Biosystematics of the Genus *Andryala* L. (*Asteraceae*)

DOCTORAL THESIS

Maria Zita Ferreira

DOCTORATE IN BIOLOGICAL SCIENCES

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Abstract

Andryala (Asteraceae: Cichorieae) is a little-known Mediterranean-Macaronesian genus whose taxonomy is much in need of revision. The aim of the present biosystematic study was to elucidate species relationships within this genus based on morphological and molecular data.

In this study several taxa are recognised: 17 species, 14 subspecies, and 3 hybrids. Among these, 5 species are Macaronesian endemics (*A. glandulosa*, *A. sparsiflora*, *A. crithmifolia* Aiton, *A. pinnatifida,* and *A. perezii*), 4 species are Northwest African endemics (*A. mogadorensis*, *A. maroccana*, *A. chevallieri,* and *A. nigricans*) and one species is endemic to Romania (*A. laevitomentosa*).

Historical background regarding taxonomic delimitation in the genus is addressed from Linnaean to present day concepts, as well as the origin of the name *Andryala*. The origin of Asteraceae and the systematic position of *Andryala* is shortly summarised.

The morphological study was based on a bibliographic review and the revision of 1066 specimens of 13 herbaria as well as additional material collected during fieldwork. The variability of the morphological characters of the genus, including both vegetative taxonomic characters (root, stem, leaf and indumentum characters) and reproductive ones (inflorescence, floret, fruit and pappus characters), is assessed.

Numerical analysis of the morphological data was performed using different similarity or dissimilarity measures and coefficients, as well as ordination and clustering methods. Results support the segregation of the recognised *taxa* and the congruence of the several analyses in the separation of the recognised *taxa* (using quantitative, binary or multi-state characters).

The proposed taxonomy for *Andryala* includes a new infra-generic classification, new *taxa* and new combinations and ranks, typifications and diagnostic keys (one for the species and several for subspecies). For each *taxon* a list of synonyms, typification comments and a detailed description are provided, just as comments on taxonomy and nomenclature, and a brief discussion on karyology. Additionally, information on ecology and conservation status as well as on distribution and a list of studied material are also presented.

Phylogenetic analyses based on different nuclear and chloroplast DNA markers, using Bayesian and maximum parsimony methods of inference, were performed. Results support three main lineages: separate ones for the relict species *A. agardhii* and *A. laevitomentosa* and a third including the majority of the *Andryala* species that underwent a relatively rapid and recent speciation. They also suggest a single colonization event of Madeira and the Canary Islands from the Mediterranean region, followed by insular speciation.

Biogeography and speciation within the genus are briefly discussed, including a proposal for the centre of origin of the genus and possible dispersal routes.

Keywords: *Andryala*, colonisation, Macaronesia, Mediterranean Basin, molecular phylogeny, taxonomy.

Sumário

Andryala (Asteraceae: Cichorieae) é um género Mediterraneo-Macaronésico pouco conhecido cuja taxonomia urgia uma revisão. O presente estudo biossistemático teve como principal objetivo esclarecer as relações entre as espécies deste género com base em dados morfológicos e moleculares.

Neste estudo são reconhecidas 17 espécies, 14 subespécies, e 3 híbridos, incluindo 5 espécies endémicas para a Macaronesia (*A. glandulosa*, *A. sparsiflora*, *A. crithmifolia*, *A. pinnatifida* e *A. perezii*), 4 espécies endémicas para o Noroeste de África (*A. mogadorensis*, *A. maroccana*, *A. chevallieri* e *A. nigricans*) e uma espécie endémica para a Roménia (*A. laevitomentosa*).

Expõem-se os antecedentes históricos da delimitação taxonómica do género, do conceito lineano ao atual, e a origem do nome *Andryala*. Apresenta-se uma sinopse sobre a origem das *Asteraceae* e a posição sistemática de *Andryala*.

O estudo morfológico baseou-se numa pesquisa bibliográfica e na revisão de 1066 espécimenes de 13 herbários bem como de material adicional colhido durante o trabalho de campo. Apresenta-se uma sinopse da variabilidade dos caracteres morfológicos do género, tendo sido alvo de estudo caracteres taxonómicos vegetativos (relativos à raiz, caule, folha e indumento) e reprodutivos (relativos à inflorescência, flor, fruto e papilho).

Apresenta-se a análise numérica realizada com diferentes coeficientes de semelhança ou dissemelhança, métodos de ordenação e métodos de agregação. Como resultados destacam-se a segregação dos *taxa* reconhecidos e a coerência das várias análises na separação dos *taxa* reconhecidos (usando caracteres quantitativos, binários e multi-estado).

A taxonomia proposta para o género *Andryala* inclui uma nova classificação infra-generica, novos *taxa* e novas combinações, tipificações e chaves dicotómicas (uma para as espécies e várias para as subespécies). Para cada *taxon* apresenta-se uma lista de sinónimos, comentários acerca de tipificação, uma descrição detalhada, assim como comentários taxonómicos e nomenclaturais. Apresenta-se ainda uma breve discussão da cariologia, informação relativa à ecologia e estado de conservação, a distribuição e uma lista do material estudado.

Foram realizadas análises filogenéticas baseadas em diferentes marcadores nucleares e cloroplastidiais, usando os métodos de inferência Bayesiana e de Máxima parsimonia. Os resultados apoiam a existência de três linhagens: duas independentes para as relíquias *A. agardhii* e *A. laevitomentosa* e uma terceira incluindo a maioria das espécies de *Andryala* as quais sofreram uma especiação relativamente rápida e recente. Sugerem ainda ocorrência de eventos únicos de colonização da Madeira e das Ilhas Canárias a partir da região do Mediterrâneo, seguidos de uma especiação insular.

Tecem-se considerações sobre a biogeografia e especiação do género, incluindo uma proposta de centro de origem e de possíveis vias de dispersão.

Palavras-chave: *Andryala*, Bacia do Mediterrâneo, colonização, filogenia molecular, Macaronesia, taxonomia.

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Abbreviations

Alt. – Altitude
asl – above sea level
auct. – *Auctoris/auctorum* (of an author or authors)
auct. non – *Auctorum non* (not of these authors, used for misapplied names)
ca. – *Circa* (about)
comb. illeg. – Illegitimate combination
comb. invalid – invalid combination
comb. nov. – *Combinatio nova* (new nomenclatural combination)
e.g. – *Exempli gratia* (for example)
emend. – *Emendavit* (correction or amendment)
et – and
f. – form
ex – validly published by
i.e. – that is
in – citation of a *taxon* in the publication of another author
ined. – *Ineditus* (not validly published)
in sched. – *In Schedae* (name observed on a herbarium specimen or label, often not validly published except for names that were distributed on sets of excicata specimens accompanied by printed diagnoses)
Loc. incert. – not assinagble to any locality.
Ma. – million years
nom. nov. – *nomen novum* (new name, e.g., proposed as a substitute for an older name)
nom. ambig. – *nomen ambiguum* (ambiguous name, to reject)
nom. illeg. – illegitimate name
nom. inval. – invalid name
nom. nud. – *nomen nudum* (published without a description or diagnosis, making the name invalid)
non – not
n. v. – *non vidi* (material not seen)
p. – page
p.p. – pro parte
SEM – scanning electron microscopy
s.l. – *sensu lato* (in the broad sense)
sp. nov. – *species novum* (new species)
s.s. or s.str. – sensu strict (in the narrow sense)
stat. nov. – *status novus* (change in rank)
subsp. – subspecies
syn. – synonym
syn. nov. – *Synonymus novum* (new synonym)
var. – *Varietas* (variety)
x – Hybrid
! – Material observed
[?] – Characters or words on herbarium labels that was not possible to interpret due to calligraphy

Acronyms of the morphometric characters

RD - Root diameter
RL - Root length
RS - Root shape
PLC - Plant life-cycle duration
SH - Stem height
SD - Stem diameter (cm)
SS - Stem shape
SCol - Stem colour
SN - Stem number
SR - Stem ramification
SNPB - Number of primary branches
SNSB - Number of secondary branches
SBP - Branch position
SloSI - Lower stem stellate indumentum
SloGI - Lower stem glandular indumentum
SmSI - Middle stem stellate indumentum
SmGI - Middle stem glandular indumentum
SuSI - Upper stem stellate indumentum
SuGI - Upper stem glandular indumentum
SNRSI - Number of rays of stem stellate hairs
Lthic - Leaf thickness
LloL - Lower leaf length
LloLBMW - Length from the base of the lower leaf to the point of maximum width
LloW - Lower leaf maximum width
LloLL - Length of the larger lobe of the lower leaf
LloWBL - Width at the base of the larger lobe of the lower leaf
LloLTLMN - Length from the tip of the larger lobe of the lower leaf to the middle nerve
LcL - Cauline leaf length
LcLBMW - Length from the base of the cauline leaf to the point of maximum width
LcW - Cauline leaf maximum width
LcLL - Length of the larger lobe of the cauline leaf
LcWBL - Width at the base of the larger lobe of the cauline leaf
LcLTLMN - Length from the tip of the larger lobe of the cauline leaf to the middle nerve
LuL - Upper leaf length
LuLBMW - Length from the base of the upper leaf to the point of maximum width (mm)
LuW - Upper leaf maximum width
LuLL - Length of the larger lobe of the upper leaf
LuWBL - Width at the base of the larger lobe of the upper leaf
LuLTLMN - Length from the tip of the larger lobe of the upper leaf to the middle nerve
LloIS- Lower leaf insertion on the stem
LcIS - Cauline leaf insertion on the stem
LuIS - Upper leaf insertion on the stem
LcB - Cauline leaf base
LuB - Upper leaf base
LloWP - Lower leaf winged petiole
LloLP - Petiole length of the lower leaf
LcLP - Petiole length of the cauline leaf
LloA - Lower leaf apex
LcA - Cauline leaf apex
LuA - Upper leaf apex
LloSI - Lower leaf stellate indumentum
LloGI - Lower leaf glandular indumentum
LcSI - Cauline leaf stellate indumentum
LcGI - Cauline leaf glandular indumentum
LuSI - Upper leaf stellate indumentum
LuGI - Upper leaf glandular indumentum
LColAD - Colour of the adaxial face of the leaf
LColAB - Colour of the abaxial face of the leaf
INC - Number of capitula per inflorescence
IT - Inflorescence type
ILGP - Length of the glandular hairs of the peduncle
ICD - Capitulum diameter at anthesis
IPL - Peduncle length
IIL - Involucre length at anthesis
IIW - Involucre width at anthesis
IISA - Involucre shape at anthesis
IISF - Involucre shape at fructification
INRIB - Number of rows of the involucral bracts
IIBeC - External involucral bracts convolution
IIBeL - External involucral bracts length
IIBeW - External involucral bracts maximum width
IIBSIo - External involucral bracts stellate indumentum on the outer face
IIBSIi - External involucral bracts stellate indumentum on the inner face
IIBGI - External involucral bracts glandular indumentum
ICGIB - Colour of the external involucral bracts glandular hairs
ICEIB - Colour of the external involucral bracts stellate hairs
IIBA - External involucral bracts apex
IIBiL - Internal involucral bracts length
IIBiW - Internal involucral bracts width
IIBiSMW - Internal involucral bracts scariose margin maximum width
ILIBGI - Length of the external involucral bracts glandular hairs
IRSL - Length of receptacle setae
IRS - Receptacle shape
IRI - Receptacle indumentum
ILL - Ligule length
ILW - Ligule width
IATL - Ligule apical teeth length
ITL - Tube length
IIBL - Indumentum at the base of the ligule
ISITL - Stellate indumentum on the teeth of the ligule
ILCFo – External ligule colour on the outer face
ILCFi - External ligule colour on the inner face
ILiC- Internal ligule colour
FrL - Cypsela length
FrW - Cypsela maximum width
FrS - Cypsela shape
FrCol - Cypsela colour
FrRS - Cypsela ribs saliency
FrAA - Cypsela apex aspect
FrAIRD - Cypsela apical inner ring disposition
FrRCol - Cypsela ribs colour
FrPL - Pappus length
FrPCol - Pappus colour
FrPB - Pappus base
FRPA - Pappus apex

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1 Introduction

Andryala L. (Asteraceae) is a little known genus and no taxonomic revision as a whole has ever been made. Available works on *Andryala* L. have focused mainly on the description of new *taxa* as well as taxonomic delimitation, constrained to certain geographic areas (e.g. Murbeck 1905; Sell 1976; Press 1994; Blanca 2011). Thus, a more comprehensive study of the genus in what concerns taxonomy and nomenclature is in need. Furthermore, no phylogenetic studies have been carried out to clarify species relationships. So far, only a few *Andryala* species were included as outgroup for phylogenetic studies of other genera of the tribe Cichorieae (Fehrer *et al.* 2007a; Fehrer 2009). Some *Andryala* species have also been used in the study of one of the most variable regions in the angiosperm chloroplast genome (psbA-trnH intergenic region) and in the development of low-copy nuclear markers with great potential for phylogeny reconstruction in the subtribe Hieraciinae (Štorchová & Olson 2007; Krak *et al.* 2012).

The genus *Andryala* L. comprises annual to perennial herbs, more or less densely stellate-hairy, sometimes with glandular hairs. The leaves are entire to pinnatisect, the lower ones occasionally arranged in a rosette, the cauline, few to numerous, often more or less amplexicaul. The capitula, solitary or arranged in corymbiform inflorescences, exhibit involucral bracts disposed in 2 to several rows. The receptacle is alveolate and provided with cilia shorter or longer than the fruits [cypsela]. The florets have yellow ligules, the external sometimes with a reddish stripe on the outer face. The fruits are oblong or obconical, truncate at the apex (rarely with a disc), with 10 prominent ribs, and the pappus is formed of whitish or greyish hairs, falling entire (Sell 1976; Talavera 1987).

The distribution area of *Andryala* L. is known from early authors such as Hooker (1873) who stated that "The genus Andryala is chiefly a Mediterranean one, and finds its south-western limit in Morocco and the Canary Islands." Indeed, *Andryala* L. occurs in the Mediterranean Region, Southwest Europe, Northwest Africa, and Macaronesia (Talavera 1987). The genus is also represented in the eastern Mediterranean, as well as in islands of the Aegean Sea (Sibthorp & Smith 1813; Sibthorp & Lindley 1837; Post 1896). Outside this area, in Romania, a rare endemic *Andryala* species can also be found (Nyárády 1963; Nyárády 1965; Sell 1976).

Some species are ruderal and are commonly found growing along roadsides, while others occur in pastures or on coastal rocks and sea-cliffs or on dry rocks and banks in inland sites. A few can be found on sandy substrates of inland and coastal areas as well as on high mountain rocks and screes (Coutinho 1939; Sell 1976; Talavera 1987; Press 1994; Blanca 2009, 2011).

Considerable intraspecific variability and ecological plasticity observed in *Andryala* led to the description of many species, according to the degree of morphological differentiation and ecology. Hence, there is no clear estimate of the number of species in the genus. Nevertheless, Sell (1976) admitted five species for Europe: *Andryala agardhii* Haens. ex DC., *Andryala laxiflora* DC., *Andryala ragusina* L., *Andryala integrifolia* L., and *Andryala laevitomentosa* (Nyár. ex Sennikov) Greuter. Several authors recognised an additional species, *Andryala arenaria* (DC.) Boiss. & Reut. (Coutinho 1939; Sampaio 1949; Franco 1984; Talavera 1987; Blanca 2009, 2011). Mabberley (1997) estimated a total of approximately twenty species for the genus, whereas Greuter (2006+) recognised thirteen species.

Furthermore, many subspecies and varieties have been described or indicated with different degrees of acceptance (De Candolle 1838; Willkomm & Lange 1865; Amo y Mora 1872; Jahandiez & Maire 1934; Dobignard 2009).

Some hybrids have also been described in *Andryala* with the particularity that in each case *Andryala integrifolia* (the most widespread species) is always one of the parental species (Maire 1926; Maire 1937; Kunkel 1980; García Adá 1992).

From the conservation point of view, four *Andryala* species were officially listed in the 1997 IUCN Red List of Threatened Plants: *Andryala nigricans* Poiret and *Andryala webbii* Sch. Bip. ex Christ as vulnerable*, Andryala crithmifolia* Aiton as endangered, and *Andryala laevitomentosa* as critically endangered (Walter & Gillett 1998). In the European Red List of Vascular Plants, *Andryala crithmifolia* and *Andryala laevitomentosa* are, respectively, considered critically endangered and data deficient (Bilz *et al.* 2011).

1.1 Historical background of the genus *Andryala* L.

Although the etymology of the term *Andryala* is uncertain (Gledhill 2008), it seems to be related to the Greek words "aner", "andros" (stamens) and "hyalos" (transparent), meaning that the fillets of the stamens are very thin (Fournier 1961).

Andryala L. was described by Linnaeus (1737: 238) in *Genera Plantarum*. Nonetheless, in conformity with the International Code of Nomenclature for algae, fungi, and plants (Mcneill *et al.* 2012) the date of valid publication of generic and infra generic names of Spermatophyta is mandatorily after 1 May 1753 (Linnaeus, *Species Plantarum*, ed. 1). Thus, the original description of *Andryala* was validly published by Linnaeus (1754: 351) in the fifth edition of *Genera Plantarum*, as follows:

> *"820. Andryala*. Eriophorus Vaill. A. G. 1721. 20.*
> *CAL. Communis multifidus, brevis, rotundus, villosus: segmentis plurimis, aequalibus, subulatis.*
> *COR. composita imbricata, uniformis: corollulis hermafroditis numerosis, aequalibus. Propria monopetala, ligulata, linearis, truncata, quinquedentata.*
> *STAM. filamenta quinque, capillaria, brevissima. Anthera cylindracea, tubulata.*
> *PIST. Germen infra corollam propriam. Stylus filiformis, longitudine staminum. Stigmata duo, reflexa.*
> *PER. nullum. Calyx connivens, globosus.*
> *SEM. solitaria, ovata, coronata, Pappo simplici, longitudine calycis.*
> *REC. villosum, planiusculum."* (Gen. Pl., ed. 5.).

The description of *Andryala* L. is quite detailed and the name *Eriophorus* Vaill. was cited as a synonym of the genus. In *Species plantarum,* Linnaeus (1753) validly published the first two species for the genus: *Andryala integrifolia* L. (Figure 1.1) and *Andryala sinuata* L. The latter was afterwards recognised as a mere variety of *Andryala integrifolia* L. by the author himself (Linnaeus 1771), according to the excerpt:

> *"Andryala sinuata. varietas est mera Andr. integrifoliae."* (Mant. Pl. p. 459).

Figure 1.1 Specimen and description of *Andryala integrifolia* L. from the Linnaean herbarium, in http://www.linnaeus.nrm.se/botany/fbo/a/andry/andrint.html.en.

Linnaeus (1759) described *Andryala lanata* L., a species that was later included in *Hieracium* L. (Villars 1788; De Candolle 1838). Later Linnaeus (1763) further described a new species for the genus, *Andryala ragusina* L., mentioning two works in which this species is illustrated and identified by means of polynomial nomenclature (*Hieracium incanum lanuginosum Ragusinum, pilosellæ florae*) (Figure 1.2).

Several later authors presented descriptions of *Andryala* L., as well as of new species, some greatly contributing to the modern concept of the genus. Scopoli (1771) described the genus *Andryala* L. in the following terms:

> *"320. Andryala. Linn. Gen. Plant. 820. Forneon. Adans. Calix unico squamarum ordine, quibus ad basin duae aut tres aliae adpressae nec patulae adsident. Semina papo simplici, sessili terminata. Receptaculum villosum, planum."* (Fl. Carniol., ed. 2. p. 115).

Figure 1.2 Reproduction of the illustrations of *Andryala ragusina* L. (A – Hermann 1687; B – Miller 1760).

Scopoli (op. cit.) stressed that the involucral bracts are organized in two or three rows and appressed at the base, enhancing the Linnaean concept of *Andryala*. This author also cited another synonym of *Andryala* L., *Forneon* Adans. Indeed, Adanson (1763) distinguished *Forneon* from other genera in Asteraceae based on the features that fit the genus *Andryala* L. However, in conformity with the *International Code of Nomenclature for algae, fungi, and plants* (Mcneill *et al.* 2012), for any *taxon* from family to genus, inclusive, the correct name is the earliest legitimate one with the same rank, except in cases of limitation of priority by conservation. Thus, the correct name for the genus is *Andryala* L. as it was validly published some years before *Forneon* Adans.

Lamarck (1783) described *Andryala* L. following the Linnaean concept:

> *"La fleur a un calice commun, velu, presque simple, & formé par un rang de folioles étroites, assez égales entr'elles; elle est composée de demi-fleurons tous hermaphrodites, & qui ont leur languette linéaire tronquée & terminée par trois ou cinq dents. Ces demi-fleurons sont situés sur un receptacule commun velu. Le fruit est un amas de semences ovales, chargées chacune d´une aigrette sessile, & renfermées dans le calice commun."* (Encycl. [Lamarck] p. 153)

Although Lamarck (1783) did not describe the morphology of the *Andryala* fruit, he clearly characterised it as a cluster of oval seeds, each provided with a sessile pappus. With regard to the florets, Lamarck (op. cit.) mentioned that the ligules end in three or five teeth, conversely to the Linnaean and the modern concepts of *Andryala.* Indeed, Linnaeus (1754) stressed that the florets exhibit 5-toothed ligules, although in *Andryala laevitomentosa* (Nyár. ex Sennikov) Greuter the ligules can have five to seven apical teeth (Nyárády 1965).

Lamarck (1783: 153) recognised *Andryala* L. as a close genus to *Hieracium* L., differing mainly by the receptacle indumentum and the florets ("*Les Andriales diffèrent des Epervières, par les poils qui couvrent le réceptacle commun de leurs demi-fleurons…*")[1]. Years later Lamarck & De Candolle (1805) contributed greatly to the taxonomic delimitation of *Andryala* L., clearly differentiating it from *Hieracium* L., as shown in the following text:

> *"CDLXXXII. Andryala. Linn. Juss. Lam. Gaertn. – Eriophorus. Vaill. Car. Les andryales ne différent des épervières que parce que leur réceptacle est garni de longs poils qui naissent entre les graines, et qui sont les prolongements des bords de l'alvéole. Obs. Leurs feuilles sont garnies d´un duvet cotonneux composé de poils rameux."* [Fl. Franc. (DC. & Lamarck), ed. 3. p. 56].

Actually, these authors distinguished *Andryala* L. based on the presence of receptacle hairs between the seeds (corresponding these to prolongations of the margins of the receptacle alveoli) and the existence of a stellate-hairy indumentum, features that are mentioned in all recent descriptions of the genus (e.g. Sell 1976; Talavera 1987; Blanca 2009; Blanca 2011).

Lamarck (1783) described several new species: *Andryala glandulosa* Lam., *Andryala laciniata* Lam. and *Andryala nudicaulis* Lam. The latter was afterwards excluded from *Andryala* L. (Steudel 1840). In spite of Lamarck (op. cit.) having considered *Andryala laciniata* Lam. and *Andryala ragusina* L. as distinct species, De Candolle (1838) recognised the first as a variety of *Andryala ragusina* L. Taxonomic instability in *Andryala* is related to the fact that new names were given to species which were previously and validly described. For instance, Lamarck (1783) described *Andryala corymbosa* Lam., stating *Andryala integrifolia* L. as a synonym. In respect to *Andryala glandulosa* Lam., Lamarck (1783) stressed that this species should be included in a separate genus, seeing that the receptacle exhibits peripheral chaffy scales and is slightly setose. However, Lamarck's collaborator Poiret (1823) recognised *Andryala glandulosa* Lam. (Figure 1.3) and described *Andryala* L. as follows:

> *"1363. Andryala. Calix rotundatus, simplex, multipartitus, subaequalis, interdum squamulis paucis cinctus; pappus sessilis, pilosus; receptaculum pilosum."* (Tabl. Encycl. p. 205).

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[1] Lamarck (1783) also distinguished *Andryala* L. from other genera (*Seriola* L., *Hypochoeris* L. and *Cichorium* L.) by receptacle features ("… elles sont distinguées des Serióles, des Porcelles, des Chicorées, &c. parce que ce sont des poils qui couvrent leur réceptacle, & non des paillettes.").

Hence, according to Poiret (op.cit.) in *Andryala* L. the receptacle can sometimes be surrounded by a few small scales.

L'Héritier (1785: 35) fully described *Andryala cheiranthifolia* L'Hér. (Figure 1.4) as a new species, adding the following diagnose: "*Planta undique induta villis glandulosis*". In the original description of *Andryala glandulosa* Lam. this feature was also highlighted: "*Andryala tomentosa, pilis glandulosa vestita*". Much later, these were recognised as belonging to the same species, although corresponding to distinct subspecies (Fernandes 1959; Greuter 2003).

Moreover, Scopoli (1787) described in detail *Andryala tomentosa* Scop., presenting an illustration (Figure 1.5) and underlining the following morphological features:

> *"Tota planta denso villo canescens, qui in superiori imprimis eiusdem loco glandula terminatus est."* (Delic. Fl. Faun. Insubr. ii. p.12).

Figure 1.3 Reproduction of the illustration of *Andryala glandulosa* Lam. on the left (Poiret 1823).

According to this description, *Andryala tomentosa* Scop. resembles the earlier described *Andryala glandulosa* Lam. and *Andryala cheiranthifolia* L'Hér., although the glandular hairs are found especially in the upper part of the plant. In agreement, Aiton (1789) recognised *Andryala cheiranthifolia* L'Hér. as a distinct species, citing both *Andryala glandulosa* Lam. and *Andryala tomentosa* Scop. as synonyms. Nonetheless, Aiton (op. cit.) clearly did not adopt the earliest validly published name, which later led to some nomenclatural instability.

Villars (1788) underlined an important diagnostic feature in *Andryala* L., the length of the receptacle setae, according to the following text:

> *"Les Andryala ont leur calice écailleux; le réceptacle est garni de poils soyeux qui sont de la longuer des semences."* [Hist. Pl. Dauphiné (Villars) iii. p. 65].

Figure 1.4 Reproduction of the illustration of *Andryala cheiranthifolia* L'Hér. (L'Héritier 1785).

Indeed, according to the modern concept of the genus, the receptacle setae can be shorter or longer than the cypsela (Sell 1976; Talavera 1987).

Aiton (1789) described two new species for the genus: *Andryala crithmifolia* Aiton, native from Madeira, and *Andryala pinnatifida* Aiton, including *Andryala pinnatifida* var. *α* from Madeira and *Andryala pinnatifida* var. *β* from the Canary Islands[2]. Later, Schultz Bipontinus (1849) described *Andryala pinnatifida* Aiton var. *β* in detail, restricting the name *Andryala pinnatifida* Aiton to the Canarian plants.

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[2] *Andryala pinnatifida* var. *α* corresponds to *A. glandulosa* subsp. *cheiranthifolia* (L'Hér.) Greuter with more divided leaves.

Figure 1.5 Reproduction of the illustration of *Andryala tomentosa* Scop. (Scopoli 1787).

Poiret (1789) described a new *Andryala* species for North Africa (Algeria), *Andryala nigricans* Poir., considering it distinct from *Andryala integrifolia* L., also present in this region.

Some authors proposed new genera including species that fit the modern concept of *Andryala* L. For instance, Roth (1790) described the genus *Voigtia*, including a single species: *Voigtia tomentosa* Roth. The description of the genus is as follows:

> *"Receptaculum subvillosum Calyx communis aequalis 5- ad 7- phyllus. Calyculi proprii marginalis, plures, uniflori. Flosculi ligulati; centrales ecalyculati. Semina radii nuda; centralia pappo plumoso coronate." [Bot. Mag. (Römer & Usteri) iv. p. 17].*

Although the description is somewhat vague, it includes features that match the modern concept of *Andryala* L., at least in what concerns some species (e.g. involucre with two series of bracts, the external and the internal, the latter numerous). Moreover, when describing *Voigtia tomentosa* Roth, Roth (1790) stated that the peripheral fruits are enclosed at the base of the external involucral bracts ("*Semina … radii calyculi proprii basi imersa…*"). Schreber (1791) also described a new genus, *Rothia* Schreb., comparing it to *Andryala* L. The following text corresponds to the original description of *Rothia* Schreb.:

> *"CAL. Communis rotundatus, villoso-tomentosus: squamis circiter septem, aequalibus, linearibus, acutis.*
> *COR. Composita imbricata, uniformis: Corollulis hermaphroditis, numerosis, aequalibus.*
> *Propria monopetala, ligulata, linearis, truncata, quínquedentata.*
> *STAM. Filamenta quinque, capillaria, brevissima. Anthera cylindracea, tubulosa.*
> *PIST. Germen ovatum. Stylus filiformis, longitudine staminum. Stigmata duo, reflexa.*
> *PER. Nullum. Calyx connivens.*
> *SEM. Solitaria.*
> *Disci cylindraceo-turbinata, striata. Pappus, capillaries, inferne plumosus, sessilis.*
> *Radii cylindracea, striata, paleis involuta. Pappus nullus.*
> *REC. Planum, disco pilosum, radio paleaceum. Paleae plurium serierum, lineares, canaliculatae, erectae, acutiusculae, basi tubulosae: exteriores longitudine calycis, interiores sensim breviores."* (Gen. Pl., ed. 8[a]. ii. p. 531).

Voigtia Roth and *Rothia* Schreb. correspond to the same *taxon* since in both the fruits found at the circumference of the involucre are enfolded by the involucral bracts and apparently devoid of pappus, contrary to the inner ones. Likewise, Gaertner (1791) recognised both *Andryala* L. and *Rothia* Schreb., including them in two different groups: the first in "*Seminibus uniformibus*" and the latter in "*Seminibus difformibus*". Gaertner (1791) replaced the name *Voigtia tomentosa* Roth. by *Rothia andryaloides* Gaertn., considering it as the only species within *Rothia* Schreb. Later Roth (1797), accepting the name *Rothia* Schreb., included in this genus two more species: *Rothia cheiranthifolia* Roth and *Rothia runcinata* Roth. Although, later authors followed this taxonomic concept (e.g.

Willdenow 1803), Persoon (1807) saw no reason to split *Andryala* L. into two distinct genera. In agreement, Steudel (1840) published a valuable list of synonyms in which *Forneon* Adans., *Voigtia* Roth and *Rothia* Schreb. are given as synonyms of *Andryala* L. Nonetheless, Persoon (1807) admitted two distinct groups for *Andryala* L.: "*Seminibus omnibus papposis*" and "*Seminibus marginalibus nudis*", corresponding the latter to the *Rothia* Schreb. Persoon (1807: 577) underlined the existence of ribbed cypselae in *Andryala* L. (*"Cal. multipartitus, subæqualis, rotundatus, Recept. villosum. Pappus simplex, sessilis. Sem. sulcata*."), as did Schreber when describing *Rothia* Schreb., thus contributing to the modern concept of the genus.

Smith in a work by Sibthorp & Smith (1813) described a new species from the East Mediterranean: *Andryala dentata* Sm. Until then only European, North African and Macaronesian species had been described[3]. The protologue of *Andryala dentata* Sm. contains a reference to an illustration from *Flora Graeca* ("*Fl. Græc. t. 811*") which can also be observed in a later publication by Sibthorp & Lindley (1837) (Figure 1.6).

Figure 1.6 Reproduction of the illustration of *Andryala dentata* Sm. (Sibthorp & Lindley 1837).

Hoffmansegg & Link (1825) briefly described the genus *Andryala* L., in conformity with the following text:

> *"Peranthodium subsimplex, phyllis acenia non involventibus, exterioribus paucis. Receptaculum hirsutum. Pappus sessilis, piliformis, saepe scaber."* [Fl. Portug. (Hoffmannsegg) ii. p. 151].

According to these authors, in *Andryala* L. the involucral bracts do not enfold the fruits. Hoffmansegg & Link (1825) described three new *Andryala* species for the Portuguese flora. Nonetheless, these correspond all to the very polymorphic *Andryala integrifolia* L. (Coutinho 1939), which indeed exhibits flat involucral bracts not enfolding a fruit (e.g. Talavera 1987). Actually, this feature is not common to all *Andryala* L. species, according to the modern concept. Similarly to earlier authors, Hoffmansegg & Link (1825) mentioned the presence of a sessile, pilose and often rough pappus in *Andryala*.

Sibthorp & Lindley (1837) provided a brief description of *Andryala* L. in which they described the fruit as a 10-ribbed and truncate achene, according to the following excerpt:

> *"Andryala. Linn. Gen Pl. 403. Juss. Gen Pl. 171. Gaertn. t. 158. Receptaculum pilosum. Involucrum simplici serie polyphyllum, subaequale, rotundatum. Achaenia decagona, truncata. Pappus sessilis serie simplici, scaber."* [Fl. Graec. (Sibthorp) ix. p. 7].

De Candolle (1838) contributed to the modern concept of *Andryala* L. presenting a quite detailed description of the genus:

> *ANDRYALA Linn. gen. n. 915. DC. Fl. fr. ed. 3. v. 4. p. 56. — Eriophorus Vaill, act. acad. par. 1721. — Forneum Adans. fam. 2. p. 112.— Andryala et Voigtia Roth in Ust. mag. 9. p. 17. — Andryala et Rothia Schreb. gen. n. 1240 et 1241, sp. 3. p. 1611. Cass. dict. 25. p. 64, 66. p. 311. Less. syn. p. 141.*

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[3] *Andryala ragusina* L. was erroneously assigned to the islands of the Aegean Sea when first described by Linnaeus.

> *Capitulum multiflorum. Invol. campanulatum, squamis numerosis linearibus 1-serialibus, nonnulis exterioribus accessoriis. Recept. alveolatum, alveolis fimbrilliferis in setas productis, interdum in ambitu paleaceum. Achaenia obovato-oblonga 10-striata erostria. Pappus pilosus scaber facilè deciduus 1- serialis rigidulus.- Herbae pleraeque australi-Europaeae biennes aut perenes, tomento brevi stellato-velutino et pilis apice glandulosis praesertim in partibus superioribus donatae. Capitula flava saepiùs corymbosa."* [Prodr. (A. P. de Candolle) vii. p. 244].

According to De Candolle (op. cit.), *Andryala* L. includes biennial and perennial herbs, covered with a stellate-hairy indumentum and with glandular hairs, especially in the upper part of the plant. Additionally, De Candolle (1838) mentioned the most frequent type of inflorescence as well as the ligule colour, and even stressed the fact that the pappus is deciduous. De Candolle (1838) admitted two sections for *Andryala* L. based on receptacle and achenes features (i.e. presence/absence of chaffy scales on the margin of the receptacle and presence/absence of pappus on the peripheral achenes) as follows:

> *- Sect. I. Euandryala - Andryala Roth. Schreb. Less. Cass. (Recept. ebracteolatum. Achaenia omnia pappigera).*
>
> *- Sect. II. Voigtia Roth in Roem. et Ust. mag. 9. p. 17. non Spreng. - Rothia Schreb. gen. n. 1241. non. Pers. nec Lam. (Recept. margine paleaceum, paleis involucro brevioribus subhyalinis. - achaenia radii à plurimis dicuntur calva, sed papposa semper vidi. Fortè ob pappum deciduum achaenia visa fuerunt nuda. Fortè interdúm reverâ ob palearum pressionem calva?).*

De Candolle (1838) included most of the *Andryala* species in section I and only five in section II (*Andryala rothia* Pers., *Andryala varia* Lowe, *Andryala sinuata* L., *Andryala integrifolia* L., and *Andryala laxiflora* DC.). Nevertheless, De Candolle (op. cit.) questioned the absence of the pappus on peripheral achenes, arguing that since the pappus is deciduous perhaps this is the reason why achenes are sometimes observed without this structure. De Candolle (op.cit.) contributed to a better taxonomic delimitation of the genus excluding several species and placing them in other genera[4].

Years later Gussone (1843), an Italian botanist who studied the Sicilian flora, described *Andryala* L. according to the following text:

> *"Andryala. Lin. gen. pl. n. 945 – Juss. 171. Anthod. multiflorum, polyphyllum; foliolis saepius 1-seriatis, subaequalis. Sem. oblonga, striata, truncata. Papp. sessilis, pilosus, scaber, facile deciduus. Recept. areolatum, interdum in ambitu paleaceum; areolis margine pilosis (Herbae in Sicilia annuae, tomento tenui stellato mollissimo adpresso obductae: flores erectis, citrini, sulphurei, aut aurei, racemoso-paniculati vel corymbosi)."* (Fl. Sic. Syn. ii. p. 407).

Gussone (op. cit.) included also annual herbs in the genus, bearing racemose-paniculate or corymbose inflorescences. Additionally, the author made reference to the different shades of yellow of the florets.

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[4] According to De Candolle (1838): "*A. chondrilloides* Scop. = *Crepis chondrilloides*, *A. lanata* L. = *Hieracium tomentosum*., *A. nemausensis* Vill. = *Pterotheca nemausensis*, *A. nudicaulis* Lam. = *Pterotheca nemausensis* and *A. pontana* Vill. = *Hieracium montanum*." De Candolle (op. cit.) did not mention the authors of all species.

