 2008).
- Ammi majus* L.² – APIUM clade (3-4) wild (RM); cult. (MJG); (Thellung 1926; Zohary 1972; Burton 2002; Menglan et al. 2005; Reduron 2008).
- Ammodaucus leucotrichus* Coss. & Durieu² – DAUCINAE (1) Gabriel s.n. (1972-01-28) [B 10 0184393], Chevallier s.n. (1902-03-23) [B 10 0184394]; <http://www.sahara-nature.com/plantes.php?aff=nom&plante=ammodaucus%20leucotrichus> [accessed: 2013-3-27] (González et al. 2003).
- Ammoides pusilla* (Brot.) Breistr.² – PYRAMIDOPTERAE? (2) cult. (MWG), Reduron s.n. (MCB); (Thellung 1926; Tutin 1986; Reduron 2008).
- Andriana marojejyensis* (Humbert) B.-E.van Wyk² – HETEROMORPHEAE (3) Humbert 22710 [B 10 0058143] (Humbert 1955; Van Wyk et al. 1999; Sales et al. 2004).
- Andriana tsaratananensis* (Humbert) B.-E.van Wyk² – HETEROMORPHEAE (3) Humbert 18374 [B 10 0114233] (Humbert 1954; Van Wyk et al. 1999; Sales et al. 2004).
- Anethum graveolens* L.² - APIEAE (2) cult. (MJG); (Mouterde 1970; Pignatti 1982; Thulin 1999; Menglan et al. 2005; Reduron 2008).
- Angelica archangelica* L.² – SELINEAE (115) cult. (MJG, F); (Burton 2002; Reduron 2008).
- Angelica breweri* A. Gray¹ – SELINEAE (115) Pollard s.n. (1936-07) [B 10 0184229]; http://www.calflora.org/cgi-bin/species_query.cgi?where-taxon=Angelica+breweri [accessed: 2013-3-27]; (Coulter & Rose 1900b) [= *Angelica arguta* Nutt. var. *breweri* (Gray) Di Tomaso].
- Angelica capitellata* (A. Gray) Spalik, Reduron & S.R. Downie² – SELINEAE (115) Duran 554 [B 10 0184267], Pollard s.n. (1936-07) [B 10 0184268], Copeland 430 [B 10 0184269]; Reduron & Downie 2004, Lavelle & Walters 2007, davesgarden.com/guides/pf/go/94236/ (Coulter & Rose 1900b; Mathias & Constance 1944; Spalik et al. 2004; Lavelle & Walters 2007).
- Angelica czernaevia* (Fisch. & C. A. Mey.) Kitag.² - SELINEAE (115) Bornmüller s.n. (1835) [B 10 0184231], Bornmüller s.n. (1835) [B 10 0184232] (Hiroe 1958; Shishkin 1974; Menglan et al. 2005) {= *Czernaevia laevigata* Turczaninow var. *laevigata*}.
- Angelica gigas* Nakai² - SELINEAE (115) cult. (MJG) (Hiroe 1958; Hiroe & Constance 1958; Ohwi 1984).
- Angelica hendersonii* J.M. Coult. & Rose¹ - SELINEAE (115) Rose 37647 [B 10 0184233]; Mathias & Constance 1944.
- Angelica hirsuta* Muhl.¹ - SELINEAE (115) Heuser s.n. (1893-07) [B 10 0184234] (Coulter & Rose 1887a; Mathias & Constance 1944; Torrey & Gray 1969; Britton & Brown 1970).
- Angelica lucida* L.¹ - SELINEAE (115) Calder & Taylor 36572 [B 10 0184228]; http://calphotos.berkeley.edu/cgi/img_query?where-genre=Plant&where-taxon=Angelica+lucida [accessed: 2013-3-27]; (Fernald 1919; Mathias & Constance 1944; Hiroe 1958; Hiroe & Constance 1958; Gleason 1968; Welsh 1974).
- Angelica pachycarpa* Lange² - SELINEAE (115) cult. (MCB); (Webb et al. 1988; Nieto Feliner et al. 2003; Reduron 2008).

- Angelica pubescens* Maxim.¹ - SELINEAE (115) Hiroe 16.575 E(A-E) [B 10 0184227] (Hiroe & Constance 1958, Ohwi 1984).
- Angelica sylvestris* L.² - SELINEAE (115) wild (RM); (Thellung 1926, Burton 2002, Menglan 2005, Reduron 2008).
- Anginon difforme* (L.) B. L. Burt² – HETEROMORPHA Clade (12) cult. (MJG); Beyers 5996 [B 10 0029335] (Allison & van Wyk 1997; Goldblatt & Manning 2000; Manning & Paterson-Jones 2007).
- Anisosciadium lanatum* Boiss.² – ECHINOPHOREAE (3) Rechinger 9812 [B 10 0184220 / Roepert 2000 – **Image ID: 244718**], Rechinger 9960 [B 10 0184221] (Hedge & Lamond 1973; Hedge & Lamond 1978; Hedge et al. 1987; Mandaville 1990).
- Anisosciadium orientale* DC.² – ECHINOPHOREAE (3) Rechinger 170 [B 10 0184222], Bornmüller 1268 [B 10 0184225], Stapf s.n. (1985-04-14) [B 10 0184226] (Mouterde 1970; Zohary 1972; Hedge & Lamond 1973; Hedge et al. 1987; Reduron 2008).
- Anisotome aromatica* Hook.f.² – ACIPHYLLEAE (16) Amr s.n. (1946-01) [B 10 0184218] (Allan 1961; Parkinson 2001; Reduron 2008).
- Anisotome* Hook.f. spec.² – ACIPHYLLEAE (16) W. Schwabe s.n. (1977-11) [B 10 01842219].
- Anthriscus caucalis* M. Bieb.³ – SCANDICINAE (9) wild (RM); (Davis 1972; Hruška 1982; Reduron & Spalik 1995; Seybold 2006; Reduron 2008).
- Anthriscus cerefolium* (L.) Hoffm.² – SCANDICINAE (9) cult. (MJG); (Davis 1972; Shishkin 1973; Reduron & Spalik 1995; Seybold 2006; Reduron 2008).
- Anthriscus fumarioides* (Waldst. & Kit.) Spreng.² – SCANDICINAE (9) wild (C), cult. (B); (Thellung 1926, Hruška 1982, Spalik 1996).
- Anthriscus kotschyi* Boiss. & Balansa² – SCANDICINAE (9); Sintenis 4.763 [B 10 0184212], Görk, Hartvig & Strid (Strid et al.) 23.943 [B 10 0184213]; (Davis 1972; Shishkin 1973; Spalik & Downie 2001).
- Anthriscus lamprocarpa* Boiss.² – SCANDICINAE (9) Danin et al. 48.012 [B 10 0184214]; (Davis 1972; Zohary 1972; Spalik & Downie 2001).
- Anthriscus nemorosa* (M. Bieb.) Spreng.² – SCANDICINAE (9) wild (C), Rechinger 57.094 [B 10 0184215], Bornmüller 2.208 [B 10 0184216], Sintenis 4.145 [B 10 0184217]; (Thellung 1926, Davis 1972, Shishkin 1973, Hruška 1982, Spalik 1996).
- Anthriscus nitida* (Wahlenb.) Hazslinszky² – SCANDICINAE (9) A (wild) (Shishkin 1973; Hruška 1982; Reduron & Spalik 1995; Spalik & Downie 2001; Reduron 2004; Seybold 2006; Reduron 2008).
- Anthriscus sylvestris* (L.) Hoffm.³ – SCANDICINAE (9) wild (RM); (Schröter 1889; Hruška 1982; Reduron & Spalik 1995; Seybold 2006; Reduron 2008).
- Aphanopleura capillifolia* (Regel & Schmalh.) Lipsky² – PIMPINELLEAE (6) Granitov 320b [B 10 0184388]; (Shishkin 1973, Menglan 2005).
- Aphanopleura leptoclada* (Aitch. & Hemsl.) Lipsky² – PIMPINELLEAE (6) Sintenis 264 [B 10 0184389]; (Shishkin 1973, Menglan 2005).
- Aphanopleura trachysperma* Boiss.¹ – PIMPINELLEAE (6) Manakjan, Gochtuni, Chandschian s.n. (1971-06-18) [B 100184387]; (Shishkin 1973).
- Apiastrum angustifolium* Nutt.² – SELINEAE (1) Clements 192 [B 10 0184391 / Roepert 2000 – **Image ID: 244921**], Brandege 3428 [B 10 0184392 / Roepert 2000 – **Image ID: 244922**] (Mathias & Constance 1944; Torrey & Gray 1969).
- Apium fernandezianum* Johow² – APIEAE (25) cult. (MCB); (Reiche 1902; Skottsberg 1928, 1956).
- Apium graveolens* L.² – APIEAE (25) cult. (MJG); (Shishkin 1973; Burton 2002; Menglan et al. 2005; Seybold 2006; Reduron 2008; Ronse et al. 2010).
- Arracacia schneideri* Mathias & Constance¹ – ARRACACIA clade (55) Schwabe s.n. (1976-12-27) [B 10 1001728]; (Mathias & Constance 1942, 1944).
- Artemisia squamata* L.² – ARTEMISIA clade (1) Class.-Bockh. 2563, Bornmüller 104.116 [B 10 0184210], Schwarz 692 [B 10 0184211] (Mouterde 1970; Davis 1972).
- Astomaea seselifolia* (DC.) Rauschert² – PYRAMIDOPTERAE (2) Amdursky s.n. (1938-05-03), [B 10 0184385], Danin et al. 05.056 [B 10 0184386]; <http://flora.huji.ac.il/browse.asp?action=specie&specie=ASTSES> [accessed 2013/3/27] (Zohary 1972).
- Astrodaucus orientalis* (L.) Drude² – TORILIDINAE (2) Callier s.n. (1896-07-20) [B 10 0184383], Rechinger 57.469 [B 10 0184384] (Mouterde 1970, Shishkin 1973).

