

# Monograph of *Arctium* L. (Asteraceae)

Generic delimitation (including *Cousinia* Cass. p.p.), revision of the species, pollen morphology, and hybrids

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## 1. Contents

1. Contents	1
2. Summary	3
<b>I. General part</b>	
3. Introduction	4
4. The tribe Cardueae within the Asteraceae	5
5. Species concept	6
6. Macromorphological characters	8
6.1 General habit and life span	8
6.2 Leaves	8
6.3 Synflorescence	9
6.4 Capitules (involucral bracts, receptacle, receptacular scales)	10
6.5 Pappus	12
6.6 Corolla	13
6.7 Stamens	14
6.8 Style	14
6.9 Achene	14
7. Pollen morphology	16
7.1 Introduction	16
7.2 <i>Arctium</i> and <i>Cousinia</i>	18
7.3 Materials and methods	19
7.4 Measurements	21
7.5 Results	21
8. Chromosomes	27
9. Reproduction	27
10. Chemistry and economic importance	28
11. Species delimitation in the <i>Arctium</i> minus-complex	29
11.1 Introduction	29
11.2 Material and methods	31
11.3 Results	31
11.4 Conclusions and discussion	38

- 12. The recognition of hybrids in *Arctium* section *Arctium* . . . . . 39
  - 12.1 Introduction . . . . . 39
  - 12.2 Delimitation of the species and determination of the hybrids in *Arctium* section *Arctium* . . . . . 41
  - 12.3 Conclusion and discussion . . . . . 43
- 13. Phylogeny and generic delimitation . . . . . 44
  - 13.1 Introduction . . . . . 44
  - 13.2 Phylogeny . . . . . 45
  - 13.3 Genus concept . . . . . 46
  - 13.4 The computer algorithm . . . . . 47
  - 13.5 Selection of the ingroup . . . . . 47
  - 13.6 Selection of the outgroup . . . . . 47
  - 13.7 Character states . . . . . 48
  - 13.8 Character states coding . . . . . 49
  - 13.9 Results . . . . . 56
  - 13.10 Conclusions and discussion . . . . . 63
- 14. Acknowledgements . . . . . 65
- 15. References . . . . . 65

**II. Taxonomic part**

- 16. Generic description . . . . . 69
- 17. Key to the species . . . . . 71
- 18. Descriptions of the sections and species . . . . . 72
- 19. Descriptions of the hybrids . . . . . 122
- 20. *Nomina dubiae* . . . . . 127
- 21. *Species excludenda* . . . . . 128
- 22. Identification list . . . . . 129
- 23. Index to taxonomic names . . . . . 140

## 2. Summary

The subject of this thesis is a monograph of the genus *Arctium*, now including also five species formerly placed into *Cousinia*. Based on herbarium material and some field observations, this study presents new insights on three subjects: a) the generic delimitation of *Arctium*, b) the species delimitation within the *A. minus*-complex, and c) the occurrence of hybridisation.

It soon became clear, rather surprisingly, that five species of *Cousinia* possess hooked involucre bracts like *Arctium* in its classical concept. The study became focussed then on the relation between *Arctium* in its classical delimitation and the large Asian genus *Cousinia*. From a macromorphological point of view the five 'arctioid' species of *Cousinia* should be placed in the extended genus *Arctium*. The pollen morphological study showed that most species of *Cousinia* have a pollen type which is different from the *Arctium* type. However, 30 species of *Cousinia* (all species of the subgenera *Cynaroides* and *Hypacanthoides*), including the five 'arctioid' species, share their pollen type with *Arctium* (see Chapter 7). In the phylogenetic analysis, including both macro- and pollen morphological characters, the arguments to rearrange *Arctium* against *Cousinia* got strong support. It was concluded that there were good reasons for a formal redescription of *Arctium*, now comprising 11 species belonging to 4 sections. *Arctium* section *Arctium* comprises all species of *Arctium* in its classical delimitation. The following 3 sections are new combinations: sect. *Pseud-arctium* [with 3 species: *A. (C.) amplissimum*, *A. (C.) pseudarctium* (comb. nov.), and *A. (C.) umbrosum*], sect. *Nanarctium* [*A. (C.) arctioides*], and sect. *Lappaceae* [*A. (C.) lappaceum*].

Especially troublesome was the specific delimitation in the *A. minus*-complex (see Chapter 11), resulting in the delimitation of three species: *A. atlanticum*, *A. minus* and *A. nemorosum*; *Arctium pubens* and *A. chaberti* are treated as synonyms of *A. minus*. Within the classical delimitation of the genus three more species are recognized, *A. lappa*, *A. palladini* and *A. tomentosum*. These six species are all included in *A. sect. Arctium*.

Regarding the question on hybridisation in the genus *Arctium* the following was observed. Contrary to the current opinion, hybrids appeared to be rare (see Chapter 12). They often have a higher percentage of abortive achenes than the parents. The hybrid between *A. minus* and *A. palladini* (*A. ×semi-constrictum* hybr. nov.) is recorded for the first time.

# I. General part

## 3. Introduction

The genus *Arctium* L. is a small genus within the Asteraceae and is included in the tribe Cardueae (Thistles). The species of *Arctium* are native in Europe, Northern Africa and non-tropical Asia. They occur as an alien in temperate regions elsewhere in the world. The most characteristic feature of the genus is the hooked apex of the involucre bracts. The genus name goes back as far as Dioscorides (first century, 'arkteion'). It is probably derived from the Greek 'arktos' which means 'bear', and refers to the woolly indumentum of the plants (Hegi, 1929).

*Arctium* was described by Linnaeus (1753). Many authors in the 18th and 19th century preferred the illegitimate synonym *Lappa* Scop., based on the prelinnaean work of Tournefort (1700: 450) and Plinius (first century, Hegi, 1929). This name is derived from the Greek 'labein' which means 'to hold' or 'to grasp'. It refers to the hooked involucre bracts which hold on furs and clothes.

Next to *Arctium lappa* ( $\alpha$  and  $\beta$ ) Linnaeus (1753, resp. 1767) included *A. persohnata* and *A. carduelis* in the genus. The latter, however, have since long been generally accepted as species in *Carduus* because of their spiny leaves and involucre bracts, and their scabrid pappus hairs which are united at base into a ring. Without these two species *Arctium* could be recognized by the large, unarmed leaves, the hooked involucre bracts, and the free pappus elements.

Boissier (1875) transferred the species he had formerly described as *Lappa amplissima* to the genus *Cousinia* in the same section as *C. umbrosa*. Both species have hooked involucre bracts and unarmed leaves, but, according to Boissier (1875), unlike the species of *Arctium*, they have anthers with fimbriate basal appendages.

Kuntze (1891) transferred the whole genus *Cousinia* to *Arctium*. At that time 187 species had been described in *Cousinia*, only six of which have hooked involucre bracts. His view was not followed by others, and *Cousinia* contains at present some 660 species, including the 'arctioid' species with hooked involucre bracts and anthers with (usually) fimbriate basal appendages. Both Rechinger (1972) and Schtepa (1971, 1973), considering macro- and pollen morphological variation, mentioned the close relationship of these 'arctioid' species to *Arctium*, but they did not transfer them. *Arctium* in its classical delimitation might not be a natural (= monophyletic) genus, and it therefore seemed better to analyse its relation to *Cousinia*, taking into account both macro- and pollen morphological characters.

On the infrageneric level there has been much more disagreement, both on the morphological delimitation and the taxonomical status of the taxa. The extraordinary variability tempted several authors to describe many taxa at or below the species level, as well as many (supposed) hybrids. A revision of *Arctium* should bring more stability in its taxonomy, and Arènes made an attempt in 1950. He divided the genus into two sections with two species each, based on the absence or presence of glandular hairs on the corolla. He described 22 taxa within the 4 species, and he recognized 11 hybrids. Unfortunately, his revision did not bring stability. The majority of the European floras recognize the taxa '*lappa*', '*tomentosum*', '*minus*', '*pubens*',

and '*nemorosum*', either as species or as subspecies. The inflorescences of the first two taxa, which are invariably recognized as species, are corymbose, whereas the other three taxa are racemose to subcorymbose. Most European authors agree about the delimitation of the corymbose species, although in Asia another six corymbose species were recognized. Considerable differences of opinion can be found in the European floras as far as the treatment of the non-corymbose species (the *Arctium minus*-complex) is concerned. The character states by which the taxa are delimited are not compatible, sometimes even conflicting, and the taxonomical rank at which the taxa are recognized differs. In many floras it is reported that hybrids would occur frequently. Sometimes *A. pubens* is supposed to be of hybrid origin. The delimitation of the species is far from clear, and a new revision of the genus is, therefore, highly needed. The results are presented in the present paper.

#### 4. The tribe Cardueae within the Asteraceae

Although containing a vast number of species on a worldwide scale, the Asteraceae are easily recognized as a family. The most obvious character is found in the capitules in which usually a number of flowers are placed on a common receptacle. The flowers are subtended by one or several rows of involucre bracts, and consist of an inferior ovary, a sympetalous corolla, five usually fused anthers, and a style with two branches. The family comprises approximately twenty thousand species in 1300 genera (Bremer, 1987).

Cassini (1816–1830) proposed a classification for the family with 19 tribes. Bentham & Hooker (1873), based on Cassini, recognized 13 tribes, and, with some modifications by Hoffmann (1890–1894), this classification has long been accepted. Recently, several authors suggested the delimitation of more tribes. I will discuss here only the tribe in which *Arctium* is included, the Cardueae.

The tribe Cardueae dates from Cassini (1816–1830), while the much used name Cynareae Less. is a later synonym. This tribe includes both armed Thistles, as *Cirsium*, *Echinops*, and *Carlina*, and unarmed representatives like *Arctium* and many species of *Centaurea*. Several authors recognized four subtribes within the tribe, the Carduinae, the Centaureinae, the Carlininae, and the Echinopsidinae (Boissier, 1875; Hoffmann, 1890–1894). As Dittrich (1977) remarked, the characterisation of both the tribe, as well as the subtribes is problematical when the characters traditionally assigned to them are used. These characters are the thickened, hairy articulation of the style (the cynaroid type), the absence of female or ligulate ray florets, a lateral or a basal hilum, the pubescence of the achene, and the arrangement of the pappus elements. Based on many more characters than the traditional ones, Dittrich divides the 'super-tribe' Cynaroideae into three tribes, Echinopeae, Carlineae, and Cardueae. The latter is further divided into two subtribes, the Carduinae (including *Arctium*), and the Centaureinae.

Bremer (1987) performed a cladistic analysis of the Asteraceae involving 27 (sub-) tribes. As a result, the Carlineae, Echinopeae, Cardueae, and the mainly South African tribe Arctoteae together constitute a monophyletic group, which is characterized by the cynaroid type of style. The phylogenetic relation between the four tribes is, how-

ever, not resolved. Petit (1990) performed a cladistic analysis of the Cynaroideae at the generic level. His results agree with the (sub-)tribal classification of Dittrich (1977). Therefore, I adhere to this classification, which divides the tribe Cardueae into two subtribes, the Carduinae and the Centaureinae.

## 5. Species concept

Many species concepts exist, which may be reduced to three basic concepts, the morphological, the evolutionary, and the internodal species concept. Each of these concepts accommodates one of the intuitions we have about species: they should be recognizable, reproductively isolated, and mutually exclusive. The problem is that the concepts are incompatible when we attempt to combine them on a footing of equality.

I largely follow the composite species concept which is developed by Kornet (1993), and which is based on the internodal species concept of Hennig (1966). Starting point of Kornet is the idea that all organisms have descended (at least indirectly) from sexually reproducing ancestors. Consequently, they are part of a genealogical network. She then divides the network into internodons by permanent splitting events. The allocation of organisms to internodons is based on parental relations only. If (the descendants of) two individuals produce offspring, they are part of the same internodon; no information about common ancestry is needed.

Internodons are mutually exclusive, which is an important criterion for species. However, they are thought to be too short-lived to be regarded as species, because every time a complete family (father, mother and all their children) is killed an internodon dies. Therefore, several internodons are grouped together to form a composite species. As a criterion for grouping Kornet introduced quality  $Q$ . The first internodon exhibiting quality  $Q$  is the start internodon of a composite species. All internodons descending from it, and not having quality  $Q$  themselves belong to the same composite species. For  $Q$  Kornet (1993) chose a morphological criterion, the first time of majority fixation of a character state. Majority fixation means that the character state outnumbered all other states of the same character present in the internodon. It follows that not all organisms of a composite species need possess that character state. Also, the presence of a character state is not evidence for an organism to belong to a certain species. The character state may well have its origin in an ancestor internodon, which split up whereby the character state was distributed over the two sister internodons. In one internodon the character state reached majority fixation, in the other it did not, but neither did it disappear entirely. This may seem very unpractical, and one may ask why not full fixation of a character state is used as a criterion. Then, at least all organisms of a species have the character state, not excluding the possibility that some organisms belonging to another composite species share this character state. This option was not chosen by Kornet (1993), because this would probably lead to entities that are too large. Especially when states follow each other rapidly, full fixation might never be reached. Thus, for an organism to belong to a certain composite species, it is neither sufficient, nor necessary to possess a certain character state.

The primary criterion for this composite species definition lays in the parenthood relationships. Morphology is used as a second level criterion. The herbarium tax-

onomist, of course, does not know the parenthood relations of the (small sample of herbarium) specimens. It is his/her task to estimate them, and the only available information is often the morphology (from molecules to macromorphology). Because a composite species does not need to have a single, unique character state, the estimation may be improved if combinations of character states are evaluated. Also, the delimitation of states, especially in quantitative characters with continuous variation, is often very difficult and subjective if the variation of other characters is not taken into consideration. This corresponds with recommendation number 14 of Van Steenis (1957: CCXXV), which is in current use by many taxonomists. It dictates that, if only one differentiating morphological character can be found, "the separation will mostly prove to be artificial."

If a (slightly overlapping) difference in morphology in only a single character is found, which is also sustained by geographical or ecological information, taxa are recognized at subspecific level (subspecies and varieties). However, there is no theoretical support in the composite species concept for the recognition of infraspecific taxa. Therefore, I do not wish to use them in the revision of *Arctium*. In some cases, however, it can be useful to classify infraspecific variation, for instance in horticulture or ecological interpretations of floristic inventarisations. But, philosophically speaking, they are not individuals, existing in nature, but artificial, purely utilitarian classes.

Agamospecies are clones of asexually reproducing organisms. These clones are so uniform and recognizable, that it is tempting to describe each 'population', which in fact exists of only one individual, as a separate species, agamospecies. In the composite species concept they cannot be regarded as real species, because they lack the parenthood relation.

The demand of permanent splittings in the definition of internodons also has serious consequences for the interpretation of hybrids, because a hybridisation makes a split in the genealogical network a temporary one. According to Kornet (1993: 49) the parents have to be united into one composite species. However, the parenthood relation can be qualified in such a way that the vitality or fertility of the offspring is taken into account, or that it excludes artificially produced hybrids as offspring uniting two internodons. This caters for the intuition of many taxonomists, who do not like the lumping of otherwise well characterized species, which only very incidentally form hybrids.

According to Stace (1989), a fertility of 0.1 % can be highly significant in evolutionary terms. A consequence could be that the assumption of hybridisation between composite species is only acceptable in case the hybrid is completely sterile. However, many hybrids with reduced fertility produce hybrid swarms which locally blur the delimitation of species which are otherwise well characterised. I mention *Anchusa*  $\times$  *baumgartenii* Nym. (= *A. officinalis*  $\times$  *A. ochroleuca*), *Dryopteris*  $\times$  *deweaveri* (J. Jansen) P. Jansen & Wachter (= *D. carthusiana*  $\times$  *D. dilatata*), *Geum*  $\times$  *xintermedium* Ehrh. (= *G. rivale*  $\times$  *G. urbanum* as examples from the Dutch flora (Van der Meijden, 1990). In some genera hybridisation, within and between sections or subgenera, with (partly) fertile offspring is known between so many species that almost all species of the genus should have to be lumped into a single species. (e.g. *Mentha*, *Salix*). Therefore, I prefer a narrower definition of the parenthood relation.

Parent species often grow together without forming hybrids. Special circumstances, such as recent disturbance of the habitat, seem to stimulate the process (Stace, 1989: 141). I suggest that hybridisations which have taken place under such special circumstances should be excluded from the parenthood relation, and that the parents may be accepted as separate species. I also suggest that hybridisations resulting in fully sterile offspring, or produced under artificial circumstances (also unwittingly, e.g. between an ornamental garden plant and a wild plant) should be excluded from the parenthood relation.

## 6. Macromorphological characters

In the following I describe the variation of the macromorphological characters of the six species of *Arctium* sect. *Arctium* (which is the genus in its classical delimitation), and the five former species of *Cousinia* with hooked involucre bracts which are now included in the extended genus *Arctium*, i.e. *A. amplissimum*, *A. arctioides*, *A. lappaceum*, *A. pseudarctium*, and *A. umbrosum* (see Chapter 13). I define *Arctium* s.l. as including all species of *Arctium* sect. *Arctium* and the five former species of *Cousinia*. I include the following species in the *A. minus*-complex: *A. atlanticum*, *A. chaberti*, *A. minus*, *A. nemorosum*, and *A. pubens*. (See Chapter 11.)

### 6.1 General habit and life span

The species of *Arctium* s.l. are usually up to 2½ m high, bushy herbs with a taproot. The main axis arises from a rosette of leaves (the basal leaves), and is generally much branched. Sometimes, as in *A. arctioides*, several axes arise simultaneously from the rosette. The stem and the branches are either glabrous or glandular-hairy and arachnoid. The glandular hairs are short. The white arachnoid indument consists of long tousled hairs which form scattered flocks along the axes.

The five former species of *Cousinia* are, as far as I know, perennials, producing flowers for several successive years. The plants of *Arctium* sect. *Arctium* are monocarpic hemicryptophytes. The seeds germinate in spring and grow into a rosette of leaves. The emergence of seedlings is reduced by the presence of litter and vegetation. The rosette leaves die back in the autumn, and, when the rosette has reached a critical minimum size in its first year, it will produce a flowering specimen the next year. If the critical size was not reached flowering will be delayed for one or several years. In places with high densities of grasses and other herbs the plants generally take four years to flower (Gross & Werner, 1983).

### 6.2 Leaves

The basal leaves of all species are unarmed, and, except in *A. lappaceum*, petiolate. The base of the petioles is hollow or solid (see Fig. 6.1). This character proved to be constant in some species (e.g. solid in *A. lappa*, hollow in *A. minus*, and *A. nemorosum*), but is variable in other species (e.g. *A. tomentosum*).

The blades of the basal leaves are in most species very large, up to 80 cm long in *A. lappa*, and cordate at base. The blades of *A. arctioides* and *A. lappaceum* are considerably smaller (and narrower) compared to those of the other species of *Arctium*



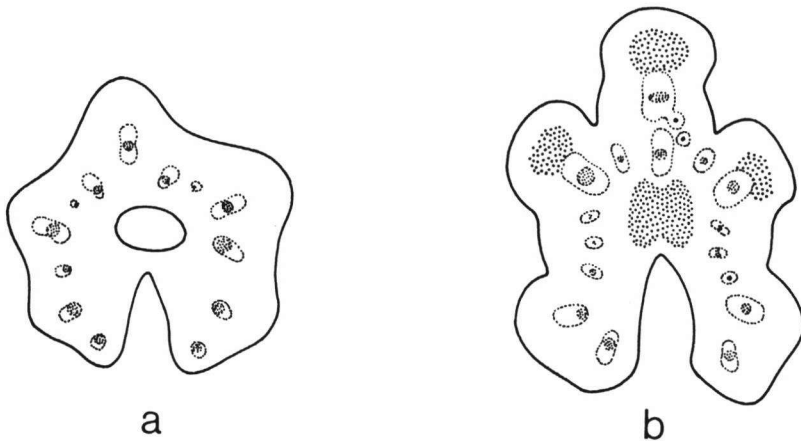


Fig. 6.1. Cross section of the base of the petiole of a basal leaf: a. hollow; b. solid.

s.l., and attenuate-cuneate at base. The shape varies from orbicular (index 1.0) to lanceolate (index 5.5). Between the species there is considerable overlap in the index. The margin varies from shallowly undulating to lobed.

The cauline leaves are alternate. Higher in the synflorescence the blades are smaller, and cuneate at base. The upper leaves, especially those on the peduncles of the capitules, are often asymmetrically developed. They are usually unarmed, but in *A. lappaceum* and *A. arctioides* they are spiny-dentate. The latter species also has 1–3 pairs of spines at the base of the upper cauline leaves. This is a unique character for the species.

The petioles have the same type of indument as the stem and branches. The lower side of the leaves, both basal and cauline, is often densely covered with white lanuginose or tomentose hairs. Between those hairs many small vitreous globules of less than 1 mm diameter can often be found, but were not observed in *A. amplissimum*, *A. lappaceum*, and *A. umbrosum*. Their origin is not known, but they are probably excretion products. In the descriptions I refer to them as ‘minute glassy globules’. The upper side of the leaves of *A. lappaceum* is glabrous. The other species have short, rather inconspicuous, uni- and multicellular hairs on the upper side of both the basal and the cauline leaves; they are only visible when using a strong handlens.

### 6.3 Synflorescence

The synflorescence of most species of *Arctium* s.l., with the exception of that of *A. arctioides*, is repeatedly branched, and consists of tens or hundreds of capitules. The type of synflorescence has always been considered very important for the identification of the species of *Arctium* sect. *Arctium*. The synflorescence ranges from strictly racemose to corymbose (see Fig. 6.2b resp. a). Corymbose are those of which the peduncles of the lower capitules are so much longer than those of the upper ones, that all capitules reach about the same level (e.g. *A. lappa*). Racemose are all those of which the lower capitules never reach the level of the apical capitules. In the latter type

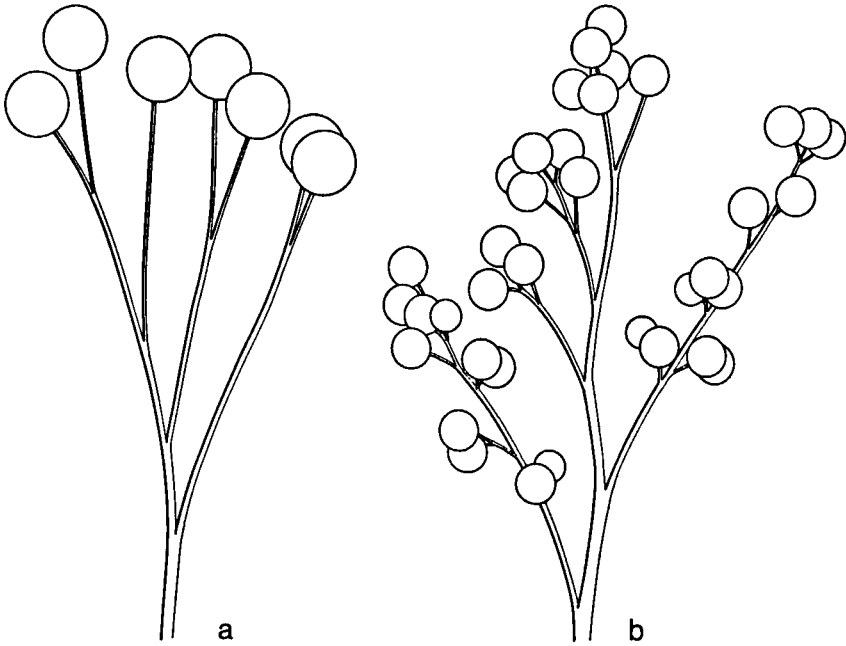


Fig. 6.2. Schematic representation of the two types of synflorescence: a. corymbose; b. racemose.

of synflorescence the sessile capitules can form dense clusters (e.g. *A. amplissimum*). In intermediate forms, often described as subcorymbose, only some capitules of the synflorescence more or less reach the same level.

The synflorescence is best developed in the terminal part of the main axis. In the lower parts the capitules are smaller, and shorter pedunculate. A corymbose specimen is often so only in the terminal part of the main axis, whereas its lower branches are often racemose. Many people tend to collect just these atypical lower branches, because they can be more easily detached from the stem than the apex, for the collection of which one at least needs a knife. Collections consisting of branches can sometimes be recognized in the herbarium by the presence of rest fibres of the stem at the base of the branch. Because collections of this type are common, and because the delimitation of racemose and corymbose is not discrete, I prefer not to use this character for the identification of the species.

6.4 Capitules (involucral bracts, receptacle, receptacular scales)

The capitules are homogamous, as is usual in the Cardueae (female or neutral ray flowers are known in *Centaurea* and related genera). Size, shape, and amount of indument of the capitules vary between the species, but also within a single species. The capitules of *Arctium* s.l. range from 0.8 to 4.7 cm diameter (including the patent parts of the involucral bracts), they may be spherical to ovoid, and glabrous to densely arachnoid tomentose. Some species have up to 25 flowers per capitule, but most species, including those of *Arctium* sect. *Arctium*, have capitules with more than 40 flowers.

The many involucre bracts are imbricate, arranged in a series of descending curves or parastichies (in the descriptions referred to as 'rows'). They are usually herbaceous, but in *A. lappaceum* they are coriaceous. The apex of at least the outer and middle involucre bracts is hooked, describing at least a semi-circle (see Fig. 6.3). The presence of the hooked apex of the involucre bracts in *Arctium* s.l. is unique within the Cardueae. *Xanthium* (Tribus Ambrosineae) has developed independently involucre bracts with somewhat hooked spines. The margin of the involucre bracts of all species of *Arctium* s.l. bears short glandular hairs; large, sessile glands on the margin of the involucre bracts are unique for *A. umbrosum*.

The length and width of the outer involucre bracts is variable within many species, and in some specimens (sometimes treated as f. *monstruosa* or f. *foliosa*) they are leaflike. They illustrate the generally accepted view of Napp-Zinn (1951, 1956) who stated that the involucre bracts should be considered as reduced leaves.

The middle involucre bracts usually are less variable. They can be divided in a basal, convex, and appressed part which is the widest part of the middle involucre bracts, and an apical part which is patent to deflexed (see Fig. 6.3). The inner involucre bracts of most species are gradually narrowing from halfway towards the apex. In *A. palladini* and *A. tomentosum*, however, they are constricted in the middle and widened just below the apex. The involucre may be entirely glabrous, as in *A. lappaceum* and often in *A. lappa*, or more or less densely hairy. The indument of the involucre may be lanate and appressed to the basal part of the involucre bracts as in *A. pseudarctium* and *A. umbrosum*. In many other species (e.g. *A. minus*, *A. nemorosum*, and *A. tomentosum*) the apical, patent to deflexed part of the involucre bracts is (densely) arachnoid hairy, while the dorsal side of the basal part is glabrous or has only very short, stiff hairs. The width of the involucre bracts is diagnostic for some species (e.g. *A. nemorosum*), whereas the length of the apical part relative to the total length of the involucre bract is of importance for the recognition of other species (e.g. *A. atlanticum*).

Within all species of *Arctium* s.l. the inner involucre bracts are variable in length, width, and index. In most species they are linear, and acute to acuminate, gradually narrowing towards the apex. In some species, however, they are widened just below the apex, and acuminate to truncate at apex (*A. palladini* and *A. tomentosum*; see Fig. 6.4).

The receptacle is flat or subconcave, and, as is the case in most Cardueae, densely covered with scale-like hairs between the ovaries. According to Warning

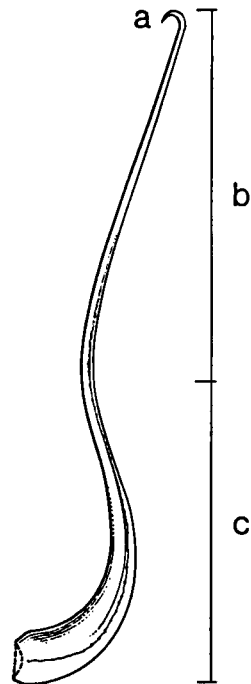


Fig. 6.3. Lateral view of middle involucre bract: a. hooked apex; b. patent or deflexed apical part; c. appressed basal part.

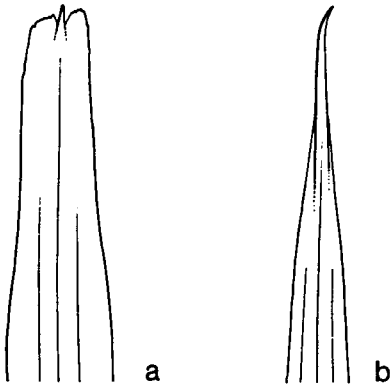


Fig. 6.4. Apex of the inner involucre bract: a. truncate; b. acute.

In *Arctium* s.l. the receptacular scales are rather uniform, linear, flat, without vascular bundles, and acute. In some species (e.g. *A. tomentosum*) they are somewhat wider than in other. Within a capitule the scales vary enormously in length. The length of the longest receptacular scales in a capitule proved to be useful in separating *A. amplissimum* and *A. umbrosum*. The receptacular scales of some species of *Cousinia* subg. *Cousinia* are slightly widened near the apex, spatulate.

(1876) [from Napp-Zinn (1951)] they are to be considered as split bracts or 'setae' (paleae). Napp-Zinn (1951, 1956), however, views them as outgrowths or appendages ('Emergenzen') of the receptacle, because of the random distribution between the flowers, their independent origin in the receptacle, the differences in anatomical structure with the real setae of the Carlininae, and the coexistence of these scale-like hairs and setae in some Dipsacaceae. The occurrence of both scales and setae in a single capitule is an argument against the theory that the two structures are homologous, and I therefore refer to them as receptacular scales.



Fig. 6.5. Pappus hair with serrate margin.

### 6.5 Pappus

At first glance it is tempting to view the pappus of the Asteraceae as homologous with the calyx in related families. A pappus consisting of five scales, as occurs in some Heliantheae, has to be considered as primitive then. From the cladistic analysis of Bremer (1987) it is very unlikely that a Heliantheae-like taxon with five pappus-scales was the ancestor of the Asteraceae. Also, a developmental study of the pappus showed that a pappus of many parts has to be considered as primitive [Robinson (1981); reference in Bremer, 1987]. Consequently, the homology of the pappus still remains uncertain.

Unlike the pappus of most Cardueae, the pappus of *Arctium* s.l. and most species of *Cousinia* (Rechinger, 1972), consists of a few rows of free, deciduous bristles with a serrate margin (Fig. 6.5). In *Arctium* s.l. they are within a flower of unequal length, the outer being shorter than the inner. This is in contradiction with Dittrich (1970), who stated that the pappus

elements of all Carduinae (*Jurinea* and *Saussurea* excepted) are of equal length. In the descriptions, I mention the length of the longest bristles only.

In most Cardueae (Dittrich 1970), and in *Cousinia tenella* (my own observation) the pappus elements are connected through a special, ring-shaped tissue, falling off as a unity. In *Cousinia astracanica* the pappus consists of a dentate corona, according to Moore in Tutin et al. (1976: 215). In *Onopordum* the bristles are basally connate, not connected through a special tissue, but also detaching as a unity.

## 6.6 Corolla

The corolla is tubular-campanulate, consisting of a tube and a limb (see Fig. 6.6). Where the tube changes into the campanulate limb the filaments of the stamens are inserted. This insertion point can be seen from the outside as a slightly darker ring. The tube of the Cardueae is generally long and S-shaped (Dittrich, 1977). However, in some species this S-shape is not always very pronounced, and in *A. amplissimum* and *A. umbrosum* the tube is only 2 mm long and straight. For the majority of the species of *Arctium* s.l. the limb takes up 2/5 to 3/5 of the total corolla length, which is usual for the Cardueae. In some species, however, this amounts to 4/5 (e.g. *A. amplissimum*, *A. umbrosum*). The corolla has normally 5 lobes, but incidentally corollas may be 4-, 6- or 7-lobed; the flowers then have the same number of stamens, and are considered as aberrations. The incisions of the limb are more or less regular, the abaxial lobes are at most 0.4 mm longer than the adaxial. In the descriptions I mention only the length of the longest (abaxial) lobe. In *A. lappa*, *A. lappaceum*, *A. palladini*, and *A. tomentosum* the lobes take up 2/5 to 3/5 of the limb; in *A. amplissimum* this is only 1/5 to 1/4. The other species are intermediate. Some taxonomical value of the relative length of the limb and the lobes was also demonstrated in *Ptilostemon* (Greuter, 1973).

The corolla may be glabrous or glandular hairy. *Arctium amplissimum*, *A. arctioides*, *A. lappaceum*, *A. palladini*, and *A. tomentosum* always have glandular hairs on the corolla. The corolla of *A. atlanticum* and *A. nemorosum* is always glabrous. The other species are variable in this respect. In the *A. minus*-complex the glandular hairs were hitherto mentioned for specimens from South Europe only. Such specimens were regarded as a separate species, *A. chaberti*. However, I have seen abundant material of *A. minus* from Northwestern Europe with glandular hairs (see Chapter 11). Arènes (1950) recognized two sections within *Arctium* sect. *Arctium*, sect. *Glandulosa* and *Eglandulosa*, based on the presence resp. absence of glandular hairs on the corolla (see Chapter 13).

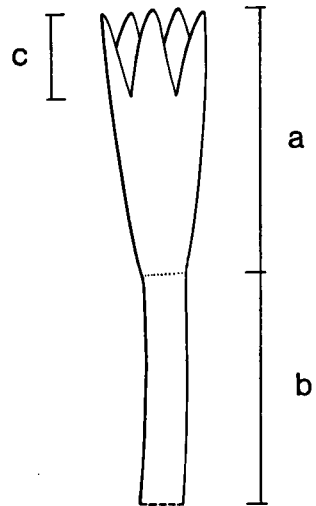


Fig. 6.6. Tubular-campanulate corolla: a. limb; b. tube; c. lobes.

### 6.7 Stamens

The five filaments of the stamens are attached to the corolla at the articulation between tube and limb, and alternating with the lobes. Arènes (1950) stated that the filaments of *Arctium* sect. *Arctium* are glabrous, and Dittrich (1977), in his systematic review of the Cynareae, mentioned this for both *Arctium* and *Cousinia*. However, I have seen glabrous, verrucate, and sometimes even papillose filaments in both genera. They are indeed never hairy as in, for instance, *Carduus*. The length of the filaments is measured from the insertion on the corolla to the split of the basal appendages.

In the Asteraceae, except in *Xanthium*, the 5 connate anthers form a tube (Gerdt, 1905). The anthers of the Cynaroideae are caudate, which means that they have sterile, branched or simple, basal appendages (see Fig. 6.7). Boissier (1875) mentioned that they are simple in *Lappa* (= *Arctium*) and fimbriate in *Cousinia* (including the 'arctioid' species). Until the present day this character has been considered as diagnostic for the two genera. However, I have seen specimens with branched basal appendages in all species of *Arctium* sect. *Arctium*, and unbranched appendages in *A. arctioides*. Sometimes, as in some specimens of *A. umbrosum*, the basal appendage is only minutely developed.

The apical appendage is not soft, but somewhat coriaceous. The apex is acuminate, and slightly bent inward as to close the anther tube. The length varies within and between the species. Generally the apical appendage is glabrous. The presence of hairs on its dorsal side in *A. amplissimum*, *A. pseudarctium*, and *A. umbrosum* is here recorded for the first time. The length of the anther is measured including the sterile basal and apical appendages.

### 6.8 Style

The typical Cynaroideae style can be divided into three parts (Briquet, 1916; Greuter, 1973; Dittrich, 1977): the base, the scape and the tip (stylar apex; see Fig. 6.8). The scape is glabrous and cylindrical. The stylar apex is defined as the apical part starting from the thickened articulation which bears a ring of sweeping hairs. The branches of *Arctium* sect. *Arctium* and *A. arctioides* take up at least 60% of the stylar apex. The species of *A. amplissimum*, *A. pseudarctium*, *A. umbrosum*, and *A. lap-paceum* have stylar branches which are shorter than 50% of the length of the stylar apex. Such variation also occurs in *Ptilostemon* (Greuter, 1973). The unbranched part of the stylar apex is often covered with stiff hairs which are shorter than the sweeping hairs. It is interesting to note that the style of (many species of) *Cousinia* subg. *Cousinia* is very different from the typical Cynaroideae style. A stylar apex cannot be recognized, because a thickened articulation with a ring of sweeping hairs is absent; the branches and the apical part of the scape are covered with long hairs. This type of style very much resembles what Bremer (1987) called the 'vernonioid' style, and has not been recorded for the Cardueae before.

### 6.9 Achene

The Asteraceae have a 1-seeded, dry fruit developed from an inferior ovary, with the pericarp more or less adhering to the testa. De Candolle (1813) proposed to restrict the term 'achene', which formerly included all dry and closed fruits, to this type

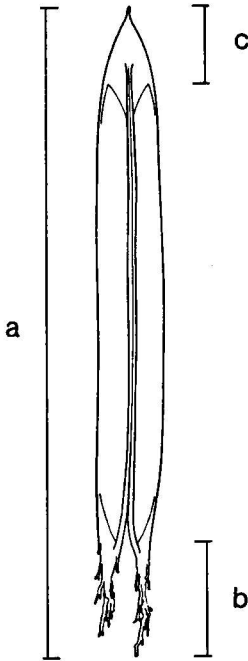


Fig. 6.7. Anther (a) with branched basal appendages (b), and acuminate apical appendage (c).

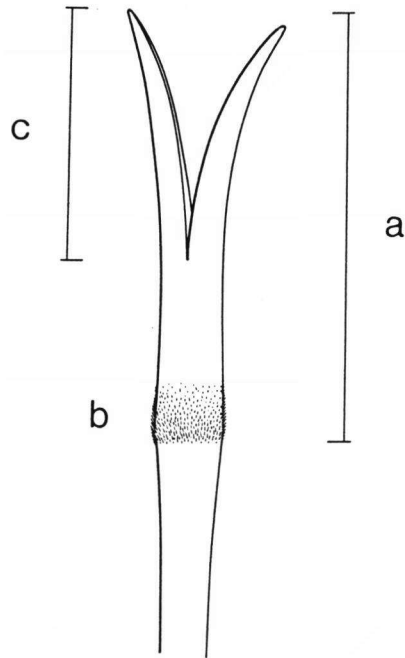


Fig. 6.8. Apical part of the style showing the styler apex (a) including the ring of sweeping hairs (b) and the branches (c).

of fruit. Mirbel (1815; from Wagenitz, 1976) introduced for the Asteraceae fruit the term 'cypsela' which is frequently used in Anglo-Saxon literature (e.g. Stearn, 1966; Fahn, 1990), while the term 'achene' was used to describe fruits which developed from a superior ovary. I follow Wagenitz (1976), who advised to use the term 'achene', as defined by De Candolle.

The achenes of the Carduinae all have a basal hilum. The embryology has been summarized by Dittrich (1977). For the anatomy of the wall of the achenes of the Cardueae the reader is referred to Dittrich (1966), Gerdts (1905), Singh & Pandey (1984; also some embryology), and Tscherneva & Shurukhina (1979; *Cousinia*).

The achenes of both *Arctium* s.l. and *Cousinia* are glabrous, and they are either smooth, or they are rugose and have longitudinal ridges. A number of species has a marginal ridge, a crown-like structure at the apex (see Fig. 6.9), which may be conspicuous (*A. arctioides*) or inconspicuous (*Arctium* sect. *Arctium*). I consider a ridge as conspicuous when it is 0.3–0.4 mm high, measured from the lowest point of the apical plate; a ridge is inconspicuous if it reaches only 0.1–0.2 mm. The ridge is often dentate, but in *Arctium* section *Arctium* sometimes entire.

The centre of the apex is called the apical plate. Dittrich (1977) recognized three different types, the Carlineae-, the Echinopeae-, and the Cardueae-type. The latter occurs in all genera of the two subtribes of the Cardueae. Within *Arctium* sect. *Arctium* and *A. arctioides* the apical plate is truncate. The apical plate of *A. amplissimum* and



Fig. 6.9. Apical part of achene without (a) and with (b) a marginal ridge. Both have a truncate apical plate.

*A. umbrosum* is flat, and a marginal ridge is not present. This is much reminiscent of the apical plate of *Notobasis* and *Ptilostemon* (Dittrich, 1970; Greuter, 1973). *Arctium pseudarctium* takes an intermediate position; the apical plate is somewhat truncate, and a margin is absent. The achenes of *A. lappaceum* are again of a different shape. The apical plate is somewhat truncate, and bordered by a slight depression around the scars of the pappus. According to Dittrich (1977) modifications to the three basic types can be diagnostic for different genera or groups of genera.

## 7. Pollen morphology

### 7.1 Introduction

*Asteraceae* — Wodehouse (1926, 1928) made the first detailed pollen morphological study of the *Asteraceae*. He described three major ornamentation types, psilate, echinate, and lophate. As the most persistent and characteristic feature he claimed the presence of three furrows each enclosing a germinal aperture. A recent overview of the pollen morphology of the *Asteraceae* is given by Skvarla et al. (1977). The following paragraph is largely based upon this work.

The pollen wall, as in most seed plants, consists of two layers, the exine and the intine. They are of different chemical composition, and the latter is not resistant to acetolysis. Within the exine two major layers can be discerned, of which the inner is the endexine. The outer layer, the ectexine, consists of the basal foot layer, followed by a columellate infratectum, and the tectum. The foot layer is uniform, showing minimal variations in thickness. The infratectum shows an enormous amount of variation with respect to internal organisation and to the form of the columellae. Between the foot layer and the infratectum a cavity may be present (exine caveate) or absent (exine non-caveate). The tectum usually consists of one or several layers of tectal columellae. Its surface is psilate, scabrate, echinate or lophate, and is often perforate. The echinae may be hollow or partly filled with tectal columellae, and their bases may be related to infratectal columellae or not. The apertural system of the family is usually denoted as tricolporate.

In the pollen of the *Asteraceae* four main exine types can be recognized, which are determined by the internal structure of the exine (Skvarla et al., 1977): the Anthemoid type, the Helianthoid type, the Arctotiid type, and the Senecioid type. According to



Skvarla et al. (1977) the species of the 'super-tribe' Cynaroideae have pollen of the Anthemoid type. This pollen type is non-caveate (columellae not separated from the foot layer), and its exine has infratectal columellae and one or several layers of tectal columellae.

*Cynaroideae* — The systematic study on the pollen of the 'super-tribe' Cynaroideae was initiated by Wagenitz (1955), working on the pollen morphology and systematics of *Centaurea*. Schtepa (1958; from Qaid, 1990) studied the 'super-tribe' Cynaroideae and Avertision (1964; from Qaid, 1990) analysed the pollen of the subtribe Centaureinae. Dittrich (1977) recognized three main pollen types in the 'super-tribe' Cynaroideae. As the basic type he denoted spherical, coarsely echinate, tricolporate pollen with an exine showing tectal as well as infratectal columellae (e.g. *Onopordum*, *Carlina*, and *Serratula*). This type corresponds to the *Serratula* type of Wagenitz (1955), and fits in the Anthemoid type of Skvarla et al. (1977). The second type evolved through reduction of the infratectal columellae (e.g. *Galactites*, *Centaurea* p.p.), which are either very short (exine non-caveate), or absent (exine caveate). In the latter case the echinae on the tectum are often reduced too. The grain shape is spherical to oblong. This type resembles the Helianthoid type of Skvarla et al. (1977), which was not mentioned by Skvarla et al. for the Cynaroideae. *Arctium* and *Cousinia* constitute, together with other genera (e.g. *Centaurea* p.p., *Echinops*), the third type, which has reduced echinae and usually an oblong grain shape. The infratectal columellae are present. This type more or less resembles the Anthemoid type of Skvarla et al. (1977). According to Dittrich (1977) the two derived types most probably have developed several times in the Cynaroideae. The reduction of echinae has independently taken place in three ('super-')tribes of the Asteraceae: in the Mutisieae where all species have pollen without echinae, in the Anthemidae in several closely related genera, and in the Cynaroideae.

Qaid (1990) analysed the pollen of 152 Mediterranean species, belonging to 39 genera of the 'super-tribe' Cynaroideae, and presented pollen keys to all genera and infrageneric taxa. Qaid performed a phenetic analysis and in his general conclusions he mentioned 7 classes (p. 157–159). He did not give detailed pollen morphological descriptions of these classes, and his data are arranged in such a manner that their characters are difficult to detect. *Arctium* is grouped with genera from various tribes, mostly from the Cynaroideae, based on the presence of branched infratectal columellae: *Atractylis* p.p., *Carlina*, *Chamaeleon*, *Cirsium*, *Cyanopsis*, *Cynara*, *Dicoma* (tribe Mutisieae), *Jurinea*, *Mantiscalca*, *Saussurea* p.p., *Serratula*, *Stemmacantha*, *Voluntaria*, and *Xeranthemum* p.p.; *Cousinia* and *Atractylis* p.p. constitute a separate class, based on the presence of obtuse echinae ('épines mousse').

Dimon (1971) studied the aperture system in the pollen of 33 species of the 'super-tribe' Cynaroideae and some species of other tribes. She described tripartite apertures, each consisting of an outer aperture in the tectum, a median aperture in the foot layer, and an inner one in the endexine. Vasanthy (1978) proposed to name these ecto-, meso-, and endoaperture respectively, and to apply these terms in a relative way, not considering their position in the stratigraphy of the exine. Thus, the mesoaperture is an aperture between the ecto- and endoaperture. Tormo-Molina & Uberta-Jiménez (1990) recognised the tripartite nature of the apertures in Cardueae pollen,

but, based on SEM and TEM observations, they associated the ectoaperture with the tectum and infratectum, the mesoaperture with the foot layer and the outer endexine, and the endoaperture with the inner endexine. They also noted that the endoapertures may be connected by endosculptured areas, which, together with the endoapertures, form a relatively thin equatorial exine zone, the endocingulum. Wagenitz (1955) described this structure in *Centaurea* pollen as a ring-shaped furrow, not always very conspicuous, and in some cases accompanied by heavy costae. Qaid (1990) distinguished an ecto-, meso-, and endoaperture, the meso- and endoaperture being sometimes hard to tell apart. Although illustrated in several of his plates as a relatively light equatorial zone, he did not mention the endocingulum.

## 7.2 *Arctium* and *Cousinia*

Pollen of *Arctium* was first studied by Ikuse (1956). He designated the pollen of *A. lappa* as tricolporate, and  $40\text{--}41 \times 39\text{--}40 \mu\text{m}$ . Qaid (1990) described the pollen of *A. lappa*, *A. minus*, and *A. sylvestris* (= *A. atlanticum*). He mentioned for *Arctium*:  $P \times E = 45\text{--}51 \times 38\text{--}48 \mu\text{m}$ ,  $P/E = 1.06\text{--}1.20$ , tectum with echinae wider than long, and not connected by ridges (ridges do occur in, for instance, *Galactites tomentosa*, l.c. pl. 27-4), average diameter of the perforations  $0.2 \mu\text{m}$ , tectal columellae in two layers, infratectal columellae simple and branched, endoaperture a pore with acute equatorial ends.

Schtepa (1966) investigated the pollen of over 160 species of *Cousinia*, and discussed the affinity with *Arctium* sect. *Arctium* based on pollen morphology. In 1971 she stated that six species of *Cousinia* (including four species and a synonym which I transfer to *Arctium*, and *C. anomala*), whose pollen is identical to that of *Arctium*, should be placed in *Arctium*. Later on she demonstrated that all investigated species of *Cousinia* (subgenera *Cynaroides* and *Hypacanthoides*) have the spheroidal, echinate pollen type of *Arctium*, whereas other species of *Cousinia* (subgenus *Cousinia*) have oblong, scabrate pollen (Schtepa, 1976).

The morphology and ultrastructure of *Cousinia* pollen has also been studied by Kuprianova & Tscherneva (1982), who selected 28 species of this vast genus and compared the pollen to that of *Arctium tomentosum* and *Centaurea cyanus*. They confirmed the results of Schtepa, that *Cousinia* has two different pollen types. The 12 species selected from *Cousinia* subg. *Cousinia* all showed to have prolate ( $P/E: 1.5\text{--}1.9$ ), scabrate or microechinate pollen with obvious equatorial costae. The polar axis  $P$  is  $(32.4\text{--})43.2\text{--}64.8(-72.0) \mu\text{m}$ ; the equatorial diameter  $E$  is  $(28.6\text{--})32.4\text{--}36.0(-45.0) \mu\text{m}$ . The exine is conspicuously thinner at the poles than at the equator. The tectum is perforated. They referred to this type as to the *Cousinia* type, which is identical to the *Centaurea cyanus* type of Faegri & Iversen (1950) and Wagenitz (1955). Qaid (1990) analysed the pollen of seven species of *Cousinia*, which all have the *Cousinia* type. His data supplement the above description of this type:  $E = 26\text{--}38 \mu\text{m}$ ,  $P/E = 1.31\text{--}1.58$ , the obtuse echinae are less than  $1 \mu\text{m}$  long and wide, the average diameter of the perforations is  $0.03 \mu\text{m}$ , the endoaperture is rhomboid, rectangular, or elliptic.

The other type of Kuprianova & Tscherneva (1982), named the *Arctiastrum* type for its resemblance with the pollen of *Arctium* (*Arctiastrum* is not the name of a taxon), is almost spheroidal to subprolate ( $P/E: 1.0\text{--}1.2$ ), and echinate. The polar axis is

(43.2–)50.4–54.0(–64.8)  $\mu\text{m}$ ; the equatorial diameter is 36.0–54.0  $\mu\text{m}$ . The equatorial costae are less conspicuous, and interrupted, being absent under the mesocolpia. The exine is only slightly thinner at the poles. The perforations in the tectum are more frequent, and wider than in the *Cousinia* type. The *Arctiastrum* type has been found in 16 species of *Cousinia* subg. *Hypacanthoides* and *C.* subg. *Cynaroides*.

Considering the preceding data it seems wise to involve pollen characters in the argumentation for the generic delimitation of *Arctium*. Below, the results of the pollen analysis of *Arctium* and *Cousinia* p.p. are presented. Pollen of *Onopordum acanthium* was studied because this taxon was selected as outgroup for the phylogenetic analysis of *Arctium* and *Cousinia* p.p. (see Chapter 13).

### 7.3 Materials and methods

A total number of 84 pollen samples has been collected from herbarium material of 73 species. These include 10 of the 11 species (21 samples) of *Arctium* s.l., 12 species of *Cousinia* subg. *Cynaroides*, 2 of *C.* subg. *Hypacanthoides*, and 49 species from 47 sections of *C.* subg. *Cousinia*. In Table 7.1 the species and collections are cited, and the method of analysis (LM, SEM) is indicated.

Table 7.1. List of studied material. 1: *Arctium* (including the five former species of *Cousinia*), 2: *Cousinia* subg. *Cynaroides*, 3: *Cousinia* subg. *Hypacanthoides*, 4: *Cousinia* subg. *Cousinia*. The last column indicates whether the material was studied with SEM or LM.

(sub-) genus	species	collector	SEM, LM
1	<i>Arctium</i> ( <i>C.</i> ) <i>amplissimum</i>	Bornmüller 7377	SEM, LM
1	<i>Arctium</i> ( <i>C.</i> ) <i>arctioides</i>	Krascheninnikov 5240	SEM, LM
1	<i>Arctium atlanticum</i>	de Wilde & Dorgelo 2850	SEM, LM
1	<i>Arctium lappa</i>	Zijlstra 69056	SEM, LM
1	<i>Arctium lappa</i>	Duistermaat 50	LM
1	<i>Arctium lappa</i>	Duistermaat 130	LM
1	<i>Arctium</i> ( <i>C.</i> ) <i>lappaceum</i>	anon. Russian 766	SEM, LM
1	<i>Arctium minus</i>	van Urk s.n., 7/08/1983	SEM, LM
1	<i>Arctium minus</i>	Sandwith & Brenan s.n., 4/08/1937	SEM, LM
1	<i>Arctium minus</i>	Anema & Roeleveld s.n., 24/08/1983	SEM, LM
1	<i>Arctium minus</i>	Reverchon 1389	SEM, LM
1	<i>Arctium minus</i>	van Uken s.n., s.d.	SEM, LM
1	<i>Arctium minus</i>	Gorter 1145	SEM, LM
1	<i>Arctium nemorosum</i>	Duistermaat 168	SEM, LM
1	<i>Arctium</i> ( <i>C.</i> ) <i>pseudarctium</i>	anon. Russian 3 (35)	SEM, LM
1	<i>Arctium tomentosum</i>	Duistermaat 84	SEM, LM
1	<i>Arctium</i> ( <i>C.</i> ) <i>umbrosum</i>	anon. Russian 96	SEM, LM
1	<i>Arctium</i> ( <i>C.</i> ) <i>umbrosum</i>	Sintenis 226	LM
1	<i>Arctium lappa</i> $\times$ <i>A. tomentosum</i>	Lampinen 3250	SEM, LM
1	<i>Arctium minus</i> $\times$ <i>A. tomentosum</i>	Jansen & van Ooststroom 1363-1365-2	SEM, LM
1	<i>Arctium minus</i> $\times$ <i>A. tomentosum</i>	Duistermaat 133	LM
2	<i>Cousinia anomala</i>	anon. Russian 937	LM
2	<i>Cousinia aurea</i>	Regel s.n.	SEM, LM
2	<i>Cousinia chlorantha</i>	anon. Russian s.n., 14/06/1929	LM
2	<i>Cousinia haesitabunda</i>	von Knorring s.n., /1914	LM
2	<i>Cousinia horrescens</i>	Granitov 478	LM
2	<i>Cousinia karatavica</i>	anon. Russian s.n., 12/06/1969	LM

(Table 7.1 continued)

(sub-) genus	species	collector	SEM, LM
2	<i>Cousinia korolkovii</i>	anon. Russian s.n., 5/06/1964	SEM, LM
2	<i>Cousinia pentacantha</i>	Regel s.n., 29/05/1880	LM
2	<i>Cousinia pentacanthoides</i>	anon. Russian 299	SEM, LM
2	<i>Cousinia refracta</i>	Lipsky 1004	LM
2	<i>Cousinia schmalhauseni</i>	Kudrjatsjev & Soemnevstsj 381	SEM, LM
2	<i>Cousinia triflora</i>	Mokeyeva & Popov 197	LM
3	<i>Cousinia macilentia</i>	Zaprzagaev 4641	SEM, LM
3	<i>Cousinia vavilovii</i>	Popov 198	LM
4	<i>Cousinia actinia</i>	Gilli 2500	LM
4	<i>Cousinia astracanica</i>	Fircher s.n.	LM
4	<i>Cousinia autrani</i>	Freitag 6831	LM
4	<i>Cousinia buphthalmoides</i>	Podlech 18393	LM
4	<i>Cousinia candolleana</i>	Rioux & Govan 488	LM
4	<i>Cousinia centauroides</i>	Korovin 44	LM
4	<i>Cousinia congesta</i>	Rechinger 16179	SEM, LM
4	<i>Cousinia crispa</i>	Rechinger 48328	LM
4	<i>Cousinia cynaroides</i>	Grant 15866	LM
4	<i>Cousinia decumbens</i>	Moussari & Karavar 33783-E	LM
4	<i>Cousinia dissecta</i>	Sintenis 1624	LM
4	<i>Cousinia dissectifolia</i>	Popov 480	LM
4	<i>Cousinia eryngioides</i>	Rechinger 4191	LM
4	<i>Cousinia eugenii</i>	Poretzky 4643	LM
4	<i>Cousinia freynii</i>	Rechinger 1752	SEM, LM
4	<i>Cousinia harazensis</i>	Amin 4118	LM
4	<i>Cousinia heliantha</i>	Rechinger 53718	LM
4	<i>Cousinia immitans</i>	Uotila 18762	LM
4	<i>Cousinia lachnosphaera</i>	Kukkonen 5888	LM
4	<i>Cousinia lepida</i>	Rechinger 53594	LM
4	<i>Cousinia macroptera</i>	anon. Russian s.n., 4/07/1958	LM
4	<i>Cousinia microcarpa</i>	Nikitin e.a., s.n., 20/05/1975	LM
4	<i>Cousinia mollis</i>	Popov 484	LM
4	<i>Cousinia neurocentra</i>	Rechinger 5951	LM
4	<i>Cousinia olgae</i>	Schmid 6263	LM
4	<i>Cousinia oligocephala</i>	Behboudi 1208-E	LM
4	<i>Cousinia oreodoxa</i>	Sintenis s.n., /07/1900	SEM, LM
4	<i>Cousinia parviceps</i>	Rechinger 18675	SEM, LM
4	<i>Cousinia pineticola</i>	Rechinger 37439	LM
4	<i>Cousinia prolifera</i>	Rechinger 16887	LM
4	<i>Cousinia pseudostenolepis</i>	Rechinger 18782	LM
4	<i>Cousinia pulchella</i>	Koelz 13054	LM
4	<i>Cousinia pygmaea</i>	Anders 6863	LM
4	<i>Cousinia raddeana</i>	anon. Russian 623	LM
4	<i>Cousinia regelii</i>	Butrov s.n., 6/05/1941	LM
4	<i>Cousinia scariosa</i>	Gilli 2534	LM
4	<i>Cousinia scheibiana</i>	Hedge & Wendelbo 5504	LM
4	<i>Cousinia sicigera</i>	Bormmüller 3454	LM
4	<i>Cousinia simulatrix</i>	anon. Russian 100	LM
4	<i>Cousinia singularis</i>	Rechinger 37240	LM
4	<i>Cousinia smirnowii</i>	Rechinger 53185	LM
4	<i>Cousinia sphaerocephala</i>	Wendelbo e.a. 14090	LM
4	<i>Cousinia stenocephala</i>	Iranshahr 13133-E	LM
4	<i>Cousinia stocksii</i>	Horreus de Haas 374 A	LM
4	<i>Cousinia tenella</i>	Jacobs 6878	SEM, LM
4	<i>Cousinia turcomanica</i>	Rechinger 53621	LM
4	<i>Cousinia vanensis</i>	Nydegger 1834	LM
4	<i>Cousinia verticillaris</i>	Griffith 3282	LM
4	<i>Cousinia wilhelminae</i>	Rechinger 49505	LM

The pollen samples were acetolysed following the method of Erdtman (1960). The grains were embedded in glycerine jelly, and the slides were sealed with Paraplast (Van der Ham, 1990). The material was studied with an Olympus type E microscope.

The preparation for SEM included the coating of the acetolysed pollen with gold in a Polaron E 5100 series II sputter-coater. Pollen grains of a selection of samples were sectioned with a Leitz freezing microtome according to Muller (1973). The observations and photography were performed with a Jeol JSM 35 and a Jeol JSM 5300 at the Rijksherbarium / Hortus Botanicus.

#### 7.4 Measurements

The terminology follows Punt et al. (1994). The following variables were scored with LM. The polar axis (P) and the corresponding equatorial diameter (E) were measured in equatorial view in 25 grains per sample. The distance between two colpi (A, apocolpium size) and the corresponding equatorial diameter were measured in polar view in as many grains as possible per sample. Exine thickness was measured in equatorial view at the pole and at the equator in the centre of the mesocolpia between the costae. The thickness of the widest infratectal columellae was also measured with LM. The SEM photographs were used to ascertain the size and morphology of the apertures, exine stratification and measurements, and details of the ornamentation (length of (micro-)echinae, diameter of perforations).

#### 7.5 Results

Two pollen types could be recognised, which in general agree with the types distinguished by Kuprianova & Tscherneva (1982): the *Arctiastrum* type and the *Cousinia* type.

*Arctiastrum* type (see Plate 1) — General shape: polar axis (P) 34 (47) 60  $\mu\text{m}$ , equatorial diameter (E) 29 (37) 44  $\mu\text{m}$ , prolate spheroidal to subprolate, P/E 1.00 (1.20) 1.52, equatorial outline subcircular to obtusely triangular with convex sides; meridional outline circular to elliptic. Apertures: tricolporate, planaperturate; ectoaperture 21 (27) 32  $\mu\text{m}$  long, rather narrow colpus, apex acute to obtuse, sometimes forked, A/E 0.30 (0.38) 0.53, in the endoapertural region often filled with coarse sexine elements or a single variously shaped operculum-like structure; mesoaperture a more or less distinct, roughly lens-shaped cavity between the lateral margins of the endoaperture and the equatorial parts of the ectoaperture margins; endoaperture a lalongate pore or colpus, 4–7  $\times$  7.5–15  $\mu\text{m}$ , polar sides obtuse to parallel, lateral sides acute. The endoapertures are connected by relatively thin scabrate zones, which, together with the endoapertures form an endocingulum. Costae present only at the polar sides of the endoapertures. Stratification: exine 5.2–8.3  $\mu\text{m}$  thick in the centres of the mesocolpia, thinning towards the colpi and usually also towards the poles, 4.2–7.3  $\mu\text{m}$  thick at the poles; tectum 1.1–1.8  $\mu\text{m}$  thick, consisting of a perforate outer tectum, a  $\pm$  granular inner tectum, and tectal columellae in between; infratectal layer columellate, 1.9–4.0  $\mu\text{m}$  thick, columellae simple or distally branched; nexine 0.9–1.3  $\mu\text{m}$  thick, in SEM often consisting of two sub-layers (probably representing foot layer and endex-

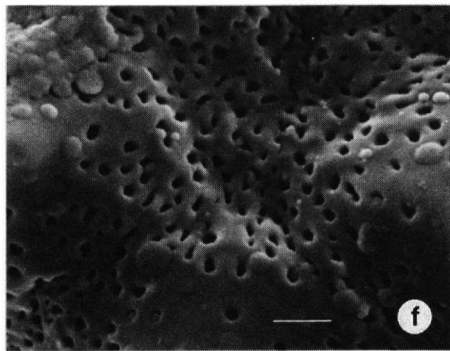
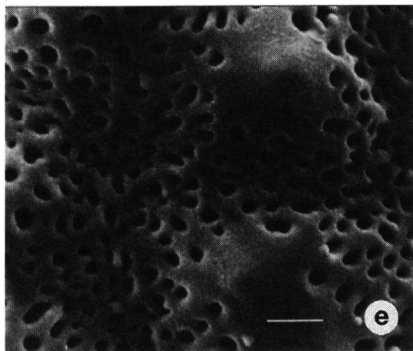
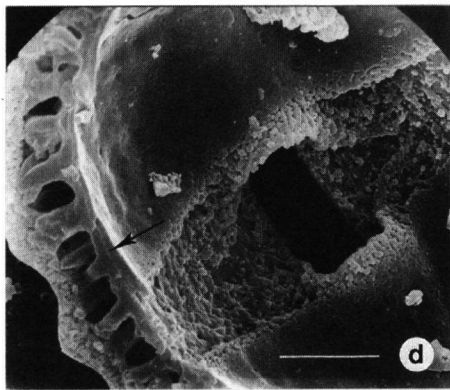
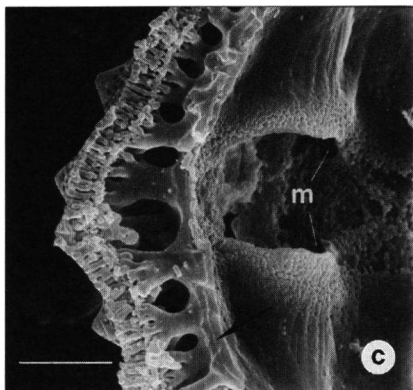
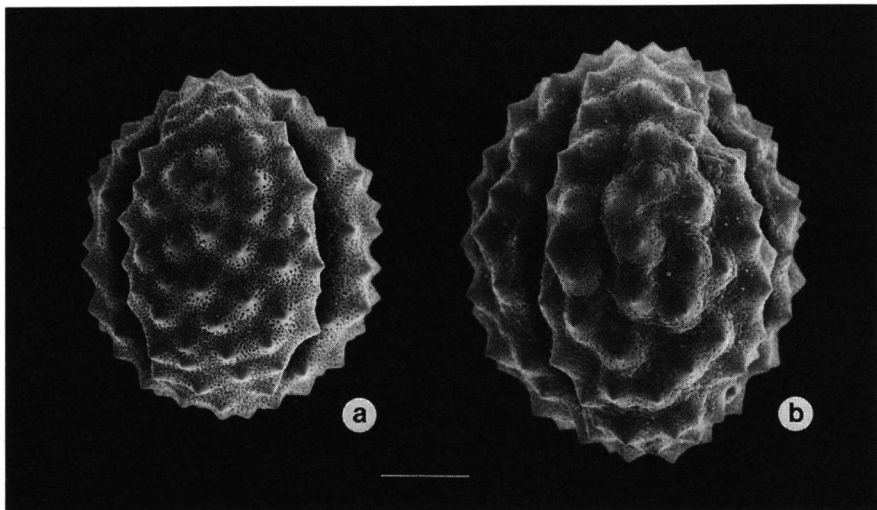
ine),  $\pm$  equally thick, but inner one much thicker at the costae endocinguli. Ornamentation: echinate or microechinate, echinae 0.8–2.1  $\mu\text{m}$  long, 27–85 per mesocolpium; largest perforations 0.17–0.67 (mean: 0.06–0.22)  $\mu\text{m}$  wide.