Schultz Bipontinus (1849) presented an emended Linnaean concept of *Andryala* L., which is indeed closer to the modern concept:

> *"Capitulum multiflorum. Involucrum 1-seriale, campanulatum. Receptaculum convexum, alveolatum, alveolarum margine in setas integras elongatas abeunte, raro margine paleatum. Achaenia columnari-turbinata, 10-costata, costis superne in cornua totidem productis, brevia. Pappus 1-serialis caducus, setis inferne barbellatis superne denticulatis, rariùs si receptaculum margine paleaceum achaenia paleis inclusa, calva. Herbae annuae, biennes, vel perennes, quandoque suffruticulosae, caule rarius monocephalo pl. corymboso-racemoso, foliato, foliis lanceolato ovatis, dentato-pinnatifidis, tomento stellato obductae: pl. pili flavo-virentes, apice glanduliferi, praecipue in plantae parte superiore, sunt intermixti. Succo lacteo scatent, e planta vulnerata emanente et in gummi rufescens coagulante."* [Hist. Nat. Iles Canaries (Phytogr. iii. p. 411)].

In effect, Schultz Bipontinus (op. cit.) included in *Andryala* L. annual to perennial herbs, sometimes exhibiting a woody habit. This author described the fruit morphology quite well: oblong-obconical achene, with 10 ribs forming a crown at the apex, bearing a pappus barbelate at the base and denticulate at the apex. Schultz Bipontinus (1849) also emphasised rare features in *Andryala* L. such as receptacle margin with chaffy bracts, cypsela enfolded by involucral bracts devoid of pappus, and monocephalus inflorescences. Actually, Schultz Bipontinus (1849) proposed a division of *Andryala* L. similar to the one suggested by De Candolle (1838):

> *A. Receptaculum setosum. Achaenia omnia pappigera. Euandryala DC., Pr. 7, p. 244 ex parte.- C.H. Schultz Bip. emend.*
> *B. Receptaculum setosum, margine paleatum, paleis achaenia calva foventibus. Rothia Schreber.*

Furthermore, in the same publication Schultz Bipontinus (op. cit.) included two groups in *Euandryala* DC. based on the colour of the fruit (yellowish brown or dark brown):

> *a. Achaenia alutacea (A. agardhii DC., A. integrifolia L., A. sinuata L.)*
> *b. Achaenia atra (A. pinnatifida Aiton, A. cheiranthifolia L'Hér.).*

In the second division, *Rothia* Schreber, Schultz Bipontinus (1849) included *A. cheiranthifolia* L'Hér. [= *A. glandulosa* Lam.]. In the same publication the author presented a detailed description of *Andryala pinnatifida* Aiton from the Canary Islands and admitted numerous forms, recognising it as a very polymorphic species.

Willkomm & Lange (1865) described the genus *Andryala* L. similarly to Schultz Bipontinus (1849), according to the following text:

> *"CCCCXLVL. Andryala L. Gen. pl. Anthodium multiflorum, squamis subbiseriatis. Receptaculum nudum alveolatum, alveolis pentagonis brevissíme marginatis, margine membranaceo lacero-dentato et in seta achaenia subaequantes v. superantes producto. Achaenia parvula cylindrica, 10 costata, apice truncata 10 dentata; pappo sordide albo caduco multo breviora. Pappi pili basi subplumosi apicem versus dentati. - Herbae v. suffrutices stellato-tomentosae, incanae v. viridi canescentes, caulibus foliatis plerumque ramosis, calathis subglobosis paniculatis v. cymosis, raro solitariis, ligulis luteis."* (Prodr. Fl. Hispan. ii. p. 270).

These authors described the *Andryala* plants as whitish or greyish green herbs or subshrubs, with leafy and usually branched stems. According to the modern concept of *Andryala* L., the stems were described as usually branched at the upper part of the plant and less frequently from the base, while the leaves are distributed along the stems, although in some cases they are mainly basal (Sell 1976; Talavera 1987; Blanca 2009, 2011). Willkomm & Lange (1865) described the receptacle in more detail highlighting that the margins of the alveoli are membranaceous lacerate-dentate and with setae, shorter or longer than the achenes. Actually, according to the modern concept the receptacle setae can surpass the cypselae or not (Sell 1976; Talavera 1987; Blanca 2009, 2011). Furthermore, Willkomm & Lange (1865) considered the involucre subglobose and, indeed, according to the modern concept the involucre has either this form or is campanulate.

Battandier (1889) contributed greatly to the knowledge of *Andryala* L. in North Africa and described the genus as follows:

> *"Pericline à écailles subunisériées, les caliculaires avortant d´ordinaire; réceptacle fibrilleux; achaines minuscules 5-8 fois plus courts que l'aigrette, atténués à la base, tronqués au sommet, noirs, à 10 côtes saillantes, claires, terminées au sommet en petite dent étalée; aigrette un peu plumeuse vers la base, très caduque.- Plantes mollement veluotées, à capitules en corymbe, médiocres, subglobuleux."* (Fl. de l 'Alger, Dicot. p. 566).

Similarly to previous authors, Battandier (1889) paid special attention to the cypsela morphology, stressing the presence of prominent light ribs, each forming an extended tooth at the apex. Following the taxonomic concept of earlier authors, Battandier (1889) also considered two sections in *Andryala* L., according to the following text:

> *1. Euandryala. - Périclinė à écailles n´embrassant pas les achaines extérieurs; receptacle fibrilleux mais sans paillettes à la périphérie.*
> *2. Rothia Schreber, non Persoon. - Achaines extérieurs enveloppés dans les écailles du péricline; pericline doublé intérieurement d´un ou deux rangs de paillettes hyalines plus courtes qui lui. Plantes annuelles.*

Moreover, Battandier (op. cit.) proposed the division of *Euandryala,* based on the plant life cycle, as follows:

> *a. Plantes sous frutescentes à la base, couverts d´un duvet court et serré. (A. ragusina L., A. spartioides Pom., A. mogadorensis Coss.)*
> *b. Plantes anuelles ou bisannuelles, jamais lignaeux à la base. (A. nigricans Poir., A. integrifolia L., A. dentata Sibth. & Sm., A. arenaria Boiss. & Reut.).*

In the section *Rothia* Schreber, Battandier (1889) included only *A. laxiflora* Salzm.[5] and *A. floccosa* Pom.

Years later, Caballero (1916) mentioned a peculiar specimen collected in Northern Morocco which he decided to include in a new genus after having consulted the illustrious botanist D. Carlos Pau. Caballero (1916) described the new genus, *Paua* Caball., according to the following text:

> *"Capitulum multiflorum campanulatum, bracteis anthodii uniserialibus post anthesim reflexis; receptaculum nudum alveolatum, alveolis pentagonis brevissime membranáceo marginatis ad ángulos pentagonorum in dentes breves achaenia granditer superatis productis; achaenia párvula, cylindracea, 10 costata, basi attenuata, ápice truncata edentata, pappo multo breviora; pappi decidui pili a basi ad apicem dentati. Planta*

---

[5] *A. laxiflora* Salzm., a herbarium name, was validly published by De Candolle (1838) as *A. laxiflora* DC.

> *maroccana perennis, ramosissima, eglandulosa, tomento sordide incano stellato ramoso tecta; foliis congestis parvis, spathulatis, integris vel parce dentatis, semiamplexicaulibus; capitulis solitariis ramos terminantibus."* [Bol. Soc. Esp. Hist. Nat. xvi. 540 (1916)].

Caballero (op. cit.) stressed the affinity of *Paua* Caball to *Andryala* L., further stating that it is quite distinct when compared to *Hieracium* L. Later Caballero (1917) illustrated several diagnostic features of *Paua* Caball. (Figure 1.7). Clearly, the fruit morphology differs from that of most of the *Andryala* species described until then. Caballero (1916) described a single species for the new genus, *Paua maroccana* Caball., that was later included in *Andryala* L. under the name *Andryala maroccana* (Caball.) Maire (Maire 1922). Therefore, Maire (1922) did not recognise *Paua* Caball. as a distinct genus, definitely placing it in *Andryala* L.

In *Flora de Portugal* Coutinho (1939) described *Andryala* L. in terms that correspond quite well to the modern concept of the genus:

> *"Capítulos multifloros com invólucro campanulado de brácteas herbáceas ou levemente escariosas na margem, bisseriadas ou sub-bisseriadas, pouco desiguais, acompanhadas ou não de uma ou duas séries de brácteas internas completamente escariosas; receptáculo alveolado, provido de sedas, grandes ou medíocres; aquénios pequenos, oblongo-cónicos, atenuados na base e troncados ou denticulados no cimo, decicostados, com papilho muito caduco de pêlos ásperos, celheados na base e denticulados na parte restante. Plantas caulescentes, vestidas de tomento estrelado, acompanhado ou não de pêlos simples glandulosos; capitulos de ordinário reunidos em cimeiras corimbiformes ou racemosas."* (Fl. Portugal, ed. 2, p. 791).

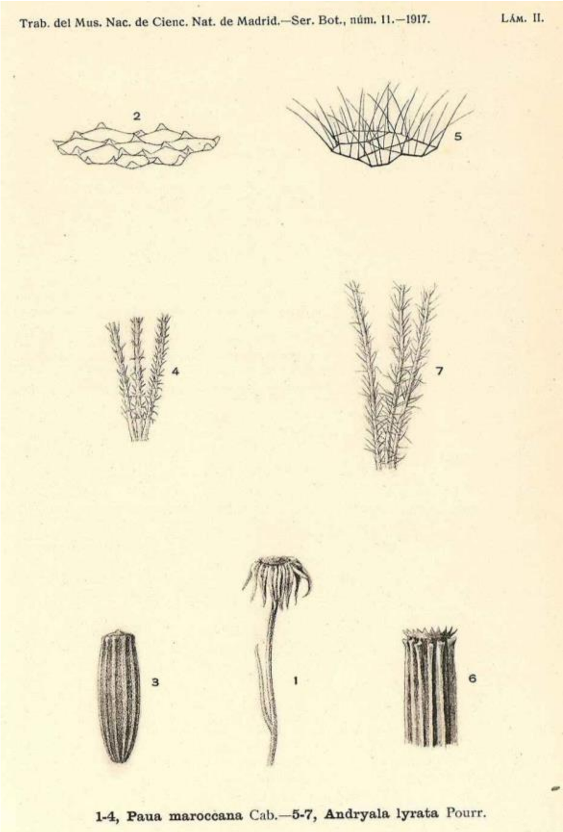

Figure 1.7 Diagnostic characters of *Paua maroccana* Caball. vs. *Andryala lyrata* Pourr. (Caballero 1917).

Coutinho (op.cit.) described the involucral bracts in some detail, considering them herbaceous or with slightly membranaceous margins, arranged in more or less two rows, accompanied or not by one or two series of completely scariose internal bracts. The latter correspond most surely to the "chaffy scales at the circumference of the receptacle", feature used by several authors in the past to divide *Andryala* L. into two sections. Similarly to previous authors, Coutinho stated *Andryala laxiflora* (Salzm.) DC. as a species provided with these scariose internal bracts, not recognising, however, two distinct groups in *Andryala* L. on account of this feature.

Nyárády (1963) described a new genus for Romania, *Pietrosia* Nyár., including a single species, *Pietrosia levitomentosa* Nyár. However, in the same publication Nyárády (op.cit.) made no reference to *Andryala* L. as a related genus. Years later, Sell (1975) combined *Pietrosia levitomentosa* Nyár. *as Andryala levitomentosa* (Nyár.) P.

D. Sell. not accepting, therefore, *Pietrosia* Nyár. Nonetheless, Sennikov (1999) proposed to restore the genus as *Pietrosia* Nyár. ex Sennikov.[6] stressing that an unusual character separates it from *Andryala*, namely that of "a monopodial rosette producing long caudex and axillary oligophyllous monocephalous generative shoots". Furthermore, Sennikov (1999) recognised two sections for *Pietrosia* Nyár. ex Sennikov, based on the receptacle and involucral bracts indumentums, as follows:

> *Sect. 1. Pietrosia. - Receptaculum squamis longis tectum. Involucri phylla pilis simplicibus longis obsita.*
>
> *Sect. 2. Andryalopsis Sennik. sect. nov. - Receptaculum nudum. Involucri phylla pilis glanduliferis brevibus obsita.*

The author included *Pietrosia laevitomentosa* Nyár. ex Sennikov.[7] in Sect. 1. *Pietrosia* Nyár. ex Sennikov and *Pietrosia agardhii* (Haens. ex DC.) Sennikov in Sect. 2. *Andryalopsis* Sennikov. Nonetheless, Greuter (2003) did not recognise *Pietrosia* Nyár. ex Sennikov as a distinct genus and presented a new combination: *Andryala laevitomentosa* (Nyár. ex Sennikov) Greuter.

Bramwell & Bramwell (1974) briefly described the genus *Andryala* L. in the publication *Wild flowers of the Canary Islands*, as follows:

> *"Leaves lobed or toothed to subentire. Involucral bracts in a single row, usually densely hairy on the outer face. Flowers yellow. Receptacle with long hairs-like scales. Pappus of simple, deciduous hairs. Cypselas with 8-10 ribs."* (Wild flowers of the Canary Islands, p. 220).

These authors contributed to the modern concept of the genus by characterising the external involucral bracts indumentum, referring specifically to the outer face of these structures.

In *Flora Europaea* Sell (1976) described the genus *Andryala* L., according to the following texto:

> *"Annual to perennial herbs. Stems usually solitary, rarely numerous. Leaves entire to pinnatissect; cauline few to numerous, often more or less amplexicaule. Capitula usually few to numerous, rarely solitary. Involucral bracts in 2 to several rows. Receptacule pitted, the margins of the pits lacinate-dentate and with cilia which are often longer than the subtending achenes, sometimes with scales enfolding some or all the florets. Ligules yellow, the outer sometimes with a reddish stripe on outer face. Achenes oblong or obconical, truncate (rarely with a disc) at apex, with 8-10 prominent ribs; pappus of greyish hairs, falling entire."* (Fl. Eur., p. 358).

Sell (op. cit.) underlined the variability of some characters within *Andryala* L. (e.g. leaf margin, the number of cauline leaves and number of capitula per inflorescence). This author characterised *Andryala* L. in what concerns the number of stems as well as the leaf insertion on the stem. In addition, Sell (1976) stressed the occasional presence of a reddish stripe on the outer face of the external ligules and the existence of a disc at the apex of the cypsela, although very rarely. The latter feature was also mentioned in the protologue of the genus *Paua* Caball. Indeed,

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[6] Sennikov (1999) considered *Pietrosia* Nyár. as an invalid name, according to the following text: "*Pietrosia Nyárády ex Sennik. gen. nov. – Pietrosia Nyárády, 1963, Rev. Biol. (Bucharest), 8,3 : 250, descr. lat., nom. invalid. (Art. 37).*"

[7] Sennikov (1999: 77) deliberately changed the original spelling of the epithet *laevitomentosa*. Actually, Sennikov (op. cit.) made the following statement: "*Due to nomenclatural reasons, the name Pietrosia levitomentosa should be validated anew, because E. I. Nyárády did not state the type in the protologue.*"

Caballero (1916) described the apex of the cypsela in these terms: "*apice achaenii edentata nec coronata*", that is, apex with no teeth or crown. Actually, in most *Andryala* L. species the cypsela apex displays a more or less conspicuous inner ring of teeth surrounded by a crown formed by the extension of the ribs. Furthermore, Sell (1975: 256) stated that "some of the N. African species of *Andryala* have a disc at the apex of the achenes …", whereas "… the achenes of *Pietrosia* [later included in *Andryala* L.] have at their apex a 2-rimmed disc."

More recent authors presented full descriptions of the genus *Andryala* L., coinciding in the essential points to that of Sell's. For instance, in *Flora vascular de Andalucía occidental* Talavera (1987) described *Andryala* L. as follows:

> *"Hierbas anuales, bienales o perennes, densamente cubiertas de pelos estrellados, a veces mezclados con pelos unicelulares simples o glandulares, caulescentes. Hojas de enteras a pinnatissectas; las inferiores a veces en roseta. Capitulos solitários o agrupados en inflorescencias corimbiformes. Involucro con 2-6 filas de bracteas. Brácteas involucrales con un mechon de pelos en el ápice y a veces con una flor axilar. Receptáculo foveolado, con numerosos pelos unicelulares más cortos ou más largos que los aquénios. Lígulas amarillas; las externas a veces con el dorso rosado. Aquénios subcilíndricos u obcónicos, negros, con 10 costillas longitudinalles blancas. Vilano formado por 1 fila de pelos subplumosos, prontamente caduco, blanco."* (Fl. Iber. p. 96).

Talavera (op.cit.) also referred the variability of the leaf margin and additionally stated that the lower leaves can be arranged in a rosette. This author clearly specified the number of rows of the involucral bracts (two to six).

In *Flora of Madeira* the description of *Andryala* L. by Press (1994: 381) resembles very much the one of Sell's authority, as shown in the excerpt below:

> *"Annual, biennial or perennial herbs, stellate-hairy. Stems solitary or numerous, branched. Leaves entire to pinnatisect, the cauline often sessile, rounded to amplexicaul. Capitula few to numerous, rarely solitary. Involucral bracts in 1-2 rows. Receptacle pitted; pits with laciniate-dentate margins. Florets sulphur-yellow, gold or orange, sometimes with a red stripe on the back of the ligule. Achenes oblong to obconical with 8-10 ribs extending into teeth at the truncate apex; pappus a ring of greyish hairs, falling entire."* (Flora of Madeira, p. 381).

This author also highlighted the colour of the florets, which range from different tons of yellow to orange.

It is worth noting that the more recent descriptions of the genus *Andryala* L. (e.g. Sell 1976; Talavera 1987) do not propose any division of the genus in sections. Actually, the divisions of *Andryala* L. in two sections suggested in the past have something in common; they all place *Andryala laxiflora* DC. (= *A. rothia* Pers.) in the second section, a distinct species that is not segregated from *Andryala* L. in any of the recent descriptions of the genus.

1.2 Higher classification and systematic position of the genus *Andryala* L.

The genus *Andryala* L. is currently included the Phylum Magnoliophyta, Class Magnoliopsida, Subclass Asteridae, Superorder Asteranae, Order Asterales and Family Asteraceae (Takhtajan 2009). It belongs to the Subfamily Cichorioideae Chevall., Tribe Cichorieae Lam. & DC. and Subtribe Hieraciinae Dumort. (Kilian *et al.* 2009).

Asteraceae (Compositae), one of the more successful angiosperm families, is represented by innumerable genera, species and individuals (Takhtajan 1997). In Asteraceae traditionally two subfamilies were recognised (Asteroideae and Cichorioideae). Currently this family includes ten more subfamilies (Funk *et al.* 2009). It represents the largest dicotyledone family, with about 25 000 species distributed worldwide (Glimn-Lacy & Kaufman 2006). Asteraceae is the alternative name for Compositae, accepted under the current Botanical Code, and deriving from the type genus, *Aster* L. The name Compositae, authored by Giseke (1792) is currently treated as validly published, since it corresponds to a name of long usage. This family is characterised by florets arranged on a receptacle in centripetally developing heads and surrounded by bracts, by anthers fused in a ring with the pollen pushed or brushed out by the style, and by the presence of achenes (cypselae) usually with a pappus (Funk *et al.* 2009). Although the family is well-defined, there is a great deal of variation among the members: the habit varies from annual and perennial herbs to shrubs, vines, or trees, although few are true epiphytes; species grow in just about every type of habitat from forests to high elevation grasslands, however, being less common in tropical wet forests and more common in open areas (Funk *et al.* 2009).

The earliest fossil record for the Asteraceae consists mainly of pollen. Based upon fossil references Bremer & Gustafsson (1997) dated the family back at least to the Oligocene-Eocene boundary of 38 million years B.P. The megafossil record of the Asteraceae is very sparse. *Viguiera cronquistii* Becker from the Tertiary (Oligocene-Miocene), appearing to correspond to a capitulum, was thought to be the first reliable megafossil of Asteraceae (as cited in Crepet & Stuessy 1978). However, Crepet & Stuessy (1978) re-examined the type specimen and concluded that it "cannot be considered unequivocally to be the remains of a Compositae". Very recent studies resulted in recognition of the oldest fossil assignable to Asteraceae an exceptionally well preserved capitulescence from the Middle Eocene found in the 47.5 million-year-old Huitrera Formation in Argentina (Barreda *et al.* 2012).

The systematic position of *Andryala* L. has been more or less stable throughout the years. De Candolle (1838) placed this genus in Suborder Ligulifloræ, Tribe Cichoraceæ and Subtribe Lactuceæ. Schultz Bipontinus (1849) included *Andryala* L. in the Tribe Cichoraceæ, similarly to De Candolle (op. cit.). However, Schultz Bipontinus (op. cit) considered *Andryala* L. as part of the Subtribe Hieracieæ Sch. Bip., and further included the genus in the division II – Andryaleæ. Much later, Sell (1976) also placed *Andryala* L. in the Subfamily Cichorioideae and the Tribe Cichorieae[8]. Mabberley (1997) included *Andryala* L. in the same subfamily and the Tribe Lactuceae[9]. In the same publication, Mabberley apparently included *Andryala* L. in the Subtribe Hieraciinae ["*Andryala L. Compositae (Lact.-Hier.)*]", along with the genera *Hieracium* L. and *Pilosella* Hill.

1.3 Related genera and origin of *Andryala* L.

The closest genera to *Andryala* L. are the ones included in the subtribe Hieraciinae: *Hieracium* L., *Hispidella* Barnad. ex Lam. and *Pilosella* Hill (Fehrer *et al.* 2007a). Actually, according to recent data from nuclear DNA three major lineages exist: genus *Pilosella* with *Hispidella* as a sister *taxon*, *Hieracium/Chionoracium* [*Hieracium* subg. *Hieracium*

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[8] Plants from the Tribe Cichorieae can de distinguished by the almost exclusive presence of homogamous capitula with 5-dentate, ligulate florets; and exclusive presence of lactiferous canals in both the subterranean and aerial parts (Funk *et al.* 2009).

[9] *Lactuceae* Cass. (1819) is an alternative name for *Cichorieae* Lam. & DC. (1806).

and *Hieracium* subg. *Chionoracium* (= *Stenotheca*)] and *Andryala*, a sister genus of the whole group (Fehrer *et al.* 2007a). *Andryala* is a member of tribe Cichorieae (Asteraceae), included in subtribe Hieraciinae, along with *Hieracium* L., *Hispidella* Barnad. ex Lam., *Pilosella* Vaill. (Fehrer *et al*., 2007a; Krak & Mráz, 2008) and *Schlagintweitia* Griseb., a segregate of *Hieracium*, including *S. intybacea* (All.) Griseb. (also known as '*Hieracium*' *intybaceum* All.), and two of its hybridogeneous derivates (Bräutigam & Greuter, 2007; Kilian *et al*., 2009).

Molecular studies showed that the origin of *Andryala* L. is related to an ancient hybridization event between *Pilosella* and the *Andryala* ancestor (Fehrer *et al.* 2007a).

1.4 Objectives

No biosystematic work on the genus *Andryala* L. as a whole has ever been performed so far. Hence, the aim of this thesis was to revise the entire genus based on morphological and molecular data. To accomplish this aim the following objectives were defined:

i) clarify the morphology of the *Andryala taxa* in all its distribution area (Mediterranean Basin and Macaronesia);
ii) elucidate taxonomy and nomenclatural aspects of *Andryala*;
iii) clarify the phylogenetic relationships of *Andryala* species by using different nuclear ribosomal and chloroplast markers as well as one single-copy nuclear gene;
iv) examine colonization patterns in the Macaronesian region.

1.5 Structure

To meet the above objectives, the thesis was organized in several capitula with references to published papers, all written during the elaboration of the thesis. **Chapter 2** includes a description of the morphological characters of the genus, comprehending both vegetative and reproductive taxonomic characters. The variability of these characters is also assessed. In **Chapter 3** taxonomic relationships within *Andryala* L. are accessed by means of numerical taxonomy techniques. Morphological resemblances between specimens are established using different similarity or dissimilarity measures and coefficients. Both ordination and clustering methods were applied in this analysis. In **Chapter 4** results of the taxonomic and nomenclatural study are presented. For each recognised taxon the accepted name [according to the International Code of Botanical Nomenclature (2011)] is followed by a list of synonyms and a detailed description. Additional information (typification, chromosome numbers, distribution, ecology and conservation status, as well as taxonomic and nomenclatural comments) is included. In **Chapter 5** a publication on phylogenetic analysis of *Andryala* is presented. This study was conducted in order to elucidate species relationships within *Andryala* L. by using two nuclear ribosomal DNA markers (ITS and ETS), two chloroplast markers (trnT–trnL and trnV–ndhC intergenic spacers), and one single-copy nuclear gene (sqs). In **Chapter 6** issues on paleobiogeography and speciation of *Andryala* are discussed. **Chapter 7** includes general conclusions and future research perspectives. Papers written during the thesis are included in the **Appendices**.

2 Taxonomic characters

Species constitute the major subdivision of a genus or subgenus and are regarded as the basic category of biological classification. A species is often defined as the largest group of organisms capable of interbreeding and producing fertile offspring. While in many cases this definition is adequate, the difficulty of defining species is known as the species problem. Moreover, the presence of specific locally adapted traits may further subdivide species into infraspecific *taxa* such as subspecies, varieties, and forms.

The species as a taxonomic unit, in the modern concept, was first proposed by John Ray in his book *Historia Plantarum* (1686-1704). According to Ray's **typological species** concept, species is a group of plants which breed true within their limits of variation (Singh 2010), and any variation that occurrs is to be treated as accidents, resulting from environmental factors or factors inherent to the species itself (Davis & Heywood 1963). According to Linnaeus, species were fixed, discrete and natural entities created by God (Van Dyke 2008). As Linnaeus, Darwin followed this concept for some time. However, both these naturalists gradually changed their species concept as they understood that this taxonomic unit often has no definite limits, because of its plastic and mutable nature (Castroviejo 2004).

Over time the concept of species has been evolving and different basic definitions emerged. The discrepancies arise largely from the purpose for which the species is used. The **morphological species** concept is broadly applied in descriptive works or catalogues (Castroviejo 2004). This concept (aka taxonomic species concept) regards the species as an assemblage of individuals with morphological features in common, and separable from other such assemblages by correlated morphological discontinuity in a number of features (Singh 2010). The **biological species** concept was first developed by Mayr in 1942 who defined species as "groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" (Beurton, 2002; Singh 2010). This concept was later amplified considering the niche occupation of a species: "species are ecological units forming lineages through time in a competitive environment" – **ecological species** concept (Mayden 1997). This concept faces two main difficulties: local populations in the more widespread species may differ in their niche occupation and two sympatric species may occupy the same niche (Mayr 2007).

Although the **biological species** is the most accepted concept among the present day taxonomists and systematists, it is not the most applied as it requires biological knowledge about the group in question, not yet available (Castroviejo 2004). The biological species concept proposed by Mayr has some limitations, acknowledged by the author himself. It does not apply to uniparental organisms or populations or those with asexual reproduction, neither the ones with spontaneous and frequent hybridization, a extremely common process especially in plants (Castroviejo 2004). Hence, a new species concept emerged, the **genetic species** concept. In accordance with this concept, the method used to delineate species is a measure of genetic differences, presumed to reflect reproductive isolation and evolutionary independence (Mayden 1997). Nevertheless, this concept has little practical use insofar as it is unthinkable that one can measure gene difference between populations on a large scale, even though new techniques allow some measurements in specific cases (Castroviejo 2004). With the intention of avoiding the inconvenience of biological species concept concerning interspecific hybridisation, the **evolutionary species** concept (aka phylogenetic species concept) arose. According to this concept, a species is "a phyletic lineage (ancestral-descendant sequence of interbreeding populations) evolving independently of others, with its own separate and unitary evolutionary role and tendencies" (Simpson 1951). The emergence of experimental taxonomy and biosystematics allowed a deeper knowledge of certain groups, which in turn showed that the categories used in traditional Linnaean classifications did not permit an explanation of the diversity and history of the group. Thus, the **biosystematic species** concept emerged and along with it countless proposals for new categories surrounding the taxonomic category, many of them referring to the internal characteristics of the populations, breeding systems, ploidy levels, etc. (Castroviejo 2004).

Taxonomy, which had fallen into a stagnation phase, similarly to other sciences became an exciting challenge with the application of new technologies, especially molecular biology and computer science. Currently DNA studies are already quite widespread and there are no doubts as to the importance of this new tool. The information obtained from DNA studies of plants or animals is crucial to understand species relationships, which opened new doors for phylogeny studies since a few hundred base pairs can give countless potential combinations (Castroviejo 2004). In taxonomy, morphology is a fundamental source of information, although any other data such as geographical, ecological, cytological and molecular must be considered. This means that taxonomists should cooperate with experts from other scientific fields (Castroviejo 2004). For instance, taxonomy (describing, naming and classifying) and phylogeny (establishing phylogenetic relationships) are distinct scientific tasks, yet they are complementary. Actually, a good taxonomy based on the establishment of species boundaries using morphometric studies can prove to be very useful in molecular biology.

Taxonomic characters constitute the basis of the procedure in numerical taxonomy. The term character is defined as a characteristic of a type of organism that will distinguish it from another type (Sneath & Sokal 1973). There are different kinds of taxonomic characters. In this work only morphological characters will be under study.

2.1 Material

The study of the morphological characters was based on the revision of herbarium material as well as material collected in the field and herborised, totalling 1066 specimens.

Most observations were performed on specimens borrowed from different herbaria, whose acronyms are the following according to Index Herbariorum (Thiers continuously updated): MA (Real Jardín Botánico), TFC (Universidad de La Laguna), TFMC (Museo de Ciencias Naturales), LISI (Instituto Superior de Agronomia), LISU (Museu Nacional de História Natural e da Ciência), MADJ (Jardim Botânico da Madeira), MADS (Museu de História Natural do Seminário do Funchal), MADM (Museu Municipal do Funchal), SEV (Universidad de Sevilla), MPU (Université Montpellier 2), P (Muséum National d'Histoire Naturelle), NMW (National Museum of Wales) and PRA (Institute of Botany, Academy of Sciences, Czech Republic). Herbarium specimens belonging to the University of Madeira (UMad) were also object of study.

The study of herbarium specimens was complemented with material obtained during fieldwork, which took place between 2006 and 2012. Living plants and specimens for the herbarium collection were gathered in Macaronesia (Madeira and the Canary Islands), the Iberian Peninsula, Morocco, Tunisia, Italy and Romania with international collaboration. Additionally, several plant structures and organs were collected in the field and preserved in 70% ethanol for scanning electron microscopy.

2.2 Methods

To carry out this morphological study it was necessary to acknowledge beforehand which entities in the genus *Andryala* L. were taxonomically recognised. For that purpose, criteria set by several authors were followed (Post 1896; Battandier & Trabut 1905; Coutinho 1939; Sell 1976; Talavera 1987; Press 1994). Various checklists and catalogues were also taken into account (e.g. Boulos 1979; Hansen & Sunding 1993; Montserrat 2002; Conti *et al.* 2005; Carazo-Montijano & Fernández-López 2006).

Subsequently, an analysis of the protologues for all the *Andryala* L. *taxa*, proposed by different authors, was undertaken. The bibliographic information gathered was stored in a database by using the software Filemaker Pro 5.0. This literature research allowed the selection of diagnostic taxonomic characters, that is, taxonomic characters that differentiate taxonomic entities from each other, known by taxonomists as operational taxonomic units (OTUs). The selected characters were registered in an Excel spreadsheet prepared for biometry purposes. The information on each herbarium specimen observed (voucher information) was stored in another database, also constructed with FileMaker 5.0.

2.2.1 Macro characters

Most of the macroscopic biometric characters were measured with the aid of a stereo binocular microscope Nikon SMZ-U ZOOM 1:10, equipped with ocular micrometer, using different amplifications according to the structure under analysis. Some macroscopic characters were measured with a digital caliper MITUTOYO (Absolute digimatic) that allowed the automatic transfer of the measurements to the excel spreadsheet.

To facilitate the observation of some macroscopic characters, certain structures of the herbarium material were submitted to a previous hydration using a microwave oven.

2.2.2 Micro characters

The observation and measurement of the microscopic characters were undertaken by using the preparation method described by Jirasek & Jozifova (1968): the material to be measured was mounted in water between slide and cover slip and the microscope slides obtained were sealed with nail polish. Likewise, the herbarium material under study was previously hydrated in a microwave oven. The slides were photographed under a Carl Zeiss Stemi SV 11 microscope, using the computer program Canon utilities – Zoom Browser EX and a digital camera Canon Powershot G6. Posteriorly, the measurements were performed by using the computer program Carl Zeiss Vision – AxioVision release 4.4.

In order to perform the Scanning Electron Microscopy (SEM), the herbarium material was subjected to a previous hydration to promote the turgescence of the structures under study. Subsequently, the dehydration of the material was carried out using solutions with increasing acetone concentrations (30%, 50%, 70%, 80%, 90%, 95%, 100%). Fresh plant material was also subjected to this dehydration process. The samples were then dried using the critical-point method and submitted to metal coating using a layer of gold of 25-30 nm. These were then mounted on sample holders and observed with a scanning electron microscope, JOEL JSM T 330 A at the Royal Botanical Garden of Madrid facilities, and SEM images were thus obtained.

2.3 Description of the characters under study

The most relevant morphologic characters are described below, with emphasis on those that were systematically registered and subsequently used in the numerical analysis (Chapter 3). These are accompanied by an acronym (in bold) by which they are referred to in the following chapter. The complete list of acronyms is provided in page viii.

2.3.1 Plant life-form and life-cycle duration

In *Andryala* L. three life-forms can be observed: chamaephytes (perennating buds above the soil surface but lower than ca. 25 cm), hemicryptophytes (renewal buds at the surface of the ground) and therophytes (perennating bud is that of the embryo contained in the seed, as no other embryonic part lives through the unfavorable season - annual plants). According to Franco (1984), *A. integrifolia* L. and *A. ragusina* L. are hemicryptophytes, whereas *A. arenaria* (DC.) Boiss. & Reut. and *A. laxiflora* DC. (= *A. rothia* Pers.) are therophytes. Similarly, Blanca (2009, 2011) considered *A. arenaria* and *A. rothia* as therophytes and *A. integrifolia* as hemicryptophyte. However, Blanca (op. cit.) classified *A. ragusina* as therophyte, in spite of considering it a perennial plant. As chamaephyte, Blanca (op. cit.) mentioned *A. agardhii* Haens. ex DC. Indeed, *A. agardhii*, *A. laevitomentosa* (Nyár. ex Sennikov) Greuter, *A. maroccana* Pau ex Caball., *A. perezii* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq., *A. mogadorensis* Coss. ex Hook.f., *A. ragusina*, *A. pinnatifida* Aiton, and *A. glandulosa* Lam. are examples of chamaephytes, although some of these can also be hemicryptophytes (*A. ragusina*, *A. pinnatifida*, and *A. glandulosa*). *Andryala arenaria*, *A. rothia*, *A. dentata* Sm. and *A. cossyrensis* Guss. are therophytes, whilst *A. integrifolia* is a hemicryptophyte.

Concerning life-cycle duration (**PLC**), three states were registered: 0-annual, 1-biennial, 2-perennial as the genus *Andryala* includes annual to perennial plants (Sell 1976; Talavera 1987; Press 1994). *Andryala integrifolia* and *A. glandulosa* include biennial to perennial herbs, while *A. crithmifolia* and *A. chevallieri* Barratte ex L. Chevall. are biennials. *Andryala sparsiflora* (Lowe) M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq.[10] includes annual to biennial plants, and some were found to be perennating.

2.3.2 Root

In *Andryala* the root system consists of a strongly developed main root which grows downwards bearing much smaller lateral roots (taproot). The study of the root characters was somewhat hampered as many specimens were incomplete. Nonetheless, several root characters were registered:

- root diameter (**RD**), measured at the transition point between root and stem in centimetres;
- root length (**RL**), measured from the tip of root to the transition point between root and stem in centimetres;

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[10] *Andryala sparsiflora* (Lowe) M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. is a new combination proposed herein and corresponds to *Andryala glandulosa* subsp. *cheiranthifolia* (L'Hér) Greuter (see Chapter 4, p. 228).

- root shape (**RS**): 0-sinuous, 1-axonomorph, 2-napiform.

Regarding the root diameter (**RD**), some species typically exhibit a thin root (e.g. *A. arenaria*, *A. dentata*, *A. cossyrensis*, and *A. rothia*), while others tend to have a thicker root (e.g. *A. glandulosa* and *A. crithmifolia*). However, this character is quite variable for some species (e.g. *A. integrifolia* and *A. pinnatifida, A. sparsiflora*). In what concerns the root length (**RL**), some species usually have shorter roots (e.g. *A. arenaria*, *A. cossyrensis*, *A. dentata*, and *A. rothia*). In other species this character exhibits great intraspecific variation (e.g. *A. glandulosa, A. sparsiflora, A. integrifolia, A. mogadorensis,* and *A. pinnatifida*). Concerning the root shape (**RS**), it can be sinuous or axonomorph (i.e. straight), being some slightly napiform (e.g. *A. integrifolia*). The root of some species is typically sinuous (e.g. *A. dentata*, *A. cossyrensis*, *A. ragusina*, and *A. maroccana*) or axonomorph (e.g. *A. arenaria* and *A. rothia*). In some cases (e.g. *A. integrifolia*, *A. crithmifolia*, *A. glandulosa*, *A. mogadorensis*, and *A. pinnatifida*) the root shape is somewhat variable.