Astrodaucus persicus (Boiss.) Drude¹ – TORILIDINAE? (DAUCINAE?) (22) Bornmüller 7177 [B 10 0184382]; Shishkin 1973.

Astydamia latifolia (L.f.) Baill.² – ANNESORHIZEAE (1) cult. (MCB, B); Asplund 139 [B 10 0184209] (Cannon 1994; Lebrun & Stork 2011; Schönfelder & Schönfelder 2011; Schönfelder & Schönfelder 2012).

Athamanta cretensis L.³ – SCANDICINAE (8) wild (A, J), cult. (MJG, F) (Thellung 1926; Reduron 2008)

Athamanta montana (Webb ex Christ) K. Spalik, Wojew. & S.R. Downie² – SCANDICINAE (8) Schwerdtfeger 8-86 [B 10 0184334] (Spalik & Downie 2001; Schönfelder & Schönfelder 2011).

Athamanta sicula L.² – SCANDICINAE (8) cult. (B); Castroviejo et al. s.n. (1981-05-30) [B 10 0029340], Greuter 17.779 [B 10 0056536], Bornmüller 388 [B 10 0184335], Todaro s.n. (s.d.) [B 10 0184336], Reverchon 43 [B 10 0184337] (Pottier-Alapetite 1979; Pignatti 1982; Tutin 1986).

Athamanta turbith (L.) Brot.² – SCANDICINAE (8) cult. (MJG, B), (Reduron 2008, Tutin 1986).

Aulacospermum gonocaulum Popov (1) – PLEUOSPERMEAE (15) Goloskokov 5780 [B 10 0184380]; (Shishkin 1973; Pimenov & Kljuykov 2000).

Aulacospermum tianschanicum (Korovin) C. Norman² – PLEUOSPERMEAE (15) Mokeeva & Popov s.n. (1924-07-08; ISOTYPUS) [B 10 0184381]; (Shishkin 1973, Pimenov & Kljuykov 2000).

B

Berula erecta (Huds.) Coville² – OENANTHEAE (3) cult. (MJG); Scholz 70322 [B 10 0184374 / Roepert 2000 – **Image ID: 244904**], Willing 33.543 [B 10 0184375/ Roepert 2000 – **Image ID: 244905**], Willing 21.730a [B 10 0184376] (Reduron 2008, Burton 2002).

Bifora radians M. Bieb.² – CORIANDREAE (3) cult. (MJG); Willing 17.329 [B 10 0184371], Willing 28.585 [B 10 0184372], Willing 28.846 [B 10 0184373] (Davis 1972, Shishkin 1973, Seybold 2006).

Bilacunaria microcarpa (M. Bieb.) Pimenov & V. N. Tikhom.¹ – CACHRYIS Clade (4) Sintenis 6.132 [B 10 0184] (Shishkin 1973; Pimenov & Tikhomirov 1983) {= *Hippomarathrum crispum* W.D.J. Koch?}.

Bonannia graeca (L.) Halácsy (= probably *B. resinifera* Guss.)² – SELINEAE? (1) cult. (MCB); Bornmüller 168 [B 10 0184368], Stroly s.n. (1873-07) [B 10 0184369] (Pignatti 1982, Tutin 1986).

Bunium alpinum Waldst. & Kit. subsp. *montanum* (W.D.J. Koch) P. W. Ball = *Bunium divaricatum* (W.D.J.) Bertol., non Ces² – PYRAMIDOPTEREAE (50) Bornmüller 538 [B 10 0184365], Marchesetti 1347 [B 10 0184366]; (Ball 1968; Tutin 1986; Qosja 1992).

Bunium alpinum subsp. *petraeum* (Ten.) Rouy & E. G. Camus = *Bunium petraeum* Ten.² – PYRAMIDOPTEREAE (50) Bornmüller 105 [B 10 0184367]; (Ball 1968, Pignatti 1982, Tutin 1986).

Bupleurum baldense Turra² – BUPLEUREAE (190) cult (MCB); (Burton 2002, Reduron 2008).

Bupleurum falcatum L.² – BUPLEUREAE (190) cult. (MJG); (Burton 2002, Seybold 2006, Reduron 2008).

Bupleurum fruticosum L.² – BUPLEUREAE (190) wild (P), cult. (MJG); (Reduron 2008).

Bupleurum ranunculoides L.² – BUPLEUREAE (190) cult. (MJG); (Seybold 2006, Reduron 2008).

Bupleurum rotundifolium L.² – BUPLEUREAE (190) cult. (MCB); (Coulter & Rose 1887b; Britton & Brown 1970; Burton 2002; Seybold 2006; Reduron 2008).

C

Cachry cristata DC.¹ – CACHRYIS Clade (4) Böhring 8.099 [B 10 0144378] (Pottier-Alapetite 1979, Pignatti 1982, Tutin 1986).

Cachry libanotis L.² – CACHRYIS Clade (4) Akeroyd et al. 3.324 [B 10 0050036] (Gruenberg-Fertig et al. 1973; Pignatti 1982; Tutin 1986; Pimenov & Kljuykov 2002; Nieto Feliner et al. 2003).

Caropsis verticillato-inundata (Thore) Rauscher² – OENANTHEAE? (APIEAE? SELINEAE?) (1) Reduron 1982-08-10-02 (MCB); (Nieto Feliner et al. 2003).

Carum carvi L.³ – CAREAE (30) Cult. (MJG); (Zijlstra 1916; Thellung 1926; Bouwmeester & Smid 1995; Németh & Pluhár 1996; Németh et al. 1997; Németh & Székely 2000; Burton 2002; Langenberger & Davis 2002b, a; Menglan et al. 2005; Reduron 2008).

Carum verticillatum W.D.J. Koch² - CAREAE (30) cult. (F, MJG); Reduron n. unkn. (MCB); (Burton 2002).

Cenolophium denudatum (Hornem.) Tutin¹ - *SINODIELSIA* Clade (1) cult. (B, BGM); (Shishkin 1973; Jonsell 2000; Menglan et al. 2005) {*Cenolophium fischeri* (Spreng.) W.D.J. Koch.}.

Cervaria rivini Gaertn.² – SELINEAE (6-7; >100) wild (RM); (Seybold 2006, Reduron 2008).

Chaerophyllum aromaticum L.³ – SCANDICINAE (40) cult. (MJG) (Shishkin 1973, Seybold 2006).

Chaerophyllum aureum L.³ – SCANDICINAE (40) wild (A, J), cult. (MJG), (Davis 1972, Hedge et al 1987, Burton 2002, Seybold 2006, Reduron 2008).

Chaerophyllum bulbosum L.³ – SCANDICINAE (40) wild (RM); (Shishkin 1973, Hedge et al 1987, Seybold 2006, Reduron 2008).

Chaerophyllum byzantinum Boiss.² – SCANDICINAE (40) cult. (B); (Davis 1972; Spalik & Downie 2001).

Chaerophyllum hirsutum L.¹ – SCANDICINAE (40) wild (A), cult (B) (Spalik & Downie 2001; Seybold 2006; Reduron 2008).

Chaerophyllum nodosum (L.) Crantz² – SCANDICINAE (40) cult. (B, MJG); Class-Bockh. s.n. (1987-6; 9e; MJG); (Davis 1972; Zohary 1972; Pignatti 1982; Spalik & Downie 2001; Reduron 2008).

Chaerophyllum temulum L.³ – SCANDICINAE (40) cult. (MJG) (Spalik & Downie 2001; Seybold 2006; Reduron 2008)..

Chaerophyllum villarsii W.D.J. Koch² – SCANDICINAE (40) wild (A), cult. (B); (Spalik & Downie 2001; Seybold 2006; Reduron 2008).