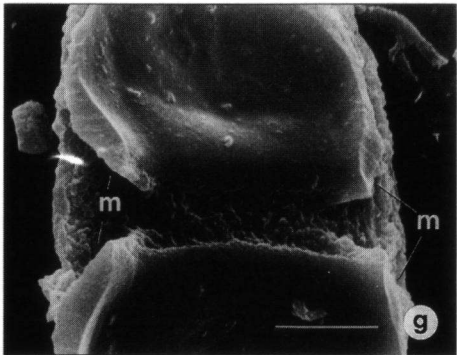
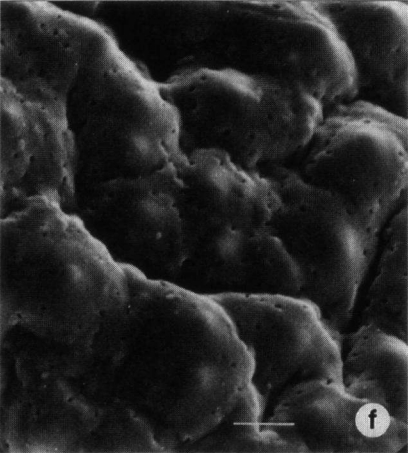
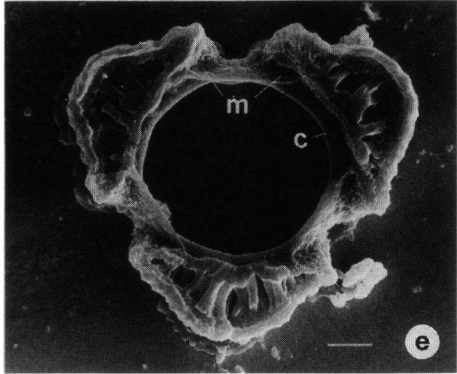
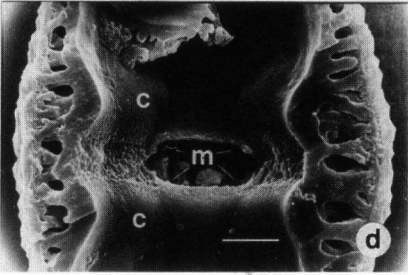
Included taxa: *Arctium* s.l., all 14 specimens examined of *Cousinia* subg. *Cynaroides* and *C.* subg. *Hypacanthoides* (see Table 7.1).

*Cousinia* type (see Plate 2) — General shape: polar axis (P) 33 (53) 70  $\mu\text{m}$ , equatorial diameter (E) 26 (36) 53  $\mu\text{m}$ , prolate spheroidal to prolate, P/E 1.06 (1.39) 1.78, equatorial outline obtusely triangular, with straight sides; meridional outline circular to elliptic. Apertures: tricolporate, planaperturate; ectoaperture 30–37  $\mu\text{m}$  long, very narrow colpus, apex acute to obtuse, A/E 0.31–0.34, in the endoapertural region often filled with coarse sexine elements or a single oblong operculum-like structure; mesoaperture a usually distinct, roughly lens-shaped cavity between the lateral margins of the endoaperture and the equatorial parts of the ectoaperture margins; endoaperture a longitudinal pore or colpus, 2.5–4.7  $\times$  5.6–10.7  $\mu\text{m}$ , polar sides usually parallel, lateral sides acute. The endoapertures are connected by relatively thin scabrate zones, which, together with the endoapertures form an endocingulum. Costae present along both sides of the endocingulum. Stratification: exine 5–11  $\mu\text{m}$  thick in the centres of the mesocolpia, thinning towards the colpi and the poles, 3–5  $\mu\text{m}$  thick at the poles; tectum 1.1–2.5  $\mu\text{m}$  thick, consisting of a perforate outer tectum, a  $\pm$  granular inner tectum, and tectal columellae in-between; infratectal layer columellate, 2.4–4  $\mu\text{m}$  thick, columellae simple or distally branched; nexine 0.9–1.5  $\mu\text{m}$  thick, in SEM often consisting of two sub-layers (probably representing foot layer and endexine),  $\pm$  equally thick, but the inner one much thicker at the costae endocinguli. Ornamentation: scabrate to verrucate; largest perforations 0.06–0.09  $\mu\text{m}$  (mean 0.03–0.06  $\mu\text{m}$ ) wide.

Included taxa: All 49 species examined of 47 sections of *Cousinia* subg. *Cousinia* (see Table 7.1).

Plate 1. SEM photographs of the *Arctiastrum* pollen type. — a, e. *Arctium minus* (*Anema & Anema-Roeleveld s.n.*, 24/07/1983). a. Equatorial view; bar = 10  $\mu\text{m}$ ; e. detail of ornamentation; bar = 1  $\mu\text{m}$ . — b, f. *Cousinia macilentia* (*Zaprjagaev 4641*). b. equatorial view; bar = 10  $\mu\text{m}$ ; f: detail of ornamentation; bar = 1  $\mu\text{m}$ . — c. *Arctium tomentosum* (*Duistermaat 84*), meridional section through mesocolpium showing exine stratigraphy, endoaperture, mesoaperture (m) and endocingulus. Note the discontinuity in the nexine (arrow) and the absence of costae along the endocingulus; bar = 5  $\mu\text{m}$ . — d. *Arctium amplissimum* (*Bornmüller 7377*), meridional section through mesocolpium showing exine stratigraphy, endoaperture, ectoaperture and endocingulus. Note the discontinuity in the nexine (arrow) and the absence of costae along the endocingulus; bar = 5  $\mu\text{m}$ .







## Key to the pollen types

- 1a. Costae endocinguli not interrupted. Tectum scabrate to verrucate, with up to 0.5  $\mu\text{m}$  high scabrae or verrucae; perforations up to 0.09  $\mu\text{m}$  diameter. Exine 5–11  $\mu\text{m}$  thick in the centres of the mesocolpia, at the poles distinctly thinner, 3–5  $\mu\text{m}$   
**Cousinia type**
- b. Costae endocinguli interrupted, present only near the mesoapertures. Tectum (micro)echinate, with 0.8–2.1  $\mu\text{m}$  long echinae; largest perforations 0.17–0.67  $\mu\text{m}$  diameter. Exine 5–8  $\mu\text{m}$  thick in the centres of the mesocolpia, at the poles only slightly thinner, 4–7  $\mu\text{m}$  ..... **Arctiastrum type**

Notes – 1. Qaid (1990) mentioned for both *Arctium* and *Cousinia* two layers of tectal columellae. I have seen only one layer in both pollen types (see Plate 1c and Plate 2d). Some granules are sometimes present halfway the tectal columellae. Perhaps Qaid interpreted this as an internal tectum separating two layers of tectal columellae. I prefer to interpret the structure as a single layer of tectal columellae.

2. According to Kuprianova & Tscherneva (1982), an important difference between the two types is the P/E ratio: 1.0–1.2 for the *Arctiastrum* type, and 1.5–1.9 for the *Cousinia* type. The gap was reduced by the work of Qaid (1990), who reported a P/E ratio of 1.3–1.6 for the latter. Figure 7.1 and 7.2 show that there is a considerable overlap in P and P/E ratio between the two types. *Cousinia eryngioides* has a mean P/E of 1.23; *Arctium* (*C.*) *amplissimum*, *C. aurea* and *C. korolkovii* have a mean P/E ratio of 1.38. Thus, these characters cannot be used to discriminate between the two pollen types. I did not include them in the phylogenetic analysis because I could not describe non-overlapping states.

3. The presence of costae endocinguli in the *Cousinia* pollen type was already mentioned by Kuprianova & Tscherneva (1982), and is confirmed here (Plate 2e, g). Until this time costae have not been mentioned for *Arctium* or the *Arctiastrum* type. I have found that costae are present here at the polar sides of the endoaperture (Plate 1c).

4. The *Cousinia* pollen type is within *Cousinia* restricted to *C.* subg. *Cousinia*, whereas the *Arctiastrum* type occurs in *Arctium* s.l., *Cousinia* subg. *Cynaroides*, and *C.* subg. *Hypacanthoides*. In order to decide on the delimitation of *Arctium*, I performed a cladistic analysis, including both macro- and pollen morphological characters in the data matrix (see Chapter 13).

Plate 2. SEM photographs of the *Cousinia* pollen type. – a, f. *Cousinia oreodoxa* (Sintenis s.n., 07/1900). a. Equatorial view; bar = 10  $\mu\text{m}$ ; f. detail of ornamentation; bar = 1  $\mu\text{m}$ . – b. *Cousinia congesta* (Rehinger 16179), equatorial view; bar = 10  $\mu\text{m}$ . – c. *Cousinia tenella* (Jacobs 6878), slightly oblique equatorial view; bar = 10  $\mu\text{m}$ . – d, e. *Cousinia freynii* (Rehinger 1752). d. Meridional section through mesocolpiums showing exine stratigraphy, endoaperture, mesoaperture (m), ectoaperture and endocingulus; note the thick costae (c) along the endocingulus; bar = 5  $\mu\text{m}$ ; e. equatorial section through the endoapertures showing exine stratigraphy and aperture structure; note the continuous circular costa (c) and the mesoapertures (m); bar = 5  $\mu\text{m}$ . – g. *Cousinia parviceps* (Rehinger 18675), meridional section through the lateral sides of two endoapertures showing endocingulus between distinct costae. Note the mesoapertures (m); bar = 5  $\mu\text{m}$ .

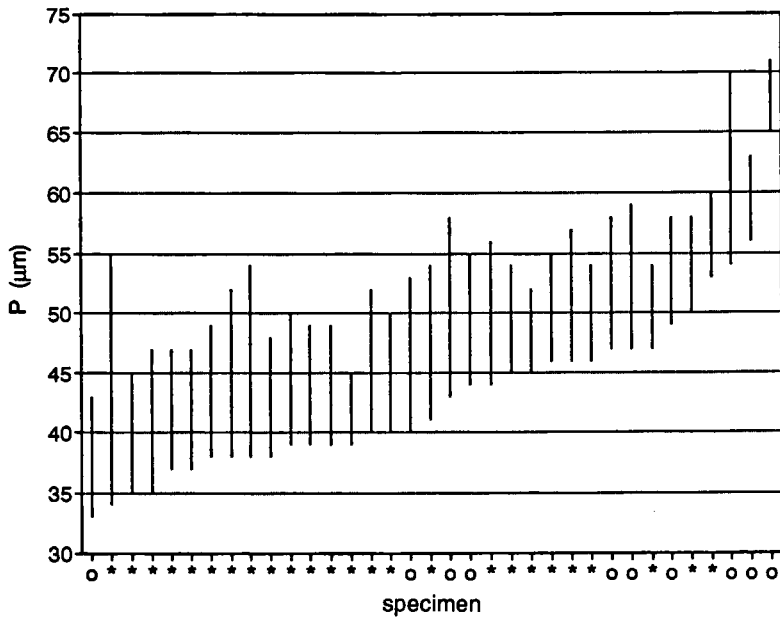


Fig. 7.1. Variation of polar diameter (P) within a specimen; the specimens are arranged according to their smallest value of P. \*: *Arctiastrum* pollen type; o: *Cousinia* pollen type.

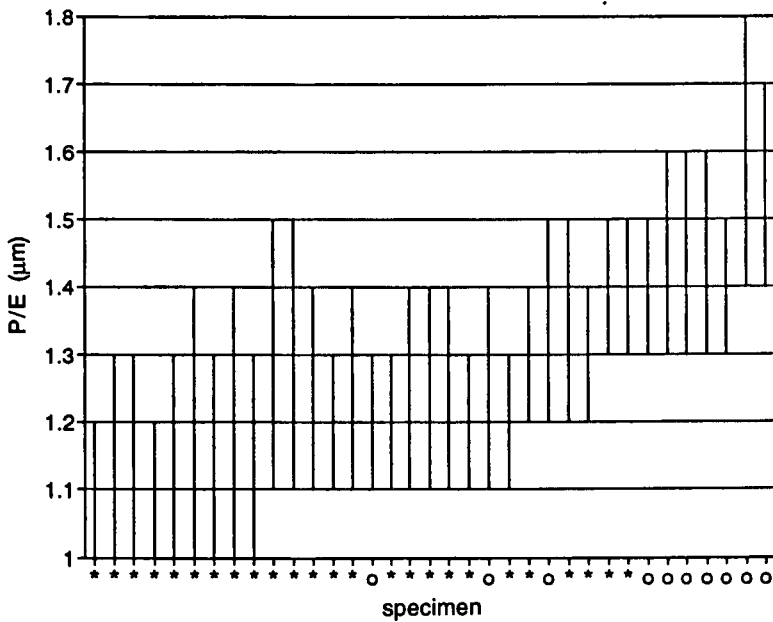


Fig. 7.2. Variation of pollen shape (P/E) within a specimen; the specimens are arranged according to their smallest value of P/E. \*: *Arctiastrum* pollen type; o: *Cousinia* pollen type.

5. The pollen of *Onopordum acanthium* is spheroidal, and has echinae of at least 2  $\mu\text{m}$  long. The endocingulum is present, but is not bordered by costae. The echinae are connected by inconspicuous ridges, and the tectum has perforations of 0.2  $\mu\text{m}$  diameter, according to the generic pollen description of Qaid (1990).

## 8. Chromosomes

Original counts of the chromosome numbers of the species of *Arctium* sect. *Arctium* were performed by Poddubnaja-Arnoldi (1931), who reported  $2n = 36$  for *A. tomentosum*. Wulff (1937) reported  $2n = 32$  for *A. minus*. Original counts for *A. lappa* were performed from Japanese material by Sugiura (1936) who reported  $2n = 32$ . Nakajima (1936) concluded that  $n = 18$ . Tarnavaschi in Tischler (1950) counted  $2n = 36$  for *A. tomentosum* and *A. minus*. Löve & Löve (1944, 1961) counted  $2n = 31$ ,  $2n = 32$ , and  $2n = 36$  from European and Japanese material. Moore (1968) performed chromosome counts for *A. nemorosum* and reported  $2n = 36$ .

Moore & Frankton (1974) argued that the (rather few) counts of 32 are errors. I think that the count of  $2n = 31$  is also erroneous. According to Moore & Frankton, the interpretation of the karyogram is difficult because the chromosomes are long and usually appear as an entangled group. Also, the variability in length within the karyome is large. This may cause erroneous counts. According to Moore & Frankton (1974) the somatic chromosome number is  $2n = 36$ .

According to Kuzmanov et al. (1991) the base number for the genus *Arctium* is  $x = 9$ . The chromosome number would thus be  $4x$ , but Grime et al. (1990) reported  $2x$ . Gametic chromosome numbers of 8, 9, 10, 11, 12, 13, 15, 17, and 19 are mentioned for the 'super-tribe' Cynaroideae (Dittrich, 1977).

Tscherneva (1988) presents the chromosome numbers for the three subgenera of *Cousinia*. *Cousinia* subg. *Cynaroides* (including the 5 species which I transfer to *Arctium*) and *C.* subg. *Hypacanthoides* have  $2n = 36$  (Tscherneva, 1985); *Cousinia* subg. *Cousinia* has  $2n = 18, 20, 22, 24, 26$  (Moore, 1973, 1977; Afzal Rafii, 1980; Goldblatt, 1981; Tscherneva, 1985).

The chromosome number and chromosome morphology could be diagnostic at the genus level (Dittrich, 1977). Tucci et al. (1994) performed a structural analysis of intergenic spacers of the rRNA genes of three species belonging to the Cardueae genera *Onopordum* and *Cynara*. The results show that this technique might also be a useful tool for the genus delimitation in the tribe Cardueae. I have not examined chromosomal characters of *Arctium* and *Cousinia*.

## 9. Reproduction

Several authors indicated that *Arctium minus* and *A. lappa* are autogamous (see Gross et al., 1980; Clapham et al., 1987). Mulligan & Findlay (1970), indeed, demonstrated that *A. minus* sets viable seed under pollination bags. Gross (in Gross et al., 1980), however, found that a significantly greater percentage of achenes with embryos was present in the unbagged control group compared to the bagged inflores-

cences. The mean weight of the filled achenes of both groups was, however, not significantly different. These results show that self-pollination is effective, but also that cross-pollination is probably predominant.

According to Mulligan & Kevan (1973) *A. minus* attracts insects. Although its flowers have no odour, they do have a high reflectance of ultraviolet and blue light, and the species has flower targets (capitules) of over 20 mm diameter. I have often seen different kinds of insects (*Lepidoptera*, *Hymenoptera*, *Coleoptera*) on several species of *Arctium*. These data also suggest that species of *Arctium* are cross-pollinators.

Apomixis has never been reported for species of *Arctium*. All species of the genus have the same chromosome number, and the ranges of the pollen diameter (see Chapter 11) also suggest that apogamy is not involved.

## 10. Chemistry and economic importance

According to Wagner (1977) the root of *A. lappa* has a high content of inulin, a fructan polysaccharide often found in Asteraceae. It also contains acetylenes with strong bactericidal and fungicidal activity (Wagner, 1977).

Beger (in Hegi, 1929) extensively discusses the uses of the genus. In Eurasia roots of mainly *A. minus* and *A. lappa* ('*Radix bardanae*') of first year's rosettes are or were used for a variety of complaints. Extract of the root has been used as a laxative, diuretic, sudorific, blood purifier, and hair restorer. It was also used as a skin care for animals, as a constituent of 'wood tea' (purpose unknown), and as an emergency coffee substitute (Beger in Hegi, 1929; Moore & Frankton, 1974). It is recorded that the leaves and fruits are also used for these purposes (references in Gross et al., 1980).

Woodcock (1925) listed *A. minus* as a poisonous plant because of its diuretic effects. Nevertheless, several parts of the plants are used for consumption. *Arctium lappa* is widely cultivated in Japan as a vegetable ('gobo'; Bailey, 1947). In the United Kingdom a lemonade 'Dandelion and Burdock' has been produced (pers. comm. Mr. & Mrs. Ball, Mr. Turner), but I do not know whether it did indeed contain extracts of *Arctium*. *Arctium lappa* has been introduced in Hawai'i for cultivation (Wagner et al., 1990; as a rootcrop?). In North America the introduction of several species of *Arctium* has probably occurred unwittingly, but the young leaves and fresh or dried roots were eaten by the Indians [Yanovsky (1936) and Rousseau and Raymond (1945), from Moore and Frankton, 1974].

Species of *Arctium* are no noxious weeds. The capitules cling to the wool of animals and may reduce the value of it (Steyermark, 1963). Because of their getting entangled so easily in hair, the capitules of *Arctium* sp. are used by children, and at new year's eve in Switzerland also by grown ups (*Van Steenis s.n.*, 31-12-1970), to throw at each other. The foliage is eaten with pleasure by cows, but it may give a bitter flavour to the milk if eaten in large quantities. The frequency with which the Dutch painter P. Potter (1625-1654) accompanied his cattle with not or poorly flowering specimens of *Arctium* spec. is striking. Artists have a preference for imperfections, but it may indicate that the plants were grazed upon. I do not know whether Burdock in pastures was actively controlled in later times.

The pappus releases from the ripe achene and the sharp bristles easily prick in the human skin. The barbs of the pappus are filled with fluid, which may cause allergic skin reactions (Gross et al., 1980).

## 11. Species delimitation in the *Arctium minus*-complex

### 11.1 Introduction

The *Arctium minus*-complex comprises all racemose to subcorymbose species of the genus *Arctium* in its traditional delimitation, i.e. without the former *Cousinia* species. I exclude from the *A. minus*-complex the corymbose species *A. lappa*, *A. tomentosum* and allied species, although hybrids between racemose and corymbose species are often mentioned in literature. Apart from the corymbose inflorescence, *A. lappa* can be recognized by the solid base of the petiole of the basal leaves, and *A. tomentosum* and *A. palladini* by the shape of the inner involucre bracts.

Arènes (1950) described 18 racemose to subcorymbose taxa within two species which he appointed to different sections. According to him *A. minus* has a glabrous corolla. He recognized seven subspecies of which the subsp. *atlanticum*, *eu-minus*, *pubens*, and *nemorosum* had been recognized before. Newly described are the three subsp. *mediterraneum* (from the Mediterranean region), *alpestre* (from the French and Italian Alps), and *tchihatchefii* (from the Middle East). A number of the subspecies is further divided into several varieties and formae. The other species, *A. chaberti*, is a Southern European species which, in contrast to *A. minus*, should have a glandular hairy corolla, and is divided into four new subspecies: subsp. *chaberti* (from Central Spain), *aellenianum* and *corsicum* (both from Corsica, and both known from one specimen each), and *balearicum* (from Mallorca). He used a wide variety of characters to delimitate the taxa of the *A. minus*-complex, including size and shape of the capitules, length of the inner bracts (absolute and relative to corolla and receptacular scales), length of peduncle, width of involucre bracts, shape of the corolla, length of tube relative to length of limb of the corolla, form and length of the basal and apical appendages of the anthers.

Arènes (1950) mentioned 11 hybrid taxa in the genus *Arctium*. He saw a few specimens from Central and Northern Europe with a racemose synflorescence and a glandular hairy corolla (e.g. *Soc. Et. Fl. Franco-Helv.* 300, leg. Camus & Franchet), and identified them as a hybrid between *A. minus* and *A. tomentosum*, rather than *A. chaberti*. He described two new hybrids, and for the other hybrid taxa he only mentioned the parent taxa, suggesting that they are intermediate between the parents.

The taxonomic treatment of Arènes (1950) has not been followed by other authors. This is mainly caused by his largely inaccessible key, and by his taxonomic views. In the first couple of questions the user has to choose between a typical racemose inflorescence, or a primarily racemose inflorescence but subcorymbiform in top. These character states are not discrete, and, unfortunately, Arènes did not give definitions of the terminology he used. When comparing the drawings of the various taxa in his publication, it appears that, for instance, *A. minus* subsp. *pubens* (Pl. 5 f, g) and *A. minus* subsp. *mediterraneum* var. *libanum* (Pl. 6 a, b) have the same type of inflorescence, namely long peduncled capitules in a loose raceme. The former is

keyed out as typical racemose, whereas the latter is classified as primarily racemose and subcorymbiform in top. Similarly, *A. minus* subsp. *tchihatchefii* is having a subcorymbose inflorescence in top according to the description. However, the drawings of the synflorescences of this subspecies and *A. lappa*, which is characterized as typically corymbose, are identical. Another shortcoming is that the descriptions of the subspecies within one species, which are presented in a key, are not mutually comparable.

Since 1950 three taxa are generally accepted at different levels within the *A. minus*-complex: *A. minus*, *A. pubens* and *A. nemorosum*. Almost always the extensive variability of the taxa is mentioned, as is the assumption that hybridisation occurs frequently. The North-African taxon *A. atlanticum* is treated as a subspecies of *A. minus* (Quézel & Santa, 1963). *Arctium chaberti* usually disappears into the synonymy of *A. minus*, but Barcelo (1980) synonymized *A. chaberti* with *A. tomentosum*.

There is no agreement on the taxonomical status of *A. minus*, *A. pubens*, and *A. nemorosum*. For instance, Flora Europaea [Perring in Tutin et al. (1976) 215] treats them as separate species, Stace (1991) as three subspecies of *A. minus*, and Oberdorfer (1990) regards *A. nemorosum* as a separate species, and *A. minus* and *A. pubens* as subspecies of *A. minus*. Finally, Rothmaler (1976) regards *A. pubens* and *A. nemorosum* as subspecies of *A. nemorosum*, and presents *A. minus* as a separate species. *Arctium pubens* is often regarded as the intermediate taxon, or it is supposed to be of hybrid origin (Pignatti, 1982; Perring in Tutin et al., 1976; Clapham et al., 1987).

The size of the capitules is often used as the diagnostic character, but the amount of indumentum, and the length of the peduncles are considered of importance too. However, the descriptions of several floras do not agree. The capitules of *A. pubens*, for instance, are 2–2.5 cm across according to Oberdorfer (1990), 2–3 cm according to Van der Meijden (1990), 3–3.5 cm according to Perring in Tutin (1976: 215) and Stace (1991), or even 3–4 cm according to various other authors (like Clapham et al. 1987, Mossberg 1992). The various floras also conflict in the given measurements of the length of the peduncles and the length of the achenes for *A. pubens*. Finally, *A. pubens* is regarded as the commonest species of the genus in the Netherlands (Van der Meijden, 1990), whereas in Belgium (De Langhe et al., 1988: 616) and Germany (Oberdorfer, 1990: 960) its distribution is said to be badly known because of confusion with *A. minus*.

The descriptions of *A. nemorosum* given by the diverse floras are more consistent. Although the size of the capitules, the amount of indumentum, and the clustering of the capitules varies, the branches are always described as long and arched, giving the (sub-)species a characteristic habit.

If hybrids within the complex occur as frequently as is suggested in literature, is it then possible to regard the parents as different species? From the discussion concerning the species concept (Chapter 5) it is clear that the answer must be negative. If the individual plants in this complex show a continuum in morphological variation, and if all specimens are normally fertile, then there is no reason to maintain that they are separate species. I examined the (dis-)continuity in morphological variation and the fertility of individuals within the *A. minus*-complex. The results are given below. I will deal with the determination of hybrids with the other species of *Arctium* sect. *Arctium* in the next Chapter (12).

I do not know of a study investigating the occurrence of apomixis in *Arctium*, nor do I know of incidental statements to this effect. It is not very likely that apomixis is involved, because agamospecies tend to show hardly any variability. If any conclusions could be drawn from Arènes' work, it should be that the recognition of more taxa leads to the occurrence of more intermediate forms. If so, this would be an indication of the presence of a more or less continuous variation within the *A. minus*-complex. Nevertheless, I did not leave out of consideration the occurrence of apomixis in my study.

### 11.2 Material and methods

I made full descriptions and drawings of 122 specimens. The material examined (indicated with an asterisk in the Identification list) comprises only herbarium specimens (both old and freshly sampled). I used only selected collections for this purpose: preferably from the apex of the inflorescence, in the same stage of development (flowering, preferably the beginning of flowering), and not too badly flattened during the drying process. In order to obtain specimens of this quality, I made collecting trips in The Netherlands, to Belgium, France, Spain, and Germany. In Germany mainly limestone areas were visited where *A. nemorosum* was supposed to grow (Haeupler & Schönfelder 1988).

In the first stage of the investigation it was difficult to decide which specimens might be regarded as intermediates or as hybrids, because the variation width of the characters of each species was still uncertain. Therefore I opted for the scatter diagram to visualize the morphological variation of the complex. With the spreadsheet programme QuatroPro scatter diagrams of all possibly relevant combinations of two characters of a datamatrix of 122 specimens and 25 characters were produced. A third character was used to see if it was possible to define groups. The characters examined are given in Table 11.1.

From all 122 specimens mentioned above pollen was collected and studied without prior acetolysis. The visibility of nuclear material, the number of deformed pollen, and the number of pollen grains with airbubbles in the cytoplasm were scored. The percentage of pollen grains which contained air or were deformed was taken as a measure for the fertility of the pollen. As in apomictic specimens the largest pollen grains are often twice as large as the smallest (e.g. Sterk et al., 1987: 91, fig. 50), I measured the pollen diameter of 25 grains per specimen as a possible indicator for the involvement of apomixis.

### 11.3 Results

In order to be able to distinguish groups of specimens, I made a large number of scatter diagrams, in which many different combinations of characters were visualized. The characters which are used in a single diagram should not be highly correlated. For instance, the width of a capitule including the apical part of the involucre bracts is very much related to the length of the middle involucre bracts; specimens with long involucre bracts will have wider capitules than specimens with short involucre bracts. (see Fig. 11.1, where the dots are situated more or less on a straight line). Only in some specimens the middle involucre bracts are shorter than would be expected from the width of the capitules; such specimens invariably proved to be ex-

Table 11.1. List of characters examined for the delimitation of species in the *A. minus*-complex.

1. Length of peduncle of capitule.
2. Capitule hairy vs. glabrous.
3. Width of capitule including the patent parts of the involucre bracts.
4. Width of capitule excluding the patent parts of the involucre bracts.
5. Length of capitule including the patent parts of the involucre bracts.
6. Length of capitule excluding the patent parts of the involucre bracts.
7. Length of middle involucre bract.
8. Relative length of apical part of middle involucre bract.
9. Width of middle involucre bract.
10. Length of receptacular scales.
11. Length of longest pappus hairs.
12. Corolla length.
13. Length of the limb of the corolla.
14. Length of longest corolla lobe.
15. Length of shortest corolla lobe.
16. Length of the tube of the corolla.
17. Corolla with / without hairs.
18. Corolla exceeding the involucre (+ mm), or exceeded by the involucre (- mm).
19. Length of filament.
20. Filament glabrous, verrucate or papillose.
21. Length of anthers.
22. Length of apical appendage of anthers.
23. Length of basal appendage of anthers.
24. Length of stylar apex.
25. Length of stylar branches.

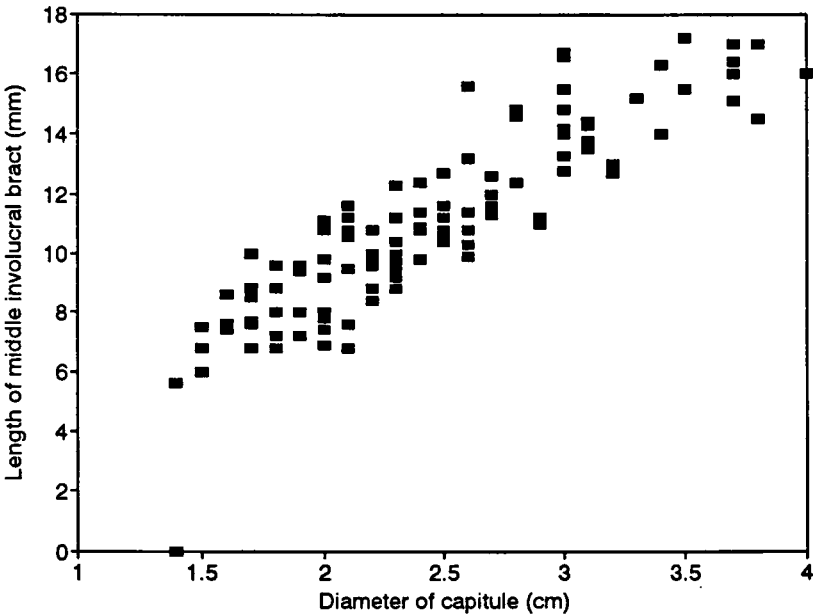


Fig. 11.1. Scatter diagram showing the relation between the width of the capitule and the length of the middle involucre bract.



cessively flattened during the process of drying, resulting in an unnatural widening of the capitules. Boiling the capitules in water is to no avail here, it will not help regaining their original shape. Therefore, I chose to use the length of the middle involucre bracts as an estimate for the width of the capitules. From Fig. 11.1 it can be concluded that the width of a capitule including the apical part of the involucre bracts is approximately twice the length of the middle involucre bracts.

Firstly, it proved to be possible to identify *A. atlanticum* with the aid of a scatter diagram (Fig. 11.2) including the character 'middle involucre bract index' on the x-axis, and the character 'relative length of middle involucre bract' (compared to its entire length) on the y-axis. This procedure shows a group A of two North African specimens, which could be identified provisionally as *A. atlanticum*. This group is characterized by the combination of relatively wide middle involucre bracts and capitules with relatively short patent apical parts. I did not succeed in finding any other single character which is exclusive to this group. When applying the combination of another two characters ('corolla exceeding the involucre' and 'corolla glabrous') this group can be nicely circumscribed as a uniform, homogenous group. None of the character states, however, is exclusive to group A, and even the combination of the states is present in specimens of group B. In the next scatter diagrams I excluded this group of North African specimens (group A) from the data matrix.

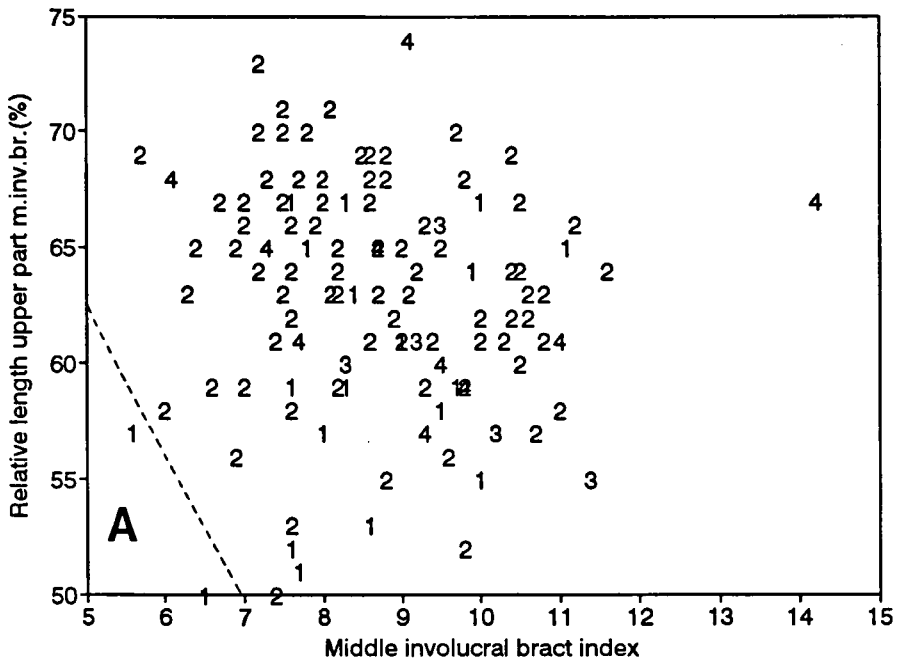


Fig. 11.2. Scatterdiagram showing the variability of 122 specimens of the *Arctium minus*-complex. Group A contains two specimens from Northern Africa. 1: corolla glabrous, and exceeding the involucre > 0.5 mm; 2: corolla glabrous, and exceeded by the involucre or exceeding the involucre up to 0.5 mm; 3: corolla hairy, and exceeding the involucre > 0.5 mm; 4: corolla hairy, and exceeded by the involucre or exceeding the involucre up to 0.5 mm.

Secondly, another rather uniform group can be distinguished. In the scatter diagram of Fig. 11.3 I put on the x-axis the character 'length of middle involucre bract' and on the y-axis the character 'length of anther'. The symbols representing the specimens also illustrate the distribution of the variation of the characters 'width of middle involucre bract', 'corolla exceeded by the involucre' and 'corolla glabrous'. This group consists of specimens with middle involucre bracts usually at least 1.7 mm wide, and with the involucre always exceeding the glabrous corollas. Only four specimens (a, b, and c, and d) showed a certain overlap with this group. The specimens a, b, and c deviate in having 1.6 mm wide middle involucre bracts; d has a hairy corolla and middle involucre bracts of only 1.1 mm wide. The habit of group B, as experienced from my own field observations, was very much like the descriptions in literature of *A. nemorosum*: a huge plant, with long, arched branches (often even inclined at the top) with large, (almost) sessile heads solitarily placed along the branches, and with three heads clustered at the top of a branch. The herbarium collections of group B, including the specimens a, b, and c, but excluding specimen d, consist of (slightly) arcuated branches, showing a clustering of capitules at the apex. They

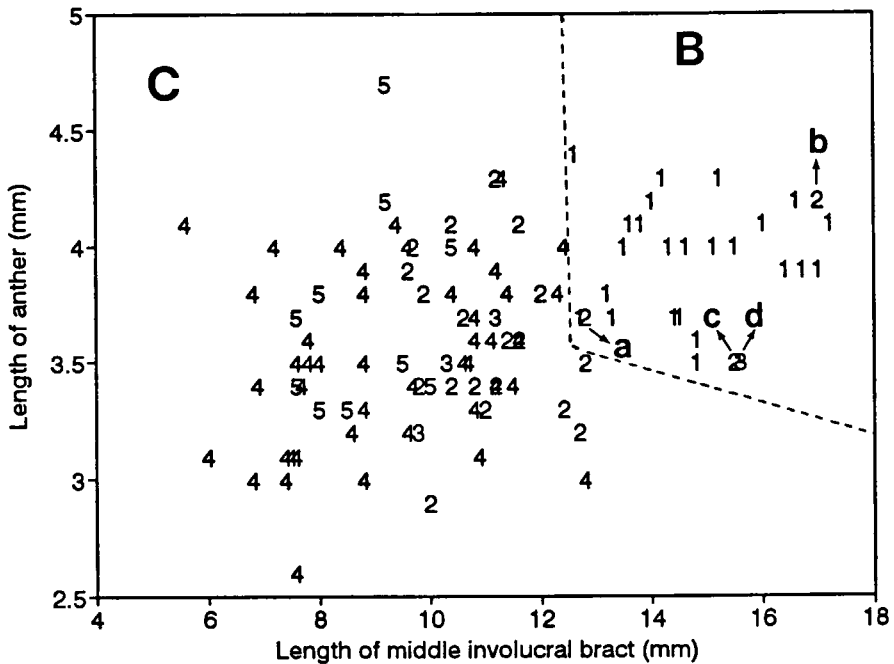


Fig. 11.3. Scatterdiagram showing the variability of the *Arctium minus*-complex, excluding group A. Group B contains specimens (excluding specimen d) which agree with descriptions of *Arctium nemorosum*. 1: middle involucre bract  $\geq 1.7$  mm wide, involucre exceeding the corolla  $\geq 1.0$  mm, corolla glabrous; 2: middle involucre bract  $\leq 1.6$  mm wide, involucre exceeding the corolla  $\geq 1.0$  mm, corolla glabrous; 3: middle involucre bract  $\leq 1.6$  mm wide, involucre exceeding the corolla  $\geq 1.0$  mm, corolla hairy; 4: middle involucre bract  $\leq 1.6$  mm wide, involucre exceeding the corolla  $< 1.0$  mm, corolla glabrous; 5: middle involucre bract  $\leq 1.6$  mm wide, involucre exceeding the corolla  $< 1.0$  mm, corolla hairy (a-d: specimens mentioned in text).

grew on open spots or along paths in woodlands, mostly on calcareous soil. It is very likely that the type specimen of *A. nemorosum*, of which I have seen a photograph, as well as a single capitule, belongs to this group B with wide involucre bracts which exceed the corolla. I exclude specimen d from the 'nemorosum'-group because it has hairy capitules, narrow middle involucre bracts, and rather short, straight branches.

After having removed the specimens of group A and B from the data matrix, group C (including specimen d) could be investigated further. The specimens of this group have middle involucre bracts of up to 1.6 mm wide. With respect to the other characters group C is still very variable. Specimens with sessile to long pedunculate, small to large, and glabrous to densely tomentose capitules are still present. I combined these characters, which are often used to differentiate *A. minus* from *A. pubens*, in a single scatter diagram (Fig. 11.4), using the length of the middle involucre bracts as an estimate for the width of the capitule. The result is a single concentration of dots, including specimens with glabrous capitules as well as specimens with hairy capitules. I tried many other combinations of characters, invariably with a similar result. The presence of glandular hairs on the corolla, on which character state *A. chaberti* was based, too could not be used to separate a homogenous group. The scatter diagram based on the characters 'length of the middle involucre bract', 'length of anther', and 'hairy corolla' (Fig. 11.5) serves as a model. Specimens from one location may

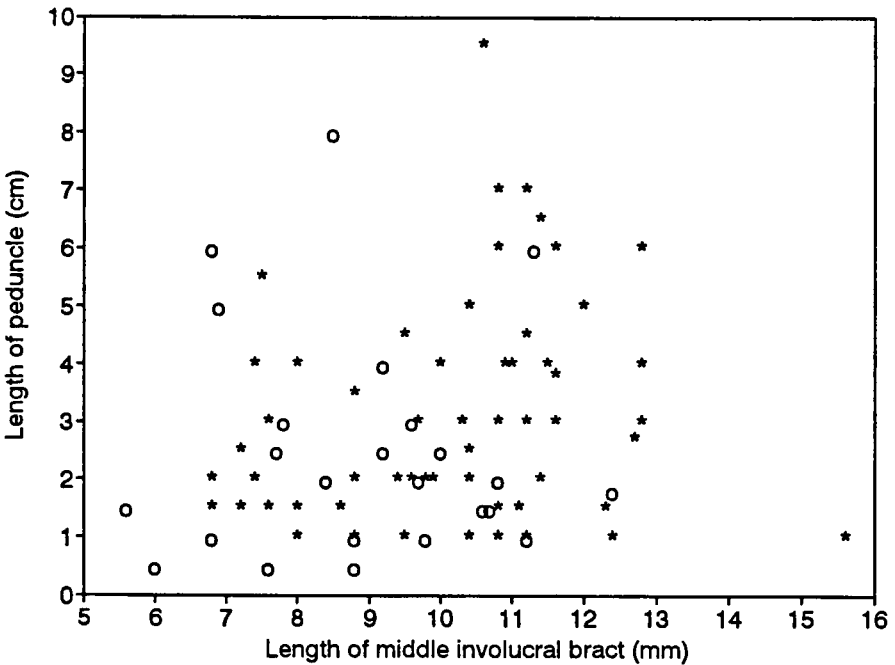


Fig. 11.4. Scatterdiagram showing the variability of the *Arctium minus*-complex, excluding group A and B. o: capitule glabrous; \*: capitule (densely) hairy.

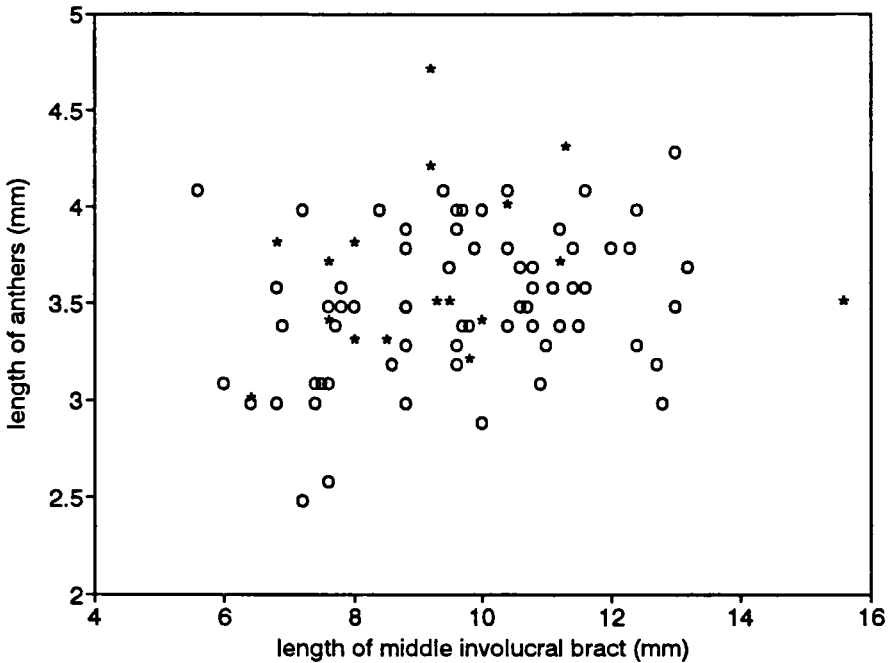


Fig. 11.5. Scatterdiagram showing the variability of the *Arctium minus*-complex, excluding group A and B. o: corolla glabrous; \*: corolla hairy.

have glandular hairs on the corolla (e.g. *Duistermaat 180* and *183* from Maaldrift near Wassenaar, The Netherlands) while other specimens of the same location (*Duistermaat 181* and *182*) may have a glabrous corolla. I have found specimens with a hairy corolla both in Southern Europe as well as in Northwestern Europe. All variation, e.g. length of peduncle, indument of capitule, length of the anthers, and length of the stylar apex, occurs (almost) throughout the geographical range of the entire group.

In order to obtain information on the fertility of the specimens, I first examined the formation of filled achenes. For the scatter diagrams I primarily examined flowering material. Nevertheless, in some of the material immature achenes were present. They were always filled, seemingly viable, suggesting that the specimen is not a hybrid between two species.

I followed by estimating the viability of pollen, by determining the percentage of deformed grains in unacetolysed samples of the specimens included in the scatter diagrams. In the two specimens of the '*atlanticum*'-group (A) 0–5% of the pollen grains are deviating. They either contain air in their cytoplasm, or they are indented. This suggests that the pollen in the '*atlanticum*'-group is viable. Of the 28 specimens of the '*nemorosum*'-group (B) 24 have 0–7% of deviating pollen grains. Four specimens of this group have 15–50% deviating pollen, suggesting that the pollen is less viable. A number of 77 specimens of the '*rest-group*' (C) has 0–9% deviating pollen

grains, and only 5 specimens have 12–30% deviating pollen grains. The pollen grains of the supposed less viable specimens are not seriously damaged, and the specimens are equally distributed in the diagrams. If they are removed from the diagram, on the assumption that they represent hybrids, still no groups could be recognized in the diagrams. Thus, there are no strong arguments for the assumption that specimens with up to 30% deviating pollen grains should be seen as hybrids.

Finally it was examined whether apomixis could be demonstrated, which might be the case if pollen grains within one sample show a great variation in size. The polar axis of the unacetolysed grains proved to be little variable within a specimen. In Fig. 11.6 the range of all specimens in polar diameter (P) is presented. The median value of all specimens together is 38  $\mu\text{m}$ , while the total range is 29–52  $\mu\text{m}$ . The difference in P between the largest and the smallest grain within a specimen ranges from 2–16  $\mu\text{m}$  (see Fig. 11.7). From this it is clear that within the *A. minus*-complex the largest pollen grains are never twice as large as the smallest grain. This indicates that apomixis is not involved.

To summarise the results, it is, based on morphological variation, possible to identify an '*atlanticum*-group', a '*nemorosum*-group', and a variable restgroup within the racemose complex. The characters 'width' and 'length of middle involucral bract' and 'length of stylar apex' proved to be of diagnostic value. The presence of glandular hairs on the corolla was shown to occur in a wider geographical region than was known until now, and to have no taxonomic significance in the racemose complex. Specimens within a population do show variation to a certain degree. The unacetolysed pollen did not show high numbers of deformed or less viable grains.

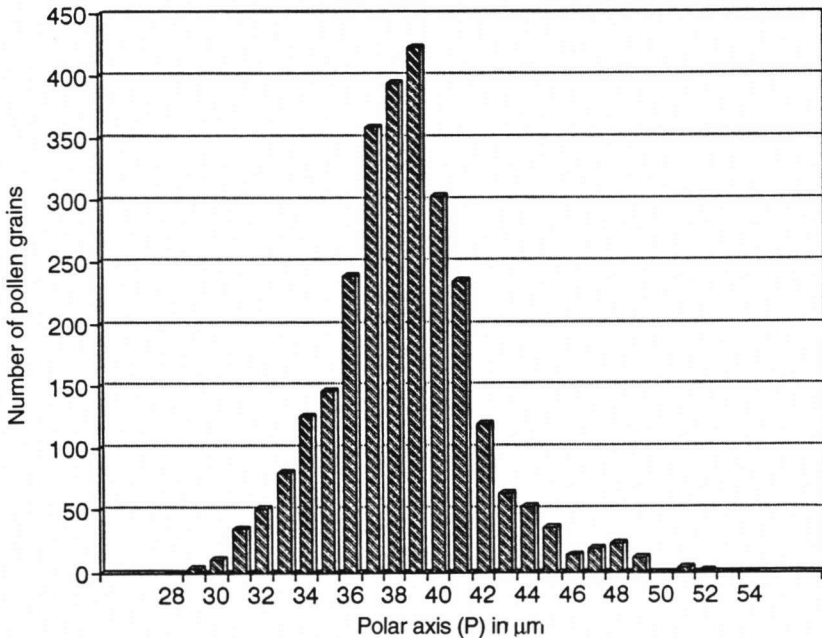


Fig. 11.6. Bar diagram showing the range of the polar diameter (P) in unacetolysed pollen grains of 122 specimens of the *Arctium minus*-complex. The median value of P = 38  $\mu\text{m}$ .

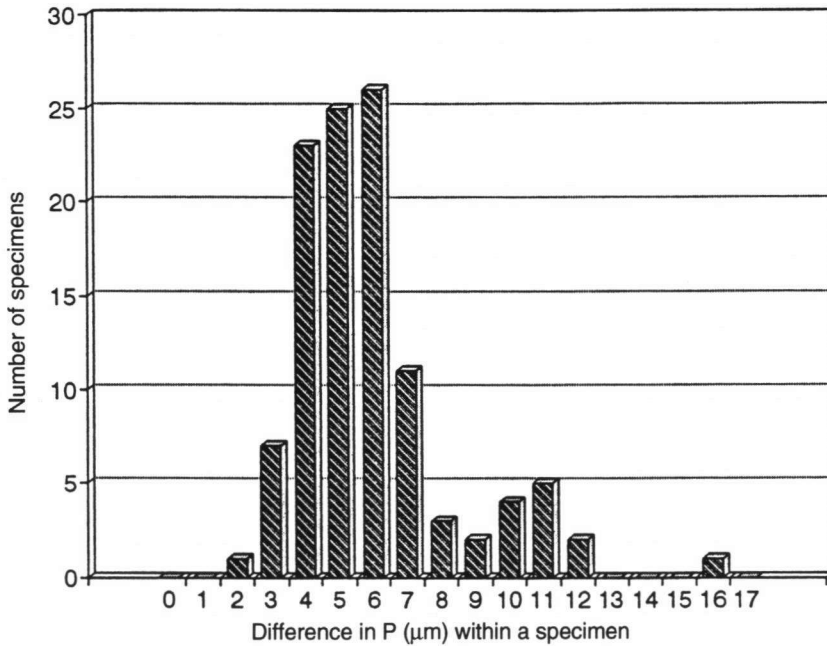


Fig. 11.7. Bar diagram showing the range of the polar diameter in unacetolised pollen grains within the 122 specimens of the *Arctium minus*-complex.

#### 11.4 Conclusions and discussion

The '*atlanticum*'-group is not characterized by unique character states. For the composite species concept this is not required. The presence of a character state is neither sufficient, nor necessary for a specimen to be included in a species (see Chapter 5). Based on the unique combination of character states (index of middle involucrel bracts up to 6.5, relatively short upper part of middle involucrel bracts (up to 57%), glabrous corolla exceeding the involucre) of the specimens of this group, I decided to treat this group as a species, *A. atlanticum*. It is restricted to Northern Africa. I have seen six specimens of this species (including the two of the scatter diagram); I have not seen intermediate specimens, indicating that they do not hybridize.

The '*nemorosum*'-group, too, can only be characterized by a unique combination of character states. The width of the middle involucrel bracts shows some overlap between this group and the rest-group. However, there is a unique combination of character states (habit, wide involucrel bracts, glabrous corolla exceeded by the involucre). Moreover, all specimens (except one which was found under a tree in a village) of this group have been found in woodlands only, mostly on calcareous soils, whereas only a small portion of the rest-group is found in this type of habitat. This suggests that the *nemorosum*-group differs in its ecology from the rest-group. I therefore treat *A. nemorosum* as a separate species. It reaches from the United Kingdom to Russia, excluding the Mediterranean and Arctic regions.

The rest-group (C) of the *A. minus*-complex is still very variable. It appears to be impossible to describe geographical races in this rest-group. Arènes (1950) identified racemose specimens from Northwestern Europe with a glandular hairy corolla as hybrids between *A. minus* and *A. tomentosum*. However, the presence of the glandular hairs is the only character present which is reminiscent of *A. tomentosum*, and in Southern Europe this single character is used to delimitate *A. chaberti* as a separate species. Moreover, specimens of one location may show variation with respect to this character only, while *A. tomentosum* itself, with its characteristic acuminate to truncate inner involucre bracts which are widened below the apex, is not known from the area where the presumed hybrids occur. Therefore, the presence of glandular hairs in racemose specimens should be interpreted as variability within the rest-group, rather than as a character emerging exclusively through hybridisation.

Within the *A. minus*-complex the pollen and achene viability offered no clues as to the hybrid origin of specimens. Both the morphological variation within a population, as well as the variation in polar axis of pollen grains indicate that no apomixy is involved. Therefore, I treat *A. pubens*, *A. chaberti*, and *A. minus* together as a single species to be called *A. minus*. The inclusion in a single species of many differing specimens may not be quite satisfactory. In such cases the question arises why some species show such extreme variability while most species do not. Unfortunately, I do not have an explanation at hand. I described the morphological variation, I did not study processes. However, it seems tempting to follow Weeda (1991: 148) in his speculations on the very variable complex of *Centaurea jacea*. He argues that *C. jacea* survived the adverse conditions prevalent during the Pleistocene in small, isolated populations on sheltered locations. Because these populations derived from different parts of the Pre-Pleistocene range of the species, their genetic properties were slightly different. This enhanced a different evolutionary development of each population during the Pleistocene. In the Holocene period the populations extended their ranges again, they met, and still proved to be interfertile, leading to numerous different forms with intermediates between them. If the same reasoning were adopted for the case of *A. minus*, this would result in abundant 'hybridisation' in the Holocene period without doubling of chromosomes. In terms of the composite species concept, the splittings in the network were only temporary, and the 'microspecies' are part of the same species. But this, of course, is only speculation.

## 12. The recognition of hybrids in *Arctium* section *Arctium*

### 12.1 Introduction

Many European floras mention that hybrids between species of *Arctium* occur frequently, and that they are fully fertile. An overview of methods for the recognition of hybrids has been given by Stace (1989); some of the methods are criticized by Wilson (1992), in particular the ability to distinguish between reticulate series (involving hybridisation) and phyletic ones (involving speciation). Most frequently the intermediacy of character states, or the possession of character states of both parents is used as evidence for hybrid origin. The latter kind of intermediacy has been explained as a phyletic series, and would, thus, be fundamentally different from the former. But this

division between reticulate and phyletic series is obscured by, for instance, extreme dominance or backcrossing. The hybrid index and principal component analysis would be most useful for identifying an intermediate hybrid specimen approaching one of the parents, e.g. in introgression or swarms, or for determination of the parent species (Wilson, 1992). The character count procedure is proposed by Wilson (1992: 19) as a powerful tool to distinguish between hybridity and divergence (phyletic series). All characters in which both parent species differ are scored. The putative hybrid is scored per character for being different with one, both, or none of the parents. The tally (intermediate/not intermediate) indicates whether or not hybridity is the case.

All above methods can be used when the delimitation and therefore the morphology and variability of both parent species are known. The recognition of species hybrids is, thus, closely dependent on the way the species are delimited. A narrow species concept may lead to numerous intermediate specimens which can be regarded as hybrids. However, if intermediate specimens always occur where the supposed parent species are present, in stable habitats, and if they are completely fertile, then they may not be the result of interspecific hybridisation (see Chapter 5). It is then more realistic to unite both supposed parent species into a single species. The specimens previously regarded as hybrids then fit into that species as intermediates in a morphological cline.

According to Wagner (1983: 70) the hybrid origin of specimens very often is obvious. This would imply that a simple evaluation of character states in a putative hybrid could give enough information about the parents of the individual. When parent species are morphologically very similar, intermediate specimens can hardly have intermediate character states. They rather tend to possess some character states of one and some of the other parent. I feel that comparison of the character states of the putative hybrid with the states of the supposed parents, and a fertility analysis are sufficient instruments to detect whether hybridisation has taken place.

Fertility of hybrids can be inferred from the production of viable pollen or seed, from chromosome behaviour at meiosis, or from the success of the F1 or F2 hybrid (Stace, 1989: 140). One has to bear in mind that reduced fertility may also have other causes, like environmental effects or mutations, rather than being of hybrid origin. Other evidence on hybridity can be gathered from F2 segregation; if the offspring of a supposed hybrid is very divergent there is reasonable evidence that the parent was indeed of hybrid origin. Finally, comparison of a putative hybrid and an artificial resynthesis of it could help.

The recognition of hybrids is closely dependent on the delimitation of the species for which we have to rely on morphological characters (see Chapter 5). Taxonomists tend to describe taxa with as little variability as possible. The late Mr. R.M. van Urk (Den Haag, an avid student of *Arctium* sect. *Arctium* in the Netherlands) stated that he could distinguish nine species of *Arctium* in Northwestern Europe (pers. comm.). In *Arctium* sect. *Arctium*, with the increase of the number of taxa recognized, the number of described hybrid taxa also increased. Since long, it has generally been stated that in this genus intermediate forms occur frequently. This could lead to the recognition of only one species, without infraspecific taxa, in the genus. However, this is felt to be very unsatisfactory, because some forms occur rather frequently.



Another possibility is that the variability which is allowed for the characters is artificially restricted. Then, often specimens will be found which conflict in one or several respects with the imposed variability. Such plants, which might be hybrids, have characters which can be considered as intermediate between two taxa. Because all species of *Arctium* have the same chromosome number, this character can not be used to ascertain whether these plants indeed are hybrids. In my opinion, F1 hybrids should be intermediate in more than one respect. If such specimens are not found, or, in other words, if all intermediate specimens are only so in a single character, it is then rather unlikely that the intermediates are hybrids. If the number of intermediate specimens strongly decreases when the characters are allowed a wider variability, it may indicate that the taxa were delimited too narrow. I tried to reach an optimum between an acceptable variability within each species, so that the species can still be characterized, on the one hand, and minimalisation of the occurrence of intermediate forms on the other hand. In the remaining of this chapter I deal with the hybrids in *Arctium* section *Arctium* only. Within *Arctium* section *Pseudarctium* I have seen the hybrid between *A. pseudarctium* and *A. umbrosum* (see the description of *A. xdualis*, H6). I have not seen the recorded hybrid (now intergeneric!) between *A. umbrosum* and *Cousinia alberti*.

### 12.2 Delimitation of the species and determination of the hybrids in *Arctium* section *Arctium*

Herbarium taxonomists start by piling specimens which look similar to the naked eye, putting aside equivocal specimens for the time being. Describing the specimens of each pile produces a 'group-description'. When all piles are described, the left-over specimens are submitted to a detailed analysis, in order to allocate them as much as possible to one of the piles. The 'group-descriptions' will approximate each other during this process, but as long as they have a unique combination of characters the groups can be considered as species.

Within *Arctium* sect. *Arctium* I started by selecting the typically corymbose specimens, and followed by dividing them into a group with glabrous, bright green capitules, and a group with (densely) hairy, dark green to purplish capitules. I prepared descriptions of the groups and found some reliable differences between them. The latter group, corresponding with *A. tomentosum* (s.l., including *A. palladini*), contains specimens with always a glandular hairy corolla which exceeds the involucre. The inner involucre bracts are widened below the apex, and truncate at the apex. In all specimens of the first group, corresponding with *A. lappa*, the involucre exceeds the usually glabrous corolla, but specimens with a hairy corolla are also present. Within this group the petiole of the basal leaves (not always present in the specimens) appears to be solid at base. Only 2% of the corymbose specimens was difficult to place. Some specimens I could not allocate to either one, and some I could allocate with similar justification to both of the corymbose groups. The latter have characters of both *A. lappa* and *A. tomentosum*, as well as intermediate characters. In those specimens the percentage of abortive achenes is higher than in 'typical' specimens of both species. It seems acceptable to conclude that these intermediate specimens are indeed hybrids between *A. lappa* and *A. tomentosum*. The other deviating corymbose specimens which I could not allocate to either of the two corymbose species are dealt with later in this chapter.

Specimens with a subcorymbose to racemose synflorescence were much more difficult to distribute over various piles. Very quickly, after some hundred specimens and using different characters (e.g. length of peduncle, indument and size of capitule), the differences between the piles became obscure. Thus, if different groups should indeed be present within this group of subcorymbose to racemose plants, more detailed characters are needed to describe them.

Therefore, I started by preparing hundreds of detailed specimen descriptions. A number of subcorymbose specimens appeared to have all characters in common with either *A. lappa*, or *A. tomentosum*, except for the type of synflorescence. I soon realised that those collections indeed belong to *A. lappa* or *A. tomentosum*, but represent the lower branches of plants of those species. As was already mentioned elsewhere (Chapter 6), the top of the synflorescence should always be checked in order to determine the way it branches. It is very probable that the collections mentioned were made from a lower branch of a plant. In some cases a closer inspection of a specimen revealed that, based on the presence of rest fibres at the base of the axis, a lateral branch was indeed involved. All specimens of this type were included either in *A. lappa* or *A. tomentosum* (s.l.).