2.3.3 Stem

A few earlier authors considered the shape of the stem cylindrical or at least sometimes subangular (e.g. Lamarck 1783; Hoffmannsegg & Link 1825; Schultz Bipontinus 1849). According to different authors (e.g. Chevallier 1900; Caballero 1916; Sell 1976; Press 1994; Blanca 2009, 2011) the *Andryala* species can be distinguished by the stem height since there are some that exhibit very short stems when compared to others. The stems are solitary or numerous or even caespitose (Caballero 1916; Sell 1976; Press 1994; Blanca 2009, 2011). Moreover, the stem may be simple, branched in the upper third, in the upper half or even from the base (Talavera 1987). The morphological study of the stem included both quantitative and qualitative characters which were systematically registered:

- stem shape (**SS**): 0-cylindrical, 1-subangular, 2-more or less flattened in the upper part;
- stem height (**SH**), measured in centimetres;
- stem diameter (**SD**), measured at 10 cm from the rosette/base of the stem in centimetres;
- stem colour (**SCol**): 0-whitish, 1-yellowish, 2-greenish, 3-purplish, 4-greyish, 5-brownish, 6-black;
- stem number (**SN**): 0-single stemmed, 1-multi stemmed (two to six stems), 2-caespitose (more than six stems);
- stem ramification (**SR**): 0-simple, 1-branched in the upper third, 2-branched in the upper half, 3-branched from the base;
- number of primary branches (**SNPB**), counted from the base to the tip of the main stem;
- number of secondary branches (**SNSB**), counted on of the lower primary branch;
- branch position (**SBP**): 0-erecto-patent, 1-ascending.

Regarding the stem shape (**SS**) in most species it is indeed cylindrical, although occasionally it varies between cylindrical and subangular (e.g. *A. glandulosa, A. integrifolia,* and *A. sparsiflora*) or is at least sometimes more or less flattened in the upper part (e.g. *A. agardhii*, *A. maroccana*, and *A. ragusina*).

Regarding the stem height (**SH**), some species exhibit short stems (e.g. *A. agardhii, A. laevitomentosa, A. maroccana*), while others have long stems (e.g. *A. crithmifolia* and *A. chevallieri*). Nevertheless, in many cases this character shows great intraspecific variation (e.g. *A. glandulosa, A. sparsiflora, A. integrifolia, A. pinnatifida,* and *A. mogadorensis*).

Relating to the stem diameter (**SD**), some species exhibit usually thin stems (e.g. *A. arenaria, A. agardhii, A. cossyrensis, A. dentata, A. rothia, A. laevitomentosa,* and *A. maroccana*), contrary to others in which this character is somewhat variable (e.g. *A. crithmifolia, A. glandulosa, A. sparsiflora, A. integrifolia, A. mogadorensis, A. pinnatifida,* and *A. ragusina*).

Regarding the stem number (**SN**), most species (e.g. *A. arenaria, A. dentata, A. glandulosa, A. sparsiflora, A. cossyrensis, A. integrifolia,* and *A. rothia*) are single stemmed or rarely multi stemmed. However, in some species intraspecific variation is considerable since these can either be single or multi stemmed (e.g. *A. nigricans, A. crithmifolia, A. mogadorensis, A. pinnatifida,* and *A. perezii*). Few species are single stemmed to caespitose (*A. ragusina*) or caespitose (*A. agardhii, A. laevitomentosa,* and *A. maroccana*).

With respect to the stem ramification (**SR**), only a few species usually have simple stems (*A. agardhii, A. levitomentosa,* and *A. maroccana*). Species such as *A. arenaria, A. integrifolia, A. crithmifolia, A. chevallieri,* and *A. mogadorensis* have stems frequently branched in the upper third, while others have stems often branched in the upper half (e.g. *A. dentata, A. cossyrensis, A. glandulosa*). Nonetheless, this character is quite variable within species such as *A. perezii, A. ragusina, A. sparsiflora,* and *A. pinnatifida*.

In what concerns the branch position (**SBP**), in most species the branches are frequently erecto-patent or more rarely ascending. Some species have branches equally erecto-patent or ascending (e.g. *A. glandulosa, A. sparsiflora, A. pinnatifida, A. ragusina*), whilst in others they are more frequently ascending (e.g. *A. perezii*).

2.3.4 Leaf

The leaf characters have been largely used in the classical taxonomy of the genus. In fact, some infraspecific taxonomic treatments were made largely based on leaf characters (e.g. Schultz Bipontinus 1849). However, some of these characters (e.g. leaf size and margin) were found to exhibit great intraspecific variation. Furthermore, in *Andryala* it is quite common to find some variation in leaf characters within the same individual allowing the distinction of lower, cauline and upper leaves (Coutinho 1939; Sell 1976; Talavera 1987; Blanca 2009, 2011). The lower leaves form a rosette at the base of the stem (Figure 2.1), often marcescent at anthesis. Generally, these are larger than the cauline (inserted along the stem) and the upper leaves (inserted on the inflorescence stem). The lower leaves are frequently withered during anthesis, which quite often hinders the study of all leave characters of an individual.

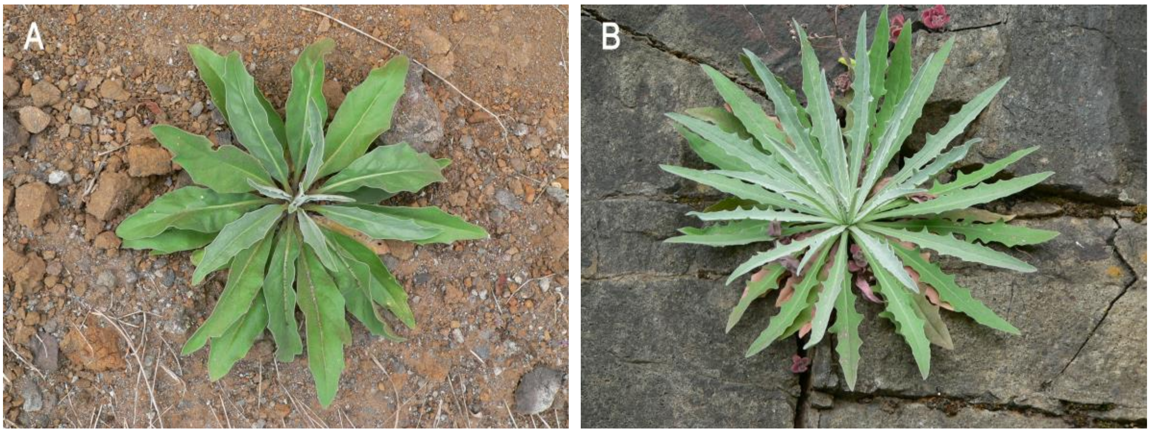


Figure 2.1 Lower leaves in rosette. A – *Andryala glandulosa*; B – *Andryala sparsiflora.*

The study of the leaf included the recording of several quantitative characters, all measured in millimetres:

- leaf length for the lower leaves (**LloL**), cauline leaves (**LcL**) and upper leaves (**LuL**), measured from the insertion point of the petiole to the apex of the leave;
- leaf maximum width for the lower leaves (**LloW**), cauline leaves (**LcW**) and upper leaves (**LuW**);
- length from the base of the leaf to the point of maximum width for the lower leaves (**LloLBMW**), cauline leaves (**LcLBMW**) and upper leaves (**LuLBMW**);
- width at the base of the larger lobe for the lower leaves (**LloWBL**), cauline leaves (**LcWBL**) and upper leaves (**LuWBL**);
- length of the larger lobe of the lower leaves (**LloLL**), cauline leaves (**LcLL**) and upper leaves (**LuLL**);
- length from the tip of the larger lobe to the middle nerve of the lower leaves (**LloLTLMN**), cauline leaves (**LcLTLMN**) and upper leaves (**LuLTLMNL**);
- petiole length of the lower leaves (**LloLP**) and cauline leaves (**LcLP**).

Several binary or multi state qualitative characters of the leaf were also registered:

- leaf thickness: 0-membranaceous, 1-not membranaceous;
- leaf insertion on the stem for the lower leaves (**LloIS**) and cauline leaves (**LcIS**): 0-amplexicaul, 1-semi-amplexicaul, 2-decurrent, 3-sessil, 4-atenuate in petiole, 5-petiolate;
- leaf insertion on the stem for the upper leaves (**LuIS**): 0-amplexicaul, 1-semi-amplexicaul, 2-sessil, 3-atenuate in petiole;
- leaf base of the cauline leaves (**LcB**) and upper leaves (**LuB**): 0-cuneate, 1-atenuate, 2-truncate, 3-redonded, 4-cordate, 5-auriculate;
- winged petiole of the lower leaf (**LloWP**): 0-absent, 1-present;
- leaf apex for the lower leaves (**LloA**) and cauline leaves (**LcA**): 0-truncate, 1-obtuse, 2-acute, 3-acuminate;
- leaf apex for the upper leaves (**LuA**): 0-truncate, 1-obtuse, 2-acute, 3-acuminate, 4-retuse.

The morphological characters leaf length (e.g. **LcL**) and leaf width (e.g. **LcW**) were used to ascertain the leaf size (Figure 2.2). In *Andryala* the leaf size is quite variable from species to species; some have rather small lower leaves (e.g. *A. maroccana*), while in other species they are quite large (e.g.

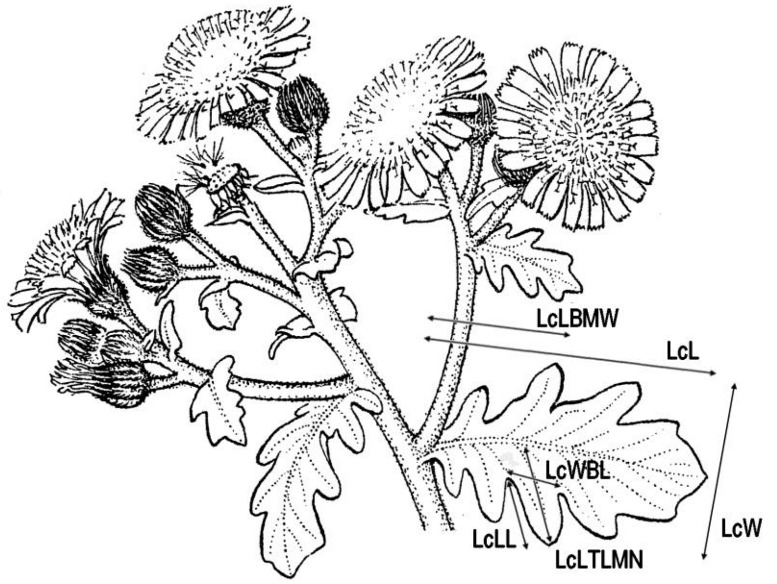


Figure 2.2 Quantitative characters used in the biometric study of the leaf: **LCL** (leaf length), **LcW** (leaf width), **LcLL** (length of the larger lobe), **LcWBL** (width at the base of the larger lobe), **LcLTLMN** (length from the tip of the larger lobe to the middle nerve of the leaf) larger [illustration taken from Die Kanarischen Inseln und ihre pflanzenwelt (Kunkel 1993)].

A. crithmifolia, A. chevallieri, A. glandulosa). Nonetheless, in most cases intraspecific variation is quite high (e.g. *A. ragusina*, *A. integrifolia*). Moreover, the lower leaves are usually larger than the cauline and upper leaves. The cauline leaves tend to decrease in size towards the upper part of the stem.

The length of the petiole was registered for both lower leaves (**LlLP**) and cauline leaves (**LcLP**). In general, a rather high intraspecific variation for the lower leaves can be observed. The leaf insertion on the stem is a morphological character that ranges from petiolate to more or less amplexicaul (Sell 1976; Press 1994; Blanca 2009, 2011). Concerning the insertion of the lower leaf on the stem (**LloIS**), in most *taxa* these are attenuate into a petiole, although there are some exceptions such as *A. glandulosa* and *A. dentata* whose lower leaves are often semiamplexicaul. In some species (e.g. *A. agardhii, A. laevitomentosa*, *A. maroccana,* and *A. pinnatifida*) the lower leaves are attenuate into a notable winged petiole as mentioned in different publications (Schultz Bipontinus 1849; Doumergue 1921; Sell 1976). Furthermore, the petiole can be broader at the base slightly embracing the stem (e.g. *A. crithmifolia, A. sparsiflora, A. perezii,* and *A. pinnatifida*). Regarding the insertion of the cauline leaves on the stem (**LcIS**), these are frequently semiamplexicaul, although some intraspecific variability is observable (e.g. *A. pinnatifida* and *A. ragusina*). In respect to the insertion of the upper leaves on the stem (**LuIS**), some intraspecific variation occurs since these can be sessile, semiamplexicaul or amplexicaul (Figure 2.3). Nonetheless, in some species the upper leaves are mainly amplexicaul (e.g. *A. dentata, A. arenaria, A. perezii, A. glandulosa,* and *A. rothia*) or semiamplexicaul (e.g. *A. crithmifolia, A. laevitomentosa, A. maroccana*).

Figure 2.3 Insertion of the upper leaves on the stem. A – *Andryala glandulosa:* amplexicaul, B – *Andryala sparsiflora*: semiamplexicaul or amplexicaul.

2.3.4.1 Leaf shape

To determine the leaf shape three quantitative characters were used (Figure 2.2): leaf length of the lower leaves (**LloL**), cauline leaves (**LcL**), and upper leaves (**LuL**); leaf maximum width of the lower leaves (**LloW**), cauline leaves (**LcW**), and upper leaves (**LuW**) as well as length from the base of the leaf to the point of maximum width for the lower leaves (**LloLBMW**), cauline leaves (**LcLBMW**) and upper leaves (**LuLBMW**). For this purpose, the ratios leaf length/width and length from the base of the leaf to the point of maximum width/leaf length (Radanachaless & Maxwell 1994) were calculated. In *Andryala* the leaf shape reveals great intraspecific variability and a certain leaf shape can hardly be assigned to a particular *taxon*. Indeed, the leaf shape varies in most species depending on whether they are lower, cauline or upper leaves. The lower leaves usually vary from oblong to lanceolate or from obovate-lanceolate to lanceolate, although sometimes they can be spatulate (e.g. *A. agardhii, A. maroccana*), obovate to elliptic (e.g. *A. laevitomentosa*) or obovate-oblong (*A. mogadorensis*). The cauline leaves are often lanceolate, ovate-lanceolate, oblong or ovate-oblong, and more rarely elliptic (e.g. *A. agardhii* and *A. pinnatifida*), linear-lanceolate (e.g. *A. sparsiflora*), spatulate (*A. maroccana*) or obovate-oblong (*A. mogadorensis*). The upper leaves vary frequently from ovate-oblong to ovate-lanceolate, linear to linear-lanceolate, but occasionally they are oblong to obovate-oblong (*A. mogadorensis*) or lanceolate (*A. integrifolia, A. maroccana*).

2.3.4.2 Leaf margin

In *Andryala* the leaf margin varies from entire to pinnatisect (Sell 1976; Press 1994; Blanca 2009, 2011). To classify the leaf margin two characters were used (Figure 2.2): the larger lobe length, measured from the base to the tip of the lobe for the lower leaves (**LloLL**), cauline leaves (**LcLL**) and upper leaves (**LuLL**) and the length from the tip of the larger lobe to the middle nerve of the lower leaves (**LloLTLMN**), cauline leaves (**LcLTLMN**), and upper leaves (**LuLTLMN**). For this purpose, the ratio larger lobe length/length from the tip of the larger lobe to the middle nerve was calculated. The leave margin shows great intraspecific variation (e.g. *A. integrifolia, A. pinnatifida, A. arenaria, A. ragusina, A. sparsiflora*) and this variability is notable among the different leaves from the same individual. Although lower leaves and cauline leaves are more variable concerning leave margin, the upper leaves tend to be less divided and in many species they are always entire. Some exceptions can be highlighted such as *A. laevitomentosa* and *A. maroccana* (only entire to lobate leaves), and also *A. agardhii* (only entire leaves).

2.3.5 Plant indumentum

The genus *Andryala* L. includes plants that are covered with stellate hairs, sometimes combined with unicellular simple eglandular or glandular hairs, the latter at least in the upper third of the stem (Sell 1976; Talavera 1987; Blanca 2009, 2011). There are species typically with no glandular hairs (*A. maroccana* and *A. ragusina*) and species always with glandular hairs (e.g. *A. crithmifolia, A. glandulosa, A. integrifolia, A. sparsiflora*) (Figure 2.4). However, some species may be glandular-hairy or scarcely so, or even devoid of glandular hairs (e.g. *A. mogadorensis, A. pinnatifida*). Furthermore, *A. laevitomentosa* can be distinguished from the remaining species by the presence of simple eglandular hairs on the involucre and external involucral bracts (see Figure 2.7H, p. 30).

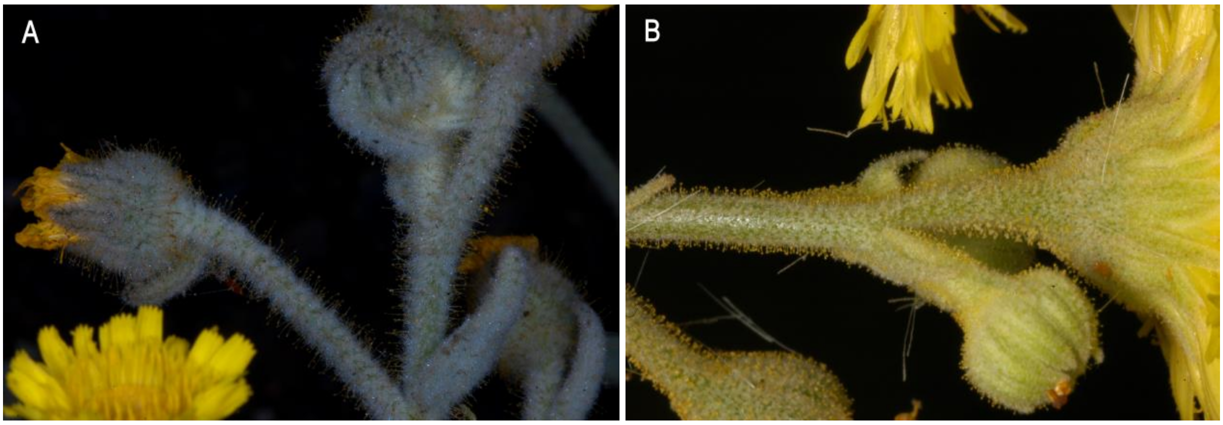


Figure 2.4 Plant indumentum. A – *Andryala glandulosa*, B – *Andryala crithmifolia*: glandular hairs always present.

Concerning the stem indumentum the following characters were registered:

- lower stem stellate indumentum (**SloSI**): 0-inexistent, 1-puberulous, 2-tomentose, 3- floccose/densely tomentose;
- middle stem stellate indumentum (**SmSI**): 0-inexistent, 1-puberulous, 2-tomentose, 3-floccose/densely tomentose;
- upper stem stellate indumentum (**SuSI**): 0-inexistent, 1-puberulous, 2-tomentose, 3-floccose/densely tomentose;
- lower stem glandular indumentum (**SloGI**): 0-inexistent, 1-puberulous, 2- pubescent, 3-villous, 4-hispid, 5-hirsute;
- middle stem glandular indumentum (**SmGI**): 0-inexistent, 1-puberulous, 2-pubescent, 3-villous, 4-hispid, 5-hirsute;
- upper stem glandular indumentum (**SuGI**): 0-inexistent, 1-puberulous, 2-pubescent, 3-villous, 4-hispid, 5-hirsute.

In most species the stellate indumentum on the lower part of the stem is tomentose, although it can vary from pubescent to tomentose (e.g. *A. crithmifolia, A. integrifolia,* and *A. rothia*) or tomentose to densely tomentose (e.g. *A. mogadorensis, A. ragusina,* and *A. laevitomentosa*). In general, towards the upper part of the stem the density of the stellate hairs tends to increase. In species bearing glandular hairs, although on the lower part of the stem the glandular indumentum is usually absent, in some species it is occasionally puberulous or pubescent (e.g. *A. arenaria, A. cossyrensis, A. integrifolia, A. rothia*). Conversely, in *A. glandulosa* the lower part of the stem is frequently pubescent and sometimes it can be villous or even hirsute. Generally, on the middle part of the stem the glandular indumentum is either puberulous or pubescent. On the upper part of the stem the glandular indumentum is pubescent or villous and in some species even hispid or hirsute. However, the glandular indumentum can be quite variable within species, comparing the same part of the stem (e.g. *A. pinnatifida* and *A. mogadorensis*).

Regarding the leaf indumentum, the following characters were systematically recorded for the abaxial face:

- lower leaf stellate indumentum (**LloSI**): 0-inexistent, 1-puberulous, 2-tomentose, 3-floccose/densely tomentose;
- cauline leaf stellate indumentum (**LcSI**): 0-inexistent, 1-puberulous, 2-tomentose, 3-floccose/densely tomentose;
- upper leaf stellate indumentum (**LuSI**): 0-inexistent, 1-puberulous, 2-tomentose, 3-floccose/densely tomentose;
- lower leaf glandular indumentum (**LloGI**): 0-inexistent, 1-puberulous, 2- pubescent, 3-villous, 4-hispid, 5-hirsute;
- cauline leaf glandular indumentum (**LcGI**): 0-inexistent, 1-puberulous, 2- pubescent, 3-villous, 4-hispid, 5-hirsute;
- upper leaf glandular indumentum (**LuGI**): 0-inexistent, 1-puberulous, 2- pubescent, 3-villous, 4-hispid, 5-hirsute.

Some species exhibit stellate-tomentose lower leaves (e.g. *A. agardhii, A. crithmifolia, A. dentata, A. mogadorensis, A. glandulosa, A. maroccana,* and *A. laevitomentosa*). However, this character shows some intraspecific variation: it can vary from puberulous to tomentose in some species (*A. arenaria, A. chevallieri, A. cossyrensis, A. perezii,* and *A. sparsiflora*) and from puberulous to densely tomentose in others (*A. pinnatifida* and *A. ragusina*). In general, the stellate indumentum tends to become denser from the lower to the upper leaves. In what concerns species provided with glandular hairs, these are present on the lower leaves of *A. glandulosa* and rarely on those of *A. integrifolia*, in contrast with the remaining species. Some species do not exhibit any glandular hairs on the upper leaves (e.g. *A. agardhii, A. chevallieri, A. mogadorensis, A. dentata*). However, in some species the glandular indumentum of the upper leaves is puberulous or pubescent (*A. arenaria, A. crithmifolia, A. cossyrensis, A. perezii, A. rothia, A. sparsiflora and A. pinnatifida*). Only in *A. glandulosa* it ranges from pubescent to hirsute. Thus, the glandular indumentum of the leaves reveals some variability within species and also between species.

2.3.6 Inflorescence

In *Andryala* the capitula are solitary or few to numerous, arranged in corymbiform inflorescences (Sell 1976; Talavera 1987; Blanca 2009, 2011). To study of the inflorescence morphology four characters were registered:

- inflorescence type (**IT**): 0-panicule, 1-corymbose panicle, 2-corymb, 3-anthela, 4-solitary capitulum, 5-racemose, 6-paniculate corymb;
- number of capitula per inflorescence (**INC**), measured in millimetres;
- capitula diameter at anthesis (**ICD**), measured in millimetres on the four largest capitula (Figure 2.5);
- peduncle length (**IPL**), measured in millimetres on the four largest capitula, from the base of the capitulum to the first ramification (Figure 2.5).

In respect to the inflorescence type (**IT**), while in some species the inflorescences are usually corymbose (e.g. *A. crithmifolia, A. dentata, A. integrifolia*, and *A. mogadorensis*), some commonly exhibit solitary capitula (e.g. *A. agardhii, A. laevitomentosa* and *A. maroccana*) or less frequently so (e.g. *A. ragusina, A. rothia*). Nonetheless, in *Andryala* the inflorescence type is quite variable as in most species the capitula are arranged in different inflorescences. For example, in *Andryala pinnatifida*, this character reveals a significant variation, even within subspecies: corymbose, paniculate-corymbose or racemose. Similarly, in *A. glandulosa* the inflorescence type varies from corymbose to paniculate-corymbose. The inflorescences are either more or less dense or rather lax (Coutinho 1939; Sampaio 1949; Franco 1984; Talavera 1987; Press 1994; Blanca 2009, 2011) depending on the number of capitula per inflorescence (**INC**). Indeed, there are species which generally exhibit few capitula per inflorescence such as *A. chevallieri, A. cossyrensis, A. dentata, A. rothia,* and *A. ragusina.* Nevertheless, this morphological character also reveals some intraspecific variation in some species (e.g. *A. glandulosa, A. sparsiflora, A. integrifolia, A. mogadorensis*, and *A. pinnatifida*).

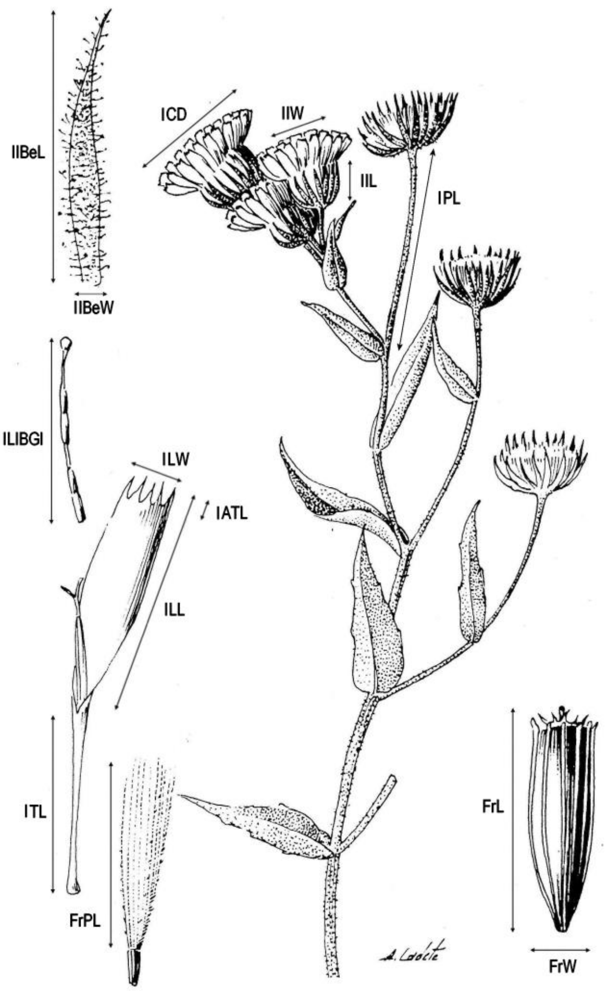


Figure 2.5 Quantitative characters used in the biometric study of the inflorescence and fruit: **ICD** (capitula diameter at anthesis), **IPL** (peduncle length), **IIBeL** (external involucral bracts length), **IIBeW** (external involucral bracts maximum width), **ILIBGI** (length of external involucral bracts glandular hairs), **ILL** (ligule length), **ITL** (tube length), **ILW** (ligule width), **IATL** (ligule apical teeth length), **FrL** (cypsela length), **FrPL** (pappus length) [illustration by A. Cadete taken from Flora Vascular de Andalucía Occidental (Talavera 1987)].

The capitula diameter at anthesis (**ICD**) shows some intraspecific variation. Nevertheless, while some species tendentiously have smaller capitula (e.g. *A. arenaria, A. dentata, A. integrifolia, A.*

cossyrensis), other species such as *A. glandulosa, A. sparsiflora, A. rothia,* and *A. ragusina* tend to exhibit larger capitula.

Concerning the length of the peduncle (**IPL**), there is a certain tendency for shorter peduncles in some species (e.g. *A. arenaria, A. crithmifolia, A. dentata, A. integrifolia, A. pinnatifida,* and *A. mogadorensis*) and longer peduncles in others (e.g. *A. glandulosa, A. sparsiflora, A. ragusina*, and *A. rothia*). However, in the latter group some intraspecific variation occurs as, although very rarely, shorter peduncles may be observed.

2.3.7 Involucre and involucral bracts

According to earlier authors the shape of the involucre at anthesis is campanulate or hemispherical (e.g. Lowe 1838; Hooker 1873; Caballero 1917; Coutinho 1939). Some authors referred the shape of this structure at fructification: campanulate, cylindrical and truncate or ovoid (e.g. Talavera 1987). For the morphological study of the involucre both quantitative and qualitative characters were registered:

- involucre length at anthesis (**IIL**) measured in millimeters (Figure 2.5);
- involucre width at anthesis (**IIW**) measured in millimeters (Figure 2.5);
- involucre shape at anthesis (**IISA**): 0-campanulate, 1-hemispherical;
- involucre shape at fructification (**IISF**): 0-campanulate, 1-cylindrical and truncate, 2-ovoid.

The size of the involucre at anthesis was inferred by the involucre length (**IIL**) and involucre width (**IIW**). In spite of the intraspecific variation observed, the involucre is frequently large in some species (e.g. *A. glandulosa, A. rothia*, and *A. ragusina*) and generally smaller in species such as *A. dentata*, *A. arenaria*, and *A. integrifolia*. Thus, the size of the involucre reveals some intraspecific as well as interspecific variation.

With reference to the shape of the involucre at anthesis (**IISA**), an interspecific variation was detected; there are indeed species with campanulate involucres or at least more or less campanulate (e.g. *A. arenaria, A. integrifolia, A. maroccana, A. cossyrensis, A. ragusina,* and *A. sparsiflora*) and species in which the involucre is hemispherical (e.g. *A. agardhii, A. chevallieri, A. glandulosa, A. rothia*, *A. mogadorensis*, *A. perezii* and *A. laevitomentosa*) (Figure 2.6). As for the shape of the involucre at fructification (**IISF**), this character was difficult to evaluate given the large number of missing data (the involucre shape at fructification is not always well defined in herbarium specimens and many specimens did not have involucres at this stage of development). Nonetheless, intraspecific variation was observed since some species exhibit more or less campanulate to cylindrical and truncate involucres (e.g. *A. cossyrensis*, *A. dentata*, *A. perezii*, *A. pinnatifida*, *A. crithmifolia*, and *A. mogadorensis*).

Figure 2.6 Shape of the involucre at anthesis. *A* – *Andryala sparsiflora*: campanulate; B – *Andryala glandulosa*, C – *Andryala crithmifolia:* hemispherical.

In regard to the involucral bracts, for both the external and the internal involucral bracts, a few characters were registered:

- number of rows of the involucral bracts (**INRIB**);
- external involucral bracts length (**IIBeL**), measured on four bracts of the largest capitulum in millimeters (Figure 2.5);
- external involucral bracts maximum width (**IIBeW**), measured on four bracts of the largest capitulum in millimeters (Figure 2.5);
- external involucral bracts convolution (**IIBeC**): 0-flat not enfolding a floret, 1-involute enfolding a floret, not enclosing a cypsela; 2-strongly involute enclosing a cypsela;
- external involucral bracts stellate indumentum on the outer face (**IIBSIo**): 0-puberulous, 1-tomentose, 2-floccose/densely tomentose;
- external involucral bracts stellate indumentum on the inner face (**IIBSIi**): 0- absent, 1-present;
- external involucral bracts glandular indumentum (**IIBGI**): 0-inexistent, 1-puberulous, 2-pubescent, 3-villous, 4-hispid, 5-hirsute;
- colour of the external involucral bracts glandular hairs (**ICGIB**): 0-yellowish, 1-greenish, 2-yellow but dark at the base, 3-dark;
- colour of the external involucral bracts stellate hairs (**ICEIB**): 0-whitish, 1-tawny;
- external involucral bracts apex (**IIBA**): 0-obtuse, 1-acute, 2-acuminate, 3-subulate;
- internal involucral bracts length (**IIBiL**), measured on four bracts of the largest capitulum in millimeters;
- internal involucral bracts width (**IIBiW**), measured on four bracts of the largest capitulum in millimeters;
- internal involucral bracts scariose margin maximum width (**IIBiSMW**), measured in millimeters;
- length of the external involucral bracts glandular hairs (**ILIBGI**), measured in millimeters on the four larger hairs (Figure 2.5).

The involucral bracts are arranged in 2 to 6 rows (e.g. Sell 1976; Talavera 1987; Blanca 2009, 2011). Indeed, in most species the number of involucral bracts (**INRIB**) ranges between 2 and 3, however, in *A. rothia* and *A. glandulosa* this number varies between 4 and 5 or 6.

As for the convolution of the external involucral bracts (**IIBeC**), there are species that can be distinguished by flat involucral bracts which do not enfold a floret (*A. integrifolia, A. agardhii, A. chevallieri, A. mogadorensis*, and *A. ragusina*). Conversely, other species exhibit involute involucral bracts, enfolding a floret (*A. arenaria, A. crithmifolia, A. cossyrensis, A. dentata, A. perezii, A. sparsiflora, A. laevitomentosa,* and *A. maroccana*). Furthermore, *A. rothia* and *A. glandulosa* exhibit strongly involute involucral bracts enclosing a cypsela. Only very rarely an intraspecific variation is observed; in *A. pinnatifida* the involucral bracts are frequently flat and occasionally involute.

The ratio between the length of the external involucral bracts (**IIBeL**) and maximum width of the external involucral bracts (**IIBeW**) was used to assess the shape of these structures. Some species have linear to linear-lanceolate (*A. integrifolia, A. laevitomentosa, A. chevallieri, A. dentata, A. rothia, A. ragusina, A. pinnatifida*) or lanceolate external involucral bracts (*A. arenaria, A. cossyrensis, A. agardhii*). However, occasionally an intraspecific variation was observed (e.g. *A. mogadorensis* exhibits lanceolate to linear-lanceolate external involucral bracts).

Regarding the external involucral bracts glandular indumentum (**IIBGI**), some species (e.g. *A. ragusina*) are devoid of glandular hairs (Figure 2.7A), while in others these are always present (e.g. *A. agardhii, A. sparsiflora, A. glandulosa*) (Figure 2.7B, M, P) or frequently observed (e.g. *A. mogadorensis, A. pinnatifida*) (Figure 2.7I, J, N, O).

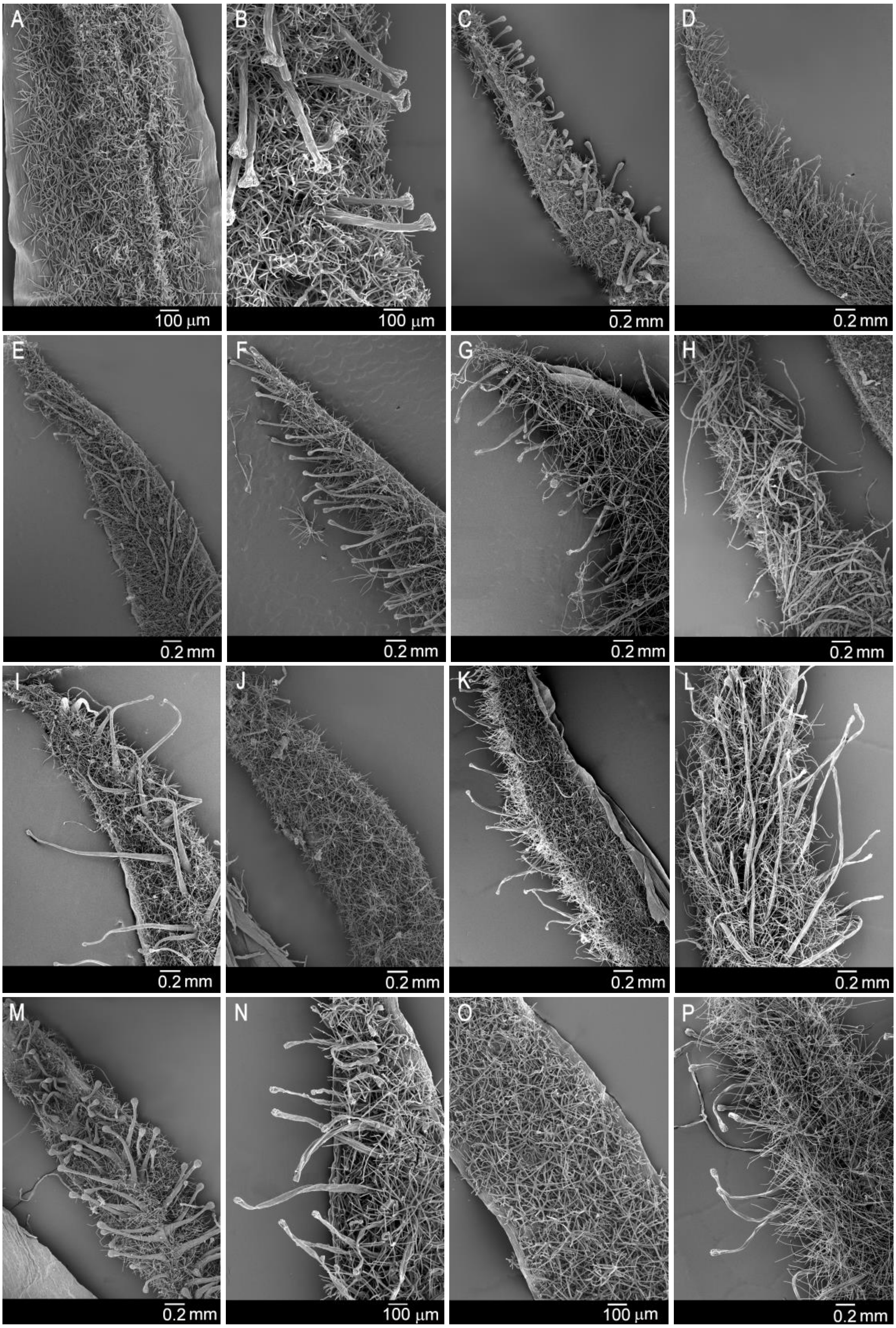


Figure 2.7 External involucral bracts glandular indumentum: A – *A. ragusina* (no glandular hairs), B – *A. agardhii,* C – *A. crithmifolia,* D – *A. cossyrensis,* E – *A. chevallieri,* F – *A. nigricans,* G – *A. arenaria,* H – *A. laevitomentosa,* I – *A. mogadorensis* subsp. *mogadorensis* J – *A. mogadorensis* subsp. *jahandiezii*, K – *A. perezii,* L – *A. integrifolia,* M – *A. sparsiflora,* N – *A. pinnatifida* subsp. *pinnatifida,* O – *A. pinnatifida* subsp. *teydensis* (no glandular hairs), P – *A. glandulosa.*

As for the length of the glandular hairs of the external involucral bracts (**ILIBGI**), some species (e.g. *A. agardhii, A. crithmifolia, A. cossyrensis, A. chevallieri, A. nigricans, A. arenaria,* and *A. laevitomentosa*) tend to exhibit short glandular hairs (Figure 2.7B – G). Nonetheless, intraspecific variation was observed in some species (e.g. *A. perezii, A. integrifolia, A. mogadorensis, A. pinnatifida, A. sparsiflora, and A. glandulosa*) (Figure 2.7I – P). Concerning the external involucral bracts stellate indumentum on the inner face (**IIBSIi**), this character was only observed in *A. rothia* and *A. glandulosa*; the remaining species do not present stellate hairs on the inner face of the external bracts.