Chamaesciadium acaule C. A. Mey.² – CAREAE (1) Class-Bockh. 2576 (MJG); (Wolff 1910-1927; Davis 1972; Shishkin 1973, 1974; Hedge et al. 1987; Menglan et al. 2005; Gabrielian & Fragman 2008).

Cicuta virosa L.² – OENANTHEAE (8) cult. (B); (Eichler 1878; Warnstorff 1896; Hiroe & Constance 1958; Tutin 1986; Burton 2002; Menglan et al. 2005).

Conioselinum chinense (L) Britton, Sterns & Poggenb.² - *CONIOSELINUM CHINENSE* clade (18) cult. (MWG) (Henderson 1925; Mathias & Constance 1944; Mathias & Constance 1945; Hiroe & Constance 1958; Welsh 1974; Hinds 1986).

Conium maculatum L.³ - *APIUM* superclade? SMYRNIEAE? *CONIUM* clade (6) Cult. (MJG) (Troll & Heidenhain 1951; Paczkowska & Chapman 2000; Burton 2002; Seybold 2006; Reduron 2008).

Conopodium glaberrimum (Desf.) Engstrand² – SCANDICINAE (8?) E. Cosson s.n. (1892-05-09), [*B 10 0184377*], Font Quer 438 [*B 10 0184378*], Sennen et Mauricio 8417 [*B 10 0184379*] (Pottier-Alapetite 1979) {*Balansaea fontanesii* Boiss. & Reut.}.

Coriandrum sativum L.³ – CORIANDREAE (2) cult. (MJG); Class-Bockh. 2553 (MJG); (Zohary 1972, Burton 2002, Menglan et al. 2005, Seybold 2006).

Coristospermum lucidum (Mill.) Reduron, Charpin & Pimenov² – *ACRONEMA* clade (3) cult. (MCB) (Reduron 2008).

Crithmum maritimum L.³ – PYRAMIDOPTEREAE (1) wild (G), cult. (MJG); (Burton 2002, Reduron 2008).

Cryptotaenia canadensis Hassk.² – OENANTHEAE (6) cult. (B, MJG) (Hiroe & Constance 1958; Hinds 1986; Tutin 1986; Baskin & Baskin 1988; Spalik & Downie 2007).

Cryptotaenia japonica (L.) DC.² – OENANTHEAE (6) cult. (MJG); (Ohwi 1984; Spalik et al. 2007).

Cyclosporum leptophyllum (Pers.) Sprague ex Britton & P. Wilson² – SELINAE? APIEAE? CAREAE? (3) Cult. (MCB); Class-Bockh. s.n. (2005-11-11, MJG) (Reduron 2008, Ronse et al. 2010).

Cymopterus anisatus A. Gray³ – PENA clade (20-40?) C.F. Baker 1369 [*B 10 0184263*], Arsène 17870 [*B 10 0184262*?]; (Coulter & Rose 1900b; Snow 2009; Sun & Downie 2010) {*Aletes anisatus* (A.Gray) Theobald & Tseng, *Pseudocymopterus anisatus* (A. Gray) J.M. Coult. & Rose, *Pseudopteryxia anisata* (A. Gray) Rydb.}.

Cymopterus duchesnensis M.E. Jones² – PENA clade (40) Weber 7404 [*B 10 0184279*], Weber 7404 [*B 10 0184280*] (Mathias & Constance 1944; Gilmartin & Simmons 1987).

Cymopterus ibapensis M.E. Jones² – PENA clade (40) Thiem 12062 [*B 10 0184278* / Roepert 2000 – **Image ID: 244816**] (Mathias & Constance 1944).

D-E

Dasispermum suffruticosum (P. J. Bergius) B. L. Burt² – *LEFEBVREA* clade (1) Class-Bockh. s.n. (2005-11-08 & 2005-11-01, MJG) (Manning & Paterson-Jones 2007, Magee et al. 2009).

Daucus carota L.³ – DAUCINAE (22) wild (RM) (Jonsell 2000, Burton 2002, Reduron 2008).

- Dethawia splendens* (Lapeyr.) Kerguelen² – clade? (1) Cult. (MCB) (Reduron 2008).
- Dichoropetalum carvifolia* (Vill.) Pimenov & Kljuykov² – *JOHRENIA* clade? SELINEAE? (5) wild (A); (Reduron 2008) {*Holandrea carvifolia* (Vill.) Reduron, Charpin & Pimenov}.
- Distichoselinum tenuifolium* (Lag.) Garcia Martin & Silvestre¹ – DAUCINAE? LASERPITIEAE? (4) cult. (MCB); (Nieto Feliner et al. 2003, Reduron 2008).
- Echinophora spinosa* L.² – ECHINOPHOREAE (11) wild (G), cult. (MJG); (Pignatti 1982, Reduron 2008).
- Endressia pyrenaica* (J. Gay ex DC.) J. Gay² – SELINEAE (2) cult. (MCB); (Tutin 1986, Reduron 2008).
- Exoacantha heterophylla* Labill.¹ – SELINEAE (1) Class-Bockh. 2573, 2576 (MJG) <http://flora.huji.ac.il/browse.asp?action=specie&specie=EXOHET&fileid=49536> [accessed 2013/3/27] (Mouterde 1970, Davis 1972, Zohary 1972).

F-H

- Falcaria vulgaris* Bernh.³ – CAREAE (1) wild (RM), cult. (MJG); (Zohary 1972, Burton 2002).
- Ferula communis* L.² – FERULINAE (175-185) wild (G); Class.-Bockh. s.n. (1987-7, 2a; MJG); (Pottier-Alapetite 1979, Tutin 1986).
- Ferula glauca* L.² – FERULINAE (175-185) cult. (MJG) (Tutin 1986, Reduron 2008).
- Ferula jaeschkeana* Vatke¹ – FERULINAE (175-185) cult. (B); (Nasir 1972; Shishkin 1974; Menglan et al. 2005).
- Ferulago nodosa* (L.) Boiss.² – *CACHRYS* clade (47) cult. (B, MBC); (Polunin 1980; Pignatti 1982; Tutin 1986; Qosja 1992).
- Ferulago sylvatica* (Besser) Rechb. subsp. *confusa* (Velen.) Hartvig² – *CACHRYS* clade (47) cult. (B) (Shishkin 1974, Polunin 1980, Tutin 1986).
- Foeniculum vulgare* Mill.³ – APIEAE (4-5) cult. (MJG) (Troll und Heidenhain 1951; Reduron 1983; Burton 2002; Menglan 2005).
- Gasparrinia peucedanoides* (M. Bieb.) Thell.¹ – ? (1?) cult. (MCB) (Reduron 2008).
- Gingidia montana* (J. R. Forst. & G. Forst.) J. W. Dawson² – ACIPHYLLEAE (8) *Schwerdtfeger* 17363 [*B 10 0184286*] (Dawson 1967; Webb & Druce 1984; Webb 1986; Parkinson 2001).
- Hausknechtia elymaitica* Boiss.¹ – PIMPINELLEAE (1) Hausknecht s.n. (1868-07) [*B 10 0184285* / **Image ID 244823**] (Boissier 1872; Hedge et al. 1987; Pimenov et al. 2004).
- Helosciadium bermejoi* (L. Llorens) Popper & M. F. Watson² – OENANTHEAE (?) cult. (MCB); (Ronse et al. 2010).
- Helosciadium nodiflorum* (L.) W.D.J. Koch³ – OENANTHEAE (?) cult. (MJG); Reuther s.n. (2008-7-9; MJG); (Burton 2002, Seybold 2006, Reduron 2008, Ronse et al. 2010).
- Helosciadium repens* (Jacq.) W.D.J. Koch³ – OENANTHEAE (?) cult. (MJG); Reuther s.n. (2008-7-9; MJG); (Burton 2002, Seybold 2006, Reduron 2008, Ronse et al. 2010)
- Heptaptera triquetra* (Vent.) Tutin² – *CACHRYS* Clade? *PHYSOSPERMOPSIS* Clade? (6) cult. (B); (Herrnstadt & Heyn 1971a; Herrnstadt & Heyn 1971b; Tutin 1986).
- Heracleum antasiaticum* Manden.² – TORDYLIINAE (65) cult. (B); (Davis 1972, Shishkin 1974).
- Heracleum candicans* Wall. ex DC.² – TORDYLIINAE (65) cult. (B), (Nasir 1972; Dhar & Kachroo 1983; Menglan et al. 2005).
- Heracleum leskovii* Grossh. (var. *angustilaciniatum* Satzyp.)² – TORDYLIINAE (65) cult. (B); (Shishkin 1974, Reduron 2008).
- Heracleum mantegazzianum* Sommier & Levier² – TORDYLIINAE (65) cult. (MJG); (Troll & Heidenhain 1951, Burton 2002).
- Heracleum pumilum* Vill.² – TORDYLIINAE (65) wild (A); (Reduron 2008).
- Heracleum sphondylium* L.³ – TORDYLIINAE (65) wild (RM); (Mathias & Constance 1944; Troll & Heidenhain 1951; Burton 2002).