For the delimitation of the species in the rest-group I selected a number of specimens covering the whole range of the variability of this group. I described the results of this analysis in Chapter 11, where I concluded that three species may be recognized in the *A. minus*-complex. I could allocate most, but not all of the material to one of the three species *A. atlanticum*, *A. minus*, and *A. nemorosum*.

A rest-group of 33 unidentified specimens remained. Most of these specimens have a (sub-)corymbose synflorescence, but one specimen has a racemose synflorescence. Nine specimens had the following combination of characters: (sub-)glabrous capitules in corymbose synflorescences, basal leaves with hollow petioles, acute inner involucre bracts, and corollas equalling the involucre. I regard these nine specimens as hybrids between *A. lappa* and *A. minus*. In *A. lappa* the petiole is solid, and the involucre exceeds the corolla; in *A. minus* the synflorescence is racemose to subcorymbose, and never corymbose. The shape of the inner involucre bracts excludes *A. tomentosum* as a possible parent.

The other subcorymbose specimens usually have normally developed pollen, but they seem to have a higher percentage (more than 50%) of aborted achenes than is usually the case. In my opinion they are also of hybrid origin. The recognition of the parents is not always easy. I compared the characters of each putative hybrid with the characters of the species known from the area where the putative hybrid was collected. I also used information from the field notes on the herbarium labels and my own field observations concerning the presence of other *Arctium* species.

One collection (*A. de Wever in hb. van Soest 2211*) with a corymbose synflorescence grew in a garden between *A. tomentosum* and *A. nemorosum*. According to the label, hybrids were formed spontaneously every year. I indeed regard this collection as the hybrid between the mentioned species.

Most of the remaining specimens with a (sub-)corymbose synflorescence have inner involucre bracts which are slightly widened below the apex, or somewhat truncate at apex. Apparently, *A. tomentosum* is one of the parents. According to the labels, some of these specimens were growing together with *A. tomentosum* as well

as either *A. lappa* or *A. minus*. If they are indeed hybrids with these respective species, it appears that the hybrid of *A. tomentosum* with *A. lappa* has longer capitules than the hybrid with *A. minus*. I included the specimens of which field notes were lacking to either of the two hybrids, based on the length of the capitule.

Finally, a specimen (*Koelz 16578*) from Iran was left with a racemose synflorescence, a glandular hairy corolla, and acute inner involucrel bracts which are somewhat widened below the apex. The subapically widened inner involucrel bracts are characteristic for both *A. palladini* and *A. tomentosum*. The length of the anthers and stylar apex of the specimen falls within the range of *A. tomentosum*, while those of *A. palladini* are longer. The collection was made in Iran, in which area both *A. minus* and *A. palladini* occur. The specimen combines characters of both *A. minus* and either *A. tomentosum* or *A. palladini*. It seems reasonable to assume that the collection is the hybrid between *A. minus* and *A. palladini*, because of the geographical distribution, and because the anther and stylar apex length are intermediate between the putative parent species.

### 12.3 Conclusion and discussion

Presumably, hybrids are formed between species of *Arctium* sect. *Arctium*, but not frequently. I have seen, out of some 2000 specimens, only 35 specimens which are of supposed hybrid origin. Moreover, hybrids are almost certainly overrepresented in the herbarium, because, in the botanically well known region of Western Europe, collectors tend to collect the odd, deviating specimens, rather than the normally developed, well known species.

Earlier authors accepted a narrower delimitation of the species than I do. They, therefore, saw more intermediate specimens which often lead to the assumption that they represented hybrids. In my opinion *A. lappa* and *A. minus*, for instance, both may have either a glandular hairy, or a glabrous corolla, whereas according to earlier authors the corolla of both species is glabrous only. Arènes (1950) interpreted the presence of hairs on the corolla of specimens of both species as a sign of their hybrid origin, even if such specimens did not deviate in any other aspect from specimens of either species with a glabrous corolla. This type of 'intermediate' specimens between *A. lappa*, *A. minus*, and *A. tomentosum* in a narrow delimitation is so abundant, that these three species should be regarded as a single species. However, it is much more plausible that both *A. minus* and *A. lappa* are variable in the indument of the corolla (glabrous to glandular hairy). There is then (taking also into account the fact that the synflorescence of the lower branches deviates fairly from those of the terminal branches) no need to have doubts on the species-status of *A. minus*, *A. lappa*, and *A. tomentosum*. The number of really intermediate specimens (to be interpreted as hybrids) is actually very small.

Within *Arctium* sect. *Arctium* six species can be distinguished. By assuming that the internal variation of each species is somewhat more extensive than in Arènes' publication, most of the plants which formerly would have been called hybrids can then be regarded as belonging to one of the six species. The species of the *A. minus*-complex do not seem to form hybrids with each other. In my opinion, hybridization does occur in *Arctium*, but on a much smaller scale than previously assumed.

### 13. Phylogeny and generic delimitation

#### 13.1 Introduction

The generic delimitation of *Arctium* has not been a serious issue of dispute, although Kuntze (1891) transferred all 187 described species of *Cousinia* to *Arctium*, because some species of *Cousinia* also possess hooked involucre bracts. The difference between the two genera would be the presence of entire (*Arctium*) versus fimbriate (*Cousinia*) basal appendages of the anthers, but my analysis showed that this difference can not be maintained (see Chapter 6). Later authors did not follow Kuntze: they kept *Arctium* and *Cousinia* separate, and they sometimes mentioned the close relationship between *Arctium* and these species of *Cousinia*. Rechinger (1972), for instance, stated that the species of section *Pseudarctium* can be understood as a 'bridge between the genera *Arctium* and *Cousinia*'. Schtepa (1971, 1973) felt that, based on palynological evidence, some species of the genus *Cousinia* should probably be placed in *Arctium*. These species are *C. arctioides* (section *Nanarctium*), *C. umbrosa*, *C. tomentella*, and *C. pseudarctium* (section *Pseudarctium*), *C. lappacea* (section *Lappacea*), and *C. anomala* (section *Ctenarctium*), although the latter species does not have the typically hooked involucre bracts of *Arctium* [sections according to Tscherneva, 1962 (in Komarov), 1988].

Kuprianova & Tscherneva (1982) referred to the pollen of the above mentioned species as the *Arctiastrum* type, and found that this type is present in all the species examined of *Cousinia* subg. *Cynaroides*, which, among others, includes the sections mentioned above, as well as *C.* subg. *Hypacanthoides* (subgenera of Tscherneva, 1988). Most species of these subgenera, however, have involucre bracts which are not hooked as in *Arctium*.

My palynological studies confirm the findings of the earlier authors (see Chapter 7). The pollen of *Cousinia* subg. *Cousinia* is very different from the pollen of the other two subgenera. I include the pollen of *Arctium*, *C.* subg. *Cynaroides* and *C.* subg. *Hypacanthoides* in one type, the *Arctiastrum* type of Kuprianova & Tscherneva (1982). However, this does not imply the inclusion of the two subgenera in *Arctium*. Pollen types generally include species of more than one genus in the Asteraceae. The pollen type of *Arctium*, for instance, also occurs in other genera of the 'super-tribe' Cynaroideae, e.g. *Cynara*, *Jurinea*, and *Cirsium* (Qaid, 1990).

The delimitation of *Arctium* is thus not very clear-cut. Should it be based on the basal appendage of the anthers, the presence of hooked involucre bracts, on the pollen type, or on other characters? I performed a phylogenetic analysis to gain insight. Of course, I could not include all 660 species of *Cousinia* in the analysis. None of the available algorithms can manage a database with over 100, let alone 600 species. I therefore selected all species of *Arctium* sect. *Arctium* and a selected number of species from *Cousinia*, including all species with hooked involucre bracts.

Greuter (1973: 175) mentioned that the relation of *Ptilostemon* to *Cousinia* still has to be studied. I do not preclude that more genera are closely related to *Cousinia* or that *Cousinia* in its present circumscription is an unnatural entity. However, the aim of the present phylogenetic analysis is to reach a natural, and recognizable delimitation of *Arctium*. The relation of *Cousinia* to other genera is not discussed here.

### 13.2 Phylogeny

Three major schools exist which all aim at a natural arrangement of species: the classical ('evolutionary') school, the phenetic school, and the phylogenetic school. The classical approach is usually atheoretical, and very heterogeneous. The phenetic approach starts with the assumption that as many characters as possible should be taken into account in a classification. It is a reaction to the lack of transparency of the classical school. Diverse mathematical algorithms have been developed which often produce very different results with the same datamatrix. There is no theoretical basis to decide which algorithm is better than another.

Phylogenetic systematics is, intentionally, not free of theory. It assumes (pattern cladistics excepted) that there is evolution which results in character changes. These character changes can be used to reconstruct relationships. A distinction is made between plesiomorphic, or earlier developed, character states, and apomorphic, or later developed, advanced character states. These terms are relative. What is an apomorphy at the family-level, is a plesiomorphy at the generic level. Only shared apomorphies are evidence of common ancestry. Both the classical and the phenetic school allow groupings based on plesiomorphic states which holds the risk of unnatural classifications. I, therefore, choose for the phylogenetic analysis.

A method to assign apomorphies is by outgroup comparison. This rule states that, if two homologous character states are found within a monophyletic group, then the state that is also found in the sister group is the plesiomorphic one. The character state that is only found within the monophyletic group is the apomorphic state (Wiley, 1981: 139).

The number of cladograms resulting from a single data matrix depends on the number of taxa. A criterion to select a cladogram among many is the principle of parsimony. This criterion minimizes parallel developments and reversals, and maximizes the number of synapomorphies. This principle guarantees that a cladogram is selected with the smallest number of character changes. The character distribution on this cladogram deviates maximally from the hypothesis that all character states originated independently, without historical constraint. The cladogram does not necessarily depict the true evolutionary history, but it is the first logical step in the search for it.

Several measures have been developed to describe the fit of the data to the tree (Siebert in Forey et al., 1992). I mention three of them, the length of the tree, the consistency index (ci), and the retention index (ri). The tree length is the summation of the number of character changes of the individual characters on the tree. The ci decreases by an increasing number of steps, and indicates the amount of homoplasy within a cladogram. It is achieved through dividing minimum possible change, if no homoplasy would occur, by actual change. If there is no homoplasy the  $ci = 1$ ; the more homoplasy, the lower the ci. The ri expresses the amount of synapomorphy in a data set. It is a measure for the sturdiness of the cladogram: character changes close to the root of the cladogram are valued higher than those at the top of the cladogram. If the  $ri = 0$  it means that the character states are either synplesiomorphies or (parallel) autapomorphies. The length of the tree, the ci, and the ri are primarily for use within an analysis.

### 13.3 *Genus concept*

It is generally agreed, at least since Linnaeus, that genera should not overlap, and that they should be exhaustive (Kornet, 1988). Each species belongs to only one genus.

Since the translation of Hennig (1966), until recently, the generally accepted idea among cladists is that natural supraspecific entities, i.e. sections, genera, families etc, should be monophyletic. The goal is to develop a classification of monophyletic groups that will disrupt the present classification as little as possible (Funk, 1985: 73). A genus, thus, should include an ancestor-species and all its descendant-species. A classification of 'natural groups' that have a common evolutionary history is maximally informative (Wiley, 1981: 239): it has predictive value. The size of the monophyletic supraspecific taxa is partly a matter of choice. This choice is influenced by practical considerations, such as the history of a group, the number of species, apomorphy without reversals, etc.

However, several taxonomists dealing with large genera felt that the requirement of strict monophyly for supraspecific taxa is untenable. I agree with this. It may lead to supra-specific groups which are only weakly characterized (e.g. Vermeulen, 1993: 44). Sosef (1994: 82) stressed that not accepting paraphyletic groups will cause an avalanche of new supraspecific taxa, or will result in excessive lumping. Examples illustrating these effects are given by Brummitt (in press). He emphasized the difference between a phylogenetic classification, based on putative phylogenetic relations, and a Linnaean classification which is based on morphological discontinuity. De Quieroz & Gauthier (1992), among others, proposed to abandon Linnaean classification. Instead, they want to introduce species names that are independent of their arrangement into higher taxa. This means that from a list of species names it is impossible to arrange the species into higher taxa without extra information. As De Quieroz & Gauthier (1992) stated, a hierarchic system is fundamental to comparative biology. Therefore, I think their aim towards a phylogenetic taxonomy is very impractical.

Taxonomists want their results to be used. Therefore, as Brummitt (in press) states, all taxa must be recognizable and identifiable. The classification should be based on a cladogram. However, Brummitt (in press) and Sosef (1994) allow such taxa to consist of the paraphyletic tail of a monophyletic group, if it improves the recognizability of the supraspecific taxa. Indeed, accepting paraphyletic taxa decreases the phylogenetic information. But, if information on the phyletic status of a group is needed, as for instance in historical biogeography, it is not necessary to have a phylogenetic classification at one's disposal. It is sufficient to have a phylogenetic reconstruction, the cladogram. I think that a classification with well-characterized genera, although some genera consist of a paraphyletic tail, is to be preferred over a classification consisting solely of monophyletic, but weakly recognizable genera.

Of course, polyphyletic taxa should be rejected as unnatural and thus uninformative classes. Hennig (1966) was not the first to formulate the desire for a natural classification. This idea goes back at least as far as Linnaeus (1753), who sometimes included species in groups because of a vague notion of phylogenetic relationship, rather than on account of characters as the number of stamens. Cladistics provides a theoretically based method to infer the phylogenetic relations.

### 13.4 The computer algorithm

I chose to apply the computer program Hennig86 (Farris, 1988), which needs a priori designation of an outgroup. The user is free in his choice of options. The basal node of the resulting cladograms is always at least a trichotomy, of which the outgroup should be considered as the most basal clade.

I entered all characters as unordered, and used the combination of the options 'mhennig\*' and 'bb\*', which is often sufficient to find all most parsimonious trees (pers. comm. van Welzen). The length, the ci, and the ri of each tree are calculated.

Usually this results in more than one cladogram. The cladograms can be summarized in a consensus tree, which shows the similarities between the trees (option 'nelsen'). Following a primary analysis as above, a second analysis can be performed, this time with a weight to each character, given according to its fit on the primary cladogram (ci x ri, rescaled between zero and 10; option 'xsteps w'). This procedure has to be repeated until the number of trees and the weighting factors do not change anymore. The process of character weighting is more or less described by Farris (1969).

### 13.5 Selection of the ingroup

The datamatrix included 26 taxa. Apart from the outgroup, it included the eleven species of *Arctium*, including the six species of the genus in its traditional delimitation (sect. *Arctium*), and the five 'arctioid' species of *Cousinia* (*A. amplissimum*, *A. arctioides*, *A. lappaceum*, *A. pseudarctium*, and *A. umbrosum*); also included are a species of each of the remaining four sections of *Cousinia* subg. *Cynaroides* (*C. anomala*, *C. triflora*, *C. korolkovii*, and *C. pentacantha*), a species of a randomly chosen section of *C.* subg. *Hypacanthoides* (*C. macilenta*), and a species each of nine randomly chosen sections of *C.* subg. *Cousinia* (*C. parviceps*, *C. eryngioides*, *C. congesta*, *C. scariosa*, *C. pseudostenolepis*, *C. oligocephala*, *C. microcarpa*, *C. freynii*, and *C. tenella*). The only selection criterion was the availability of good material. It is, of course, preferable to use the character states at the basal node of the assumedly monophyletic section or subgenus, but these are not available. Unfortunately, a cladistic analysis of *Cousinia* has never before been performed, and is beyond the scope of the present project.

### 13.6 Selection of the outgroup

An analysis of the phylogenetic relationships of the genera within the 'super-tribe' Cynaroideae, including 40 of the 89 genera, was performed by Petit (1990). He executed his analysis with PHYLIP. This is a compatibility analysis which does not need an outgroup. Siebert (in Forey et al., 1992: 81) states that the resulting cladograms may not be the most parsimonious. Also, Petit (1990) did not include all genera of the 'super-tribe' in the analysis. His results may nevertheless serve as a guide in the search for an outgroup for my analysis.

The first analysis of Petit (1990) was performed with a selection of genera of the Cynaroideae and resulted in five groups. The subtribe Carduinae, including *Arctium* and *Cousinia*, together with *Serratula* (Centaureinae) form one group. A second analysis involving this subgroup resulted in a cladogram which excluded *Serratula*, *Jurinea* and *Saussurea* from the Carduinae. *Arctium* and *Cousinia* are more closely related

to each other than each is to any of the other genera of the Carduinae. The clade of these two genera branches off at the base, followed by a clade including the genera *Onopordum*, *Cynara* and *Ptilostemon*.

Dittrich (1970, 1977), who studied the fruit characters including the pappus, showed that the apical plate of the achenes of the Cynaroideae is considerably variable, and he recognized within the subtribe Carduinae four groups of genera. According to him *Arctium* and *Cousinia* constitute one group together with *Onopordum*, *Myopordon*, and *Tiarocarpus*.

The genus *Tiarocarpus* is a split genus of *Cousinia*. Its phylogenetic relation to *Cousinia* is unclear, it may be a derivative of *Cousinia*, but it may also take a position at the root of the genus. I therefore did not select *Tiarocarpus* as an outgroup for *Arctium* and *Cousinia* p.p.

The pappus of *Onopordum* and *Myopordon* is connate at base. This is unique within the Carduinae, but seems more similar to the free pappus of *Arctium* and *Cousinia* than to the pappus of the other Carduinae, of which the pappus hairs are inserted on a basal ring-shaped tissue. The receptacle of *Onopordum* and *Myopordon* has a honeycomb structure, and has no receptacular scales. The species of *Myopordon* are compact, strongly branched shrublets with unarmed leaves. Within the Asteraceae shrubs (versus trees and annual herbs) are generally considered the plesiomorphic state (Bremer, 1987). I do not know whether this holds also for the Carduinae, where many genera, including *Arctium* and many species of *Cousinia* are herbs. The woody habit of *Myopordon* favoured the selection of the genus *Onopordum* as outgroup, of which the species are monocarpic. This is not in contradiction with the results of Dittrich (1977) and Petit (1990).

The phylogeny of *Onopordum* has so far not been analysed. I have rather arbitrarily chosen *Onopordum acanthium* as outgroup.

### 13.7 Character states

For a cladistic analysis character states of taxa (often species) have to be entered in a data matrix. Morphological characters can be qualitative (discrete) and quantitative (discrete or continuous). Pimentel & Riggins (1987), among others, argue that continuous quantitative data should not be included in the analysis. The use of discrete quantitative variation is also advised against.

What remains are the qualitative characters. Many authors severely felt a general shortage of qualitative characters (see references in Stevens, 1991), resulting in cladograms which are badly resolved. Sometimes quantitative characters were used in sub-analyses, in order to resolve the polytomies of the initial analysis. Others used or developed statistical techniques to 'detect' gaps in the variation. Simple methods include comparisons of midpoints or means; generalized gap coding (Archie, 1985) is one of the more sophisticated methods. Intermediate states are sometimes coded as a separate state.

Stevens (1991) discusses the nature of the various types of characters in cladistics, and the delimitation into character states. I agree with him that many so-called qualitative characters are only semantically so, because measurements have been replaced by terminology. I mention leaf shape and flower colour as examples. Basically, these characters are, often continuous, quantitative characters.



The delimitation of character states, the basis of the cladistic analysis, usually receives very little attention in publications. Stevens shows that in at least some cases the delimitation is arbitrary. He presents as a general rule that character states in a phylogenetic analysis should be discrete and without overlap. If the boundary between two discrete states is blurred by only a few taxa these taxa may be scored as having missing data or as having both states, rather than scoring only one or the other state. According to him intermediates should not be coded as a separate state. In the process of delimitation he also advises to take the variation of the outgroup into account. If the character states will overlap when the outgroup is also considered, Stevens advises to exclude these characters from the initial analysis, and use them at lower level analyses. The strongest plea of Stevens, however, is to extensively document the justification of the delimitation of the character states, a recommendation I will follow here.

### 13.8 Character states coding

I will give here the argumentation for the delimitation of the character states. Missing values, and taxa with variable characters I coded both as a '?'. Unlike PAUP, Hennig86 does not offer the option of coding polymorphism. The character states present in the outgroup, *Onopordum acanthium*, are coded '0'.

- 0 — Life span:
  - 0: monocarpic
  - 1: annual
  - 2: perennial

The 'arctioid' and many more species of *Cousinia* are all perennial, whereas five species of *Arctium* sect. *Arctium* are monocarpic. The life span of *A. atlanticum* is unknown. *Cousinia tenella* is the only annual species that is included in the analysis.

- 1 — Lower cauline leaves
  - 0: decurrent
  - 1: sessile
  - 2: petiolate

The character states do not show overlap.

- 2 — Petiole of basal leaf
  - 0: absent
  - 1: hollow
  - 2: solid

The character states show overlap only in *A. tomentosum*, of which the petiole may be hollow or solid. I have not seen petioles of the basal leaves of *A. (C.) arctioides* and *C. tenella*. In all other species the petiole is either hollow or solid.

Note – I treated the absence of the petiole as a separate character state; perhaps, it would have been better to score the species in which a petiole is absent as '?' for this character.

- 3 — Margin of cauline leaves incision
  - 0: pinnatifid
  - 1: entire to sinuous dentate
  - 2: pinnatipartite

A quantitative character showing no overlap.

- 4 — Margin of cauline leaves: presence of spines  
0: present  
1: absent

I included as spines all spiny projections of the leaf margin. I have not seen species with both character states, for instance leaves with margins with and leaves with margins without spines in one specimen.

- 5 — Capitule peduncle  
0: present  
1: absent

This character is taken from the capitules in the apex of the inflorescence. Only the capitules of the very variable species *A. minus* range from sessile to rather long pedunculate. All other species are not variable for this character.

- 6 — Middle involucre bract: presence of appendage  
0: absent  
1: present

The appendage of the middle involucre bract is, as in e.g. *Centaurea*, defined as an abruptly widened apical part. The character states show no overlap.

- 7 — Apex of middle involucre bract: presence of spines  
0: one spine present  
1: several spines present  
2: absent

The presence of more spines occurs in some of the species with an appendage. There is no overlap between the character states.

- 8 — Apex of middle involucre bract: presence of a hook  
0: absent  
1: present

A hook is defined as a bend of more than 180°. Sometimes, as in *C. anomala*, a bend of ca. 90° is present; they are coded as not hooked. There is no overlap between the character states.

- 9 — Receptacle  
0: with ridges  
1: with receptacular scales

All species of the ingroup have receptacular scales.

- 10 — Receptacular scales  
0: absent  
1: acute  
2: narrowly spatulate

There is no overlap between the character states.

Note – Only after I performed the analyses, I realized that in fact the characters 9 and 10 are the same character; character 9 has to be eliminated. The inclusion does not influence the topology of the cladograms, because only the outgroup does not have receptacular scales. It does, albeit not seriously, influence the length, the ci, and the ri of the cladograms.

- 11 — Pappus  
0: connate at base  
1: free, falling off separately  
2: inserted on a ring-shaped tissue which falls off as a whole  
3: absent

There is no overlap between the character states. *Cousinia congesta* is the only species without a pappus.

- 12 — Capitule: number of flowers  
0: more than 30  
1: less than 30

I do not know the ranges of the number of flowers of all species. Of several species of *Cousinia* I know only the lower limit, *C. macilenta*: more than 50 flowers, *C. pseudostenolepis*: more than 70 flowers, *C. freynii*: more than 80 flowers, and *C. scariosa*: more than 100 flowers. At the present delimitation the character states show no overlap. Within the character state 'more than 30 flowers per capitule' no further division is possible because of shortage of data.

- 13 — Corolla: colour  
0: pink to purple  
1: cream coloured to golden or greenish yellow

The examined species have either purplish or yellowish flowers. The only exception is *A. (C.) amplissimum*, which has normally purple flowers, but rarely yellowish flowers also occur. The character is coded as '?'. The information in the literature on the colour of the flowers of *A. (C.) arctioides* is equivocal. Several authors mention either yellow or purple corollas. It is therefore also coded as '?'

- 14 — Corolla: presence of multicellular hairs  
0: absent  
1: present

I did not make any subdivision for the distribution of the hairs over the corolla (only at the lobes, over the entire limb, or limb and apical part of the tube), because this showed too much overlap. With the present delimitation of character states only three species show overlap: *A. minus*, *A. (C.) pseudarctium*, and *A. (C.) umbrosum* can have either glabrous or hairy corollas. In *A. lappa* a glandular hairy corolla is so rare that I coded them as absent for this species.

- 15 — Limb: part of total length of corolla  
0: 2/5–3/5  
1: 3/5–4/5

See Fig. 13.1. With this delimitation only *A. (C.) arctioides* shows some overlap. I did not score this taxon as variable because only one out of seven specimens has a limb which is slightly longer than 3/5 of the total length of the corolla. Of *C. subg. Cousinia* unfortunately the full range of each state is unknown, but the data do not blur the delimitation. For *A. (C.) lappaceum* this character is scored as missing value, because of this species I have only seen juvenile flowers, of which the tube was not yet full-grown.

- 16 — Longest lobe: part of total length of the limb  
0: 2/5–3/5  
1: 1/5–2/5

See Fig. 13.2. This delimitation of the character states shows overlap only in *A. nemorosum* which is coded as '?'.

- 17 — Anthers: colour  
0: pink to purple  
1: yellow(ish)

The character states do not show overlap. The anthers of *A. (C.) amplissimum* are purple, never yellow, whereas the corolla of this species may be yellow or purple (see character 13). Some species with yellow corollas, as *C. pentacantha* and *C. congesta*, have purple anthers. I do not know the colour of the anthers of *A. (C.) arctioides*.

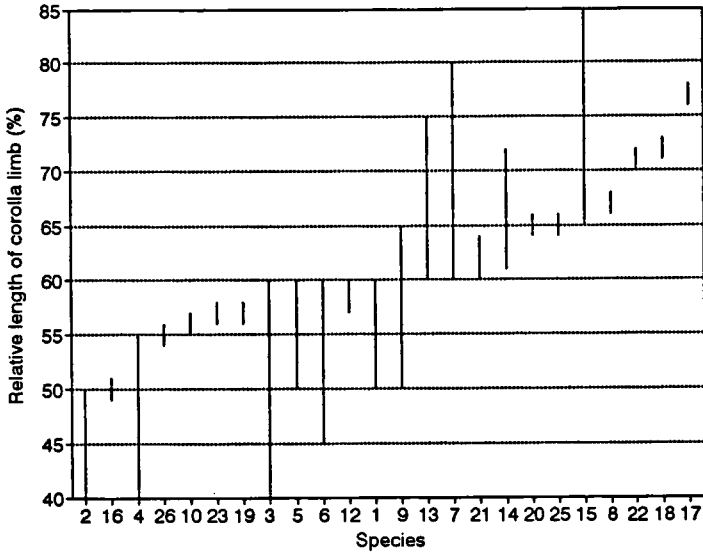


Fig. 13.1. High/low Diagram showing the range of the relative length of the corolla limb within the 26 species which are included in the phylogenetic analysis. The numbers on the x-axis refer to the species as follows: 1: *Arctium atlanticum*; 2: *A. lappa*; 3: *A. minus*; 4: *A. nemorosum*; 5: *A. palladini*; 6: *A. tomentosum*; 7: *Cousinia amplissima*; 8: *C. anomala*; 9: *C. arctioides*; 10: *C. korolkovii*; 11: *C. lappacea*; 12: *C. pentacantha*; 13: *C. pseudarctium*; 14: *C. triflora*; 15: *C. umbrosa*; 16: *C. macilentia*; 17: *C. congesta*; 18: *C. eryngioides*; 19: *C. freynii*; 20: *C. microcarpa*; 21: *C. oligocephala*; 22: *C. parviceps*; 23: *C. pseudostenolepis*; 24: *C. scariosa*; 25: *C. tenella*; 26: *Onopordum acanthium*.

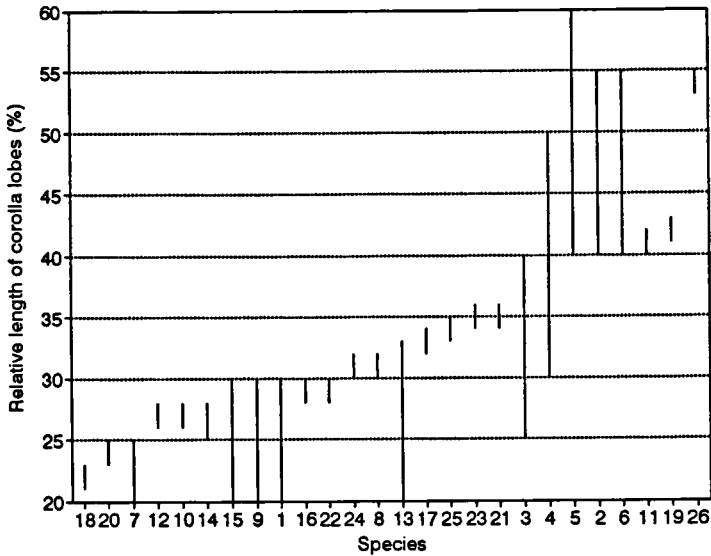


Fig. 13.2. High/low Diagram showing the range of the relative length of the corolla lobes within the 26 species which are included in the phylogenetic analysis. The numbers on the x-axis refer to the species (see the legend of Fig. 13.1).

- 18 — Anther: filament  
0: glabrous  
1: verrucate to papillose

Both the outgroup and many species of *Cousinia* have glabrous filaments. In several species of *Arctium* both glabrous and verrucate filaments occur. I have interpreted this character as having not yet reached full fixation, and I have appointed the state '1' if verrucate filaments occur at all in the species.

- 19 — Anther: apical appendage  
0: glabrous  
1: dorsally with slender hairs

Hairs on the dorsal side of the apical appendage occur in only three species. *A. (C.) umbrosum* is coded as '1', but glabrous appendages also occur. Fixation is, again, not yet completed.

- 20 — Style: position of sweeping hairs  
0: a concentrated ring of sweeping hairs near a thickened apical portion  
1: sweeping hairs in region below branches, without a thickening  
2: branches dorsally with many scattered sweeping hairs

In this delimitation the character states do not show any overlap. The plesiomorphic state is the cynaroid type of style, which is typical for the Cardueae. The other two states were hitherto unknown in the Cardueae (and other tribes of the Cynaroideae).

- 21 — Styler branches: part of styler apex  
0: more than 3/5th  
1: less than 3/5th  
2: ring of sweeping hairs absent

See Fig. 13.3. The styler apex is the apical part of the style, downwards to the ring of sweeping hairs. The absence of this ring in *C. subg. Cousinia* is coded as a separate state. I have found no overlap between the character states.

Note – I treated the absence of the ring of sweeping hairs as a separate character state; perhaps, it would have been better to score the species in which this ring is absent as '?' for this character.

- 22 — Achene  
0: with (inconspicuous) ridges  
1: smooth  
2: 'winged'

In fact, the difference between ridges and wings is gradual. I have coded species as having 'winged' achenes if the extremities are at least 0.1 mm wide. In this delimitation the character states show no overlap.

- 23 — Apical plate  
0: flat  
1: truncate

The taxonomic significance of the apical plate at the (supra-) generic level, including the presence and shape of protuberances, is known since Dittrich (1970). In the above delimitation the character states show no overlap.

- 24 — Apical plate: marginal ridge  
0: absent  
1: conspicuous (0.3–0.4 mm high)  
2: inconspicuous (0.1–0.2 mm high)

I have not seen intermediates of these character states, and within a species only one of the states is present. The presence or absence of a marginal ridge is unknown for *C. congesta* and *C. eryngioides*. *Arctium (C.) lappaceum* does not have a marginal ridge; the presence of a slight depression around the scars of the pappus is not included in the datamatrix because it is an autapomorphy of the species.

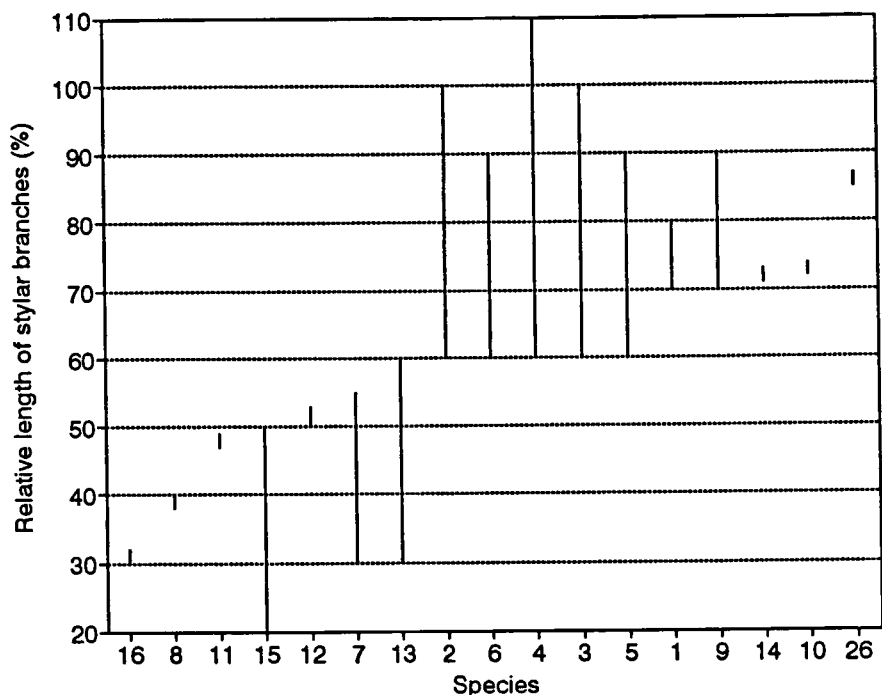


Fig. 13.3. High/low Diagram showing the range of the relative length of the stylar branches within 17 of the 26 species which are included in the phylogenetic analysis. The species of *Cousinia* subg. *Cousinia* are not included because, lacking a thickened ring of sweeping hairs, they do not have a stylar apex. The numbers on the x-axis refer to the species (see the legend of Fig. 13.1).

- 25 — Pollen grains: costae equatoriales  
 0: absent  
 1: costae only near mesoaperture  
 2: present

The character state 'costae only near mesoaperture' can be seen as an intermediate character state. I coded it as a separate state, because it is always present in all species of *Arctium* and several species of *Cousinia*. There is no overlap between the character states in the present delimitation; the '?' for *A. palladini* is a missing value, because I, unfortunately, did not include this species in the palynological analysis.

- 26 — Pollen: echinae or scabrae  
 0: echinae, at least 0.8  $\mu\text{m}$  long  
 1: scabrae, less than 0.5  $\mu\text{m}$  long or absent

The present delimitation into character states shows no overlap, and agrees with the pollen types. It is very difficult to say whether the tectum is scabrate or psilate. Therefore, the absence of echinae has not been treated as a separate state.

- 27 — Tectum: diameter of largest perforations  
 0: 0.17–0.67  $\mu\text{m}$   
 1: 0.06–0.11  $\mu\text{m}$

The present delimitation into character states shows no overlap, and agrees with the pollen types. The diameter of the perforations in the tectum of the *Arctiastrum* type shows a considerable amount of variation. Therefore, I took only the largest perforations of a pollen grain into account.

28 — Somatic (2n) chromosome number

- 0: 34
- 1: 36
- 2: 26

These character states do not show overlap, but the information is incompletely available. The number of chromosomes of two species of *Arctium*, and eight species of *C.* subg. *Cousinia* has not been counted. They are coded as '?'.  


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Tabel 13.1. Datamatrix on which the phylogenetic analyses are based.

OTU	Character																	
	1									2								
	0	1	2	3	4	5	6	7	8	0	1	2	3	4	5	6	7	8
<i>O. acanthium</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>A. lappa</i>	0	2	2	1	1	0	0	2	1	1	1	1	0	0	0	0	0	1
<i>A. minus</i>	0	2	1	1	1	?	0	2	1	1	1	1	0	0	?	0	1	0
<i>A. atlanticum</i>	?	2	1	1	1	0	0	2	1	1	1	1	0	0	0	1	0	1
<i>A. nemorosum</i>	0	2	1	1	1	1	0	2	1	1	1	1	0	0	0	?	0	1
<i>A. tomentosum</i>	0	2	?	1	1	0	0	2	1	1	1	1	0	0	1	0	0	0
<i>A. palladini</i>	0	2	2	1	1	0	0	2	1	1	1	1	0	0	1	0	0	0
<i>A. (C.) arctioides</i>	2	2	?	0	0	0	0	2	1	1	1	1	0	?	0	0	1	?
<i>A. (C.) lappaceum</i>	2	1	0	1	1	1	0	2	1	1	1	1	1	0	1	?	0	0
<i>A. (C.) pseudarctium</i>	2	2	2	1	1	1	0	2	1	1	1	1	1	0	?	1	1	0
<i>A. (C.) amplissimum</i>	2	2	2	1	1	1	0	2	1	1	1	1	1	1	?	1	1	0
<i>A. (C.) umbrosum</i>	2	2	2	1	1	1	0	2	1	1	1	1	1	1	0	?	1	0
<i>C. macilenta</i>	2	2	2	2	0	0	0	0	1	1	1	0	0	0	0	1	0	0
<i>C. anomala</i>	2	2	2	2	1	1	1	1	0	1	1	1	1	1	1	1	1	0
<i>C. triflora</i>	2	1	2	1	0	1	1	1	0	1	1	1	1	1	1	1	0	0
<i>C. korolkovii</i>	2	2	2	2	0	0	0	0	1	1	1	1	1	1	1	0	1	0
<i>C. pentacantha</i>	2	2	2	1	0	0	1	1	0	1	1	1	0	1	1	0	1	0
<i>C. parviceps</i>	2	1	2	2	0	0	0	0	1	2	1	1	0	0	1	1	0	0
<i>C. eryngioides</i>	2	1	2	2	0	1	0	0	0	1	1	1	0	1	1	0	0	2
<i>C. congesta</i>	2	1	2	0	0	1	0	0	0	1	3	1	1	1	1	1	0	0
<i>C. scariosa</i>	2	2	2	0	0	0	1	0	0	1	2	1	0	0	1	0	1	0
<i>C. pseudostenolepis</i>	2	2	2	2	0	0	0	0	0	1	2	1	0	0	0	0	1	0
<i>C. oligocephala</i>	2	0	2	1	0	0	0	0	0	1	2	1	0	0	0	1	1	0
<i>C. microcarpa</i>	0	0	2	1	0	0	0	0	0	1	2	1	0	0	0	1	1	0
<i>C. freynii</i>	2	1	2	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
<i>C. tenella</i>	1	2	?	1	1	0	0	0	0	1	1	2	1	0	0	1	1	0

---

### 13.9 Results

Run with the options 'mhennig\*' and 'bb\*' the matrix of all 26 above mentioned species produces 168 trees. The strict consensus tree of the first 100 trees ('nelsen') is a cladogram with three polytomies including most of the species (Fig. 13.4). *Cousinia* subg. *Cousinia* appears to be a monophyletic group. This group is poorly resolved, which increases the number of trees. Two options (I and II, see below) to

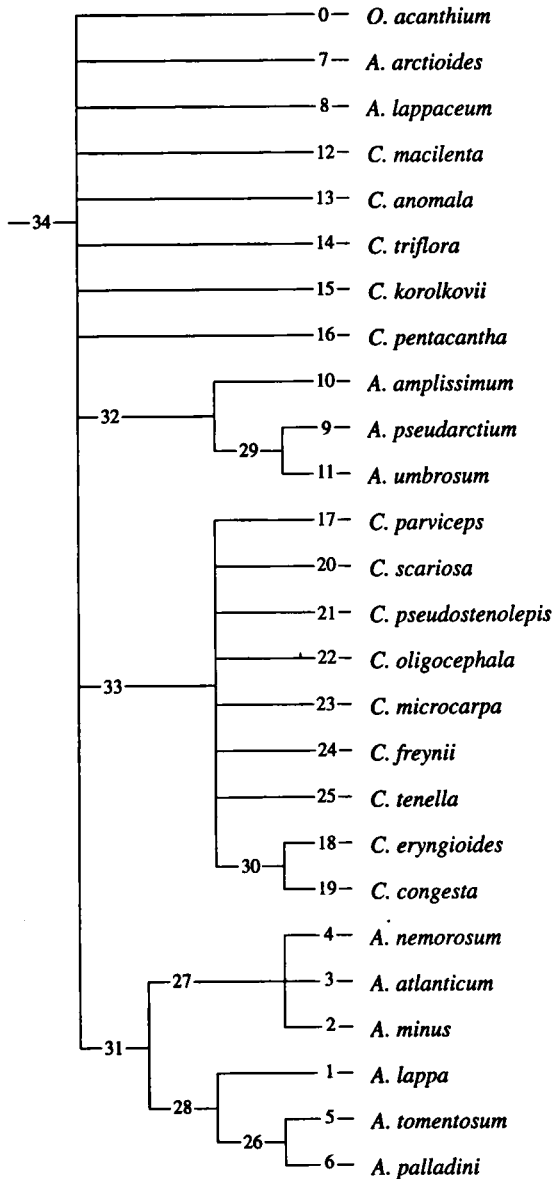


Fig. 13.4. Strict consensus tree of over 100 trees which resulted from the initial analysis.



proceed with the analysis are open at this point; both were carried out. The first is to replace the nine species of *C. subg. Cousinia* by the root (node 33) of this clade in Fig. 13.4. However, there is a possibility that other topologies, with other character states for node 33, exist in the 'overflow'-trees.

Therefore, I also tried the second option. I simply removed all nine species of *C. subg. Cousinia* from the datamatrix. Many species of this subgenus, including all that are included in this analysis, do not have the typical 'cynaroid' style, which is characterized by the presence of a thickened ring with sweeping hairs below the branches. The branches, or sometimes only the upper part of the shaft, usually are covered with sweeping hairs, while a thickening is absent. This 'vernonioid' style was unknown in the Cardueae, but it is common in other tribes of the Asteraceae (e.g. Vernonieae, Lactuceae, Liabeae; see Bremer, 1987). Bremer (1987) excluded for the same reason the genus *Gundelia*, which has the vernonioid type of style, from the Arctoteae which have the cynaroid type of style. Also, the pollen of *C. subg. Cousinia* is very different from pollen of *Arctium*, *Onopordum*, and the other species of *Cousinia*. Therefore, the supposed close relationship to *Arctium* *C. subg. Cynaroides* and *C. subg. Hypacanthoides*, and by that its inclusion in this analysis, is debatable.

#### Option I

With 'tread' and 'xsteps hclm' I imported the strict consensus tree of Fig. 13.4. This command presents the character states of the internal nodes. I replaced the nine species of *C. subg. Cousinia* in the data matrix by the root of the clade, node 33. The character states of this node are shown in Table 13.2.

Table 13.2. Character states of the root of *C. subg. Cousinia*, node 33 from Fig. 13.4.

	0			1			2																					
Character	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8									
Croocous	2	2	2	1	0	0	0	0	0	1	2	1	0	0	0	1	1	0	0	2	2	0	1	0	2	1	?	?

This matrix resulted in 52 equally parsimonious trees (length = 63, ci = 57%, ri = 70%). After three times of character weighting ('xsteps w', 'ccode', 'ie') eight equally parsimonious trees were left (length = 251, ci = 78%, ri = 85%). The strict consensus tree of these eight trees is shown in Fig. 13.5. The most basal node, but excluding the outgroup, is a polytomy of four clades (node 30). Two of them consist of only one OTU. Both the genus *Arctium* including the 'arctioid' former species of *Cousinia* and the rest of *C. subg. Cynaroides* are each monophyletic. From this cladogram it is impossible to make statements about sistergroup relations.

The presence of unarmed, and hooked middle involucre bracts is a synapomorphy for *Arctium* and the 'arctioid' former species of *Cousinia*, in the following referred to as *Arctium* s.l. The yellow corolla and yellow anthers are synapomorphies for the rest of *C. subg. Cynaroides*, *C. pentacantha* showing a reversal to pink anthers. Within *Arctium* s.l. the groups are supported mainly by parallel developments. The spe-

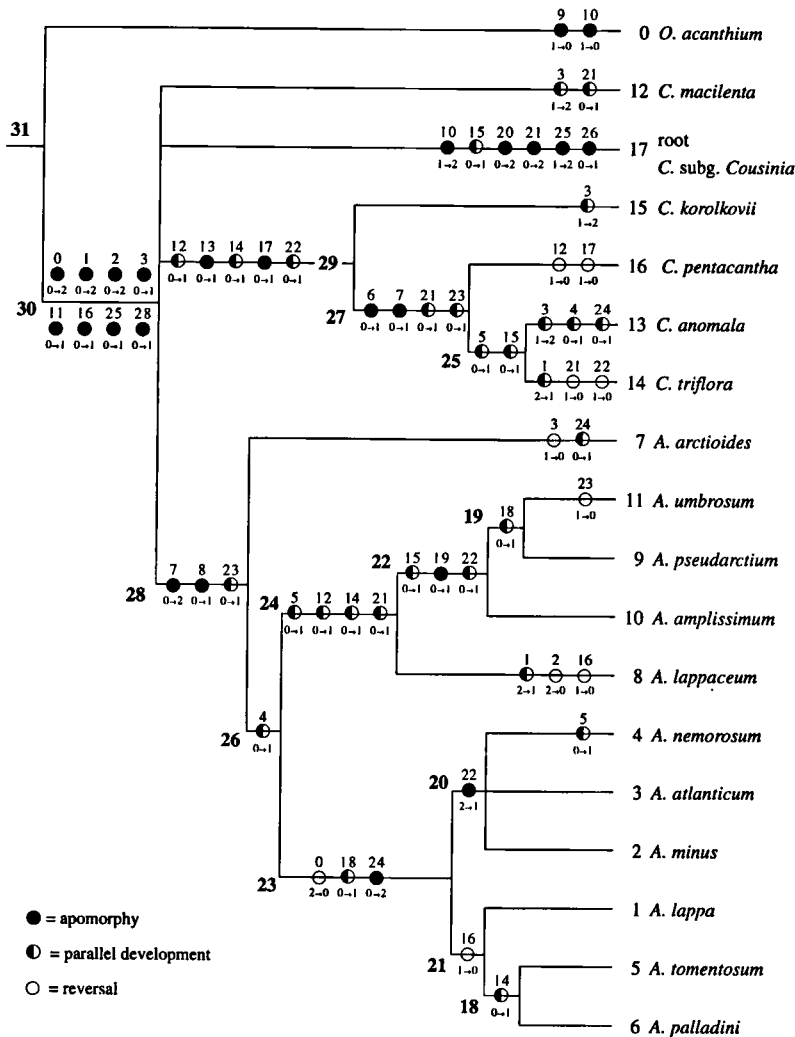


Fig. 13.5. Strict consensus tree of eight trees resulting from option I (see text). *Cousinia* subg. *Cousinia* is in this analysis replaced by its root (node 33 in Fig. 13.4).

cies of *Arctium* sect. *Arctium* form a clade based on the inconspicuous marginal ridge on the apical plate (character 24). The trio *A. (C.) umbrosum*, *A. (C.) pseudarctium*, and *A. (C.) amplissimum* share the relatively long corolla limb (character 15), the hairy apical appendage of the anther (character 19), and the smooth achenes (character 22). The root of *C. subg. Cousinia* is supported by several synapomorphies, including the spatulate receptacular scales (character 10), the style type (characters 20, 21), and the pollen type (characters 25, 26).

**Option II**

IIa – I entirely eliminated *Cousinia* subg. *Cousinia* from the data matrix. The analysis of the remaining 17 OTUs resulted in 12 equally parsimonious trees (length = 56, ci = 55%, ri = 71%). After three times of iterative weighting two trees remained, which differ in the degree in which the triplet *A. minus*, *A. atlanticum*, and *A. nemorosum* is resolved. The strict consensus tree is shown in Fig. 13.6 (length = 199, ci = 74%, ri = 85%). The ci is not higher than in the first analysis, which means that the homoplasies are spread regularly over the cladogram. The genus *Arctium* s.l. is, of course, again a monophyletic group. It has the same synapomorphies as in the cladogram of Fig. 13.5. Also, its internal structure is identical to the results of Option I. Its sistergroup is formed by the clade of *C.* subg. *Hypacanthoides* (*C. macilenta*) and *C.* subg. *Cynaroides* (node 29). The synapomorphy for this group is the pinnatifid leaf (character 3), showing reversals to pinnatifid in *C. pentacantha* and *C. triflora*.

IIb – In a following analysis I included all nine species of *C.* subg. *Cousinia*, and I replaced the species of *Arctium* s.l. by the root of the genus (node 28 in Fig. 13.6). The character states of this node are shown in Table 13.3.

Table 13.3. Character states of the root of *Arctium* s.l., node 28 in Fig. 13.6.

	0									1									2											
Character	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	
Aroot	2	2	2	0	0	0	0	2	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1

This matrix resulted in 21 equally parsimonious trees (length = 75, ci = 54%, ri = 60%). One time of character weighting was sufficient to leave only one tree (length = 304, ci = 73%, ri = 76%). More times of weighting did not alter this result. In this completely resolved cladogram, shown in Fig. 13.7, *C.* subg. *Cousinia* (node 26) and *C.* subg. *Cynaroides* (node 25) are sistergroups. Together they form the sistergroup to *Arctium* s.l.. These groups, which exclude *C.* subg. *Hypacanthoides* (*C. macilenta*), share the truncate apical plate (character 23) as a synapomorphy, in this cladogram showing only once a reversal in *C. korolkovii*. Compared to the results of Option I the synapomorphies ‘receptacular scales spathulate’ (character 10), and ‘limb more than 3/5 of the total corolla length’ (character 15) have disappeared from the root of *C.* subg. *Cousinia* (node 26 in Fig. 13.7). The receptacular scales of *C. freynii* are acute, and the limb of *C. freynii*, *C. microcarpa*, *C. scariosa*, and *C. pseudostenolepis* is less than 3/5 of the total corolla length. The characters 27 (tectum perforations) and 28 (chromosome number), although very incompletely known, show up as synapomorphies at this level. The yellow corolla of *C.* subg. *Cynaroides* is now a homoplasy, also present in *C. congesta*. The yellow anthers are now a synapomorphy without reversals because *C. korolkovii* and *C. pentacantha* changed position in the cladogram. The root of *Arctium* s.l. has, of course, the same apomorphies as in the earlier cladograms.

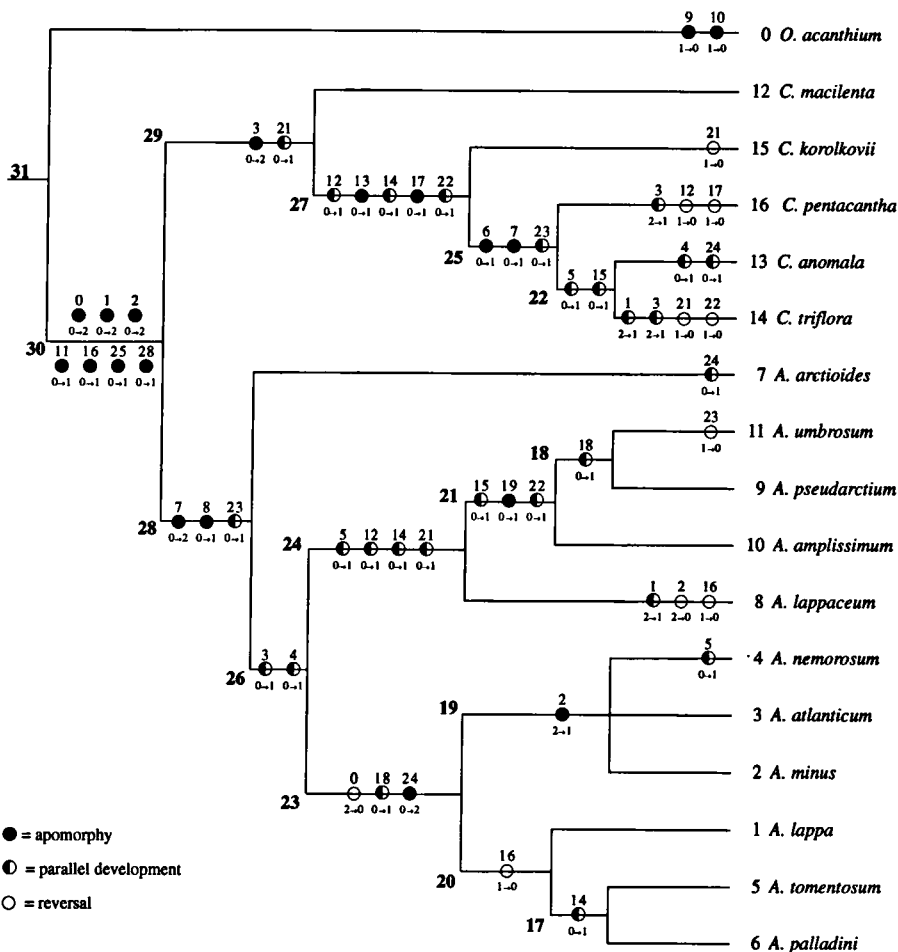


Fig. 13.6. Strict consensus tree of two trees resulting from option IIa (see text). *Cousinia* subg. *Cousinia* is excluded in this analysis.

IIc – In the final analysis I again (as in Option I) included all species of *Arctium* s.l., and replaced the nine species of *Cousinia* subg. *Cousinia* by the root (node 26 of Fig. 13.7). The character states of this node are shown in Table 13.4.

The result was 22 equally parsimonious trees (length = 61, ci = 57%, ri = 72%). Character weighting resulted in 2 equally parsimonious trees (length = 247, ci = 77%, ri = 85%), again (as in IIa) only different in the degree in which the triplet of *A. minus*, *A. atlanticum*, and *A. nemorosum* is resolved. The strict consensus tree is shown in

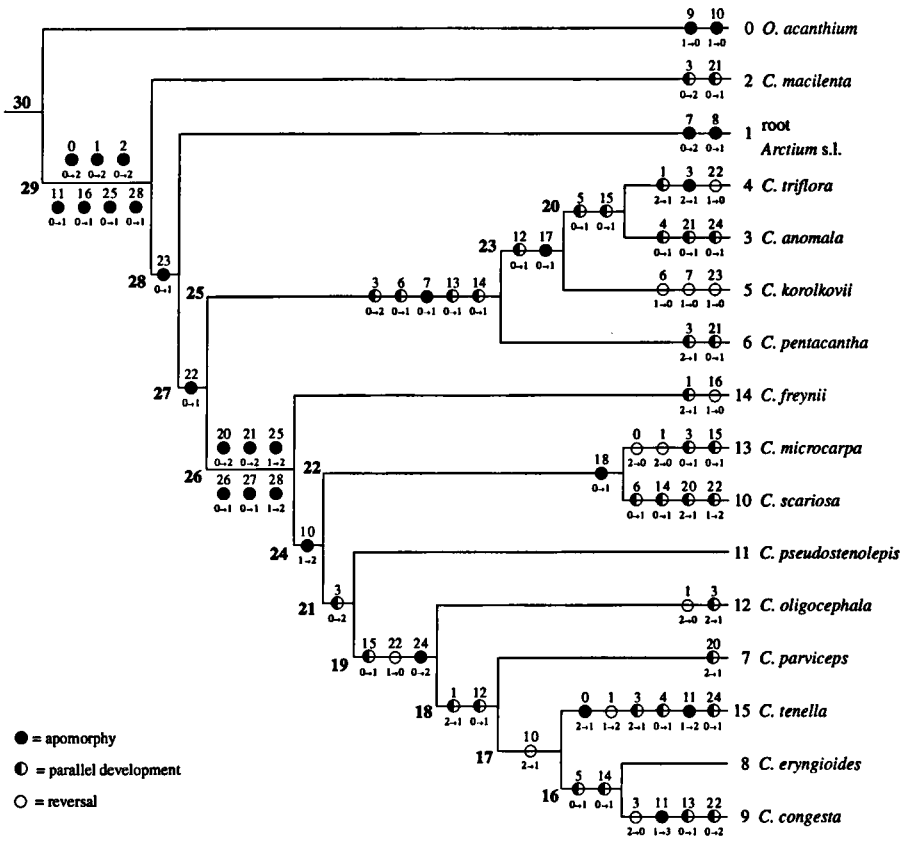


Fig. 13.7. Cladogram resulting from option IIb (see text). The species of *Cousinia* subg. *Cousinia* are in this analysis included, and *Arctium* is replaced by its root (node 28 in Fig. 13.6).

Table 13.4. Character states of the root of *C.* subg. *Cousinia*, node 26 of Fig. 13.7.

	0									1									2										
Character	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8
Crootcous	2	2	2	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	2	2	2	1	1	0	2	1	?	?

Fig. 13.8. *Arctium* s.l. is again monophyletic, based on the same synapomorphies as in the preceding subanalyses. Its sistergroup is *C.* subg. *Cousinia* in this cladogram, based on the truncate apical plate (character 23, homoplasy). *Cousinia* subg. *Cynaroides* (node 28) is the sistergroup of *C.* subg. *Hypacanthoides*, as in Op-

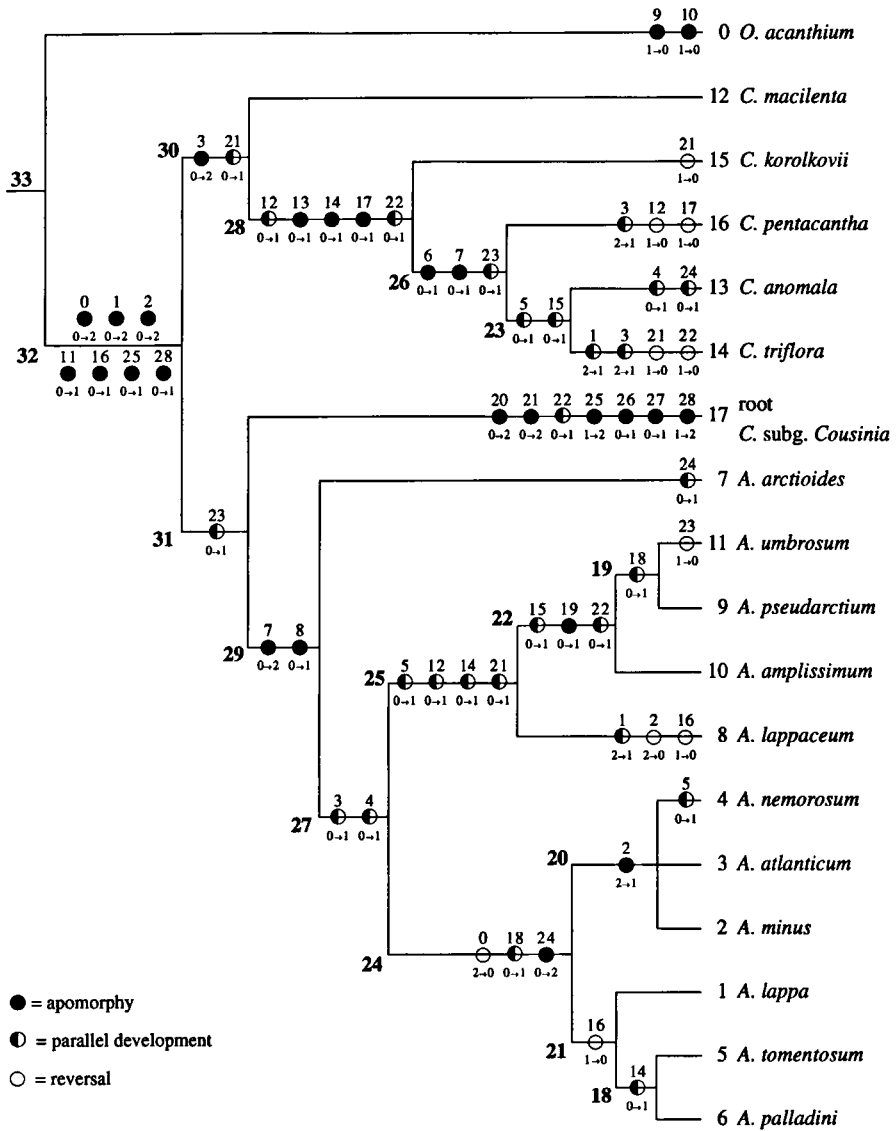


Fig. 13.8. Strict consensus tree of two trees resulting from option IIc (see text). The species of *Arctium* are in this analysis included, and *Cousinia* subg. *Cousinia* is replaced by its root (node 26 in Fig. 13.7).

tion IIa based on character 3. The internal structure of *Arctium* s.l., and the distribution of character states are the same as in the resulting cladograms of Option I (Fig. 13.5), and IIa (Fig. 13.6).

### 13.10 Conclusions and discussion

I feel that my results are not necessarily influenced in a negative way by the lack of phylogenetic information of the genus *Cousinia*. The ci and ri are always rather high. This means that the data fit the tree rather well, and that many character changes occur on the internal nodes. The characters 9 (receptacle), 10 (receptacular scales), 11 (pappus), 19 (apical appendage of anther), 20 (position of hairs on style), 25, 26, 27 (pollen) always fit the tree for 100%. This applies also for character 28 (chromosome number), but here it is caused by the many missing values. Most characters needed one extra step to fit the tree, and character 21 (length of stylar branches relative to length of stylar apex) needed 2 or 3 extra steps.

Qaid (1990) tried to fit the palynological characters which resulted from his analysis of the pollen morphology of the 'super-tribe' Cynaroideae on the cladogram of Petit (1990), but this was only possible if many homoplasies and reversals were allowed. He concluded that palynological information contains little phylogenetic information. Contrary, in my cladistic analysis of a subgroup of the subtribe Carduinae the characters describing the variation in pollen morphology always fitted the cladograms for 100%. They constitute synapomorphies for *C.* subg. *Cousinia*.

The cladograms resulting from option I and option II all agree in the resolution of *Arctium* s.l. (Fig. 13.5, and 13.8). In the following I will draw my conclusions concerning the generic and infrageneric division of *Arctium* from Fig. 13.8.