2.3.8 Receptacle

In *Andryala* L. the receptacle is pitted (i.e. alveolate) (Figure 2.8). The margins of the pits are laciniate-dentate and have silky hairs (setae) longer or shorter than the cypselae (Sell 1976; Talavera 1987). For this structure the following characters were registered:

- receptacle shape (**IRS**): 0-convex, 1-more or less flat;
- receptacle indumentum (**IRI**): 0-puberulous, 1-pubescent, 2-tomentose, 3-villous;
- length of the receptacle setae (**IRSL**), measured in millimeters on the four largest setae.

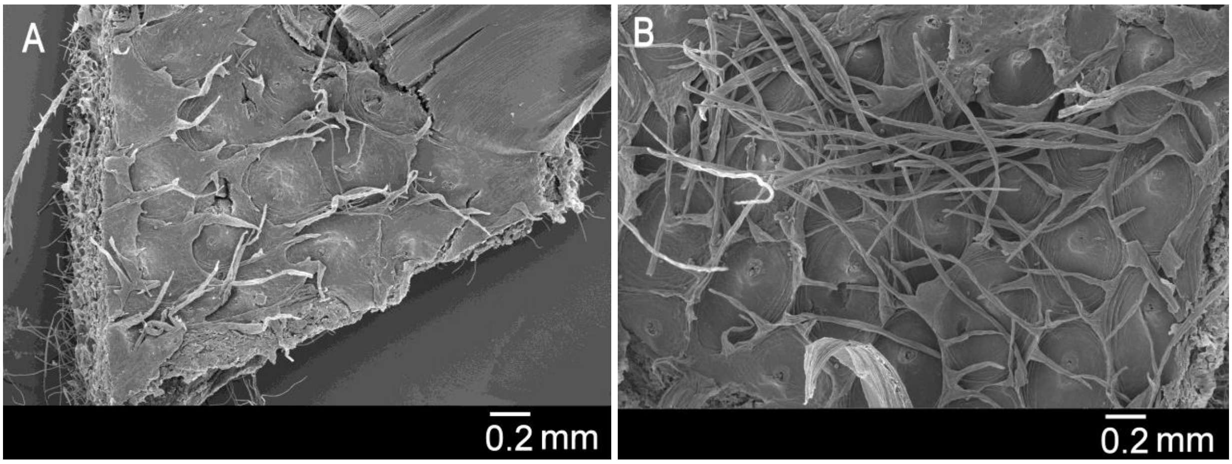


Figure 2.8 Detail of the receptacle. A – *Andryala arenaria*: pit margins with short setae, B – *Andryala glandulosa*: pit margins with long setae.

The shape of the receptacle (**IRS**) in most species is convex, with the exception of *A. crithmifolia* and *A. dentata* which usually exhibit a more or less flat receptacle or only slightly convex.

Regarding the receptacle indumentum (**IRI**), despite the intraspecific variability observed in some species (e.g. *A. arenaria*, *A. dentata*, *A. glandulosa*, *A. rothia*), it is commonly puberulous in species such as *A. maroccana*, *A. ragusina*, and *A. agardhii* and villous in others (e.g. *A. crithmifolia*, *A. chevallieri*, *A. sparsiflora*, *A. mogadorensis*, and *A. laevitomentosa*) (Figure 2.9).

In what concerns the length of the receptacle setae (**IRSL**), these are typically short in some species (e.g. *A. arenaria*, *A. agardhii*, *A. cossyrensis*, *A. dentata*, *A. maroccana*, and *A. ragusina*) and usually rather long in others (e.g. *A. crithmifolia*, *A. perezii*, *A. glandulosa*, *A. sparsiflora*, and *A. pinnatifida*) (Figure 2.9).

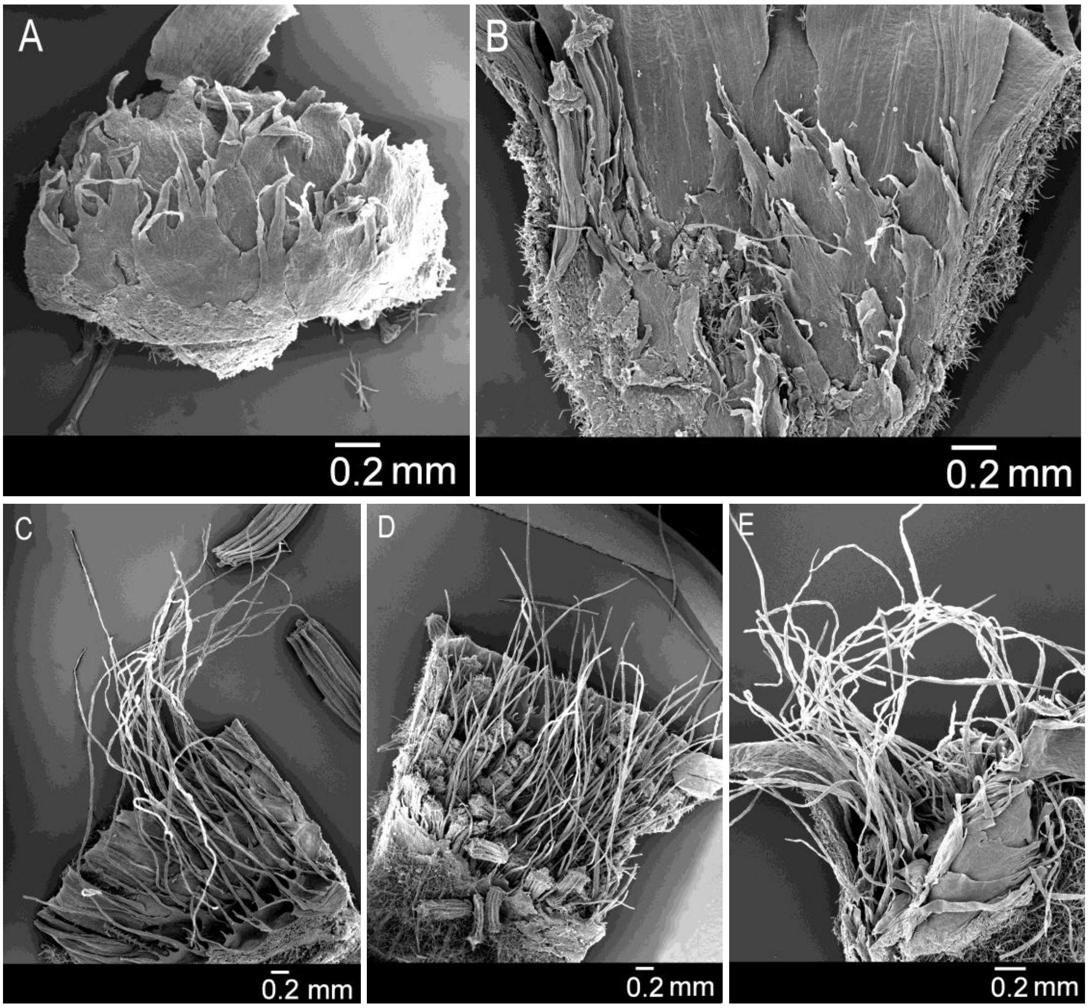


Figure 2.9 Receptacle indumentum. A – *Andryala agardhii*, B – *Andryala ragusina*: with short setae; C – A*ndryala crithmifolia*, D – *Andryala perezii*, E – *Andryala pinnatifida*: with long setae.

2.3.8.1 Florets

The florets are numerous, hermaphrodite, with linear ligules, usually with five fused petals forming teeth at the apex (Figure 2.10). In each floret the androecium comprises five stamens with short and transparent filaments, fused to the tube of the floret, and anthers forming a tube around the two styles partially fused and with two reflexed stigmas. The ligules have different shades of yellow and the external ones sometimes present a reddish stripe on the outer face (Sell 1976; Talavera 1987; Press 1994).

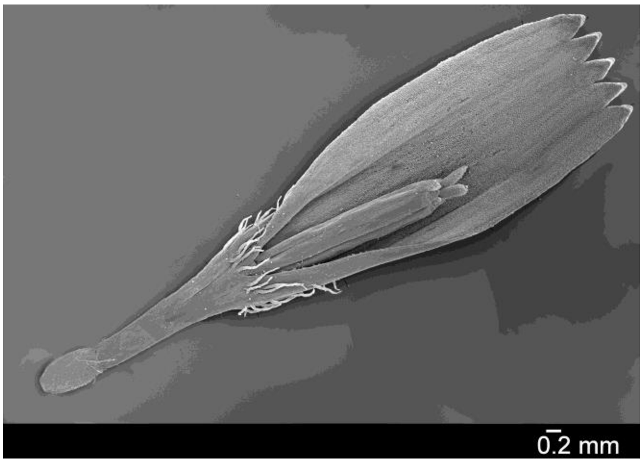


Figure 2.10 Aspect of the floret (*Andryala sparsiflora*).

Concerning the floret, several quantitative characters were registered (Figure 2.5):

- ligule length (**ILL**) and ligule width (**ILW**), measured on four external florets in millimeters;
- ligule apical teeth length (**IATL**), measured on four external florets in millimeters;
- tube length (**ITL**), measured on four external florets in millimeters.

Additionally, qualitative binary and multi state characters of the floret were recorded:

- indumentum at the base of the ligule (**IIBL**): 0-glabrous, 1-villous, 2-hirsute, 3-subglabrous;
- stellate indumentum on the teeth of the ligule (**ISITL**): 0-absent or very rare, 1-present in all teeth;
- external ligule colour on the outer face (**ILCFo**): 0-pale yellow, 1-bright yellow, 2-golden yellow, 3-dark yellow, 4-orange yellow, 5-with a reddish stripe;
- external ligule colour on the inner face (**ILCFi**): 0-pale yellow, 1-bright yellow, 2-golden yellow, 3-dark yellow, 4-orange yellow, 5-with a reddish stripe;
- internal ligule colour (**ILiC**): 0-pale yellow, 1-bright yellow, 2-golden yellow, 3-dark yellow, 4-orange yellow, 5-with a reddish stripe.

Regarding the length of the ligule (**ILL**) some species are worthy of notice: *A. glandulosa, A. sparsiflora,* and *A. laevitomentosa* usually exhibit long ligules, contrary to *A. dentata* in which these are excepcionally short. However, in some species this character is quite variable (e.g. *A. pinnatifida*, *A. ragusina*, and *A. rothia*).

As for the colour of the external ligule on the outer face (**ILCFo)** and the inner face (**ILCFi**), these characters are hard to determine on herbarium specimens especially the ones that are very old. Information was provided mainly by recently collected material. Although some intraspecific variation was observed, in some species the external ligules are usually golden yellow (*A. arenaria, A. cossyrensis, A. crithmifolia, A. chevallieri, A. glandulosa, A. perezii, A. sparsiflora, A. ragusina,* and *A. maroccana*), pale yellow (*A. integrifolia*, *A. dentata, A. rothia*) or bright yellow (e.g. *A. agardhii*, *A. laevitomentosa*). Conversely, *A. mogadorensis* exhibits orange yellow ligules. No significant difference was detected between the two faces of the external ligule regarding the colour. Nonetheless, the presence of a reddish stripe on the outer face of the external ligules was observed more or less frequently in species such as *A. arenaria, A. agardhii, A. mogadorensis, A. integrifolia, A. rothia, A. maroccana,* and *A. ragusina*, although there are species that express this character only occasionally (e.g. *A. pinnatifida*) or do not reveal it at all (e.g. *A. crithmifolia, A. glandulosa,* and *A. sparsiflora*). Although, the internal ligule colour (**ILiC**) usually corresponds to that of the external ligule, sometimes these may be lighter than the internal ligules (e.g. *A. integrifolia*).

Relating to the stellate indumentum on the teeth of the ligule (**ISITL**), this character separates quite clearly both *A. crithmifolia* subspecies from the rest of the *Andryala taxa* (Figure 2.11). Indeed, in *A. crithmifolia* stellate hairs are present on all five teeth of the ligule, contrary to the rest of the *Andryala* species in which these hairs are absent with the exception of *A. sparsiflora* in which they are rarely observed and even so not on all teeth of the ligule.

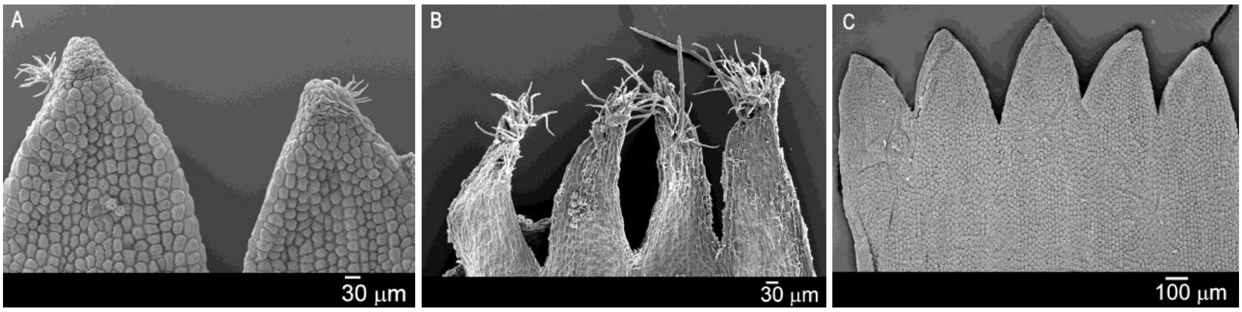


Figure 2.11 Ligule indumentum: A – *Andryala crithmifolia* subsp. *crithmifolia,* B – *Andryala crithmifolia* subsp. *coronopifolia:* all teeth stellate-hairy; C – *Andryala glandulosa*: teeth not stellate-hairy.

2.3.8.2 Fruit

According to most authors, the fruit is an achene whose shape varies between oblong and obconical, provided with ten ribs extending into teeth at the truncate apex or more rarely with an apical disc (e.g. Sell 1975; Sell 1976; Talavera 1987; Press 1994). Franco (1984) and Bramwell & Bramwell (2001) considered the fruit as a cypsela and, indeed, it is a small, dry, one-seeded, indehiscent fruit derived from an inferior ovary composed of two fused carpels. The morphological study of the cypsela was somewhat hindered by the absence of mature fruits in some specimens. However, in this study the following quantitative and qualitative characters were registered:

- cypsela length (**FrL**), measured in millimeters (Figure 2.5);
- cypsela maximum width (**FrW**), measured in millimeters (Figure 2.5);
- cypsela shape (**FrS**): 0-oblong, 1-obconical;
- cypsela colour (**FrCol**): 0-brownish yellow, 1-light-brown, 2-dark brown, 3-black;
- cypsela ribs saliency (**FrRS**): 0-slightly salient; 1-very salient;
- aspect of the cypsela apex (**FrAA**): 0-inner ring eroded, 1-inner ring with conspicuous teeth;
- cypsela apical inner ring disposition (**FrAIRD**): 0-at a lower level than the prolongation of the ribs, 1-at the same level as the prolongation of the ribs, 3-at a higher level than the prolongation of the ribs;
- cypsela ribs colour (**FrRCol**): 0-whitish, 1-light-brown, 2-reddish brown/brown.

The cypsela length (**FrL**) revealed some interspecific variability. In effect, *A. agardhii* and *A. ragusina* stand out by their remarkably long cypsela, conversely to other species which tend to develop short cypselae (e.g. *A. arenaria, A. cossyrensis, A. dentata*, and *A. perezii*). With reference to the cypsela shape (**FrS**), some intraspecific variation was observed, especially in *A. pinnatifida* and *A. ragusina*. In some species the cypsela is frequently oblong (*A. arenaria* and *A. integrifolia*) or obconical (*A. crithmifolia, A. glandulosa*, and *A. sparsiflora*). Nevertheless, it is clearly oblong in *A. agardhii, A. maroccana, A. perezii,* and *A. rothia,* whereas in *A. chevallieri, A. dentata, A. nigricans, A. mogadorensis,* and *A. laevitomentosa* it is obconical (Figure 2.12).

In respect to the cypsela colour (**FrCol**), although it is generally dark brown, in some species it can vary from dark brown to black (e.g. *A. mogadorensis*, *A. glandulosa*, and *A. pinnatifida*), while in others (e.g. *A. agardhii*, *A. laevitomentosa*, and *A. ragusina*) it is light-brown or brownish yellow. Regarding the cypsela ribs colour (**FrRCol**), in spite of some intraspecific variability (e.g. *A. glandulosa* with white or light-brown ribs), in most species these are often white. Nonetheless, in *A. crithmifolia*, *A. perezii*, and *A. maroccana* the ribs are reddish brown or brown. With respect to cypsela ribs saliency (**FrRS**), despite the intraspecific variability in a few species, *A. pinnatifida* stands out as in this species these are quite salient (Figure 2.12B) when compared to the remaining species, except for *A. agardhii* and *A. integrifolia* with more or less salient ribs (Figure 2.12A, F).

Concerning the cypsela apex aspect (**FrAA**), most species exhibit a inner ring constituted by more or less conspicuous teeth, conversely to *A. agardhii* with a rather eroded inner ring and *A. laevitomentosa* with a 2-rimmed disc (i.e. a broad eroded ring, overlying another prominent ring) (Figure 2.12E, F).

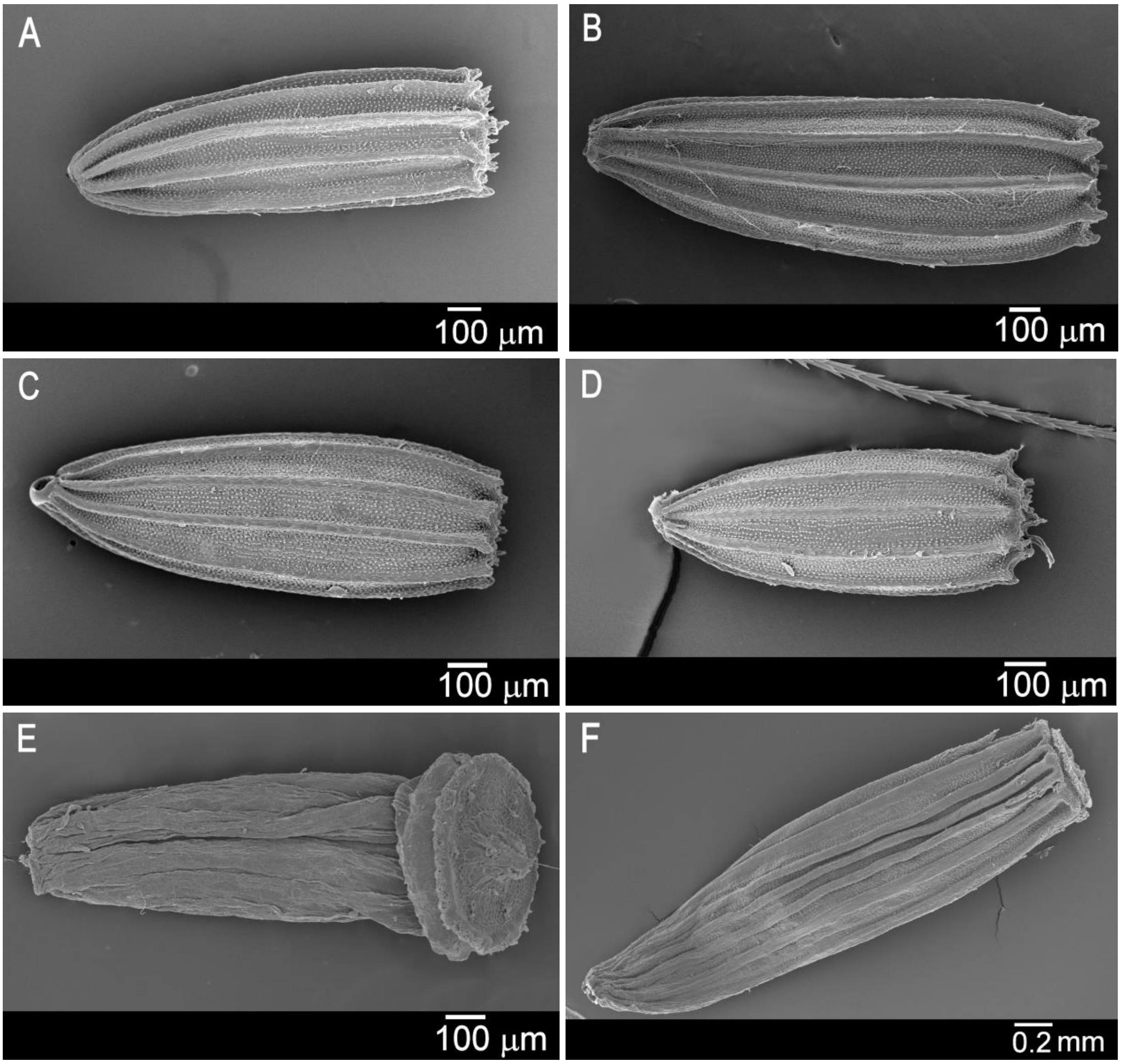


Figure 2.12 Cypsela morphology. A – *Andryala integrifolia,* B – *Andryala pinnatifida*, C – *Andryala chevallieri,* D – *Andryala dentata*, E – *Andryala laevitomentosa,* F – *Andryala agardhii.*

As for the cypsela apical inner ring disposition (**FrAIRD**), in some species the apical inner ring of teeth lays more or less at the same level of the prolongation of the ribs (e.g. *A. integrifolia*, *A. chevallieri*, *A. perezii*, *A. glandulosa*, and *A. sparsiflora*). However, in *A. pinnatifida* the inner ring of teeth is often greatly surpassed by the prolongation of the ribs, whereas in other species it is found at a higher level than the prolongation of the ribs (e.g. *A. dentata, A. laevitomentosa, A. agardhii*) (Figure 2.12D, E, F).

2.3.8.3 Pappus

The pappus (Figure 2.13) is deciduous and is formed by one row of whitish and scabrid bristles (Coutinho 1939; Talavera 1987; Blanca 2009, 2011).

For this structure several morphological characters were registered:

- pappus length (FrPL), measured in millimiters (Figure 2.5)
- pappus colour (FrPCol): 0-white, 1-dirty-white;
- pappus base (FrPB) and apex (FrPA): 0-denticulate, 1-pilose.

In respect to the pappus length (**FrPL**), despite the intraspecific variation quite often observed, some species usually exhibit a long pappus (e.g. *A. agardhii, A. laevitomentosa*, and *A. chevallieri*). The pappus colour (**FrPCol**) varied between white (e.g. *A. agardhii, A. perezii, A. sparsiflora, A. dentata*, and *A. laevitomentosa*) and dirty-white (e.g. *A. crithmifolia, A. integrifolia,* and *A. cossyrensis*). Few species reveal some intraspecific variability in what concerns this character .

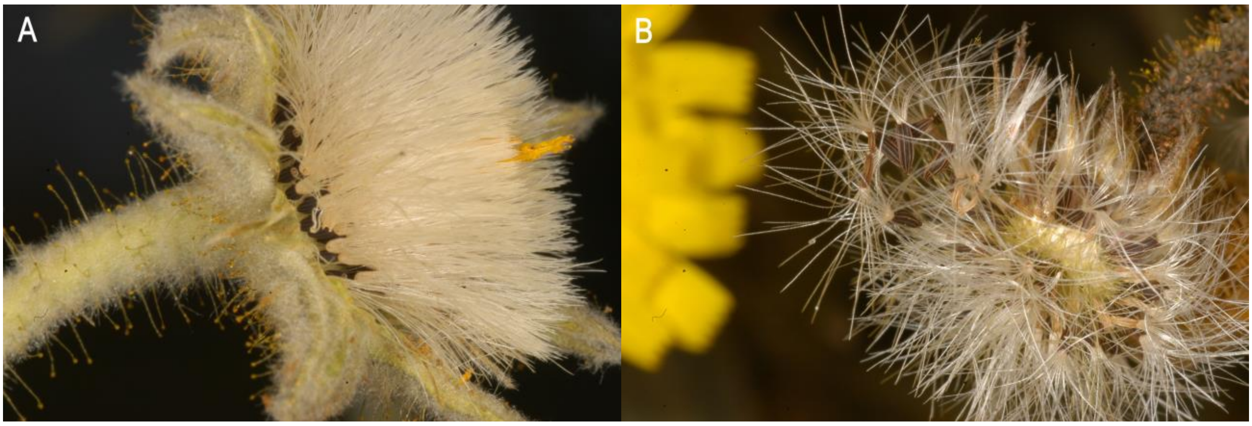
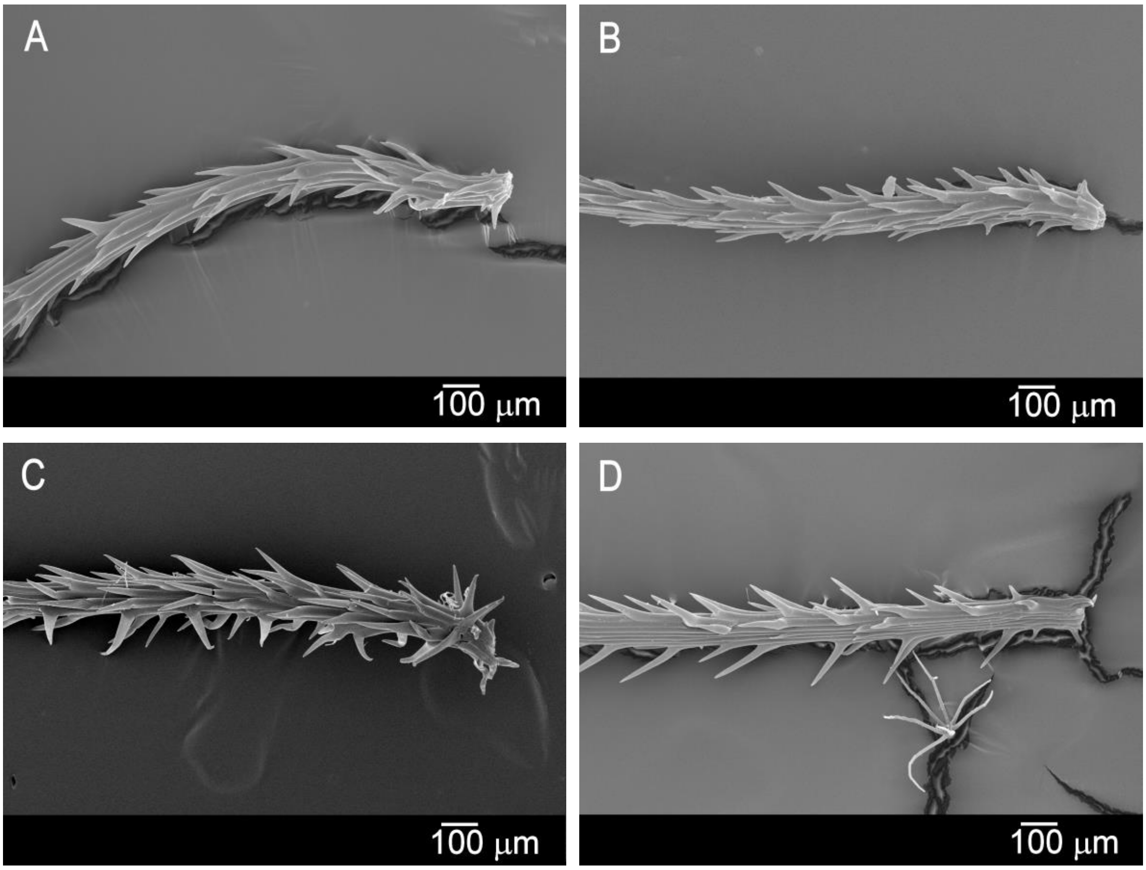


Figure 2.13 Pappus. A – *Andryala glandulosa*; B – *Andryala sparsiflora.*

As for the pappus base (**FrPB**), in some species it is often denticulate (e.g. *A. agardhii, A. cossyrensis, A. sparsiflora, A. laevitomentosa,* and *A. maroccana*) or pilose (e.g. *A. chevallieri, A. arenaria, A. crithmifolia, A. rothia, A. mogadorensis*, and *A. ragusina*) (Figure 2.14). The pappus apex is always more or less denticulate.



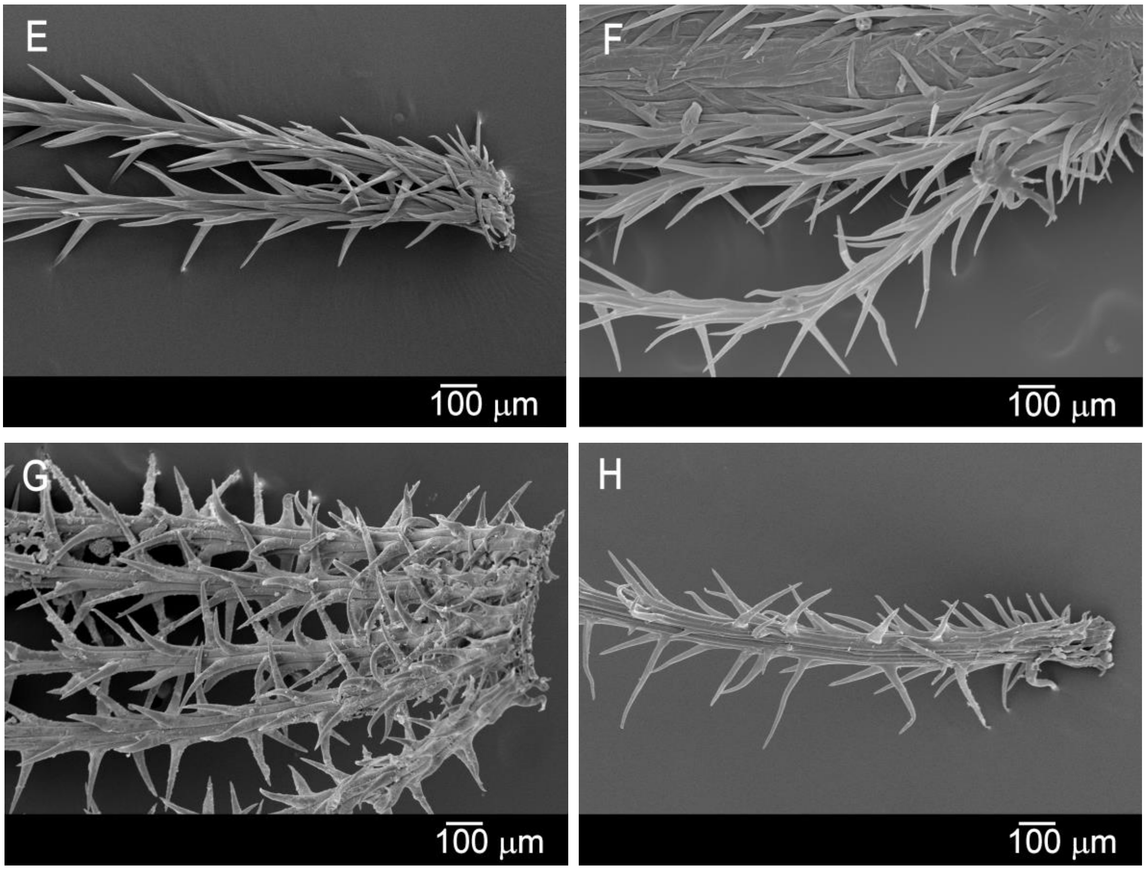


Figure 2.14 Base of the pappus. A – *Andryala agardhii*, B – *Andryala laevitomentosa*, C – *Andryala maroccana*, D – *Andryala sparsiflora*: denticulate; E – *Andryala arenaria*, F – *Andryala perezii*, G – *Andryala mogadorensis*, H – *Andryala ragusina:* pilose.

3 Multivariate morphometric study

Andryala L. (Asteraceae) is a well-defined Mediterranean-Macaronesian genus, comprising from 13 (Greuter 2006+) to 20 species (Mabberley 1997), depending on taxonomic concept, as mentioned before. It is a rather complex plant group concerning taxonomy. Indeed, the traditional concept of the genus included an assemblage of numerous descriptions of "new species" which actually correspond to *taxa* with high intraspecific variation. As *Andryala* includes species with poorly defined taxonomic boundaries, more recent literature has shown a lumping approach to the genus, instead of a splitting one. For example, Sell (1976) preferred to treat *A. integrifolia* as a highly variable species, including possibly very closely allied *taxa*, until detailed experimental work was carried out. The most recent taxonomic concept in the framework of the Euro+Med PlantBase (Greuter 2006+) recognises, for instance, *A. integrifolia* with further 8 species and 2 subspecies as "included *taxa*" and considers these as "preliminary accepted". Similar confusing classifications are presented in several floras, checklists or identification keys (e.g. Fiori 1928; Pottier-Alapetite 1981; Pignatti 1982; Conti *et al.* 2005). In addition, the inclusion of some species in *Andryala*, namely *A. agardhii* and *A. laevitomentosa*, has been quite controversial (Sennikov 1999; Greuter 2003).

The taxonomic complexity in *Andryala* results mainly from intricate morphological variation. It includes morphologically more or less homogeneous species (e.g. *A. agardhii*, *A. laevitomentosa* and, *A. maroccana*) as well as morphologically similar species (*A. cossyrensis* and *A. arenaria*), aside from polymorphic species with complex infraspecific variation (e.g. *A. integrifolia* and *A. pinnatifida*). Extensive morphological variation (including large phenotypic plasticity), a more or less broad distribution area and ecological amplitude, have been the main factors hampering a sound infraspecific treatment of some *Andryala* species such as *A. pinnatifida and A. mogadorensis.* Several examples of natural hybrids have also been described in *Andryala* (Maire 1926; Maire 1937; García Adá 1992), but hybridization and its possible influence on the morphological variation have never been studied further by biosystematists.

In earlier taxonomic treatments of the genus *Andryala* L. two sections were defined within the genus (De Candolle 1838; Battandier 1889): Sect. 1. *Euandryala* (involucral bracts not enclosing the outer cypselae; receptacle villous, without scales at the margin) and Sect. 2. *Voigtia* Roth or *Rothia* Schreb. (involucral bracts enclosing the outer cypselae; receptacle with 2 or 3 series of short hyaline scales). However, recent taxonomic treatments do not suggest any infra generic division of the genus.

Taxonomic relationships are often accessed by means of numerical taxonomy techniques. To date, no numerical taxonomic study has been conducted on *Andryala*, a genus including some species which are difficult to distinguish from each other and for which no infra generic classification is yet been established. Numerical taxonomy can be defined as "the numerical evaluation of the affinity or similarity between operational taxonomic units (OTUs) and the ordering of these units into *taxa* on the basis of their characters states" (Sneath & Sokal 1963). The number of taxonomic characters required to obtain stable classifications is debatable. Sneath & Sokal (1963) argued that one should use as many features as possible. However, although it is often suggested that at least 50, but preferably 100 or more characters, should be used to produce a fairly stable classification, in certain circumstances it might be possible to obtain a stable classification using fewer characters (Dunn & Everitt 1982).

Polymorphic plant species with large intraspecific variation are undoubtedly a challenge for taxonomic research. Sound taxonomic concepts are usually difficult to establish and, traditionally, these *taxa* are surrounded by taxonomic controversies. In recent decades, significant advances have been made in species-level systematics, mainly due to large scale-sampling of material and comparative approaches employing several methods and techniques simultaneously (e.g. morphometric, molecular, karyological, or genome size data). These data along with detailed knowledge on distribution patterns, ecological requirements and mating systems, facilitate the delimitation of closely related *taxa* (Slovák *et al.* 2012). To assess pronounced morphological variation within species groups or complexes, several morphometric studies have been performed using numerical taxonomy techniques (e.g. Chiapella 2000; Cron *et al.* 2007; Flann *et al.* 2008; Olšavská *et al.* 2009; Mráz *et al.* 2011; Slovák *et al.* 2012). The aim of this study is to clarify the taxonomic relationships of closely related species in *Andryala* and to establish an infra generic delimitation using numerical taxonomy techniques.