Heteromorpha arborescens (Spreng.) Cham. & Schltdl. var. *abyssinica* (A. Rich.) H. Wolff² – HETEROMORPHA Clade (7) Faulkner 4061 [B 10 0184292], Gillett 14223 [B 10 0184293], Le Houérou 08-10 [B 10 0184294], www.rbghkew.org.uk/efloras/ [accessed: 2013-3-27] (Cannon 1978; Townsend 1985; Winter & Van Wyk 1996; Spalik & Downie 2001; Burrows & Willis 2005) {*Heteromorpha arborescens* (Spreng.) Cham. & Schltdl. var. *trifoliata* (Wendl.) Sonder = *Heteromorpha trifoliata* (H. L. Wendl.) Eckl. & Zeyh }.

Hohenackeria excaspa (Steven) Koso-Pol.² – BUPLEUREAE (2?) Class.-Bockh. 26/2012 (MJG); <http://floradealmeria.es/index.php/flora-de-almeria/flora-endemica-rara-o-amenazada-de-la-provincia-de-almeria/129-hohenackeria-excaspa> [accessed: 2013-3-27] (Davis 1972; Shishkin 1973; Tutin 1986; Gabrielian & Fragman 2008).

I-L

Imperatoria ostruthium L.³ – SELINEAE (3) wild (A), cult. (MJG) (Mathias & Constance 1944; Reduron & Nigaud 1987; Burton 2002; Reduron 2008).

Itasina filifolia (Thunb.) Raf.² – ANNESORHIZEAE (1) Class.-Bockh s.n. (2005-11-02 & 2005-11-04, MJG) (Manning & Paterson-Jones 2007).

Kadenia dubia (Schkuhr) Lavrova & V. N. Tikhom.² – SELINEAE (4) cult. (MJG) (Reduron 2008).

Katapsxus silaifolia (Jacq.) Raf. - SELINEAE (4) cult. (MJG) (Reduron 2008).

Kitagawia baicalensis (Redow. ex Willd.) Pimenov² – ACRONEMA clade (9?) Hand 1517 [B 10 0184289], Kedowsky? 2901 [B 10 0184290]; (Shishkin 1974; Mukherjee & Constance 1993; Menglan et al. 2005) {*Peucedanum baicalense* (Redow) C. Koch}.

Kitagawia terebinthacea (Fisch. ex Trevir.) Pimenov² – ACRONEMA clade (9?) Karo 253 [B 10 0184287], Karo s.n. (1906) [B 10 0184288]; (Hiroe & Constance 1958; Shishkin 1974; Ohwi 1984; Mukherjee & Constance 1993; Menglan et al. 2005) {*Peucedanum terebinthaceum* Fisch.}.

Komarovia anisosperma Korovin² – KOMAROVIA clade (1) cult. (MWG) (Shishkin 1974).

Krasnovia longiloba (Kar. & Kir.) Popov ex Schischk.² – SCANDICINAE (1) anonymous collector s.n. (s.d.) [B 10 0184295] (Mukherjee & Constance 1993; Spalik & Downie 2001; Menglan et al. 2005).

Kruberia peregrina (L.) Hoffm. = *K. leptophylla*² – OPOPANAX Clade (1) cult. (MJG); Rigo 296 [B 10 0184364 / **Image ID: 244893**], Ariault s.n. 1992-04-30 (MCB), Reduron 1990-09-28 (MCB); (Magee et al 2009^{a+b}, Plunkett et al. in press).

Kundmannia sicula (L.) DC.² –? (3) cult. (B), cult. (MJG); (Pottier-Alapetite 1979, Pignatti 1982, Tutin 1986, Reduron 2008).

Lagoecia cuminoides L.² – PYRAMIDOPTEREAE (1) cult. (MJG); Reuther s.n.(s.d.; MJG), Class.-Bockh. s.n. (1987-6, 1a; MJG); (Mouterde 1970; Davis 1972; Zohary 1972; Meikle 1977; Pignatti 1982; Hedge et al. 1987).

Laser trilobum (L.) Borkh. ex Gaertn., B. Mey & Scherb³ – DAUCINAE (1) cult. (B, (F, MCB, MJG) (Shishkin 1974; Reduron 2008).

Laserpitium halleri Crantz² – DAUCINAE (35) cult. (B) (Tutin 1986, Reduron 2008).

Laserpitium siler L.³ – DAUCINAE (35) cult. (B); (Tutin 1986, Reduron 2008).

Levisticum officinale W.D.J. Koch³ – SINODIELSIA clade (1) cult. (MJG) (Burton 2002, Menglan 2005, Reduron 2008).

Libanotis pyrenaica (L.) O. Schwarz³ – SELINEAE (10-30) wild (A), cult. (MJG) (Mathias & Constance 1944, Burton 2002, Reduron 2008).

Lichtensteinia interrupta E. Mey¹ – LICHTENSTEINIEAE (7) Bayliss 6955 [B 10 0184296] (Sonder 1862; Goldblatt & Manning 2000; van Wyk & Tilney 2003).

Lisaea heterocarpa (DC.) Boiss.² – TORILIDINAE (3) Froebe 2539 (MJG); (Davis 1972; Shishkin 1973; Hedge et al. 1987)(Davis 1972; Shishkin 1973; Hedge et al.).

Lomatium angustatum H. St. John² – PENA clade (86) Constance 3445 [B 10 0184298] (Mathias & Constance 1944).

Lomatium nevadense (Wats.) J.M. Coult. & Rose var. *parishii* (J.M. Coult. & Rose) Jeps.² – PENA clade (86) Schmidt & Merello 2671 [B 10 0184299] (Mathias & Constance 1944).

Lomatium nudicaule (Pursh) J.M. Coult. & Rose² – PENA clade (86) cult. (MWG)?; Rose 54080 [B 10 0184300] (Mathias & Constance 1944).

Lomatium parryi (Wats.) J. F. Macbr.² – PENA clade (86) Clokey 7614 [B 10 0184301] (Mathias & Constance 1944).

Lomatium roseanum Cronquist² – PENA clade (86) Tiehm 12079 [B 10 0184302].

Lomatium utriculatum (Nutt.) J.M. Coult. & Rose² – PENA clade (86) Baker 2621 [B 10 0184303], Pollard s.n. (1936-03) [B 10 0184304] (Mathias & Constance 1944, Lavelle & Walters 2007).

M-O

Meum athamanticum Jacq.² – SELINEAE (1-3) wild (V), cult. (B); (Pignatti 1982, Jonsell 2000, Burton 2002, Reduron 2008).

Meum nevadense Boiss.² – SELINEAE (1-2) Quintana, Mari & López 12396 [B 10 0184308], Bourgeau 1197 [B 10 0184307] (Tutin 1986).

Molopospermum peloponnesianum (L.) W.D.J. Koch² – ANNESORHIZEAE (1) cult. (B ; F); (Drude 1898; Thellung 1926; Reduron 2008).

Monizia edulis Lowe² – Daucinae (1) cult. (MCB); (Lowe 1868; Vieira 1992; Cannon 1994).

Musineon tenuifolium Nutt. ex Torr. & A. Gray¹ – PENA clade (4) Thilenius 69 [B 10 0184305] (Mathias & Constance 1944, Britton & Brown 1970).

Mutellina adonidifolia (J. Gay) Gutermann [var. *mutellina* (L.) Reduron]³ – CONIOSELINUM CHINENSE clade (3) Cult. (MJG) (Reduron 2008).

Myrrhidendron donnell-smithii J.M. Coult. & Rose² – ARRACACIA clade (5) (Mathias & Constance 1944; Standley & Williams 1966; Webb 1984; Wiedmann & Weberling 1993)

Myrrhidendron glaucescens J.M. Coult. & Rose² – ARRACACIA clade (5) Cazalet & Pennington 5419 [B 10 0184306] (Mathias & Constance 1976).

Myrrhis odorata (L.) Scop.³ – SCANDICINAE (1) cult. (MJG) (Burton 2002, Seybold 2006, Reduron 2008).

Naufraga balearica Constance & Cannon² – APIEAE (1) Cult. (MCB) (Constance & Cannon 1967; Botey 2005; Reduron 2008; Cursach & Rita 2012).

Notobubon laevigatum (Aiton) Magee² – LEFEBVREA Clade (6-7; >100) Class.-Bockh. s.n. (2005-11-08, MJG) <http://www.plantzafrica.com/plantnop/notobuboncap.htm> [accessed: 2013-3-27]; (Sonder 1862; Goldblatt & Manning 2000) {*Peucedanum capense* (Thunb.) Sond.}.

Oenanthe fistulosa L.² – OENANTHEAE (40) cult. (MJG) (Burton 2002, Reduron 2008).