From the cladogram (Fig. 13.8) it is clear that *Arctium* sect. *Arctium* is a monophyletic group, based on the synapomorphy 'apical plate with an inconspicuous marginal ridge'. It is, thus, possible to retain the classical delimitation of *Arctium*, excluding the 'arctioid' species of *Cousinia* from it. This would leave the 'arctioid' species as a paraphyletic group of perennial species. If classifying the 'arctioid' species as one or more separate genera, characters like life span (char. 0), the number of flowers per capitule (char. 12), apical appendage of the anthers (char. 19), and the marginal ridge of the apical plate (char. 24) have to be used. The presence of hooked involucre bracts (char. 8) is a synapomorphy not only in the tribe Cardueae, but in the whole family Asteraceae. As this character is also visible with the naked eye, the inclusion of all species with this character into one genus seems an elegant solution of the problem concerning the genus delimitation of *Arctium*. Therefore I include the 'arctioid' species of *C.* subg. *Cynaroides* in *Arctium* s.l., which then contains 11 species. It is a monophyletic, and very recognizable genus. Descriptions of the eleven species are given in the taxonomic part (Chapter 18) of this publication.

I do not include *C. anomala* in *Arctium* s.l., as was suggested by Schtepa (1971, 1973). This suggestion was based on palynological evidence only. The pollen type found in *C. anomala* occurs not only in *Arctium*, but in numerous other species of *Cousinia* as well. According to the cladogram (Fig. 13.8), the inclusion of *C. anomala* in *Arctium* would mean that at least the entire subgenus *Cynaroides* of *Cousinia* has to be included in the genus *Arctium*. I do not wish to do this, because it would result in a poorly recognizable genus.

At the infrageneric level a division into sections in *Arctium* s.l. is sustained by the cladogram (see Fig. 13.8). *Arctium* in its classical delimitation may indeed be interpreted as one section (section *Arctium*), recognizable by the inconspicuous marginal ridge of the apical plate (char. 24). It may also be divided into two sections, one con-

taining *A. atlanticum*, *A. minus* and *A. nemorosum*, and another containing *A. lappa*, *A. palladini*, and *A. tomentosum*. The first group could be recognized by the hollow petiole of the basal leaves (char. 2). The other group has solid petioles (hollow petioles also occur in *A. tomentosum*), but so have the species which were formerly included in *Cousinia*; the lobes of the corolla are relatively long, but so are those of *A. (C.) lappaeum* (char. 16); the inflorescence is corymbose, but (sub-) corymbose inflorescences also occur in the first group (character not included in the data matrix). Therefore, I prefer to include the species of *Arctium* in its classical delimitation in a single section (sect. *Arctium*).

The subdivision of *Arctium* sect. *Arctium* into two sections as in the cladogram differs from the one proposed by Arènes (1950). His sections were characterized by the absence or presence of glandular hairs on the corolla only. According to the cladogram, this character (14) has developed three times within *Arctium* (Fig. 13.8: on node 25 and node 18, and in *A. minus* p.p.). The sectional division of Arènes is not compatible with the cladogram because species with a glandular hairy corolla as *A. palladini* and *A. tomentosum* (section *Glandulosa* Arènes) constitute a monophyletic group together with *A. lappa* which usually has a glabrous corolla (section *Eglandulosa* Arènes).

The species which were formerly placed in *Cousinia* and are transferred by me to *Arctium*, were distributed over three different sections (Tscherneva, 1962, 1988; Rechinger, 1972). *Arctium (C.) arctioides* was the only species in the section *Nanarctium* Juz. ex Tscherneva. *Arctium (C.) amplissimum*, *A. (C.) pseudarctium*, and *A. (C.) umbrosum* were placed in the section *Pseudarctium* Juz., while *A. (C.) lappaceum* was included in the monotypic section *Lappacea* Schrenk. These three supraspecific groups are all monophyletic according to the cladogram (see Fig. 13.8), and, following the sequencing convention of Nelson (Wiley, 1981: 206), may all be treated as sections. Section *Nanarctium* is characterized by having achenes with a conspicuous marginal ridge on the apical plate. Section *Pseudarctium* is recognized by the smooth achenes, and by the hairy apical appendages of the anthers (but glabrous apical appendages sometimes occur in *A. umbrosum*). Section *Lappacea* is recognized by its sessile lower cauline leaves, and by the coriaceous involucre bracts. I accept these three sections in *Arctium*, which thus is composed of the following four sections (listed in order of their branching sequence):

section *Nanarctium*  
section *Lappaceum*  
section *Pseudarctium*  
section *Arctium*

Accepting *Arctium* s.l. as a separate genus leaves *Cousinia* as a paraphyletic tail. Both *C.* subg. *Cynaroides* (s.s.) Tschern. and *C.* subg. *Cousinia* seem to be monophyletic. The relation of *C.* subg. *Hypacanthoides*, in this analysis represented by only one of the approximately ten species, to the other two subgenera is uncertain. It seems advisable to further divide the speciose, and polymorphic genus *Cousinia*. However, I did not aim at a natural classification of *Cousinia*, and the results of this analysis, which included only 19 of the ca. 660 species of *Cousinia*, cannot pass



judgement on a generic delimitation of it. A further study of *Cousinia* should include a detailed study of the stylar apex and the achenes, and should be followed by a phylogenetic analysis, including many sub-analyses to ascertain the character states at the root of assumed monophyletic sections.

#### 14. Acknowledgements

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## II. Taxonomic part

### Introduction

In this revision a description of the genus *Arctium* is followed by the key to the species. The species are treated in alphabetical order per section. In a separate chapter the known hybrids are listed by their parents in alphabetical order, followed by the nomina dubiae and the species excludenda.

The description of the genus and species starts with the synonymy, including all infraspecific taxa, in chronological order. The morphological descriptions are based on herbarium material, my own field observations and information from herbarium labels. If a character, e.g. life form, is only known from literature, it is mentioned between square brackets. A note following the description will elaborate on this.

For the geographical distribution, habitat, ecology, and altitude mainly information from herbarium labels is used. The enumeration of the distribution is limited to country, and provinces or districts. The political boundaries are following the Times Atlas of the World (Dutch version, 1978). The republics of the former Soviet Union are treated as countries. For widespread species (occurring in ten or more countries) I describe the distribution less detailed. Maps illustrate their distribution patterns.

In the notes following the Distribution, I distinguish notes on Taxonomy, notes on Nomenclature and Synonymy, notes on Variation, notes on Hybrids, and other Notes.

### 16. Generic description

#### ARCTIUM

*Arctium* L., Sp. Pl. 2 (1753) 816; Benth. & Hook., Gen. Pl. 2, 1 (1873) 466; Kuntze, Revis. Gen. 1 (1891) 307, p.p.; Hoffm. in Engl. & Prantl, Natürl. Pflanzenfam. 4, 5 (1893) 318; Post & Kuntze, Lex. Gen. Phan. (1904) 708; Arènes, Bull. Jour. Bot. Brux. 20 (1950) 73. — *Arcium* Rupr., Fl. Ingr. 1 (1860) 538, nom. illeg. — *Arcion* Bubani, Fl. Pyren. 2 (1899) 123, nom. illeg. — Type: *Arctium lappa* L. — See note 5.

*Lappa* [Tourn., Inst. (1700) 450, tab. 256]; Scop., Meth. Pl. 19 (1754); Adans., Fam. Pl. (1763) 116; Juss., Gen. Pl. (1789) 173; Cass., Dict. Sc. Nat. 4, Suppl. (1816) 16; Less., Syn. Gen. Compos. (1832) 8; DC., Prodr. 6 (1838) 661. — Type: *Lappa major*, *Arctium Dioscoridis* C. Bauh. — See note 6.

*Bardana* Hill, Herb. Brit. 1 (1756) 79; Veg. Syst. ed. 1, 4 (1762) 28. — Type: *Bardana lappa* Hill.

Monocarpic or perennial, medium-sized to tall, branched herbs, geophytic, with a taproot. *Basal leaves* in a rosette, unarmed, sometimes sessile; *cauline leaves* usually unarmed. *Synflorescence* racemose or corymbose, with 6-numerous capitules. *Capitules* solitary or in clusters, sessile to long pedunculate, with 6 to more than 40 flowers, spherical to ovoid, glabrous to densely arachnoid hairy. *Involucral bracts* imbricate, the outer and middle subulate or caudate, 1-veined, basal part appressed, apical part patent to deflexed, apex hooked, the inner linear. *Receptacle* flat to sub-concave, with numerous long, narrow scales. *Pappus* short, of simple, flat bristle hairs, in 2–4 irregular rows, falling off separately. *Flowers* uniform, hermaphrodite, shorter than to exceeding the involucre, protandrous. *Corolla* tubulose-campanulate,

white, yellow or (red-)purple, glabrous or with glandular hairs; tube often somewhat widened at base, limb campanulate, lobes (4 or) 5(-7), slightly unequal. *Stamens* as many as corolla-lobes, inserted at the demarcation of tube and  $\pm$  campanulate limb, alternating with the lobes, filaments free, anthers connate, apically and basally with appendages, basal appendage tail-like, entire to multifurcate, apical appendage deltoïd, glabrous or dorsally villose. *Style* below the branches with a hairy thickening which is covered with stiff sweeping hairs, branches linear, scabrid, scape glabrous. *Achene* oblong-obovoid, somewhat compressed, abaxial side of the outer achenes in the upper third often somewhat bossed, glabrous, smooth or rugose and with (inconspicuous) longitudinal ridges, brown, often with dark brown spots, detachment area basal, hilum basal, at apex with or without a marginal ridge, marginal ridge entire or dentate, apical plate flat to truncate.

Distribution – Europe, Northern Africa (Morocco, Algeria, Egypt), temperate Asia (West and Central Asia, Himalaya, China, Japan).

Habitat & Ecology – Disturbed, nutrient-rich habitats. Alt.: sea-level up to 3300 m; in Central Asia often restricted to higher altitudes.

Taxonomy – 1. As a result from the phylogenetic analysis (see Chapter 13) I include five species, which were formerly included in the genus *Cousinia*, in the genus *Arctium*. Typical for *Arctium* are: the hooked apex of the involucre bracts, usually rather large leaves with unarmed margin, and a usually purplish corolla. The shape of the basal appendages of the anthers is variable. They may be simple, bifurcate or fimbriate, and cannot be used to characterize the genus.

2. Arènes (1950) divided the genus into two sections, based on the absence or presence of glandular hairs on the corolla. However, this character is not even diagnostic at the species level. I have shown that *A. chaberti* ["sect. *Glandulosa*"] is a synonym for *A. minus* ["sect. *Eglandulosa*"] (see Chapter 11) and that specimens with a hairy corolla also occur in *A. lappa* ["sect. *Eglandulosa*"].

3. I recognize four sections in *Arctium* (see Chapter 13), of which *A.* section *Arctium* includes all six species of the genus *Arctium* in its traditional delimitation, based on the presence of an inconspicuous marginal ridge at the apex of the achene. They have capitules with more than 40 flowers. The monotypic section *Nanarctium*, including only *A. arctioides*, also has capitules with more than 40 flowers. The achenes, however, have a conspicuous marginal ridge at the apex, and the cauline leaves have spines at the base. *Arctium* section *Lappaceum* is also a monotypic section, including only *A. lappaceum*. This species has capitules with up to 10 flowers, and is the only species with coriaceous involucre bracts. The three species of *A.* section *Pseudarctium* share the presence of anthers with dorsally hairy apical appendages (but sometimes glabrous in *A. umbrosum*), which is unique within the genus. The capitules of the species of this section have up to 25 flowers.

Nomenclature – 4. *Arctium lappa* L. is the type species of the genus. As already noticed by Kupicha in Davis (1975, 354) material in the original herbaria cannot be identified with the species generally known as *A. lappa*. Kupicha treated the name therefore as a nomen confusum under *A. tomentosum*. In my opinion, however, the identification of *A. lappa* has never caused any confusion, and therefore I will propose to conserve this name.

5. Both Ruprecht (1860) and Bubani (1900) rejected the spelling of the genus name of Linnaeus (1753), and used the prelinnean spelling of Dioscorides (first century).

6. Authors use either *Arctium* or *Lappa* in their publications; the two names are never used simultaneously. Several authors, even into the twentieth century, did not accept the work of Linnaeus as a starting point as we do today and preferred to use the Tournefortian name of *Lappa*. This name is therefore a nomen superfluum. Most of these authors did not intend to describe new species, but rather transferred already described species to the 'right' genus. Often the original author of the species is not cited, but from the epitheton and the description it can be deduced that a new combination and not a new species was meant.

## 17. Key to the species

For measurements of the capitule, the involucre, and the floral structures, a capitule from the *terminal part of the synflorescence* should be studied; for explanation of the terms used the reader is referred to Chapter 6. The size of the capitules includes the patent or deflexed spines; the size excluding the spines is given between brackets. Relative sizes of capitules (e.g. smaller capitules) are always including the spines.

- 1a. Capitule with less than 30 flowers ..... 2  
 b. Capitule with 40 or more flowers ..... 5
- 2a. Basal leaves attenuate, sessile. Involucral bracts coriaceous. Corolla lobes 2/5 of the length of the limb ..... 7. *A. lappaceum*  
 b. Lamina of basal leaves cordate or cuneate at base, distinctly stalked. Petiole at least 5 cm long. Involucral bracts herbaceous. Corolla lobes 1/5–3/10 of the length of the limb ..... 3
- 3a. Capitule with 15–25 flowers, 1.9–2.7 cm wide. Achenes 6.2–7.4 mm long  
     10. *A. pseudarctium*  
 b. Capitule with 7–15 flowers, 0.8–1.8 cm wide. Achenes 4.9–6.1 mm long ..... 4
- 4a. Lamina of basal leaves 37–42 cm long. Middle involucral bracts with glandular hairs only. Longest receptacular scales 6.8–7.0 mm long. Longest pappus hairs 2.0–2.5 mm long ..... 9. *A. amplissimum*  
 b. Lamina of basal leaves 18–28 cm long. Middle involucral bracts with glandular hairs and 1–3 pairs of 0.5 mm large, sessile glands. Longest receptacular scales 8.0–10.3 mm long. Longest pappus hairs 3.5–4.0 mm long ..... 11. *A. umbrosum*
- 5a. Upper cauline leaves at base with 1–3 pairs of sharp, up to 6 mm long marginal spines, sessile. Achene with a conspicuous marginal ridge, ridge 0.3–0.4 mm high ..... 8. *A. arctioides*  
 b. Upper cauline leaves not spiny, petiolate or sessile. Achene with an inconspicuous marginal ridge, 0.1–0.2 mm high ..... 6
- 6a. Inner involucral bracts constricted above the middle, and widened below the apex, apex truncate or acuminate. Corolla limb (usually densely) covered with glandular hairs, never glabrous ..... 7  
 b. Inner involucral bracts never constricted above the middle, gradually narrowing towards the apex, apex acute to acuminate. Corolla limb glabrous to densely covered with glandular hairs ..... 8

- 7a. Corolla lobes 3.0–4.2 mm long. Anthers 6.3–7.1 mm long. Capitules glabrous to sparsely hairy ..... 5. *A. palladini*
- b. Corolla lobes 2.0–3.0 mm long. Anthers 3.8–5.4 mm long. Capitules almost glabrous to densely arachnoid hairy ..... 6. *A. tomentosum*
- 8a. Petiole of basal leaves solid (at least at the base). Capitules at the terminal parts of the synflorescence at least 2.5 cm pedunculate. Synflorescence corymbose  
2. *A. lappa*
- b. Petiole of basal leaves hollow (at least at the base). Capitules at the terminal parts of the synflorescence sessile or up to 2 cm pedunculate; if longer pedunculate, then synflorescence racemose ..... 9
- 9a. Capitules at the terminal parts of the synflorescence sessile. Middle involucre exceeding the corolla by 1.2–6.0 mm. Corolla glabrous ..... 4. *A. nemorosum*
- b. Capitules pedunculate or sessile. Middle involucre exceeding the corolla by 1.2–6.0 mm. If capitules sessile and middle involucre bracts 1.6–1.8 mm wide, then either corolla equalling or exceeding the involucre, or corolla hairy, or both. .... 10
- 10a. Index of middle involucre bracts 5.4–7.0. Styler apex 2.3–2.7 mm long. Corolla glabrous (from N Africa) ..... 1. *A. atlanticum*
- b. Index of middle involucre bracts 7.0–14.2. If styler apex longer than 2.2 mm, then (at least in Southern Europe and N Africa) usually corolla with glandular hairs ..... 3. *A. minus*

## 18. Descriptions of the sections and species

(The species are described per section in alphabetical order)

### Section *Arctium*

*Arctium* section *Arctium*.

*Arctium* section *E glandulosa* Arènes, Bull. Jour. Bot. Brux. 20 (1950) 74, nom. illeg. — Syntype species: *A. lappa* L., *A. minus* Bernh.

*Arctium* section *Glandulosa* Arènes, Bull. Jour. Bot. Brux. 20 (1950) 74. — Syntype species: *A. tomentosum* Mill., *A. chaberti* Briq. & Cav.

Monocarpic (but see *A. atlanticum*?). *Leaves* irregularly undulate, dentate, unarmed. *Capitules* solitary or clustered, sessile to long pedunculate, with more than 40 flowers. *Involucre bracts* herbaceous. *Corolla*: limb up to 3/5 of the total length of the corolla. *Stamens*: apical appendage of anthers glabrous. *Styler branches* more than 3/5 of the total length of the styler apex. *Achene* rugose, with longitudinal ridges, marginal ridge inconspicuous. 0.1–0.2 mm high. entire or dentate. apical plate truncate.

Including *A. atlanticum*, *A. lappa*, *A. minus*, *A. nemorosum*, *A. palladini*, and *A. tomentosum*.



1. *Arctium atlanticum* (Pomel) H. Lindb. – Fig. 18.1.

*Arctium atlanticum* (Pomel) H. Lindb., Acta Soc. Sci. Fenn., n. s. B, 1, 2 (1932) 153. — *Lappa atlantica* Pomel, Nouv. Mat. Fl. Atl. (1875) 285. — *Arctium minus* (Hill) Bernh. subsp. *atlanticum* (Pomel) Maire in Jahand. & Maire, Cat. Pl. Mar. 3 (1934) 794; Arènes, Bull. Jard. Bot. Brux. 20 (1950) 105; Quézel & Santa, Nouv. Fl. Alger. 2 (1963) 1003, fig. 2921. — *Arctium minus* (Hill) Bernh. subsp. *atlanticum* (Pomel) Maire var. *eu-atlanticum* Maire in Jahand. & Maire, l. c.; Arènes, Bull. Jard. Bot. Brux. 20 (1950) 105. — Neotype (assigned here): *Faure s. n.*, 1932, Algeria, Tlemcen (P!).

*Lappa sylvestris* Pomel, Nouv. Mat. Fl. Atl. (1875) 284. — Type: unknown.— See note 2.

*Arctium minus* (Hill) Bernh. subsp. *atlanticum* (Pomel) Maire var. *grandiceps* Maire in Jahand. & Maire, Cat. Pl. Mar. 3 (1934) 794. — Type: *M. A. Talsent* : n., s. d., Algeria (n.v.).— See note 3.

[Biennial or perennial]. *Stem* 80–150 cm long. *Basal leaves*: petiole 17–30 cm long, hollow, glabrous or glandular-hairy; lamina 22–52 × 15–33 cm (index 1.4–1.6), margin irregularly undulate, with sparse mucronate teeth, apex acute, with mucro, lower side arachnoid hairy, without minute glassy globules, silvery white, upper side sparsely hairy, with short uni- and multicellular hairs; *cauline leaves* like basal leaves but lamina cuneate at base, lower side with many minute glassy globules. *Synflorescence* (sub-)corymbose or racemose, with many capitules, branches patent (otherwise unknown). *Capitules* more or less solitary, 0.3–2.0 cm pedunculate, with more than 40 flowers, 2.3–2.7 × 1.4–2.1 (1.3–1.5 × 1.2–1.5) cm, glabrous to sparsely hairy. *Involucral bracts* in 8–14 rows, herbaceous, the upper part often tinged with red; outer involucral bracts triangular, 6.5–7 × 2 mm, patent or deflexed, glabrous or somewhat villose, margin with some glandular hairs in the lower half; middle involucral bracts 9.1–11.9 × 1.6–1.8 mm, linear-triangular (index 5.4–7.0), margin with glandular and eglandular hairs, the upper 2/5–3/5 patent; inner involucral bracts 8.0–11.5 × 1.2–2.3 mm, linear-ovate to -obovate (index 4.6–9.6), membranaceous, dorsal side with short hairs, the upper part slightly recurved, apex acute to acuminate, straight or (slightly) hooked. Longest *receptacular scales* 5.4–9.0 × 0.1–0.4 mm, glabrous, entire, acute. Longest *pappus hairs* 2.0–3.4 mm long, margin minutely dentate, acute. *Corolla* 9.4–10.6 mm long, pale or red-purple, glabrous, equalling or exceeding the involucral bracts by 1.0–2.5 mm, tube 3.8–4.8 mm long, not widened at base, limb 5.3–6.0 mm long (= 1/2–3/5 of total length), gradually widening, longest lobe 1.3–2.0 mm long (= 1/5–3/10 of limb). *Stamens*: filaments 3.0 mm long, smooth to somewhat verrucate, anthers 3.8–4.5 × 0.4–0.5 mm, (colour unknown), basal appendage 0.1–0.5 mm long, entire to multi-furcate, apical appendage 0.6–0.9 mm long, glabrous, acuminate. *Stylar apex* 2.3–2.7 mm, (colour unknown), branches 1.6–2.0 mm long (= c. 3/4 of stylar apex), sweeping hairs 0.6–0.8 mm below the branches. *Achene* 6.8 × 3.0 mm, obovate (index 2.3), rugose, with up to 5 longitudinal ridges, brown, with black spots, apex with inconspicuous marginal ridge, apical plate truncate.

Distribution – Morocco (Moyen Atlas, Haut Atlas), Algeria (Tlemcen, Constantine).

Habitat & Ecology – Waste places, roadsides, along fields, moist *Quercus ilex* forests, forest clearings, alluvial plains. On calcareous, nitrate rich soil. Alt.: 800–1900 m. Flowering in July and August.

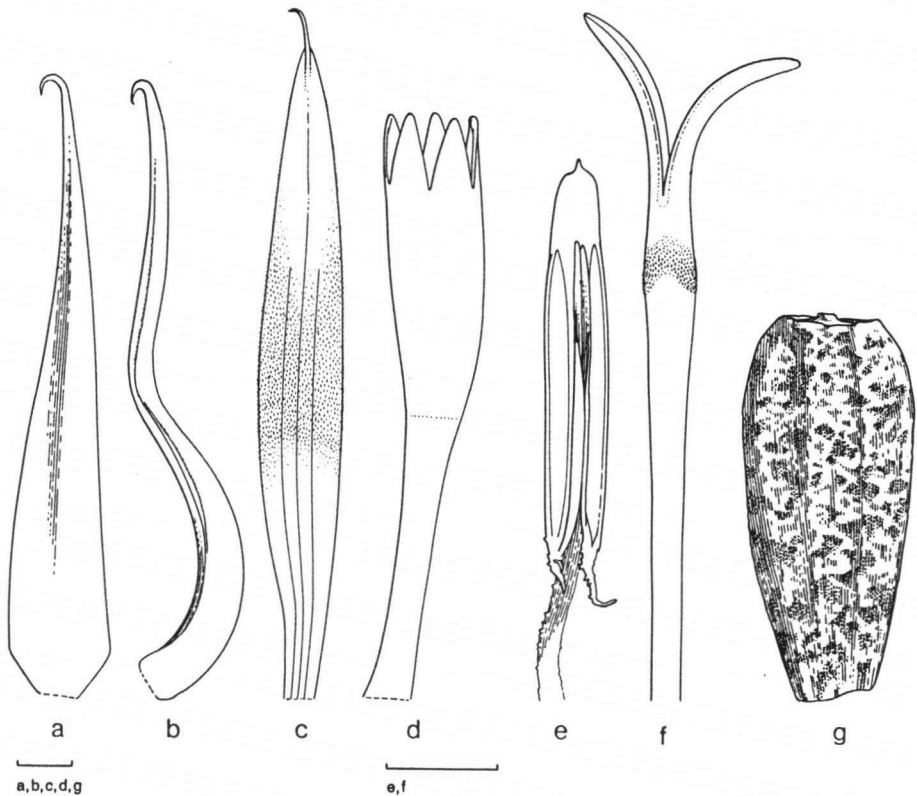


Fig. 18.1. *Arctium atlanticum* (Pomel) H. Lindb. – a. Dorsal view of middle involucre bract; b. lateral view of middle involucre bract; c. dorsal view of inner involucre bract; d. corolla; e. anther with apical part of filament; f. apical part of style; g. achene (a–f: Davis 54976; g: Faure s.n., 24-08-1932). Bar indicates 1 mm.

**Taxonomy – 1.** The capitules at the terminal parts of the synflorescence of *A. atlanticum* are up to 2 cm pedunculate, often almost arranged in a corymb. *Arctium atlanticum* differs from *A. tomentosum* in the shape of the inner involucre bracts which are constricted above the middle in *A. tomentosum*, and the glabrous corolla; it differs from *A. lappa* in the corollas which exceed the involucre bracts, and in the smaller capitules; from *A. nemorosum* in the smaller capitules which are longer pedunculate, and in the corollas which exceed the involucre bracts; from *A. minus* in the combination of relatively wide involucre bracts (*A. minus* index more than 7), and the glabrous corolla which exceeds the involucre (see Chapter 1, Fig. 11.2).

**Nomenclature & Synonymy – 2.** *Arctium sylvestris*, with glabrous involucre bracts, and *A. atlanticum*, with pubescent-glandulous involucre bracts, were described by Pomel (1875) at the same time. I have not seen the type specimens. The herbarium specimens I examined, indeed, had either a glabrous involucre or were somewhat arachnoid hairy with marginal glandular hairs at the involucre bracts. Otherwise the

specimens were similar. Because the amount of indument on the involucre is very variable in most of the other species of *Arctium*, I consider the above described variation as infraspecific, and I treat the two names as synonyms.

3. According to the very short original description of Maire (1934), *Arctium minus* subsp. *atlanticum* var. *grandiceps* differs from the type-variety in having larger (2.0–2.2 in stead of 1.3–1.5 cm), and somewhat longer pedunculate capitules. It is not clear whether the diameter includes or excludes the patent apical parts of the involucral bracts. I have not seen the type specimen. Based on the available material, the variety does not seem to merit recognition as a separate taxon.

Variation – 4. The colour of the anthers and style are mentioned neither in literature nor on herbarium labels.

5. Only one specimen of the material which I have examined had mature achenes (*A. Faure s.n.*, 24-08-1932). They are longer and wider than Arènes (1950) mentioned for this species: “5.5–6.0 mm long, 2 mm wide”.

Hybrids – 6. I have not seen specimens which originated through the hybridisation of *A. atlanticum* and any other species.

Notes – 7. Arènes (1950, 73) described all species of *Arctium* as biennial. Contrary to this, Pomel (1875) and Quézel & Santa (1963, 1003) characterized *A. atlanticum* as perennial. In the present concept of *Arctium*, both biennial and perennial species are included in the genus, but all other species of the section *Arctium* are biennial. I have not been able to check this on the available material.

8. *Arctium atlanticum* is the only species of the genus that is restricted to (the north-western part of) the African continent. *Arctium minus* is also known from Africa, but not restricted to it.

## 2. *Arctium lappa* L. – Fig. 18.2, 3, 4.

*Arctium lappa* L., Sp. Pl. (1753) 816 (incl. var. a); Mill., Gard. Dict. ed. 8 (1768); Willd., Spec. Pl. ed. 4, 3, 3 (1803) 1631; Schkuhr, Bot. Handb. 3 (1803) 48; Pers., Syn. Pl. 2 (1807) 383; Schweigg. & Körte, Fl. Erlang. (1811) 74; Weiss in Koch, Syn. Deutsch. Fl. ed. 3, 2 (1897) 1510; Druce, List Brit. Pl. ed. 1 (1908) 39; Fernald & Wiegand, Rhodora 12 (1910) 44; A. H. Evans, Jour. Bot. (London) 51 (1913) 116; Schinz & R. Keller, Fl. Schweiz ed. 3, 2 (1914) 348; Beger in Hegi, Ill. Fl. Mitteleur. 6, 2 (1928) 827; Briq. & Cavill. in Burnat, Fl. Alp. Marit. 7 (1931) 266; Grossh., Fl. Kavkaza 4 (1934) 164; Fernald, Gray's Man. Bot. ed. 8 (1950) 1537; Ross-Craig, Draw. Brit. Pl. 17 (1962) pl. 2; Tscherneva in Komarov, Fl. URSS 27 (1962) 97, tab. 7, fig. 10, 11; Klovov, Fl. URSS 11 (1962) 436; Rothm., Exkurs.fl. Deutschl. ed. 4 (1963) 331; Soó, Syn. Syst.-Geobot. Fl. Veg. Hung. 4 (1970) 122; Hess & Landolt, Fl. Schweiz 3 (1972) 411; Takht. & Fed., Fl. Erevana (1972) 288; Perring in Tutin et al., Fl. Eur. 4 (1976) 215; Rech. f., Fl. Iran. 139a (1979) 107; Hultén, Vår Svenska Fl. 19 (1958) 617. — *Lappa vulgaris* Hill, Veg. Syst. 4 (1762) 28, fig. 1 a, b; F. N. Williams, Prodr. Fl. Brit. 2 (1901) 53. — *Lappa glabra* Lam. var. a, Fl. Fr. 2 (1778) 37; Lam., Tabl. Encycl. Méth. Bot. 1, 2 (1785) 337 (8). — *Lappa officinalis* All., Auct. Fl. Pedem. 1 (1785) 145; Rchb. f., Ic. Fl. Germ. 15 (1853) 54; Körn., Schr. phys.-ökon. Ges. Königsb. 5 (1864) 67; Crép., Man. Fl. Belgique ed. 2 (1866) 209; Blytt, Norg. Fl. ed. 1, 2 (1874) 611; Crép., Man. Fl. Belgique ed. 5 (1884) 259; Greml. Excurs.-Fl. Schweiz ed. 9 (1901) 240; A. Blytt, Haandb. Norg. Fl. (1906) 711; Erdner, Fl. Neuburg (1911) 489. — *Lappa major* Gaertn., Fruct. Sem. Pl. 2 (1791) 379, tab. 162, fig. 3; Lam. & DC., Fl. Fr. ed. 3, 4 (1805) 77; G. Mey., Chlor. Hanov. (1836) 447; Kar., Bull. Soc. Nat. Moscou (1839) 160; Steud., Nomencl. Bot. ed. 2, 3 (1840) 9; Lange in Liebm., Fl. Dan. 14 (1844) tab. 2424 (text fasc. 41, p. 7); Boiss., Fl. Or. 3 (1875) 457; Cariot & St.-Lag., Étude fl. ed. 8, 2 (1889) 439; Vuyck, Prodr. Fl. Bat. ed. 2, 1, 2

- (1902) 899. — *Lappa bardana* Moench, Meth. (1794) 552. — *Arctium majus* Bernh., Syst. Verz. Erfurt (1800) 154, nom. illeg.; Schkuhr, Handb. 3 (1808) 49; Courtois, Mag. Hort. (1833) 290; Lej. & Courtois, Comp. Fl. Belg. 3 (1836) 127; Hartm., Handb. Skand. Fl. ed. 4 (1843) 260; Lange, Haandb. Danske Fl. (1851) 464; Bab., Ann. Mag. Nat. Hist., sér. 2, 17 (1856) 372; De Wild. & Durand, Prodr. Fl. Belg. 3 (1899) 778; Rouy, Fl. Fr. 9 (1905) 94; Fourn., Fl. Compl. Plaine Fr. (1928) 289; Senay, Bull. Soc. Bot. Fr. 83 (1936) 330. — *Lappa glabra* Lam. var. *major* (Gaertn.) DC., Bot. Gall. 1 (1828) 282; Mathieu, Fl. Gén. Belg. 1 (1853) 294. — *Lappa communis* Coss. & Germ. var. *major* (Gaertn.) Coss. & Germ., Fl. Paris, ed. 1 (1845) 389. — *Lappa vulgaris* Hill var. *major* (Gaertn.) Neilr., Fl. Wien (1846) 267. — *Lappa bardana* Moench var. *major* (Gaertn.) Čelak., Prodr. Fl. Böhm. (1871) 249. — *Lappa major* (Bernh.) Lange, Haandb. Danske Fl. ed. 4 (1886) 358. — *Lappa minor* Hill f. *major* (Gaertn.) Knuth, Fl. Nordfr. Inseln (1895) 81. — *Arctium majus* Bubani ex Schkuhr, Fl. Pyren. 2 (1899) 125. — *Arctium lappa* L. var. *majus* (Bernh.) Fiori in Fiori & Paol., Fl. Anal. It. 3 (1904) 317. — *Arctium vulgare* (Hill) Druce, Ann. Scott. Nat. Hist. 60 (1906) 222. — *Arctium lappa* L. subsp. *majus* (Bernh.) Arènes, Bull. Jard. Bot. Brux. 20 (1950) 75. — Type: Non Hb. Linn. 964.1: *A. tomentosum*. — See note 2, 3.
- Arctium ruderales* Salisb., Prod. (1796) 184, nom. superfl.
- Lappa kotschyi* Boiss. ex Crép., Notes Pl. rares ou crit. 2 (1862) 53; Boiss., Fl. Or. 3 (1875) 458 (in syn. of *L. major* Gaertn.). — Type: *Kotschy 356*, (1836) "Asie mineure, Taurus" (W!).
- Lappa platylepis* Boiss. & Balansa in Boiss., Fl. Or. 3 (1875) 458. — *Arctium platylepis* (Boiss. & Balansa) Sosn. ex Grossh., Fl. Kavkaza 4 (1934) 164; Tscherneva in Komarov, Fl. URSS 27 (1962) 95, tab. 7, fig. 1; Kupicha in Davis, Fl. Turkey 5 (1975) 354; Rech. f., Fl. Iran. 139a (1979) 106. — *Arctium lappa* L. subsp. *platylepis* (Boiss. & Balansa) Arènes, Bull. Jard. Bot. Brux. 20 (1950) 77. — Type: *Balansa s.n.*, "hab. circa Khabackhar Ponti Lazici 6000" (G, holo, n.v., LE!, P!). — See note 4.
- Lappa major* (Bernh.) Lange var. *subtomentosa* Lange, Haandb. Danske Fl. ed. 4 (1886) 358. — *Lappa vulgaris* Hill var. *subtomentosa* (Lange) F.N. Williams, Prod. Fl. Brit. 2 (1901) 54. — *Arctium lappa* L. var. *subtomentosum* (Lange) Druce, List Brit. Pl. ed. 1 (1908) 39 — Type: *J. Lange 320*, 18/08/1867, "in silva ad Juelsberg Frondo" (P!).
- Arctium majus* Bernh. subvar. *purpurascens* Legrand, Bull. Assoc. Fr. Bot. 2 (1899) 69; Rouy, Fl. Fr. 9 (1905) 95. — *Arctium lappa* L. var. *purpurascens* (Legrand) Fernald & Wiegand, Rhodora 12 (1910) 44. — *Arctium lappa* L. f. *purpurascens* (Legrand) Marsh, litt. unknown; Gross et al., Canad. Jour. Pl. Sci. 60 (1980) 623. — Type: unknown.
- Arctium lappa* L. f. *subtomentosum* A.H. Evans, Jour. Bot. (London) 51 (1913) 116. — Type: unknown.
- Arctium edule* [Sieb. ex Miq.] Beger in Hegi, Ill. Fl. Mitteleur. 6, 2 (1928) 829; Nakai, Bull. Nat. Sci. Mus., Tokyo 31 (1952) 112. — *Lappa edulis* Sieb. ex Miq., Ann. Mus. Bot. Lugd.-Bat. 2 (1866) 185, in synonymy of *Lappa major* Gaertn.: nom. nud. — Lectotype (assigned here): *Siebold s.n.*, s.d. (L!, sheet 900.74-218).
- Arctium majus* Bernh. subvar. *album* Bonnier, lit. unknown; Senay, Bull. Soc. Bot. Fr. 83 (1936) 331. — Type: unknown.
- Arctium lappa* L. f. *albiflorum* Beger in Hegi, Ill. Fl. Mitteleur. 6, 2 (1928) 829. — Type: unknown.
- Arctium minus* (Hill) Bernh. subsp. *tchihatchefii* Arènes, Bull. Jard. Bot. Brux. 20 (1950) 107, pl. 6, fig. e, f, h, i; fig. 15n; Kupicha in Davis, Fl. Turkey 5 (1975) 355, in syn. — Type: *Tchihatchef 950*, 1858, Asia minor, Olst (P, holo!). — See note 5.
- Arctium leiospermum* Juz. & Serg., Not. Syst. Herb. Inst. Bot. Acad. Sci. URSS 18 (1957) 299; Tscherneva in Komarov, Fl. URSS 27 (1962) 98. — Holotype: *O. & B. Fedtschenko s.n.*, 15/08/1901, "Jugum montium Alaicum, inter pag. Guleza et Langar" (LE!). Paratype: *W. L. Nekrassova 39*, 19/09/1921, "Distr. Aulieata regionis Syr-Dariensis, pag. Kljutschevka in oleraceis" (LE!). — See note 6.
- Arctium chaorum* Klokov, Fl. URSS 11 (1962) 437, 560. — Type: *Klokov s.n.*, 3/8/1957, RSS Ucr., *Tauria meridionalis*, Alupka, "in rupestris loco <<chaos>> dicto" (n.v.). — See note 6.
- Arctium lappa* L. f. *foliosum* (Wallr.) Beger in Hegi, Ill. Fl. Mitteleur. 6, 2 (1928) 829 (teratologic form), nom. illeg. — Type: unknown.



Fig. 18.2. *Arctium lappa* L. – Apical part of synflorescence and basal leaf (Duistermaat & Vermeulen 137). Bar indicates 5 cm.

Biennial. *Stem* 40–210 cm long. *Basal leaves*: petiole 15–36 cm long, solid, glabrous to shortly arachnoid hairy; lamina 25–80 × 20–70 cm (index 1.0–1.4), base cordate, margin irregularly undulate, with sparse mucronate teeth, apex obtuse, sometimes acuminate and somewhat hooked, lower side arachnoid hairy, with minute glassy globules, silvery white, upper side sparsely hairy, with short uni- and multicellular hairs; *cauline leaves* like basal leaves but lamina at base cuneate. *Synflorescence* corymbose, with many capitules, branches patent or deflexed, the longest 30–150 cm. *Capitules* solitary, 2.5–26 cm pedunculate, with more than 40 flowers, (2.4–)3.0–4.7 × 2.0–3.3 ((1.1–)1.3–2.2 × 1.4–2.2) cm, glabrous to sparsely hairy. *Involucral bracts* in (9 or) 10–16 rows, herbaceous, bright green, the upper part yellow or straw-coloured, sometimes dark green and purple at apex; outer involucral bracts 8–11.8 × 0.9–2 mm, linear-triangular, sometimes foliose, patent or deflexed, margin with some glandular hairs in the lower half; middle involucral bracts (9.2–)10.6–16.0 × 0.9–1.7 mm, linear-triangular (index 6.9–13.3), margin in the lower half membranaceous, with some to many glandular hairs, the upper 3/5–3/4 patent; inner involucral bracts 13.4–21.0 × 1.0–2.6 mm, linear-ovate to -obovate (index 6.0–22.5), membranaceous, abaxially in the middle third with club-shaped hairs, margin with rather few to many (glandular) hairs, the upper part slightly recurved, apex acute to (sharply) acuminate, straight or (slightly) hooked. *Longest receptacular scales* 5.8–9.6 × 0.1–0.7 mm, glabrous, near apex scabrid, apex rarely split, margin at apex rarely dentate, acute. *Longest pappus hairs* (2.1–)2.3–4.9 × 0.1–0.2 mm wide, margin minutely dentate, at apex rarely 3-fid, acute. *Corolla* 9.5–14.7 mm long, white, pink, lilac, crimson, pale blue, (deep) purple, or deep purple at apex and pale purple to white at base, exceeded by the involucral bracts by 1.0–5.0 mm, rarely equalled by them, tube 5.0–8.5 mm long, not or slightly widened at base, glabrous, limb 4.4–6.6 mm long (= 2/5–1/2 of total length), gradually widening, glabrous or with 1 to many glandular hairs at the apex of (some of) the lobes, rarely limb with glandular hairs (*Koelz 18453*); lobes 5, sometimes 6, longest lobe 2.0–2.9 mm long (= 2/5–1/2 of limb). *Stamens* 5, sometimes 6, filaments 1.9–4.8 mm long, smooth to verrucate or (very) papillose, anthers 3.5–6.0 × 0.3–0.4 mm, blue, deep to pale (blue-)purple, or pale purple with dark blue stripes, basal appendage 0.3–1.7 mm long, entire or bifurcate or with 2 very short fimbriae, apical appendage 0.7–1.4 mm long, glabrous, acuminate. *Stylar apex* 1.8–3.0(–4.3, *Jardine 866*) mm, white, pink, pale lilac, or pale purple, branches 1.4–2.9(–4.3) mm long (= 3/5–1 of stylar apex), sweeping hairs 0–1.0 mm below the branches. *Achene* 6.2–7.7 × 2.4–3.2 mm, obovoid (index 2.2–2.7), rugose, with up to 5 longitudinal ridges, chestnut brown, sometimes with dark brown spots, with inconspicuous marginal ridge, apical plate truncate.

Distribution – Europe and Western Asia northwards to 65° latitude (excluding Iceland), southwards to the Mediterranean (very rare), Iran, Pakistan, and Northern India, and eastwards to Japan.

Introduced – Canada (Québec). USA (Pennsylvania). [Hawai'i; see Fernald, 1950; Wagner et al., *Man. Fl. Pl. Hawai'i* 1 (1990) 258].

Habitat & Ecology – Neglected places in or near industrial or human settlements, sides of roads etc., along streams and ditches, marshlands, forest edges. Dry to moist, nitrate rich limestone soil, (heavy) clay, sandy clay, or (calcareous) sand, in shadow or full sun. Alt.: 0–3200 m. Flowering from June to August.

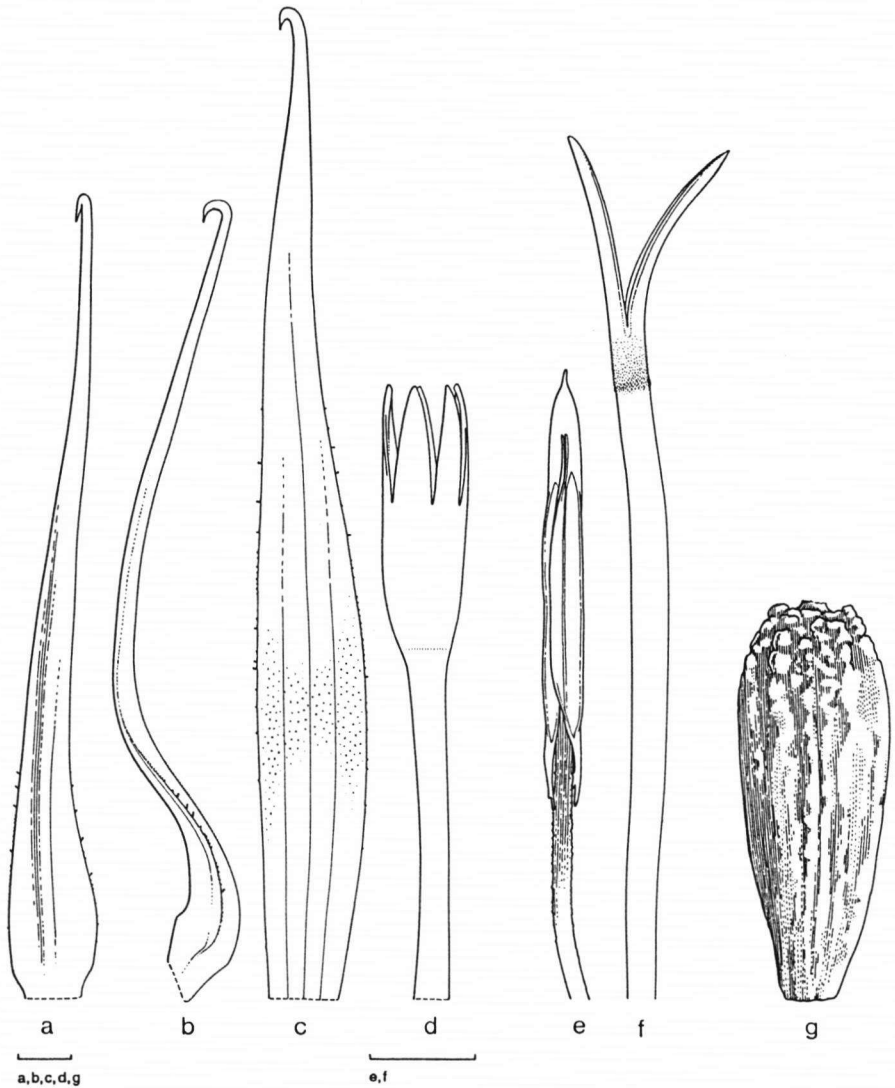


Fig. 18.3. *Arctium lappa* L. – a. Dorsal view of middle involucre bract; b. lateral view of middle involucre bract; c. dorsal view of inner involucre bract; d. corolla; e. anther with apical part of filament; f. apical part of style; g. achene (a–g: *Duistermaat & Vermeulen 55*). Bar indicates 1 mm.

**Taxonomy – 1.** In the field *A. lappa* can generally be recognised by its bright green capitules, gathered in loose, corymbose synflorescences. The differences with *A. minus* include the basal leaves which have a solid petiole, the larger capitules (those of *A. minus* rarely reach 3.2 cm), and a corymbose synflorescence. From *A. tomentosum* and *A. palladini* it differs in having usually a glabrous corolla which is exceeded by the involucre bracts, and acute inner involucre bracts.

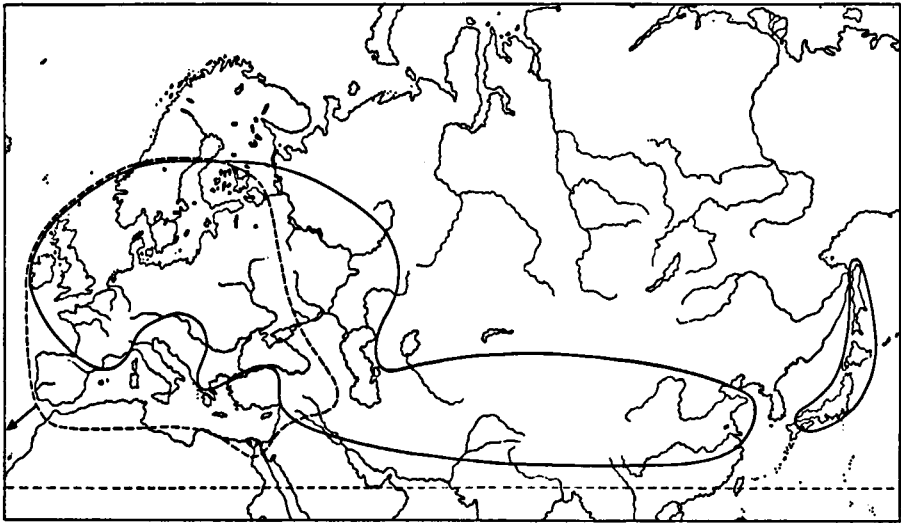


Fig. 18.4. Distribution map of two widespread species. — *Arctium lappa* L. - - - *Arctium minus* (Hill) Bernh. The arrow indicates the occurrence of *A. minus* on Madeira.

Nomenclature & Synonymy – 2. The specimens which are labeled as *A. lappa* in the Linnaean herbarium do not agree with the generally accepted concept of the species. I identified the specimens as *A. minus* or *A. tomentosum*. Kupicha (1975) noticed this also, and therefore treats *A. lappa* as a ‘nomen confusum’ in the synonymy of *A. tomentosum*. However, *A. lappa* has never since Linnaeus been confused with either of the two above mentioned species. I therefore propose to conserve this name (in prep.).

3. Bernhardt (1800) described *A. minus* and *A. majus* simultaneously. In the synonymy of both species he mentioned *A. lappa* L., and therefore one of them is illegitimate. *Arctium minus* refers to a taxon which is different from the generally accepted concept of *A. lappa* in having a racemose to sub-corymbose synflorescence. It is the first name that is available for this taxon, and I therefore prefer to accept *A. minus* as the legitimate of the two. *Arctium majus* is, in fact, a later synonym for *A. lappa*. Therefore, I treat *A. majus* as the illegitimate name.

4. *Lappa platylepis* was described in 1875 by Boissier and Balansa, and said to be differing from *A. lappa* and other species by its flattened and very wide involucre bracts. It is recorded from NE Turkey, Iran and the Caucasus. Both the Flora of Turkey (Kupicha, 1975) and the Flora Iranica (Rechinger, 1979) state that *A. platylepis* has wider capitules, wider involucre bracts, and flowers equalling (instead of exceeded by) the purple green involucre bracts. The Flora of the URSS (Tscherneva, 1962) adds that achenes of *A. platylepis* are 7 mm long, of *A. lappa* (and *A. pleiospermum*) 5–6(–6.5) mm long. Figure 18.5 shows a scatter-diagram in which specimens of *A. platylepis* (as cited by the above authors) and *A. lappa* are included. In this diagram the length and width of the middle involucre bracts, and the length of the corolla relative to the involucre are visualized. It seems impossible to describe



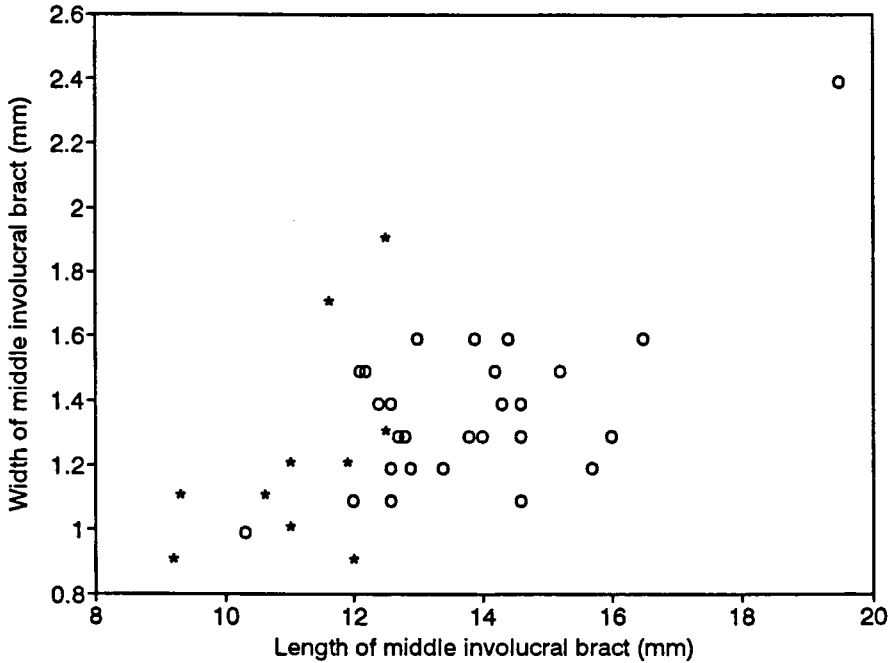


Fig. 18.5. Scatterdiagram showing the variability of *Arctium lappa*, including *A. platylepis*. o: corolla exceeded by the involucre; \*: corolla equalling the involucre.

more than one group from this diagram. Contrary to what is stated in literature, the specimens with small capitules more often have flowers which equal the involucre (\*\*\*) than specimens with larger capitules. I therefore treat *A. platylepis* as a synonym for *A. lappa*.

5. The type specimen of *A. minus* Bernh. subsp. *tchihatchefii* Arènes, *Tchihatchef* 950, is a collection from Western Asia, of a plant which was c. 35 cm high. Its synflorescence is very poorly developed, but, in contrast with *A. minus*, it seems to be corymbose, and the capitules are c. 3.5 cm wide. In my opinion it is a poorly developed specimen of *A. lappa*, and I regard the subspecies as a synonym of *A. lappa*.

6. Juzepczuk & Sergievskaja (1957, 299) described *Arctium leiospermum* as a close relative of *A. lappa* with shorter pedunculate capitules and shorter involucrel bracts. I have seen neither the holotype, nor the paratype.

Klokov (1962, 560) described *A. chaorum* for the Ucrain. I have not seen the type specimen. According to the author the capitules and all other parts are smaller than in *A. lappa*, the capitules are 20–22 mm wide, and with 1–6 cm long peduncles. Also, its general appearance would be different. No reference is made to *Arctium leiospermum*.

I have not seen specimens with a (sub-)corymbose synflorescence with capitules narrower than 2.4 cm (*Mandenova & Kuthatheladze s.n.*, 11-08-1952; *Anon. (Russian) s.n.*, 29-07-1961). The width of the capitule did not correspond with any other

character. Therefore, and because the original descriptions of both above mentioned species fall within the range of *A. lappa*, I treat both *A. leiospermum* and *A. chaorum* as synonyms for *A. lappa*.

Variation & Hybrids – 7. Specimens which are interpreted as a hybrid with as one of the parents *A. lappa* are frequently found in the herbarium. However, even when the specimen is reported growing among its putative parents, such an interpretation is often not justified in my opinion. Mown specimens of *A. lappa*, and specimens consisting of lateral branches, which are often easier to collect than the diagnostically important end branch, may somewhat resemble other species. These specimens do very often have smaller capitules which are arranged in an intermediate type of synflorescence between racemose and corymbose, described as subcorymbose. A hybrid between *A. lappa* and a species with a racemose synflorescence (*A. minus*, *A. pubens* or *A. nemorosum*) was postulated several times, based on insufficient herbarium material (e.g. Guétrot, *Pl. Hybr. Fr.* 81 (leg. Fouillade); Lambinon 81/305 (11739); van Soest 23279; Bakhuizen van den Brink 5577).

8. Also, specimens corresponding to *A. lappa* except for having slightly hairy or purple coloured capitules were considered to be of hybrid origin (Arènes, in sched.). Usually either *A. pubens* (= *A. minus*) or *A. tomentosum* is mentioned as the other parent. On locations where *A. lappa* is abundant, such slightly aberrant specimens can be observed among numerous normal specimens. If such 'intermediates' are regarded as hybrids, *A. lappa*, *A. minus* and *A. tomentosum* should be synonymized. However, I include in *A. lappa* specimens which differ from *A. lappa* only in having slightly hairy or purple coloured capitules. This increases the variability within *A. lappa*, but it decreases the number of intermediate, supposed hybrid specimens dramatically. In Chapter 12 I conclude that hybrids are rare within the genus *Arctium*.

9. I have seen a few specimens which are probably the hybrid between *A. lappa* and *A. minus* (H1) or *A. tomentosum* (H2). They seem to produce at least some fertile seeds.

Notes – 10. The collection *Haveman 593* from The Netherlands is annotated 'petiole hollow'. This could not be checked because the petiole was not collected, but I think that this refers to a lower cauline leaf, and not to a rosette leaf.

11. *Arctium lappa* is cultivated in Japan (Okinawa Island) for roots and young shoots, which are eaten commonly and sold in markets. It is said that cultivated forms always have white flowers (coll. Walker, Tawada & Amano 5792).

12. Hohenacker (in sched.) mentions that the root or 'Radix Bardanae' is collected for pharmaceutical purposes.

### 3. *Arctium minus* (Hill) Bernh. – Fig. 18.4, 6, 7.

*Arctium minus* (Hill) Bernh., *Syst. Verz. Erfurt* (1800) 154; Schkuhr, *Handb.* 3 (1808) 49, tab. 227; Courtois, *Mag. Hort.* (1833) 290; Lej. & Courtois, *Comp. Fl. Belg.* 3 (1836) 128; Lange, *Haandb. Danske Fl.* ed. 1 (1851) 463; Bab., *Ann. Mag. Nat. Hist.*, sér. 2, 17 (1856) 375; sér. 3, 15 (1865) 11; Nyman, *Consp.* 1 (1879) 402; *Suppl.* 2 (1889) 179; Weiss in Koch, *Syn. Deutsch. Fl.* ed. 3, 2 (1897) 1512 (as a var?); Durand in De Wild. & Durand, *Prodr. Fl. Belg.* 3 (1899) 779; Bubani, *Fl. Pyren.* 2 (1899) 125 (sub *Arcium*); Teyber, *Verh. Zool.-Bot. Ges. Wien* 52 (1902) 590; Rouy, *Fl. Fr.* 9 (1905) 95; A. H. Evans, *Jour. Bot. (London)* 51 (1913) 118; Beger in Hegi, *Ill. Fl. Mitteleur.* 6, 2 (1928) 831; Fourn., *Fl.*

Compl. Plaine Fr. (1928) 291; Briq. & Cavill. in Burnat, Fl. Alp. Marit. 7 (1931) 271; Senay, Bull. Soc. Bot. Fr. 83 (1936) 335; Máthé, Acta Geobot. Hung. 1 (1937) 230; Fernald, Gray's Man. Bot. (1950) 1538; Hultén, Vår Svenska Fl. 19 (1958) 617; W. Stevens, Kansas Wild flowers ed. 2 (1961) 424; Ross-Craig, Draw. Brit. Pl. 17 (1962) pl. 4; Tscherneva in Komarov, Fl. URSS 27 (1962) 100, tab. 7, fig. 8, 9; Klokov, Fl. URSR 11 (1962) 442; Rothm., Exkurs.fl. Deutschl. ed. 4 (1963) 331; Craighead et al., Field Guide to Rocky Mt. wild flowers (1963) 191; Soó, Syn. Syst.-Geobot. Fl. Veg. Hung. 4 (1970) 122; Hess & Landolt, Fl. Schweiz 3 (1972) 410; Moore & Frankton, Canad. Dept. Agric. Monogr. 10 (1974) 14; Kupicha in Davis, Fl. Turkey (1975) 355; Perring in Tutin et al., Fl. Eur. 4 (1976) 215; Rech. f., Fl. Iran. 139a (1979) 107. — *Lappa minor* Hill, Veg. Syst. 4 (1762) 28, pl. 25, fig. 3a; Lam. & DC., Fl. Fr. 4 (1805) 77; DC., Prodr. 6 (1838) 661; Steud., Nomencl. Bot. ed. 2, 3 (1840) 9; Wallr., Linnaea 14 (1840) 639; Rchb. f., Ic. Fl. Germ. 15 (1853) 53; Schur, Verh. Mitt. Siebenb. Ver. Naturw. 4, 6 (1853) 35; Lange, Haandb. Danske Fl. ed. 2 (1856–59) 530; Boreau, Fl. Centre Fr. ed. 3, 2 (1857) 363; Lange in Liebm. & Lange, Fl. Dan. 15, (1866) tab. 2662 (text fasc. 45, p. 7); Marsson, Fl. Neu-Vorpomm. (1869) 262; Blytt, Norg. Fl. ed. 1, 2 (1874) 610; Crép., Man. Fl. Belgique ed. 5 (1884) 259; Lange, Haandb. Danske Fl. ed. 4 (1886) 357; Gustave & Héríb., Fl. Auv. (1888) 236; Cariot & St.-Lag., Étude fl. ed. 8, 2 (1889) 439; Knuth, Fl. Nordfr. Ins. (1895) 80; Eeden, Fl. Bat. 20 (1898) pl. 1587; Gremli, Excurs.-Fl. Schweiz. ed. 9 (1901) 240; F. N. Williams, Prod. Fl. Brit. 2 (1901) 54; Vuyck, Prodr. Fl. Bat. ed. 2, 1, 2 (1902) 900; A. Blytt, Haandb. Norg. Fl. (1906) 710; Erdner, Fl. Neuburg (1911) 490. — *Lappa glabra* Lam., Fl. Fr. 2 (1778) 37 (B); Tabl. Encycl. Méth. Bot. 1, 2 (1785) 337 (a); Crép., Man. Fl. Belg. ed. 5 (1884) 259. — *Arctium lappa* L. *β minus* (Hill) Pers., Syn. Pl. 2 (1807) 383. — *Arctium majus* Bernh. var. *minus* (Hill) Gray, Nat. Arr. 2 (1821) 435. — *Lappa glabra* Lam. a *minor* (Hill) DC., Bot. Gall. 1 (1828) 282; Mathieu, Fl. Gen. Belg. (1853) 294. — *Lappa major* Gaertn. Spielart b *minor* (Hill) G. Mey., Chlor. Hanov. (1836) 447. — *Lappa communis* Coss. & Germ. var. *minor* (Hill) Coss. & Germ., Fl. Paris ed. 1 (1845) 389. — *Lappa vulgaris* Hill var. *minor* (Hill) Neilr., Fl. Wien (1846) 267. — *Arctium minus* (Hill) Bernh. subsp. *eu-minus* Syme, Engl. Bot. ed. 3, 5 (1866) 26, tab. 702; Arènes, Bull. Jard. Bot. Brux. 20 (1950) 83. — *Lappa bardana* Moench e *minor* (Hill) Čelak., Prodr. Fl. Böh. (1871) 249. — *Arctium lappa* L. var. *minus* (Bernh.) Fiori in Fiori & Paol., Fl. Anal. Ital. 3 (1904) 317. — Type: Hill l.c., pl. 25, fig. 3a.

*Arctium montanum* Schweigg. & Körte, Fl. Erlang. (1811) 74 (L. *minor* in syn.). ex Steud., Nomencl. Bot. ed. 2 (1840) 120, in syn.: L. *minor*. — Type: unknown.

*Lappa major* Gaertn. Spielart a *racemosa* G. Mey., Chlor. Hanov. (1836) 447. — Type: Engl. Bot. tab. 1228. — See note 5.

*Lappa repens* DC. ex Kar., Bull. Soc. Nat. Moscou (1839) 160. — Type: unknown.

*Lappa communis* Coss. & Germ., Fl. Paris ed. 1 (1845) 389 (a, b, t). — Type: unknown.

*Lappa minor* DC. var. *montana* Fr., Summa Veg. Scand. (1846) 5, nom. nud.

*Lappa minor* DC. var. *campestris* Lange apud Fr., Summa Veg. Scand. (1846) 5, nom. nud.