3.1.1 Plant material

The morphometric study was performed on herbarium material as well as specimens collected during fieldwork. Most observations were performed on specimens obtained as a loan from different herbaria: MA, TFC, TFMC, LISI, LISU, MADJ, MADS, MADM, SEV, MPU, P, NMW and PRA (Thiers continuously updated). All European, North African and Macaronesian *taxa* were included. Specimens were chosen in order to obtain a representative set including the greatest possible number of *taxa* recognised in the consulted literature and, simultaneously, the largest geographical natural distribution area. In total 473 OTUs were included in this study. Species with high intraspecific variation were represented by a great number of OTUs, whereas some *taxa* were represented only by a few OTUs due to sampling difficulties and/or rarity.

3.1.2 Morphometric data

The morphological characters included in this study are those traditionally used for *Andryala taxa* delimitation in the literature. Both vegetative and reproductive characters were assessed, including micro and macro characters (see Chapter 2). In total 105 characters, including 48 quantitative characters, 43 qualitative (multistate) characters, and 14 qualitative (binary) characters, were measured or scored on each OTU (Table 3.1). Characters of peduncles, capitula and involucre were measured on the four largest capitula of each specimen and characters of involucral bracts and florets were measured on four bracts/florets of the largest capitulum (see Chapter 2). In each case the maximum values were used for the morphometric analysis.

3.1.3 Statistical analysis

Before undertaking any technique of multivariate analysis the data set was inspected for outliers (unusual observation that may be due to variability in the measurement or may indicate experimental error). For each measured or scored character a box-and-whisker plot was obtained through the software application SPSS 14.0. Some measurement errors were detected and corrected in order to perform exploratory analysis. This procedure also allowed assessing intraspecific and interspecific variability for each character (see Chapter 2).

Multivariate analysis was performed with the following software applications: Gower's coefficient (**G**) was calculated by using the MVSP 3.22 program, while the remaining calculations were made with the NTSYSpc 2.21c program (Rolf 2009). As ordination methods the principal component analysis (**PCA**) and principal coordinate analysis (**PCoA**) were used, whereas **UPGMA** ("unweighted Pair-Group Method using Arithmetic averages") was chosen to perform cluster analysis.

Table 3.1 Characters measured or scored for the root, stem, inflorescence, and fruit (Character type: Q – quantitative; B – binary; M – multistate).

Character acronym	Character type	Description
		ROOT
RD	Q	Root diameter (cm)
RL	Q	Root length (cm)
RS	M	Root shape: (0) sinuous main root, (1) straight main root, (2) napiform
PLC	M	Plant life-cycle duration: (0) annual, (1) biennial, (2) perennial
		STEM
SH	Q	Stem height (cm)
SD	Q	Stem diameter (cm)
SS	M	Stem shape: (0) cylindrical, (1) subangular, (2) more or less flattened in the upper part
SCol	M	Stem colour: (0) whitish, (1) yellowish, (2) greenish, (3)purplish, (4) greyish, (5) brownish, (6)-black
SN	M	Stem number: (0) single stemmed, (1) multi stemmed (two to six stems), (2) caespitose (more than six)
SR	M	Stem ramification: (0) simple, (1) branched in the upper third, (2) branched in the upper half, (3) branched from the base
SNPB	Q	Number of primary branches
SNSB	Q	Number of secondary branches
SBP	B	Branch position: (0) erecto-patent, (1) ascending
SloSI	M	Lower stem stellate indumentum: (0) inexistent, (1) puberulous, (2) tomentose, (3) floccose/densely tomentose
SloGI	M	Lower stem glandular indumentum: (0) inexistent, (1) puberulous, (2) pubescent, (3) villous, (4) hispid, (5) hirsute
SmSI	M	Middle stem stellate indumentum. (0) inexistent, (1) puberulous, (2) tomentose, (3) floccose/densely tomentose
SmGI	M	Middle stem glandular indumentum: (0) inexistent, (1) puberulous, (2) pubescent, (3) villous, (4) hispid, (5) hirsute
SuSI	M	Upper stem stellate indumentum: (0) inexistent, (1) puberulous, (2) tomentose, (3) floccose/densely tomentose
SuGI	M	Upper stem glandular indumentum: (0) inexistent, (1) puberulous, (2) pubescent, (3) villous, (4) hispid, (5) hirsute
SNRSI	Q	Number of rays of stem stellate hairs
		LEAF
Lthic	B	Leaf thickness: (0) membranaceous; (1) not membranaceous
LloL	Q	Lower leaf length (mm)
LloLBMW	Q	Length from the base of the lower leaf to the point of maximum width (mm)
LloW	Q	Lower leaf maximum width (mm)
**LloLL	Q	Length of the larger lobe of the lower leaf (mm)
*LloWBL	Q	Width at the base of the larger lobe of the lower leaf (mm)
*LloLTLMN	Q	Length from the tip of the larger lobe of the lower leaf to the middle nerve (mm)
LcL	Q	Cauline leaf length (mm)
LcLBMW	Q	Length from the base of the cauline leaf to the point of maximum width (mm)
LcW	Q	Cauline leaf maximum width (mm)
**LcLL	Q	Length of the larger lobe of the cauline leaf (mm)
*LcWBL	Q	Width at the base of the larger lobe of the cauline leaf (mm)
*LcLTLMN	Q	Length from the tip of the larger lobe of the cauline leaf to the middle nerve (mm)
LuL	Q	Upper leaf length (mm)
LuLBMW	Q	Length from the base of the upper leaf to the point of maximum width (mm)
LuW	Q	Upper leaf maximum width (mm)
**LuLL	Q	Length of the larger lobe of the upper leaf (mm)
*LuWBL	Q	Width at the base of the larger lobe of the upper leaf (mm)
*LuLTLMN	Q	Length from the tip of the larger lobe of the upper leaf to the middle nerve (mm)
LloIS	M	Lower leaf insertion on the stem: (0) amplexicaul, (1) semi-amplexicaul, (2) decurrent, (3) sessil, (4) atenuate in petiole, (5) petiolate
LcIS	M	Cauline leaf insertion on the stem: (0) amplexicaul, (1) semi-amplexicaul, (2) decurrent, (3) sessil, (4) atenuate in petiole, (5) petiolate
LuIS	M	Upper leaf insertion on the stem: (0) amplexicaul, (1) semi-amplexicaul, (2) sessil, (3) atenuate in petiole
LcB	M	Cauline leaf base: (0) cuneate, (1) atenuate, (2) truncate, (3) redonded, (4) cordate, (5) auriculate
LuB	M	Upper leaf base: (0) cuneate, (1) atenuate, (2) truncate, (3) redonded, (4) cordate, (5) auriculate
LloWP	B	Lower leaf winged petiole: (0) absent, (1) present
LloLP	Q	Petiole length of the lower leaf (mm)
LcLP	Q	Petiole length of the cauline leaf (mm)
LloA	M	Lower leaf apex: (0) truncate, (1) obtuse, (2) acute, (3) acuminate
LcA	M	Cauline leaf apex: (0) truncate, (1) obtuse, (2) acute, (3) acuminate, (4) retuse
LuA	M	Upper leaf apex: (0) truncate, (1) obtuse, (2) acute, (3) acuminate, (4) retuse
LloSI	M	Lower leaf stellate indumentum: (0) inexistent, (1) puberulous, (2) tomentose, (3) floccose/densely tomentose
LloGI	M	Lower leaf glandular indumentum: (0) inexistent, (1) puberulous, (2) pubescent, (3) villous, (4) hispid, (5) hirsute
LcSI	M	Cauline leaf stellate indumentum: (0) inexistent, (1) puberulous, (2) tomentose, (3) floccose/densely tomentose
LcGI	M	Cauline leaf glandular indumentum: (0) inexistent, (1) puberulous, (2) pubescent, (3) villous, (4) hispid, (5) hirsute
LuSI	M	Upper leaf stellate indumentum: (0) inexistent, (1) puberulous, (2) tomentose, (3) floccose/densely tomentose
LuGI	M	Upper leaf glandular indumentum: (0) inexistent, (1) puberulous, (2) pubescent, (3) villous, (4) hispid, (5) hirsute

LColAD	M	Colour of the adaxial face of the leaf: (0) white, (1) greyish white, (2) pale green, (3) glaucous, (4) dark green, (5) brownish
LColAB	M	Colour of the abaxial face of the leaf: (0) white, (1) greyish white, (2) pale green, (3) glaucous, (4) dark green, (5) brownish
		INFLORESCENCE
INC	Q	Number of capitula per inflorescence
IT	M	Inflorescence type: (0) panicule, (1) corymbose panicle, (2) corymb, (3) anthela, (4) solitary capitulum, (5) racemose, (6) paniculate corymb
**ILGP	Q	Length of the glandular hairs of the peduncle (mm)
ICD	Q	Capitulum diameter at anthesis (mm)
IPL	Q	Peduncle length (mm)
IIL	Q	Involucre length at anthesis (mm)
IIW	Q	Involucre width at anthesis (mm)
IISA	B	Involucre shape at anthesis: (0) campanulate, (1) hemispherical
IISF	M	Involucre shape at fructification: (0) campanulate, (1) cylindrical and truncate, (2) ovoid
INRIB	Q	Number of rows of the involucral bracts
IIBeC	M	External involucral bracts convolution: (0) flat, not enfolding a floret (1) involute, enfolding a floret, not enclosing a cypsela (2) strongly involute enclosing a cypsela
IIBeL	Q	External involucral bracts length (mm)
IIBeW	Q	External involucral bracts maximum width (mm)
IIBSIo	M	External involucral bracts stellate indumentum on the outer face: (0) puberulous, (1) tomentose, (2) floccose/densely tomentose
IIBSIi	B	External involucral bracts stellate indumentum on the inner face: (0) absent, (1) present
IIBGI	M	External involucral bracts glandular indumentum: (0) inexistent, (1) puberulous, (2) pubescent, (3) villous, (4) hispid, (5)-hirsute
*ICGIB	M	Colour of the external involucral bracts glandular hairs (0) yellowish, (1) greenish, (2) yellow but dark at the base, (3) dark
ICEIB	B	Colour of the external involucral bracts stellate hairs: (0) whitish, (1) tawny
IIBA	M	External involucral bracts apex: (0) obtuse, (1) acute, (2) acuminate, (3) subulate
IIBiL	Q	Internal involucral bracts length (mm)
IIBiW	Q	Internal involucral bracts width (mm)
IIBiSMW	Q	Internal involucral bracts scariose margin maximum width (mm)
**ILIBGI	Q	Length of the external involucral bracts glandular hairs (mm)
IRSL	Q	Length of receptacle setae (mm)
IRS	B	Receptacle shape: (0) convex, (1) more or less flat
IRI	M	Receptacle indumentum: (0) puberulous, (1) pubescent, (2) tomentose, (3) villous
ILL	Q	Ligule length (mm)
ILW	Q	Ligule width (mm)
IATL	Q	Ligule apical teeth length (mm)
ITL	Q	Tube length (mm)
IIBL	M	Indumentum at the base of the ligule: (0) glabrous, (1) villous, (2) hirsute, (3) subglabrous
ISITL	B	Stellate indumentum on the teeth of the ligule: (0) absent or very rare, (1) present in all teeth
ILCFo	M	External ligule colour, outer face: (0) pale yellow, (1) bright yellow, (2) golden yellow, (3) dark yellow, (4) orange yellow, (5) reddish stripe
ILCFi	M	External ligule colour, inner face: (0) pale yellow, (1) bright yellow, (2) golden yellow, (3) dark yellow, (4) orange yellow, (5) reddish stripe
ILiC	M	Internal ligule colour: (0) pale yellow, (1) bright yellow, (2) golden yellow, (3) dark yellow, (4) orange yellow, (5) reddish stripe
		FRUIT
FrL	Q	Cypsela length (mm)
FrW	Q	Cypsela maximum width (mm)
FrS	B	Cypsela shape: (0) oblong, (1) obconical
FrCol	M	Cypsela colour: (0) brownish yellow, (1) light-brown, (2) dark brown, (3) black
FrRS	B	Cypsela ribs saliency: (0) slightly salient, (1) very salient
FrAA	B	Cypsela apex aspect: (0) inner ring eroded, (1) inner ring with conspicuous teeth
FrAIRD	M	Cypsela apical inner ring disposition: (0) at a lower level than the prolongation of the ribs, (1) at the same level as the prolongation of the ribs, (2) at a higher level than the prolongation of the ribs
FrRCol	M	Cypsela ribs colour: (0) whitish, (1) light-brown, (2) reddish brown/brown
FrPL	Q	Pappus length (mm)
FrPCol	B	Pappus colour : (0) white, (1) dirty-white
FrPB	B	Pappus base: (0) denticulate, (1) pilose
*FrPA	B	Pappus apex: (0) denticulate, (1) pilose

* Characters excluded from morphometric analysis for expressing similar features, for being non-coding or due to invariability.

** Characters recoded as binary: (0) absent (1) present - for being non-coding (e.g. length of the larger lobe of the leaf when the leaf margin is entire).

3.1.4 Similarity and dissimilarity coefficients

Similarity estimation is the most important step of numerical taxonomy. Relations of similarity or dissimilarity were calculated between all pairs of OTUs by using different similarity or dissimilarity coefficients: Gower's coefficient (**G**), Simple Matching (**SM**) coefficient, Jaccard's (**J**) coefficient, Correlation (**CORR**) coefficient, Average "taxonomic" (**DIST**) distance, Average Manhattan (**MANHAT**) distance, and Euclidean (**EUCLID**) distance. Both the **SM** and **J** coefficients were used for the binary characters. For the multistate characters only the **SM** coefficient was applied. Regarding the quantitative characters, the **CORR** coefficient was used as a similarity measure. This coefficient provides information on the similarity between the OTUs, minimizing the effect of the scale factor (Dunn & Everitt 1982). It was also utilised to determine the correlation between characters in order to, for example, calculate the eigenvalues and eigenvectors in a principal component analysis. The **EUCLID** distance for quantitative characters is widely applied in numerical taxonomy, but various measures derived from it can also be used (e.g. **DIST** distance[11] and the **MANHAT** distance). Hence, besides the **CORR** coefficient, these coefficients were also applied on the quantitative data set. On the combined set of binary, multistate and quantitative characters the similarity measure applied was **G** coefficient[12].

3.1.5 Matrix transformations

The application of Gower's coefficient (**G**) on the total matrix was preceded by the logarithmic transformation of the quantitative data, according to the equation $y_i = \log_{10}(x_i)$ in order to reduce the skewness of the data. As these characters were measured on different scales, they were standardised by dividing the difference between the mean and the actual measurement by the standard deviation [$y = (x - \bar{x})/s$].

The multistate characters were transformed into binary characters according to the procedure suggested by Legendre & Legendre (1998)[13]. For example, the multistate character external involucral bracts apex (**IIBA**) with four character states – (0) obtuse, (1) acute, (2) acuminate, (3) subulate – was transformed into three new binary characters: IIBA0, IIBA1, and IIBA2. If the apex was obtuse, then IIBA0 was coded 1 and the remaining characters 0; if the apex was acute then IIBA1 was coded 1 and the remaining characters 0, and if the apex was acuminate then IIBA2 was coded 1 and the remaining characters 0. The fourth character state was excluded as its information is totally linearly dependent on the first three characters. This transformation was performed in order to apply the Jaccard coefficient to a larger set of binary characters[14].

3.1.6 Types of matrices

The original matrix (473 OTUs by 105 characters) was split into several subsets in order to calibrate the different usefulness of each type of character and the following matrices were obtained:

- matrix of binary characters, including the multistate characters binary-coded (473 OTUs by 166 characters);
- matrix of the multistate characters (43 characters and 473 OTUs);
- matrix of the quantitative characters (473 OTUs by 48 characters).

An additional quantitative data set was assembled including all the original quantitative data as well as the ratio characters shown in Table 3.2. To apply Gower's similarity coefficient (**G**) a total matrix was constructed (473 OTUs

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[11] The elimination of OTUs with missing values makes the average "taxonomic" distance coincide with the Euclidean distance.

[12] Gower's coefficient was proposed by Gower in 1971 and is a particularly useful similarity measure when OTUs are described by a mixture of binary, multistate, and quantitative characters (Dunn & Everitt 2012 and references therein).

[13] Multistate qualitative characters may be binary-coded as dummy variables. A multistate qualitative character with *s* states is decomposed into (*s – 1*) dummy variables (Legendre & Legendre 1998).

[14] The simple matching coefficient is more useful when 0s and 1s are merely used as codes of two alternative states of a binary character. When 0s indicate the absence of a character and 1s its presence, it is necessary to consider the Jaccard coefficient, because if, on one hand, the presence of a character in two OTUs is a strong indication of similarity, on the other, the absence of a character in two OTUs does not necessarily reflect their similarity. Hence, the Jaccard coefficient attributes importance only to the characters that are present in both the OTUs, while the simple matching coefficient also values the characters absent in both OTUs (Branco 2004).

by 97 characters) containing all types of characters, excluding non-coding or invariant characters as well as characters expressing similar features (see Table 3.1).

Table 3.2 Ratio characters included in the quantitative dataset.

Character acronym	Description
*LloL/LloW	Lower leaf length/Lower leaf maximum width (mm)
**LloLL/LloLTLMN	Length of the larger lobe of the lower leaf/Length from the tip of the larger lobe of the lower leaf to the middle nerve (mm)
*LloLBMW/LloL	Length from the base of the lower leaf to the point of maximum width/Lower leaf length (mm)
*LcL/LcW	Cauline leaf length/Cauline leaf maximum width (mm)
**LcLL/LcLTLMN	Length of the larger lobe of the cauline leaf/Length from the tip of the larger lobe of the cauline leaf to the middle nerve (mm)
*LcLBMW/LcL	Length from the base of the cauline leaf to the point of maximum width/Cauline leaf length (mm)
*LuL/LuW	Upper leaf length/ Upper leaf maximum width (mm)
**LuLL/LuLTLMN	Length of the larger lobe of the upper leaf/Length from the tip of the larger lobe of the upper leaf to the middle nerve (mm)
*LuLBMW/LuL	Length from the base of the upper leaf to the point of maximum width/Upper leaf length (mm)
ILL/ILW	Ligule length/Ligule width(mm)
*IIBel/IIBeW	External involucral bracts length/External involucral bracts maximum width (mm)
*IIBil/IIBiW	Internal involucral bracts length/Internal involucral bracts width (mm)
***IIBiSMW/(IIBiW/2)	Internal involucral bracts scariose margin maximum width/(Internal involucral bracts width)/2 (mm)
IRSL/FrL	Length of receptacle setae/Cypsela length (mm)
FrL/FrW	Cypsela length/Cypsela maximum width (mm)

Ratio characters used to determine: *leaf and involucral bracts shape; **leaf margin; *** broadness of internal involucral bracts scariose margin (see Chapter 4).

3.1.7 Missing data

According to Legendre & Legendre (1998), missing values may be represented in data matrices by numbers that do not correspond to possible data values. Therefore, given the high number of missing data in the original matrix (resulting from improper sampling procedures, incorrectly preserved specimens, and wither of certain structures during anthesis), these were replaced by the number 999 so as to perform a multivariate analysis with the NTSYSpc 2.21c program (Rolf 2009). Another way of dealing with missing data is to eliminate rows and columns of the original data matrix containing missing values (Legendre & Legendre 1998). Following this procedure a reduced total matrix (322 OTUs by 64 characters) was obtained, on which Gower's similarity coefficient (**G**) was applied. Although, this method of treating missing data is quite simple, it is important to bear in mind that it is also the most costly since a great deal of precious information is lost (Legendre & Legendre 1998).

3.1.8 Multivariate techniques

Two main approaches have been used in numerical taxonomy based on morphological data, ordination and cluster analysis. **Ordination methods** are frequently used in numerical taxonomic studies as they summarise large amounts of information in a reduced number of dimensions. They can be very useful for displaying the relationships between the OTUs in a low-dimensional space, thus enabling direct visual examination of the relative positions of the OTUs (Dunn & Everitt 1982).

Principal Component Analysis (**PCA)** transforms the original characters into new and non correlated characters, sorted in ascending order of variance. These new characters (variables) are called principal components. The aim of PCA is to ascertain if the first few principal components are responsible for most of the total variance and, therefore, being reasonable to use these first components to explain the initial data system. In this case, this technique can be used to summarize the original data with little loss of information, thus obtaining a reduced dimensionality of the data (Dunn & Everitt 1982). **PCA** has a great advantage compared to Principal Coordinates Analysis (**PCoA)**: the possibility of projecting the characters (besides the OTUs) in the same space defined by the principal components. In this case the projection of each character (represented by a vector) over each axe is equal to the loading coefficient of the respective principal component. Hence, it is possible to perform a first direct observation of the weight of the several characters on the segregation of the OTUs.

Concerning **PCoA**, the principal coordinates are also functions of the original variables, although mediated by the similarity or dissimilarity coefficient employed. **PCoA** is an alternative ordination method to **PCA** when many missing values are present[15]. Moreover, **PCoA** can be used with all types of variables (quantitative, qualitative or both) while **PCA** is used only with quantitative data (Legendre & Legendre 1998). Thus, in this study **PCoA** was preferred over **PCA.** The goodness of fit of the results obtained with **PCoA** can be ascertained through the calculation of a correlation matrix of the data with the SIMINT module of the software program NTSYS by using the **CORR** coefficient. This new matrix can then be compared with the original similarity matrix using the MXCOMP module. The correlation coefficient obtained from this comparison (product-moment correlation, *r*) indicates the degree of overlap and, simultaneously, the degree of distortion between the correlation matrix and the original similarity matrix.

Clustering methods are used to separate organisms into groups that may be applied in a classification. The clustering method **UPGMA**[16] (unweighted Pair-Group Method using Arithmetic averages) was used in this study in order to group the OTUs, defining levels of similarity between them. In **UPGMA** the dissimilarity between two groups is the mean of dissimilarities between all pairs of objects, formed with an object of each group (Branco 2004). The clustering method **UPGMA** was applied to the similarity matrices using the SAHN module in order to produce a tree matrix. With the TREE PLOT module this matrix can be represented as a phenogram (dendrogram representing phenetic relations). To perform this study the **UPGMA** clustering method was chosen due to the fact that it is the most widely used and also the one that produces the least distortion when the resulting phenograms are compared with the original similarity matrices (Sneath & Sokal 1973). The degree of distortion between the similarity matrices and the resulting phenograms can be determined through the cophenetic correlation (Sneath & Sokal, 1973). From the phenogram a symmetrical matrix of cophenetic similarity or dissimilarity values (cophenetic value matrix) can be produced using the COPH module of the software program NTSYS. This new matrix can be compared with the similarity matrix upon which the clustering was based using MXCOMP module. The cophenetic correlation has high values for small degrees of distortion and low values for high degrees of distortion. According to Rohlf & Sokal (1981), the cophenetic correlation can be evaluated as follows:

CC> 0.9 Excellent overlap of the two matrices
0.8 <CC <0.9 Good overlap
0.7 <CC <0.8 Low overlap
CC <0.7 Very low overlap

UPGMA clustering method was implemented on both the similarity and dissimilarity matrices and the following coefficients were applied: **G** coefficient (for the total matrix including all character types); **CORR** coefficient as well as

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[15] In this situation, PCoA is preferable as, in addition to the standardisation of data, the symmetric similarity or dissimilarity matrix is "double centered" using DCENTRE module and, thus, transformed to scalar product form so that its eigenvalues and eigenvectors can be computed with the EIGEN module.

[16] The clustering methods enable the identification of discrete subsets of individuals with similar characteristics ("clusters"). In contrast, ordination methods simply depict a data representation and may or not show evidence of "clustering" (Shaw 2003).

DIST distance, **MANHAT** distance, and **EUCLID** distance (for the matrix of quantitative characters); **J** and **SM** coefficients (for the total matrix of binary characters, including also the multistate characters transformed into binary characters); and **SM** coefficient (for the matrix of multistate characters).

3.2 Results

3.2.1 Exploratory data analysis

As mentioned before, prior to the exploratory analysis the data were inspected through box-and-whisker plots so as to detect possible outliers. These preliminary results (not shown) were fundamental to eliminate any possible sources of error.

3.2.1.1 Results for the total matrix (TM)

The application of **G** coefficient on the total matrix (containing all types of characters) allowed the construction of a similarity triangular matrix which was used to explorer the spatial ordination by **PCoA** and the possible aggregation of OTUs into species and large groups through **UPGMA** cluster analysis.

The projection of the 473 OTUs on the first two and three principal coordinate axes are shown in Figure 3.1 and Figure 3.2, respectively. The product-moment correlation obtained by comparison of the correlation matrix to the original similarity matrix was low (r = 0.54) indicating some degree of distortion between these two matices. Both projections show a clear segregation of *A. glandulosa* Lam. and some tendency of segregation of *A. rothia* Pers., *A. mogadorensis* Coss. ex Hook.f. and, to a lesser extent, of *A. integrifolia* L. and *A. sparsiflora* (Lowe) M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. Moreover, *A. agardhii* DC., *A. laevitomentosa* (Sennikov) Greuter, *A. maroccana* Pau ex Caball., and *A. ragusina* L. tend to segregate from the rest of the *Andryala* species. However, most species reveal an unclear segregation including, for example, *A. arenaria* (DC.) Boiss. & Reut., *A. dentata* Sm., *A. cossyrensis* Guss., *A. pinnatifida* Aiton, and *A. perezii* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq.

The **UPGMA** clustering method applied on the similarity matrix obtained by using **G** coefficient on the total matrix yielded a phenogram showing a more or less fair segregation of the OTUs by species including *A. integrifolia*, *A. arenaria*, *A. dentata, A. rothia*, *A. crithmifolia* Aiton, *A. sparsiflora* (Lowe) M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq., *A. nigricans* Poir., *A. perezii, A. agardhii, A. maroccana, A. ragusina, A. laevitomentosa,* and *A. glandulosa.* A somewhat unclear segregation is observed for *A. cossyrensis, A. pinnatifida,* and *A. chevallieri* Barratte ex L. Chevall., *A. mogadorensis* Coss. ex Hook.f. (Figure 3.3). Moreover, in the phenogram four large groups comprising several species are clearly distinguishable: Group 1 – *A. arenaria*, *A. cossyrensis,* and *A. dentata*; Group 2 – *A. crithmifolia* and *A. sparsiflora*; Group 3 – *A. chevallieri*, *A. mogadorensis*, *A. perezii*, and *A. pinnatifida* (the latter splitting somewhat from the first three); Group 4 – *A. agardhii*, *A. maroccana*, *A. ragusina,* and *A. laevitomentosa* (the latter appearing to split from the first three species). Group 1 clearly separates from *A. integrifolia* and *A. rothia*. Similarly, Group 2 segregates quite well from *A. glandulosa*. The cophenetic correlation obtained by comparison of the original similarity matrix to the cophenetic value matrix equalled 0.71, which means that the **UPGMA** clustering method imposed on the original similarity matrix led to some distortion causing low but acceptable overlap of the two matrices.

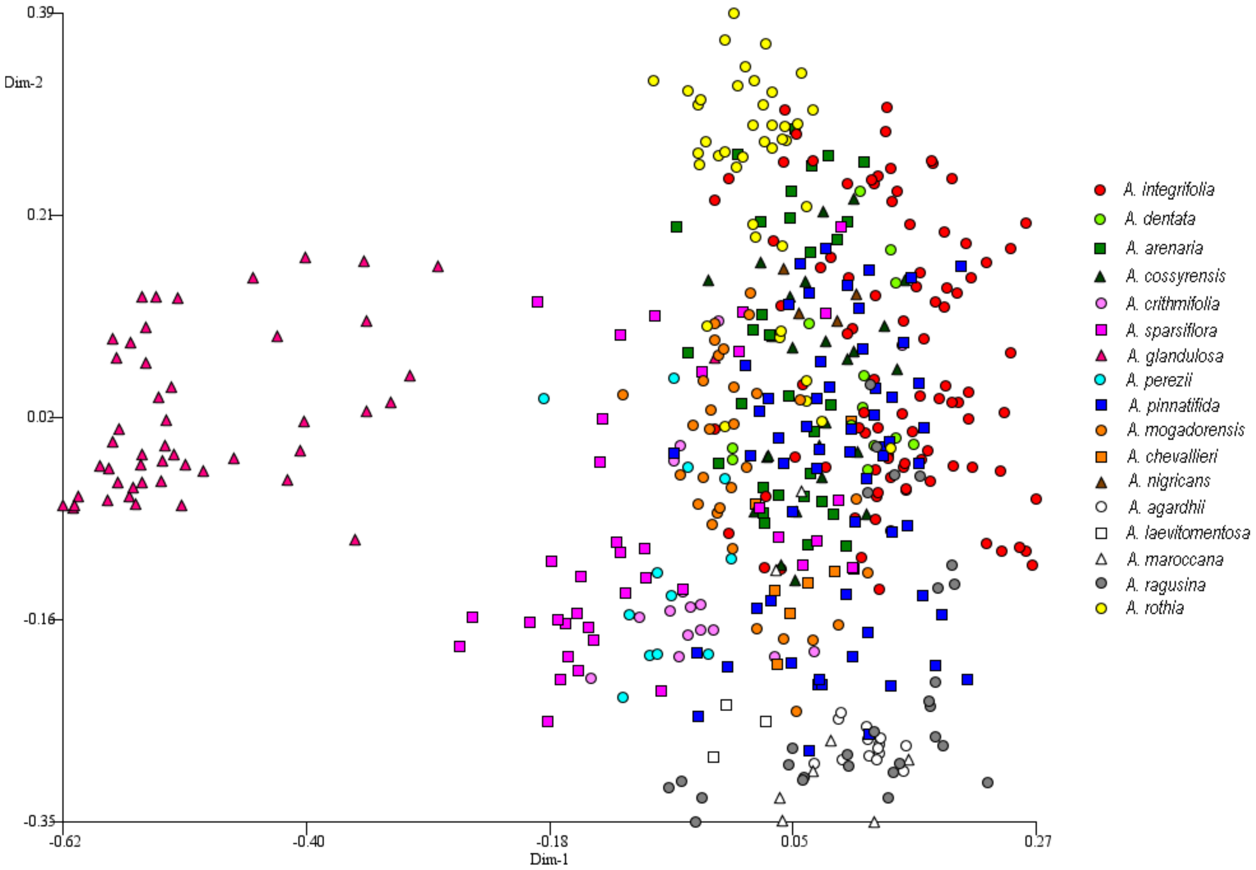


Figure 3.1 Principal coordinates analysis (PCoA) performed on the similarity matrix obtained from the total matrix (TM) using Gower's coefficient: 2-dimensional projection of the OTUs.

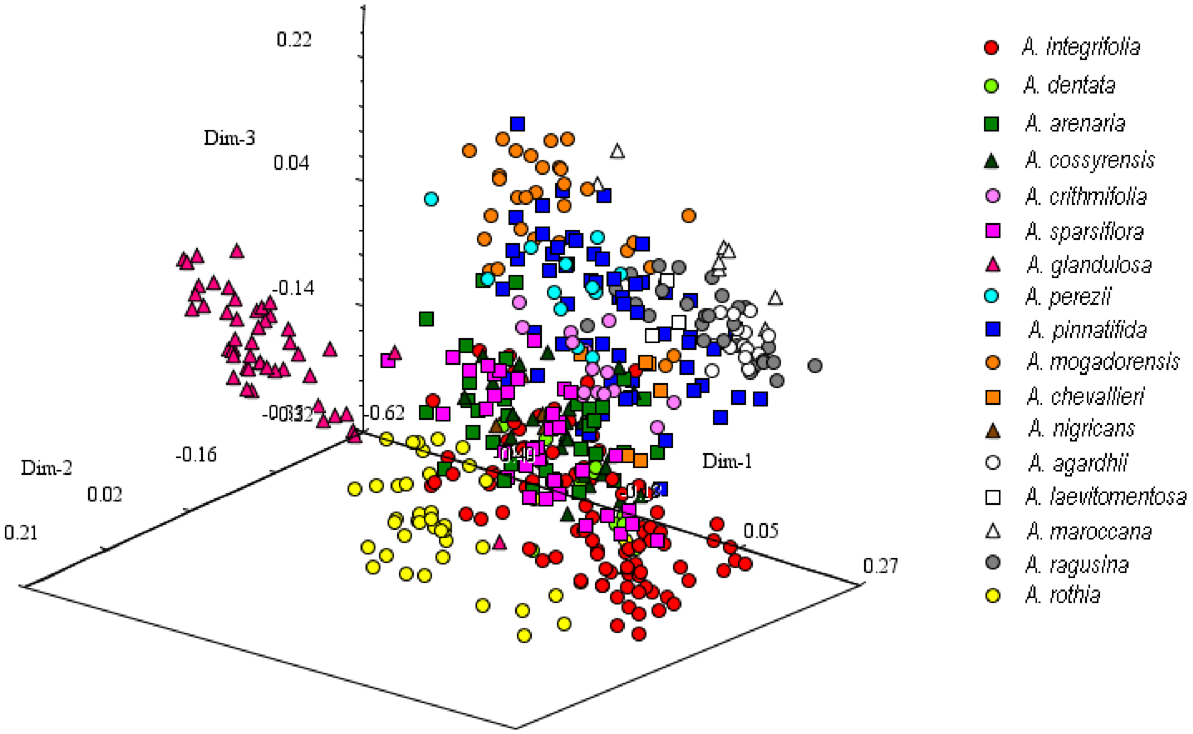


Figure 3.2 Principal coordinates analysis (PCoA) performed on the similarity matrix obtained from the total matrix (TM) using Gower's coefficient: 3-dimensional projection of the OTUs.

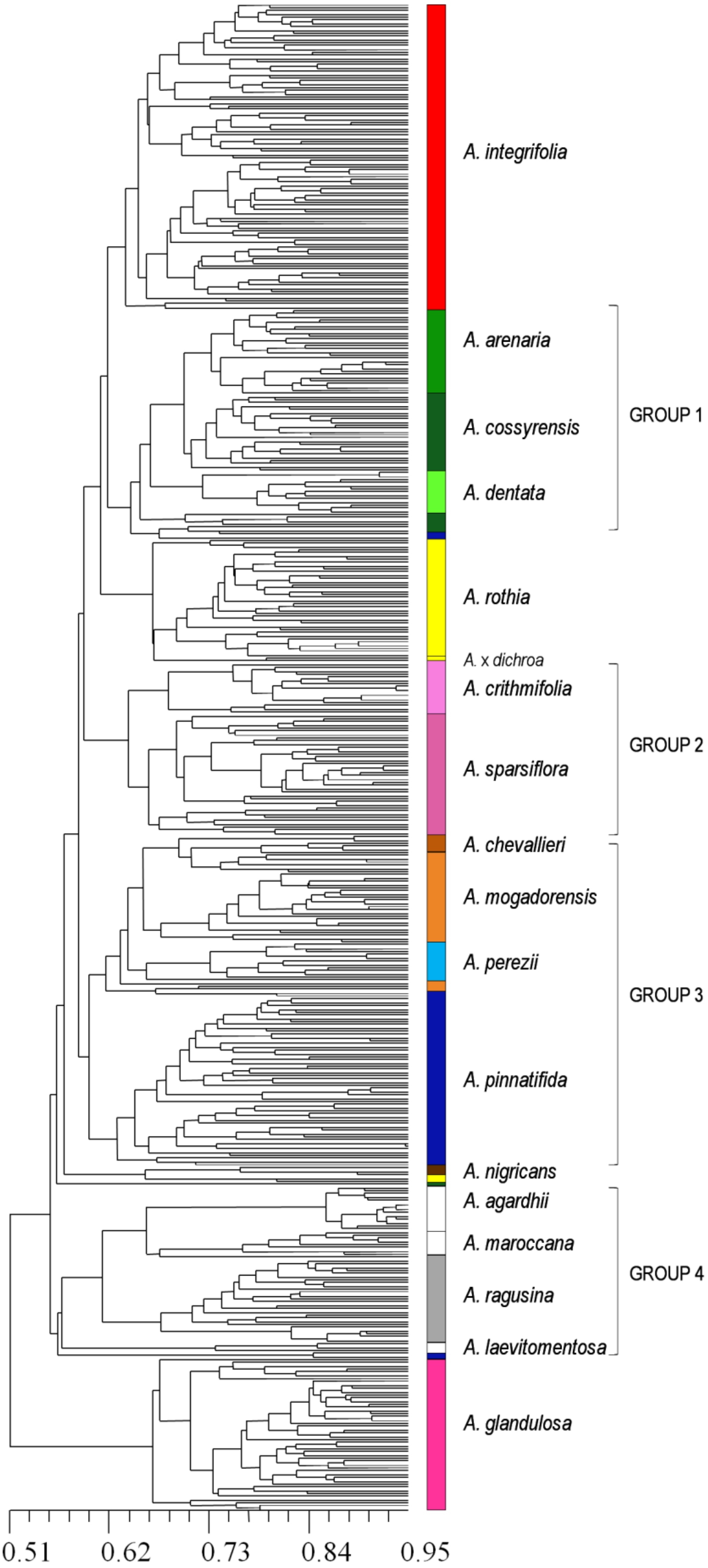


Figure 3.3 Phenogram constructed by performing UPGMA cluster analysis on the similarity matrix obtained from the total matrix (TM) using Gower's coefficient. Cophenetic correlation 0.71.