Oenanthe pimpinelloides L.³ – OENANTHEAE (40) wild (G), cult. (MJG) (Shishkin 1973, Burton 2002, Reduron 2008).

Opopanax chironium (L.) W.D.J. Koch² – OPOPANAX clade (3) cult. (MJG), Reduron 1979-07-19-01 (MCB), Reduron 26 (2000-07-17; MCB); <http://sophy.u-3mrs.fr/photohtm/TI8174.HTM> [accessed: 2013-3-27] (Tutin 1986, Reduron 2008).

Oreoselinum nigrum Delarbre³ – SELINEAE (1) cult. (MJG); (Spalik et al. 2004; Reduron 2008).

Oreoxis humilis Raf.² – PENA clade (4) Fisher s.n. (1925-06-23) [B 10 0184305]; (Coulter & Rose 1900).

Orlaya grandiflora (L.) Hoffm.³ – DAUCINAE (3) cult. (MJG) Class-Bockh. 2550 (MJG); ((Spalik & Downie 2001; Seybold 2006; Reduron 2008).

Ormosolenia alpina (Sieber ex Schultes) Pimenov³ – SELINEAE (*JOHRENIA* group) (1) Böhling 8750 [B 10 0126674], Görk, Hartvig & Strid 23599 [B 10 0184310] (Davis 1972, Pimenov 1992).

Orogenia fusiformis S. Watson² – PENA clade (2) Sonne s.n. (1897-05-09) [B 10 0184312]; (Coulter & Rose 1900b; Jepson 1923a, b; Gilmartin & Simmons 1987).

Orogenia linearifolia S. Watson² – PENA clade (2) Suksdorf 7668 [B 10 0184311] (Coulter & Rose 1900; Gilmartin & Simmons 1987).

Osmorhiza chilensis Hook. & Arn.² – SCANDICINAE (10) cult. (B); (Welsh 1974; Moss & Packer 1983; Hinds 1986; Constance 1988).

Osmorhiza longistylis (Torr.) DC.² – SCANDICINAE (10) cult. (MJG); (Torrey & Gray 1969; Moss & Packer 1983; Hinds 1986; Spalik & Downie 2001).

Ostericum sieboldii (Miq.) Nakai¹ – SELINEAE? (12) cult. (MJG) (Ohwi 1984, Menglan et al. 2005).

Oxypolis filiformis (Walter) Britton² – OENANTHEAE (6) Froebe 2542 (MJG); (Mathias & Constance 1944, Britton & Brown 1970).

P

Palimbria salsa Besser² – SELINEAE? (3) Skvortsov, Bochkina, Klinkova & Sagalaev 18.240 [B 10 0184313], Becker s.n. (1896) [B 10 0184314], Becker s.n. (s.d.) [B 10 0184315], Becker s.n. (1896) [B 10 0184316]; (Shishkin 1974; Mukherjee & Constance 1993)

Pancicia serbica Vis.² – PIMPINELLEAE (1) Class-Bockh. 2558 (MJG) (Vladimirov et al. 2007).

Parasilau asiaticus (Korovin) Pimenov² – KOMAROVIA clade (1) cult. (MWG); (Gilli 1959; Leute & Speta 1972).

Pastinaca sativa L.³ – TORDYLIINAE (16) wild (RM), cult. (MJG); (Mathias & Constance 1944 28B 2; Troll & Heidenhain 1951; Burton 2002; Menglan 2005).

Petroselinum crispum (Mill.) Fuss³ – APIEAE (1-3) cult. (MJG); (Burton 2002; Menglan et al. 2005; Reduron 2008).

Peucedanum officinale L.³ – SELINEAE (6-7; >100) wild (RM); www.blumeninschwaben.de [accessed 2013/3/27] (Burton 2002; Reduron 2008).

Phlojodicarpus sibiricus (Fisch. ex Spreng.) Koso-Pol.² – SELINEAE (2) – SELINEAE (3-4) Treviranus s.n. (1822) [B 10 0184323] (Shishkin 1974; Mukherjee & Constance 1993; Menglan et al. 2005) [*Cachrys sibirica* Fischer ex Spreng. = *Libanotis cachroides* DC.].

Physospermopsis obtusiuscula (DC.) C. Norman¹ – PHYSOSPERMOPSIS clade (15) Pradhan & Rai 153 [B 10 0184320] (Watson 1999; Menglan et al. 2005).

Physospermopsis rubrinervis (Franch.) C. Norman² – PHYSOSPERMOPSIS clade (15) Delavay s.n. (s.d.) [B 10 0184319] (Menglan et al. 2005).

Physospermum cornubiense (L.) DC.² – PLEUROSPERMEAE (2) BGMw, Willing 18.603 [B 10 0184248], Maly 4890 [B 10 0184249], Heldreich 2097 [B 10 0184250], Sintenis & Bornmüller 1026 [B 10 0184251], Eisenblätter & Willing 69.821 [B 10 0184324] (Pignatti 1982, Tutin 1986, Reduron 2008).

Physospermum verticillatum (Waldst. & Kit.) Vis. = *Danaa verticillata* (Waldst. & Kit.) Janchen² – PLEUROSPERMEAE (2) BGM, Baschant 51.080 [B 10 0184321], Todoró? s.n. (s.d.) [B 10 01843222] (Pignatti 1982, Tutin 1986).

Pimpinella anagadendron Bolle² – PIMPINELLEAE (170-180) Cult. (MCB) (Schönfelder & Schönfelder 2012).

Pimpinella anisum L.² – PIMPINELLEAE (170-180) Cult. (MJG) (Mathias & Constance 1944 28B 2, Jonsell 2000; Menglan 2005; Reduron 2008).

Pimpinella bicknellii Briq.² – PIMPINELLEAE (170-180) cult. (B) ; (Knoche 1923; Tutin 1986).

Pimpinella major (L.) Huds.³ – PIMPINELLEAE (170-180) wild (RM), cult. (MJG); (Knuth 1898, Burton 2002, Reduron 2008).

Pimpinella peregrina L.³ – PIMPINELLEAE (170-180) wild (RM); (Zohary 1972; Reduron 2008).

Pimpinella saxifraga L.² – PIMPINELLEAE (170-180) wild (RM); Class-Bockh. s.n. (1987-6, 2°, 13°; MJG); (Burton 2002).

Pleurospermum austriacum (L.) Hoffm.³ – PLEUROSPERMEAE (2) cult. (MJG); (Hiroe & Constance 1958, Shishkin 1973, Seybold 2006, Reduron 2008).

Polytaenia nutallii DC.² – PENA clade (2) Horr & McGregor E514 [B 10 0184252], Damaree 2734 [B 10 0184253], Clark 2435 [B 10 0184254 / Röpert 2000 – **Image ID 244753**] (Mathias & Constance 1944; Torrey & Gray 1969; Britton & Brown 1970).

Prangos trifida (Mill.) I. Herrnst. & Heyn² – CACHRYS clade (45) B_{BG}; [*Prangos ferulaceae*? <http://flora.huji.ac.il/browse.asp?action=specie&specie=PRAFER> [accessed 2013/3/27] (Herrnstadt & Heyn 1977; Pimenov & Tikhomirov 1983; Reduron 2008).

Prionosciadium pringlei S. Watson² – ARRACACIA clade (10) Schiede s.n. (s.d.) [B 10 0184255], Schiede s.n. (s.d.) [B 10 0184256] (Mathias & Constance 1942).

Pseudocymopterus montanus (A. Gray) J.M. Coult. & Rose² – PENA clade (1) Arsène s.n. (1930-06-16) [B 10 0184259], Howell & True 45177 [B 10 0184257], Pase 1746 [B 10 0184258] (Coulter & Rose 1900; Mathias & Constance 1944).

Pseudocymopterus montanus J.M. Coult. & Rose var. *multifidus* Rydb.² – PENA clade (1) Arsène 17728 [B 10 0184260].

Pteroselinum austriacum (Jacq.) Rechb.² – SELINEAE (1) cult. (B, MJG); (Reduron & Nigaud 1987; Seybold 2006; Reduron 2008) {*Peucedanum austriacum* (Jacq.) W.D.J. Koch, *Peucedanum rablense* W.D.J. Koch}.

Pteryxia hendersonii (J.M. Coult. & Rose) Mathias & Constance² - PENA clade (5) Cronquist 7959 [B 10 0184261]; (Mathias & Constance 1944; Kartesz 1994; Scott 1995).

Ptychotis saxifraga (L.) Loret & Barrandon² – related to *Ammoides*; PYRAMIDOPTEREAE? (1-2) wild (P); cult. (MCB); (Tutin 1986, Reduron 2008).

Pyramidoptera cabulica Boiss.² – PYRAMIDOPTEREAE (1) Rechinger 17.572 [B 10 0184281], Rechinger 18.063 [B 10 0184282], Rechinger 19.134 [B 10 0184283], Rechinger 37.211 [B 10 0184284] (Leute 1972, Hedge et al. 1987).