*Arctium pubens* Bab., Ann. Mag. Nat. Hist., sér. 2, 17 (1856) 376; Rouy, Fl. Fr. 9 (1905) 96; Beger in Hegi, Ill. Fl. Mitteleur. 6, 2 (1928) 834; Fourn., Fl. Compl. Plaine Fr. (1928) 291; Briq. & Cavill. in Burnat, Fl. Alp. Marit. 7 (1931) 273; Senay, Bull. Soc. Bot. Fr. 83 (1936) 336; Ross-Craig, Draw. Brit. Pl. 17 (1962) pl. 5; Perring in Tutin et al., Fl. Eur. 4 (1976) 215. — *Lappa pubens* (Bab.) Boreau, Fl. Centre Fr. ed. 3, II (1857) 758. — *Arctium nemorosum* Lei. var. *pubens* (Bab.) Nyman, Consp. 1 (1879) 402; Máthé, Acta Geobot. Hung. 1 (1937) 233. — *Lappa minor* DC. var. *pubens* (Boreau) Gustave & Héríb., Fl. Auv. (1888) 237; Cariot & St.-Lag., Étude fl. ed. 8, 2 (1889) 440; Gremli, Exkurs.-Fl. Schweiz (1901) 240. — *Arctium tomentosum* Mill. subsp. *pubens* (Bab.) Nyman, Suppl. 2 (1889) 179. — *Arctium minus* Bernh. var. *pubens* (Bab.) Weiss in Koch, Syn. Deutsch. Fl. ed. 3, 2 (1897) 1513. — *Arctium lappa* L. e *pubens* (Bab.) Fiori in Fiori & Paol., Fl. Anal. Ital. 3 (1904) 317. — *Arctium nemorosum* Lej. var. *pubens* (Bab.) Fiori, Nuovo Gior. Bot. Ital., n. s., 13 (1906) 197, 198. n.v. — *Lappa minor* DC. f. *pubens* (Bab.) A. Blytt, Haandb. Norg. Fl. (1906)

710. — *Arctium minus* Bernh. subsp. *pubens* (Bab.) Arènes, Bull. Jard. Bot. Brux. 20 (1950) 89; Kupicha in Davis, Fl. Turkey 5 (1975) 355. — *Arctium nemorosum* Lej. subsp. *pubens* (Bab.) Fiori, Nuovo Gior. Bot. Ital. 13 (1906) 197; Rothm., Exkurs.fl. Deutschl. ed. 4 (1963) 332; Soó, Syn. Syst.-Geobot. Fl. Veg. Hung. 4 (1970) 123. — *Arctium intermedium* auct. non Lange: Bab., Ann. Mag. Nat. Hist., sér. 3, 15 (1865) 9; Bab., Man. Brit. Bot. ed. 6 (1867) 196. — Lectotype (assigned by Kupicha, 1975, 355): *Babington s.n.*, 30/8/1853, "Middle Hill Drove, near Upware Ferry, Cambridgeshire, England". (CGE, holo!). — See notes 8, 10, and 13.
- Lappa conglomerata* Schur in Fuss, Verh. Mitt. Siebenb. Ver. Naturw. 10 (1859) 79. — *Arctium conglomeratum* (Schur) Schur ex Nyman, Syll. Suppl. (1865) 4. — *Arctium minus* Bernh. var. *conglomeratum* (Schur) Nyman, Consp. 1 (1879) 402; Suppl. 2 (1889) 179. — Type: ?Schur, "auf den Hügeln um Thorda, Hermannstadt u. s.w." (? , n.v.).
- Arctium minus* (Hill) Bernh. var. *macrocephalum* Rupr., Fl. Ingrica (1860) 541; Máthé, Acta Geobot. Hung. 1 (1937) 231. — Type: unknown.
- Arctium minus* (Hill) Bernh. var. *microcephalum* Rupr., Fl. Ingrica (1860) 541; Máthé, Acta Geobot. Hung. 1 (1937) 232; Soó, Syn. Syst.-Geobot. Fl. Veg. Hung. 4 (1970) 123. — Type: unknown.
- Lappa minor* Hill var. *broquetii* Martinis, Bull. Soc. Bot. Belg. 2 (1863) 155, n.v.; Heurck & Martinis, Herb. Pl. rares ou crit. Belg. (1862) 33 (in sched.?). — *Arctium minus* (Hill) Bernh. var. *broquetii* (Martinis) Durand in De Wild. & Durand, Prodr. Fl. Belg. 3 (1899) 779. — Type: *Van Heurck* (Martinis), Herb. Pl. rares ou crit. Belg. (1862) 33 (BM!).
- Lappa bardana* Moench e *minor* (Hill) Čelak. f. *macrocephala* Čelak., Prodr. Fl. Böhm. (1871) 249. — *Arctium minus* (Hill) Bernh. var. *macrocephalum* (Čelak.) Weiss in Koch, Syn. Deutsch. Fl. ed. 3, 2 (1897) 1513. — Type: unknown.
- Lappa minor* Hill f. *purpurascens* Blytt, Norg. Fl. ed. 1, 2 (1874) 610. — *Arctium vulgare* A. H. Evans f. *purpurascens* (Blytt) A. H. Evans, Jour. Bot. (London) 51 (1913) 118; Máthé, Acta Geobot. Hung. 1 (1937) 233. — Type: unknown.
- Lappa minor* Hill a *virescens* Blytt, Norg. Fl. ed. 1, 2 (1874) 610. — Type: unknown.
- Lappa minor* Hill var. *araneosa* Lamotte, Prodr. Fl. Plat. Centr. (1881) 445. — *Arctium minus* (Hill) Bernh. subvar. *araneosa* (Lamotte) Rouy, Fl. Fr. 9 (1905) 96; Senay, Bull. Soc. Bot. Fr. 83 (1936) 336. — Type: unknown.
- Lappa minor* Hill var. *alba* Christ in Gremli, Excurs.-Fl. Schweiz. ed. 5 (1885) 249 (n.v.); Gremli, Excurs.-Fl. Schweiz ed. 9 (1901) 240. — *Arctium minus* (Hill) Bernh. var. *album* (Christ) Weiss in Koch, Syn. Deutsch. Fl. ed. 3, 2 (1897) 1513; Schinz & R. Keller, Fl. Schweiz ed. 3, 2 (1914) 348; Beger in Hegi, Ill. Fl. Mitteleur. 6, 2 (1928) 832. — *Arctium minus* (Hill) Bernh. var. *subteralbatum* P. Fourn., Fl. Compl. Plaine Fr. (1928) 291. — Type: unknown.
- Lappa minor* Hill var. *paniculata* Lange, Haandb. Danske Fl. ed. 4 (1886) 357. — *Arctium minus* (Hill) Bernh. f. *paniculata* (Lange) A. H. Evans, Jour. Bot. (London) 51 (1913) 118. — Type: unknown.
- Arctium intermedium* auct. non Lange var. *subtomentosum* A. Benn., Bot. Exch. Cl. Br. Isl. Rep. (1892) 328. n.v.; Druce, List Brit. Pl. ed. 1 (1908) 39. — *Arctium vulgare* A. H. Evans f. *subtomentosum* (A. Benn.) A. H. Evans, Jour. Bot. (London) 51 (1913) 117. — *Arctium pubens* Bab. subvar. *subtomentosum* (A. Benn.) Senay, Bull. Soc. Bot. Fr. 83 (1936) 336. — Type: unknown.
- Lappa nemorosa* Körn. var. *microcephala* Erdner, Mitt. Bayer. Bot. Ges. 1, 31 (1904) 373. — *Arctium nemorosum* Lei. var. *microcephalum* (Erdner) Beger in Hegi, Ill. Fl. Mitteleur. 6, 2 (1928) 829; Máthé, Acta Geobot. Hung. 1 (1937) 233. — *Arctium pubens* Bab. var. *microcephalum* Wilpert, Monogr. Arctium (1928), n.v. — Type: unknown.
- Lappa minor* Hill f. *lanaria* A. Blytt, Haandb. Norg. Fl. (1906) 710. — Type: unknown.
- Lappa minor* Hill f. *purpurea* A. Blytt, Haandb. Norg. Fl. (1906) 710. — *Arctium minus* (Hill) Bernh. f. *purpurea* (A. Blytt) A. H. Evans, Jour. Bot. (London) 51 (1913) 118; Gross et al., Canad. Jour. Pl. Sci. 60 (1980) 622. — Non Moore & Frankton, Canad. Dept. Agric. Monogr. 10 (1974) 16. — Type: unknown.
- Arctium minus* (Hill) Bernh. f. *laciniatum* Clute, Amer. Botanist 15 (1909) 83, n.v.; Fernald & Wiegand, Rhodora 12 (1910) 43; Fernald, Gray's Man. Bot. (1950) 1538; Moore & Frankton,

- Canad. Dept. Agric. Monogr. 10 (1974) 16; Gross et al., Canad. Jour. Pl. Sci. 60 (1980) 622. — Type: unknown.
- Lappa minor* Hill f. *macrocephala* Erdner, Fl. Neuburg (1911) 491. — *Arctium minus* (Hill) Bernh. var. *macrocephalum* (Erdner) Beger in Hegi, Ill. Fl. Mitteleur. 6, 2 (1928) 832. — Type: unknown.
- Arctium minus* (Hill) Bernh. f. *albiflorum* Beger in Hegi, Ill. Fl. Mitteleur. 6, 2 (1928) 832. — *Arctium minus* (Hill) Bernh. subsp. *eu-minus* Syme f. *albiflora* (Beger) Arènes, Bull. Jard. Bot. 20 (1950) 85. — Type: unknown.
- Arctium minus* (Hill) Bernh. var. *melanoceps* Beger in Hegi, Ill. Fl. Mitteleur. 6, 2 (1928) 832 (var. *macrocephala* Rupr. in syn.). — Type: unknown.
- Arctium minus* (Hill) Bernh. f. *majus* Beger in Hegi, Ill. Fl. Mitteleur. 6, 2 (1928) 832. — Type: unknown. Non *Lappa minor* Hill var. *majus* Knuth, Fl. Nordfr. Ins. (1895) 81 (*L. major* Gaertn. in syn.).
- Arctium chaberti* Briq. & Cavill. in Burnat, Fl. Alp. Marit. 7 (1931) 269. — *Arctium chaberti* Briq. & Cavill. subsp. *chaberti* Arènes, Bull. Jard. Bot. Brux. 20 (1950) 120. — Type: *Reverchon 1389*, pl. Esp. ann. 1907 (W!, BM!). — See note 11.
- Arctium degeni* H. Lindb., Acta Soc. Sci. Fenn., n.s. B, 1, 2 (1932) 153. — *Lappa degeni* Chabert Hervier ex H. Lindb., in sched. — Type: *Lindberg 1115*, 21–24/7/1926, “Hispanien, Sierra Nevada, in ruderatis juxta monasterium, c. 1400 m” (W!).
- Arctium minus* (Hill) Bernh. var. *tibidatensis* Sennen, Pl. Esp. (1936) 7151. — Type: *Sennen 7151*, 1929, “Barcelone, Massif du Tibidabo, carrefours, marges élargies” (W!, BM!).
- Arctium pubens* Bab. subvar. *album* Senay, Bull. Soc. Bot. Fr. 83 (1936) 336. — *Arctium minus* (Hill) Bernh. subsp. *pubens* (Bab.) Arènes f. *albiflora* (Senay) Arènes, Bull. Jard. Bot. Brux. 20 (1950) 90. — Type: *P. Senay 3611*, Seine-Inférieure: Rogerville, Sandouville (P, holo!).
- Arctium nemorosum* Lej. var. *italicum* Máthé, Acta Geobot. Hung. 1 (1937) 233; Soó, Syn. Syst.-Geobot. Fl. Veg. Hung. 4 (1970) 124. — Type: *Fiori s.n.* (n.v.).
- Arctium minus* (Hill) Bernh. subsp. *eu-minus* Syme var. *pycnanthum* Arènes, Bull. Jard. Bot. Brux. 20 (1950) 86, pl. 5, fig. b. — Lectotype (assigned here): Arènes, Herbar. norm. Cynar. 3383; cotypes: Arènes, Herbar. norm. Cynar. 3384, 3385, 3386, 3387. (P, holo!).
- Arctium minus* (Hill) Bernh. subsp. *mediterraneum* Arènes, Bull. Jard. Bot. Brux. 20 (1950) 108. — *Arctium minus* (Hill) Bernh. subsp. *mediterraneum* Arènes var. *eumediterraneum* Arènes, Bull. Jard. Bot. Brux. 20 (1950) 108, pl. 5, fig. d, e; fig. 15 f. — Syntypes: several specimens in Herb. de Litardière (G?, n.v.).
- Arctium minus* (Hill) Bernh. subsp. *mediterraneum* Arènes var. *libanum* Arènes, Bull. Jard. Bot. Brux. 20 (1950) 111, pl. 6, fig. a, b. — Type: *R. P. Mouterde s.n.*, “Liban, Haouch près de Zahlé, dans un boisement très humide” (in herb. Mouterde; n.v.).
- Arctium minus* (Hill) Bernh. subsp. *alpestre* Arènes, Bull. Jard. Bot. Brux. 20 (1950) 94, pl. 4, fig. a, b; pl. 6, fig. g; fig. 15 h. — Lectotype (assigned here): *Herb. J. Milliat 885*; syntypes: *Herb. J. Milliat 886, 1149, 1425, 1426, 1933*. (n.v.).
- Arctium chaberti* Briq. & Cavill. subsp. *aellenianum* Arènes, Bull. Jard. Bot. Brux. 20 (1950) 121. — Type: *Aellen s.n.*, 1930, Fl. Cors., in herb. R. de Litardière. (G?, n.v.).
- Arctium chaberti* Briq. & Cavill. subsp. *corsicum* Arènes, Bull. Jard. Bot. Brux. 20 (1950) 121. — Type: *Aellen s.n.*, 1932, Fl. Cors., in herb. de Litardière. (G?, n.v.).
- Arctium chaberti* Briq. & Cavill. subsp. *balearicum* Arènes, Bull. Jard. Bot. Brux. 20 (1950) 122. — *Arctium tomentosum* non Mill., sensu var. *balearicum* (Arènes) Barcélo, Fl. Mallorca 4 (1980) 272. — Type: *Sennen 1265* (leg. *Bianor*, 1911), Pl. Espagne, in herb. de Litardière. (BM!).
- Arctium xbatavum* Arènes, Bull. Jard. Bot. 20 (1950) 127. — Type: *Anon., s.n.*, 08/1935, The Netherlands, Friesland, Muldenburg and Jelsum (L, holo!). — See note 14.
- Arctium nemorosum* Lej. f. *mathei* Soó, Acta Bot. Acad. Sci. Hung. 13 (1967) 308; Soó, Syn. Syst.-Geobot. Fl. Veg. Hung. 4 (1970) 123; Soó, Acta Bot. Acad. Sci. Hung. 18 (1973) 176. — Type: unknown.
- Arctium minus* (Hill) Bernh. f. *purpurea* Moore & Frankton, Canad. Dept. Agric. Monogr. 10 (1974) 16. — Type: unknown. Non *Lappa minor* Hill f. *purpurea* A. Blytt (1906).

- Lappa minor* Hill var. *alba* A. & G. Camus, in sched. — \* var. *alba* Debaire, litt. unknown; Fourn., Fl. Compl. Plaine Fr. (1928) 291. — *Arctium minus* (Hill) Bernh. subvar. *album* A. & G. Camus ex Senay, Bull. Soc. Bot. Fr. 83 (1936) 336. — Type: A. & G. Camus, exss. Fr.-Helv., 1784 (G, holo, n.v., BM!).
- Arctium minus* (Hill) Bernh. f. *pallidum* Farw., litt. unknown; Fernald, Gray's Man. Bot. (1950) 1538; Moore & Frankton, Canad. Dept. Agric. Monogr. 10 (1974) 16; Gross et al., Canad. Jour. Pl. Sci. 60 (1980) 622. — Type: unknown.
- Arctium minus* (Hill) Bernh. var. *corymbosum* Wieg., litt. unknown; Fernald, Gray's Man. Bot. (1950) 1538. — Type: unknown.
- Arctium gallicum* Chabert in sched.; Burnat, Fl. Alp. Marit. 7 (1931) 273, nom. illeg., in syn.: *Arctium pubens* Bab.
- Arctium personata* auct. non L., Sp. Pl. (1753) 816 (= *Carduus personata*): Mill., Gard. Dict. ed. 8, 2 (1768). — Type: unknown (Vaillant, *lappa vulgaris capitulo minore*).
- Lappa nemorosa* auct. non Körn.: Vuyck, Prodr. Fl. Bat. ed. 2, 1, 2 (1902) 900.
- Arctium intermedium* auct. non Lange: Bab., Ann. Mag. Hist., sér. 3, 15 (1865) 9; Syme, Engl. Bot. ed. 3, 5 (1866) 25, tab. 700 (sub *A. minus*). — See note 6.
- Lappa intermedia* auct. non (Lange) Rchb. f.: Eeden, Fl. Bat. 20 (1898) pl. 1588; F.N. Williams, Prod. Fl. Brit. 2 (1901) 54.
- Arctium lappa* auct. non L.: Smith, Eng. Bot. 18 (1804) pl. 1228; Hartm., Handb. Skand. Fl. ed. 4 (1843) 260.
- Lappa glabra* auct. non Lam.: Asch., Fl. Brandenb. (1864) 353; Asch. & Graebner, Flor. Nordostd. Flachl. (1899) 743.
- Arctium vulgare* auct. non (Hill) Druce: A.H. Evans, Jour. Bot. (London) 51 (1913) 117. — See note 7.
- Arctium tomentosum* auct. non Mill.: Barcélo, Fl. Mallorca 4 (1980) 272, fig. 1.498.

Biennial. *Stem* 50–250 cm long. *Basal leaves*: petiole 16–50 cm long, hollow (sometimes only at base), ribbed, slightly to densely arachnoid hairy, rarely with short glandular hairs; lamina 28–58 × 16–34 cm (index 1.3–2.2), base cordate, margin irregularly undulate, with sparse up to 1 mm long mucronate teeth, apex retuse to acute, with up to 2 mm long mucro, straight, lower side sparsely arachnoid, with minute glassy globules, grey-white or pale green, upper side sparsely hairy, with short multicellular hairs; *cauline* leaves like basal leaves but lamina cordate to cuneate at base, margin somewhat undulate, entire or with mucronate teeth, apex acute to acuminate, the upper leaves with up to 3 mm long mucro. *Synflorescence* racemose to subcorymbose, with many capitules, branches patent or deflexed, longest 26–200 cm long. *Capitules* 2–10 in clusters or solitary at the terminal part of branches, sessile or up to 9.5 cm pedunculate, with more than 40 flowers, 1.5–3.2 × 1.1–2.4 (0.8–1.8 × 1.0–2.1) cm, glabrous to densely (woolly) silvery hairy. *Involucral bracts* in 9–17 rows, herbaceous, (dark or purple) green, the upper part often tinged with red or yellowish; outer involucral bracts 3.5–8.0 × 0.8–2.2 mm, linear-triangular, sometimes foliose, patent to deflexed, margin with some glandular hairs in the lower half; middle involucral bracts 6.0–15.6 × 0.6–1.6 mm, linear-triangular (index 7.0–14.2), abaxially sometimes with short hairs, margin in the lower half with (glandular) hairs, the upper 1/2–3/4 patent; inner involucral bracts 7.8–17.1 × (0.6–)0.8–1.9 mm, linear-triangular or -ovate (index 6.1–19.2), membranaceous, glabrous or abaxially in the middle part with short hairs, margin dentate from 2 mm above base, straight or the upper part slightly recurved, apex acute or acuminate, straight or (slightly) hooked. Longest *receptacular scales* 4.0–11.0 × 0.1–0.4 mm, glabrous, sometimes scabrid in the upper half, margin entire or at apex sometimes with 1 tooth, apex rarely split, acute.



Fig. 18.6. *Arctium minus* (Hill) Bernh. – Apical part of synflorescence (from fresh material collected in Leiden, The Netherlands). Bar indicates 5 cm.

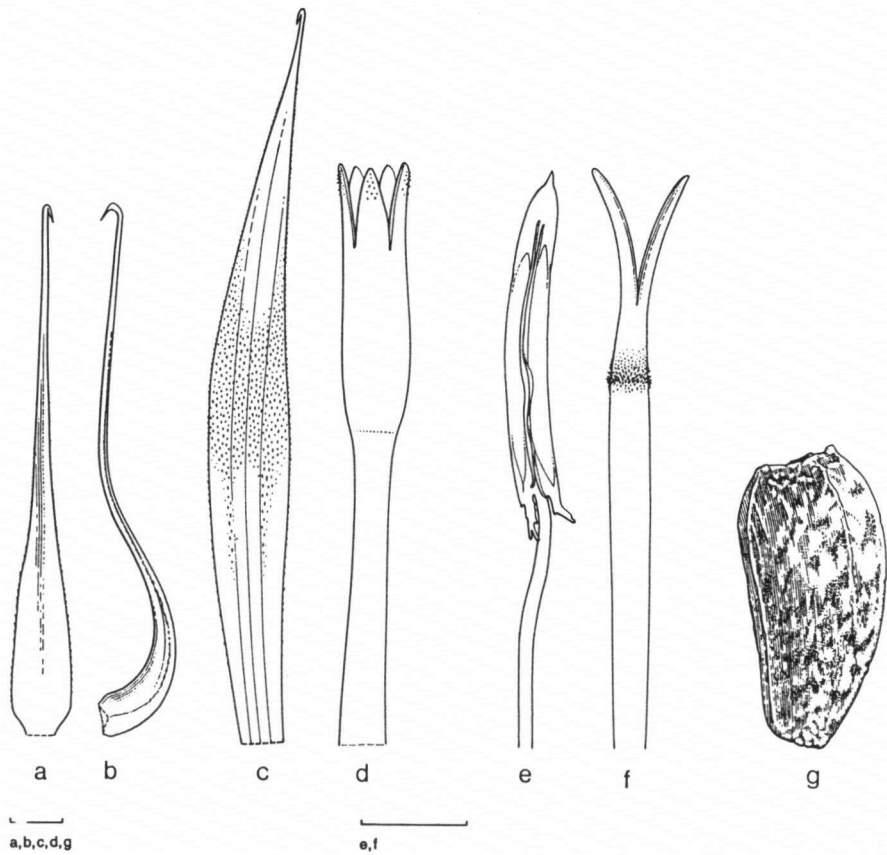


Fig. 18.7. *Arctium minus* (Hill) Bernh. – a. Dorsal view of middle involucre bract; b. lateral view of middle involucre bract; c. dorsal view of inner involucre bract; d. corolla; e. anther with apical part of filament; f. apical part of style; g. achene (a–f: *Duistermaat 180*; g: *Duistermaat & Bruinsma 76*). Bar indicates 1 mm.

Longest *pappus hairs* 1.2–3.7 mm long, margin minutely dentate, acute. *Corolla* 7.6–12.3 mm long, white to (pale) pink, lilac, purple, or velvet-red, more pale at base, more pale or blue when young, sometimes white and purple corollas in one capitule or in different capitules of one plant, either equalling or exceeding the involucre bracts up to 2.5 mm, or exceeded by involucre bracts up to 3.6 mm, tube 3.4–6.3 (–7.0) mm long, slightly widened at base, glabrous, or sometimes the upper part with glandular hairs, limb 3.9–6.1 mm long (= 2/5–3/5 of total length), glabrous to entirely covered with glandular hairs; lobes 5, sometimes 4 or 6, longest lobe 1.1–2.2 mm long (= 1/4–1/2 of limb). *Stamens* 5, sometimes 4 or 6, filaments 2.0–4.1 mm long, smooth to verrucate, anthers 2.6–4.4(–5.1) × 0.3–0.4 mm, (creamy) white, blue- or dark purple (in white corollas too), apically dark purple-blue, pale purple and white at base, basal appendage 0.2–1.0(–1.5) mm, entire or bifurcate



to multifurcate, apical appendage 0.4–1.1 mm long, glabrous, acuminate. *Stylar apex* 1.4–2.8 mm, (creamy) white with pale lilac apex or base, pink, or pale purple, branches 1.1–2.5 mm long (= 3/5–1 of stylar apex), sweeping hairs 0–0.8 mm below the branches. *Achene* 5.0–8.0 × 1.7–3.5 mm, obovate (index 2.0–2.9), often rugose, with 2–5 longitudinal ridges, pale to chestnut brown, unicoloured or with (inconspicuous) dark brown dots, at apex with inconspicuous marginal ridge, apical plate truncate.

Distribution – Europe eastwards to Ukraine, and except North of 65° latitude, Madeira, Africa (Morocco, Algeria, Egypt), Asia (Turkey, Syria, Iraq, Iran). See note 15.

Introduced and naturalized in many parts of both North and South America (Fernald, 1950; Stevens, 1961; Craighead et al., 1963). Canada (British Columbia, Ontario, Québec). USA (Oregon, North Dakota, Kansas, Ohio, New York, Massachusetts, New Jersey, Washington, North Carolina). Brazil (Santa Catarina, Parana). Argentina (Corrientes).

Habitat & Ecology – Neglected places in or near industrial or other human settlements, sides of roads etc., along streams and ditches, forest edges and clearings. On nitrate-rich, damp, calcareous or siliceous, argillaceous or siltish sand, clay, loam, or alluvial soil, in shadow or exposed to the sun. Alt.: 0–1500 m. Flowering from June to September; frequented by bumblebees and butterflies.

Taxonomy – 1. *Arctium minus* differs from *A. nemorosum* in the narrower middle involucre bracts, and the usually smaller capitules. Also, in *A. minus* the capitules may be sessile or long pedunculate at the terminal parts of the synflorescence, and the corolla may be glabrous or hairy, and longer or shorter than the involucre, whereas in *A. nemorosum* the capitules are sessile at the terminal parts of the synflorescence, and the corolla is glabrous and shorter than the involucre (see also Chapter 11, Fig. 11.3).

2. The differences between *A. minus* and *A. atlanticum* include the relatively narrow involucre bracts (*A. atlanticum*: index less than 7), the relatively long apical part of the middle involucre bracts (up to 1/2 in *A. atlanticum*), and the indument and relative length of the corolla (always glabrous and longer than the involucre in *A. atlanticum*; see Chapter 11, Fig. 11.2).

3. To establish whether a specimen belongs to *A. minus* or to *A. lappa* the petiole of the basal leaves has to be examined. In *A. minus* it is, at least at the base, hollow; in *A. lappa* it is solid. Also, the synflorescence of *A. minus* is racemose to subcorymbose, and (sub-)corymbose in *A. lappa*. Finally, the capitules of *A. lappa* (wider than 3.0 cm) are usually larger than those of *A. minus*, which rarely reach 3.2 cm diameter.

4. From *A. tomentosum* the species differs in the shape of the inner involucre bracts, which are constricted above the middle, and widened below the apex in *A. tomentosum* and gradually narrowing from the middle to the apex in *A. minus*. *Arctium tomentosum*, contrary to *A. minus*, has a corymbose synflorescence.

5. Arènes (1950) treated *Lappa major* Gaertn. “Spielart” a *racemosa* G. Mey. as a synonym of *A. nemorosum*. I consider it as a synonym for *A. minus*, because the type (Smith (1804), English Botany, table 1228) shows a specimen in which the corollas

clearly exceed the involucre. I never observed this character state in *A. nemorosum*, in which species the corolla is always 1–6 mm shorter than the involucre.

Nomenclature & Synonymy – 6. Babington (1865) interpreted *A. intermedium* not in the sense of Lange (1851), which is *A. nemorosum*. In the synonymy of *A. intermedium* he placed *A. pubens* Bab., a species he had described himself in 1856, and which is placed in the synonymy of *A. minus* in this revision (see note 10). *Arctium intermedium* sensu Babington (1865) is therefore not identical with *A. nemorosum* Lej., but refers to *A. minus*.

7. Evans (1913) felt that *Arctium pubens* Bab. is synonymous with *A. intermedium* Lange and *Lappa vulgaris* Hill. As *vulgaris* is then the oldest available epitheton he made the combination *Arctium vulgare*. However, *A. intermedium* Lange is a synonym for *A. nemorosum* Lej. (see note 4 under that species), and *L. vulgaris* Hill is identical with *A. lappa* L. The description of Evans (1913) mentions the same character states as Babington (1856) did in his description of *A. pubens*. I therefore treat *A. vulgare* A.H. Evans as a synonym of *A. pubens* (= *A. minus*).

8. From his treatment of *Arctium* in the Flora of Turkey it is not clear what Kupicha (in Davis, 1975: 356) meant with *A. minus* subsp. *pubens*. His description covers both *A. minus* and *A. lappa*. He cited several specimens of which I have seen only two (*Davis 20765*; *Tchihatcheff 950*). In my opinion they both belong to *A. lappa*, although the synflorescence is subcorymbose in its terminal parts. I prefer to cite this reference for *A. minus* because I have seen only a selection of the cited material.

Variation – 9. *Arctium minus* is a very variable species. The synflorescence is usually racemose, but less often it may be subcorymbose. The capitules range from 1.5–3.2 cm wide, they may be glabrous to densely arachnoid hairy, and sessile to long pedunculate. The corolla may be glabrous to densely glandular hairy, and is longer to shorter than the involucre. This excessive variability resulted in the description of many taxa.

10. *Arctium pubens* was described by Babington (1856) as a species with stalked, hemispherical heads which are open and much ‘webbed’ in fruit, and with the inner involucre bracts equalling the corollas in length. In a number of recent floras *A. minus* is regarded as a complex species, which might be divided into two entities, “*minus* s.s.” and “*pubens*”. The latter entity would be characterized by its larger and more hairy capitules. However, different authors give different distinctions between the two supposed entities. In Figure 11.4 the whole variation for these characters in the material which I examined is shown. It is obvious that not the slightest discontinuity is present regarding the size of the capitules. In fact, I did not find any other character state having a correlation with smaller or larger capitules. Thus, the size of the capitules is not a discriminating character within this variable species. Also, with other characters and character combinations I did not encounter discontinuities. Therefore, I treat *A. pubens* as a synonym of *A. minus*.

11. *Arctium chaberti* would be characterized by a glandular hairy corolla, and should have a range limited to Southern Europe. I did not find any other character state having a correlation with a glabrous or a glandular hairy corolla (see Fig. 11.5). It serves no purpose to distinguish *A. chaberti* as a separate taxon. Arènes (in sched.) considered the specimens from Northwestern Europe as hybrids between *A. minus*

(or *A. pubens*) and *A. tomentosum* (e.g. *Oudemans s.n.*, 1863). However, I found that specimens of *A. minus* with a glandular hairy corolla are rather common throughout the range of the species, also in Western Europe. No further evidence supports the hybridogenal status of such specimens.

12. As usual in European botany, various extreme forms have been described on varietal or formal rank. A form with white leaves underneath was described by Christ (1885) as var. *alba*. The subvariety *album* of Senay (1936) and forma *pallidum* Farw. were used for plants with white flowers. Blytt (1906) described a forma *purpurea* for specimens with purple involucre bracts. This epitheton was also used by Moore & Frankton (1974) to describe the occurrence of deep purple corollas. On very dry, and exposed places, e.g. dunes, extremely compact forms occur frequently (*van Soest 2212*). Arènes (1950, 86, pl. 5, fig. b) described these compact forms as *A. minus* subsp. *eu-minus* var. *pycnanthum*. Monstruous forms with sharply dentate to lacinate leaves have been found (*de Jongh s.n.*, 07-1950; *van Ooststroom 15233*), and were described as *A. minus* f. *laciniatum* Clute (1909). The flowers of this form are said to be sterile. None of these forms merit recognition as infraspecific taxa at whatever rank.

Hybrids – 13. *Arctium pubens* is often regarded as a hybrid between *A. minus* and either *A. nemorosum* or *A. lappa* (e.g. Perring, 1976). According to Evans (1913), in many cases the postulated hybrids are specimens that have grown under poor conditions. He also stated that the capitules of herbarium specimens are often so much pressed that they look wider than they really are. I fully agree with him here, that hybrids are much rarer than is stated generally. However, I have seen hybrids of *A. minus* with *A. lappa*, *A. palladini*, and *A. tomentosum* (See descriptions of the hybrids H1, H3, and H4).

14. The anonymous collections nr. 2 and 3 (L) from the Netherlands, 'Kerkhof Jelsum/op Nuldenburg', were appointed by Arènes (1950) as syntypes of his newly described hybrid *A. xbatavum*. It would be a hybrid between *A. minus* and *A. pubens*. I included both specimens in *A. minus*, because in my opinion the supposed parent species are synonymous, and because the specimens agree with the above description of *A. minus*.

Notes – 15. Both *A. minus* and *A. atlanticum* reach the African continent, but Arènes (1950) mentioned only the latter. He identified *Cosson s.n.* (12-07-1861 from Algeria), although it has maturing achenes, as a juvenile state of *A. atlanticum*. This specimen has narrow middle involucre bracts, a glandular hairy corolla, and a shorter stylar apex than *A. atlanticum*, and in my opinion belongs therefore to *A. minus*. I have also seen specimens of *A. minus* from Morocco and Egypt. It is not known from the Caucasus region or Central Asia.

16. Hohenacker (in sched.) mentions that the root, or 'Radix Bardanae', is collected for pharmaceutical purposes. According to Feuilleaubeis (in sched.) the whole plant is mildly sudorific, diuretic, 'résolutive', and restorative. A photograph on a herbarium sheet (*LEPS 16706*) shows that *A. minus* was cultivated in Belgium in 1947. I do not know whether this was for pharmaceutical or agricultural use.

#### 4. *Arctium nemorosum* Lej. – Fig. 18.8, 9.

- Arctium nemorosum* Lej. in Courtois, Mag. Hort. (1833) 289; Lej. & Courtois, Comp. Fl. Belg. 3 (1836) 129; Bab., Ann. Mag. Nat. Hist., sér. 3, 15 (1865) 10; Bab., Man. Brit. Bot. ed. 6 (1867) 196; Nyman, Consp. 1 (1879) 402; Suppl. 2 (1889) 179; Weiss in Koch, Syn. Deutsch. Fl. ed. 3, 2 (1897) 1513; Teyber, Verh. Zool.-Bot. Ges. Wien 52 (1902) 590; Beger in Hegi, Ill. Fl. Mitteleur. 6, 2 (1928) 829; Fourn., Fl. Compl. Plaine Fr. (1928) 291; Briq. & Cavill. in Burnat, Fl. Alp. Marit. 7 (1931) 275; Senay, Bull. Soc. Bot. Fr. 83 (1936) 337; Máthé, Acta Geobot. Hung. 1 (1937) 232; Fernald, Gray's Man. Bot. (1950) 1537; Ross-Craig, Draw. Br. Pl. 17 (1962) pl. 3; Tscherneva in Komarov, Fl. URSS 27 (1962) 99, tab. 7, fig. 2, 3; Klokov, Fl. URSS 11 (1962) 438, fig. 82; Moore & Frankton, Canad. Dept. Agric. Monogr. 10 (1974) 17; Perring in Tutin et al., Fl. Eur. 4 (1976) 215. — *Lappa nemorosa* Körn. ex Griewank, Schr. phys.-ökon. Ges. Königsb. 5 (1864) 63; Körn., Arch. Ver. Naturg. Mecklenb. 23 (1870) 189; Lange, Haandb. Danske Fl. ed. 4 (1886) 357; Gremli, Excurs.-Fl. Schweiz. ed. 9 (1901) 240; A. Blytt, Haandb. Norg. Fl. (1906) 711. — *Arctium minus* (Hill) Bernh. subsp. *nemorosum* (Lej.) Syme, Engl. Bot. 5 (1866) 25, pl. 701; Arènes, Bull. Jard. Bot. Brux. 20 (1950) 96. — *Lappa glabra* Lam. var. *nemorosa* (Lej.) Crép., Man. Fl. Belgique ed. 2 (1866) 209. — *Lappa minor* Hill var. *nemorosa* (Lej.) Crép., Man. Fl. Belgique ed. 5 (1884) 259. — *Arctium minus* (Hill) Bernh. var. *nemorosum* (Lej.) Durand in De Wild. & Durand, Prodr. Fl. Belg. 3 (1899) 779. — *Arctium lappa* L. *δ nemorosum* (Lej.) Fiori in Fiori & Paol., Fl. Anal. Ital. 3 (1904) 317. — *Arctium majus* Bernh. subsp. *nemorosum* (Lej.) Rouy, Fl. Fr. 9 (1905) 95. — *Lappa nemorosa* Körn. 'var. *typica*' Erdner, Mitt. Bayer. Bot. Ges. 1, 31 (1904) 373; Erdner, Fl. Neuburg (1911) 490. — *Arctium minus* (Hill) Bernh. subsp. *nemorosum* (Lej.) Syme var. *eunemorosum* Arènes, Bull. Jard. Bot. Brux. 20 (1950) 96. — *Arctium nemorosum* Lej. subsp. *nemorosum* Rothm., Exkurs.fl. Deutschl. ed. 4 (1963) 331; Soó, Syn. Syst.-Geobot. Fl. Veg. Hung. 4 (1970) 123. — Type: *Lejeune s.n.*, s.d. (BRUX, holo, n.v., W!). — See note 3.
- Lappa macrosperma* Wallr., Linnæa 14 (1840) 639; Asch., Fl. Brandenb. (1864) 353. — *Lappa bardana* Moench *d macrosperma* (Wallr.) Čelak., Prodr. Fl. Böhm. (1871) 249. — *Arctium macrospermum* (Wallr.) Hayek, Sched. fl. stiriac. 13–14 (1908) 29; Dalla Torre & Sarnth., Farn- und Blütenpfl. Tirol 6, 3 (1912) 595. — Type: ?*Wallroth*, "in den Schlüchten der Gypsvorberge des südlichen Harzes stellenweise". (n.v.). — See note 6.
- Arctium lappa* *β majuscula* Hartm., Handb. Skand. Fl. ed. 4 (1843) 260. — *Lappa minor* Hill f. *majuscula* (Hartm.) A. Blytt, Haandb. Norg. Fl. (1906) 710. — Type: Schkuhr, Handb., tab. 227.
- Arctium intermedium* Lange, Haandb. Danske Fl. ed. 1 (1851) 463; Bab., Ann. Mag. Nat. Hist., sér. 2, 17 (1856) 374; [non Bab., Ann. Mag. Nat. Hist., sér. 3, 15 (1865) 9 (= *A. minus*)]; Druce, List Brit. Pl. ed. 1 (1908) 39. — *Lappa intermedia* (Lange) Rchb. f., Ic. Fl. Germ. 15 (1852–53) 54, tab. 81; Schur, Verh. Mitt. Siebenb. Ver. Naturw. 4, 6 (1853) 35; Boreau, Fl. Centre Fr. ed. 3, II (1857) 758; Lange in Liebm. & Lange, Fl. Dan. 15, (1866) tab. 2663 (text fasc. 45, p. 8); F.N. Williams, Prod. Fl. Brit. 2 (1901) 54. — *Arctium majus* Bernh. subsp. *intermedium* (Lange) Nyman, Consp. 1 (1879) 402. — *Lappa minor* Hill var. *intermedium* (Lange) Cariot & St.-Lag., Étude fl. ed. 8, 2 (1889) 440. — Type: *Lange s.n.*, "in sylvis Daniae" (W!). — See note 4 and 5.
- Lappa* × *maassii* Schultze, Mitt. Thüring. Bot. Ver. 2 (1884) 214. — *Arctium* × *maassii* (Schultze) Rouy, Fl. Fr. 9 (1905) 98. — Type: *Maass s.n.*, 08/1883 (P!). — See note on the nomenclature below. — See note 11.
- Lappa intermedia* (Lange) Rchb. f. var. *newbouldii* F.N. Williams, Prod. Fl. Brit. 2 (1901) 54. — *Arctium newbouldii* (F.N. Williams) Druce, List Brit. Pl. ed. 1 (1908) 39; Benn., Jour. Bot. (London) 37 (1899) 342. — Type: *W.W. Newbould s.n.*, 1862, Llanberis, Caernarvonshire, United Kingdom. (CGE, holo!). — See note 7.
- Arctium austriacum* Teyber, Verh. Zool.-Bot. Ges. Wien 52 (1902) 590. — *Arctium nemorosum* Lej. var. *austriacum* (Teyber) Beger in Hegi, Ill. Fl. Mitteleur. 6, 2 (1928) 831. — Type: ?*A. Teyber s.n.*, "ende Juli 1902. Mehreren Exemplaren in einer Au bei Baumgarten an der March, Niederösterreich". (n.v.). — See note 6.

- Arctium vulgare* A. H. Evans subvar. *pycnocephalum* A. H. Evans, Jour. Bot. (London) 51 (1913) 117 ('British nemorosum'). — *Arctium pubens* Bab. f. *pycnocephalum* (A. H. Evans) Senay, Bull. Soc. Bot. Fr. 83 (1936) 336. — Type: unknown.
- Arctium nemorosum* Lej. f. *ar(t)isticum* Rapaics, Erd. Kisérletek 18 (1916) 66 (in syn.: *A. pubens* Bab. and *A. austriacum* Teyber). n.v. — Type: *Rapaics s.n.*, 10/8/1916, "comit. Hajdu in silvaticis 'Nagyerdő' ad opp. Debrecen, solo arenoso". (W!, LE!).
- Arctium nemorosum* Lej. var. *microcephalum* Arènes, Cynar. Fr. (1942) 531; non Erdner. n.v.
- Arctium minus* (Hill) Bernh. subsp. *nemorosum* (Lej.) Syme var. *orientale* Arènes, Bull. Jard. Bot. Brux. 20 (1950) 105. — Type: *Mouterde s.n.*, s.d., "Liban, dans un boisement très humide à Haouch près de Zahlé" (n.v.). — See note 8.
- Arctium vulgare* auct. non. Hill (sub *Lappa*; = *A. lappa*), non A. H. Evans (= *A. minus*): Hultén, Vår Svenska Flora 19 (1958) 617; Hess & Landolt, Fl. Schweiz 3 (1972) 411.

Biennial. *Stem* 95–210 cm long. *Basal leaves*: petiole 30–47 cm long, at least at base hollow, glabrous to glandular-hairy; lamina 36–56 × 22–38 cm (index 1.4–1.8), base cordate, margin irregularly undulate, with sparse mucronate teeth, apex acute, with 1 mm long mucro, lower side sparsely arachnoid hairy, with minute glassy globules, greyish white, upper with some short uni- and multicellular hairs; *cauline leaves* as basal leaves but lamina cuneate at base. *Synflorescence* racemose, with many capitules, branches deflexed, arcuate, longest 35–120 cm long. *Capitules* at terminal part of branch in clusters of 2–5 or solitary, sessile, the lower solitary, up to 2.0(–9.5) cm pedunculate, with more than 40 flowers, 2.7–4.0 × 1.9–2.9 (1.2–1.9 × 1.8–2.3) cm, glabrous to densely arachnoid hairy. *Involucral bracts* in 9–14 rows, herbaceous, (dark to reddish) green, the upper part often tinged with red or purple; outer involucral bracts 6.8–9.4 × 1.2–2.6 mm, linear-triangular, patent or deflexed, somewhat villose, abaxially glabrous or with glandular hairs, margin with some eglandular hairs in the lower half; middle involucral bracts 10.0–17.2 × (1.6–)1.7–2.5 mm, linear-triangular (index 5.6–8.6(–9.7)), margin with (glandular) hairs, the upper 3/5–3/4 patent; inner involucral bracts 12.9–22.0 × 1.2–2.3 mm, linear-ovate (index 6.8–13.0), membranaceous, abaxially in the middle part with short hairs, margin with eglandular and, at least in the upper half of basal part, with glandular hairs, the upper part slightly recurved, apex acute, straight or hooked. Longest *receptacular scales* (5.4–)7.9–15.1 × 0.1–0.4 mm, glabrous, near apex dentate, acute, sometimes retuse. Longest *pappus hairs* 1.8–3.4 mm long, margin minutely dentate, acute. *Corolla* (8.5–)9.2–12.4 mm long, (red-)purple, glabrous, exceeded by involucral bracts by 1.2–6.0 mm, tube (3.9–)4.5–6.9 mm long, not or slightly widened at base, limb 4.3–5.7 mm long (= 2/5–1/2 of total length); lobes 5, sometimes 4, 6 or 7, longest lobe (1.5–)1.7–2.7 mm long (= 3/10–1/2 of limb). *Stamens* 5, sometimes 4, 6 or 7, filaments 2.4–3.8 mm long, smooth to somewhat verrucate, anthers (2.9–)3.4–5.4 × 0.3–0.5 mm wide, (grey- or blue-) purple, basal appendage 0.3–1.1 mm long, bifurcate to multifurcate, apical appendage 0.4–1.0 mm long, glabrous, acuminate. *Stylar apex* 1.9–3.0 mm, creamy white or pale pink, branches 1.4–2.6 mm long (= 3/5–1(–11/10) of stylar apex), sweeping hairs 0.1–0.8 mm below the branches to 0.2–0.5 mm above split branches. *Achene* 6.7–8.7 × 2.6–3.9 mm, obovate (index 1.9–3.1), with 4–5 inconspicuous longitudinal ridges, pale to chestnut brown, with (inconspicuous) dark brown dots, at apex with inconspicuous marginal ridge, apical plate truncate.

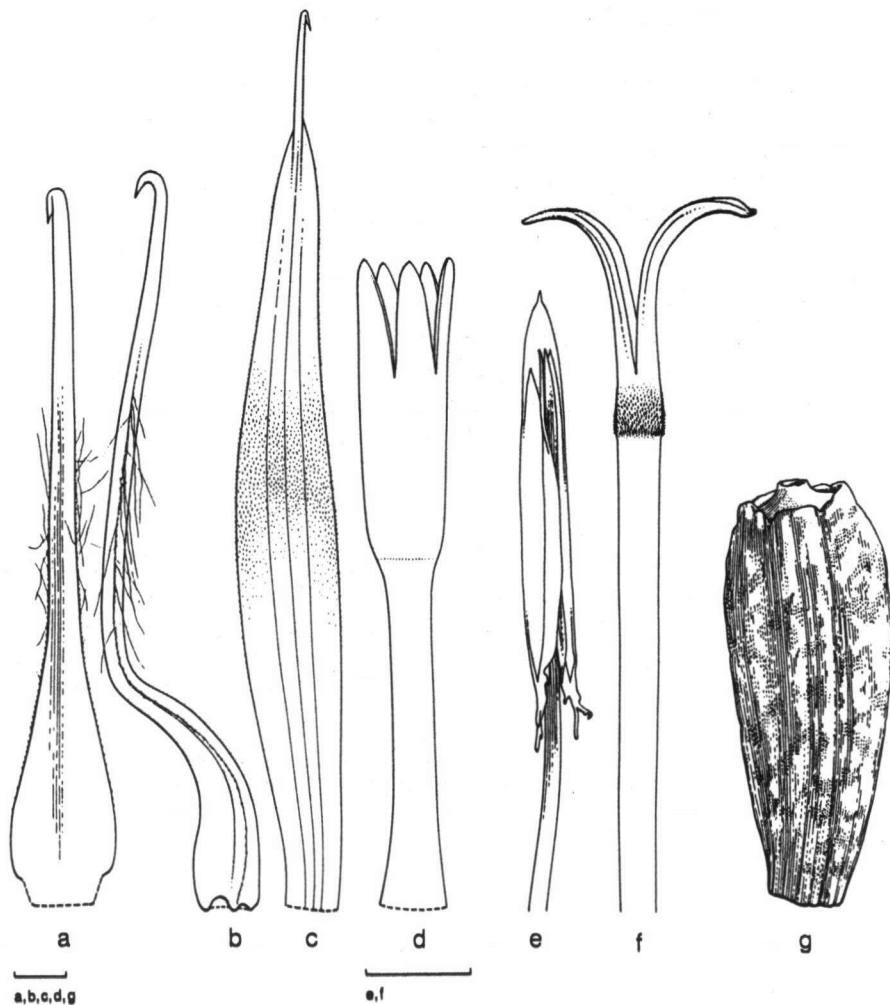


Fig. 18.8. *Arctium nemorosum* Lej. – a. Dorsal view of middle involucre bract; b. lateral view of middle involucre bract; c. dorsal view of inner involucre bract; d. corolla; e. anther with apical part of filament; f. apical part of style; g. achene (a–f: *Duistermaat 173*; g: *Duistermaat, Cortenraad & van der Meijden 70*). Bar indicates 1 mm.

Distribution – *Arctium nemorosum* is a mainly Central European species extending westwards to the United Kingdom, northwards to Southern Sweden, southwards to Southern Italy and Northern Greece (montane), and eastwards to Western Russia (Kaliningrad). The species has not been recorded from Spain or Portugal. It is very rare in areas with acid soils. *Arctium nemorosum* would be the most common taxon of the genus in the United Kingdom where it is absent from the SW.

Introduced – Recently introduced in the Netherlands (see note 13). Although Fernald (1950) mentioned that *A. nemorosum* is naturalized in the United States, I doubt that this species is introduced there. I have not seen material of this species from the American continent.



Fig. 18.9. Distribution map of two widespread species.  
 — *Arctium nemorosum* Lej. - - - *Arctium tomentosum* Mill.

**Habitat & Ecology** – Nearly always occurring in woodlands, in disturbed habitats, but sometimes also in shaded roadsides in villages. Mostly on calcareous soil (limestone, marl), rarely on siliceous soil (*Polatschek s.n.* 07/08-1981; *Fiori* 383, 384, 28-07-1904), usually in (half-)shadow. Alt.: 50–1400 m. Flowering from June to August, earlier than *A. minus*.

**Taxonomy** – 1. *Arctium nemorosum* differs from *A. minus* in the middle involucre bracts which are usually wider than 1.6 mm, and in the capitules which are often wider than 3 cm and (almost) sessile at the terminal parts of the synflorescence. The corolla of *A. nemorosum* is glabrous and never exceeds the involucre, whereas in *A. minus* the corolla may be hairy or glabrous and it may or may not exceed the involucre.

2. Both *A. nemorosum* and *A. atlanticum* have an entirely glabrous corolla. Differences with *A. atlanticum* include the larger, often sessile capitules, the upper, patent, part of the middle involucre bracts being more than 3/5 of the total length, and the corolla being exceeded by the involucre bracts. Differences with *A. lappa* include a strictly racemose synflorescence with in its terminal parts the capitules sessile, and

the hollow petiole of the basal leaves. In contrast to *A. nemorosum*, *A. tomentosum* is strictly corymbose, has inner involucre bracts which are constricted above the middle, and widened below the apex, and a glandular hairy corolla.

Nomenclature & Synonymy – 3. I have not seen the type specimen of *A. nemorosum* Lej. from Spa (Belgium), which is kept in the herbarium of Bruxelles (BRUX). However, photographs of this specimen on two different sheets (*Baenitz s.n.*, 1868; *Grantzow s.n.*) show an arched branch with a cluster of 3 capitules at the terminal part. The lower capitules are solitary, sessile or shortly pedunculate. A short branch and 3 capitules of the Bruxelles type specimen are stored in the herbarium of Vienna (W). Both the photographs and the Vienna material are in accordance with my description of *A. nemorosum*.

4. *Arctium intermedium* was described by Lange in 1851. His description is not very exact. He mentioned that the capitules are roundish, and that the plant is taller than the other W. European species. Liebmann & Lange (1866) published a plate of this taxon (sub *Lappa*), showing a plant with an arcuate synflorescence, and rather large and somewhat hairy capitules, which are sessile and in a cluster of two at the terminal part of the branch. Lower down the branch the capitules are longer pedunculate. The oldest herbarium collection identified as (*L.*) *intermedia* by Lange that I have seen dates from 07-1857 (*Lange s.n.*, in hb. Oudemans, L!). This specimen has large capitules which are sessile at the terminal part of branches. The involucre exceeds the corolla, and the middle involucre bracts are wider than 1.7 mm. Another collection of Lange (ex herbario Reichenbach fil.) of *A. intermedium* was annotated 'inflorescentia ab *A. majus*, statue elata forme calathium et ab *A. minor* differ, in sylvis Daniae'. It has only one capitule, which is 4.1 (1.9) cm wide, and the corolla is exceeded by involucre bracts. Both the plate and the herbarium specimens fall within the range of *A. nemorosum* Lej., and I therefore treat *A. intermedium* Lange as a synonym of this species.

5. Reichenbach (1853) described *L. intermedia*. He made no reference to the publication of Lange (1851), but Lange had sent material of this species to him. They undoubtedly wrote to each other about this taxon, and used the epitheton *intermedium* for it. I therefore treat them as homotypic synonyms. The description of Reichenbach is illustrated with a plate, which depicts a specimen with capitules almost as large as those of *A. lappa*. The capitules are sessile and clustered at the end of the branch. The corolla is exceeded by the involucre. Therefore I conclude that *L. intermedia* Rchb. f. is a synonym for *A. nemorosum* Lej.

6. I have not seen the type specimens of *L. macrosperma* Wallr. and *A. austriacum* Teyber. I do not know whether the respective authors kept any herbarium material of their described species. The remarks of Wallroth (1840) concerning *L. macrosperma* are rather vague, but his observation 'die sehr verlängerten, arm- und entfernt blüthigen Zweigen hängen während der Saamenreife ruthenförmig herab' points to *A. nemorosum*. Teyber (1902) described *A. austriacum* as a form of *A. nemorosum* with 2.5 cm wide capitules, whereas true *A. nemorosum* would have 4.0 cm wide capitules. However, I have found a whole range between the extreme values. I therefore synonymise both names with *A. nemorosum*.

7. *Lappa intermedia* Rchb. f. var. *newbouldii* is described by Williams (1901) from specimens collected by Newbould in the United Kingdom. The author stated



that the specimens do not agree with the concept of *A. nemorosum* as understood by "Continental authors". However, both the description and the material of Newbould in the herbarium of Cambridge (CGE) are in accordance with *A. nemorosum* in my revision. I thus treat the taxon *newbouldii* as a synonym of this species.

8. Arènes (1950) based his newly described *A. minus* subsp. *nemorosum* var. *orientale* on only one specimen. According to the original description, the differences with the type variety include longer pedunculate capitules, narrower patent part of the involucre bracts, relatively short corolla tube, anthers with shorter apical appendages, and bi- to multifurcate basal appendages. I have not seen the type, but it seems very likely that this variety has to be included in *A. nemorosum*.

Variation – 9. *Arctium nemorosum* is less variable than *A. minus*. The plants reach usually to a man's height, and have long, arcuated and deflexed branches, of which the terminal parts sometimes almost reach the ground. The glabrous to densely arachnoid hairy capitules are 2.7–4.0 cm wide, often sessile and in clusters of 2 or 3 at the end of the branches. The middle involucre bracts are at least (1.6–)1.7 mm wide at base. The corolla is glabrous, and is always exceeded by the involucre.

10. In literature achenes of 8–11 mm long are often mentioned for *A. nemorosum* (e.g. Gremli, 1901; Fiori & Paol., 1904). I have not seen any specimen with achenes longer than 8.7 mm.

Hybrids – 11. *Lappa* × *maassii* was described by Schultze (1884) as the hybrid between *L. macrosperma* (= *A. nemorosum*) and *L. minor* (= *A. minus*). The type specimen (*Maass s.n.*, 8-1883) was said to have grown among the parents in Thüringen. The capitules at the terminal part of the branch are sessile, and the involucre bracts are more than 1.7 mm wide. The identification of the specimen as *A. nemorosum* is unproblematical. Therefore, I regard this "hybrid" as a synonym of *A. nemorosum*.

12. I have not found hybrids including *A. nemorosum* as one of the parents under natural conditions. Moreover, I have never seen it growing together with any other species of *Arctium*. However, in the garden of De Wever, where *A. nemorosum* and *A. tomentosum* grew side by side, the hybrid between the two was formed 'spontaneously' every year according to the label on the herbarium specimen (*A. de Wever* in hb. *van Soest 2211*; L!). I confirm that this collection is the mentioned hybrid (see also H5).

Notes – 13. In the Netherlands *A. nemorosum* is not a native species. It is known from all surrounding countries, and is found only a few kilometers south of the Dutch border in Belgium (Kelmis). In The Netherlands a specimen of *A. nemorosum* was collected a century ago in Steenwijkerwold (*Unio s.n.*, 08-1892), and it grew several years in the garden of A. de Wever in S. Limburg. For several years now it has been growing in Montferland (*A. Hertog s.n.*, 13-08-1989) where it was probably introduced with forest litter from Germany. Although the specimen has middle involucre bracts of 1.6 mm wide, the capitules of the terminal part of the synflorescence are 3.5 cm wide and sessile, the branches are arcuate, and the glabrous corolla is exceeded by the involucre. I therefore include this specimen in *A. nemorosum*.

## 5. *Arctium palladini* (Marcow.) R.E. Fr. & E.S. Söderb. – Fig. 18.10, 11.

- Arctium palladini* (Marcow.) R.E. Fr. & E.S. Söderb., Delect. Spor. Sem. Hort. Bot. Berg. (1923); Grossh., Fl. Kavkaza 4 (1934) 164; Söderb., Svensk Bot. Tidskr. 42 (1948) 497; Tscherneva in Komarov, Fl. URSS 27 (1962) 103, tab. 7, fig. 4, 5, 6; Rech. f., Fl. Iran. 139a (1979) 106. — *Lappa palladini* Marcow., Acta Horti Bot. Univ. Jurjev. 1, 3 (1900) 147. — *Arctium tomentosum* Mill. subsp. *palladini* (Marcow.) Takht. in Takht. & Fed., Fl. Erevana (1972) 288. — Lectotype (assigned here): *Marcowicz s.n.*, ?1898, Ossetien, Czecznia and Imeretien (LE!). Syntypes (assigned by Rechinger, 1979): *Kolenati*, Szovitz (LE!). — See notes 1 and 2.
- Lappa tomentosa* (Mill.) Lam. var. *glabra* Körn., Schr. phys.-ökon. Ges. Königsb. 5 (1864) 67. — *Arctium tomentosum* Mill. var. *glabrum* (Körn.) Arènes, Bull. Jard. Bot. Brux. 20 (1950) 118, p.p.; Kupicha in Davis, Fl. Turkey 5 (1975) 354. — Syntypes: *Szovitz s.n.*, “prov. Aderbeidzan, an Zäunen bei Khoi”; *Kolenati s.n.*, “von Lars bis Kasbeck” (LE!). — See note 1.
- Arctium radula* Juz. & Serg., Not. Syst. Herb. Inst. Bot. Acad. Sci. URSS 18 (1957) 300; Tscherneva in Komarov, Fl. URSS 27 (1962) 106. — Type: *Choziatowsky s.n.*, 28/7/1897, “in viciniis lac. Sevan, Tshingyly” (LE!). — See note 3.

[Biennial]. *Stem* 35–120 cm long. *Basal leaves*: petiole 14–50 cm long, solid at least at base, glabrous to glandular-hairy; lamina 27–42 × 19–31 cm (index 1.2–1.4), base cordate, margin irregularly shallowly undulate, with sparse mucronate teeth, apex somewhat emarginate or obtuse, mucronate, lower side arachnoid, with minute glassy globules, silvery white, upper side sparsely hairy, with (sometimes very few) short uni- and multicellular hairs; *cauline leaves* like basal leaves but lamina at base cuneate. *Synflorescence* corymbose, with many capitules, (branches unknown). *Capitules* solitary, 0.5–5 cm pedunculate, with more than 40 flowers, 2.1–3.0 × 1.7–2.2 (1.1–1.4 × 1.4–1.6) cm, glabrous to sparsely hairy. *Involucral bracts* in 9–15 rows, herbaceous, green; outer involucral bracts 5.2–8.0 × 1.2–1.4 mm, linear-triangular, patent or deflexed, margin with some glandular hairs in the lower half; middle involucral bracts 8.4–11.6 × 0.8–1.2 mm, linear-triangular (index 9.7–10.5), the upper 3/5 patent; inner involucral bracts 12.4–16.6 × 1.1–1.3 mm, linear-obovate (index 9.5–13.8), constricted above the middle, and widened below the apex, membranaceous, the upper part slightly recurved, apex acuminate to truncate, straight. Longest *receptacular scales* 4.0–7.2 × 0.1–0.4 mm, glabrous, acute. Longest *pappus hairs* 1.8–2.2 mm long, margin minutely dentate, acute. *Corolla* 10.8–14.7 mm long, lilac, (pink-)purple, exceeding the involucral bracts by 0.4–4.0 mm, tube 5.2–6.9 mm long, (slightly) widened at base, glabrous, limb 5.6–7.9 mm long (= 1/2–3/5 of total length), with glandular hairs at the lobes and at the base of the limb, longest lobe 3.0–4.2 mm long (= 2/5–3/5 of limb). *Stamens*: filaments 3.5 mm long, (somewhat) verrucate or in the upper half papillose, anthers 6.3–7.1 × 0.4–0.5 mm, (colour unknown), basal appendage 0.7–1.6 mm long, entire or bifurcate, apical appendage 0.9–1.3 mm long, glabrous, acuminate. *Stylar apex* 3.3–4.9 mm, (colour unknown), branches 2.2–3.8 mm long (= 3/5–1/1 of stylar apex), sweeping hairs 0.1–1.5 mm below the branches. *Achene* 7.2 × 2.8 mm, obovate (index 2.6), with 4–5 inconspicuous longitudinal ridges, (colour unknown), at apex with inconspicuous marginal ridge, apical plate truncate.

Distribution – Russia (Osetinskaya, Dagestania). Turkey (Gümüsane, Erzurum, Kurdistan, Van, Hakkâri). Gruzija. Armenia. Azerbaijan. Iran (Azerbaijan, Mazenderan).