3.2.1.2 Results for the reduced total matrix (RTM)

A reduced total matrix (64 characters by 322 OTUs) was constructed by eliminating OTUs and characters of the total data matrix containing missing values. Likewise, from this matrix a similarity matrix was produced based on **G** coefficient. The reduced total matrix was also subjected to **PCoA** and the **UPGMA** clustering method. Regarding **PCoA,** the product-moment correlation obtained by comparison of the correlation matrix to the original similarity matrix was slightly higher (r = 0.58) than the value obtained with the total matrix, showing still some degree of distortion of the distances between OTUs. Nonetheless, the 3-dimensional projection of the 322 OTUs on the first three axes (Figure 3.4) reveals a segregation of the OTUs by species resembling the one obtained from the total matrix. Nonetheless, the separation of *A. sparsiflora*, *A. mogadorensis*, and *A. integrifolia* seems somewhat clearer. Additionally, *A. arenaria*, *A. dentata*, and *A. cossyrensis* Guss. seem to show some tendency to segregate from each other.

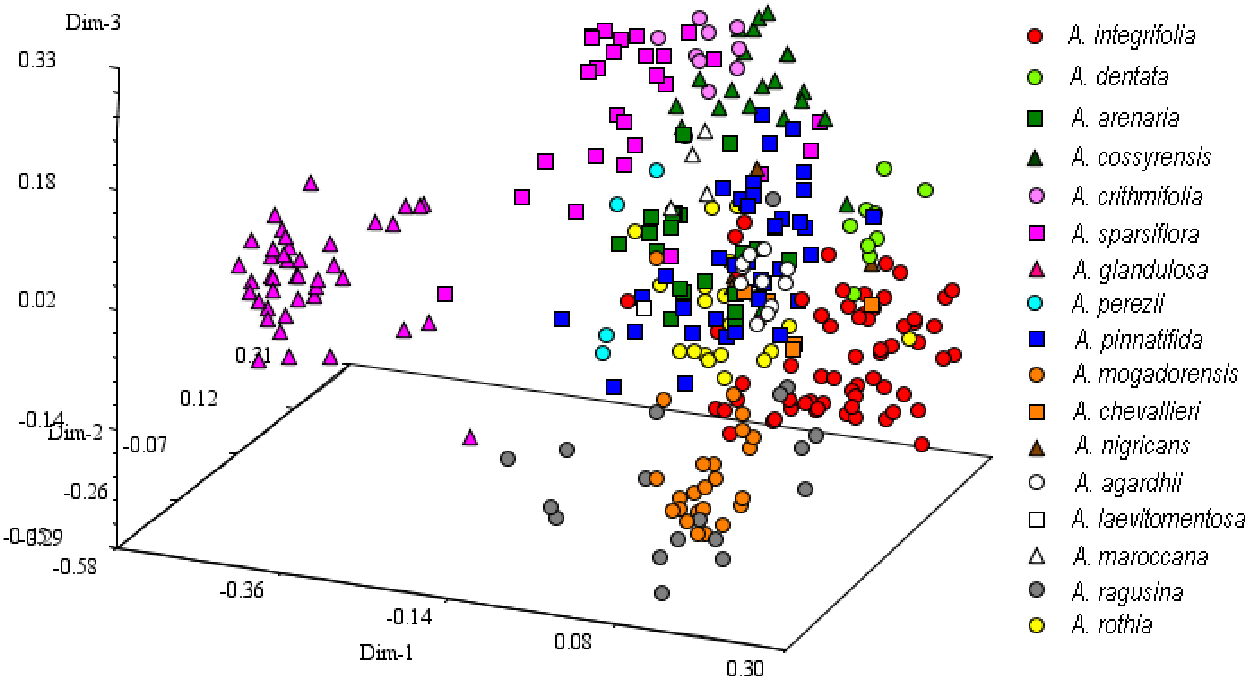


Figure 3.4 Principal coordinates analysis performed on the similarity matrix obtained from the reduced total matrix using Gower's coefficient.

The phenogram constructed by using the **UPGMA** clustering method on the similarity matrix obtained through Gower's coefficient applied on reduced total matrix shows a similar phenetic structure of the data with the same four large groups as observed for the total matrix (Figure 3.5). Furthermore, this phenogram shows a very similar segregation of the OTUs by species. However, it shows that the *A. cossyrensis* OTUs form a fairly good cluster compared with the phenogram obtained from the total matrix. Similarly to this phenogram, *A. integrifolia* does not cluster with either *A. arenaria, A. dentata* or *A. nigricans.* Additionally, *A. pinnatifida* and *A. perezii* do not form a cluster, neither do *A. pinnatifida* and *A. mogadorensis.* Furthermore, *A. glandulosa* and *sparsiflora* do not group together. The cophenetic correlation obtained by comparison of the original similarity matrix to the cophenetic value matrix almost equalled the one obtained for the total matrix (r = 0.75).

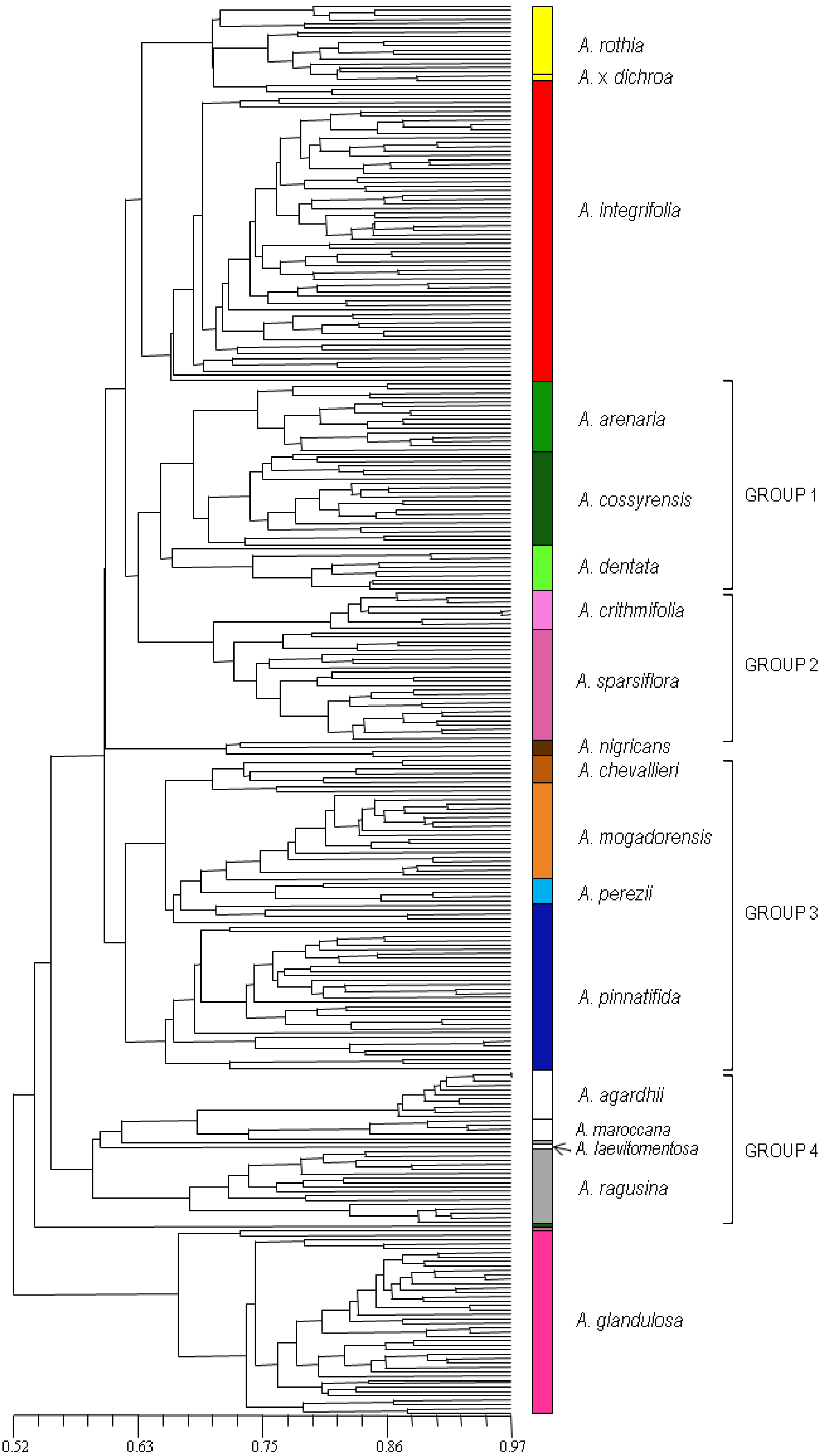


Figure 3.5 Phenogram constructed by performing UPGMA cluster analysis on the similarity matrix obtained from the reduced total matrix (TMR) using Gower's coefficient. Cophenetic correlation 0.75.

3.2.1.3 Results for the complete matrix of the binary characters (CBM)

The complete matrix of binary characters (166 characters by 473 OTUs) included, as mentioned before, the original binary characters and the multistate characters transformed into binary characters. Numerical analysis was performed on this matrix by calculating the triangular similarity matrix using the **SM** and **J** coefficients. The **PCoA** yielded similar results using either of the similarity coefficients. The product-moment correlation obtained by comparison of the correlation matrix to the original similarity matrix showed a low value (r = 0.54 and r = 0.55, respectively for the **SM** and **J** coefficients), reflecting some distortion of the results by the application of **PCoA.** Nevertheless, the 3-dimensional projection of the OTUs using **J** coefficient reveals a segregation of the OTUs by species resembling the one obtained with the total matrix. However, conversely to the latter matrix, the separation of *A. dentata* from *A. arenaria* and *A. cossyrensis* is more evident (Figure 3.6). Furthermore, *A. sparsiflora* tends to group with *A. crithmifolia* and segregate from *A. glandulosa.*

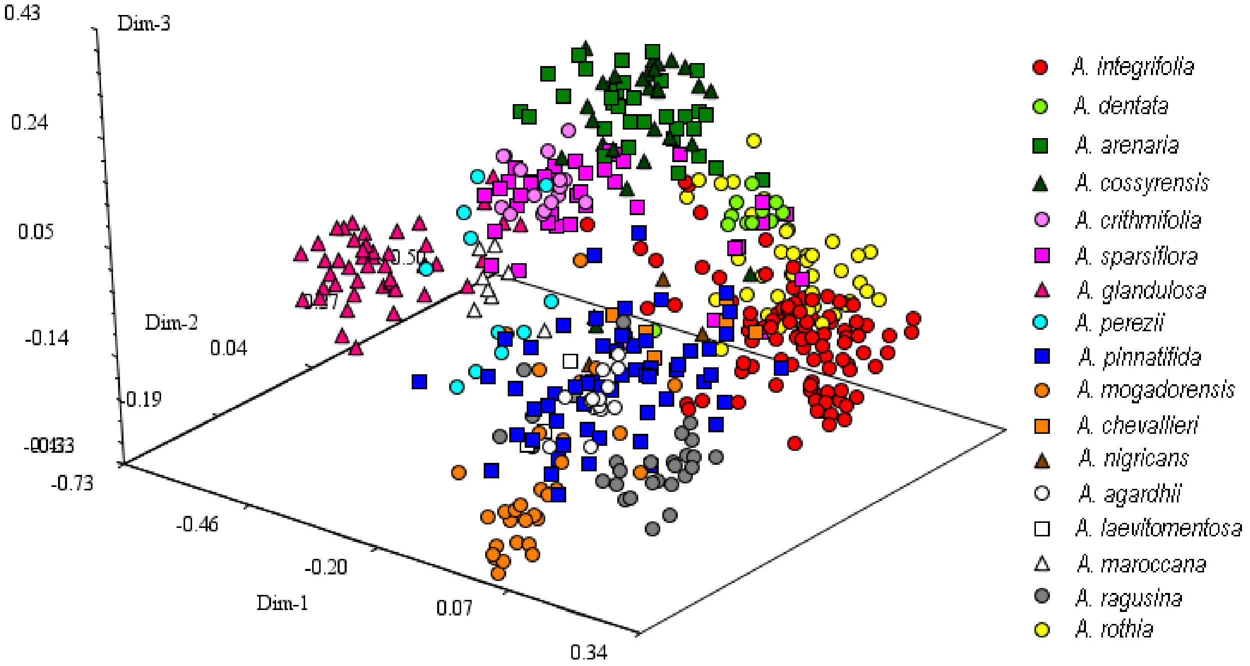


Figure 3.6 Principal coordinates analysis (PCoA) performed on the similarity matrix obtained from the complete matrix of binary characters (CMB) using Jaccard's coefficient.

UPGMA cluster analysis was applied to the similarity matrices (retrieved by using the **SM** and **J** coefficients). The phenogram constructed with **J** coefficient shows a segregation of the OTUs by species and by large groups very similar to the one observed for the results obtained with the total matrix (Figure 3.7). Most OTUs segregate by species quite well except for *A. chevallieri, A. mogadorensis, A. nigricans, A. cossyrensis*, and *A. perezii* which nonetheless show a moderately fair separation. The phenogram constructed with the **SM** coefficient disclosed the same large groups but a less clear segregation of the OTUs by species was observed (results not shown). The cophenetic correlations obtained by comparison of the original similarity matrices, produced by using the **SM** and **J** coefficients on the complete matrix of binary characters, to the cophenetic value matrices were, respectively, r = 0.72 and r = 0.73, revealing some distortion of the phenograms.

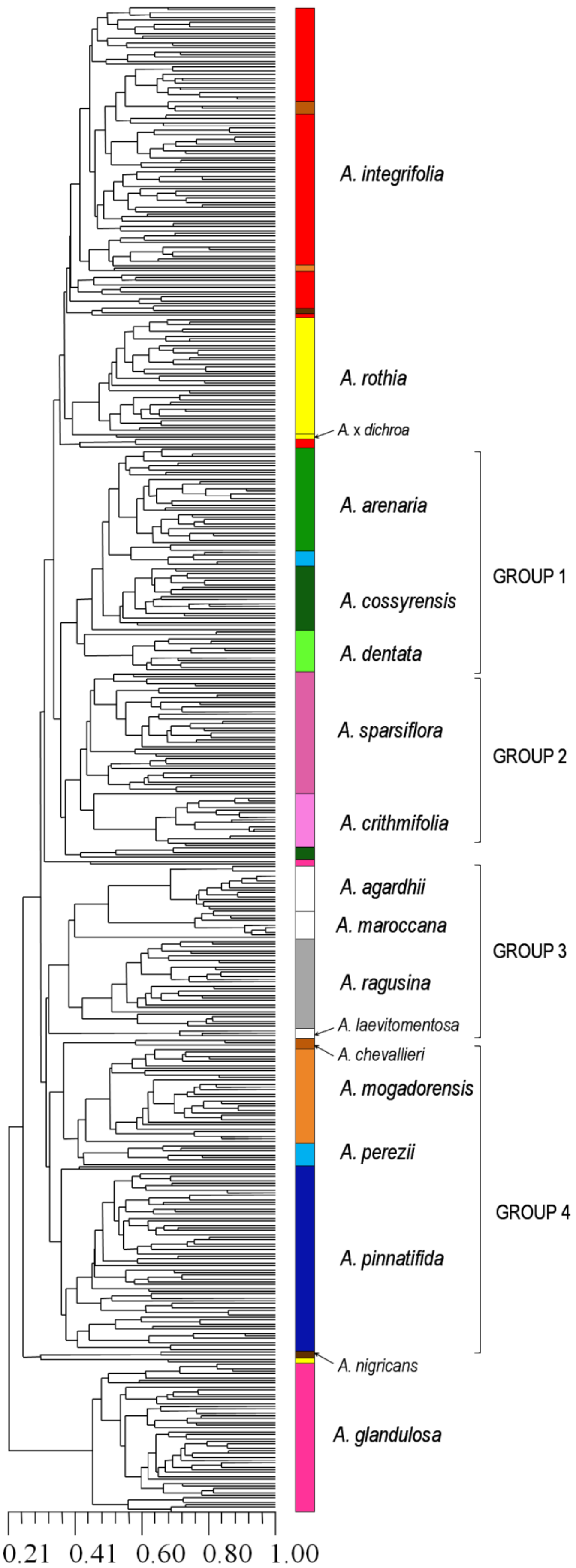


Figure 3.7 Phenogram constructed by performing UPGMA cluster analysis on the similarity matrix obtained from the complete matrix of binary characters using J coefficient. Cophenetic correlation 0.74.

3.2.1.4 Results for the matrix of the multistate characters (MM)

Numerical analysis was performed on the matrix of multistate characters (43 characters by 473 OTUs) by calculating the triangular similarity matrix using the **SM** coefficient. **PCoA** was performed on this matrix yielding a 3-dimensional projection of the OTUs which revealed a segregation of the OTUs by groups resembling very much the one obtained with the complete matrix of binary characters using the **J** coefficient. Similarly the separation of *A. glandulosa* is quite evident. A moderately fair segregation of *A. dentata* and *A. arenaria* from *A. integrifolia* is observed as well (Figure 3.8). Moreover, the *A. perezii* OTUs show some tendency to segregate from those of *A. pinnatifida*. The product-moment correlation obtained by comparison of the correlation matrix to the original similarity matrix (r = 0.55) reflects some degree of distortion of the results by application of **PCoA.**

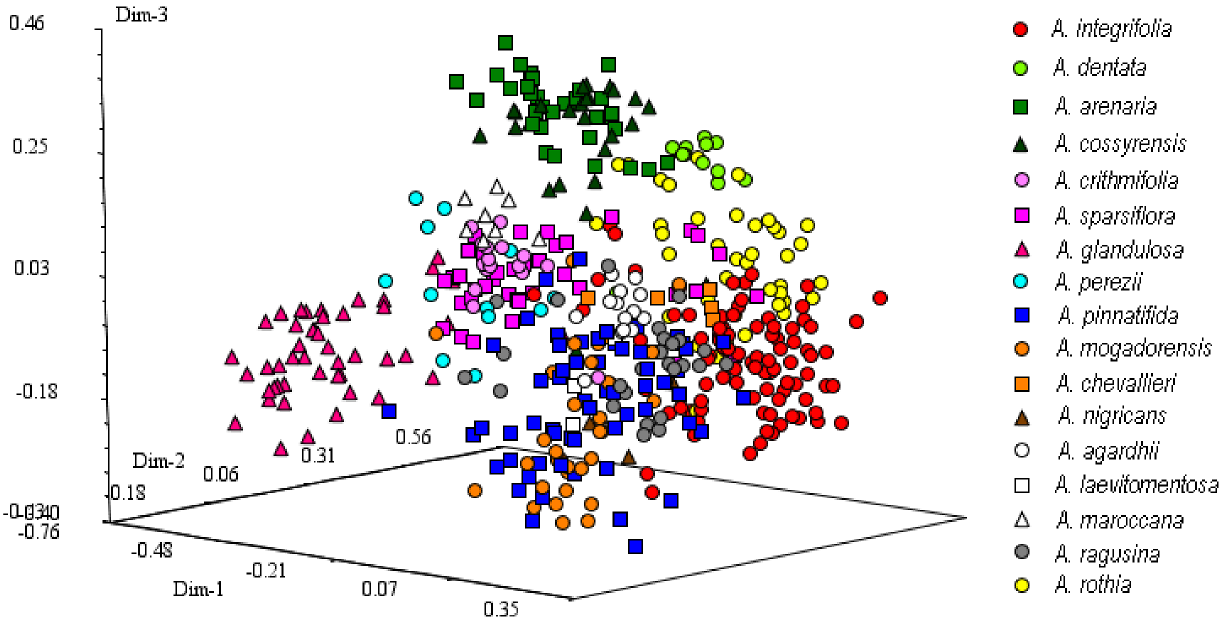


Figure 3.8 Principal coordinates analysis (PCoA) performed on the similarity matrix obtained from the complete matrix of multistate characters using the SM coefficient.

The phenogram constructed by applying the **SM** coefficient on the same similarity matrix obtained from the complete matrix of multistate characters shows a less clear segregation of the OTUs by species, namely *A. arenaria A. cossyrensis* (mostly included in Group 1) as well as *A. pinnatifida* and *A. chevallieri* (mostly included in Group 3) (Figure 3.9). Conversely, species included in Group 2 and Group 4 show a very clear separation. As in the results obtained with the application of the **G** coefficient to the total matrix and the **J** coefficient to the complete matrix of binary characters, *A. laevitomentosa* clusters with *A. agardhii, A. maroccana* and *A. ragusina,* forming all four species a large group (Group 4). Likewise, *A. laevitomentosa* segregates well from the remaining three species of this large group. Regarding *A. nigricans,* the OTUs segregate quite well from all species including *A. integrifolia.* Again, *A. pinnatifida* and *A. mogadorensis* reveal a rather clear segregation as well as *A. perezii*. The cophenetic correlation obtained by comparison of the original similarity matrix of multistate characters, obtained through the **SM** coefficient, to the cophenetic value matrix was r = 0.69, representing some distortion of the results by the application of **UPGMA** clustering method.

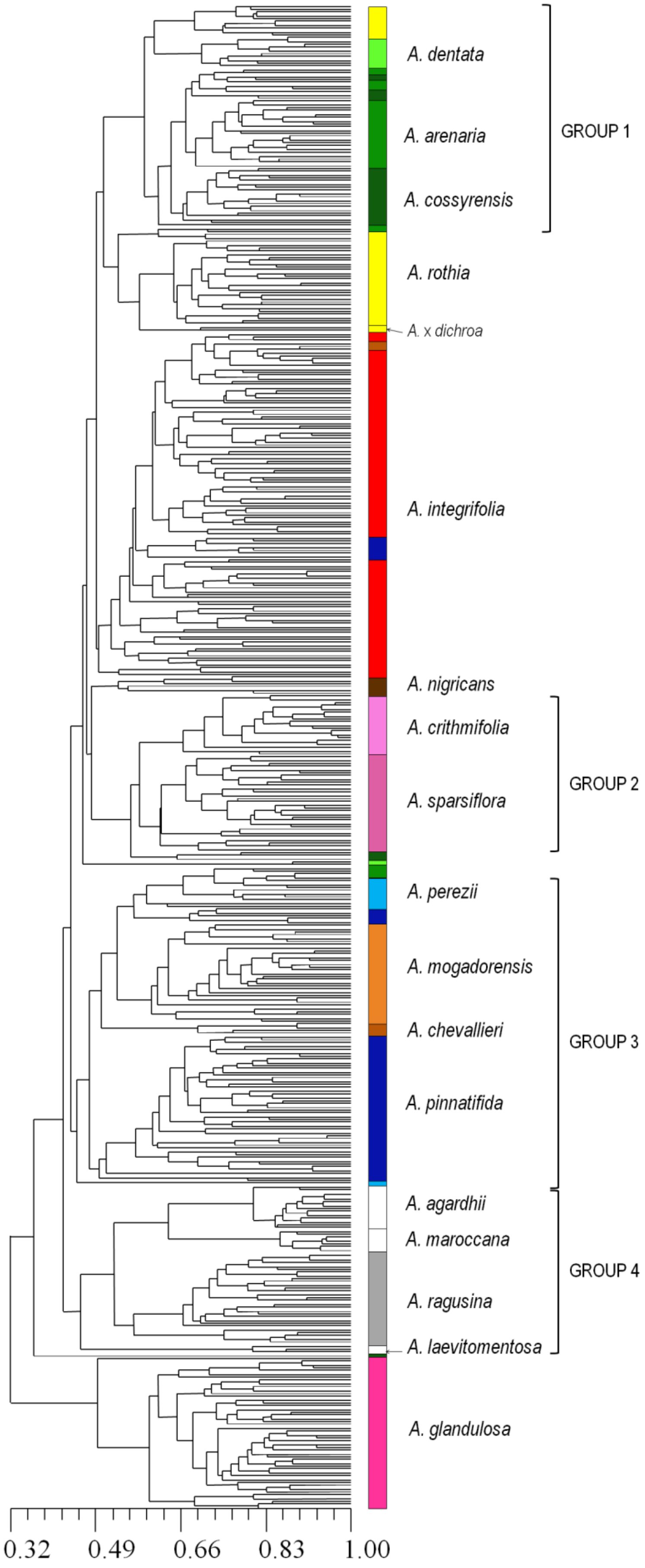


Figure 3.9 Phenogram constructed by performing UPGMA cluster analysis on the similarity matrix obtained from the matrix of multistate characters using the SM coefficient. Cophenetic correlation 0.69.

3.2.1.5 Results for the complete matrix of quantitative characters (CQM)

From the complete matrix of quantitative characters (48 characters and 473 OTUs), after the standardisation of the variables, a similarity matrix was obtained by using the **CORR** coefficient. This matrix of correlations between OTUs was utilized to explore the spatial ordination of these by means of **PCoA** and their possible clustering by means of **UPGMA** analysis. The projection of the 473 OTUs on the first three axes reveals a tendency of segregation of some species, namely, *A. glandulosa* and *A. rothia* (Figure 3.10). Additionally, *A. agardhii, A. maroccana, A. ragusina,* and *A. laevitomentosa* tend to cluster together and segregate from the remaining species which, in turn, show no evident separation. The product-moment correlation calculated by comparison of the correlation matrix to the original similarity matrix (r = 0.66) indicated a very low overlap of these two matrices due to some distortion of the results obtained.

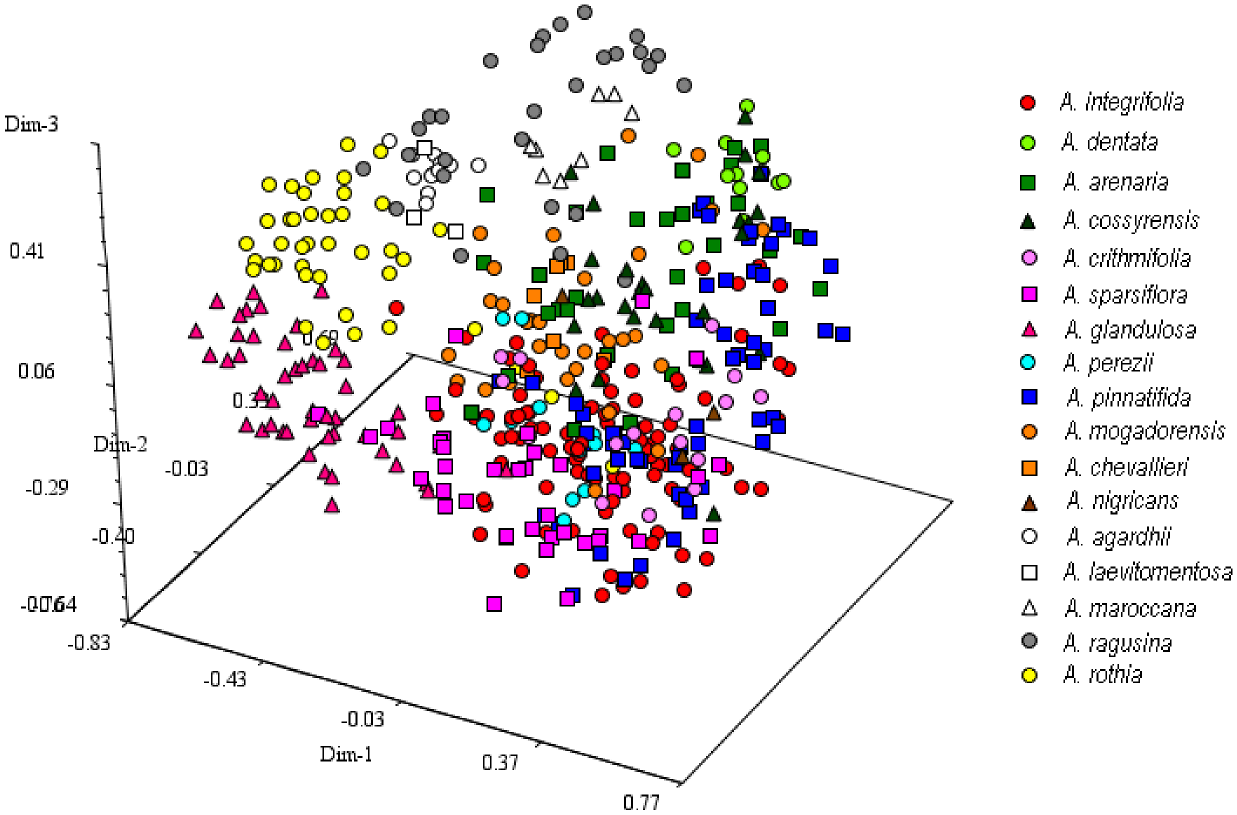


Figure 3.10 Principal coordinates analysis (PCoA) performed on the similarity matrix obtained from the complete matrix of quantitative characters (CMQ) using the correlation coefficient.

The phenogram produced through the application of the **UPGMA** clustering method on the similarity matrix obtained by using the **CORR** coefficient between OTUs on the complete matrix of quantitative characters shows a clear segregation only for some species: *A. dentata, A. perezii*, *A. agardhii, A. laevitomentosa, A. maroccana, A. ragusina, A. glandulosa*, and *A. rothia* (Figure 3.11).

In contrast to the UPGMA analysis applied on the similarity matrices obtained from the total matrix, the complete matrix of binary characters and the matrix of multistate characters, no clear segregation of the four large groups is evident except for the one comprising *A. agardhii, A. laevitomentosa, A. maroccana* and *A. ragusina*, the latter separating from the cluster including the first three species. Nonetheless, in this phenogram another large group, including *A. glandulosa*, *A. rothia,* and *A.* x *dichroa*, is noticeable. As in all the preceding UPGMA analyses, *A.* x *dichroa* Maire clusters with *A. rothia*. The cophenetic correlation coefficient obtained by comparison of the matrix of correlations to the cophenetic matrix showed a low value (r = 0,59) revealing some distortion of the results.

PCoA was also performed on the complete matrix of the quantitative characters obtained by employing other similarity coefficients, namely **DIST** distance, **MANHAT** distance and **EUCLID** distance. A similar OTU segregation produced by using the **CORR** coefficient was observed (results not shown).

UPGMA analysis performed on the same matrix subjected to the similarity coefficients mentioned above yielded phenograms showing a similar segregation by species; however, in general, the segregation of OTUs by large groups is unclear (results not shown).

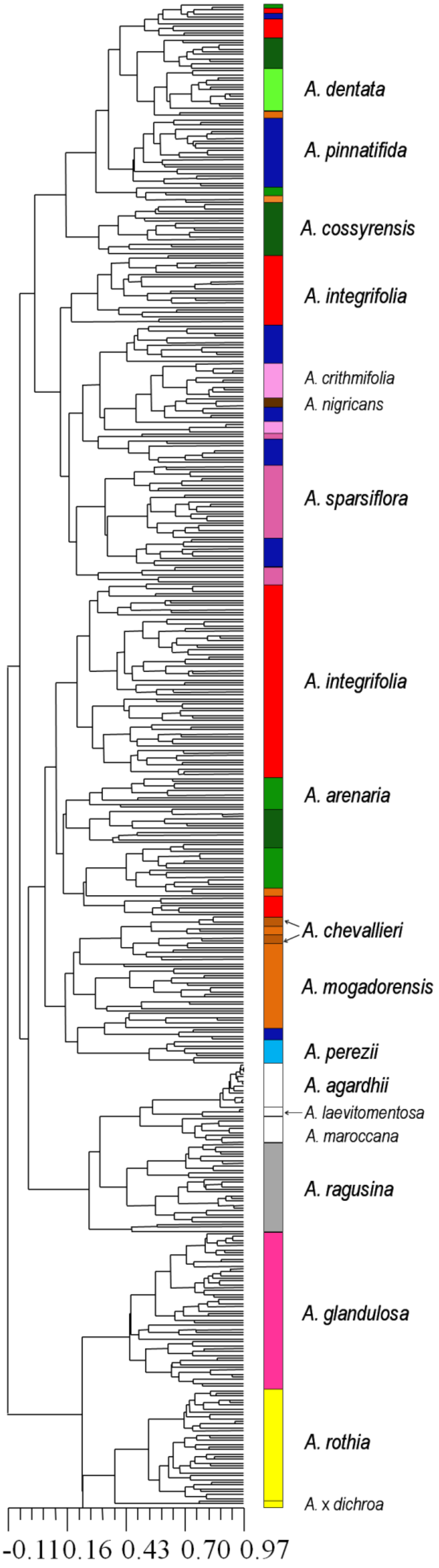


Figure 3.11 Phenogram constructed by performing UPGMA cluster analysis on the similarity matrix obtained from the complete matrix of quantitative characters (CMQ) using the correlation coefficient. Cophenetic correlation 0.59

3.2.1.6 Results for the reduced matrix of quantitative characters (RQM)

From the complete matrix of the quantitative characters a reduced matrix (36 characters by 473 OTUs) was assembled by eliminating characters with more than 10% of the missing values. A similarity matrix was obtained by applying the **CORR** coefficient to the reduced matrix of quantitative characters in order to perform a **PCA**. The first three eigenvectors explained 48% of the total variance (Table 3.3). The 3-dimensional projection obtained shows a tendency of segregation of the OTUs by species only in a few cases, in particular *A. crithmifolia*, *A. glandulosa,* and *A. dentata* (Figure 3.12). The separation of *A. agardhii*, *A. laevitomentosa*, *A. maroccana* and *A. ragusina* is somewhat tenuous. However, they tend to segregate from the rest of the OTUs forming a large group.

Table 3.3 Principal component analysis (PCA) based on the correlation coefficient applied on the reduced matrix of quantitative characters. Eigenvalue, variance and cumulative variance for the first ten eigenvectors.

Eigenvector	Eigenvalue	Variance (%)	Cumulative variance (%)
1	7.82064346	21.7240	21.7240
2	5.69170143	15.8103	37.5343
3	3.82950099	10.6375	48.1718
4	2.53623986	7.0451	55.2169
5	2.41916578	6.7199	61.9368
6	1.44047804	4.0013	65.9381
7	1.21636952	3.3788	69.3169
8	1.11590277	3.0997	72.4167
9	0.98916297	2.7477	75.1643
10	0.90597790	2.5166	77.6810

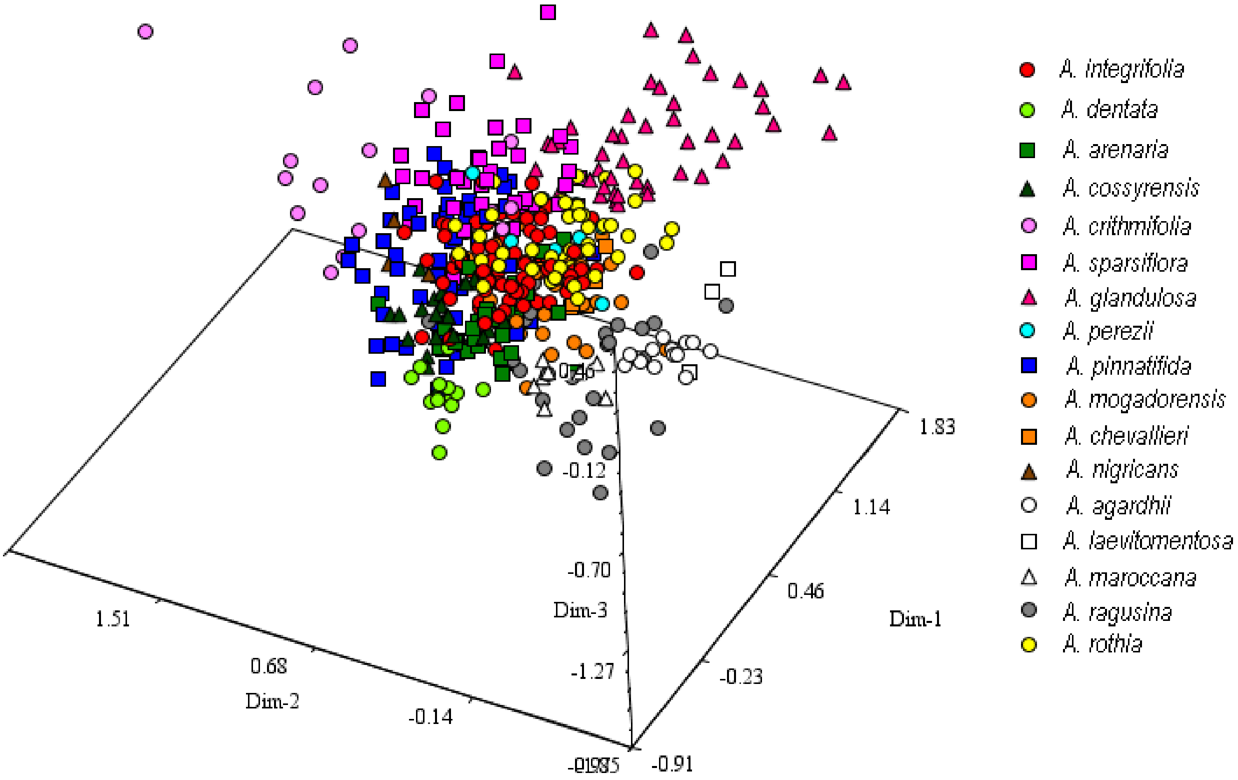


Figure 3.12 Principal component analysis (PCA) performed on the similarity matrix obtained from the reduced matrix of quantitative characters using the correlation coefficient.