Q-S

Ridolfia segetum (Guss.) Moris² – APIEAE (1) cult. (B); (Zohary 1972, Tutin 1986, Mandaville 1990, Reduron 2008).

Rouya polygama (Desf.) Coincy² – DAUCINAE? (1) cult. (MCB) (Pignatti 1982, Tutin 1986).

Saposhnikovia divaricata (Turcz.) Schischk.² – SELINEAE (1) Bojko7339 [B 10 0021105], Karo 209 [B 10 0184266] Roepert 2000 - **Image IDs: 244767, 249440**, Reduron s.n. (1986-07-29), Reduron 1984-08-23-02, Herbar J.-P. Reduron (Shishkin 1974; Mukherjee & Constance 1993; Menglan et al 2005).

Scaligeria tripartita (Kalenicz.) Tamamsch.³ – PYRAMIDOPTEREAE (5) cult. (MJG) (Shishkin 1973, Pils 2006) {*Pimpinella tripartita*}.

Scandia rosifolia (Hook.f.) J. W. Dawson² – ACIPHYLLEAE (2) Lush s.n. (1946-12-01) [B 10 0184265].

Scandix balansae Reut. ex Boiss.² – SCANDICINAE (>7) cult. (MCB) (Davis 1972; Spalik & Downie 2001; Reduron 2008).

Scandix pecten-veneris L.³ - SCANDICINAE (>7) cult. (MJG) (Zohary 1972, Burton 2002, Seybold 2006, Reduron 2008).

Selinum carvifolia (L.) L.³ – SELINEAE (2-3) cult. (MJG) (Jonsell 2000, Burton 2002, Reduron 2008).

Seseli gummiferum Pall. ex Sm.² – SELINEAE (125-140) cult. (MJG) (Shishkin 1973).

Seseli hippomarathrum Jacq.² - SELINEAE (125-140) cult. (MJG) (Shishkin 1973, Reduron 2008).

Seseli praecox (Gamisans) Gamisans² - SELINEAE (125-140) cult (MCB); (Reduron 2008).

Seseli webbii Coss.¹ – APIEAE (125-140) cult. (MCB) (Schönfelder & Schönfelder 2011; Schönfelder & Schönfelder 2012).

Silaum silaus (L.) Schinz. & Thell.² – *SINODIELSIA* clade (2) cult. (B) (Pignatti 1982, Burton 2002, Menglan 2005, Reduron 2008).

Silaum tenuifolium (DC.) Reduron³ – *SINODIELSIA* clade? (2) cult. (MJG) (Shishkin 1973; Reduron 2008).

Sison amomum L.² – PYRAMIDOPTEREAE (3) wild (P), cult. (B); (Webb et al. 1988; Burton 2002; Seybold 2006; Reduron 2008).

Sium latifolium L.³ – OENANTHEAE (14) cult. (MJG) (Burton 2002, Menglan 2005, Reduron 2008).

Sium sisarum L.³ – OENANTHEAE (14) cult. (B); (Hiroe & Constance 1958; Ohwi 1984; Mukherjee & Constance 1993; Reduron 2008).

Smyrniolum olusatrum L.² – SMYRNIEAE (7) Reduron n. unknown (MCB) (Mouterde 1970, Zohary 1972, Burton 2002, Reduron 2008).

Smyrniolum perfoliatum L.³ – SMYRNIEAE (7) cult. (MJG) (Burton 2002, Seybold 2006, Reduron 2008).

Spermolepis divaricatus (Walter) Raf. ex Ser.² – SELINEAE (5) Schallert 11125 [B 10 0184270], Dale Thomas 83988 [B 10 0184271] (Mathias & Constance 1944; Britton & Brown 1970).

Spermolepis echinatus (Nutt. ex DC.) A. Heller¹ – SELINEAE (5) Shinnars 18852 [B 10 0184272 / Roepert 2000 - **Image ID: 244773**]; (Mathias & Constance 1944; Britton & Brown 1970).

Steganotaenia araliacea Hochst.² – STEGANOTAENIEAE (3) Schimper s.n. (1894) [B 10 0184273], Greuter 20.340 [B 10 0184317], Peter 47.319 [B 10 0184318], Class.-Bockh. s.n. (2005-10-31, MJG)(Cannon 1978; Thulin 1999; Burrows & Willis 2005; Magee et al. 2010a).

Synclinostyles denisjordanii Farille & Lachard² – APIEAE? *ACRONEMA* Clade? (25?) Reduron n. unknown (MCB); (Farille & Lachard 2002).

T

Taenidia integerrima (L.) Drude¹ - PENA clade (1) Blake 9422 [*B 10 0184325*] (Henderson 1925; Mathias & Constance 1944; Gleason 1968; Britton & Brown 1970).

Taenidia montana (Mack.) Cronq. = *Pseudotaenidia montana* Mack.¹ – PENA clade (1) Davis 4844 [*B 10 0184264*] (Mathias & Constance 1944; Britton & Brown 1970; Kartesz 1994).

Tauschia arguta (Torr. & A. Gray) J. F. Macbr² - PENA clade (31) Wester 413 (MJG).

Tauschia filiformis J.M. Coult. & Rose² - PENA clade (31) Pringle 4714 [TYPUS; *B 10 0184274*] (Mathias & Constance 1944; Standley & Williams 1966).

Tauschia kelloggii (A. Gray) J. F. Macbr.¹ - PENA clade (31) Pollard s.n. (1935-04) [*B 10 0184275*] (Mathias & Constance 1944).

Tauschia nudicaulis Schldt.² - PENA clade (31) Hinton et al. 11868 [*B 10 0184276*] (Mathias & Constance 1944, 1976).

Tauschia parishii (J.M. Coult & Rose) J. F. Macbr.¹ - PENA clade (31) Clark 5144 [*B 10 0184277*] (Mathias & Constance 1944).

Thaspium barbinode (Michx.) Nutt.² - PENA clade (3) Biltmore Herbarium 1036b [*B 10 0184327*], Loughridge 3439 [*B 10 0184328*], Leonard & Radford 1439 [*B 10 0184329*], Bornmüller 71 [*B 10 0184330*] (Coulter & Rose 1887c; Mathias & Constance 1944; Gleason 1968; Britton & Brown 1970; Bell 1971).

Thaspium pinnatifidum (Buckley) A. Gray¹ - PENA clade (3) Radford 45404 [*B 10 01843*] (Coulter & Rose 1887c; Mathias & Constance 1944; Gleason 1968; Britton & Brown 1970).

Thaspium trifoliatum (L.) A. Gray¹ - PENA clade (3) Schrader s.n. (1844) [*B 10 0184333*] (Coulter & Rose 1887c; Mathias & Constance 1944; Gleason 1968; Britton & Brown 1970).

***Todaroa aurea* Parl.³** – SCANDICINAE (1) Cult. (MJG); Greuter 247 [*B 10 0021633*], Greuter 20.136 [*B 10 0069857*] (Schönfelder I. & P. 2011/P. & I. 2012)

Tommasinia altissima (Mill.) Reduron² – SELINEAE (1) cult. (B); Prefferg s.n. (1880?) [*B 10 0184338*], Šafer s.n. (1894-06-28) [*B 10 0184339*] (Leute 1966, Seybold 2006, Reduron 2008) (= *Peucedanum verticillare* (L.) Mert. & W.D.J. Koch).

Tordylium apulum L.³ – TORDYLIINAE (18) wild (G); Reduron s.n. (2001-05-05), Reduron 01 (1982-04-23), Reduron 19820423-01), Reduron s.n. (1994-04-27) (Davis 1972, Pottier-Alapetite 1979, Al-Eisawi et Jury 1988, Reduron 2008).

Tordylium cordatum (Jacq.) Poiret.² – TORDYLIINAE (18) Rilke 1.245 [*B 10 0184397*] (Zohary 1972, Al-Eisawi et Jury 1988)

Tordylium maximum L.² - TORDYLIINAE (18) wild (G); Reduron s.n. (1974-07-30), Reduron 09 (MCB) Coulom s.n. (1977-07-07; MCB), Reduron s.n. (1988-07-08; MCB), Reduron 34 (Al-Eisawi et Jury 1988, Burton 2002, Seybold 2006, Reduron 2008).

Tordylium syriacum L.² - TORDYLIINAE (18) cult. (MJG); (Mouterde 1970, Davis 1972, Zohary 1972, Al-Eisawi et Jury 1988).

Tordylium trachycarpum (Boiss.) Al-Eisawi & Jury² - TORDYLIINAE (18) Samuelsson 981 [*B 10 0184236*], Reching 60.740 [*B 10 0184237*], Reduron 19860427-01 (Zohary 1972, Al-Eisawi et Jury 1988).