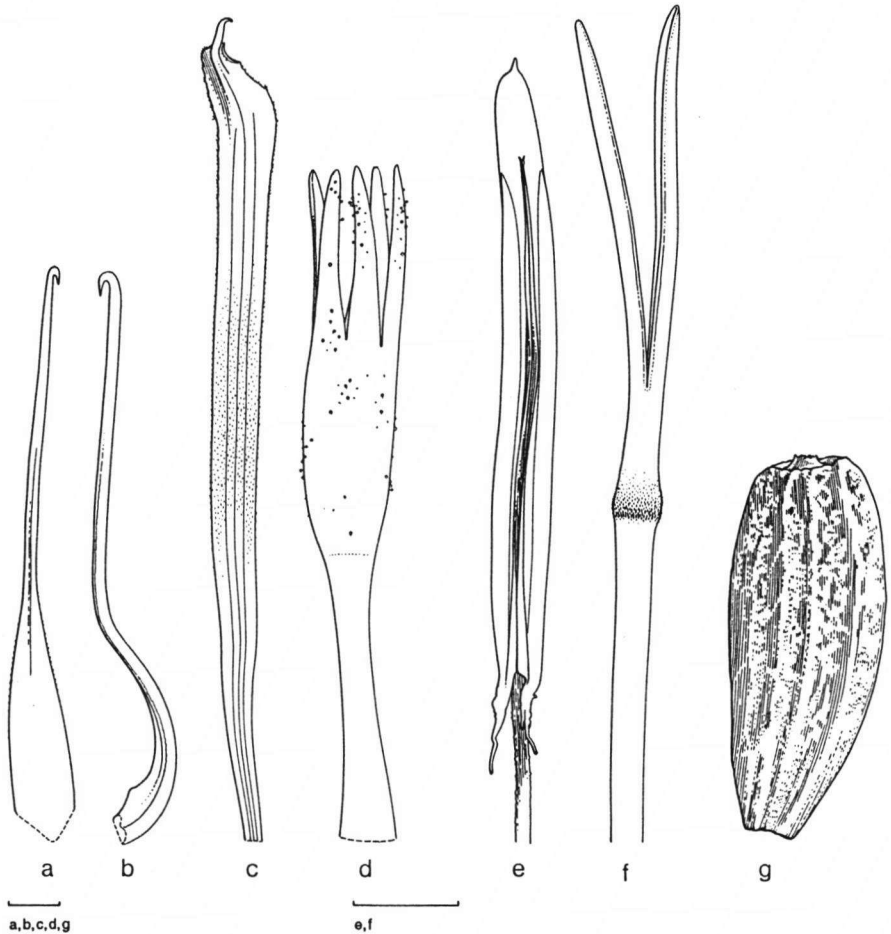


Fig. 18.10. *Arctium palladini* (Marcow.) R.E. Fr. & E.S. Söderb. – a. Dorsal view of middle involucre bract; b. lateral view of middle involucre bract; c. dorsal view of inner involucre bract; d. corolla; e. anther with apical part of filament; f. apical part of style; g. achene (a–f: *de Wilde s.n.*, 1989; g: *Ruprecht 43*). Bar indicates 1 mm.

**Habitat & Ecology** – Waste places and fallow land, gardens, road sides, along streams, in forests. Stony mountain slopes, shady. Alt.: 900–2300 m. Flowering in August.

**Taxonomy & Variation** – 1. *Arctium palladini* much resembles *A. tomentosum*. Both have inner involucre bracts which are constricted above the middle and widened below the apex, a corymbose synflorescence, and a glandular hairy limb of the corolla. The shape of the inner involucre bracts is within the genus unique to these two species.

Several authors (Fries 1828, Körnicke 1864, Arènes 1950, Kupicha in Davis 1975) felt that all specimens of this “*tomentosum*” group which have a glabrous involucre

together constitute a separate taxon, referred to as *A. tomentosum* forma or variety *glabrum*, or *A. palladini* (auct. non Grossh). It is recorded from scattered localities throughout Europe and Western Asia as well as South Central Asia. I have established that the character state 'involucre glabrous' does not coincide with any other character. Therefore, in this revision the indumentum of the involucre is not used as a distinguishing character between *A. palladini* and *A. tomentosum*. Fig. 18.11 shows that, based on floral characters, two groups can be discerned which merit recognition at the species level. The group of specimens with the longer anthers and longer corolla lobes includes the type specimen of *A. palladini* and the syntypes of *A. tomentosum* var. *glabrum*. *Arctium palladini* thus including the var. *glabrum*, has always (almost) glabrous capitules. The other group of specimens, *A. tomentosum*, has capitules which usually are (densely) arachnoid hairy, but specimens with a glabrous involucre also occur. In the present delimitation the two species occur allopatric. According to Tscherneva in Komarov (1962) both species grow in the Caucasus, but I have not seen any material of *A. tomentosum* from that region.

Nomenclature & Synonymy – 2. Rechinger (1979) assigned two specimens, *Kolenati s. n.* and *Szovitz s. n.*, as neotypes to *A. palladini*. However, these specimens are already the syntypes of *Lappa tomentosa* var. *glabra*. The type specimen of the basionym *L. palladini* Marcow. is present in the Leningrad herbarium (*Marcowicz s. n.*, ?1898, "Ossetien, Czecznia und Imeretien", LE!), and I assigned it as the lectotype.

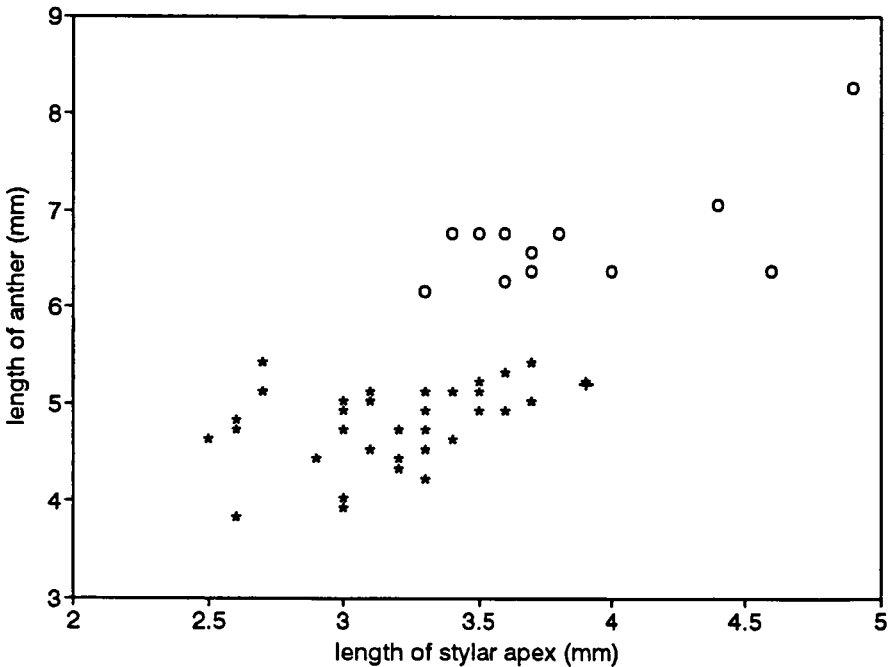


Fig. 18.11. Scatterdiagram showing the variability of *Arctium palladini* and *A. tomentosum*. o: corolla lobe 3.0–4.2 mm long; \*: corolla lobe 2.0–2.9 mm long.

3. According to the original description of Juzepczuk & Sergievskaja (1957) *A. radula* differs from *A. tomentosum* and *A. palladini* in the greater roughness ('asperitas') of stem and branches, in the thicker leaves with more rigid marginal spines, in the involucre which is always glabrous, and in differently shaped inner involucre bracts. Moreover, the general shape of the synflorescence would be different from *A. palladini*, and the capitules would have up to 1.4 cm long peduncles. My analysis of material that was cited by the authors (*Heydeman & Isaev s.n.*, 23-07-1931, *Choziatowski s.n.*, 1897) shows a slightly longer stylar apex and anthers than in other specimens of *A. palladini*. However, the capitules are 2–4 cm pedunculate, and the inner involucre bracts are similarly shaped as in *A. palladini*. I have not seen leaves with marginal spines, and also otherwise the specimens agree with my description of *A. palladini*. I therefore treat *A. radula* as a synonym of *A. palladini*.

Hybrids – 4. Kupicha (1975) regards *Rechinger 37696* from Turkey as a possible hybrid between "*A. platylepis*" (= *A. lappa*) and "*A. tomentosum* var. *glabrum*" (= *A. palladini*). However, the corolla is exceeding the involucre bracts, its limb is hairy and has long lobes (3.2 mm), the stylar apex is long, and its inner involucre bracts are similarly shaped as in *A. palladini*. The characters of *Rechinger 37696* fall within the range of the variability of *A. palladini*. The specimen does not show any typical characters of *A. lappa*, and I conclude that it is not a hybrid, but a "normal" specimen of *A. palladini*.

5. I have recognized a single specimen as a hybrid between *A. palladini* and *A. minus* (see description of hybrid H3). This hybrid is new to literature. I do not know of any other hybrids with *A. palladini*.

Note – 6. *Arctium palladini* is probably a biennial (Rechinger, 1979). I did not see herbarium material including the base of the stem, and could therefore not ascertain the life span of this species. One herbarium label indicated the presence of a 'tap root'.

## 6. *Arctium tomentosum* Mill. – Fig. 18.9, 11, 12.

*Arctium tomentosum* Mill., Gard. Dict. ed. 8, 3 (1768) tab. 159; Bernh., Syst. Verz. Erfurt (1800) 154; Pers., Syn. Pl. 2 (1807) 383; Schkur, Handb. 3 (1808) 49; Courtois, Mag. Hortic. (1833) 290; Hartm., Handb. Skand. Fl. ed. 4 (1843) 260; Lange, Haandb. Danske Fl. (1851) 463; Bab., Ann. Mag. Nat. Hist., sér. 2, 17 (1856) 371; De Wild. & Durand, Prodr. Fl. Belg. 3 (1899) 778; Weiss in Koch, Syn. Deutsch. Fl. ed. 3, 2 (1897) 1511; Bubani, Fl. Pyren. 2 (1899) 125 (sub *Arcion*); Rouy, Fl. Fr. 9 (1905) 96; Fernald & Wiegand, Rhodora 12 (1910) 44; Schinz & R. Keller, Fl. Schweiz ed. 3, 2 (1914) 348; Beger in Hegi, Ill. Fl. Mitteleur. 6, 2 (1928) 832; Fourn., Fl. Compl. Plaine Fr. (1928) 290; Briq. & Cavill. in Burnat, Fl. Alp. Marit. 7 (1931) 267; Grossh., Fl. Kavkaza 4 (1934) 164; Senay, Bull. Soc. Bot. Fr. 83 (1936) 331; Arènes, Bull. Jard. Bot. Brux. 20 (1950) 113, pl. 7, fig. a, b, c; Fernald, Gray's Man. Bot. (1950) 1537; Tscherneva in Komarov, Fl. URSS 27 (1962) 104, tab. 7, fig. 7; Klovov, Fl. URSS 11 (1962) 433; Rothm., Exkurs.fl. Deutschl. ed. 4 (1963) 331; Soó, Syn. Syst.-Geobot. Fl. Veg. Hung. 4 (1970) 121; Hess & Landolt, Fl. Schweiz 3 (1972) 410; Perring in Tutin et al., Fl. Eur. 4 (1976) 215; Hultén, Vår Svenska Fl. 19 (1958) 617. — *Arctium lappa* L. *β* L., Sp. Pl. ed. 1 (1753) 816. — *Lappa arctium* Hill, Veg. Syst. 4 (1762) 28, pl. 25, fig. 2a, b. — *Lappa tomentosa* (Mill.) Lam., Fl. Fr. ed. 1, 2 (1778) 37; Tabl. Encycl. Méth. Bot. 1, 2 (1785) 337; All., Auct. Fl. Pedem. 1 (1785) 144; Lam. & DC., Fl. Fr. ed. 3, 4 (1805) 77; DC., Bot. Gall. 1 (1828) 282; G. Mey., Chlor. Hanov. (1836) 447; Steud., Nomencl. Bot. ed. 2, 3 (1840) 9; Lange in Liebm., Fl. Dan. 14 (1844) tab. 2423 (text fasc. 41, p. 7); Rchb. f.,

- Ic. Fl. Germ. 15 (1853) 54; Mathieu, Fl. Gén. Belg. 1 (1853) 294; Schur in Fuss, Verh. Mitt. Siebenb. Ver. Naturw. 10 (1859) 79; Hartsen in F.W. van Eeden, Fl. Bat. 13 (1868) pl. 1016; Crép., Man. Fl. Belgique ed. 2 (1866) 209; Blytt, Norg. Fl. ed. 1, 2 (1874) 609; Boiss., Fl. Or. 3 (1875) 457; Crép., Man. Fl. Belgique ed. 5 (1884) 260; Lange, Haandb. Danske Fl. ed. 4 (1886) 356; Cariot & St.-Lag., Étude fl. ed. 8, 2 (1889) 440; Gremlí, Excurs.-Fl. Schweiz. ed. 9 (1901) 240; Vuyck, Prodr. Fl. Bat. ed. 2, 1, 2 (1902) 900; A. Blytt, Haandb. Norg. Fl. (1906) 711; Erdner, Fl. Neuburg (1911) 490. — *Arctium bardana* Willd., Sp. Pl. 3 (1803) 1632; Smith, Engl. Bot. 19 (1804) pl. 2478; Schweigg. & Körte, Fl. Erlang. (1811) 75; Lej. & Courtois, Comp. Fl. Belg. 3 (1836) 128. — *Lappa communis* Coss. & Germ. var. *tomentosa* (Mill.) Coss. & Germ., Fl. Paris, ed. 1 (1845) 389. — *Lappa vulgaris* Hill var. *tomentosa* (Mill.) Neilr., Fl. Wien (1846) 267. — *Lappa bardana* Moench var. *tomentosa* (Mill.) Čelak., Prodr. Fl. Böhm. (1871) 249. — *Arctium lappa* L. var. *tomentosum* (Mill.) Fiori in Fiori & Paol., Fl. Anal. It. 3 (1904) 317. — Type: Herb. Linnaeus 964.1 (LINN, n.v.; microfiche L!).
- Lappa tomentosa* (Mill.) Lam. var. *glaberrima* Fr., Nov. Fl. Suec. ed. 2 (1828) 264; Erdner, Fl. Neuburg (1911) 490. — *Arctium tomentosum* Mill. f. *glaberrimum* (Fr.) Beger in Hegi, Ill. Fl. Mitteleur. 6, 2 (1928) 833. — Type: unknown.
- Lappa tomentosa* (Mill.) Lam. var. *oligocephala* Lange in Liebm., Fl. Dan. 14 (1844) tab. 2423 (fig. A, B); Lange, Haandb. Danske Fl. ed. 4 (1866) 357. — Type: Plate of Lange in Liebm.
- Lappa tomentosa* (Mill.) Lam. var. *denudata* Lange, Haandb. Danske Fl., ed. 3 (1864) 288; ed. 4 (1886) 356. — *Arctium tomentosum* Mill. var. *denudatum* (Lange) Beger in Hegi, Ill. Fl. Mitteleur. 6, 2 (1928) 833. — Type: unknown.
- Lappa tomentosa* (Mill.) Lam. var. *calva* Fischer in Marsson, Fl. Neu-Vorpomm. (1869) 263. — *Arctium tomentosum* Mill. var. *calvum* (Fischer) Weiss in Koch, Syn. Deutsch. Fl. ed. 3, 2 (1897) 1511; Fourn., Fl. Compl. Plaine Fr. (1928) 290. — Type: *Fischer s.n.*, 21/9/1924, Pommern, Stralsund (LE, holotype!).
- Lappa tomentosa* (Mill.) Lam. var. *umbrosa* Erdner, Fl. Neuburg (1911) 490. — Type: unknown.
- Arctium tomentosum* Mill. f. *glabrescens* Thell. in Schinz & R. Keller, Fl. Schweiz ed. 3, 2 (1914) 348. — Type: unknown.
- Lappa crispa* J. Wolff ex Borza, Bul. Grád. Bot. Muz. Bot. Univ. Cluj 1 (1921) 40, nom. nud. — *Arctium crispum* Cretz., Acta Fauna Flora Univ., Bucuresti, ser. 2 Bot., 1 (1933) 7. — Type: *J. Wolff s.n.*, 07/1904, Romania, Turda Distr., "prope urben Turda, Sant-Mihai". (LE!, W!). — See note 2.
- Arctium tomentosum* Mill. subvar. *album* P. Fourn., Fl. Compl. Plaine Fr. (1928) 290; Senay, Bull. Soc. Bot. Fr. 83 (1936) 331. — Type: unknown.
- Arctium tomentosum* Mill. f. *albiflora* Arènes, Bull. Jard. Bot. Brux. 20 (1950) 116. — Type: *Baenitz, Herb. Eur. 25* (Koenigsberg), sub *A. tomentosum* var. *alba* (P!).
- Arctium leptophyllum* Klokov, Fl. URSS 11 (1962) 434, 559. — Type: *Klokov s.n.*, 16/7/1959, RSS Ucr., "Tauria praemontana, prope pag. Krasnolissja, in silva". (n.v.). — See note 3.

Biennial. *Stem* 30–250 cm long. *Basal leaves*: petiole 10–15 cm long, hollow or solid, glandular-hairy; lamina 29–39 × 16–28 cm (index 1.3–1.8), margin irregularly undulate, with mucronate teeth, apex acute to obtuse, mucronate, lower side arachnoid, with minute glassy globules, silvery white, upper side sparsely hairy, with short uni- and multicellular hairs; *cauline leaves* like basal leaves but lamina at base cuneate, lower side sparsely arachnoid hairy, margin almost entire. *Synflorescence* corymbose, with many capitules, branches patent, the longest 25–100 cm long. *Capitules* solitary, 1.5–12.0 cm pedunculate, with more than 40 flowers, 2.0–3.8 × 1.4–2.6 (1.2–2.0 × 1.2–1.9) cm, (densely) arachnoid hairy or sometimes almost glabrous. *Involucral bracts* in 10–14 rows, herbaceous, the upper part often tinged with red; outer involucral bracts 3.6–12.0 × 0.8–2.8 mm, linear-triangular, sometimes leaflike, patent or deflexed, margin with some glandular hairs in the lower half; middle involucral bracts 8.0–13.3 × 1.0–1.8 mm, linear-triangular (index 6.8–10.4), margin in the

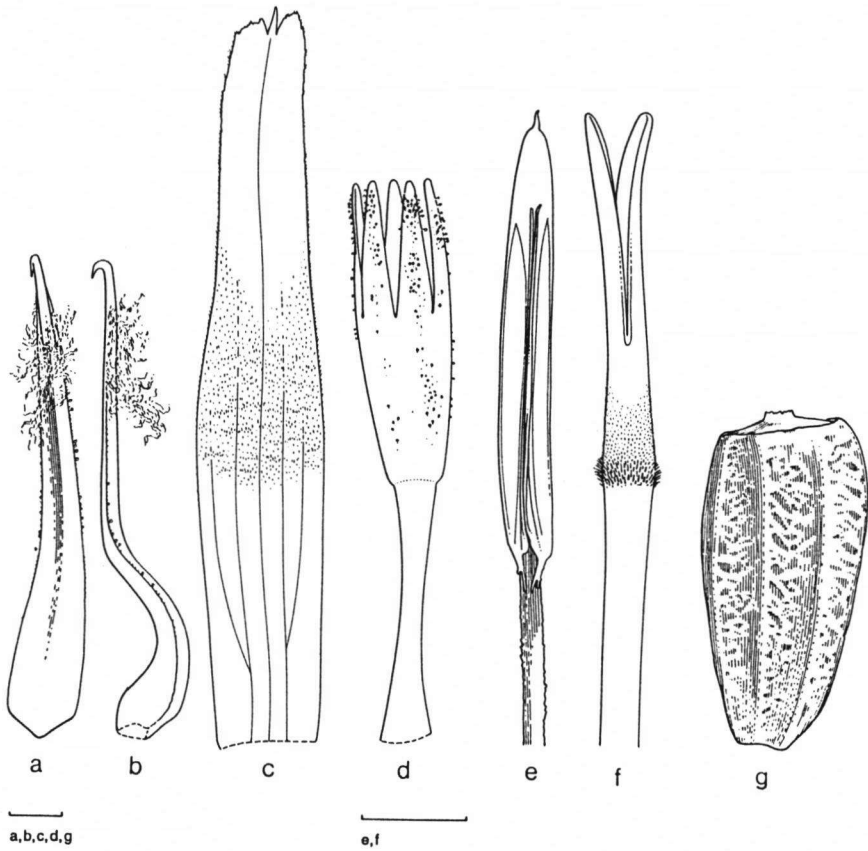


Fig. 18.12. *Arctium tomentosum* Mill. – a. Dorsal view of middle involucre bract; b. lateral view of middle involucre bract; c. dorsal view of inner involucre bract; d. corolla; e. anther with apical part of filament; f. apical part of style; g. achene (a–f: *Duistermaat & Vermeulen 147*; g: *Duistermaat & Nieuwenhuijs 83*). Bar indicates 1 mm.

lower half membranaceous, with many glandular hairs, the upper 3/5–7/10 patent; inner involucre bracts 11.0–16.0 × 1.2–3.2 mm, linear-obovate (index 4.4–10.0), (slightly) constricted above the middle, and widened below the apex, membranaceous, glabrous or abaxially in the middle part with short hairs, margin from 2 mm above base with rather many acute teeth, the upper part slightly recurved, dark red or green-purple near apex, apex truncate, rarely acuminate, straight or slightly curved. Longest *receptacular scales* 4.9–10.0 × 0.1–0.6 mm wide, apex glabrous or verrucate, sometimes dentate or split, acute. Longest *pappus hairs* 1.4–3.0 mm long, margin minutely dentate, acute. *Corolla* 10.3–13.6 mm long, white, (wine-)red, or (pale) red-purplish, exceeding the involucre bracts by (0–)0.4–3.4 mm, tube 4.7–7.0 mm long, not to (slightly) widened at base, glabrous or near apex with some

glandular hairs, limb 5.0–6.6 mm long (= 2/5–3/5 of total length), abruptly or gradually widening towards apex, with glandular hairs at least at the lobes and at the base of the limb, rarely only at the lobes or at the base of the limb, longest lobe 2.0–3.0 mm long (= 2/5–1/2 of limb). *Stamens*: filaments 2.4–4.0 mm long, verrucate, anthers 3.8–5.4 × 0.3–0.5 mm, (dark) blue(-purple), basal appendage 0.4–1.1 mm long, entire or bifurcate, apical appendage 0.8–1.2 mm long, glabrous, (slightly) acuminate. *Stylar apex* 2.5–3.9 mm, pink, branches 1.6–3.3 mm long (= 3/5–9/10 of stylar apex), sweeping hairs 0.1–1.5 mm below the branches. *Achene* 6.2–8.0 × 2.7–3.6 mm, obovate (index 1.8–2.5), rugose, with 4–5 longitudinal ridges, chestnut brown, unicoloured or with (inconspicuous) dark brown dots, at apex with inconspicuous marginal ridge, apical plate truncate.

Distribution – Europe northwards to 65° latitude, southwards to Northern Italy, casually in Western Europe (see note 10), eastwards to Western Asia (Kirgizia).

Introduced – United States of America (Fernald, 1950).

Habitat & Ecology – Neglected places in or near industrial or human settlements, sides of roads etc., along streams, forest edges. On sunny places, on siliceous or calcareous sand or clay. Alt.: 0–1500 m. Flowering from June to August.

Taxonomy – 1. *Arctium tomentosum* much resembles *A. palladini*. The shape of the inner involucre bracts, which are constricted above the middle and widened below the apex, distinguishes both species from all the other species of *Arctium*. Furthermore, both species have a corymbose synflorescence, and a glandular hairy limb of the corolla. The limb of the corolla is very often slightly to densely covered with glandular hairs, only incidentally the corolla is glabrous (*Jansen e.a. 1363-1*). *Arctium tomentosum* differs from *A. palladini* in having shorter anthers and shorter corolla lobes (see Fig. 18.11).

Nomenclature & Synonymy – 2. *Lappa crispa* was first published as a nomen nudum by Borza (1921), then described in *Arctium* by Cretziou (1933). The type specimen, *Wolff s.n.*, has very short corolla lobes (1.0–1.5 mm long), only 9 rows of involucre bracts, and rather small capitules (1.8 cm [1.1 cm excluding spines] wide). The name refers to the pinnatipartite leaves. I do not maintain this aberrant form of *A. tomentosum* as a separate taxon; it occurs so rarely that I have not included its characters in the above description.

3. *Arctium leptophyllum* is described by Klokov (1962) as different from *A. tomentosum* by the tender, sparsely arachnoid, green leaves, and by the smooth and unicoloured achenes. I have not seen the type specimen (*Klokov s.n.*, 16-07-1959) which is probably kept in the herbarium of Kiev. I have observed that the amount of indumentum on the leaves and the colouring of the achenes is variable within *A. tomentosum*, as it is in most species of *Arctium*. Therefore, I treat *A. leptophyllum* as a synonym of *A. tomentosum*.

Variation – 4. The petiole of the basal (rosette) leaves is often solid, but may also be hollow (e.g. *Duistermaat 190*). This character is valuable for the recognition of *A. lappa* (solid petiole), *A. nemorosum* and *A. minus* (both hollow petiole), but it is not diagnostic for *A. tomentosum*.

5. The capitules of *A. tomentosum* are usually (densely) covered with an arachnoid hairy indumentum, but specimens with almost glabrous capitules were described



by Erdner (1911) as var. *umbrosa*. Specimens with glabrous capitules are sometimes treated as forma or var. *glabrum*. For a discussion of *A. tomentosum* var. *f. glabrum* in relation to *A. palladini* the reader is referred to note 1 of *A. palladini*.

Hybrids – 6. Hybrids with *A. tomentosum* are probably less common than is mentioned in literature (see Chapter 12). Most records are due to a too narrow species concept. Specimens with almost glabrous or rather small capitules in a corymbose synflorescence were identified as hybrids of *A. tomentosum* with *A. lappa* (e.g. *van Soest* 2208, L!), or with *A. minus* (e.g. *Anon.* (Russian) 317, LE!). If such specimens are regarded as hybrids, *A. lappa*, *A. minus* and *A. tomentosum* should be synonymized. However, I include specimens with almost glabrous or rather small capitules, and otherwise not different from *A. tomentosum*, in *A. tomentosum*. This increases the variability within *A. tomentosum*, but it decreases the number of intermediate (= hybrid) specimens dramatically.

7. Specimens from Northwestern Europe with a racemose synflorescence and a glandular hairy corolla were identified as hybrids between *A. minus* and *A. tomentosum* (e.g. *Oudemans s.n.*, 1863). For argumentation of the inclusion of those specimens in *A. minus* the reader is referred to note 11 of *A. minus*.

8. I have confirmed the hybrids of *A. tomentosum* with *A. lappa*, *A. nemorosum* (only in a garden), and *A. minus*. See also the notes below the descriptions of the hybrids H2, H4, and H5.

Notes – 9. *Arctium tomentosum* is a European species, reaching as far east as Eastern Kirgizia. According to Tscherneva (1962) this species is also found in the Caucasus, but I have not seen any material of *A. tomentosum* from that region.

In literature there is some doubt about its occurrence in the United Kingdom, but I rely on the opinion of Stace (1991) that it is a rare casual (*Hodgson s.n.*; 18-07-1959 (BM!); *Brenan & Sandwith s.n.*, 2-08-1934 (L!); *Sherrin* 43230 (BM!); *Thomas Morong s.n.*, 16-07-1885 (BM!)). In the western parts of The Netherlands, Belgium and France it is very rare. I have not seen specimens from Spain and Portugal from this species.

10. Hohenacker (in sched.) mentions that from this species the root or 'Radix Bardanae' is collected for pharmaceutical purposes.

### Section *Lappaceum* (Bunge) Duist., *comb. nov.*

*Arctium* section *Lappaceum* (Bunge) Duist. — *Cousinia* section *Lappacea* Bunge, Mém. Acad. Sci. Pétersb., ser. 7, 9, 2 (1865) 9, p.p.; Tscherneva, Not. Syst. Inst. Bot. Acad. Sci. Uzb. 17 (1962) 80; in Komarov, Fl. URSS 27 (1962) 180. — *Cousinia* section *Uncinata* C. Winkl., Acta Horti Petrop. 12, 7 (1892) 186, p.p. — *Cousinia* section *Xerarctium* Juz., Trudy Tadshikskoj Bazy Akad. Nauk URSS 8 (1940) 510, in adnot. nomen, n.v. — Type species: *Arctium lappaceum* (Schrenk) Kuntze.

Perennial. *Leaves* shallowly lobed, unarmed or spiny dentate. *Capitules* with up to 10 flowers, sessile to shortly pedunculate, solitary. *Involucral bracts* coriaceous, caudate. (*Corolla* imperfectly known). *Stamens*: apical appendage of anthers glabrous. *Stylar branches* up to 3/5 of the total length of the stylar apex. *Achene* with (incon

spicuous) longitudinal ridges, with a slight depression around the scars of the pappus, apical plate truncate.

Including *A. lappaceum*.

## 7. *Arctium lappaceum* (Schrenk) Kuntze – Fig. 18.13, 14.

*Arctium lappaceum* (Schrenk) Kuntze, Revis. Gen. 1 (1891) 308; Tscherneva in Komarov, Fl. URSS 27 (1962) 180 (in syn.). — *Cousinia lappacea* Schrenk, Enum. pl. nov. Schrenk 1 (1841) 42; Ledeb., Fl. Ross. 2, 2 (1845) 679; Bunge, Mém. Acad. Sci. Pétersb., ser. 7, 9, 2 (1865) 10; C. Winkl., Acta Horti Petrop. 12, 7 (1892) 187; 14 (1898) 191; Tscherneva in Komarov, Fl. URSS 27 (1962) 180, 182; Bot. Zhurn. 64, 12 (1979) 1739; 73, 6 (1988) 870; Nov. Syst. Pl. Vasc. 25 (1988) 146. — Type: *Schrenk s.n.*, “hab. in Sibiriae altaicae deserto soongoro-kirghisico ad radicem m. Alatau et Karatau” (LE, holol, P!).

Perennial. *Stem* 85–100 cm long. *Basal leaves* sessile, lamina 20–25 × 4–5 cm (index 5.0–5.5), attenuate, (otherwise unknown); lower *cauline leaves* sessile, semi-amplexicaul, lamina at base cuneate, margin shallowly lobed, with mucronate teeth, lower side arachnoid hairy, without minute glassy globules, upper side glabrous, apex acute, sometimes pungent; higher cauline leaves (in the synflorescence) similar, but smaller and spiny-dentate. *Synflorescence* racemose, with many capitules, (branches unknown). *Capitules* more or less solitary, sessile to 0.4 cm pedunculate, with less than 10 flowers, 0.9–1.1 × 1.3–1.7 (0.6–0.7 × 1.3–1.7) cm, glabrous. *Involucral bracts* in 8 or 9 rows, coriaceous; outer involucral bracts 5.1–5.2 × 2.6 mm, linear-triangular, caudate, patent, glabrous, margin with some glandular hairs in the lower half; middle involucral bracts 8.8–9.4 × 4.0 mm, linear-triangular (index 2.2–2.4), caudate, margin in the middle third with glandular hairs, 1/4–3/10 patent; inner involucral bracts 10.2–13.0 × 2.1–2.8 mm, linear-obovate (index 3.6–6.2), caudate, papery, the upper part slightly recurved, apex hooked. Longest *receptacular scales* 5.5–9.3 × 0.2 mm, glabrous, acute. Longest *pappus hairs* 3.7–5.7 mm long, minutely dentate, acute. *Corolla* purple, limb 7.4 mm long, gradually widening, with many glandular hairs, longest lobe 3.0 mm long (= 2/5 of limb), (otherwise unknown). *Stamens*: filaments smooth, (otherwise unknown), anthers 7.0–7.2 × 0.7 mm, basal appendage 1.2 mm long, multi-furcate, apical appendage 1.3 mm long, glabrous, acuminate, (otherwise unknown). *Stylar apex* 2.3–2.5 mm, (colour unknown), branches 1.1–1.2 mm long (= 1/2 of stylar apex), sweeping hairs 1.2–1.3 mm below the branches. *Achene* 5.1–5.7 × 3.2–3.7 mm, obovate (index 1.5–1.6), dark brown, with several longitudinal (inconspicuous) ridges, at apex with a slight depression around the scars of the pappus, apical plate truncate.

Distribution – Kirgizia (Alayskiy Khr., Tyan Shan). Kazakhstan. Tadzhikistan (Pamir).

Habitat & Ecology – In mountains. Alt.: no data available.

Note – *Arctium lappaceum* is incompletely known. Many specimens in the herbarium have suffered severely from voracious insect larvae. Flowers, including style and stamens, and achenes are very often destroyed. Only in juvenile specimens, collected in May and June, the floral structures could be studied. But in these specimens the corolla tube and filaments are still very short. However, *A. lappaceum* can easily



Fig. 18.13. *Arctium lappaceum* (Schrenk) Kuntze – a. Base of the stem and top of the root (a, b: Lipski 766). Bar indicates 5 cm.

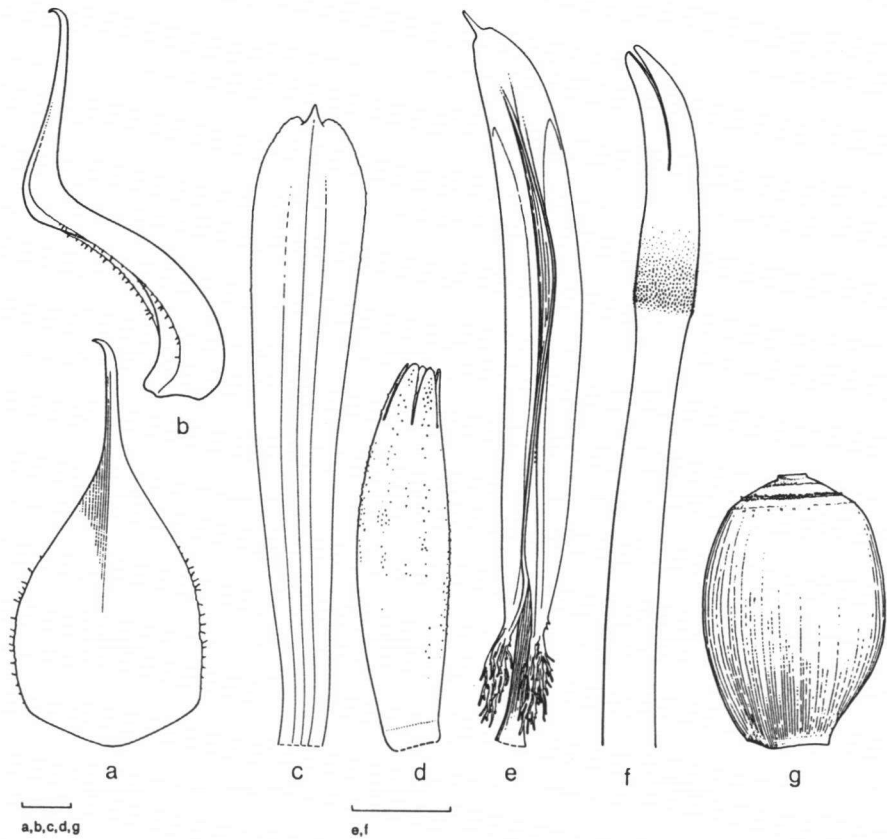


Fig. 18.14. *Arctium lappaceum* (Schrenk) Kuntze – a. Dorsal view of middle involucre bract; b. lateral view of middle involucre bract; c. dorsal view of inner involucre bract; d. juvenile corolla; e. anther with apical part of filament from juvenile flower; f. apical part of style from juvenile flower; g. achene (a–c: Schrenk s.n., 1842; d–f: Lipski 766; g: Schrenk 245). Bar indicates 1 mm.

be recognized by its sessile, lanceolate basal leaves, its coriaceous, and caudate involucre bracts, and its up to 1.1 cm wide capitules (including the patent apical part of the involucre bracts!).

**Section *Nanarctium* (Tscherneva) Duist., comb. nov.**

*Arctium* section *Nanarctium* (Tscherneva) Duist. — *Cousinia* section *Nanarctium* Juz., Trudy Tadshikskoj Bazy Akad. Nauk URSS 8 (1940) 510, in adnot. nomen, n.v.; Tscherneva, Not. Syst. Inst. Bot. Acad. Sci. Uzb. 17 (1962) 80; in Komarov, Fl. URSS 27 (1962) 176. — *Cousinia* section *Lappacea* Bunge, Mém. Acad. Sci. Pétersb., ser. 7, 9, 2 (1865) 9, p.p. — *Cousinia* section *Uncinatae* C. Winkl., Acta Horti Petrop. 12, 7 (1892) 186, p.p.; Bornm., Beih. Bot. Centralbl. 34 (1917) 134. — Type species: *Arctium arctioides* (Schrenk) Kuntze.

Perennial. *Cauline leaves* pinnatifid, armed. *Capitules* with more than 40 flowers, pedunculate, solitary. *Involucral bracts* herbaceous. *Corolla*: limb up to 3/5 of the total length of the corolla. *Stamens*: apical appendage of anther glabrous. *Stylar branches* more than 3/5 of the total length of the stylar apex. *Achene* rugose, with longitudinal ridges, marginal ridge conspicuous, 0.3–0.4 mm high, dentate, apical plate truncate. Including *A. arctioides*.

## 8. *Arctium arctioides* (Schrenk) Kuntze – Fig. 18.15, 16.

*Arctium arctioides* (Schrenk) Kuntze, Revis. Gen. 1 (1891) 307; Tscherneva in Komarov, Fl. URSS 27 (1962) 177 (in syn.). — *Cousinia arctioides* Schrenk, Bull. Phys.-Math. Acad. (Pétersb.) 2 (1844) 115; Ledeb., Fl. Ross. 2, 2 (1845) 679; Bunge, Mém. Acad. Sci. Pétersb., ser. 7, 9, 2 (1865) 10; C. Winkl., Acta Horti Petrop. 12, 7 (1892) 187; 14 (1898) 191; Bornm., Beih. Bot. Centralbl. 34 (1917) 134; Tscherneva in Komarov, Fl. URSS 27 (1962) 177; Tscherneva, Bot. Zhurn. 73, 6 (1988) 870; Nov. Syst. Pl. Vasc. 25 (1988) 147. — Type: *Schrenk s.n.*, Sibiria altaica, in deserto soongoro-kirghisico pr. Saryssu (LE, holol, P!).

Perennial. *Stem* 17–40(–70) cm long. *Basal leaves*: (petiole unknown); lamina 8.5 × 2.5 cm (index 3.4), base cuneate, margin lobed, with mucronate teeth, (apex unknown), lower side sparsely arachnoid, with many yellow minute glassy globules, greyish white, upper side sparsely hairy, with short uni- and multicellular hairs; lower *cauline leaves* like basal leaves but lamina decurrent, margin pinnatifid, spiny dentate, upper cauline leaves similar but sessile, semi-amplexicaul, at base with 1–3 pairs of sharp, up to 6 mm long spines. *Synflorescence* (sub-)corymbose, with 6–8 capitules, branches patent, up to 6–12 cm long. *Capitules* solitary, 1.5–7.0 cm pedunculate, with more than 40 flowers, 1.8–2.4 × 1.6–2.0 (1.1–1.5 × 1.2–1.6) cm, glabrous. *Involucral bracts* in 12–15 rows, herbaceous, (colour unknown); outer involucral bracts 3.0–4.0 × 1.2 mm, linear-triangular, deflexed, margin with some glandular hairs; middle involucral bracts 6.4–8.2 × 0.9–1.0 mm, linear-triangular (index 7.1–8.2), margin with glandular hairs, the upper 3/5 patent; inner involucral bracts 11.1–12.6 × 0.8 mm, linear-triangular (index 13.9–15.8), membranaceous, glabrous, the upper part slightly recurved, apex acute, straight or hooked. Longest *receptacular scales* 7.0–7.4 × 0.1–0.2 mm, glabrous, entire, acute. Longest *pappus hairs* 3.2–5.3 mm long, margin minutely dentate, acute. *Corolla* 8.2–11.4 mm long, [colour: white, pale yellow, or pale purple] exceeding the involucral bracts by 0.9–4.0 mm, tube 3.0–5.2 mm long, not widened at base, glabrous, limb 5.2–7.1 mm long (= 1/2–3/5 of total length), gradually widening, with many glandular hairs, longest lobe 1.2–1.7 mm long (= 1/5–3/10 of limb). *Stamens*: filaments 2–4 mm long, smooth, anthers 4.6–5.4 × 0.3–0.4 mm, (colour unknown), basal appendage 0.3–0.9 mm long, entire to multi-furcate, apical appendage 0.9–1.2 mm long, glabrous, retuse to acuminate. *Stylar apex* 2.1–3.1 mm, (colour unknown), branches 1.6–2.4 mm long (= 7/10–9/10 of stylar apex), sweeping hairs 0.3–1.0 mm below the branches. *Achene* 5.8–6.2 × 1.4–1.8 mm, oblong-cylindrical (index 3.4–4.1), rugose, with 4–5 longitudinal ridges, brown, with (inconspicuous) dark brown dots, at apex with conspicuous marginal ridge, apical plate truncate.

Distribution – Kazakhstan (Turgayskaya Oblast, Tselinograd, Dzhezhkhang).



Fig. 18.15. *Arctium arctioides* (Schrenk) Kuntze – Flowering plant and top of the root (*Ledebour 181*). Bar indicates 5 cm.

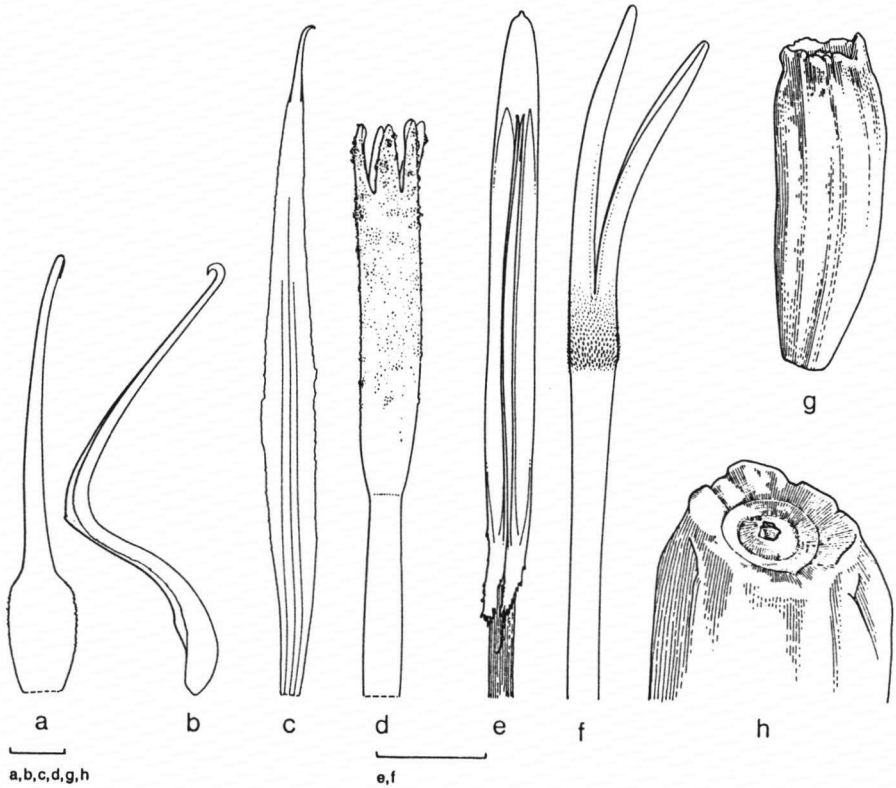


Fig. 18.16. *Arctium arctioides* (Schrenk) Kuntze – a. Dorsal view of middle involucre bract; b. lateral view of middle involucre bract; c. dorsal view of inner involucre bract; d. corolla; e. anther with apical part of filament; f. apical part of style; g. achene; h. apical view of achene (a–h: *Krascheninnikov 5240*). Bar indicates 1 mm.

**Habitat & Ecology** – River banks. Alt.: no data available. Flowering in June.

**Taxonomy** – 1. *Arctium arctioides* is a perennial species with a rather short stem. In the herbarium I have not seen specimens with a stem exceeding 40 cm, but according to Tscherneva (1962) the stem reaches up to 70 cm. It is the only armed species of the genus, the upper cauline leaves at base having 1–3 pairs of sharp, up to 6 mm long spines. The achenes are the most slender found within the genus.

**Variation** – 2. Field notes on the colour of the flowers are lacking. Bunge (1865) claims that 'flores pallide purpurascetes fere albidi', and Bornmüller (1917) states that the species has 'gelbblühenden Köpfe'. According to Tscherneva (1962) *Cousinia* section *Nanarctium* Juz. ex Tscherneva, in which *A. arctioides* is included, has white or pale yellow flowers.

## Section *Pseudarctium* (Juz.) Duist., *comb. nov.*

*Arctium* section *Pseudarctium* (Juz.) Duist. — *Cousinia* section *Pseudarctium* Juz., Trudy Tadshikskoj Bazy Akad. Nauk URSS 8 (1940) 512, 545, n.v.; Tscherneva, Not. Syst. Inst. Bot. Acad. Sci. Uzb. 17 (1962) 80; in Komarov, Fl. URSS 27 (1962) 177; Rech. f., Fl. Iran. 90 (1972) 203. — *Cousinia* section *Lappacea* Bunge, Mém. Acad. Sci. Pétersb., ser. 7, 9, 2 (1865) 9, p.p.; Boiss., Fl. Or. 3 (1875) 462. — *Cousinia* section *Uncinatae* C. Winkl., Acta Horti Petrop. 12, 7 (1892) 186, p.p.; Bornm., Beih. Bot. Centralbl. 34 (1917) 134. — Lectotype species (probably assigned by Tscherneva, 1962): *Arctium umbrosum* (Bunge) Kuntze.

Perennial. *Leaves* irregularly undulate to pinnatipartite, unarmed. *Capitules* with up to 25 flowers, sessile or up to 1.5 cm pedunculate, usually in clusters. *Involucral bracts* herbaceous. *Corolla*: limb more than 3/5 of the total length of the corolla. *Stamens*: apical appendage of anther at dorsal side with slender hairs (rarely glabrous in *A. umbrosum*). *Stylar branches* up to 3/5 of the total length of the stylar apex. *Achene* smooth, without marginal ridge, apical plate flat or somewhat truncate.

Including *A. amplissimum*, *A. pseudarctium*, and *A. umbrosum*.

### 9. *Arctium amplissimum* (Boiss.) Kuntze – Fig. 18.17.

*Arctium amplissimum* (Boiss.) Kuntze, Revis. Gen. 1 (1891) 307. — *Lappa amplissima* Boiss., Diagn. Pl. Orient. Nov. 6 (1845) 108–109; Kotschy, Reise in die cilicischen Taurus (1858) 412; Körn., Schr. phys.-ökon. Ges. Königsb. 5 (1864) 67; Benth. & Hook., Gen. Pl. 2 (1873) 467. — *Cousinia amplissima* (Boiss.) Boiss., Fl. Or. 3 (1875) 463; C. Winkl., Acta Horti Petrop. 12, 7 (1892) 188; 14 (1898) 191; Bornm., Beih. Bot. Centralbl. 34 (1917) 136; Rech. f., Fl. Iran. 90 (1972) 205; Fl. Iran. 139a (1979) 132. — Type: *Kotschy 735, 27/7/1842*, “hab. prope pagum Dusekurd ad radices montis Kuh-Daëna in Persia australis” (BM!, G (holo), K, LE!, P!, W!).

*Cousinia schiraziaca* Stapf ex Parsa, Kew Bull. (1948) 207. — Holotype: *Stapf 2862, 16/6/1885*, “Iran, near Shiraz” (n.v.). — See note 3.

Perennial. *Stem* 60–120 cm long. *Basal leaves*: petiole 38–40 cm long, solid, glabrous to glandular-hairy; lamina 37–42 × 23–32 cm (index 1.2–1.8), base cordate, margin irregularly undulate to pinnatilobed, lobes up to 1.5–5 cm long, 2–7 cm wide, with sparse mucronate teeth, apex acute, lower side (sparsely) arachnoid hairy, without minute glassy globules, greyish, upper side glabrous; *cauline leaves* like basal leaves but petiolate to sessile, lamina at base cordate to cuneate, upper side slightly hairy, with uni- and multicellular hairs. *Synflorescence* racemose, with many capitules, (branches unknown). *Capitules* at the terminal part of branches in rather loose to dense clusters of 3–10, lower heads often solitary, up to 0.5 cm pedunculate, with 9–11 flowers (less in capitules lower in the synflorescence), 1.1–1.8 × 1.2–1.7 (0.6–1.0 × 1.1–1.5) cm, glabrous. *Involucral bracts* in 7–9 rows, herbaceous; outer involucral bracts 3.4–5.5 × 0.7–1.4 mm, linear-triangular, patent, aculeate, margin with glandular hairs in the lower half; middle involucral bracts 7.2–8.6 × 1.3–1.6 mm, linear-triangular (index 4.8–6.1), aculeate, margin with glandular hairs, the upper 2/5–3/5 patent; inner involucral bracts 9.4–10.0 × 0.6–1.2 mm, linear-obovate (index 11.2–15.7), membranaceous, dorsal side aculeate in upper half, margin in the upper half serrate, apex acuminate, straight. Longest *receptacular scales* 6.8–7.0 × 0.1–0.2 mm, glabrous or scabrid near apex, entire, acute. Longest *pappus hairs* 2.0–2.5 mm long,



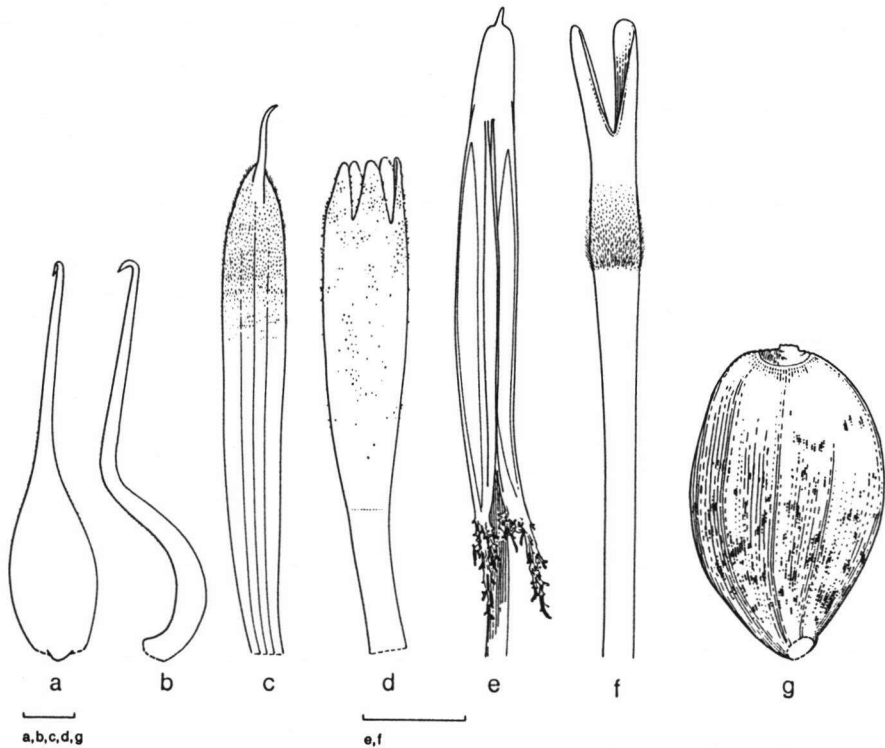


Fig. 18.17. *Arctium amplissimum* (Boiss.) Kuntze – a. Dorsal view of middle involucre bract; b. lateral view of middle involucre bract; c. dorsal view of inner involucre bract; d. corolla; e. anther with apical part of filament; f. apical part of style; g. achene (a–c, g: Kotschy 735; d–f: J. & A. Bornmüller 7377). Bar indicates 1 mm.

margin minutely dentate, acute. *Corolla* 7.2–10.0 mm long, white, pink or rose-red, rarely yellow, exceeding the involucre bracts by 6–8 mm, tube 1.5–3.6 mm long, not widened at base, glabrous, limb 5.5–7.0 mm long ( $= 3/5$ – $4/5$  of total length), gradually widening, with glandular hairs in the upper half or only at the lobes, longest lobe 1.1–1.5 mm long ( $= 1/5$ – $1/4$  of limb). *Stamens*: filament 2.8 mm long, smooth, anthers 4.6–6.4  $\times$  0.5–0.6 mm, pink-purple, basal appendage 0.6–1.5 mm long, multi-furcate, apical appendage 1.1–1.9 mm long, dorsally with slender hairs, acuminate. *Stylar apex* 1.3–2.4 mm, (colour unknown), branches 0.6–1.1 mm long ( $= 3/10$ – $1/2$  of stylar apex), sweeping hairs 0.6–1.4 mm below the branches. *Achene* 5.1–6.1  $\times$  2.9–3.7 mm, obovoid (index 1.5–1.9), smooth, (pale) brown, with dark brown dots, apex without a marginal ridge, apical plate slightly truncate, with 5 elliptic spots.

Distribution – S. & W. Iran (Azarbaijan, Mazandaran, Tehran, Lorestan, Bakhtiari, Boyer Ahmadi, Fars).

Habitat & Ecology – River valleys, seepage areas, gardens. On moist and shaded places, on calcareous substrate. Alt.: 1000–2400 m. Flowering in June and July.

Taxonomy – 1. *Arctium amplissimum* differs from *A. umbrosum* by the absence of large, sessile glands on the middle involucre bracts, the longer lamina of the basal leaves (18–28 cm long in *A. umbrosum*), the shorter receptacular scales (up to 8.0–10.3 mm long), and the shorter pappus (up to 3.5–4.0 mm long). The number of capitules in one cluster has been used by Boissier (1875) to differentiate between *A. umbrosum* (2–3) and *A. amplissimum* (5–10). Generally this is true, but sometimes the clusters in *A. amplissimum* are very loose. Winkler (1892) thought that the length of the radical leaves could serve as the differentiating character: in *A. umbrosum* 15–20 cm long, in *A. amplissimum* longer than 30 cm. Bornmüller (1917) mentioned a considerable overlap, but I have not found any overlap in this character.

2. The differences with *A. pseudarctium* include the diameter of the capitules (*A. pseudarctium* wider than 2 cm [1 cm excluding spines]), the number of flowers per capitule (15–25), the length of the achenes (6.7–7.4 mm), the length of the corolla lobes ( $\geq 1.6$  mm), and the length of the stylar apex ( $\geq 2.2$  mm).

Nomenclature & Synonymy – 3. I have not seen the type specimen of *C. schiraziaca* Stapf ex Parsa. According to the description (Parsa, 1948) it differs from *A. amplissimum* in having firmer cauline leaves which are cuneate at base, and sinuate-dentate (rather than lobate-dentate). However, these states do not deviate from the above description of *A. amplissimum*, and I therefore regard *C. schiraziaca* as a synonym of *A. amplissimum*.

Variation – 4 Several authors mentioned that *A. amplissimum* has (4–)6–9 flowers per capitule, whereas I have always found 9–11 flowers per capitule in the terminal part of the synflorescence. Capitules lower in the synflorescence are often smaller, and have less flowers. I did not include them in the above description.

5. A specimen with yellow flowers (Bornmüller 7378) has been described as var. *chrysea* Bornm. Although I have not seen this specimen I included the presence of yellow corollas in the description.

Hybrids – 6. I have not seen hybrid specimens including *A. amplissimum* as one of the parents.

Notes – 7. A record from Afghanistan (Franchet 661) belongs to *A. pseudarctium* (see note 4 below that species).

8. A specimen collected by Zerny 'gepflanzt im botanischen Garten in Wien' was identified as *Cousinia uncinata* Reg. (= *A. umbrosum*). Large sessile glands on the involucre bracts are, however, lacking. The specimen is intermediate between *A. amplissimum* and *A. pseudarctium*. It has the size of the capitules of the first, the long corolla lobes and stylar apex of *A. pseudarctium*. This cultivated specimen is the only intermediate specimen I found between the two species. Because of its unusual provenance I prefer not to use it as an argument for treating the two species as synonyms, or to treat it as a hybrid between the two species.

## 10. *Arctium pseudarctium* (Bornm.) Duist., *comb. nov.* – Fig. 18.18, 19, 20.

*Cousinia pseudarctium* Bornm., Beih. Bot. Centralbl. 34 (1917) 135; Juz., Acta Inst. Bot. Acad. Sci. URSS, ser. 1, 3 (1937) 296; Tscherneva in Komarov, Fl. URSS 27 (1962) 179; Rech. f., Fl. Iran. 90 (1972) 205; Fl. Iranica 139a (1979) 132, tab. 124; Tscherneva, Bot. Zhurn. 64, 12

(1979) 1738; Bot. Zhurn. 73, 6 (1988) 870; Nov. Syst. Pl. Vasc. 25 (1988) 147. — Lectotype (assigned here): *Bornmüller 562*, Prov. Samarkand (Pamiro-Alai), "in ditione fluvii Jagnob, abunde ad pagum Warsout, alt. 2400 m" (LE, holo!, W!). Syntypes: *Bornmüller 564, 614, B. Fedtschenko 340a*. (LE!, W!).

*Cousinia pseudarctium* Bornm. var. *leiocephala* Bornm., Beih. Bot. Centralbl. 34 (1917) 136; Tscherneva in Komarov, Fl. URSS 27 (1962) 179 (in syn.). — Syntypes: *B. Fedtschenko 340b, Bornmüller 613, 28/7/1913*, Prov. Samarkand, Pamiro-Alai, "in vallis fluvii Jagnob regionibus superioribus inter Piskan et Nowobad"; *Michelson 2111, 10/6/1913*, prov. Samarkand ad Chasr-Sultan. (LE?, WU?, n.v.). — See note 5.

*Cousinia spuria* Juz., Acta Inst. Bot. Acad. Sci. URSS, ser. 1, 3 (1937) 296; Tscherneva in Komarov, Fl. URSS 27 (1962) 179 (in syn.). — Type: *Juzepczuk 1212, 7/8/1930*, "jugum Alaicum, pag. Taldyk." (n.v.). — See note 3.

*Cousinia amplissima* auct. non (Boiss.) Boiss.: Franchet, Ann. Sci. Nat., sér. 6, Bot. 16 (1883) 314; Bornm., Beih. Bot. Centralbl. 34 (1917) 137 (in syn.); Tscherneva in Komarov, Fl. URSS 27 (1962) 179 (in syn.). — See note 4.

[Perennial]. *Stem* 86–180 cm long. *Basal leaves*: petiole 34 cm long, solid, glabrous to (glandular-)hairy; lamina 46 × 26 cm (index 1.8), base cordate, margin irregularly undulate, with up to 1.5 mm long mucronate teeth, apex acute or obtuse, lower side greyish arachnoid, with a few minute glassy globules, greyish white, upper side almost glabrous, with some short uni- and multicellular hairs; *cauline leaves* like basal leaves but lamina at base cuneate, lower side greyish arachnoid hairy, upper side glabrous. *Synflorescence* racemose, with many capitules, (branches unknown). *Capitules* 2–9 at terminal parts of branches loosely clustered, sessile or up to 1.5 cm pedunculate, with 15–25 flowers, 1.9–2.7 × 1.6–2.2 (1.0–1.7 × 1.3–1.7) cm, glabrous to densely hairy. *Involucral bracts* in 7–11 rows, herbaceous, the upper part sometimes somewhat tinged with red; outer involucral bracts 4.0–9.2 × 0.8–2.0 mm, linear-triangular, patent or deflexed, margin with some glandular hairs; middle involucral bracts 7.2–12.4 × 1.2–2.0 mm, linear-triangular (index 3.6–8.7), margin in the lower half with (many) glandular hairs, the upper 1/2–3/4 patent; inner involucral bracts 9.8–14.4 × 1.2–2.8 mm, linear-obovate (index 5.7–10.2), membranaceous, often the upper part slightly recurved, apex acute or truncate, mucronate, mucro straight or hooked. Longest *receptacular scales* 8.0–12.0 × 0.1–0.2 mm wide, glabrous or verrucate near apex, acute. Longest *pappus hairs* 3.3–5.0 mm long, margin minutely dentate, acute. *Corolla* 8.2–13.2 mm long, pink- or violet-purple, exceeding the involucral bracts by 0.6–6.0 mm, tube 2.1–5.2 mm long, glabrous, not widened at base, limb 6.6–8.4 mm long (= 3/5–3/4 of total length), glabrous or with glandular hairs; lobes 5, sometimes 6, longest lobe 1.6–2.8 mm long (= 1/5–3/10 of limb). *Stamens* 5, sometimes 6, filaments 2.6–4.4 mm long, smooth or somewhat verrucate, anthers 5.6–7.5 × 0.4–0.8 mm, (colour unknown), basal appendage 0.4–1.0 mm long, bifurcate to multifurcate, apical appendage 1.0–2.0 mm long, dorsally with slender hairs, apex acuminate. *Stylar apex* 2.2–3.3 mm long, (colour unknown), branches 0.6–1.7 mm long (= 1/4–3/5 of stylar apex), sweeping hairs 1.1–2.1 mm below the branches. *Achene* 6.2–7.4 × 3.0–3.5 mm, obovoid (index 1.8–2.2), smooth, brown, with (inconspicuous) dark brown dots, at apex without a marginal ridge, apical plate slightly truncate.



Fig. 18.18. *Arctium pseudarctium* (Bornm.) Duist. – Apical part of synflorescence (*Botschantsev & Egorova 1406*). Bar indicates 5 cm.



Fig. 18.19. *Arcetium pseudarctium* (Bornm.) Duist. – a. Basal leaf and upper part of petiole; b. dorsal view of anther with hairs at the apical part (a, b: Botschantsev & Egorova 1406).

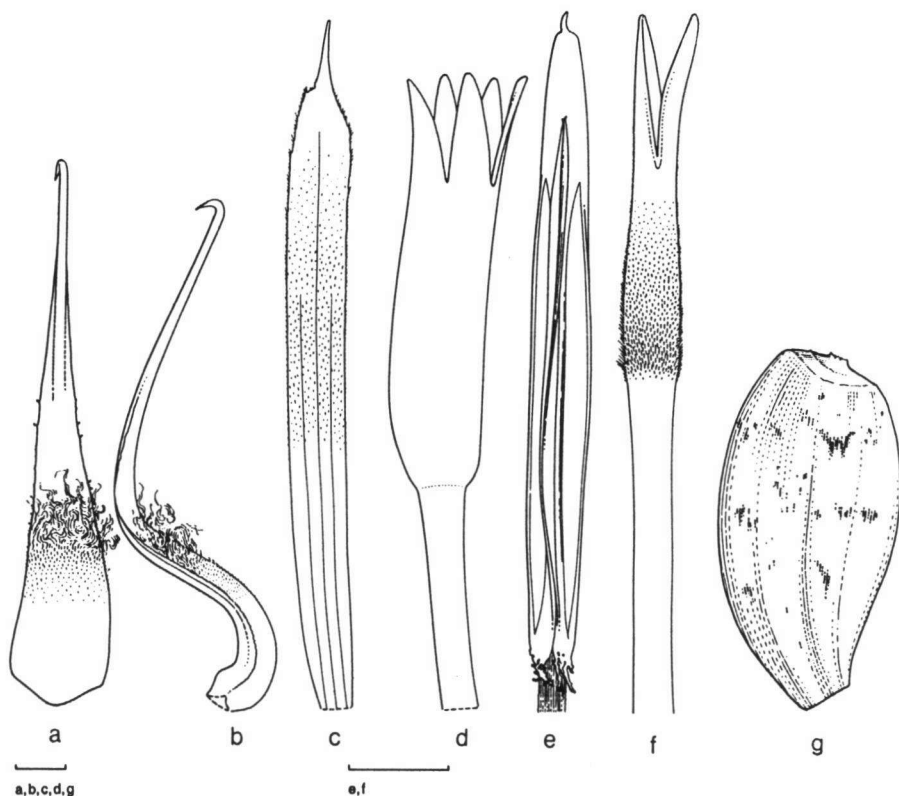


Fig. 18.20. *Arctium pseudarctium* (Bornm.) DuRoi. – a. Dorsal view of middle involucre bract; b. lateral view of middle involucre bract; c. dorsal view of inner involucre bract; d. corolla; e. anther with apical part of filament; f. apical part of style; g. achene (a–f: Botschantsev & Egorova 1406; g: Lindberg 873). Bar indicates 1 mm.