3.2.1.7 Results for the matrix of transformed and non transformed quantitative characters (MTnTQ)

The matrix of transformed and non transformed quantitative characters was assembled from the complete matrix of quantitative characters by including ratio characters (Table 3.2). From this matrix a triangular similarity matrix was originated using the **CORR** coefficient and submitted to **PCoA** in order to explore the ordination of the OTUs in a low dimensional space. The product-moment correlation obtained by comparison of the correlation matrix to the original similarity matrix (r = 0.67) showed a low overlap of these matrices due to some distortion of the results through the application of **PCoA**. The projection of the 473 OTUs on the first three axes shows an unclear segregation of the OTUs into large groups and the limits between species are rather blurred (results not shown). On the matrix of transformed and non transformed quantitative characters other similarity coefficients were applied: **DIST**, **MANHAT** and **EUCLID** coefficients. All three similarity matrices obtained were subjected to **PCoA** and the results were very similar. As an example, the 3-dimensional projection constructed by means of the **EUCLID** distance shows the segregation of a large group comprising *A. agardhii, A. laevitomentosa, A. maroccana,* and *A. ragusina* which in turn display a more or less clear segregation (Figure 3.13). Additionally, OTUs corresponding to *A. glandulosa, A. crithmifolia,* and *A. dentata* segregate a little better, compared to the results obtained with the complete matrix of quantitative characters. Despite the fuzzy boundaries, the separation between *A. mogadorensis* and *A. pinnatifida* is more evident as well as between *A. dentata* and *A. integrifolia*.

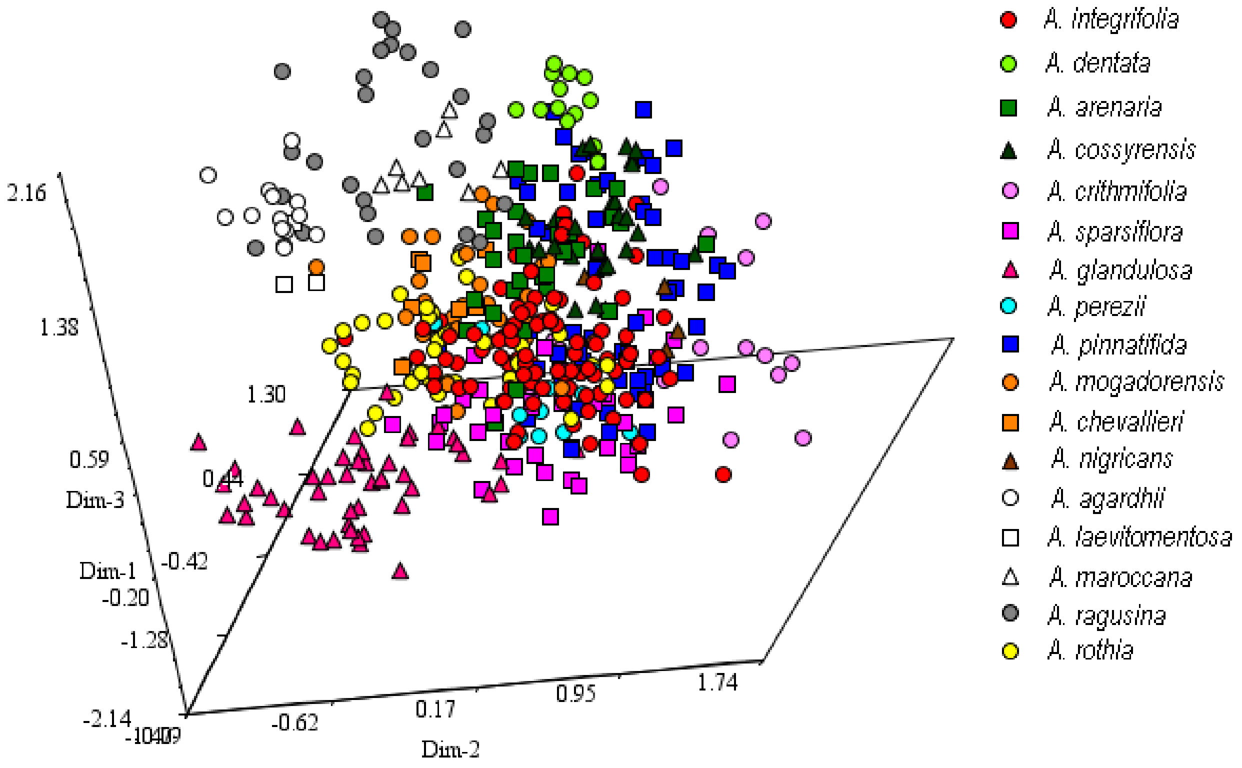
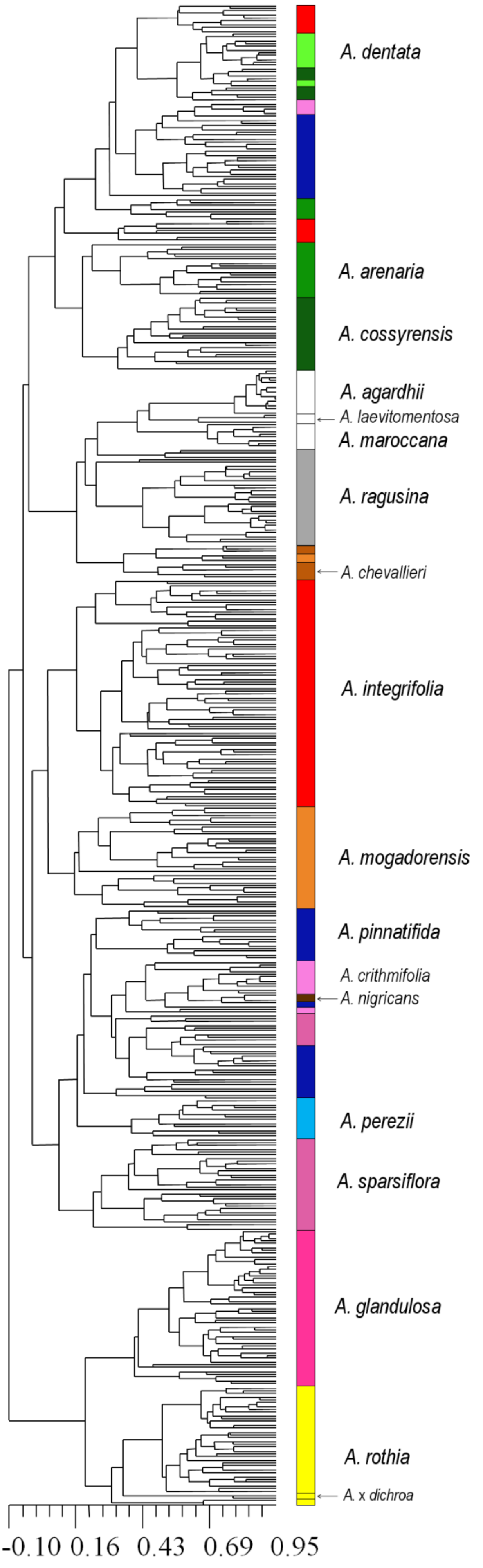


Figure 3.13 Principal coordinates analysis (PCoA) performed on the similarity matrix obtained from the matrix of transformed and non transformed quantitative characters (MTnTQ) using the Euclidean distance.



UPGMA cluster analysis performed on the matrix of transformed and non transformed quantitative characters (MTnTQ) using each of these four measures of similarity yielded phenograms more or less alike. As an example, the phenogram constructed through the **CORR** coefficient is presented (Figure 3.14). No clear segregation of the OTUs by the large groups mentioned before is evident, except for the one including *A. agardhii, A. laevitomentosa, A. maroccana,* and *A. ragusina.* Conversely to all previous UPGMA analysis, *A. chevallieri* also clusters with this group. Regarding *A. dentata, A. arenaria,* and *A. cossyrensis*, these are nested in the same large group which, however, is not well defined as it includes OTUs corresponding to other species. Nevertheless, compared to the phenogram obtained from the complete matrix of quantitative characters, this large group segregates better from the remaining OTUs. Similarly to the complete matrix of quantitative characters, a large group containing *A. glandulosa*, *A. rothia* and *A.* x *dichroa* is distinguishable. The segregation of the OTUs by species is quite clear in some cases (e.g. *A. agardhii, A. laevitomentosa, A. maroccana, A. ragusina, A. mogadorensis, A. perezii, A. glandulosa,* and *A. rothia*). The cophenetic correlation calculated by comparison of the original similarity matrix of transformed and non transformed quantitative characters, obtained through the **CORR** coefficient, to the cophenetic value matrix was r = 0.58, representing some distortion of the results.

Figure 3.14 Phenogram constructed by performing UPGMA cluster analysis performed on similarity matrix obtained from the matrix of transformed and non transformed quantitative characters (MTnTQ) using the Correlation coefficient. Cophenetic correlation 0.58

3.2.1.8 Results for the reduced matrix of transformed and non transformed quantitative characters (RMTnTQ)

Owing to the large number of missing values a reduced matrix of transformed and non transformed quantitative characters was constructed by eliminating characters with missing values higher than 30%. Likewise, from this matrix four triangular similarity matrices were obtained by using different similarity measures (**CORR**, **DIST**, **MANHAT** and **EUCLID** coefficients) and subsequently subjected to PCoA. The projections of the 473 OTUs obtained for all four similarity measures on a low dimensional space are very similar. For the sake of an example, the 3-dimensional projection of the OTUs obtained by using the average **MANHAT** distance also reveals a large group including *A. agardhii, A. laevitomentosa, A. maroccana,* and *A. ragusina* with species boundaries that are more or less defined (Figure 3.15). The limits between the remaining species are clearer compared to the plot obtained for the complete matrix of transformed and non transformed quantitative characters. The OTUs corresponding to *A. mogadorensis, A. sparsiflora*, *A. cossyrensis,* and *A. rothia* also segregate more clearly.

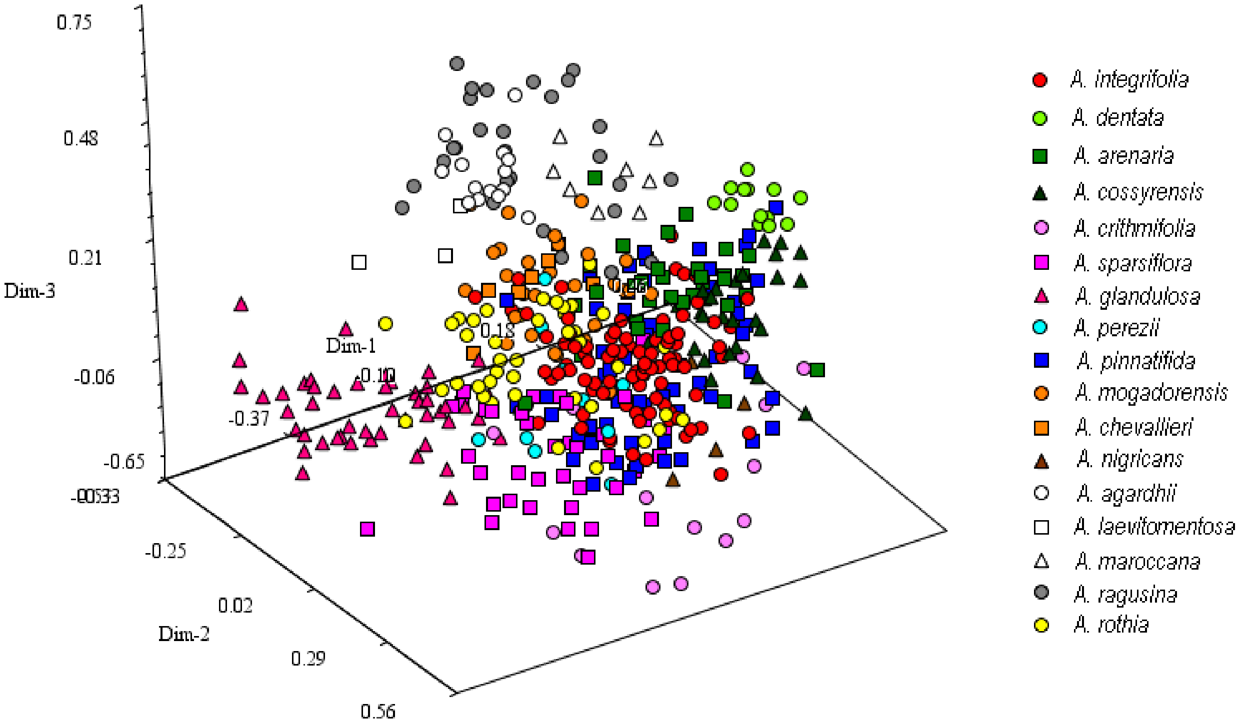


Figure 3.15 Principal coordinates analysis (PCoA) performed on the similarity matrix obtained from the reduced matrix of transformed and non transformed quantitative characters (RMTnTQ) using the average Manhattan distance

UPGMA cluster analysis performed on the reduced matrix of transformed and non transformed quantitative characters (RMTnTQ) using the same measures of similarity gave rise to phenograms resembling more or less each other. Results are very close to the ones obtained from the matrix of transformed and non transformed quantitative characters (MTnTQ). In the phenogram constructed by using the **CORR** coefficient, again no clear segregation by large groups is evident except for the one comprising *A. agardhii, A. laevitomentosa, A. maroccana, A. ragusina* as well as *A. chevallieri* (results not shown). Likewise, the less defined group including *A. dentata, A. arenaria,* and *A. cossyrensis* is observable as well as the large group containing *A. glandulosa*, *A. rothia* and *A.* x *dichroa*. The only significant difference is that *A. perezii* clusters with *A. mogadorensis* while in the phenogram obtained from the matrix of transformed and non transformed quantitative characters (MTnTQ) by using the **CORR** coefficient this species groups with *A. pinnatifida*.

3.2.1.9 Results for partial matrices obtained from the total matrix

From the total matrix (comprising all types of characters) several partial matrices, corresponding to subsets of *Andryala* comprising morphologically close species, were constructed. The subsets were chosen based on previous results, namely the ones obtained for the total matrix and the complete matrix of binary characters. The similarity matrices were obtained from the partial matrices by using **G** coefficient and, subsequently, subjected to **PCoA** and **UPGMA** clustering method.

3.2.1.9.1 Results for the partial matrix relating to the subset "*Arenaria*" (PMARe)

This subset includes species that have been treated by several authors (e.g. Emberger & Maire 1941; Sell 1976) as closely allied *taxa*: *A. arenaria*, *A. cossyrensis* and *A. dentata.* Greuter (2006+) referring to *A. integrifolia*, considered the latter three species as "included *taxa*". Consequently, this analysis will also include *A. integrifolia* in order to establish the taxonomic position of this species relatively to the other three. Phylogenetic studies support the inclusion of *A. atlanticola* in *A. integrifolia* (Ferreira *et al.* 2015a, see Chapter 5). Therefore, OTUs identified as such will be included in the analysis in order to ascertain whether the morphological data are consistent with the molecular data.

The 3-dimensional projection of the OTUs obtained by performing PCoA on the similarity matrix assembled from the partial matrix "*Arenaria*" using **G** coefficient reveals a quite clear segregation of *A. integrifolia* from the large group comprising *A. dentata, A. arenaria*, and *A. cossyrensis* (Figure 3.16). Moreover, *A. dentata* shows a tendency to segregate from both *A. cossyrensis* and *A. arenaria*. As expected, *A. atlanticola* falls into the large group *A. integrifolia.*

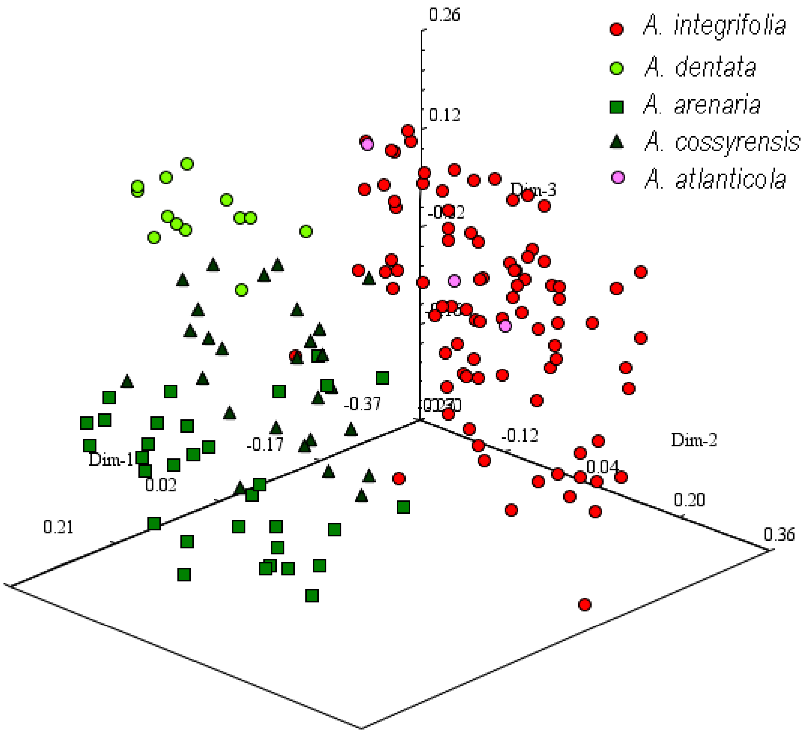


Figure 3.16 Principal coordinates analysis (PCoA) performed on the similarity matrix obtained from the partial matrix "*Arenaria*" using Gower's coefficient.

The phenogram constructed by means of **UPGMA** analysis shows a similar segregation of the OTUs by large groups: the large group *A. integrifolia* (containing *A. atlanticola*) and another comprising *A. arenaria, A. cossyrensis* and *A. dentata* (Figure 3.17). The cophenetic correlation obtained by comparison of the original similarity matrix to the cophenetic value matrix equalled 0.67 meaning that **UPGMA** cluster analysis caused some distortion of the results.

3.2.1.9.2 Results for partial matrix relating to the subset "*Pinnatifida*" (PMPin)

The subset "*Pinnatifida*" corresponds to a large group also obtained in the preceding multivariate analysis. It includes the North African *A. mogadorensis* and *A. chevallieri* as well as the Canarian *A. pinnatifida* and *A. perezii*.

The 3-dimensional projection of the OTUs obtained by performing PCoA on the similarity matrix assembled from the partial matrix "*Pinnatifida*" using G coefficient illustrates an obvious segregation between *A. pinnatifida* and *A. mogadorensis.* Furthermore, *A. perezii* segregates fairly well from *A. pinnatifida*. Similarly, *A. chevallieri* stands out as a well delimited species, and appears closer to *A. mogadorensis* (Figure 3.18).

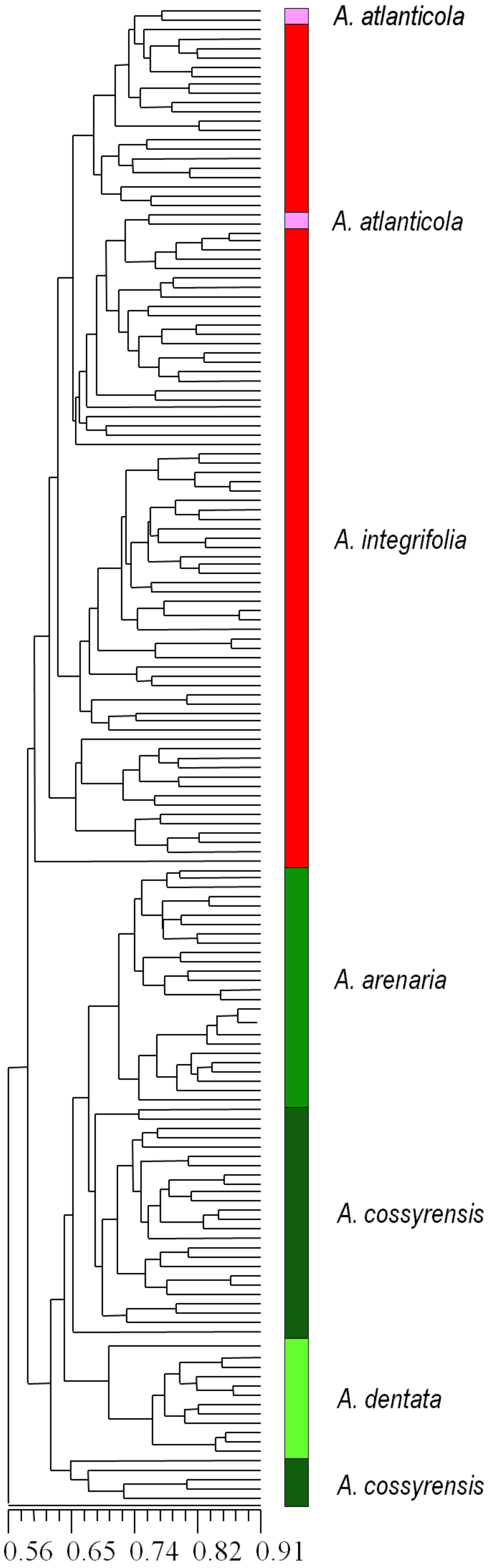


Figure 3.17 Phenogram constructed by performing UPGMA cluster analysis on the similarity matrix obtained from the partial matrix "*Arenaria*" using Gower's coefficient. Cophenetic correlation 0.67.

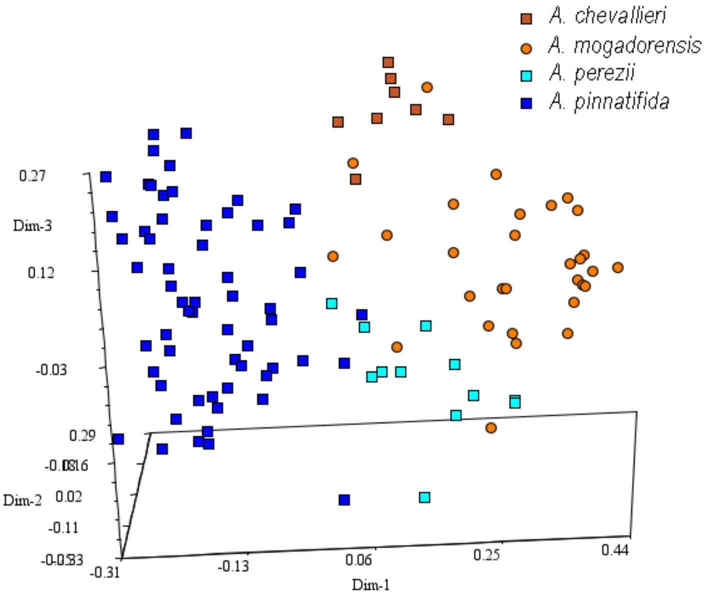


Figure 3.18 Principal coordinates analysis (PCoA) performed on the similarity matrix obtained from the partial matrix "Pinnatifida" using Gower's coefficient.

The phenogram based on the **UPGMA** clustering method shows a more or less similar aggregation of the OTUs. *Andryala chevallieri* clusters with the large group consisting of *A. mogadorensis* and *A. perezii,* whereas the segregation of *A. pinnatifida* from the rest of the OTUs is quite evident (Figure 3.19). The cophenetic correlation obtained by comparison of the original similarity matrix, based on the partial matrix PMPi, to the cophenetic value matrix equalled 0.72 revealing some distortion of the results.

3.2.1.9.3 Results for the partial matrix relating to the subset "*Paua*" (PMPaua)

The subset "Paua" corresponds to a large group which was observed in previous results obtained through the **UPGMA** cluster analysis performed on the similarity matrices based on all types of matrices, including the total matrix, the complete matrix of binary characters, the matrix of multistate characters, the matrix of quantitative characters as well as the matrix of transformed and non transformed quantitative characters. This large group is composed of several species including *A. agardhii, A. laevitomentosa, A. maroccana,* and *A. ragusina.*

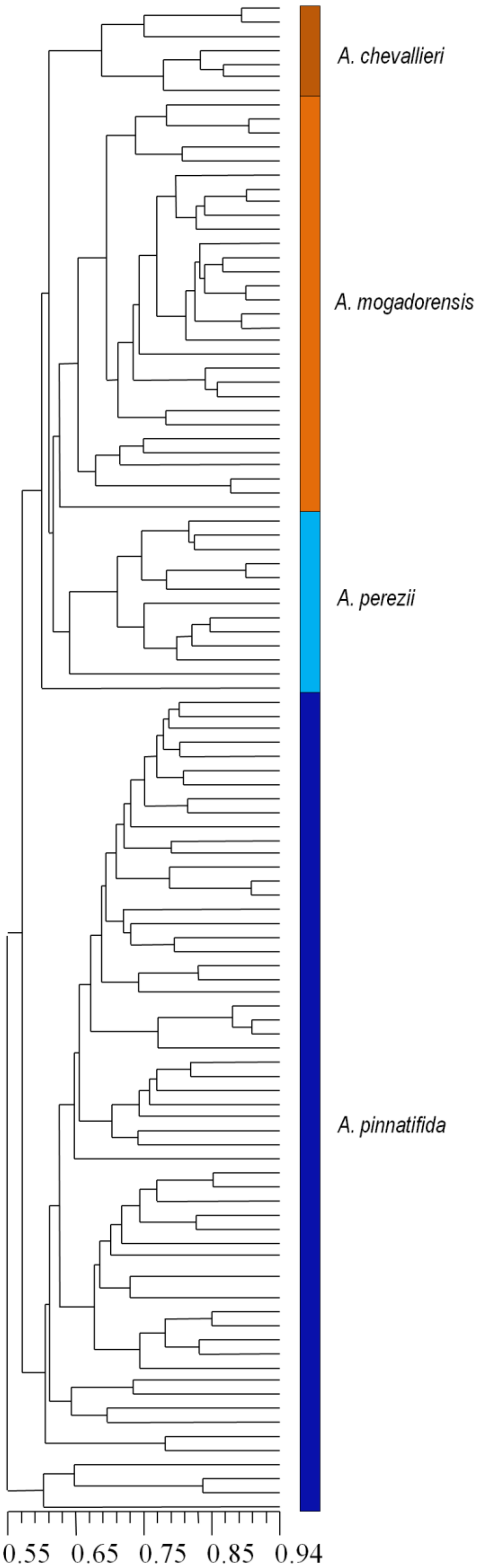


Figure 3.19 Phenogram constructed by performing UPGMA cluster analysis on the similarity matrix obtained from the partial matrix "*Pinnatifida*" using Gower's coefficient. Cophenetic correlation 0.72.

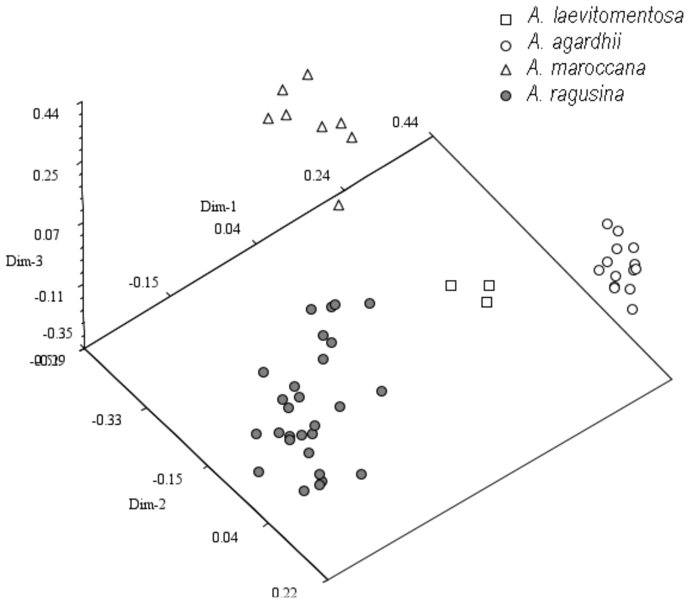


Figure 3.20 Principal coordinates analysis (PCoA) performed on the similarity matrix obtained from the partial matrix "Paua" using Gower's coefficient.

The projection of the OTUs in a 3-dimensional space, obtained through **PCoA** performed on the similarity matrix constructed from the partial matrix "*Paua*" using Gower's coefficient, shows that these segregate clearly well by species (Figure 3.20).

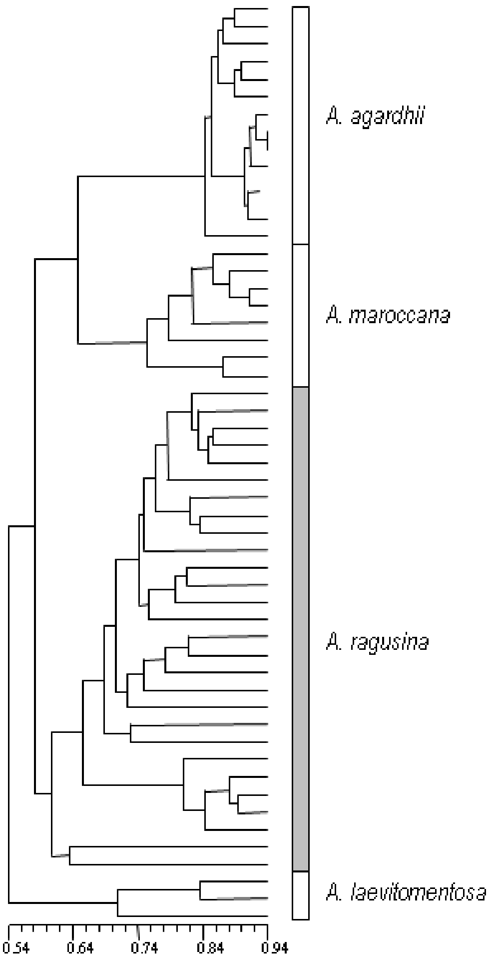


Figure 3.21 Phenogram constructed by performing UPGMA cluster analysis on the similarity matrix obtained from the partial matrix "Paua" using Gower's coefficient. Cophenetic correlation 0.88.

The phenogram based on the **UPGMA** clustering method shows a segregation of the OTUs by large groups: (1) consisting of *A. agardhii* and *A. maroccana* and (2) including *A. ragusina*, while *A. laevitomentosa* segregates quite well from both (Figure 3.21). The cophenetic correlation obtained by comparison of the original similarity matrix, based on the partial matrix PMPaua, to the cophenetic value matrix equalled 0.88, revealing a good overlap of these matrices.

3.2.1.9.4 Results for the partial matrix relating to the subset "*Crithmifolia*" (PMCrith)

The subset "*Crithmifolia*" comprises the Madeiran species *A. crithmifolia* and *A. sparsiflora*. Indeed, these formed a large group in phenograms resulting from previous UPGMA analyses performed on various similarity matrices. As mentioned before, according to the species concept followed herein, *A. sparsiflora* corresponds to the *taxon* which has formerly been recognised as *A. glandulosa* subsp. *cheiranthifolia.* Therefore, the Madeiran *A. glandulosa* (treated until now as *A. glandulosa* subsp. *glandulosa*) will be included in this analysis in order to establish its taxonomic position. The projection of the OTUs in a 3-dimensional space, based on **PCoA** performed on the similarity matrix obtained from the partial matrix "*Crithmifolia*" using Gower's coefficient, shows that these clearly segregate by species corresponding to *A. glandulosa, A. sparsiflora* and *A. crithmifolia* (Figure 3.22). Furthermore, the segregation between *A. glandulosa* and *A. sparsiflora* is quite noticeable.

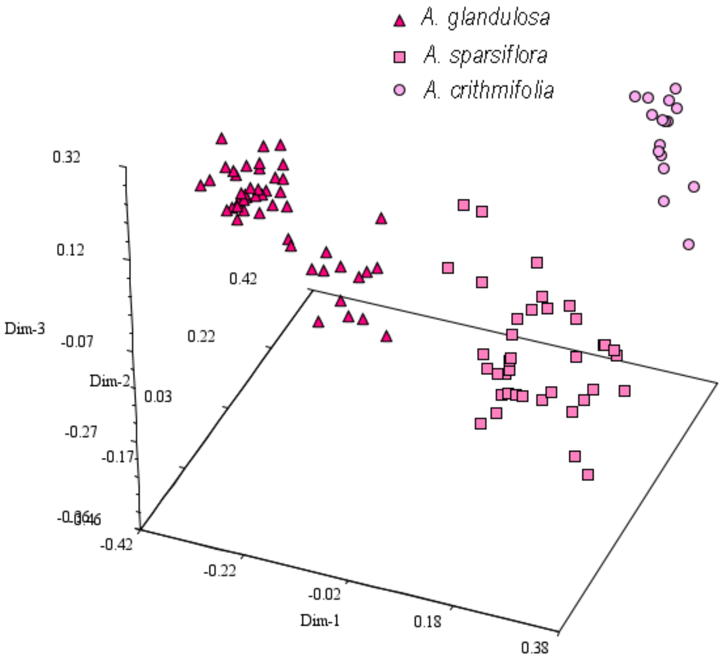


Figure 3.22 Principal coordinates analysis (PCoA) performed on the similarity matrix obtained from the partial matrix "Paua" using Gower's coefficient.

The phenogram constructed with the **UPGMA** clustering method discloses a similar segregation of the OTUs by species (Figure 3.23). Additionally, the cluster composed of *A. sparsiflora* and *A. crithmifolia* is quite evident, segregating very well from *A. glandulosa*. The cophenetic correlation obtained by comparison of the original similarity matrix, based on the partial matrix PMCrith, to the cophenetic value matrix equalled 0.85, revealing a relatively good overlap of these matrices.

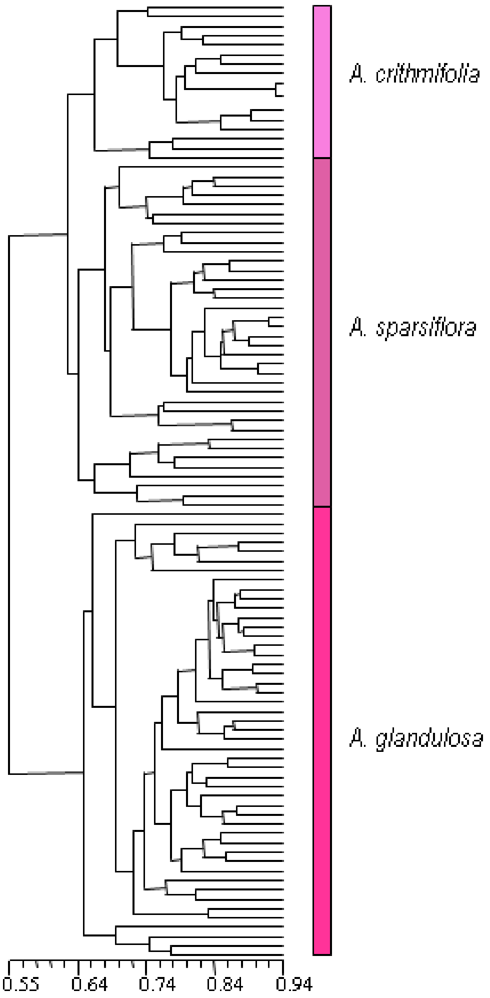


Figure 3.23 Phenogram constructed by performing UPGMA cluster analysis on the similarity matrix obtained from the partial matrix "Paua" using Gower's coefficient. Cophenetic correlation 0.88.

3.2.1.10 Results for species with high intraspecific morphological variation

The genus *Andryala* includes species with great intraspecific morphological variation. For instance, quite a few subspecies were until recently accepted for *A. mogadorensis* (Greuter 2003)[17]. Currently, only two subspecies are recognised: *A. mogadorensis* subsp. *mogadorensis* and *A. mogadorensis* subsp. *jahandiezii* (Maire) M. Z. Ferreira, Álv. Fern. & M. Seq. (Ferreira *et al.* 2014b). Other examples of highly variable species are *A. integrifolia*, *A. pinnatifida* and *A. ragusina*.

Several subsets were assembled from the total matrix or the complete matrix of binary characters in order to ascertain the intraspecific variability within the species mentioned above. The similarity matrices were obtained either from the total matrix using **G** coefficient or the partial matrices based on **SM** and **J** coefficients and subjected to

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[17] Still under *A. pinnatifida*, Greuter recognised four subspecies: *A. pinnatifida* subsp. *mogadorensis* (Hook. f.) Greuter, *A. pinnatifida* subsp. *ducellieri* (Batt.) Greuter, *A. pinnatifida* subsp. *maroccana* (Maire) Greuter, and *A. pinnatifida* subsp. *jahandiezii* (Maire) Greuter.

PCoA as well as to the **UPGMA** clustering method. In some cases the complete matrix of binary characters was chosen over the total matrix seeing it yielded better results.