***Torilis arvensis* (Huds.) Link³** – TORILIDINAE (15) wild (RM) (Zohary 1972, Thulin 1999, Burton 2002, Seybold 2006).

Torilis nodosa (L.) Gaertn.² – TORILIDINAE (15) wild (G), cult. (MJG); Reduron 26 (MCB); (Zohary 1972, Meikle 1977, Seybold 2006).

***Trinia glauca* (L.) Dumort.³** – SELINEAE (8-10) wild (RM); Reduron 06? (1987-07-22; MCB); (Burton 2002, Seybold 2006).

Trochiscanthes nodiflora (All.) W.D.J. Koch² – *CONIOSELINUM CHINENSE* clade (1) wild (A); Bernard, s.n. (1894-08-13) [*B 10 0184340*], Bernard, s.n. (1894-08-13) [*B 10 0184341*], Bourgeois, s.n. (1918-07-29) [*B 10 0184342*], Reduron 38 (MCB), Spieß, s.n. (1872-07) [*B 10 0184343*], Rehsteiner, s.n. (s.d.) [*B 10 0184344*] / Roepert 2000 – **ImageIDs 244869-244873**] (Pignatti 1982, Tutin 1986, Käsermann 1999).

Turgenia latifolia (L.) Hoffm.² – TORILIDINAE (2) cult. (MJG) (Mouterde 1970; Zohary 1972; Pottier-Alapetite 1979; Menglan et al. 2005; Seybold 2006; Reduron 2008).

U-Z

Visnaga daucooides Gaertn.² – *OPOPANAX* clade (1-2) wild (G); (Davis 1972, Zohary 1972, Shishkin 1973, Reduron 2008).

Xanthogalum purpurascens Ave-Lall.² – SELINAE (?) cult. (MJG); (Shishkin 1974).

Xanthoselinum alsaticum (L.) Schur³ – SELINAE (1) cult. (MJG); (Reduron 2008, Seybold 2006).

Xatartia scabra (Lapeyr.) Meisn.² – SELINEAE? (1?) Sennen s.n. (1898-08-19) [*B 10 0184345*], Endress s.n. (1829-08) [*B 10 0184346*], de Retz 11.496 [*B 10 0184347*]; Roepert 2000 – [**ImageID 0184346, 244877**] (Reduron 2008, Tutin 1986) {*Angelica scabra* (Lapeyr.) Petit, *Selinum scabrum* Lapeyr.}.

Zeravschania aucheri (Boiss.) Pimenov² – PIMPINELLEAE (6) Bornmüller 7243 [*B 10 0184348*], Bornmüller 7241 [*B 10 0184349*], Bornmüller 7242 [*B 10 0184350*] (Hedge et al. 1987, Spalik & Downie 2007; Ajani et al. 2008; Zhou et al. 2008).

Zizia aptera (A. Gray) Fernald² - PENA clade (4) Anonymous collector s.n. (s.d.) [*B 10 0184362*], Chase 9367 [*B 10 0184353*], Clarkson 3652-A [*B 10 0184355*], Coile 2642 [*B 10 0184354*] Moffat 238 [*B 10 0184363*] (Coulter & Rose 1887c; Mathias & Constance 1944; Britton & Brown 1970; Moss & Packer 1983; Lavelle & Walters 2007) {*Zizia cordata* W.D.J. Koch ex DC.}.

Zizia aurea (L.) W.D.J. Koch² - PENA clade (4) cult. (MJG); Birkenholz 96 [*B 10 0184356*], McGregor E311 [*B 10 0184357*], Forbes s.n. (1914-05-30) [*B 10 0184358*], Marie-Victorin & Rolland-Germain 70063 [*B 10 0184359*], Schallert 2001 [*B 10 0184360*]; missouriplants.com [accessed: 2013-3-27] (Coulter & Rose 1887c; Baten 1935; Mathias & Constance 1944; Britton & Brown 1970; Cooperrider 1985; Hinds 1986; Lavelle & Walters 2007).

Zizia trifoliata (Michx.) Fernald = ² - PENA clade (4) Anonymous collector 5526 [*B 10 0184361*] (Mathias & Constance 1944, Britton & Brown 1970) {*Ziizia bebbii* (J.M. Coulter & Rose) Britton}.

Appendix 2. Species selection, comprising 31 (of 38?) clades and subclades, based on Downie et al 2010 and citations therein; underlined find species that were placed by the author because information on their position is not available.

clade	name	species investigated
	Choritaenidae, Marlothiellae, Phlyctidocarpeae, Saniculeae, <i>Hermas</i>	
0	Steganothaenidae	<i>Steganothaenia araliaceae</i>
1	Lichtensteiniae (monogeneric)	<i>Lichtensteinia interrupta</i>
2	Annesorhizeae	<i>Astydamia latifolia</i> , <i>Itasina filifolia</i> , <i>Molopospermum peloponnesianum</i>
3	Malagasy Clade	<i>Andriana marojejensis</i> , <i>Andriana tsaratananensis</i>
4	Heteromorpha Clade	<i>Anginon difforme</i> , <i>Heteromorpha arborescens</i>
[clade 3-4: Heteromorpheae]		
5	Bupleureae (bigeneric?)	<i>Bupleurum baldense</i> , <i>Bupleurum falcatum</i> , <i>Bupleurum fruticosum</i> , <i>Bupleurum ranunculoides</i> , <i>Bupleurum rotundifolium</i> , <i>Hohenackeria exscapa</i>
6	<i>Pleuropermopsis</i> Clade	
7	<i>Chamaesium</i> Clade (monogeneric)	
8	<i>Diplophium</i> Clade (monogeneric)	
9	Pleurospereae	<i>Aulacospermum gonocaulum</i> , <i>Aulacospermum tianschanicum</i> , <i>Physospermum cornubiense</i> , <i>Physospermum verticillatum</i> , <i>Pleuropermum austriacum</i>
10	Komarovieae	<i>Komarovia anisosperma</i> , <i>Parasilaus asiaticus</i>
11	<i>Physospermopsis</i> Clade (monogeneric)	<i>Physospermopsis obtusiuscula</i> , <i>Physospermopsis rubrinervis</i>
12	Erigenieae (monotypic)	
13	Oenantheae	<i>Berula erecta</i> , <i>Caropsis verticillato-inundata</i> , <i>Cicuta virosa</i> , <i>Cryptotaenia canadensis</i> , <i>Cryptotaenia japonica</i> , <i>Helosciadium bermejoi</i> , <i>Helosciadium nodiflorum</i> , <i>Helosciadium repens</i> , <i>Oenanthe fistulosa</i> , <i>Oenanthe pimpinelloides</i> , <i>Oxypolis filiformis</i> , <i>Sium latifolium</i> , <i>Sium sisarum</i>
14	Smyrnieae	<i>Smyrniolum olusatrum</i> , <i>Smyrniolum perfoliatum</i>
15	Torilidinae	<i>Astrodaucus orientalis</i> , <i>Astrodaucus persicus</i> , <i>Lisaea heterocarpa</i> , <i>Torilis arvensis</i> , <i>Torilis nodosa</i> , <i>Turgenia latifolia</i>
16	Scandicinae	<i>Anthriscus caucalis</i> , <i>Anthriscus cerefolium</i> , <i>Anthriscus fumarioides</i> , <i>Anthriscus kotschyi</i> , <i>Anthriscus lamprocarpa</i> , <i>Anthriscus nemorosa</i> , <i>Anthriscus nitida</i> , <i>Anthriscus sylvestris</i> , <i>Athamanta cretensis</i> , <i>Athamanta montana</i> , <i>Athamanta sicula</i> , <i>Athamanta turbith</i> , <i>Balansaea fontanesii</i> , <i>Chaerophyllum aromaticum</i> , <i>Chaerophyllum aureum</i> , <i>Chaerophyllum bulbosum</i> , <i>Chaerophyllum byzantinicum</i> , <i>Chaerophyllum hirsutum</i> , <i>Chaerophyllum nodosum</i> , <i>Chaerophyllum temulum</i> , <i>Chaerophyllum villarsii</i> , <i>Conopodium glaberrimum</i> , <i>Krasnovia longiloba</i> , <i>Myrrhis odorata</i> , <i>Osmorhiza chilensis</i> , <i>Osmorhiza longistylis</i> , <i>Scandix balansae</i> , <i>Scandix pecten-veneris</i> , <i>Todaroa aurea</i>
17	<i>Glaucosciadium</i> Clade (monogeneric)	
18	Ferulinae	<i>Ferula communis</i> , <i>Ferula glauca</i> , <i>Ferula jaeschkeana</i>
19	Daucinae	<i>Ammodaucus leucotrichus</i> , <i>Daucus carota</i> , <i>Distichoselinum tenuifolium</i> , <i>Laser trilobum</i> , <i>Laserpitium halleri</i> , <i>Laserpitium sile</i> , <i>Monizia edulis</i> , <i>Orlaya grandiflora</i> , <i>Rouya polygama</i>
20	<i>Artedia</i> Clade (monotypic)	<i>Artedia squamata</i>
[clade 15-20: Scandiceae]		
21	<i>Conioselinum chinense</i> Clade	<i>Conioselinum chinense</i> , <i>Mutellina adonidifolia</i> , <i>Trochiscanthes nodiflora</i>
22	<i>Arcuaopterus</i> Clade (monogeneric)	
23	<i>Acronema</i> Clade	<i>Coristospermum lucidum</i> , <i>Kitagawia baicalensis</i> , <i>Kitagawia terebinthacea</i>