Distribution – Uzbekistan (Samarkand). Kirgizia (Alayskiy Khr.). Tadzhikistan (Pamir). Afghanistan (Badakhshan, Herat, Kopisa).

Habitat & Ecology – Roadsides, near villages. Alt.: 1720–2550 m. Flowering from June to August.

Taxonomy – 1. *Arctium pseudarctium* is very similar to *A. amplissimum* and *A. umbrosum*. The capitules are sessile, and often clustered at the terminal parts of the branches. *Arctium amplissimum* differs in having smaller (up to 2 cm [1 cm excluding spines]) capitules, fewer (9–12) flowers per capitule, shorter achenes (5.1–6.1 mm), shorter corolla lobes (up to 1.5 mm), and a shorter styler apex (up to 2.0 mm).

2. *Arctium umbrosum* differs in the presence of large, sessile glands on the involucre bracts, the smaller capitules (up to 1.6 cm [1.0 cm excluding spines]), and in having fewer flowers per capitule (up to 15).

Nomenclature & Synonymy – 3. *Cousinia spuria* was described by Juzepczuk (1937) as different from *C. pseudarctium* in the larger, subglobose capitules (2.5 cm)

and the larger number of flowers per capitule (35). The type is from Southern Kirgizia, from where *C. pseudarctium* was not known until then. Only the number of flowers does not agree with my description of *A. pseudarctium*. I have not seen the type specimen, and I examined only one of the other specimens which were cited by the author (*Juzepczuk 173*). The capitules of this specimen measure 2 cm in diameter and have only c. 15 flowers per capitule. This specimen falls entirely in the variability of *A. pseudarctium*, and I agree with Tscherneva (1962) that *C. spuria* has to be treated as a synonym of *A. pseudarctium*.

4. Franchet (1883) erroneously cited *Franchet 661* as belonging to *Cousinia amplissima*. I agree with Bornmüller (1917) and Tscherneva (1962) that it belongs to *A. pseudarctium*.

Variation – 5. Bornmüller (1917) described *Cousinia pseudarctium* with hairy capitules, and the variety *leiocephala* including all specimens with a glabrous involucre. I have seen the whole range, from a glabrous to a densely tomentose involucre. Therefore, I do not accept this variety.

Hybrids – 6. Juzepczuk (1937) described the hybrid between *Cousinia spuria* (= *pseudarctium*) and *C. umbrosa* (*C. x dualis*) (see description and notes of H6).

Note – 7. According to Rechinger (1972) this is a perennial species. I have not been able to check this, as I have seen only herbarium material which did not include the base of the stem.

## 11. *Arctium umbrosum* (Bunge) Kuntze – Fig. 18.21.

*Arctium umbrosum* (Bunge) Kuntze, Revis. Gen. 1 (1891) 308; Tscherneva in Komarov, Fl. URSS 27 (1962) 178 (in syn.). — *Cousinia umbrosa* Bunge, Mém. Acad. Sci. Pétersb., ser. 7, 9, 2 (1865) 10; Boiss., Fl. Or. 3 (1875) 463; C. Winkl., Acta Horti Petrop. 10, 2 (1887) 469; 12, 7 (1892) 188; 14 (1898) 191; Bornm., Beih. Bot. Centralbl. 34 (1917) 135; Juz., Acta Inst. Bot. Acad. Sci. URSS, ser. 1, 3 (1937) 296; Tscherneva in Komarov, Fl. URSS 27 (1962) 178; Rech. f., Fl. Iran. 90 (1972) 204; 139a (1979) 132; Tscherneva, Bot. Zhurn. 73, 6 (1988) 870; Nov. Syst. Pl. Vasc. 25 (1988) 147. — Holotype: *Bunge s.n.*, 6/7/1858, "in umbrosis montium (inter Nischapur et Meschhed) circa pagum Dschegar in provincia Meschedensi Persiae boreali-orientalis". (P!).

*Cousinia uncinata* Regel, Bull. Soc. Nat. Moscou 40, 2 (1867) 145; Franchet, Ann. Sci. Nat., sér. 6, Bot. 16 (1883) 314; C. Winkl., Acta Horti Petrop. 10, 2 (1887) 469; Tscherneva in Komarov, Fl. URSS 27 (1962) 178 (in syn.); Rech. f., Fl. Iran. 90 (1972) 204 (in syn.). — *Arctium uncinatum* (Regel) Kuntze, Revis. Gen. 1 (1891) 308; Tscherneva in Komarov, Fl. URSS 27 (1962) 178 (in syn.). — Holotype: *Regel 593* (n.v.). — See note 2.

*Cousinia tomentella* C. Winkl., Acta Horti Petrop. 10, 2 (1887) 469; 12, 7 (1892) 188; 14 (1898) 191; Bornm., Beih. Bot. Centralbl. 34 (1917) 136; Juz., Acta Inst. Bot. Acad. Sci. URSS, ser. 1, 3 (1937) 296; Tscherneva in Komarov, Fl. URSS 27 (1962) 179; Tscherneva, Bot. Zhurn. 73, 6 (1988) 870; Nov. Syst. Pl. Vasc. 25 (1988) 147. — *Arctium tomentellum* (C. Winkl.) Kuntze, Revis. Gen. 1 (1891) 308; Tscherneva in Komarov, Fl. URSS 27 (1962) 179 (in syn.). — Syntypes: *Regel s.n.*, 06/1882, "habitat in terrae Hissar valle fluminis Karatag prope pagum Hakimi altitudine circa 5000"; *Regel s.n.*, 8/9/1884, "nec non in Bucharae valle Tschitschichud in declivibus montium Sigdy sita altitudine 6–7000" (n.v.). — See note 3.

*Cousinia umbrosa* Bunge var. *virescens* Bornm., Beih. Bot. Centralbl. 34 (1917) 135; Tscherneva in Komarov, Fl. URSS 27 (1962) 178 (in syn.). — Holotype: *Bornmüller 390*, 24/7/1913, prov. Samarkand, "in ditione fluvii Jagnob in alpinis inter pagos Takfon et Simarl, alt. 2400 m." (WU)?

[Perennial]. *Stem* 65–90 cm long. *Basal leaves*: petiole 10 cm long, solid, somewhat arachnoid hairy, lamina 18–28 × 14–18 cm (index 1.3–1.6), base cordate to cuneate, pinnatilobed, lobes 3–3.5 cm long, 4 cm wide, acute, mucronate, apex acute, with up to 2 mm long, more or less spiny mucro, lower side arachnoid, without minute glassy globules, greyish, upper side glabrous; *cauline leaves* like basal leaves but pinnatifid to pinnatipartite, apex obtuse, mucronate. *Synflorescence* racemose, with many capitules, (branches unknown). *Capitules* solitary or in clusters of 2–6, 0–1.5 cm pedunculate, with 7–15 flowers, 0.8–1.6 × 1.1–2.2 (0.6–1.0 × 0.9–1.6) cm, glabrous to densely arachnoid-tomentose. *Involucral bracts* in 7–11 rows, herbaceous; outer involucral bracts 2.4–4.0 × 0.9–2.0 mm, linear-triangular to -cuspidate, patent or somewhat deflexed, margin dentate; middle involucral bracts 6.4–8.0 × 1.3–2.2 mm, linear-triangular to -cuspidate (index 3.6–5.0), margin of basal part with short (glandular) hairs, at apex with 1–3 pairs of large (up to 0.5 mm wide) sessile glands, the upper 3/10–1/2 patent; inner involucral bracts 10.3–12.4 × 1.1–2.0 mm, obovate (index 6.2–9.9), membranaceous, not recurved, apex acuminate, straight. Longest *receptacular scales* 8.0–10.3 × 0.1–0.2 mm, glabrous or with some multicellular hairs, acute. Longest *pappus hairs* 3.5–4.0 mm long, margin minutely dentate, acute. *Corolla* (7.6–)8.0–11.5(–13.3) mm long, pink- or red-purple, or blue, exceeding the involucral bracts by 0–4 mm, tube 1.5–3.2(–4.0) mm long, not widened at base, glabrous, limb 6.3–8.6(–9.3) mm long (= 7/10–9/10 of total length), glabrous or with (e-)glandular hairs at the lobes, longest lobe 1.4–2.4 mm long (= 1/5–3/10 of limb). *Stamens*: filaments 3.0–3.3 mm long, smooth to (somewhat) verrucate, anthers 4.8–7.1(–8.8) × 0.4–0.6 mm, (colour unknown), basal appendage 0.2–1.3(–1.9) mm long, multi-furcate, apical appendage 0.9–1.7(–1.9) mm long, glabrous or dorsally with slender hairs, acuminate. *Stylar apex* 1.6–3.7 mm, (colour unknown), branches 0.6–1.5 mm long (= 1/4–1/2 of stylar apex), sweeping hairs 0.8–2.2 mm below the branches. *Achene* 4.9–6.0 × 2.9–4.0 mm, obovoid (index 1.4–2.0), smooth, (pale) brown, with dark brown dots, at apex without marginal ridge, apical plate flat, with 5 ellipsoid spots.

Distribution – Iran (Khorasan). Kazakhstan (Almaty). Uzbekistan (Bukhara, Samarkand, Tashkent, Fergana). Turkmenia (Krasnovodsk, Ashkhabad). Kirgizia (Osh, Tyan Shan). Tadzhikistan (Leninabad, Dushanbe, Pamir). Afghanistan (Herat, Badghis, Balkh, Baghlan, Konar, Kabul). Pakistan (Baluchistan).

Habitat & Ecology – Roadsides, field borders, gardens, valleys and gorges, riversides, steep hillsides. On clayey and calcareous soil, shaded. Alt.: 500–3300 m. Flowering from April (!) to August.

Taxonomy – 1. *Arctium umbrosum* much resembles *A. amplissimum*, with which it shares the small, clustered capitules of up to 2.0 cm diameter. The clusters of *A. amplissimum* tend to be more dense, and include more capitules than in *A. umbrosum*. Characteristic for the latter is the presence of 1–3 pairs of 0.5 mm large, sessile glands on the middle involucral bracts. The middle involucral bracts of all other species of *Arctium* are (glandular) hairy to almost glabrous at the margin, and do not have large sessile glands on the margin.

Nomenclature & Synonymy – 2. I have not seen the type specimen of *Cousinia uncinata* Regel. The latter author also identified another collection, *Regel s.n.* (06-



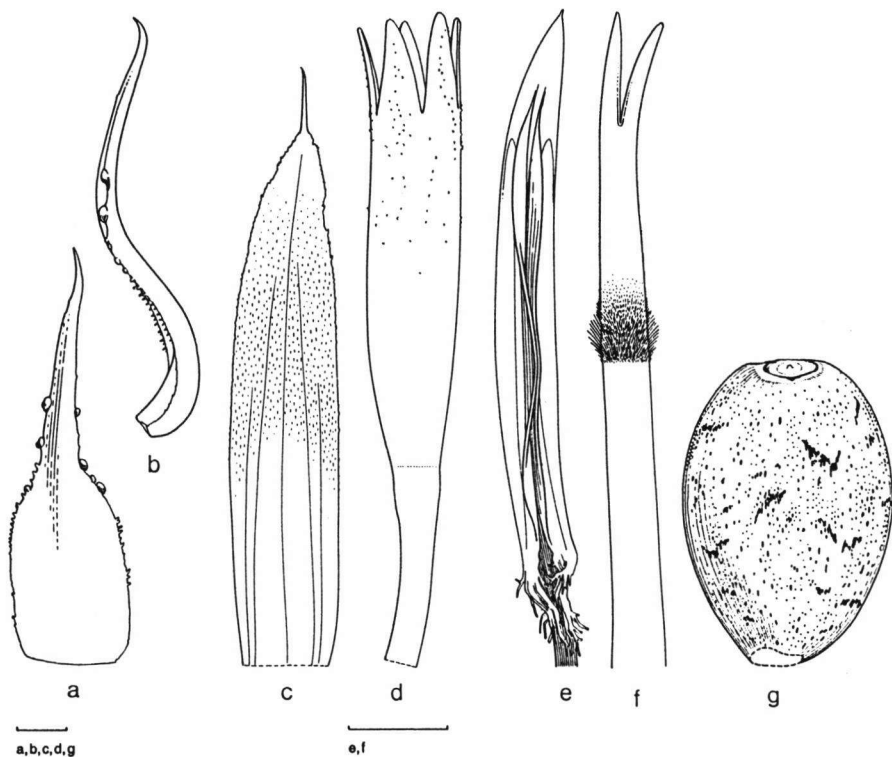


Fig. 18.21. *Arctium umbrosum* (Bunge) Kuntze – a. Dorsal view of middle involucre bract; b. lateral view of middle involucre bract; c. dorsal view of inner involucre bract; d. corolla; e. anther with apical part of filament; f. apical part of style; g. achene (a–c, g: Krause s.n., s.d.; d–f: Podlech 15956). Bar indicates 1 mm.

1883; P!), as *C. uncinata*. This specimen is identical to *A. umbrosum*, and I therefore agree with Tscherneva (1962) and Rechinger (1972) that *C. uncinata* is a synonym of *A. umbrosum*.

3. *Cousinia tomentella* differs only from *A. umbrosum* in having more densely tomentose capitules. I have not seen the type specimens (Regel s.n., 1882, 1884). Tscherneva (1962) thought that *C. tomentella* has its own well-defined range, being endemic to Pamir-Alay. However, specimens with arachnoid hairy involucre have been found outside the Pamir-Alay region (e.g. Edmondson 1314, NE Iran, W!). Moreover, I found glabrous and densely tomentose involucre to be the extremes of a range of intermediate forms. The character does not show correlation with any other character, and I therefore consider *C. tomentella* as a synonym of *A. umbrosum*.

Variation – 4. When Bunge (1865) described *C. umbrosa*, he did not know whether the species is biennial or perennial. According to Tscherneva (1962) it is a perennial species. Rechinger (1972) thinks it is probably a perennial. I have only seen the base of the stem of a single specimen. From this specimen I could not trace its life span.

5. *Fedtschenko 2435* has some capitules of normal size, and many of very small size which are tinged red. According to Bommüller (in sched.) this specimen probably grew on an extremely sun-exposed location.

Hybrids – 6. According to literature, *A. umbrosum* forms hybrids with two other species. *Arctium* × *dualis* is the product of *A. pseudarctium* × *A. umbrosum* (see description and notes of hybrid H6). *Cousinia* × *triacantha* is said to be formed by crossing *A. umbrosum* with *C. alberti*. I have not seen material of this hybrid, which should now be regarded as an intergeneric one. See under *Nomina Dubiae* (D6).

Note – 7. *Arctium umbrosum* is strictly allopatric from *A. amplissimum*. Both species occur in Iran, the first only in Northeast, the second in Southwest, West and central North Iran. *Arctium umbrosum* is sympatric with *A. pseudarctium* only in the Pamir-Alay region.

## 19. Descriptions of the hybrids

The hybrids are listed in alphabetical order of the parents. I regard specimens which are intermediate between two species as hybrids. These specimens have not been subjected to a cytological investigation, nor have crossing experiments been performed. I have examined the viability of pollen and achenes. In Chapter 12 I present the determination of the hybrid specimens of *Arctium* section *Arctium*.

### H1. *Arctium lappa* × *A. minus* = *A. xnothum* (Ruhm.) Weiss

*Lappa xnotha* Ruhm. in Eichler, *Jahrb. Bot. Gart. Berl.* (1881) 238. — *Arctium xnothum* (Ruhm.) Weiss in Koch, *Syn. Deutsch. Fl.* ed. 3, 2 (1897) 1512. (= *A. minus* × *A. lappa*).

*Lappa xsubracemosa* Simonk., *Enum. Fl. Transsilv.* (1886) 340. (= *L. major* × *L. minor*). — *Arctium xsubracemosum* (Simonk.) Nyman, *Suppl.* 2, 1 (1889) 179.

*Lappa xmixta* E. G. Camus, *Bull. Soc. Bot. Fr.* 44 (1897) 63. (= *L. major* × *L. minor*). Non Simonk. (= *A. minus* × *A. tomentosum*).

*Lappa xjanczewskii* Dyb., *Wszzechswiat* (1904) 731; Arènes, *Bull. Jard. Bot. Brux.* 20 (1950) 124 [in syn.: *A. xnothum*].

*Lappa xruhmerio* Guétrot, *Pl. Hybr. Fr.* 3 (1929) 101; Senay, *Bull. Soc. Bot. Fr.* 83 (1936) 339 (= *A. majus* × *A. minus*); Arènes, *Bull. Jard. Bot. Brux.* 20 (1950) 124 (= *A. xnothum*).

*Arctium xdebrayi* Senay, *Bull. Soc. Bot. Fr.* 83 (1936) 341. — Authentic material: *Senay 3605* (P!). (= *A. pubens* × *A. majus*)

*Arctium xdelphinense* Arènes, *Bull. Jard. Bot. Brux.* 20 (1950) 125. — Authentic material: *Milliat* (Herbar. norm. Cynar.) 3192, 3276, 5950–5954. (= *A. lappa* subsp. *majus* × *A. minus* subsp. *alpestre*).

*Stem* 50–150 cm long. *Basal leaves*: petiole at base hollow or solid (and then sometimes hollow towards lamina), lamina 48 × 26 cm (index 1.8), apex obtuse, mucronate. *Synflorescence* corymbose. *Capitules* 1.5–10.0 cm pedunculate, 2.4–3.1 × 2.2–2.6 (1.6–1.8 × 1.5–1.8) cm, glabrous to slightly arachnoid hairy. *Involucral bracts* in 10–12 rows, the upper part tinged with purple; outer involucral bracts linear-triangular, sometimes leaflike; middle involucral bracts 10.6–12.2 × 1.1–1.4 mm (index 7.8–11.1), c. the upper 3/5 patent; inner involucral bracts 13.3–16.5 × 1.7–2.0 mm, linear-ovate (index 7.6–8.3), abaxially in the middle part with short hairs, margin

dentate from 2 mm above base, the upper part slightly recurved, apex acute or slightly acuminate, straight or somewhat hooked. Longest *receptacular scales* 7.3–8.8 × 0.1–0.4 mm, verrucate at apex, sometimes dentate, acute to acuminate. Longest *pappus hairs* 2.4–3.0 mm long, acute. *Flowers* exceeded by the involucre bracts by 0–2.5 mm. *Corolla* 9.2–10.2 mm long, lilac or purple, tube 4.6–5.4 mm long, not widened at base, glabrous, limb 4.2–5.4 mm long (= c. 1/2 of total length), glabrous or with at least some glandular hairs at the lobes or at the base of the limb, longest lobe 1.8–2.3 mm long (= 2/5–1/2 of limb). *Stamens*: filaments 1.9–2.2 mm long, smooth, anthers 3.6–5.3 mm long, (deep purple-)blue, basal appendage 0.5–1.1 mm long, entire or bifurcate, apical appendage 0.6–1.0 mm long, glabrous, (slightly) acuminate. *Stylar apex* 1.7–2.5 mm, white or pale lilac, branches 1.2–1.9 mm long, sweeping hairs 0.1–0.8 mm below the branches. *Achene* 5.7–7.2 × 2.7–3.1 mm, obovoid index 2.0–2.4), with 4–5 inconspicuous longitudinal ribs, with dark brown dots, at apex with dentate marginal ridge, apical plate truncate.

Distribution – Sweden. United Kingdom. Netherlands. Germany. France.

Habitat & Ecology – Neglected places in or near human settlements, roadsides, forest edges. Alt.: no data available.

Notes – 1. The hybrid between *A. lappa* and *A. minus* is variable. Usually, the specimen combines the corymbose synflorescence of *A. lappa* and the hollow petiole of *A. minus*. The involucre is glabrous or somewhat hairy, and the corolla is often equalling the involucre bracts.

2. The above description is based on 9 specimens. This hybrid occurs occasionally throughout Western Europe, often among its parents, but also together with either *A. lappa* or *A. minus*. The pollen that is produced by these hybrid specimens does not look as if it is abortive. The achenes are often abortive.

## H2. *Arctium lappa* × *A. tomentosum* = *A. xambiguum* (Čelak.) Nyman

*Lappa xambigua* Čelak., Prodr. Fl. Böhm. (1871) 249. — *Arctium xambiguum* (Čelak.) Nyman, Suppl. 2 (1889) 179.

*Lappa xrehmanni* Dyb., Wszechswiat (1904) 732; Arènes, Bull. Jard. Bot. Brux. 20 (1950) 126 [in syn.: *A. xambiguum*]. — *Arctium xrehmanni* (Dyb.) Iljin, Fl. Yugo-Vost. Evr. Chast SSSR 6 (1936) 384.

*Arctium xleiobardana* Juz. & Serg. in Komarov, Fl. URSS 27 (1962) 105 (= *A. leiospermum* × *A. tomentosum*).

*Synflorescence* (sub-)corymbose. *Capitules* 1.5–7 cm pedunculate, 2.5–3.8 × 2.2–2.9 (1.2–2.1 × 1.7–2.1) cm, glabrous to rather densely arachnoid hairy. *Involucre bracts* in 9–12 rows, (dark) green, the upper part (often) tinged with red; outer involucre bracts 9 × 1.6–1.8 mm, linear-triangular, sometimes leaflike; middle involucre bracts 12.4–15.3 × 1.3–1.7 mm (index 7.8–11.8), the upper 3/5–7/10 patent; inner involucre bracts 15.4–16.9 × 1.1–2.3 mm, linear-obovate (index 7.3–13.1), often slightly constricted above the middle, and widened below the apex, margin dentate from 2 mm above base, the upper part slightly recurved, sometimes purple coloured near apex, apex truncate or acuminate, straight or slightly hooked. Longest *receptacular scales* 6.4–10.0 × 0.1–0.5 mm wide, verrucate at apex, sometimes dentate, acute. Longest *pappus hairs* 1.4–2.7 mm long, acute. *Flowers* exceeded by the involucre

bracts with 0.5–3.0 mm, or equalling or exceeding the involucre bracts by 1 mm. *Corolla* 10.7–12.8 mm long, tube 5.8–7.2 mm long, slightly widened at base, glabrous, limb 4.1–5.6 mm long (= 2/5–1/2 of total length), glandular hairs at least either at the lobes or at the base of the limb, longest lobe 2.1–3.0 mm long (= c. 1/2 of limb). *Stamens*: filaments 2.0–3.5 mm long, smooth or verrucate, anthers 4.0–5.1 × 0.4 mm, basal appendage 0.4–1.3 mm long, entire or bifurcate, apical appendage 0.8–1.1 mm long, glabrous, acuminate. *Stylar apex* 2.8–3.5 mm, branches 1.9–2.6 mm long, sweeping hairs 0.5–1.2 mm below the branches. *Achene* 7.1 × 3.1 mm, obovoid (index 2.3), with 4–5 longitudinal ridges, chestnut brown, at apex with an inconspicuous marginal ridge, apical plate truncate.

Distribution – Sweden. Finland. United Kingdom. Netherlands. France. Germany. Poland.

Habitat & Ecology – Neglected places in or near human settlements, roadsides. Alt.: no data available. Flowering in June and July; it would be simultaneous with *A. lappa*, and somewhat earlier than *A. tomentosum* (in sched.).

Notes – 1. The hybrid between *A. lappa* and *A. tomentosum* is very variable. It combines a few characters of both species, other characters are intermediate between the parents. In most cases the hybrid has a corymbose synflorescence, a (slightly) hairy corolla limb, inner involucre bracts which are slightly constricted above the middle and widened below the apex, and (slightly) truncate at apex, and has flowers which do not exceed the involucre. Within a population hybrid specimens may differ from each other. The three hybrid specimens I collected from one locality in Hessen (Germany, *Duistermaat 165 B, C, D*) differ from each other in colour and indumentum of the capitules. In some specimens the corolla may be entirely glabrous (*Dandy 1138; Samuelsson, G. (Hasslow) 1571*). The latter is the only specimen with flowers exceeding the involucre as in *A. tomentosum*, but the inner involucre bracts differ in shape from *A. tomentosum*.

2. I have seen 11 specimens of the hybrid between *A. lappa* and *A. tomentosum* from Western and Central Europe. It is often growing among its parents, but it is also recorded that only *A. lappa* was present (*Samuelsson, G. (Hasslow) 1571; Duistermaat 165A*).

3. The pollen of the hybrid specimens does not seem to be abortive. Compared to the parent species, a higher percentage of the achenes seems to be abortive. However, I have also seen apparently ripe achenes.

### H3. *Arctium minus* × *A. palladini* = *A. xsemiconstrictum* Duist., *hybr. nov.*

Synflorescentiae racemosae. Phyllariae interiores supra medio parum constrictae, infra apicem dilatatae, apex acutus strictus. — Authentic material: *Koelz 16578 (W!)*.

*Synflorescence* racemose. *Capitules* up to 1.5 cm pedunculate, ca 3 cm wide, somewhat hairy. Inner *involucre bracts* slightly constricted above the middle, and widened below the apex, apex acute, straight. *Flowers* exceeding the involucre bracts. *Corolla* 10.8 mm long, tube 5.2 mm long, glabrous, limb 5.6 mm long (= 1/2 of total length), with glandular hairs at the base, lobes 3.1 mm long (= c. 1/2 of limb). *Stamens*: filaments smooth, anthers 5.0 × 0.5 mm, basal appendage 0.6 mm long, entire, api-

cal appendage 1.0 mm long, glabrous. *Stylar apex* 2.8 mm, branches 2.3 mm long, sweeping hairs 0.5 mm below the branches. *Achene* 7.2 × 2.8 mm, obovoid (index 2.6), with longitudinal ridges, unicoloured, at apex with an inconspicuous marginal ridge, apical plate truncate.

Note – The above description is based on only one specimen, *Koelz 16578* (25-7-1940. Iran. Mazenderan). which was cited by Rechinger (1979) as *A. palladini*. Its synflorescence is racemose, unlike *A. palladini* or *A. tomentosum*. It has 5.0 mm long anthers, and a 2.8 mm long stylar apex, which is characteristic for *A. tomentosum* and too short for *A. palladini*. The inner involucre bracts are somewhat widened below the apex, and acute, rather than truncate at apex, as is characteristic for both *A. palladini* and *A. tomentosum*. I have seen similarly shaped inner involucre bracts only in hybrids of either *A. tomentosum* and *A. lappa*, or *A. tomentosum* and *A. minus*. The racemose synflorescence indicates that *A. minus* is involved in this hybrid. The length of the anthers and the stylar apex are intermediate between *A. minus* and *A. palladini*. I therefore regard this specimen as the hybrid between *A. palladini* and *A. minus*. This hybrid has, to my knowledge, never been published before. The name 'semiconstrictum' refers to the shape of the inner involucre bracts, which are only slightly constricted above the middle.

#### H4. *Arctium minus* × *A. tomentosum* = *A. ×mixtum* (Simonk.) Nyman

*Lappa ×mixta* Simonk., Term. Füz. 2 (1878) 145. (= *L. intermedia* × *L. tomentosa*). — *Arctium ×mixtum* (Simonk.) Nyman, Suppl. 2 (1889) 179. (= *A. minus* × *A. tomentosum*).

*Lappa ×ritschliana* Asch., Ber. Deutsch. Bot. Ges. 10 (1891) 99. (= *L. glabra* × *L. tomentosa*).

*Lappa ×media* E.G. Camus, Bull. Soc. Bot. Fr. 44 (1897) 63. (= *L. minor* × *L. tomentosa*). —

Authentic material: E.G. Camus & Franchet (Soc. Ét. Fl. Fr.-Helvet.) 300 (P!).

*Arctium ×bretoni* Rouy, Fl. Fr. 13 (1912) 517. (= *A. pubens* × *A. tomentosum*).

*Stem* 60–160 cm long. *Synflorescence* (sub-)corymbose. *Capitules* 0.5–10.0 cm pedunculate, 2.0–3.0 × 1.4–1.8 (1.2–1.4 × 1.2–1.6) cm, glabrous to slightly arachnoid hairy. *Involucre bracts*: the upper part often tinged with red; outer involucre bracts 3.6–6.8 × 0.8–1.0 mm, linear-triangular, sometimes leaflike, patent, margin with some glandular hairs in the lower half; middle involucre bracts 8.0–10.8 × 1.0–1.2 mm (index 8.0–9.0), c. the upper 3/5 patent; inner involucre bracts 11.0–14.0 × 1.2 mm, linear-ovate (index 9.2–11.7), sometimes slightly constricted above the middle and widened below the apex, margin dentate from 2 mm above base, the upper part slightly recurved, sometimes purple near apex, apex acute to (slightly) truncate, straight or hooked. Longest *receptacular scales* 5.3–7.6 × 0.1–0.3 mm, the widest sometimes split from apex halfway down, glabrous, sometimes dentate, acute. Longest *pappus hairs* 1.8–3.5 mm long, acute. *Flowers* exceeded by the involucre bracts by 0–1.0 mm, or exceeding the involucre bracts by up to 3.4 mm. *Corolla* 9.8–11.6 mm long, purple, tube 4.5–6.5 mm long, slightly widened at base, glabrous, limb 4.8–5.9 mm long (= 2/5–1/2 of total length), glabrous or with glandular hairs at least at the lobes and at the base of the limb, rarely only at the lobes, longest lobe 1.7–2.6 mm long (= 3/10–1/2 of limb). *Stamens*: filaments 3.5 mm long, smooth or papillose, anthers 3.5–5.1 × 0.3–0.4 mm, (deep purple-)blue, basal appendage 0.4–1.1 mm long, entire or bifurcate, apical appendage 0.7–1.2 mm long, glabrous,

acuminate. *Stylar apex* 2.1–3.3 mm, pale purple, branches 1.5–2.8 mm long, sweeping hairs 0.1–1.2 mm below the branches. *Achene* 6.0–6.2 × 2.1–2.6 mm, obovoid (index 2.4–2.9).

Distribution – Sweden. Netherlands. France. Austria. Poland. Romania.

Habitat & Ecology – Ruderal places, on silicate soil. Alt.: 0–850 m. Flowering from July to August.

Notes – 1. I have seen 11 specimens which I regard as the hybrid between *A. minus* and *A. tomentosum*. They have the (sub-)corymbose synflorescence of *A. tomentosum*, whereas the shape of the inner involucre bracts is similar to those of *A. minus*. This hybrid differs from the hybrid between *A. lappa* and *A. tomentosum* in having capitules which are only 1.2–1.6 cm high (excluding the deflexed outer involucre bracts); the hybrid between *A. lappa* and *A. tomentosum* has larger capitules (1.7–2.1 cm high; see also Chapter 12). Apart from the above mentioned characters, the specimens are variable in their characters. In some specimens the corolla is not exceeding the involucre (e.g. *van der Ploeg 1363x1365-2*, 10-08-1953; *Möller s.n.*, 11-08-1894), in most specimens it is.

2. Most specimens have normal pollen, but *Möller s.n.* (11-08-1894) has pollen which is luted into a band of tissue. Most (but not all) achenes seem to be abortive.

3. The hybrid occurs on scattered localities throughout Europe. It is not certain that always at least one of the parents is present. In Gex (France) the hybrid (*Duistermaat 133, 134*) was accompanied by *A. minus* (*Duistermaat 131, 132*).

##### H5. *Arctium nemorosum* × *A. tomentosum* = *A. xneumani* Rouy

*Arctium xneumani* Rouy, Fl. Fr. 9 (1905) 98. (= *A. majus* subsp. *nemorosum* × *A. tomentosum*).

*Synflorescence* corymbose. Inner *involucre bracts* slightly constricted above the middle, and widened below the apex, abaxially in the middle part with short hairs, margin entire, apex acuminate, straight. *Corolla*: limb 4.6 mm long with glandular hairs at some of the lobes, longest lobe 2.4 mm long (= 1/2 of limb). *Stamens*: anthers 5.4 mm long, basal appendage 1.5 mm long, apical appendage 1.0 mm long. *Stylar apex* 2.0 mm, branches 1.7 mm long, sweeping hairs 0.3 mm below the branches. *Achene* abortive.

Note – I know this hybrid from only one specimen which was collected in the garden of De Wever (Maastricht, The Netherlands). The parents grew close to each other, and the hybrid was said to be formed every year spontaneously (*A. de Wever s.n.*, 1928; in hb. *van Soest 2211*). The achenes are abortive.

##### H6. *Arctium pseudarctium* × *A. umbrosum* = *A. xdualis* (Juz.) Duist., *comb. nov.*

*Cousinia xdualis* Juz., Acta Inst. Bot. Acad. Sci. URSS, ser. 1, 3 (1937) 297; Tschereva in Komarov, Fl. URSS 27 (1962) 179. (= *C. spuria* × *C. umbrosa*). — Authentic material: *Juzepczuk 162, 164, 194, 313, 318*. (LE!)

*Capitules* with 14–16 flowers, 1.9–2.3 (1.0–1.2) cm wide. Middle *involucre bracts* with 2–3 pairs of large (0.5 mm), sessile glands.

Notes – 1. I have seen only 2 collections of this hybrid, *Juzepczuk 162* and *318*. Both specimens have the characteristic large sessile glands of *A. umbrosum*, and the wide capitules of *A. pseudarctium*. I therefore agree that they are the hybrid between *A. pseudarctium* and *A. umbrosum*.

2. Juzepczuk (1937) mentions 4–8 pairs of sessile glands on the middle involucre bracts. However, I have seen on both specimens only 2–3 pairs.

3. It is not known whether the above cited collections grew among their parents. The hybrid is only known from Alay. Both parents are known from this region.

## 20. Nomina dubiae

(The taxa are listed in chronological order)

D1. *Arctium adhaerens* Gilib., Fl. Litan. 1 (1781) 182, nom. illeg. — Type: unknown.

Note – I found this reference in the Index Kewensis. I have not been able to study the original publication, and I do not know whether a type specimen is extant.

D2. *Arctium grandiflorum* Desf., Cat. Hort. Par. ed. 3 (1829); Steud., Nomencl. (1840) 120 (in syn. of *Lappa major*). — Type: unknown.

Note – This reference is from the Index Kewensis. Desfontaines (1829) cited for this taxon DC., Fl. Suppl. Gall. I have not been able to trace this publication. Steudel (1840) suggested that it is a synonym for *Lappa major* (= *A. lappa*) but I can not confirm this.

D3. *Lappa ximbrica* Asch. & Graebner, Fl. Nordostd. Flachl. (1899) 743 (= *L. officinalis* × *L. nemorosa*). — *Arctium ximbricum* (E.H.L. Krause) Hayek in Hegi, Ill. Fl. Mitteleur. 6, 2 (1928) 834.

Note – I have not seen any specimen that I could identify as *A. lappa* × *A. nemorosum*, and I therefore treat this hybrid taxon as nomen dubium.

D4. *Lappa xzalewski* Dyb., Wszechswiat (1904) 732. — *Arctium xzalewskii* (Dyb.) Arènes, Bull. Jard. Bot. Brux. 20 (1950) 128 (= *A. tomentosum* × *A. lappa* subsp. *majus* × *A. minus* subsp. *eu-minus*).

Note – I have never seen a double hybrid, and I therefore treat this name as a nomen dubium.

D5. *Arctium xscanicum* Rouy, Fl. Fr. 9 (1905) 98 (= *A. majus* × *A. nemorosum*).

Note – I have not seen any specimen that I could identify as *A. majus* (= *A. lappa*) × *A. nemorosum*, and I therefore treat this hybrid taxon as nomen dubium.

D6. *Arctium umbrosum* × *Cousinia alberti* (*Cousinia xtriacantha* Kult.), Gos. Univ., ser. 8b, 6 (1929) 2, n.v.; Tscherneva in Komarov, Fl. URSS 27 (1962) 179 (*C. alberti* × *C. umbrosa*).

Note – As *Cousinia umbrosa* is treated now as a true *Arctium* species, *C. xtriacantha* should be regarded as an intergeneric hybrid. I have seen neither the original description, nor material that I could identify as the hybrid. Further study should reveal whether such intergeneric hybrids are formed indeed.

D7. *Arctium flabrescens* Klokov, Fl. URSS 11 (1962) 440, 560, fig. 83. — Holotype: *N. Pitzyn s.n.*, 22/6/1914, RSS Ucr., “Tauria praemontana, prope St. Alma, ad fl. Alma” (n.v.).

Note – I have not been able to examine the holotype which is probably kept in the herbarium of Kiev. According to Klokov (1962) it is related to *A. nemorosum*, and the Latin description suggests the same. However, the cited figure depicts a specimen with a corymbose synflorescence of probably *A. lappa*.

## 21. Species excludenda

(The taxa are listed in chronological order)

E1. *Arctium personata* L., Sp. Pl. (1753) 816. — *Lappa personata* (L.) Lam., Encyc. 1 (1785) 378. — Type: hb. *Linnaeus* 946.2 (LINN, microfiche L!) = *Carduus personata* (L.) Jacq.

E2. *Arctium carduelis* L., Mant. 1 (1767) 108. — *Lappa carduelis* (L.) Lam., Encyc. 1 (1785) 378. — Type: hb. *Linnaeus* 964.3 (LINN, microfiche L!) = *Carduus carduelis* (L.) Gren.

E3. *Arctium lanuginosum* Lam., Fl. Fr. 2 (1778) 70. — Type: *Dalechamp* (n.v.) = *Berardia subacaulis* Vill.

E4. Kuntze (Revis. Gen. 1, 1891) transferred 187 species of *Cousinia* to *Arctium*. All his combinations, except the ones mentioned in my revision, are excluded from *Arctium*. For the argumentation, which is based on a cladistic analysis, the reader is referred to Chapter 13 of this publication.



## 22. Identification list

This identification list includes all collections examined for this revision. The collections marked with an \* are used in Chapter 11). The identifications are given between brackets: species-number for the species, H + number for the hybrids, and a question mark for the indeterminatae. The numbers, which correspond with the numbers in the revision, are given below.

### *Arctium* section *Arctium*

- 1 *atlanticum* (Pomel) H. Lindb.
- 2 *lappa* L.
- 3 *minus* (Hill) Bernh.
- 4 *nemorosum* Lej.
- 5 *palladini* (Marcow.) R.E. Fr. & E.S. Söderb.
- 6 *tomentosum* Mill.

### *Arctium* section *Lappaceum*

- 7 *lappaceum* (Schrenk) Kuntze

### *Arctium* section *Nanarctium*

- 8 *arctioides* (Schrenk) Kuntze

### *Arctium* section *Pseudarctium*

- 9 *amplissimum* (Boiss.) Kuntze
- 10 *pseudarctium* (Bornm.) Duist.
- 11 *umbrosum* (Bunge) Kuntze

### Hybrids (S = species)

- H1  $\times$ *nothum* (Ruhm.) Weiss (= S2  $\times$  S3)
- H2  $\times$ *ambiguum* (Čelak.) Nyman (= S2  $\times$  S6)
- H3  $\times$ *semiconstrictum* Duist. (= S3  $\times$  S5)
- H4  $\times$ *mixtum* (Simk.) Nyman (= S3  $\times$  S6)
- H5  $\times$ *neumani* Rouy (= S4  $\times$  S6)
- H6  $\times$ *dualis* (Juz.) Duist. (= S10  $\times$  S11)

AZ s.n., s.d. (NBV 303) (6); Th.H.A.J. Abeleven s.n., s.d. (NBV 108) (2); s.n., s.d. (NBV 109) (2); s.n., s.d. (NBV 115) (2); s.n., s.d. (NBV 116) (2); s.n., s.d. (NBV 117) (2); s.n., s.d. (NBV 119) (2); s.n., s.d. (NBV 4936-44) (3); s.n., 1850 (3); s.n., 07/1850 (2); s.n., 08/1880 (2); s.n., 08/1880 (3); 374 (3); 574 (3); 575 (3); F. Adema 1092 (3)\*; 1257 (2); 1260 (3); 1265 (2); 1266 (2); 1277 (3); 1278 (3); 1285 (3); 1287 (3); P. Aellen (A. Manoutcheri & P. Aellen) 582 (2); Agosto s.n., 1847 (3); F. Ahlberg s.n., 08/1867 (3); Ahles 64614 (2); J. Akkerman s.n., 04/07/1970 (3); 04/07/1970 (6); Alexeenko 12266 (2); C.G. Alm 1590 (H1); Alpherts s.n., s.d. (NBV 4936-77) (2); s.n., 07/1846 (2); Alston & Sandwith 2545 (2); A.H.G. Alston s.n., 01/08/1941 (H1); Amin-Bazargan 3514 (?); 18579 (9); N.J. Andersson s.n., s.d. (HLB 900.74-210) (6); s.n., s.d. (HLB 900.74-214) (2); s.n., s.d. (HLB 900.74-230) (3); s.n., s.d. (HLB 900.74-231) (2); O. Anders 10628 (2); 11145 (2); L. André s.n., s.d. (HLB) (3); Anema, W. & J. Anema-Roeleveld s.n., 24/07/1983 (3)\*; s.n., 30/07/1983 (2); Ank. s.n., 1872 (3); Anon. s.n., s.d. (008814) (3); s.n., s.d. (HBU 046034) (6); s.n., s.d. (HLB 409676) (?); s.n., s.d. (HLB 900.74-199) (3); s.n., s.d. (HLB 900.74-249) (?); s.n., s.d. (HLB 908.359-37) (6); s.n., s.d. (HLB 944.264-92) (3); s.n., s.d. (HLB 3) (6); s.n., s.d. (NBV 148) (2); s.n., s.d. (NBV 149) (2); s.n., s.d. (NBV 161) (2); s.n., s.d. (NBV 302) (3); s.n., s.d. (NBV 304) (6); s.n., s.d. (NBV 307) (3); s.n., s.d. (NBV 905.10-61) (3); s.n., 00/09/ (3); s.n., 09/1832 (2); s.n., 08/1834 (3); s.n., 08/1835 (3); s.n., 1839 (3); s.n., 1840 (3); s.n., 10/1846 (2); s.n., 03/08/1850 (?); s.n., 21/07/1853 (?); s.n., 1866 (2); s.n., 1870 (3); s.n., 08/1870 (3); s.n.,

28/07/1883 (3); s.n., 10/08/1889 (4); s.n., 1891 (3); s.n., 01/09/1891 (2); s.n., 1896 (?); s.n., 24/07/1899 (4); s.n., 07/08/1901 (2); s.n., 09/1903 (3); s.n., 09/08/1905 (3); s.n., 08/1909 (3); s.n., 28/08/1929 (2); s.n., 17/07/1937 (3); s.n., 01/08/1937 (3); s.n., 17/08/1937 (3); s.n., 23/08/1937 (3); s.n., 07/08/1938 (3); s.n., 21/08/1938 (3); s.n., 22/07/1939 (3); s.n., 24/07/1939 (3); s.n., 28/07/1940 (3); s.n., 12/09/1940 (3); s.n., 05/08/1942 (3); s.n., 19/07/1944 (6); s.n., 31/08/1944 (6); s.n., 25/07/1946 (2); s.n., 26/07/1976 (3); s.n., 10/07/1979 (3); s.n., 17/08/1991 (3); s.n., 26/08/1991 (3); s.n., 08/xx33 (3); 574 (3); 788 (2); 1022 (6); 2436 (2); L. s.n., s.d. (HLB 900.74-200) (3); in H.Sieb. s.n., 1855 (3); in hb Behrendsen s.n., 08/1883 (3); in hb Behrendsen s.n., 08/1918 (3); in hb. F. Fischer s.n., 1859 (3); in hb. Gatt. s.n., s.d. (HLB 900.74-247) (3); in hb. Gatt. s.n., s.d. (HLB 900.74-248) (3); in hb. Gravet. s.n., 09/09/1895 (3); in hb. J.K. Hasskarl s.n., s.d. (HLB 900.74-228) (3); in hb. J.K. Hasskarl 718 (3); in hb. van Soest (sub 23266) 2438 (3); (russian) s.n., 20/07/1905 (2); (russian) s.n., 28/07/1961 (4); (russian) s.n., 29/07/1961 (2); (russian) s.n., 29/07/1961 (4); (russian) 18 (2); (russian) 96 (11); (russian) 102 (11); (russian) 117 (11); (russian) 151 (2); (russian) 182 (11); (russian) 295 (6); (russian) 317 (6); (russian) 1629 (11); (russian) 1799 (11); (russian) 1998 (10); (russian) 3-35 (10); Arazm-Bazargan 3513 (9); E. Arnolds s.n., 10/09/1970 (3); 1427 (2); 1619 (3); 2119 (2); 2168 (3); Ascherson s.n., 25/04/1870 (2); Aucher-Eloy s.n., s.d. (P) (2).

BM Mull Survey 393 (3); L.H. Baas Becking s.n., 09/1902 (3); Babakhanlou-Amin 3510 (9); Babakhanlou-Amin 3512 (2); Babinpton s.n., 26/08/1843 (2); s.n., 27/09/1847 (2); s.n., 02/10/1860 (2); s.n., 12/08/1864 (6); P. Backer de Wit s.n., 1852 (3); C. Baenitz s.n., 08/1866 (4); s.n., 1868 (6); s.n., 08/1872 (4); s.n., 07/08/1872 (4); s.n., 04/08/1877 (4); 25 (6); 27 (4); 28 (6); Bafu 83 (11); C. Bakels & W. Kuyper s.n., 09/1989 (3); J.G. Baker s.n., 08/1871 (3); s.n., 09/1898 (2); R.C. Bakhuizen v.d. Brink fil. s.n., 31/07/1964 (4)\*; 3864 (3); 5230 (2); 5277 (?); 5537 (3); 5546 (6); 5554 (3); 5555 (2); 5560 (2); 5577 (2); 5606 (3); 6985 (2); 6989 (3); 7028 (3); D. Bakker s.n., 04/08/1967 (3); s.n., 27/08/1967 (6); 841 (3); 891 (2); 1326 (6); 1332 (3); 1337 (2); 1340 (3); 2149 (6); 2478 (3); 2479 (6); 2543 (3); 3300 (6); 3358 (3); 4103 (3); 4400 (2); 4401 (2); B. Balansa s.n., 09/1866 (2); 900 (2); Baldacci, A. 180 (2); 278 (4); N.P.W. Balke 0 05/08/1929 (3); s.n., 31/08/1937 (2); s.n., 30/07/1941 (3); E.B. Bangerter & E.W. Groves 286 (4); N. Barabas, D. Mititelu & V. Barabas 114 (H4); Y. Barkoudah 33 (3); K. Bauer & F. Spitzenberger 1923 (?); H. Bavelaar s.n., 07/1955 (3); s.n., 07/1955 (6); A. Becker s.n., 03/08/1878 (2); W.G. Beeftink s.n., 08/08/1960 (3); A. van der Beek s.n., 08/1967 (3); s.n., 07/1970 (2); s.n., 13/08/1970 (2); s.n., 17/09/1970 (3); s.n., 21/09/1970 (2); s.n., 11/07/1971 (3); 2846 (3); 3335 (6); Beelen, J. s.n., 09/09/1965 (3); Behrendsen s.n., 08/1883 (2); s.n., 08/1883 (4); s.n., 09/1913 (6); F.J. Benjamins s.n., 06/08/1915 (3); Bento Rainha 2734 (3); E. Bergmeier s.n., 07/07/1984 (2); s.n., 23/09/1984 (3)\*; s.n., 07/08/1986 (2); s.n., 08/08/1986 (6); s.n., 09/08/1986 (6); s.n., 15/08/1986 (6); s.n., 05/09/1986 (4); s.n., 20/09/1986 (6); s.n., 12/08/1987 (4)\*; s.n., 12/08/1987 (2); s.n., 11/08/1990 (H1); s.n., 08/09/1990 (2); 3819-23 (2); 3819-23 (3); 4519-43 (3); 4617-42 (3); 4918-22 (3); A. de Beyn s.n., s.d. (NBV 4936-80) (3); U.C. Bhattacharyya 45121 (2); F. Bianor s.n., 1911 (3); 1265 (3); S.H. Bickham s.n., 19/08/1869 (3); s.n., 15/08/1901 (3); 853 (3); C. Billot (Ayraud) 1904 (2); (Vendrely) 3741 (6); (Vendrely) 3742 (3); Billups 9/853 (3); 9/854 (3); W. Bird 64 A (?); K. Bisschop van Tuinen s.n., s.d. (NBV 8553.2) (3); s.n., s.d. (NBV) (3); s.n., 10/09/1868 (3); s.n., 07/1872 (3); Blaas s.n., 1852 (3); Blijdenstein s.n., 08/1900 (3); Bloembergen 1540 (3); 1630 (2); C. Blom s.n., 19/07/1947 (H2); A. Blonam (in hb. Bab.) s.n., 1864 (2); G. Bocquet 16892 (3); E. Boel, K. & S.S. Larsen 256 (2); J.G. Boerlage s.n., s.d. (NBV 4936-49) (3); s.n., 18/08/1871 (2); s.n., 08/1872 (3); s.n., 09/1892 (3); R. de Boer & A. Kooi s.n., s.d. (NBV 4936-106) (3); E. Boissier s.n., 1837 (2); s.n., 1837 (?); D. Bolten s.n., 24/07/1893 (3); R. Bondam s.n., s.d. (NBV 160) (2); s.n., s.d. (NBV 270) (6); s.n., s.d. (NBV 272) (6); s.n., s.d. (NBV 4936-37) (3); s.n., s.d. (NBV 4936-52) (3); s.n., s.d. (NBV 4936-54) (3); s.n., s.d. (NBV 4936-73) (3); s.n., s.d. (NBV 4936-81) (3); s.n., s.d. (NBV) (3); s.n., 09/1848 (3); s.n., 01/09/1848 (6); s.n., 08/1895 (3); (in hb. D. Lako) s.n., s.d. (HLB 926.350-54) (3); B.K. Boom 15131 (6); 20117 (3); B.K. Boom & S.J. van Ooststroom 12126 (3)\*; F. Boon s.n.,

14/08/1921 (2); Borczow s.n., 1852 (2); s.n., 01/08/1859 (2); A. Boriseva s.n., 27/07/1927 (6); 1284 (2); J. Bornmüller 207 (11); 562 (10); 564 (10); 614 (10); 4033 (2); J. & A. Bornmüller 7299 (2); 7377 (9); 7378 (9); 7380 (9); J. van Borssum Waalkes 5247 (6); 5778 (3); 5779 (3); 5780 (6); N.L. Bor 13188 (2); van den Bosch s.n., 1840 (?); (in hb. Coster) s.n., 1840 (3) van den Bosch, Knuttel, van der Sande Lacoste & Cop s.n., 24/07/1859 (3); v.d. Bosch, v.d. Sande Lacoste & Suringar s.n., 21/07/1860 (3); s.n., 20/07/1861 (2); Boswell-Syme s.n., 31/07/1871 (3); Botanisches Versandhaus (A. de Selmons) s.n., 1913 (?); W. Botschantsev & T. Egorova 1406 (10); 1485 (10); D.E. Boufford 21196 (2); Boursse-Wils s.n., s.d. (NBV 295) (?); s.n., 08/1740 (6); v. d. Bout s.n., s.d. (NBV 158+159) (2); C.G.S. Braat 432 (3); C. Brakman s.n., 12/08/1943 (3); P. Brakman 203 (H1); Brandhorst, Braun Blanquet, Siertsema & van Soest 9498 (3); J. Brand, J. s.n., s.d. (HLB 955.187-990) (2); s.n., 09/08/1915 (2); s.n., 23/07/1930 (3); R. Bremer s.n., 07/1976 (3); s.n., 26/07/1976 (3)\*; s.n., 11/08/1976 (3); 2 (3); 3 (3); 5 (3); I.P.M. Brenan & C.I. Sandwith s.n., 02/08/1934 (6); J.F. Brenckle s.n., 30/09/1912 (3); D. Brinton-Lee 999 (3); Britton s.n., 27/07/1910 (3); A.N.Ch. Broek t. 142 (3); 1334 (3); C. v. d. Broek s.n., 22/08/1882 (3); S.P. Brookes, R.S. Haddad & S.L. Jury 5668 (4); J. Bruinsma s.n., s.d. (6); s.n., 28/08/1985 (3); s.n., 29/08/1985 (3); s.n., 29/08/1985 (3); s.n., 02/09/1985 (3); s.n., 04/09/1985 (3); s.n., 10/09/1985 (3); s.n., 11/09/1985 (3); s.n., 20/09/1985 (3); s.n., 24/07/1986 (3); s.n., 25/07/1986 (2); s.n., 02/08/1986 (3)\*; s.n., 26/08/1986 (2); s.n., 29/09/1986 (3); s.n., 01/10/1986 (3); s.n., 08/10/1986 (2); s.n., 04/08/1987 (3); s.n., 28/12/1987 (3); s.n., 08/04/1988 (4); s.n., 04/09/1988 (3); s.n., 08/09/1988 (3); s.n., 19/09/1988 (3); s.n., 30/10/1988 (3); s.n., 14/12/1988 (2); s.n., 14/12/1988 (3); s.n., 21/12/1988 (3); s.n., 26/12/1988 (3); s.n., 1989 (?); s.n., 15/01/1989 (2); s.n., 18/01/1989 (3); s.n., 12/03/1989 (3); s.n., 02/08/1989 (3); s.n., 21/08/1989 (3); s.n., 28/08/1989 (3); s.n., 08/09/1989 (3); s.n., 08/09/1989 (3); s.n., 12/09/1989 (2); s.n., 12/09/1989 (2); s.n., 15/09/1989 (2); s.n., 19/09/1989 (3); s.n., 25/09/1989 (3); s.n., 25/09/1989 (3); s.n., 26/09/1989 (2); s.n., 28/09/1989 (?); s.n., 28/09/1989 (3); s.n., 28/09/1989 (3); s.n., 29/09/1989 (2); s.n., 29/09/1989 (3); s.n., 29/09/1989 (3); s.n., 04/10/1989 (3); s.n., 04/10/1989 (3); s.n., 04/10/1989 (3); s.n., 08/10/1989 (3); s.n., 20/10/1989 (3); s.n., 20/10/1989 (3); s.n., 29/11/1989 (3); s.n., 24/07/1990 (3); s.n., 31/07/1991 (3); s.n., 31/07/1991 (3); s.n., 09/08/1991 (3); s.n., 31/08/1991 (3); s.n., 14/09/1991 (3); s.n., 12/09/1993 (2); J. Bruinsma & J. Spronk s.n., 12/07/1994 (3); s.n., 30/07/1994 (3); H. de Bruyn s.n., 11/08/1944 (6); s.n., 27/08/1944 (2); s.n., 01/09/1944 (6); H. de Bruyn & W. Vervoort s.n., 15/07/1944 (4)\*; P. de Bruyne s.n., 05/08/1963 (3); G.J. v. Br. s.n., 05/09/1896 (2); s.n., 11/09/1896 (3); Buchenau s.n., 08/1871 (3); Buhse s.n., 07/1847 (6); s.n., 07/1847 (2); A. Bulavkina & Ikonnikov-Galitzky s.n., 15/06/1921 (6); Bunge s.n., 06/1858 (11); s.n., 28/07/1858 (2); J.E.L. & R.J. Burdon s.n., 27/09/1919 (2); Burkill Willis 115 (3); H.M. Burkill 1578 (3); L.H. Buse s.n., s.d. (NBV 4936-32) (3); 1941 (3); L.J.M. Butot s.n., 28/07/1944 (3); P. Buwalda 308 (3); M. Buysman 605 (3); 726 (2); 1043 (3); Bürgener s.n., 21/09/1924 (6); B.G. in hb. A.P. De Candolle s.n., s.d. (P 93-232) (3).

Caijiaux s.n., s.d. (NBV 268) (6); s.n., s.d. (NBV 4936-86) (3); J.A. Calder & R.L. Taylor 36971 (3); A. & C. Camus 1784 (3); Cannon & Kendrick 339 (3); Cantonspark Baarn '53- 973 (6); Capus 660 (11); 661 (9); Carnel s.n., s.d. (P) (3); Casborne s.n., 22/08/1832 (2); A.O. Chater s.n., 24/08/1978 (2); s.n., 24/08/1978 (3); Chavin s.n., s.d. (BM) (3); I. Chociatowski s.n., 1897 (5); J.R. Churchill s.n., 15/08/1922 (6); Ch.C. s.n., 08/1890 (2); s.n., 09/1892 (2); s.n., 09/1892 (3); E.W. Clason s.n., 18/07/1952 (3); s.n., 18/07/1953 (6); s.n., 30/07/1953 (2); s.n., 29/07/1955 (3); J. Comber s.n., 08/1912 (2); E. Cosson s.n., 17/08/1848 (3); s.n., 12/07/1861 (3); 18 (4); D.C. Coster s.n., s.d. (NBV 128) (2); s.n., s.d. (NBV 132) (2); R. van Crevel s.n., 08/1989 (6); s.n., 08/1989 (3); s.n., 08/1989 (2); s.n., 09/1989 (3); A.J. Crosfield s.n., 30/07/1910 (4); E. Czerniakowska 267 (2); & Reinecke 134 (6).

J.E. Dandy 1138 (H2); Danser (Jansen & Wachter) 2075 (6); Danser, Henrard & Kloos s.n., 11/07/1915 (2); Dassen s.n., s.d. (HLB 941.185-852) (3); P.H. Davis 14202 (3); 20765 (2); (T. Bent) 54976 (1)\*; P.H. Davis & I.C. Hedge 31432 (2); 32064 (2); 32064 (2); 32473 (5); P.H. Davis & O. Polunin 23008 2 (5); 24329 (5); 24329 (5); T.A.W. Davis s.n., 13/09/1962 (3); 62/572

- (2); M.A. Day 5 (3); A.P. De Candolle s.n., s.d. (HMP 93-232) (2); (Bot. Gall.) s.n., s.d. (HMP 93-232) (6); Delavray s.n., 06/08/1885 (2); T. Denters s.n., 20/08/1992 (3); F.A. Des Tombe 776 (6); (W.W. Schipper) 777 (6); 778 (3); G. Desplantes s.n., 09/09/1910 (3); P. Dieleman 338 (3); 373 (3); S.J. Dijkstra s.n., 04/08/1938 (3); 422 (3); 777 (3); 778 (6); 802 (6); 958 (2); 1128 (2); W.M. Docters van Leeuwen s.n., 06/08/1897 (3); W.F. Dorgelo s.n., 08/1920 (3); Dorsett & Morse 1133 (2); N. Downar s.n., 1862 (2); H. Duistermaat s.n., 12/07/1990 (3); 39 (3); 42 (3)\*; 43 (3)\*; 44 (3); 45 (3); 46 (3)\*; 47 (3)\*; 48 (2); 49 (H1); 50 (2); 51 (2); 52 (2); 53 (3)\*; 64 (3); 65 (3); 66 (3)\*; 93 (3); 96 (3)\*; 97 (3); 98 (3); 99 (3); 158 (3); 160 (4)\*; 161 (4)\*; 162 (3)\*; 163 (4)\*; 164 (4)\*; 165A (2); 165B (H2); 165C (H2); 165D (H2); 166 (4)\*; 167 (6); 168 (4)\*; 169 (4)\*; 170 (6); 171 (4)\*; 172 (4)\*; 173 (4)\*; 174 (4)\*; 175 (3)\*; 176 (3)\*; 177 (3)\*; 178 (3)\*; 179 (3)\*; 180 (3)\*; 181 (3)\*; 182 (3)\*; 183 (3)\*; 192 (3)\*; 193 (3)\*; 194 (3)\*; 195 (6); 196 (2); 225 (2); H. Duistermaat & J. Bruinsma 73 (3); 74 (3); 75 (3); 76 (3); 77 (3); 78A (2); 78B (2); 79 (3); 80 (2); H. Duistermaat, J. Cortenraad & R. van der Meijden 59 (3); 60 (H1); 61 (H1); 62 (3)\*; 68 (4); 69 (4); 70 (4); 71 (3); H. Duistermaat, J. Cortenraad & T. Mulder 188 (3)\*; 189 (3)\*; 190 (6); 191 (2); H. Duistermaat & R. van der Meijden 72 (2); H. Duistermaat & A. Nieuwenhuijs 81 (6); 82 (6); 83 (6); 84 (6); 85 (6); 86 (6); 87 (6); 88 (6); 89 (6); 90 (6); 91 (6); H. Duistermaat, S. Postma, J.J. Vermeulen & M. Sosef 224 (6); H. Duistermaat & R.M.v. Urk 148 (3); 149 (3); 150 (3)\*; 151 (3)\*; 152 (3)\*; 153 (3); 154 (3); 155 (3); 156 (3)\*; H. Duistermaat & J.J. Vermeulen 15 (3)\*; 16 (3); 17 (3); 31 (3); 33 (3); 34 (3); 35 (3); 37 (3)\*; 54 (3); 55 (2); 56 (3)\*; 57 (2); 58 (3); 102 (3); 103 (3); 104 (3); 105 (3); 106 (3)\*; 107 (3)\*; 108 (3); 109 (3); 110 (3); 111 (3); 112 (3); 113 (3); 114 (3); 115 (3); 116 (3)\*; 117 (3); 118 (3); 119 (3); 120 (3); 121 (3); 122 (3); 123 (3); 124 (3); 125 (3); 126 (3)\*; 127 (3)\*; 128 (3); 129 (3)\*; 130 (2); 131 (3)\*; 132 (3)\*; 133 (H4); 134 (H4); 135 (2); 136 (2); 137 (2); 138 (3); 139 (3); 140 (3); 141 (3); 142 (6); 143 (6); 144 (3); 145 (3); 146 (3); 147 (6); 157 (3); 159 (3); 184 (4)\*; 185 (4)\*; 186 (4)\*; 187 (4)\*; W. Dybowski s.n., 20/00/1894 (2); 650 (2); 651 (H2); 745 (6); 836 (3); S. Dzevanovsky s.n., 02/./1925 (2).
- H. Ebberts s.n., 1990 (2); s.n., 1990 (3); J.R. Edmondson 1314 (11); G.Ch. Ehrenberg s.n., 06/1824 (3); E. Ellman & N.Y. Sandwith 1231 (6); W.C. van Embden s.n., 05/09 (2); s.n., 22/07/1902 (6); s.n., 09/1902 (2); s.n., 08/07/1907 (6); Erab. 239 (3); J. Erikson s.n., 07/1906 (3); s.n., 27/08/1915 (H2); s.n., 27/08/1915 (2); s.n., 08/1918 (6); s.n., 08/1928 (6); P.V. Estival 581 (3); A.H. Evans s.n., 19/08/ (3); s.n., 20/07/1949 (3); (Lejeune & Courtois) s.n., s.d. (HMB 43196) (?); E. Everts s.n., s.d. (HLB 908.359-25) (6); s.n., s.d. (HLB 908.359-38) (6); s.n., s.d. (HLB 908.359-39) (3); s.n., /08/ (2); Excursie N.B.V. s.n., 15/08/1911 (2); Exc. Leidsche biol. 3949 (3); Exc. Plantenk. s.n., 14/07/1903 (2); P.J. Eyma 44 (3); E.S.M. s.n., 07/08/1887 (3); s.n., 11/08/1887 (3); s.n., 03/08/1888 (3); s.n., 09/07/1889 (2); s.n., 02/09/1889 (2); s.n., 15/07/1893 (4); 2568 (3); v. E. s.n., 08/1871 (3).
- C.S. Fan & Y.Y. Li 349 (2); A. Faure s.n., 24/08/1932 (1); Faurie 735 (2); 736 (2); B.A. Fedtschenko (A.I. Michelson) s.n., 15/08/1901 (2); 340A (10); 1939 (2); (A.I. Michelson) 2111 (10); (A.I. Michelson) 2435 (11); B.A. Fedtschenko et al. 274 (2); 331 (6); 335 (6); O.A. Fedtschenko s.n., 15/07/1897 (2); s.n., 14/08/1901 (11); O.A. Fedtschenko & B.A. Fedtschenko s.n., 09/07/1891 (3); s.n., 10/07/1891 (2); s.n., 11/07/1891 (2); s.n., 22/07/1891 (2); s.n., 25/07/1893 (2); Feuilleaubois s.n., s.d. (HLB 902800) (3); s.n., 28/07/1878 (4); (Nauol) s.n., 09/1890 (2); Fiet s.n., 23/07/1902 (3); Figert 1309 (H4); 1310 (6); 1311 (?); A. Fiori 383 (4); 384 (4); 1170 (6); Fischer s.n., 1859 (2); s.n., 1859 (6); s.n., 21/09/1924 (6); Flora Belgii Septentrionalis s.n., s.d. (NBV 150) (?); Floron s.n., 27/07/1989 (3); A.D. Fokin 63 (6); 116 (2); Font Quer. 685 (3); W. Forstner s.n., 17/10/1965 (H4); s.n., 11/10/1966 (3); Fowles 54 (3); A. Franchet s.n., 08/1894 (6); D. Franke & D.T.E. van der Ploeg s.n., 23/07/1957 (6); s.n., 29/07/1957 (6); Fraser s.n., 07/09/1877 (2); Fries XIII no 6 (3); E.Th. Fries s.n., 09/1902 (2); Fritzsche & Stiefelhagen 1218 (6); 1220B (H1); Frivald s.n., s.d. (LE s.n.) (2); H. Fürth s.n., 08/1956 (3).
- H. Gaasenbeek s.n., 12/08/1971 (3); s.n., 12/08/1971 (3); Gandoger s.n., s.d. (HBPV 1888-9427 (3)); S.S. Ganesjien s.n., 11/07/1924 (2); E.A. Garcavi 217 (6); M.F. & S.G. Gardner 3281

(2); Garjeanne s.n., s.d. (NBV 127) (2); s.n., 07/1891 (3); Gatt s.n., 1801 (2); M.B. Gerrans 736 (3); Gibbons 6 (2); Gibson (in hb Babington) s.n., 25/07/1856 (3); J. van Giersbergen & A.W. Kloos jr. s.n., 07/08/1936 (3); Gladkova & Leonova 154 (2); Goethart & Jongen s.n., s.d. (NBV 903.40-698) (3); Goethart, Jong & Vuyck s.n., s.d. (NBV 903.40-698) (3); N. Gontscharow & V. Michajlovski 107 (11); A.C.J. van Goor s.n., 08/1899 (3); M. Gortani 1170 (6); A. Gorter 1145 (3); 1592 (3); A. Gorter, P. van Nieuwenhoven & M. Maas 2097 (6); T. Gottenbos s.n., 21/07/1963 (2); Grantzow s.n., 07/1862 (4); M.L. Grant 17689 (9); Graven s.n., 30/07/1899 (3); T. Gregor s.n., s.d. (3); S. Grigorjev s.n., 30/07/1894 (2); s.n., 02/07/1897 (6); 184 (2); H.W. Groll s.n., 16/08/1871 (3); s.n., 1879 (3); s.n., 24/07/1891 (3); L. Gross s.n., 26/07/1904 (6); s.n., 27/07/1904 (2); E.W. Groves 797 (3); 2670 (4); Guétrot, plantes hybrides de France (Fouillade) 81 (2); F. Guiol 717 (3); Guirao s.n., 07/1894 (3); Gunz., E. s.n., 10/09/1879 (4); Gussev, J.D. 18 (3); 104 (6); 106 (2); 180 (2); 407 (6); 461 (3); G.B. in hb. Bisschop 2650 (3).

van Hall s.n., s.d. (NBV 129) (2); s.n., s.d. (NBV 4936-30) (3); s.n., 08/1828 (3); s.n., 1834 (3); L. van der Hammen s.n., 08/08/1976 (3); R.W.J.M. van der Ham s.n., 02/09/1980 (6); s.n., 23/06/1982 (6); s.n., 06/09/1982 (3); Hanburry s.n., 07/1872 (3); F.A. Hanbury s.n., 07/1863 (2); s.n., 27/07/1891 (3); M. Haradjian 549 (2); Haring s.n., 08/1833 (3); Hariot s.n., 21/07/1912 (6); I.H.A.E. Harshagen s.n., 07/1964 (3); s.n., 08/1966 (3); A. Harting s.n., 04/07/1857 (3); s.n., 06/07/1857 (3); A. Hartog s.n., s.d. (3); s.n., s.d. (2); s.n., 1976 (3); s.n., 01/09/1976 (3); s.n., 01/09/1976 (?); s.n., 01/09/1976 (2); F.A. Hartsen s.n., 22/08/1857 (6); J.K. Hasskarl s.n., 08/ (2); T.A. Hattink s.n., s.d. (3); s.n., 26/08/1981 (3); 723 (3); H.J. van Hatum 656 (3); 665 (3); 691 (3); 2534 (3); 4769 (3); 5404 (2); C. Haussknecht s.n., 1865 (2); s.n., 07/1868 (9); R. Haveman 346 (3); 593 (2); R. Haveman & K. Meijer 583 (3); , A. & F. v. Hayek 691 (4)\*; E. Hällström s.n., 11/07/1953 (3); Hb. Amsterdam s.n., s.d. (NBV 286) (3); s.n., s.d. (NBV 287) (?); Hb. Franeker s.n., s.d. (HLB 14) (6); Hb. Hortus Pisani s.n., 1869 (3); Hb. Persoon s.n., s.d. (HLB 900.74-216) (3); van Heijningen s.n., s.d. (NBV 4936-60) (3); Heiland s.n., 08/1878 (4); F. Hekker s.n., 16/07/1963 (3); s.n., 17/07/1963 (6); s.n., 05/08/1973 (3); W.H.A. Hekking s.n., 30/08/1955 (3); s.n., 31/08/1955 (3); s.n., 26/07/1958 (2); s.n., 26/09/1959 (2); W.H.C. Hekking 1959 (3); J.C. de Hek 401 (3); Heldreich s.n., 31/07/1871 (3); Henrard s.n., 08/1909 (2); Henslow s.n., 12/08/1824 (3); Heribaud s.n., 08/07/1894 (3); A. Hertog s.n., 01/09/1976 (3); s.n., 13/07/1989 (4)\*; Herzing s.n., 08/1900 (4); P. Hessel, J. Klein & W.V. Rubers 1493 (3)\*; H. Heukels s.n., s.d. (NBV 4936-57) (3); P. Heukels 1639 (6); 1868 (3); van Heurck 33 (3); W.C. van Heurn s.n., 05/1940 (3); s.n., 05/08/1940 (6); T. Heydeman & J. Isaev s.n., 23/07/1931 (2); s.n., 23/07/1931 (5); Hérault s.n., 10/08/1887 (3); G. Hibon 2375 (4); 2376 (4); E. Hodgson s.n., 18/07/1959 (6); K. Hoek s.n., 03/10/1974 (3); Hohenacker 357 (3); 650 (6); 651 (6); Holkema s.n., 28/09/1863 (3); L. Holm-Nielsen & P. Pedersen 642 (2); L.B. Holthuis s.n., 10/08/1939 (3); W. Holverda s.n., 20/08/19.. (3); D.A. Hoogbruijn s.n., 08/1871 (3); R.D. Hoogland 2539 (3); 1947-282 (6); 1947-335 (3); 1947-336 (2); 1947-337 (2); J.J. Hooker s.n., s.d. (HLB 900.74-209) (2); s.n., s.d. (P) (2); W.H. Horr 3181 (3); van Hoven s.n., 1847 (2); J.J. Huizing s.n., 16/11/1953 (2); F.W.T. Hunger s.n., 08/1894 (3); s.n., 19/04/1905 (3).

H. Icke s.n., 24/07/1903 (2); J. van Iersel s.n., 07/1938 (3); Iljin 60 (3); A.P. Iljinskii s.n., 12/07/1912 (6); B. Ingenhousz & H. Korthof s.n., 26/08/1981 (3); Inst. v. Prehistorie 110 (3); 430 (2); 513 (3); Iranshahr 34038 E (11); Iranshahr & Moussari 34002 E (9); Irvine 687 (3); W. Iven s.n., 11/09/1979 (2); s.n., 11/09/1979 (6).

J.J. Jackson s.n., 14/08/1881 (2); Jacquet s.n., s.d. (HASP) (6); s.n., s.d. (HASP) (3); E. Jahandiez 626 (1); 737 (1)\*; A. Janata s.n., 05/1969 (11); Jansen, Kern, Kloos & Reichgelt s.n., 07/08/1930 (6); Jansen, Kloos, Kern & Reichgelt s.n., 07/08/1930 (2); Jansen, van Ooststroom, Reichgelt & van der Ploeg 1363-1 (6); 1363-2 (6); 1363-3 (6); 1363-4 (6); 1363-65-1 (H4); 1363-65-2 (H4); Jansen & Wachter s.n., 08/1933 (?); 3340 (6); 3341 (3); 3342 (3); 5056 (6); 9234 (2); 20701A (3); 20701B (3); 20702 (3); 20703 (6); 20704 (6); 20705A (6); 20705B (6); H. Jansen s.n., 20/08/1985 (2); J. Jansen s.n., 09/09/1946 (3); (Unio) s.n., 08/1931 (2); J. Jansen & P. Ruigrok s.n., 16/08/1947 (3); J. Jansen & J.G. Sloff s.n., 02/08/1935 (3); s.n.,

04/08/1935 (2); N.J.L. Jansonius s.n., 16/07/1950 (6); N. Jardine 866 (2); Jeanpert s.n., 02/08/1897 (6); s.n., 29/09/18.. (2); s.n., 09/1907 (6); s.n., 08/1908 (6); s.n., 15/07/1915 (6); V. Jehlík & A. Radkowsch s.n., 13/07/1989 (3); H. Jerónimo 231 (3); Johansson s.n., 08/1903 (2); G. Johansson s.n., 07/1890 (4); s.n., 08/1914 (6); J.W. Jongepier s.n., 02/08/1980 (2); s.n., 14/10/1980 (3); s.n., 18/08/1981 (3); s.n., 30/07/1990 (3); s.n., 04/08/1990 (3); , S.E. de Jongh jr. s.n., 1933 (2); s.n., 1945 (3); s.n., 1945 (2); s.n., 1948 (6); s.n., 1950 (3); s.n., 16/07/1950 (3); s.n., 1955 (3); s.n., 22/06/1957 (H2); s.n., 16/07/1960 (6); S.E. de Jongh jr. & Kloos s.n., 05/08/1937 (2); A.H.C. Jonkindt Coninck s.n., 14/08/1869 (3); Joruan s.n., 02/08/1941 (2); W.B. Jurvill s.n., 02/08/1956 (3); A. de Jussieu s.n., 07/1837 (4); S. Juzepczuk 157 (10); 162 (H6); 173 (10); 318 (H6); 3089 (2); 3108 (2).

Kappel s.n., 19/07/1908 (4)\*; C. Kausch s.n., 1885 (2); s.n., 1885 (3); L. Keller s.n., 08/1891 (6); Kendrick & Moyes 60 (3); 489 (3); G.J. Kerbert s.n., s.d. (NBV 4936-56) (3); s.n., s.d. (NBV 4936-97) (3); J. Kern s.n., 1920 (3); 595 (3); 596 15/09/1936 (3); 2836 (4); 9339 (4); 19321 (3); 19389 (4)\*; J. Kern & B. Reichgelt s.n., 23/08/1924 (3); 597 (3); 598 (3); 9335 (3); J. Kern & Th. Reichgelt s.n., 02/08/1928 (6); s.n., 04/08/1949 (2); 495 (2); 504 (2); 505 (2); 506 (2); 590 (6); 591 (6); 592 (2); 593 (2); 594 (3); 4586 (6); 5845 (6); 9336 (3); 9337 (3); 9341 (6); 9342 (3); 9343 (6); 9344 (2); 9347 (6); 9357 (6); 9358 (6); 9360 (6); 13223 (6); 16633 (4)\*; 19322 (2); 19323 (3); 19700 (3); J. Kern, Th. Reichgelt & J. Jansen s.n., 06/08/1943 (6); J. Kers 1306 (3); Kielloman s.n., 21/07/1885 (2); s.n., 26/07/1887 (2); N. Kierkegaard s.n., 30/07/1949 (H1); H.C. Kindberg s.n., 14/08/1919 (H4); J. Kirk (in hb Babington) s.n., 09/1834 (3); M.D. Kirk 114 (3)\*; Klinkert s.n., s.d. (HBU 046051) (3); s.n., s.d. (HBU 046051) (2); A.W. Kloos jr. s.n., 08/09/1913 (2); s.n., 08/09/1913 (3); s.n., 08/1914 (3); s.n., 03/08/1915 (3); s.n., 16/08/1918 (3); s.n., 31/08/1919 (2); s.n., 02/06/1920 (3); s.n., 20/07/1920 (3); s.n., 28/07/1920 (3); s.n., 30/07/1920 (6); s.n., 09/1927 (3); s.n., 04/08/1931 (3); s.n., 09/08/1931 (3); s.n., 24/08/1947 (6); A.W. Kloos jr. & van Soest 4628 (3); 4635 (3); O. von Knorring 682 (?); O. von Knorring & Z. von Minkwitz 1393 (?); J.D. Kobus s.n., 07/1877 (?); 328 (3); W.D.J. Koch s.n., s.d. (HLB 909.244-728) (6); s.n., s.d. (HLB 909.244-731) (3); s.n., 1849 (2); (Anon.) s.n., s.d. (HLB 909.244-583) (2); W. Koelz 13048 (10); 13092 (?); 13714 (11); 14111 (11); 15873 (9); 16211 (?); 16578 (H3); W.N. Koelz 18063 (9); 18453 (2); 18626 (9); H.J. Kok Ankersmit s.n., s.d. (09926 B) (3); s.n., s.d. (BMU 09927) (6); s.n., s.d. (BMU 9925 B) (2); s.n., 13/08/1851 (3); s.n., 28/10/1851 (3); s.n., 05/08/1877 (2); s.n., 07/1878 (6); s.n., 07/1879 (3); s.n., 13/08/1879 (3); s.n., 02/08/1897 (3); s.n., 1898 (6); (Kern & Reichgelt sub 9345) s.n., 08/1881 (2); Kolenati 1025 (5); 2070 (5); W.J.C. Kooper s.n., 07/1919 (2); D. Koopmans-Forstmann & A.N. Koopmans s.n., 24/07/1928 (3); s.n., 08/1931 (2); s.n., 27/08/1931 (2); s.n., 29/08/1931 (3); 155 (3); 1929-738 (3); 1930-527a (3); 1930-564 (3); 1931-602 (3); J. Koornneef s.n., s.d. (NBV 4936-20) (3); s.n., 08/1922 (6); J. van der Kooy s.n., 01/08/1976 (3); s.n., 03/08/1976 (3); s.n., 12/08/1976 (3); A.H. Koper s.n., 08/08/1990 (3)\*; s.n., 20/08/1990 (3); s.n., 21/08/1990 (3); S. Korshinsky s.n., 15/07/1884 (2); s.n., 29/07/1884 (2); s.n., 27/08/1884 (2); s.n., 08/07/1885 (2); s.n., 13/07/1885 (2); s.n., 22/07/1885 (2); 1711 (2); C. Kossinski 300 (2); 634 (3); 804 (2); J.Th. Koster 3488 (3); 3621 (3); T. Kotschy s.n., 07/1843 (9); s.n., 20/08/1859 (2); 356 (2); 425 (9); 735 (9); Kouh-Tchehel Dokhteran 610 (11); W. Kozlowsky s.n., 05/08/1920 (2); E. Köhler s.n., 09/1902 (H2); Körnicke s.n., s.d. (HLB 900.74-237) (4); s.n., 08/1857 (2); s.n., 17/07/1864 (4); s.n., 29/07/1864 (4)\*; s.n., 29/08/1868 (4); K.V. Kramer 104 (2); 463 (6); H. Krascheninikov 5240 (8); Krassnow s.n., 1885 (2); Krause s.n., s.d. (LE) (11); W. Kreczetowicz 937 (2); J. Kroon s.n., 20/01/1991 (3); J.D. Kruijer s.n., 15/08/1990 (6); 1 (3); 2 (3); 8 (3); G. Kruseman s.n., 10/08/1927 (3); G. Kruseman & J.G. Stoff s.n., 29/07/1934 (3); H. Kuhbier s.n., 15/07/1990 (6); Kunovsky 639 (2); Kühlewein s.n., s.d. (P) (3); G. Küenthal 64 (11).

LEP (R. Hegnauer) 4948 (3); (R. Hegnauer & J.H. Wieffering) 5011 (3); (H. Ruychrok & H.P. Nooteboom) 5411 (2); (R. & M. 44) 5413 (3); (J.H. Wieffering) 6891 (3); 7121 (3); 7172 (?); (G.A. Jasperse) 16695 (3); (R. Hegnauer) 16697 (2); (R. Hegnauer) 16698 (3); (F. Struykenkamp) 16699 (6); (R. Hegnauer) 16700 (3); (G.A. Jasperse) 16701 (3); (J.B. Haag) 16702 (3); (R. Hegnauer) 16704 (6); (R. Hegnauer) 16705 (2); (R. Hegnauer) 16706 (3); (R. Heg-

- nauer) 16707 (3); (R. Hegnauer) 16708 (3); (R. Hegnauer) 16709 (3); 16710 (3); (R. Hegnauer) 16711 (3); (J.H. Wieffering) 21478 (3); (Excursie Wales) 24756 (3); (R. Hegnauer) 27677 (3); D. van der Laan s.n., 10/1990 (3); Labohm s.n., 07/1946 (6); D. Lako s.n., 28/07/1867 (2); s.n., 08/1878 (3); s.n., 08/1887 (3); s.n., 09/1892 (3); s.n., 08/1893 (3); s.n., 09/1893 (3); s.n., 09/1893 (?); s.n., 09/1894 (2); s.n., 08/1898 (6); s.n., 08/1905 (3); s.n., 08/1910 (3); (in hb. Schipper) s.n., 07/1910 (2); J. Lambinon 11739 (2); 12583 (4); 12584 (3); H. Lammers s.n., 21/08/1980 (3); R. Lampinen 3250 (H2); 3349 (3); 3660 (2); R. Lampinen & T. 3496 (6); C. Langeveld 1 (3); 2 (3); 3 (3); W. Lang s.n., 23/07/1990 (6); J. Lange s.n., s.d. (HASP) (3); s.n., s.d. (HMPV 1889-21792) (4); s.n., 19/09/1851 (3); s.n., 07/1857 (3); s.n., 07/1857 (4); s.n., 20/08/1871 (2); s.n., 01/09/1881 (4)\*; 320 (2); 439 (3); R. Larsson s.n., 08/1904 (4)\*; Laurellard s.n., 08/1905 (3); Laurillard s.n., 09/1902 (3); Ledebour 181 (8); 559.1 (2); A.J.M. Leeuwenberg s.n., 24/08/1953 (3); W.C. de Leeuw s.n., 21/07/1928 (3)\*; C. Legros s.n., 07/07/1929 (4); Lejeune s.n., s.d. (HMPV 1889-341709) (4); 787 (3); Lejeune & Courtois 129 (6); 129 (2); 787 (3)\*; 788 (2); Lemann s.n., 08/1846 (3); J.F. Leve in hb. v.d. Ploeg s.n., 07/07/1959 (3); J. Lewalle 12189 (1); Libbenga 179 (4); A.S.N. Liem s.n., 25/08/1965 (6); Limdiau s.n., 08/1906 (6); H. Lindberg s.n., 24/07/1926 (3); 985 (3); K. Lindberg 873 (10); Lindemann s.n., 20/07/1865 (6); s.n., 1871 (6); s.n., 08/07/1884 (2); E. Lindeman s.n., 02/08/1937 (3); J.C. Lindeman & J.H. de Haas 3247 (3); N. Lindsay 1267 (2); K. Linkola 1397 (2); Lipski 766 (7); Little s.n., 10/08/1892 (3); s.n., 03/08/1912 (3); s.n., 05/08/1912 (3); D. Litwinow s.n., 01/07/1916 (2); 1527 (11); 1589 (11); J. Lloyd s.n., 16/08/1890 (2); G. Lorinser s.n., s.d. (HLB 900.74-204) (6); Lousley 720 (3); A. Louwe Kooymans s.n., 08/08/1994 (3); Loway s.n., 16/08/1884 (3); R.T. Lowe s.n., 29/07/1832 (3); s.n., 18/07/1833 (3); D. Lumeunov s.n., 06/1899 (11).
- R.A. Maas Geesteranus 4283 (3); Maass s.n., 08/1883 (4); Maires s.n., s.d. (NBV 309) (6); E.E. Maire s.n., 08/1910 (2); 565 (2); M.O. Malte 632 23 (3); I. Mandenova & S. Kuthatheladze s.n., 11/08/1952 (2); G. Mandon s.n., 07/1866 (3); Marcowicz s.n., 24/09/1899 (5); s.n., 1900 (5); s.n., 08/1900 (5); 927 (5); U. v. d. Mark s.n., 08/1954 (3); E.S. Marshall 726 (3); W. Marshall s.n., 1877 (2); N.H. Mason s.n., 1856 (3); s.n., 07/1856 (3); 92 (3); Matveeva, Rodin & Schiptschinskii 152 (6); Matveeva & Schiptschinskii 16 (6); Maximowicz s.n., 1862 (2); McArthur 17A (11); R. van der Meijden s.n., 08/08/1973 (3); s.n., 26/08/1975 (3); s.n., 12/08/1985 (3); s.n., 07/1989 (6); 12/07/1989-A (4)\*; 12/07/1989-B (4)\*; s.n., 24/07/1993 (6); Meijer s.n., s.d. (HASP) (H4); E. Meijer Drees 294 (6); 417 (2); Meijer in hb. W.D.J. Koch s.n., s.d. (HLB 909.244-577) (3); K. Meijer s.n., 10/08/1991 (3); 1080 (3); 1081 (3); 1082 (3); 1083 (3); 1084 (3)\*; 1085 (3)\*; 1086 (3); 1087 (3); 1088 (3); 1089 (4); 1090 (3)\*; 1091 (2); 1092 (3); 1093 (3); 1258 (3); 1278 (6); 1279 (6); 1280 (3); 1281 (6); 1282 (3); R.S. Meikle s.n., 02/08/1956 (3); Meinshausen s.n., /07/ (2); s.n., 1860 (6); 348B (6); Meissner s.n., 03/08/1869 (4); J.C. Melvill 293 (3); Menell s.n., 09/1882 (3); E.A. Mennega s.n., 26/08/1949 (2); 666 (3); Mennell s.n., 09/1882 (3); J. Mennema 1632 (2); Mertens s.n., s.d. (LE) (6); Meyer s.n., s.d. (HLB 909.244-725) (2); Michelson s.n., 23/08/1903 (3); s.n., 16/07/1915 (2); s.n., 10/08/1915 (3); Mills s.n., s.d. (HMB 43227) (3); B (3); C (3); D (3); Z. von Minkwitz s.n., 29/06/1918 (6); 887 (2); 910 (2); 1398 (2); 1548 (2); D. Mititelu, N. Barabas & L. Mititelu 308 (3); A.L. & H.N. Moldenke 30954 (3); H.N. Moldenke 7434 (3); G.A.F. Molengraaff s.n., 07/1857 (2); s.n., 07/1857 (3); Molkenboer s.n., s.d. (NBV 151) (2); s.n., 07/1835 (3); s.n., 08/1835 (3); s.n., 08/1838 (6); Moll s.n., 27/07/1874 (2); V.A. Monjoesjko 1427 (2); Montmorrency s.n., 1840 (4); More s.n., 08/1859 (3); T. Morong s.n., 16/07/1885 (6); Morton 3555 (11); C.E. Moss s.n., 02/08/1912 (2); H. Möller s.n., 11/08/1894 (H4); Muster s.n., 07/1915 (6).
- E.T. Nannenga s.n., 18/08/1934 (6); N.E. Nannenga-Bremekamp s.n., 17/08/1936 (3); s.n., 25/07/1941 (6); s.n., 19/09/1941 (2); M.I. Nasarow 3223 (2); 3226 (2); 5331 (2); 6057 (2); 6201 (2); W.L. Nekrassowa 21 (3); 39 (2); G.N. Nepli s.n., 29/05/1929 (11); H.F. Neubauer 3160 (11); W.W. Newbould s.n., s.d. (CGE) (4); (in hb. Bab.) s.n., 1844 (2); Niemann s.n., 22/06/1898 (3); s.n., 02/08/1898 (6); J. Noorman 3 (2); H.P. Nooteboom 164 (6); 177 (6); Nyman s.n., s.d. (P) (6); N.J. s.n., 01/09/1850 (3).

- O.A. Obrabotano & B.A. Fedtschenko s.n., s.d. (HBIP) (2); A. Ogterop s.n., 13/08/1890 (3); s.n., 07/1892 (3); s.n., 29/07/1892 (3); s.n., 08/1894 (2); V.J. Oinonen s.n., 08/08/1963 (3); s.n., 27/07/1964 (3); S.J. van Ooststroom 1987 (3); 3586 (3); 3744 (4); 6285 (3)\*; 6785 (2); 6830 (3)\*; 7206 (6); 7962 (3); 7965 (2); 7980 (3); 7994 (2); 9021 (6); 9230 (6); 10838 (3)\*; 10839 (3)\*; 11014 (6); 14929 (3); 15233 (3); 17372 (3); 18600 (6); 18601 (H4); 19831 (2); 19832 (2); 21483 (3); 21509 (3); S.J. van Ooststroom & Reichgelt 23359 (6); Otten & Brugman s.n., 23/06/1904 (?); B.G. Otten s.n., 08/08/1989 (3); s.n., 21/08/1989 (3); C.A.J.A. Oudemans s.n., 1835 (3); s.n., 1843 (2); s.n., 08/1859 (3); s.n., 08/1861 (3); s.n., 09/1863 (3); s.n., 10/1863 (6); s.n., 10/1863 (3); s.n., 08/1864 (3); s.n., 11/08/1870 (3); s.n., 25/08/1870 (2); s.n., 08/1872 (6); s.n., 08/1876 (3); 581 (3); 589 (2); P.N. Ovczinnikov & K.S. Afanassjev 438 (10).
- I. Paczowski s.n., 05/07/1892 (3); Pallas s.n., 19-BM (2); Pankhurst 83-16 (3); R.J. Pankhurst & P.W. James 83 (11); J. Pape & J.G. Sloff s.n., 07/08/1936 (2); A.R. Paul s.n., 08/1909 (3); Pavkova 9 (5); Pavnov 1014 (2); 1162 (2); J.P.D.W. Payens 35 (3); T.M. Pedersen 11374 (3); Perin s.n., /09/ (?) ; Perring s.n., 10/09/1961 (2); 3 (2); Persoon s.n., s.d. (HLB 900.74-246) (6); s.n., s.d. (HLB 900.74-250) (2); Petrak s.n., 08/1914 (4); W.A. Petrov s.n., 07/08/1909 (2); H.J. Petten s.n., 31/08/1891 (3); J.J. Piet s.n., 19/07/1952 (6); L.H.W. van der Plas s.n., 23/07/1967 (3)\*; D.T.E. van der Ploeg s.n., 22/08/1969 (2); s.n., 09/1969 (2); 1365 (3)\*; 1365-1 (3); 1366 (3); 1366-1 (3); 1366-2 (3); 1366-3 (3); 1366-4 (3); 1367-1 (2); D. Podlech 11686 (11); 15956 (11); A. Polatschek s.n., 07/09/1976 (3); s.n., 08/08/1978 (3); s.n., 09/08/1980 (3)\*; s.n., 22/08/1980 (3)\*; s.n., 07/1981 (3); s.n., 18/07/1981 (4); s.n., 04/08/1985 (4)\*; s.n., 02/09/1987 (H4); H. Poplawska 447 (4); Popov s.n., 13/08/1913 (6); C.M.L. Poppta s.n., 07/09/1892 (4); s.n., 21/07/1901 (6); A. Poretzky s.n., 30/07/1927 (3); s.n., 01/08/1927 (2); 797 (6); G.N. Potanin s.n., 24/07/1876 (6); H. Prell s.n., 12/08/1978 (3); s.n., 02/09/1978 (3); J. Prins 293 (3); 699 (6); 857 (3); E. Psarides s.n., 1868 (3); Puget s.n., 07/1862 (4); N. Puring s.n., 10/08/1895 (2); s.n., 08/07/1896 (2); s.n., 27/07/1897 (2); s.n., 04/08/1900 (2).
- A.E. Radford 45034 (3); B.V. Rainha 6212 (3); J. Ramsbottom s.n., 1917 (2); R. Rapaiacs 590 (4); Raven & Cannon 16440 (3); H. Raven s.n., 15/08/1990 (2); 1 (3); 2 (3); 3 (3); 3 (3); K.H. Reching s.n., 16/09/1942 (4); 519 (9); 616 (9); (Barum) 1745 (11); (E. Gauba) 1769 (11); 2034 (2); 11029 (3); 16228 (11); 16473 (11); 18267 (2); 32927 (2); 34043 (11); 37696 (5); 38667 (3); (J. Lamond & M. Iranshahr) 40825 (9); 48914 (2); K.H. & F. Reching (Aellen, P.) 4640 (11); (Aellen, P.) 4963 (11); 5004 (11); (Aellen, P.) 5044 (11); 5695 (6); 5788 (2); 6261 (2); 10588 (4); A. Regel s.n., 29/07/1867 (6); s.n., 09/1876 (6); s.n., 05/07/1877 (2); s.n., 06/1883 (11); Th. Reichgelt s.n., 08/1963 (3); s.n., 08/1963 (2); P.R. Reitz 6622 (3); E. Reverchon s.n., 07/1907 (3)\*; 439 (3); 1389 (3); Rhätische excursie 1932 279 (3); P.A. Richard s.n., 24/07/1845 (3); J. Ridder-Numan s.n., 08/1990 (3); H.J. Riddlesell s.n., 07/08/1909 (2); G.A. Ringselle 0 03/08/1927 (3); s.n., 29/07/1929 (3)\*; L. Rodin & D. Lebedev 251 (2); 253 (6); J.G. Roeleveld 7149 (3); A.P. Roesaljejev (Fokin) 354 (2); Rombouts s.n., 1838 (2); s.n., 07/1838 (3); R.J. Roshevitz 245 (6); 1661 (6); 1832 (6); E. Rostan s.n., 07/1859 (4); s.n., 1880 (3); G. Rouy (A. Guinet) s.n., 17/08/1879 (4); E. Roy 3294 (2); 3868 (2); 4155 (3); P. van Royen 98 (3)\*; 2051 (6); Rozema 1 (3); 2 (3); 3 (3); 4 (3); 5 (3); Ruprecht 43 (5); J.M. Ruys s.n., 05/08/1891 (2).
- L. Sambon s.n., 10/1924 (3); G. Samuelsson 1569 (2); (O.J. Hasslow) 1570 (2); (O.J. Hasslow) 1571 (H2); (E. Asplund) 1572 (3); (R. Ohlsén) 1573 (6); (O.J. Hasslow) 1574 (3); (V. Samuelsson) 1575 (6); C.M. van der Sande Lacoste s.n., s.d. (NBV 294) (6); s.n., s.d. (NBV 4936-45) (3); s.n., 20/07/1858 (3); s.n., 09/1885 (2); 895 (2); C.M. van der Sande Lacoste, Rombouts & Merkus Doornik s.n., s.d. (NBV 133) (2); s.n., s.d. (NBV 4936-31) (4); C.M. van der Sande Lacoste & W.F.R. Suringar s.n., 10/07/1859 (3); C.I. Sandwith s.n., 06/08/1915 (2); s.n., 21/07/1933 (3)\*; s.n., 04/03/1937 (?); s.n., 11/05/1938 (?); s.n., 08/08/1950 (2); C.I. Sandwith & J.P.M. Brenan s.n., 04/08/1937 (3)\*; s.n., 10/08/1948 (2); C.I. & N.Y. Sandwith s.n., 15/09/1920 (2); s.n., 11/10/1922 (3); 3162 (4); N.Y. Sandwith 1970 (4); 3099 (3); 3100 (H1); 3101 (H1); V.P. Savicz 1243 (3); M.C. Schakel s.n., 08/07/1969 (6); J. Schell



267A (2); 455 (2); Schiffuer s.n., 24/07/1923 (6); Schiffum s.n., 07/1924 (2); W.W. Schipper s.n., s.d. (HLB 927.346-496) (6); s.n., 1889 (6); s.n., 22/08/1905 (3); s.n., 25/09/1907 (3); s.n., 09/1908 (6); s.n., 18/09/1910 (3); (in hb. D. Lako) s.n., 08/1908 (3); W.W. Schipper & B. Sypkens s.n., 1897 (6); Schlagintweit s.n., 27/07/1856 (2); s.n., 06/08/1856 (2); I. Schmalhausen s.n., 08/1886 (4); Schmidt (in hb. J. Klinge) s.n., 1857 (2); C. Scholz s.n., 12/07/1897 (H2); A. Schrenk s.n., s.d. (WU 9453) (8); s.n., 1835 (6); s.n., 1842 (7); 245 (7); J. Schreurs s.n., 25/08/1990 (3); M. Schuitemaker s.n., 17/08/1941 (3); Schultz (Bipont) 217A (2); Schur s.n., s.d. (HLB 926.236-1089) (3); s.n., s.d. (HLB 926.236-1104) (6); s.n., ..08/.... (H4); s.n., ..08/.... (2); 1772 (6); R. Seipka s.n., 20/07/1974 (4)\*; s.n., 31/08/1975 (4); P.D. Sell 61-525 (2); 61-528 (3); 61-608 (3); 61-609 (2); 61-613 (2); 61-616 (3); 61-653 (2); 62-614 (3); 62-665 (3); 62-717 (3); 62-718 (3); 62-770 (2); 67-1601 (2); 67-1742 (2); 81-81 (3); R. Seipka et al. 82-212 (3); P. Senay 462 (6); 1070 (H2); 3605 (H1); 3611 (3); Sennen (Bianor) s.n., 27/07/1911 (3); s.n., 11/08/1912 (3); s.n., 19/08/1916 (3); (Bianor) 1265 (3); 5502 (3); 7151 (3); Sennen & Gonzalo 5502 (3); C. Sergievskaja & G. Kiknadze 4099 (5); Shahrakhi 34003 E (11); Sharif 231 (2); W.D. Sherrin s.n., 08/1936 (6); M.J. Short 149 (3); Shrubbs s.n., 09/1888 (3); Siebold s.n., s.d. (HLB 900.74-218) (2); s.n., s.d. (HLB 900.74-221) (2); s.n., 1855 (3); Sierot s.n., s.d. (NBV) (3); L.H. Siertsema 3722 (2); 3723 (3); 3724 (3); 3725 (3); L.H. Siertsema & van Soest 25206 (3); P. Sintenis 226 (11); 691 (2); 1885 (11); Sjirajevskago s.n., 12/08/1904 (2); C.J.M. Sloet 21 (3)\*; J.G. Sloff s.n., 19/08/1931 (3); s.n., 20/08/1931 (3); s.n., 06/08/1933 (3); s.n., 25/08/1933 (3); s.n., 29/08/1933 (2); s.n., 29/08/1933 (3); s.n., 04/09/1933 (3); s.n., 05/09/1933 (2); s.n., 05/08/1934 (3); s.n., 23/08/1934 (3); s.n., 05/08/1935 (3); 5237 (3); N. Smirnoff s.n., 07/1921 (6); H. Smith 6035 (2); Soc. Ét. Fl. Franco-Helv. (G. Camus & Franchet) 300 (H4); (Jeanpert) 505 (4); (P. Hariot) 749 (3); (P. Hariot) 2243 (H1); Soc. dauph. (Fray.) 2944 B (4); van Soest (in hb. A. de Wever) 2207 (2); 2208 (6); 2209 (3); 2210 (4); (A. de Wever) 2211 (H5); 2212 (3); 2213 (3); 2214 (3); 2215 (3); 2216 (3); 4620 (3); 4621 (3); (Kloos & van Soest) 4622 (?); (Kloos & van Soest) 4623 (3); (Kloos & van Soest) 4624 (2); (Kloos & van Soest) 4625 (2); (Kloos & van Soest) 4626 (2); (Kloos & van Soest) 4627 (?); (Kloos & van Soest) 4629 (2); (Kloos & van Soest) 4630 (2); (Kloos & van Soest) 4631 (2); (Kloos & van Soest) 4632 (3); (Kloos & van Soest) 4633 (2); (Kloos & van Soest) 4634 (2); (Kloos & van Soest) 4636 (?); (Kloos & van Soest) 4637 (?); (Kloos & van Soest) 4638 (3); 9499 (3); 9500 (3); 9501 (3); 9502 (3); 9503 (3); (P.D. Groot) 9504 (3); (Sloff & van Soest) 10974 (3); 12214 (3); (J. Giersberg & A.W. Kloos jr.) 12215 (3); 17201 (3); 17202 (3); (Anon. 2438) 23262 (3); (J. Jansen) 23264 (3); 23265 (3); 23267 (3); 23268 (3); (Voigt) 23273 (6); (C.M.A. Jusje) 23274 (3); 23276 (2); 23277 (3); 23278 (2); 23279 (2); (A. de Wever) 25201 (3); 25202 (2); (Siertsema & van Soest) 25203 (2); (Siertsema & van Soest) 25205 (3); 25207 (3); 25208 (2); 25209 (3); 25210 (2); 25211 (3); 25211 (2); 25212 (3); 25213 (?); 25214 (3); 25215 (3); 25216 (6); 25217 (3); 25218 (3); 25219 (3); 25220 (3); 25221 (3); 25222 (3); 25223 (3); (Rechinger f.) 26706 (3); 27597 (6); 28144 (3); 28291 (?); 29934 (3); (Clason, Th. Reichgelt & van Soest) 32583 (3); 32588 (3); 32589 (3); 32590 (3); 32591 (3); 32592 (3)\*; 32594 (3)\*; 32595 (6); 34127 (3); 38136 (3); 38142 (2); 42304 (6); 42328 (2); 50414 (3); 50415 (3); 50416 (3); (S.E. de Jongh) 50417 (3); M.S.M. Sosef 23 (3); 316 (3); 323 (2); van Spijk Vermeulen s.n., s.d. (NBV 301) (3); s.n., s.d. (NBV 301) (2); M.D. Spiridonow s.n., 09/06/1913 (8); s.n., 09/06/1914 (8); s.n., 07/08/1914 (8); F.L. Splitgerber s.n., s.d. (HLB 900.74-223) (3); s.n., ..08/.... (306932B) (3); s.n., ..09/.... (3); s.n., 07/1832 (3); Sprygin s.n., 31/07/1908 (2); s.n., 03/07/1910 (2); s.n., 25/07/1910 (2); s.n., 29/07/1915 (2); Stainton, Sykes & Williams 1498 (2); A. Stalin s.n., 18/08/1917 (4); C.G.C.J. van Steenis s.n., 31/12/1970 (3); s.n., 28/07/1918 (3); 6982 (2); 20212 (3); H. Steffen s.n., 17/09/1911 (3); s.n., 17/08/1913 (4); Steudel s.n., 08/1838 (3); C.A. Stevens s.n., 1840 (2); A.N. Steward & T. Ishimoto 6602 (3); R.R. Stewart 24715 (2); J. Stoffer 137-58 (3)\*; M.J. Stokman s.n., 08/1919 (2); P.F. Stolwijk 1520 (3); S.E. Stratingh s.n., 08/1856 (6); 575 (6); 895 (3); 896 (6); F.J. Struykenkamp s.n., 09/09/1885 (3); s.n., 08/1892 (3); Stud. biol. Rheno-Trai. in itinere 231 (3); 1505 (3); 54-104 (3); 64-2281 (4)\*; 64-2453 (2); 68-159 (3); St. Supéry s.n., 1855 (2); W.N. Suksdorf s.n., 07/1909 (3); 135 (3); W.F.R. Suringar s.n., 08/1849 (3);

- s.n., 10/08/1859 (3); s.n., 07/09/1860 (3); P.L. Swan-born s.n., s.d. (L) (?); Swart in hb. van Soest (sub 13797) 2013 (3); J.J. Swart 1371 (3); 2013 (3); Szovits (in hb Fischer) s.n., s.d. (LE) (5); S.W.B. 851 (2); 854 (2).
- Tarn. s.n., 07/08/1961 (3); G. Taylor s.n., 24/07/1937 (3); Tchihatchef 950 (2); O. Tedin s.n., 01/08/1914 (6); F.R. Tennant s.n., 07/1898 (3); s.n., 07/1901 (3); s.n., 07/1901 (2); Termé 34007 E (5); W. Thesiger 1249 (2); 1497 (11); M. Thomson 895 (3); V. Tichomirov et al. 518 2 (2); Tilanus s.n., 05/1842 (2); A. Timmermans s.n., s.d. (HLB 420502) (3); s.n., 10/07/1948 (3); s.n., 30/07/1948 (3); W.G. Top s.n., s.d. (NBV 273) (6); s.n., s.d. (NBV 4936-68) (3); s.n., 1850 (2); s.n., 1850 (3); W. Tranzschel s.n., 07/07/1900 (11); Trautvetter s.n., 09/07/1851 (2); C.L. Treviran s.n., s.d. (HLB 900.74-203) (6); Tribe s.n., 16/08/1963 (3); Tripet s.n., 20/07/1886 (3)\*; A.S. Troelstra s.n., 22/08/1981 (3); s.n., 11/08/1990 (3); C. Tucker 302 (3).
- H. Uittien s.n., 1916 (2); s.n., 31/07/1924 (2); van Uken s.n., s.d. (NBV 4936-23) (3)\*; Um. s.n., s.d. (HLB 900.74-213) (3); Unio s.n., 08/1892 (4); s.n., 20/07/18.3 (3); 1900 (3); R.M. van Urk s.n., s.d. (3); s.n., 11/07/ (3); s.n., 11/07/ (3); s.n., 11/07/ (3); s.n., 11/07/ (3); s.n., 03/08/ (3); s.n., 11/08/ (3); s.n., 16/08/ (3); s.n., 17/08/ (3); s.n., 17/08/ (3); s.n., 17/08/ (3); s.n., 17/08/1975 (3); s.n., 08/1976 (3); s.n., 29/08/1976 (3); s.n., 05/09/1976 (3); s.n., 26/07/1983 (3); s.n., 27/07/1983 (3)\*; s.n., 02/08/1983 (3); s.n., 02/08/1983 (3)\*; s.n., 03/08/1983 (3); s.n., 05/08/1983 (3)\*; s.n., 07/08/1983 (3)\*; s.n., 14/08/1983 (3); s.n., 15/08/1983 (3); s.n., 17/08/1983 (3)\*; s.n., 22/08/1983 (3)\*; s.n., 22/08/1983 (3); s.n., 23/08/1983 (3); s.n., 07/08/1984 (3)\*; s.n., 17/08/1984 (3); s.n., 20/08/1984 (3); s.n., 20/08/1984 (3); s.n., 21/08/1984 (3); s.n., 27/08/1984 (3); s.n., 27/08/1984 (3); s.n., 27/08/1984 (3); s.n., 28/08/1984 (3); s.n., 30/08/1984 (3); s.n., 30/08/1984 (3); s.n., 30/08/1984 (3); s.n., 30/08/1984 (3); s.n., 02/09/1984 (3); s.n., 02/09/1984 (3); s.n., 09/09/1984 (3); s.n., 04/10/1984 (3); s.n., 16/08/1985 (3); s.n., 17/08/1985 (3); s.n., 17/08/1985 (3); s.n., 18/08/1985 (3); s.n., 28/08/1985 (3); s.n., 28/08/1985 (3); s.n., 30/08/1985 (3); s.n., 02/08/1987 (3); s.n., 07/08/1987 (3); s.n., 07/08/1987 (3); s.n., 15/08/1987 (3); s.n., 15/08/1987 (3); s.n., 01/09/1987 (3); s.n., 28/07/1988 (3)\*; s.n., 06/08/1988 (3); s.n., 06/08/1988 (3)\*; s.n., 09/08/1988 (3); s.n., 09/08/1988 (3)\*; s.n., 12/08/1988 (3); s.n., 12/08/1988 (3); s.n., 12/08/1988 (3); s.n., 12/08/1988 (3); s.n., 12/08/1988 (3); s.n., 18/08/1988 (3); s.n., 26/08/1988 (3); s.n., 06/09/1988 (3); s.n., 06/09/1988 (3); s.n., 06/09/1988 (3); A s.n., 29/08/1976 (3); B s.n., 29/08/1976 (3); 2 (3); 3 (3); 4 (3); 5 (3); 6 (3); 7 (3); 8 (3); 9 (3); 10 (3); 11 (3); 12 (3); 13 (3).
- Vaillant s.n., s.d. (HMP 93-232) (3); J. Valckenier Suringar s.n., 09/1892 (3); s.n., 28/07/1920 (3); Vandown s.n., 08/1847 (3); L. Vanhecke 6600 (2); V. Vasák s.n., 08/07/1973 (11); s.n., 21/05/1974 (2); s.n., 23/07/1977 (3); V. Vasák & G. Esvandzia s.n., 24/07/1979 (H4); J.F. Veldkamp s.n., 09/1989 (3); J.J. Vermeulen s.n., 16/08/1989 (3); W. Vervoort s.n., 07/1939 (3); s.n., 04/07/1945 (3); s.n., 04/07/1945 (6); s.n., 25/08/1958 (3); W. Vervoort & de Bruyn s.n., 01/08/1941 (2); J.A.C. Veth & A.N. Koopmans s.n., 15/08/1957 (3); s.n., 24/08/1960 (3); s.n., 10/09/1961 (3); s.n., 04/09/1962 (2); s.n., 12/08/1968 (3); J.J. Videler s.n., s.d. (HLB 396101) (3); s.n., 21/07/1966 (3); E. Vilpa s.n., 07/07/1953 (6); U.A. Vincent s.n., 04/09/1938 (3); A. de Visser s.n., 14/08/1958 (2); s.n., 21/07/1959 (6); s.n., 21/07/1959 (6); E.E. van der Voo 335 (3); 1277 (3); 1314 (2); 1315 (2); 1993 (3); 3250 (3); Vvedensky 489 (11).
- L. Waddington s.n., 08/1836 (2); Wagner s.n., 08/1922 (4); E.H. Walker, S. Tawada & T. Amano 5792 (2); A. Walraven s.n., 08/1880 (2); Walters & Tutin s.n., 09/09/1949 (3); A.K. Warshelewski s.n., 1876 (6); Watkins s.n., 08/1872 (3); J. Wattel s.n., 21/09/1956 (6); E.J. Weeda s.n., 06/08/1977 (3); s.n., 19/08/1978 (3); s.n., 18/08/1980 (3); s.n., 22/08/1981 (3); s.n., 23/08/1981 (2); s.n., 26/07/1983 (3); s.n., 23/07/1987 (2); s.n., 30/07/1987 (6); s.n., 30/07/1987 (3); s.n., 26/07/1990 (3); s.n., 15/08/1991 (3)\*; s.n., 16/08/1991 (3)\*; s.n., 16/08/1991 (3)\*; s.n., 20/08/1992 (3); Th. Weevers s.n., 29/07/1893 (3); A. Wesmael s.n., 08/1863 (6); V. Westhoff s.n., 07/1930 (3); F.S. van Westreenen s.n., 28/08/1991 (6); A. de Wever s.n., s.d. (HLB 954.277-184) (6); s.n., 01/08/1912 (2); s.n., 01/08/1913 (6); s.n., 18/08/1913 (2); s.n., 1914 (4); s.n., 08/1929 (3); J.A. Wheldon s.n., 16/08/1913 (3); White s.n., 21/07/1924 (3); Whitmore s.n., 17/07/1961 (3); s.n., 24/07/1961 (3); J. Whittaker s.n., 23/09/1952 (2);

J.H. van Wijk s.n., 20/07/1956 (3)\*; A.J. van Wijngaarden s.n., 12/08/1913 (3); s.n., 17/08/1932 (2); s.n., 29/08/1935 (6); A.G. de Wilde s.n., 17/07/1963 (6); 1673 (3); 3004 (2); 4523 (2); 4829 (3); 5125 (3); 5238 (?); 5240 (2); 5490 (6); 6143 (3); 6335 (3); 7144 (3)\*; 7496 (3)\*; J.J.F. de Wilde, P.A.W.J. de Wilde & J. Dorgelo 2850 (1); , P.A.W.J. de Wilde & W.C. de Kock 247 (3); W.J.J.O. de Wilde, & B.E.E. de Wilde-Duyfjes 21027 (5); A.J. Wilmott 36710 (3); Windler & Keenan 3161 (3); C. Winkler 299 (2); N. Winter s.n., 06/1927 (2); 9452 (6); Wirtgen (A. Martinis) 607 (6); de Wit Hamer s.n., s.d. (L) (3); J. Wolff s.n., s.d. (LE) (6); H.J. Wolters s.n., 29/07/1977 (3); s.n., 09/08/1977 (2); s.n., 03/09/1978 (?); Wtte-waal s.n., s.d. (NBV 125) (2); s.n., 1829 (6); s.n., 05/1835 (2); v. d.W. in hb. Coster s.n., s.d. (NBV) (3).

Yorksh. Schools expl. soc. 26 (3).

G. van d. Zanden s.n., 08/08/1944 (6); Zehzad 1311 (5); H. Zerny s.n., 02/06/1920 (10); G. Zijlstra s.n., 31/07/1969 (2); G. Zinserling 15 (3); 322 (2); 726 (3); C. Zuurdeeg s.n., 17/08/1977 (6); s.n., 17/08/1977 (2).

## 23. Index to taxonomic names

Summary: accepted names only.

- Arctium sect. Arctium p.72
- 1 A. atlanticum (Pomel) H. Lindb. p. 73
  - 2 A. lappa L. p.75
  - 3 A. minus (Hill) Bernh. p. 82
  - 4 A. nemorosum Lej. p. 92
  - 5 A. palladini (Marcow.) R.E. Fr. & E.S. Söderb. p. 98
  - 6 A. tomentosum Mill. p. 101
- Arctium sect. Lappaceum (Bunge) Duist. p. 105
- 7 A. lappaceum (Schrenk) Kuntze p. 106
- Arctium sect. Nanarctium (Tscherneva) Duist. p. 108
- 8 A. arctioides (Schrenk) Kuntze p. 109
- Arctium sect. Pseudarctium (Juz.) Duist. p. 112
- 9 A. amplissimum (Boiss.) Kuntze p. 112
  - 10 A. pseudarctium (Bornm.) Duist. p. 114
  - 11 A. umbrosum (Bunge) Kuntze p. 119
- Hybrids (S = species number)
- H1 A. ×nothum (Ruhm.) Weiss (= S2 × S3) p. 122
  - H2 A. ×ambiguum (Čelak.) Nyman (= S2 × S6) p. 123
  - H3 A. ×semiconstrictum Duist. (= S3 × S5) p. 124
  - H4 A. ×mixtum (Simk.) Nyman (= S3 × S6) p. 125
  - H5 A. ×neumani Rouy (= S4 × S6) p. 126
  - H6 A. ×dualis (Juz.) Duist. (= S10 × S11) p. 126

### Index to all names

Whatever their ranks, all *infra* specific names are presented in alphabetical order, too. Accepted names are in roman type; new taxa and combinations are in **bold** type; synonyms are in *italics*. The numbers refer to the number of the accepted taxon. D = doubtful species, E = excluded species, H = hybrid taxa. Page numbers are presented only for accepted names (as well as for synonyms of genus and section names).

*Arcion* p. 69

*Arcion majus* 2

*Arctium* p. 69

*minus* var. *macrocephalum* 3

var. *microcephalum* 3

*Arctium* p. 69

sect. *Arctium* p. 72

sect. *Eglandulosa* p. 72

sect. *Glandulosa* p. 72

sect. *Lappaceum* p. 105

sect. *Nanarctium* p. 108

sect. *Pseudarctium* p. 112

(*Arctium*)

*adhaerens* D1

*×ambiguum* H2, p. 123

*amplissimum* 9, p. 112

*arctioides* 8, p. 109

*atlanticum* 1, p. 73

*austriacum* 4

*bardana* 6

*×batavum* 3

*×bretoni* H4

*carduelis* E2

*chaberti* 3

(*Arctium chaberti*)

- subsp. *aellenianum* 3
- subsp. *balearicum* 3
- subsp. *chaberti* 3
- subsp. *corsicum* 3
- chaorum* 2
- ×*cimbricum* D3
- conglomeratum* 3
- crispum* 6
- ×*debrayi* H1
- degeni* 3
- ×*delphinense* H1
- ×*dualis* H6, p. 126
- edule* 2
- flabrescens* D7
- gallicum* 3
- grandiflorum* D2
- intermedium* Lange 4
- intermedium* auct. 3
  - var. *subtomentosum* 3
- lanuginosum* E3
- lappa* L. 2, p. 75
  - f. *albiflorum* 2
  - f. *foliosum* 2
  - subsp. *majus* 2
  - var. *majus* 2
  - β *majuscula* 4
  - var. *minus* 3
  - β *minus* 3
  - δ *nemosum* 4
  - subsp. *platylepis* 2
  - e pubens* 3
  - var. *purpurascens* 2
  - f. *purpurascens* 2
  - var. *subtomentosum* 2
  - f. *subtomentosum* 2
  - var. *tomentosum* 6
  - β 6
  - × *A. minus* H1
  - × *A. tomentosum* H2
- lappa* auct. 3
- lappaceum* 7, p. 106
- ×*leibardana* H2
- leiospermum* 2
- leptophyllum* 6
- ×*maassii* 4

(*Arctium*)

- macrosperrum* 4
- majus* 2
  - subvar. *album* 2
  - subsp. *intermedium* 4
  - var. *minus* 3
  - subsp. *nemosum* 4
  - subvar. *purpurascens* 2
- minus 3, p. 82
  - f. *albiflorum* 3
  - var. *album* 3
  - subvar. *album* 3
  - subsp. *alpestre* 3
  - subvar. *araneosa* 3
  - subsp. *atlanticum* 1
  - var. *broquetii* 3
  - var. *conglomeratum* 3
  - var. *corymbosum* 3
  - subsp. *eu-minus* 3
  - f. *laciniatum* 3
  - var. *macrocephalum* 3
  - f. *majus* 3
  - subsp. *mediterraneum* 3
  - var. *melanoceps* 3
  - subsp. *nemosum* 4
  - var. *nemosum* 4
  - f. *pallidum* 3
  - f. *paniculata* 3
  - subsp. *pubens* 3
  - var. *pubens* 3
  - f. *purpurea* 3
  - var. *subteralbatum* 3
  - subsp. *tchihatchefii* 2
  - var. *tibidatensis* 3
  - × *A. palladini* H3
  - × *A. tomentosum* H4
- ×*mixtum* H4, p. 125
- montanum* 3
- nemosum* 4, p. 92
  - f. *ar(t)isticum* 4
  - var. *austriacum* 4
  - var. *italicum* 3
  - f. *mathei* 3
  - var. *microcephalum* (Erdner) Beger 3
  - var. *microcephalum* Arènes 4
  - subsp. *nemosum* 4

(*Arctium nemorosum*)  
 subsp. *pubens* 3  
 var. *pubens* 3  
 × *A. tomentosum* H5  
 × *neumani* H5, p. 126  
*newbouldii* 4  
 × *nothum* H1, p. 122  
*palladini* 5, p. 98  
*personata* L. E1  
*personata* auct. 3  
*platylepis* 2  
*pseudarctium* 10, p. 114  
 × *A. umbrosum* H6  
*pubens* 3  
 subvar. *album* 3  
 var. *microcephalum* 3  
 f. *pycnocephalum* 4  
 subvar. *subtomentosum* 3  
*radula* 5  
*ruderales* 2  
 × *scanicum* D5  
 × *semiconstrictum* H3 p. 124  
 × *subracemosum* H1  
*tomentellum* 11  
*tomentosum* Mill. 6, p. 101  
 f. *albiflorum* 6  
 f. *glaberrimum* 6  
 f. *glabrescens* 6  
 subsp. *palladini* 5  
 subsp. *pubens* 3  
 subvar. *album* 6  
 var. *calvum* 6  
 var. *denudatum* 6  
 var. *glabrum* 5  
*tomentosum* auct. 3  
 var. *balearicum* 3  
*umbrosum* 11, p. 119  
 × *Cousinia alberti* D6  
*uncinatum* 11  
*vulgare* (Hill) Druce 2  
*vulgare* A.H. Evans 3  
 subvar. *pycnocephalum* 4  
*vulgare* auct. non (Hill) Druce 3  
*vulgare* auct. non Hill, non A.H. Evans 4  
*Bardana*, p. 69  
*Berardia subacaulis* E3

*Carduus carduelis* E2  
*personata* E1  
*Cousinia* sect. *Lappacea* p. 106  
 sect. *Nanarctium* p. 105  
 sect. *Pseudarctium* p. 112  
 sect. *Uncinatae* p. 105  
 sect. *Xerarctium* p. 105  
*amplissima* (Boiss.) Boiss. 9  
*amplissima* auct. 10  
*arctioides* 8  
 × *dualis* H6  
*lappacea* 7  
*pseudarctium* 10  
 var. *leiocephala* 10  
*schiraziaca* 9  
*spuria* 10  
*tomentella* 11  
 × *triacantha* D6  
*umbrosa* 11  
 var. *virescens* 11  
*uncinata* 11  
*Lappa* Scop. p. 69  
 × *ambigua* H2  
*amplissima* 9  
*arctium* 6  
*atlantica* 1  
*bardana* 2  
 d *macrosperma* 4  
 var. *major* 2  
 e *minor* 3  
 var. *tomentosa* 6  
*carduelis* E2  
 × *cimbrica* D3  
*communis* 3  
 var. *major* 2  
 var. *minor* 3  
 var. *tomentosa* 6  
*conglomerata* 3  
*crispa* 6  
*degeni* 3  
*edulis* 2  
*glabra* Lam. 3  
 var. *a* 2  
 var. *major* 2  
 a *minor* 3  
 var. *nemorosa* 4

(*Lappa*)

- glabra* auct. 3
- intermedia* (Lange) Rchb.f. 4
  - var. *newbouldii* 4
- intermedia* auct. 3
- ×*janczewskii* H1
- kotschyi* 2
- ×*maassii* 4
- macrosperma* 4
- major* (Bernh.) Lange 2
  - var. *subtomentosa* 2
- major* Gaertn. 2
  - Spielart b *minor* 3
  - Spielart a *racemosa* 3
- ×*media* H4
- minor* Hill 3
  - var. *alba* 3
  - var. *araneosa* 3
  - var. *broquetii* 3
  - var. *intermedium* 4
  - f. *lanaria* 3
  - f. *macrocephala* 3
  - f. *major* 2
  - f. *majuscula* 4
  - var. *nemorosa* 4
  - var. *paniculata* 3
  - f. *purpurascens* 3
  - f. *purpurea* 3
  - a *virescens* 3
- minor* DC. var. *campestris* 3
- var. *montana* 3
- var. *pubens* 3

(*Lappa minor*)

- f. *pubens* 3
- ×*mixta* E.G. Camus H1
- ×*mixta* Simonk. H4
- nemorosa* Körn. 4
  - var. *microcephala* 3
  - var. *typica* 4
- nemorosa* auct. 3
- notha* H1
- officinalis* 2
- palladini* 5
- personata* E1
- platylepis* 2
- pubens* 3
- ×*rehmanni* H2
- repens* 3
- ×*ritschliana* H4
- ×*ruhmerio* H1
- ×*subracemosa* H1
- sylvestris* 1
- tomentosa* 6
  - var. *calva* 6
  - var. *denudata* 6
  - var. *glaberrima* 6
  - var. *glabra* 5
  - var. *oligocephala* 6
  - var. *umbrosa* 6
- vulgaris* var. *major* 2
- var. *minor* 3
- var. *subtomentosa* 2
- var. *tomentosa* 6
- ×*zalewski* D4