24	Aciphyllae	<i>Aciphylla glacialis</i> , <i>Aciphylla horrida</i> , <i>Aciphylla simplicifolia</i> , <i>Aciphylla squarrosa</i> , <i>Anisotome aromatica</i> , <i>Gingidia montana</i> , <i>Scandia rosifolia</i>
25	<i>Lefebvrea</i> Clade	<i>Dasispermum suffruticosum</i> , <i>Notobubon laevigatum</i>
26	<i>Cymbocarpum</i> Clade (3 genera)	
27	Tordyliinae	<i>Heracleum antasiaticum</i> , <i>Heracleum candicans</i> , <i>Heracleum leskovii</i> (var. <i>angustilacinatum</i>), <i>Heracleum mantegazzianum</i> , <i>Heracleum pumilum</i> , <i>Heracleum sphondylium</i> , <i>Pastinaca sativa</i> , <i>Tordylium apulum</i> , <i>Tordylium cordatum</i> , <i>Tordylium maximum</i> , <i>Tordylium syriacum</i> , <i>Tordylium trachycarpum</i>
[clade 25-27: Tordylieae]		
28	<i>Sinodielsia</i> Clade	<i>Cenolophium denudatum</i> , <i>Levisticum officinale</i> , <i>Silaum silaus</i> , <i>Silaum tenuifolium</i>
29	Selineae	<i>Aethusa cynapium</i> , <i>Angelica archangelica</i> , <i>Angelica breweri</i> , <i>Angelica capitellata</i> , <i>Angelica czernaevia</i> , <i>Angelica gigas</i> , <i>Angelica hendersonii</i> , <i>Angelica hirsuta</i> , <i>Angelica lucida</i> , <i>Angelica pachycarpa</i> , <i>Angelica pubescens</i> , <i>Angelica sylvestris</i> , <i>Apiastrum angustifolium</i> , <i>Cervaria rivini</i> , <i>Endressia pyrenaica</i> , <i>Exoacantha heterophylla</i> , <i>Imperatoria ostruthium</i> , <i>Kadenia dubia</i> , <i>Katapsuxis silaifolia</i> , <i>Libanotis pyrenaica</i> , <i>Meum athamanticum</i> , <i>Meum nevadense</i> , <i>Oreoselinum nigrum</i> , <i>Ostericum sieboldii</i> , <i>Peucedanum officinale</i> , <i>Phlojodicarpus sibiricus</i> , <i>Pteroselinum austriacum</i> , <i>Saposhnikovia divaricata</i> , <i>Selinum carvifolia</i> , <i>Seseli gummiferum</i> , <i>Seseli hippomarathrum</i> , <i>Seseli praecox</i> , <i>Spermolepis divaricatus</i> , <i>Spermolepis echinatus</i> , <i>Tommasinia altissima</i> , <i>Trinia glauca</i> , <i>Xanthogalum purpurascens</i> , <i>Xanthoselinum alsaticum</i>
	<i>Arracacia</i> Clade	<i>Arracacia schneideri</i> , <i>Myrrhidendron donnell-smithii</i> , <i>Myrrhidendron glaucescens</i> , <i>Prinosciadium pringlei</i>
	Perennial Endemic North American (PENA) Clade	<i>Aletes acaulis</i> , <i>Cymopterus anisatus</i> , <i>Cymopterus duchesnensis</i> , <i>Cymopterus ibapensis</i> , <i>Lomatium angustatum</i> , <i>Lomatium nevadense</i> var. <i>parishii</i> , <i>Lomatium nudicaule</i> , <i>Lomatium parryi</i> , <i>Lomatium roseanum</i> , <i>Lomatium utriculatum</i> , <i>Musineon tenuifolium</i> , <i>Oreoxis humilis</i> , <i>Orogenia fusiformis</i> , <i>Orogenia linearifolia</i> , <i>Polytaenia nutallii</i> , <i>Pseudocymopterus montanus</i> , <i>Pseudocymopterus montanus</i> var. <i>multifidus</i> , <i>Pteryxia hendersonii</i> , <i>Taenidia integerrima</i> , <i>Taenidia montana</i> , <i>Tauschia arguta</i> , <i>Tauschia filiformis</i> , <i>Tauschia kelloggii</i> , <i>Tauschia nudicaulis</i> , <i>Tauschia parishii</i> , <i>Thaspium barbinode</i> , <i>Thaspium pinnatifidum</i> , <i>Thaspium trifoliatum</i> , <i>Zizia aptera</i> , <i>Zizia aurea</i> , <i>Zizia trifoliata</i>
	<i>Johrenia</i> group	<i>Dichoropetalum carvifolia</i> , <i>Ormosolenia alpina</i>
30	Pyramidoptereae	<i>Ammoides pusilla</i> , <i>Astomaea seselifolia</i> , <i>Bunium alpinum</i> ssp. <i>montanum</i> , <i>Bunium petraeum</i> , <i>Crithmum maritimum</i> , <i>Cyclospermum leptophyllum</i> , <i>Lagoecia cuminoides</i> , <i>Pyramidoptera cabulica</i> , <i>Scaligeria tripartita</i> , <i>Sison amomum</i>
31	Pimpinelleae	<i>Aphanopleura capillifolia</i> , <i>Aphanopleura leptoclada</i> , <i>Aphanopleura trachysperma</i> , <i>Hausknechtia elymaitica</i> , <i>Pancicia serbica</i> , <i>Pimpinella anagodendron</i> , <i>Pimpinella anisum</i> , <i>Pimpinella bicknellii</i> , <i>Pimpinella major</i> , <i>Pimpinella peregrina</i> , <i>Pimpinella saxifraga</i> , <i>Zeravschania aucheri</i>
32	<i>Opopanax</i> Clade	<i>Kruberia peregrina</i> , <i>Opopanax chironium</i> , <i>Visnaga daucooides</i>
33	Echinophoreae	<i>Anisosciadium lanatum</i> , <i>Anisosciadium orientale</i> , <i>Echinophora spinosa</i>
34	Coriandreae	<i>Bifora radians</i> , <i>Coriandrum sativum</i>
35	<i>Conium</i> Clade (monogeneric)	<i>Conium maculatum</i>
36	Careae	<i>Aegokeras caespitosa</i> , <i>Aegopodium podograria</i> , <i>Carum carvi</i> , <i>Carum verticillatum</i> , <i>Chamaesciadium acaule</i> , <i>Falcaria vulgaris</i>
37	<i>Cachrys</i> Clade	<i>Alococarpum erianthum</i> , <i>Bilacunaria microcarpa</i> , <i>Cachrys cristata</i> , <i>Cachrys libanotis</i> , <i>Ferulago nodosa</i> , <i>Ferulago sylvatica</i> subsp. <i>confusa</i> , <i>Prangos trifida</i>
38	Apiaceae	<i>Ammi majus</i> , <i>Anethum graveolens</i> , <i>Apium fernandezianum</i> , <i>Apium graveolens</i> , <i>Foeniculum vulgare</i> , <i>Naufraga balearica</i> , <i>Petroselinum crispum</i> , <i>Ridolfia segetum</i> , <i>Seseli webbi</i> .
Unknown (presumptions in parentheses)		<i>Agasyllis latifolia</i> , <i>Bonannia graeca</i> , <i>Dethawia splendens</i> , <i>Gasparrinia peucedanoides</i> , <i>Heptaptera triquetra</i> (<i>Cachrys</i> clade? <i>Physospermopsis</i> clade?), <i>Kundmannia sicula</i> , <i>Palimbia salsa</i> , <i>Ptychotis saxifraga</i> , <i>Synclinostyles denisjordani</i> (<i>Apiaceae</i> ? <i>Acronema</i> clade?), <i>Xatartia scabra</i> (<i>Selineae</i> ?)

Appendix 4 (attached on CD)

- (1) Detailed data on each of my Apiaceae-Apioideae study species
- (2) Processed raw data of the *Chaerophyllum bulbosum* manipulation experiments

Thanks to ...

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ERKLÄRUNG

Hiermit versichere ich, dass ich die vorliegende Arbeit selbständig angefertigt/verfasst und außer den genannten keine weiteren Quellen und Hilfsmittel verwendet habe.

Mainz

März, 2013

Kerstin Reuther