3.2.1.10.1 Results for *Andryala integrifolia* L.

Numerical analysis was carried out on the similarity matrix obtained from the complete matrix of binary characters, including only OTUs corresponding to putative varieties *A. integrifolia* L.[18] and also *A. atlanticola* H.Lindb., by using **J** coefficient.[19]

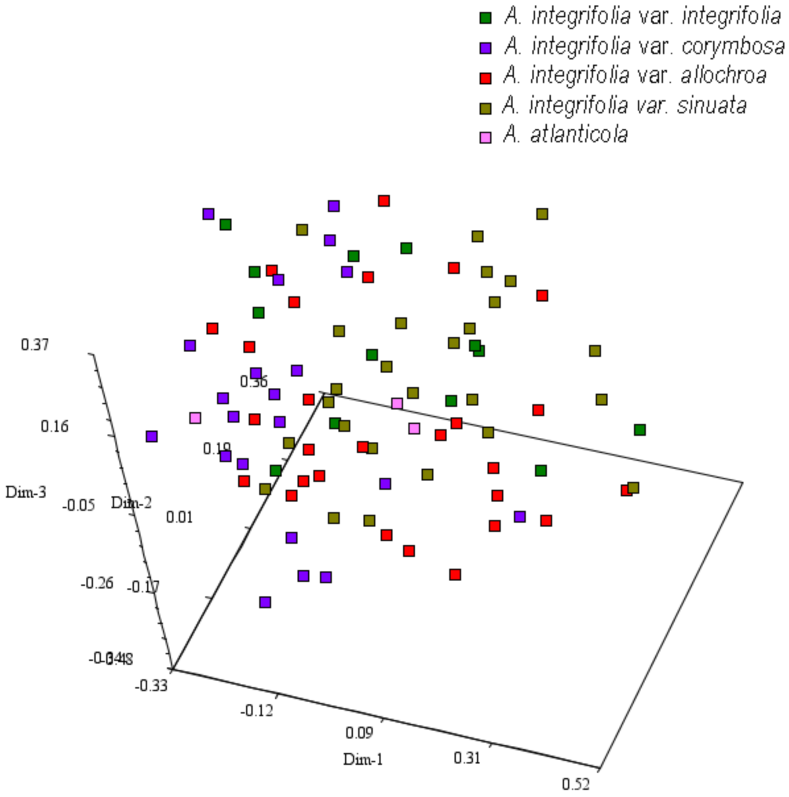

Figure 3.24 Principal coordinates analysis (PCoA) performed on the similarity matrix of binary characters including putative varieties of *A. integrifolia* and *A. atlanticola* OTUs based on J coefficient.

PCoA was performed on this matrix yielding a 3-dimensional projection of the OTUs which reveals no real segregation of *A. integrifolia* var. *integrifolia*, *A. integrifolia* var. *sinuata* (L.) Willk., *A. integrifolia* var. *allochroa* (Hoffmanns. & Link) Cout.*,* and *A. atlanticola*. However, *A. integrifolia* var. *corymbosa* (Lam.) Willk. shows some separation, although the boundaries are not clear (Figure 3.24). Similar results were obtained based on the **SM** coefficient (not shown). The product-moment correlation calculated by comparison of the correlation matrix to the original similarity matrix was quite low (r = 0.49 and r = 0.47, respectively for **J** and the **SM** coefficients), reflecting distortion of the results by the application of PCoA.

UPGMA cluster analysis was applied to the similarity matrices of binary characters including only *A. integrifolia* and *A. atlanticola* OTUs based on **J** and the **SM** coefficients. The phenogram produced with the **SM** coefficient discloses considerable chaining and no segregation of the putative varieties of *A. integrifolia* is evident (results not shown). Results obtained with **J** coefficient are quite similar (not shown). The cophenetic correlations obtained by comparison of the original similarity matrices, based on the **SM** and **J** coefficients, to the cophenetic value matrix were, respectively, r = 0.59 and r = 0.61, values which reveal some distortion of the results.

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[18] Coutinho (1939) recognised *A. integrifolia* var. *corymbosa* (Lam.) Willk., *A. integrifolia* var. *allochroa* (Hoffmanns. & Link) Cout., and *A. integrifolia* var. *sinuata* (L.) Willk. Dobignard (2009) recognised *A. integrifolia* var. *integrifolia* besides two other varieties which correspond to *A. integrifolia* var. *corymbosa* and *A. integrifolia* var. *allochroa*.

3.2.1.10.2 Results for *Andryala mogadorensis* Coss. ex Hook.f.

PCoA was performed on the complete matrix of binary characters including only OTUs corresponding to *A. mogadorensis* by calculating the triangular similarity matrix using the **SM** and **J** coefficients. The 3-dimensional projection obtained with **J** coefficient shows a clear segregation of the OTUs by subspecies: *A. mogadorensis* subsp. *mogadorensis* and *A. mogadorensis* subsp. *jahandiezii* (Figure 3.25). Results based on the **SM** coefficient resemble very much the ones obtained with **J** coefficient (not shown). The product-moment correlation calculated by comparison of the correlation matrix to the original similarity matrix showed a low value (r = 0.72 for **J** coefficient and r = 0.62 for the **SM** coefficient), reflecting some distortion of the results.

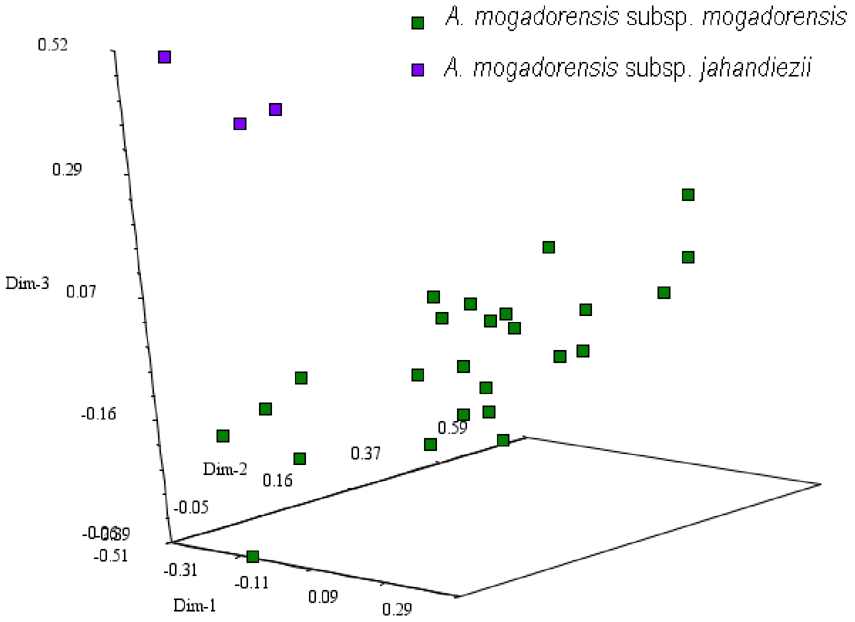

Figure 3.25 Principal coordinates analysis (PCoA) performed on the similarity matrix of binary characters including only *A. mogadorensis* OTUs based on Jaccard's coefficient.

UPGMA cluster analysis performed on the similarity matrix of the complete matrix binary characters including only *A. mogadorensis* OTUs, based on the **SM** and **J** coefficients, yielded similar phenograms that reveal a poor segregation of the OTUs by subspecies (results not shown). The cophenetic correlations obtained by comparison of the original similarity matrices, based on the **SM** and **J** coefficients, to the cophenetic value matrix are both equalled to 0.82, representing a good overlap of the two matrices.

3.2.1.10.3 Results for *Andryala pinnatifida* Aiton

Traditionally several subspecies are accepted for the Canarian *A. pinnatifida*, including *A. pinnatifida* subsp. *pinnatifida*, *A. pinnatifida* subsp. *preauxiana* (Sch. Bip.) G. Kunkel, *A. pinnatifida* subsp. *teydensis* (Sch. Bip.) S. Rivas-Martínez, Wildpret, del Arco, O. Rodr., P. Pérez, Garciá-Gallo, Acebes, T. E. Díaz & Fern. Gonz., *A. pinnatifida* subsp. *latifolia* (Bornm.) G. Kunkel and *A. pinnatifida* subsp. *webbii* (H. Christ) G. Kunkel (Kunkel 1980; Acebes Ginovés *et al.* 2004; Greuter 2006+)[20]. More recently a new subspecies (including *A. pinnatifida* subsp. *latifolia*) was

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[20] A revision of these subspecies is presented in Chapter 4 (pp. 180-205).

recognised: *A. pinnatifida* subsp. *cuneifolia* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq. (Ferreira *et al.* 2014a, see Appendix 2).

PCoA was performed on the complete matrix of binary characters including only OTUs corresponding to *A. pinnatifida* subspecies by calculating the triangular similarity matrix using the **SM** and **J** coefficients. The 3-dimensional projection obtained with the **SM** coefficient shows that there is some tendency of the OTUs to segregate by groups corresponding to the above mentioned subspecies, but the boundaries are quite fuzzy (Figure 3.26).

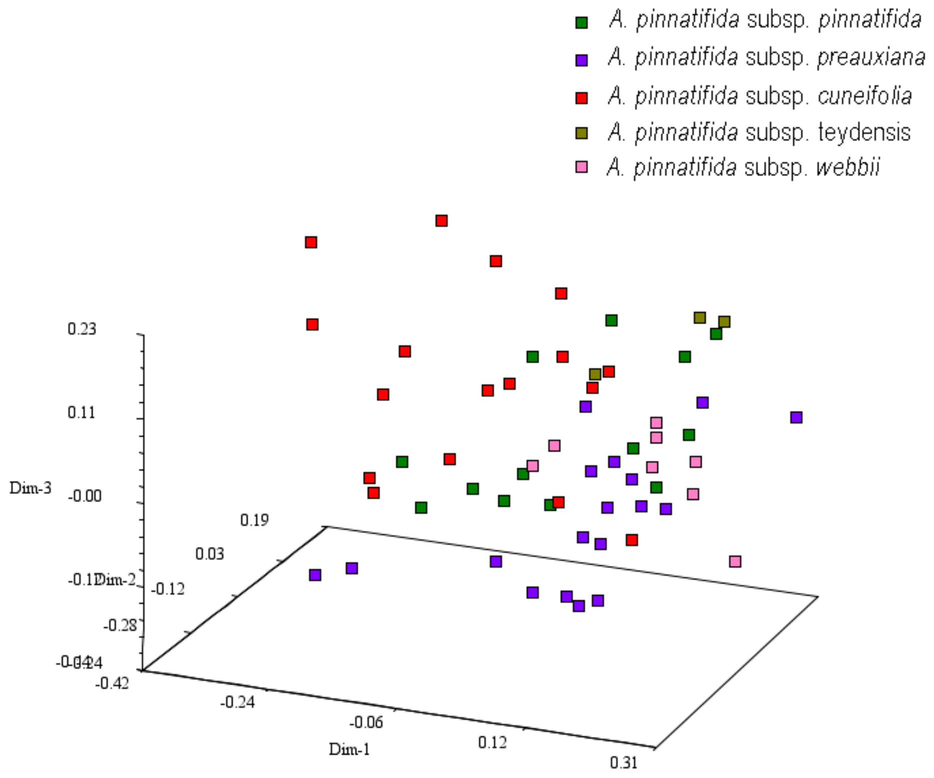

Figure 3.26 Principal coordinates analysis (PCoA) performed on the similarity matrix of binary characters including OTUs corresponding to *A. pinnatifida* subspecies based on the SM coefficient.

Nonetheless, segregation of *A. pinnatifida* subsp. *preauxiana* and *A. pinnatifida* subsp. *cuneifolia* are relatively evident. Results obtained by using the **J** coefficient are very similar (not shown). The product-moment correlation calculated by comparison of the correlation matrix to the original similarity matrix showed a low value (r = 0.48 for both **J** and the **SM** coefficients), reflecting some distortion of the results.

UPGMA cluster analysis performed on the similarity matrices of binary characters including only OTUs corresponding *A. pinnatifida* subspecies based on the **SM** and **J** coefficients yielded similar phenograms showing considerable chaining. Although there is some tendency of the OTUs to aggregate by subspecies, no well defined clusters were observed (results not shown). The cophenetic correlations obtained by comparison of the original similarity matrices, based on the **SM** and **J** coefficients, to the cophenetic value matrix were equal to 0.68 and 0.72, respectively, showing some distortion of the results.

3.2.1.10.4 Results for *Andryala ragusina* L.

This analysis included *A. ragusina* var. *ragusina* and *A. ragusina* var. *ramosissima* Boiss. ex DC., two varieties currently recognised (Sell 1976; Franco 1984; Blanca 2009, 2011). *Andryala ragusina* subsp. *spartioides* Pomel ex

Batt. described much earlier by Battandier (1889) was also included. The hybrid *A.* x *brievaensis* García Adá, whose parental species are *A. ragusina* L. and *A. integrifolia,* is morphologically very close to *A. ragusina*. In order to ascertain the taxonomic position of *A. ragusina taxa* only, it was excluded from the numerical analysis. **PCoA** was performed on the total matrix by calculating the triangular similarity matrix using **G** coefficient. The product-moment correlation calculated by comparison of the correlation matrix to the original similarity matrix showed a low value (r = 0.54). The 3-dimensional projection of the OTUs obtained shows that the *A. ragusina* var. *ramosissima* OTUs do not separate clearly from the rest of the OTUs (Figure 3.27). Regarding *A. ragusina* subsp. *spartioides*, its segregation from the remaining OTUs may only be apparent as only one specimen was included in this study. Similar results were obtained by means of **UPGMA** cluster analysis performed on the total matrix based on **G** coefficient (not shown). The cophenetic correlation obtained by comparison of the original similarity matrix, based on the **G** coefficient, to the cophenetic value matrix was r = 0.79 revealing a low distortion of the results. **PCoA** was also performed on the similarity matrix of binary characters based on the **SM** and **J** coefficients. The product-moment correlation obtained by comparison of the correlation matrix to the original similarity matrix showed a low value (r = 0.63 for both **J** and the **SM** coefficients), reflecting some distortion of the results by the application of **PCoA.** The 3-dimensional projection of the OTUs obtained with **J** coefficient showed the aggregation of the *A. ragusina* var. *ramosissima* OTUs but *A. ragusina* subsp. *spartioides* did not segregate well from the rest of the OTUs (results not shown).

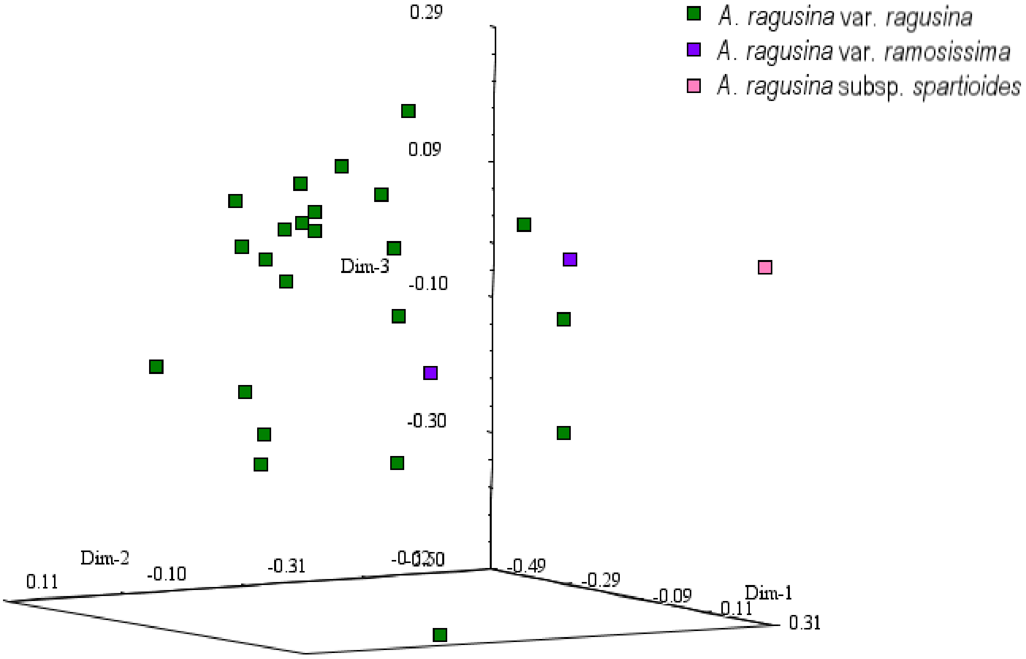

Figure 3.27 Principal coordinates analysis (PCoA) performed on the similarity matrix obtained from the total matrix using Gower's coefficient.

UPGMA cluster analysis was performed on the similarity matrices of binary characters based on the **SM** and **J** coefficients. The phenograms produced revealed the grouping of the *A. ragusina* var. *ramosissima* OTUs, however, the separation of *A. ragusina* subsp. spartioides from the rest of the *A. ragusina* OTUs was not evident (results not shown). The cophenetic correlations obtained by comparison of the original similarity matrices, based on the **SM** and

J coefficients, to the cophenetic value matrix were, respectively, r = 0.77 and r = 0.8, values which reveal a low distortion of the results.

3.3 Discussion

Based on the present morphometric analysis, species delimitation in *Andryala* will be analysed as well as an infra generic division. Infraspecific variability in highly variable species will also be object of discussion.

3.3.1 Species delimitation in *Andryala*

Multivariate methods have been successfully employed to investigate species delimitation (e.g. Hodálová & Marhold 1998; Parnell & Needham 1998; Fernández & Feliner 2001; Pedersen 2010). Hence, a similar approach was applied to *Andryala* which includes morphologically distinguishable species as well as taxa with rather unclear taxonomy. Results obtained with the total matrix, using **G** coefficient resemble very much the ones obtained with the complete matrix of binary characters, using either the **SM** coefficient or **J** coefficient. The application of **G** coefficient allowed the analysis of different types of characters simultaneously. Therefore, it was possible to explore the segregation of OTUs by species using a larger number of characters. **PCoA** performed on both matrices show that the limits between species are blurred to some extent. This result can be explained by the extensive intraspecific polymorphism observed in some *Andryala* L. species (e.g. *A. integrifolia*, *A. mogadorensis*, *A. pinnatifida*) and the close morphological resemblance of others (e.g. *A. arenaria*, *A. cossyrensis*). Nevertheless, **UPGMA** cluster analysis performed on total matrix and on the complete matrix of the binary characters, using the coefficients mentioned above, showed that most species here accepted are well delimited. The reduced total matrix, by application of **G** coefficient, gave similar results compared to the total matrix, but species delimitation was clearer in some cases (e.g., *A. arenaria, A. dentata, A. cossyrensis, A. integrifolia*). These results sustain the recognition of *A. arenaria* and *A. cossyrensis* as distinct species as proposed by Murbeck (1905). They also support the specific distinction of *A. arenaria* and *A. dentata* and, therefore, these should not be included in *A. integrifolia* as proposed by Sell (1976). Furthermore, *A. dentata* should not be treated as a synonym of *A. integrifolia,* as proposed by Mouterde (1983). In fact, these four species can be distinguished by several morphological features, especially the upper leaf shape and base, involucre indumentum, external involucral bracts convolution, receptacule indumentum, external ligule colour and length (see Chapter 5, p. 257). Moreover, although traditionally with a controversial taxonomic delimitation, phylogenetic analysis support the recognition of these species (Fereira *et al* 2015a, see Chapter 5). Results of the reduced total matrix, similarly to the total matrix, showed that *A. nigricans* and *A. integrifolia* did not cluster together. Hence, they do not support the inclusion of *A. nigricans* in *A. integrifolia*, contrary to the taxonomic point of view of some authors (e.g. Barratte 1896; Battandier & Trabut 1905). In reality, these two species differ by the lower leaf margin, upper leaf glandular indumentum, length of the glandular hairs of the peduncle, external bracts convolution, external and involucral bracts width, external involucral bracts apex, and ligule colour.

As mentioned before, the analysis performed on the complete matrix of binary characters (including the multistate characters converted into binary ones) yielded similar results to those obtained with the total matrix, which suggests the great taxonomic value of the qualitative characters. The **UPGMA** cluster analysis performed on the complete matrix of binary characters using **J** coefficient showed a clear segregation of *A. pinnatifida* and a moderately fair separation of *A. chevallieri*, *A. mogadorensis*, and *A. perezii*. These results support the treatment of *A. mogadorensis* and *A. pinnatifida* as distinct species as proposed very recently (Ferreira *et al.* 2014b, see Appendix 3), conversely to the taxonomic placement proposed by Greuter (2003)[21]. In fact, these species differ mainly by the involucre indumentum, leave shape and cypselae apex (Ferreira *et al*. 2014b, see Appendix 3). Additionally, *A. mogadorensis* and *A. chevallieri* can be distinguished by the upper leaf shape, base and apex as well as the peduncle length, external involucral bracts length and apex, cypsela apex morphology. The recently recognised *A. perezii* (Ferreira *et al.* 2014a, see Appendix 2) segregated very well from *A. pinnatifida*. These results support the treatment of *A. perezii* as a distinct species rather than a subspecies of *A. pinnatifida* as suggested in Greuter & Von Raab-Straube (2009). Actually, *A. perezii* and *A. pinnatifida* can be distinguished by the stem height and indumentum, leaf margin and indumentum, peduncle length and indumentum, cypsela length and apex morphology (Ferreira *et al*. 2014a, see Appendix 2). In agreement, phylogenetic analysis support the specifc distinction of *A. perezii*, *A. pinnatifida* and *A. mogadorensis*[22] (Ferreira *et al.* 2015a, see Chapter 5).

The **UPGMA** cluster analysis performed on the matrix of multistate characters using the **SM** coefficient showed a less clear segregation by species such as *A. pinnatifida*, *A. rothia*, and *A. cossyrensis.* Nonetheless, delimitation remains quite clear for *A. agardhii*, *A. ragusina*, *A. maroccana*, *A. laevitomentosa*, *A. crithmifolia*, *A. sparsiflora*, and *A. glandulosa*. *Andryala laevitomentosa* segregates quite well from *A. agardhii, A. maroccana* and *A. ragusina* as in the results obtained for the complete matrix of binary characters and the total matrix. Indeed, it is a very distinct Romanian species and more recent authors even proposed to include it in a separate genus along with *A. agardhii* (Sennikov 1999; Negrean 2004). However, even though very few specimens of *A. laevitomentosa* were included in the morphometric study due to collection limitations, our results support the inclusion of this species in *Andryala*, as suggested by Greuter (2003). In agreement, molecular data sustain the inclusion of both *A. agardhii* and *A. laevitomentosa* in this genus as two independent ancient lineages (Ferreira *et al.* 2015a, see Chapter 5). Indeed, these species can be distinguished by several morphological features including the external involucral bracts indumentum, receptacule indumentum, ligule length, number and length of the ligule apical teeth, cypsela length and width, and cypsela apex aspect. Concerning *A. crithmifolia*, *A. sparsiflora*, and *A. glandulosa*, these are indeed morphologically distinct species. *Andryala glandulosa* and *A. sparsiflora* differ especially by the stem and leaf glandular indumentum, leaf margin, involucre shape at anthesis, number of rows of the involucral bracts external, involucral bracts convolution, and the external involucral bracts stellate indumentum on the inner face. In turn, *A. crithmifolia* can be distinguished by the lower leaf margin, upper leaf shape, length of the glandular hairs of the peduncle, length of the external involucral bracts glandular hairs, and stellate indumentum on the teeth of the ligule. Phylogenetic analysis based on nuclear markers supported the monophyly of these three taxa, although molecular markers did not separate them completely (Ferreira *et al.* 2015a, see Chapter 5)[23].

In respect to the results obtained with the complete matrix of quantitative characters, PCoA revealed a tendency of segregation regarding *A. glandulosa* and *A. rothia,* contrary to the rest which showed a somewhat unclear

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[21] Inclusion of *A. mogadorensis* in *A. pinnatifida.*

[22] Due to difficulties in collecting new material in some countries/regions, *A. chevallieri* was not included in this phylogenetic study.

[23] In the phylogenetic study *A. sparsiflora* was treated by the earlier name *A. glandulosa* subsp. *cheiranthifolia.*

separation. **UPGMA** cluster analysis showed a clear segregation of the same species plus *A. laevitomentosa, A. agardhii, A. maroccana,* and *A. ragusina.* As in all previous **UPGMA** analysis, *A.* x *dichroa* Maire clusters with *A. rothia*. In fact, morphologically this hybrid is much closer to *A. rothia* than to *A. integrifolia* (Maire 1937). The reduced matrix of quantitative characters was submitted to **PCA** and the results showed that the first three eigenvectors only explain 48% of the total variance and, therefore it is not reasonable to use these three components to explain the initial system. However, results are very close to those obtained with the **PCoA** performed on the similarity matrix obtained from the complete matrix of quantitative characters using the correlation coefficient, although some species already show a tendency to segregate (*A. crithmifolia* and *A. dentata*). The results obtained for the quantitative characters allow inferring that these are taxonomically less informative than the qualitative characters which revealed better species delimitation. Actually, some quantitative characters display a wide infraspecific variation devaluing them to some degree in terms of taxonomic delimitation. Quantitative characters involving size and number (e.g. root size, stem height, leaf size, capitula number) show extensive plasticity within some *Andryala* species. For example, species with great or at least some phenotypic plasticity, such as *A. integrifolia*, *A. glandulosa*, *A. mogadorensis*, *A. pinnatifida* and *A. arenaria*, may show large variation in stem height and leaf size and margin. Studies have demonstrated that size characters are more plastic than shape characters, at least for leaf and floral characters (e.g. Andersson 1989). Conversely to size, the variation in shape has been proven useful for *taxa* discrimination (e.g. leaf shape in *Uvaria* L., Meade & Parnell 2003). Moreover, in numerical analysis ratio-transformed data have been successfully used to assess shape (e.g. Huamán & Spooner 2002; Meade & Parnell 2003; Cron *et al.* 2007). Hence, a matrix including all the original quantitative data as well as the ratio-transformed data was constructed. In fact, in general the results of **PCoA** performed on the similarity matrix obtained from the matrix of transformed and non transformed quantitative characters using the Euclidean distance revealed clearer species segregation compared with the results obtained for the complete quantitative matrix. Delimitation of *A. glandulosa* is clearer, while the separation between *A. mogadorensis* and *A. pinnatifida* is more evident as well as between *A. integrifolia* and *A. dentata.* The phenogram constructed from the original quantitative data and the ratio-transformed data using the Correlation coefficient showed better delimitation between *A. cossyrensis* and *A. arenaria* as well between *A. mogadorensis* and *A. pinnatifida.* Conversely, *A. pinnatifida* seems closer to *A. perezii* than to *A. mogadorensis*. Thus as in most organisms, in *Andryala,* species delimitation based on size and number is frequently less effective than the one based on shape.

3.3.2 Morphometric evidence for an infra generic division of *Andryala*

The phenograms obtained with the total matrix using **G** coefficient and the complete matrix of binary characters, using either the **SM** coefficient or **J** coefficient showed four large groups each containing several well delimited species: Group 1 – *A. arenaria*, *A. cossyrensis*, and *A. dentata;* Group 2 – *A. crithmifolia* and *A. sparsiflora*[24]; Group 3 – *A. chevallieri, A. mogadorensis, A. perezii*, and *A. pinnatifida*; and Group 4 – *A. agardhii, A. laevitomentosa, A.*

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[24] This group comprises Madeiran endemics except for *A. glandulosa* which is a quite distinct species in *Andryala* separating well from the remaining taxa.

maroccana, and *A. ragusina.* Subsets of the total matrix were constructed based on these four groups and treated separately in order to assess an infra generic division of *Andryala* based on morphological data.

For the subset "*Arenaria*", both **PCoA** and **UPGMA** analysis showed two large groups: one including *A. integrifolia* and *A. atlanticola* and another composed of *A. arenaria*, *A. cossyrensis* and *A. dentata*. Similarly to molecular data, these results advocate the inclusion of *A. atlanticola* in *A. integrifolia.* Although phylogenetic analysis support the recognition of *A. integrifolia*, *A. dentata, A. arenaria,* and *A. cossyrensis* as distinct species (Ferreira *et al* 2015a, see Chapter 5), these did not form a group which could be explained by the extremely low level of genetic divergence observed among most of the *Andryala* species, suggesting their relatively recent and rapid speciation. Nonetheless, based on morphometric data, it seems plausible to consider these three species as members of a section within *Andryala*, while *A. integrifolia*, together with *A. atlanticola*, should be included in an independent section (see Chapter 4, p. 80).

Regarding subset "*Pinnatifida*", **PCoA** and **UPGMA** cluster analysis showed a clear segregation of the North African species *A. chevallieri* and *A. mogadorensis* as well as the Canarian *A. pinnatifida* and *A. perezii*. Furthermore, *A. pinnatifida* formed a cluster segregating quite well from another including *A. chevallieri*, *A. mogadorensis* and *A. perezii*, with the latter two grouping together. Phylogenetic analysis based on the *sqs* nuclear marker revealed a sister relationship and monophyly for *A. perezii* and *A. pinnatifida.* Moreover, analysis based on rDNA markers (ITS+ETS) showed a well-supported group comprising *A. perezii* and *A. mogadorensis* subsp. *jahandiezii,* besides *A. cossyrensis* (Ferreira *et al.* 2015a, see Chapter 5). However, the inclusion of *A. chevallieri* in future phylogenetic analysis as well as the use of additional DNA markers could help clarifying interspecific relationships among the major radiation group (containing all *Andryala* species except the oldest two lineages). Based mainly on the morphometric study and to some extent on the molecular data, it seems reasonable to consider a section comprising *A. pinnatifida*, *A. perezii, A. mogadorensis,* and *A. chevallieri* (see Chapter 4, p. 81).

Subset "*Paua*" corresponds to a quite distinct large group observed in all **PCoA** and **UPGMA** analysis performed. It includes four very distinct species: *A. agardhii, A. laevitomentosa, A. maroccana* and *A. ragusina.* According to molecular data, the most divergent species in *Andryala* are *A. laevitomentosa*, *A. agardhii* and *A. maroccana*. Actually, *A. agardhii and A. laevitomentosa* are the two oldest lineages in the genus (relict species), while both *A. maroccana* and *Andryala ragusina* are part of a third lineage comprising all other *Andryala* species, most of them rather recent. Within this group *A. maroccana* seems to represent a relatively old lineage and can probably be considered as a potential relict (Ferreira *et al*. 2015a, see Chapter 5). Phylogenetic analysis based on nuclear ribosomal markers (ITS + ETS) also showed *A. ragusina* (along with *A. maroccana*) occurring in an early branching position within this lineage. Taking into account both morphometric and molecular data, it seems warrantable to include all four species in a larger division within *Andryala*, possibly a sub genus. To a certain extent, this taxonomic point of view is in conformity with the proposal of Sennen (1936) of including *A. maroccana* in a sub genus: *Paua* (Caball.) Sennen. As in previous multivariate analysis, the results obtained for the subset "*Paua*" support the inclusion of *A. laevitomentosa* and *A. agardhii* in a subgenus rather than a separate genus as proposed by some authors (Sennikov 1999; Negrean 2004). Interestingly, in this subset *A. agardhii* and *A. maroccana* formed a cluster that segregated from *A. ragusina*. Based on these results as well as on molecular data (Ferreira *et al*. 2015a, see Chapter 5) it is possible to consider two sections within this subgenus (see Chapter 4, p. 80).

The subset "*Crithmifolia*" included the Madeiran species *A. glandulosa*, *A. crithmifolia*, and *A. sparsiflora*. The segregation *A. glandulosa* from the latter two species as well as clustering of *A. crithmifolia* and *A. sparsiflora* in a large group is quite evident from previous analysis. Thus, this subset was assembled to enforce the taxonomic position of these three species. As before, both **PCoA** and **UPGMA** cluster analysis showed a quite evident segregation of the cluster formed by *A. sparsiflora* and *A. crithmifolia* from *A. glandulosa.* These results strongly support the recognition of *A. sparsiflora* and *A. glandulosa* as independent species. Furthermore, PCoA performed on the similarity matrices obtained from the complete matrix of quantitative characters using the correlation coefficient and from the matrix of transformed and non transformed quantitative characters using the Euclidean distance showed the aggregation of *A. glandulosa* and *A. rothia* in a large group. However, phylogenetic analysis based on nuclear data showed a well-supported group comprising *A. crithmifolia*, *A. glandulosa* and *A. sparsiflora* Thus, the inclusion of *A. crithmifolia*, *A. glandulosa* and *A. sparsiflora* in an independent section may be warrantable (see Chapter 4, p. 81).

3.3.3 Intraspecific morphological variability in *Andryala* and infraspecific division

In *A. integrifolia* intraspecific variation is quite high, mainly concerning leave size, shape and margin. Nonetheless, the results obtained with **PCoA** and **UPGMA** cluster analysis showed that the putative varieties included in this study (*A. integrifolia* var. *integrifolia*, *A. integrifolia* var. *sinuata* and *A. integrifolia* var. *allochroa*) do not form distinct clusters, except for *A. integrifolia* var. *corymbosa* which showed some separation although without clear boundaries. Therefore, only the latter may be worthy of a varietal distinction, following the taxonomic concept of several authors (e.g. Willkomm & Lange 1865; Jahandiez & Maire 1934; Coutinho 1939; Sampaio 1949) or even a subspecific distinction. Curiously, some authors even recognised this *taxon* at a species level, distinguishing *A. corymbosa* Lam. from *A. integrifolia* (e.g. Franco 1984). Likewise, since *A. atlanticola* did not form a cluster, it may not be worthy of a varietal distinction. However, it is important to note that these results are based on very few specimens and that a more extensive sampling could yield a different outcome.

Concerning *A. mogadorensis*, **PCoA** performed on the similarity matrix of the complete matrix binary characters including only *A. mogadorensis* OTUs, based on the **SM** and **J** coefficients, showed a clear segregation of *A. mogadorensis* subsp. *mogadorensis* and *A. mogadorensis* subsp. *jahandiezii.* These results are in agreement with the taxonomic concept recently proposed by Ferreira *et al*. (2014c). However, **UPGMA** cluster analysis yielded revealed a poor segregation of these subspecies. Due to collection limitations few specimens of *A. mogadorensis* subsp. *jahandiezii* were included in this study and, undoubtedly, a more extensive sampling could yield clearer results.

Regarding the extremely polymorphic *A. pinnatifida* from the Canary Islands, both **PCoA** and **UPGMA** analysis performed on the similarity matrix of binary characters including OTUs corresponding to *A. pinnatifida* subspecies, based on the **SM** and **J** coefficients, showed some tendency of the OTUs to segregate by subspecies. Although boundaries between subspecies were very fuzzy, the segregation of *A. pinnatifida* subsp. *preauxiana* and *A. pinnatifida* subsp. *cuneifolia* was relatively more evident. The same analysis was performed on the similarity matrix obtained from the total matrix using **G** coefficient but did not yield better results, meaning that the qualitative characters are more important for subspecies delimitation in *A. pinnatifida* than quantitative characters. Despite the results obtained, *A. pinnatifida* subsp. *webbii* and *A. pinnatifida* subsp. *teydensis* are morphologically distinct *taxa*. The inclusion of a larger set of specimens probably would have yielded better results, especially regarding *A. pinnatifida* subsp. *teydensis*. As for *A. pinnatifida* subsp. *webbii,* according to the results this *taxon* is not worthy of a specific distinction as suggested by some authors (Ceballos Fernández De Córdoba & Ortuño Medina 1976; Santos 1983). Overall results may be related to the fact that there are many intermediate forms between this subspecies[25]. Indeed, Schultz Bipontinus (1849) who performed a comprehensive study of the Canarian *A. pinnatifida* described more than ten distinct forms. A broader set of samples, excluding all intermediate forms, should be included in future morphometric and molecular studies in order to better clarify subspecies delimitation within *A. pinnatifida.* A deeper knowledge of the ecological plasticity could further enlighten taxonomic delimitation. In Chapter 4 a new infraspecific treatment of *A. pinnatifida* (including new combinations and new ranks) is proposed, based not only on this morphometric study but also on additional morphological observations and geographic distribution.

Similarly, *A. ragusina* exhibits a great deal of intraspecific variability and several *taxa* have been described and accepted by different authors over the years (e.g. De Candolle 1838; Boissier 1841; Willkomm & Lange 1865; Amo y Mora 1872; Nyman 1879). As mentioned before, only *A. ragusina* var. *ragusina* and *A. ragusina* var. *ramosissima* (here treated as *A. ragusina* subsp. *ragusina* and *A. ragusina* subsp. *ramosissima*, see Chapter 4, p. 208) are presently recognised. As for *A. ragusina* subsp. *spartioides*, this *taxon* was transferred to a species rank by Barratte (1893) who emphasised its striking resemblance to *A. ramosissima* Boiss., that is, *A. ragusina* var. *ramosissima.* While **PCoA** performed on the similarity matrix obtained from the total matrix using **G** coefficient, showed an evident segregation of *A. ragusina* subsp. *spartioides*, in the **UPGMA** analysis this *taxon* did not segregate from the remaining specimens. Thus, it does not seem worthy of a specific distinction as suggested by Barratte (op. cit.). In the UPGMA analysis *A. ragusina* var. *ramosissima* OTUs grouped together, results that support the recognition of this *taxon*. Although results support the recognition of both *A. ragusina* var. *ramosissima* and *A. ragusina* subsp. *spartioides*, more extensive sampling in the future could help better clarify intraspecific variation in *A. ragusina*.

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[25] The subspecies of *Andryala pinnatifida*, except for *Andryala pinnatifida* subsp. *teydensis,* were not distinguished in the phylogenetic study due to difficulties in their delimitation. Some specimens turned out to be intermediate forms between the traditionally recognised subspecies.

4 Taxonomy

Based on a bibliographic revision, field observations and an extensive study of herbarium material as well as on the results of the multivariate analyses and in part on the phylogenetic analyses, 17 *Andryala* species are recognised, including 14 subspecies and 3 hybrids. An infra generic structure for *Andryala* L. is proposed comprehending two sub-genera and new sections.

4.1 Material and methods

The taxonomic information assembled for each *Andryala* L. species here accepted is arranged alphabetically. Each *taxon* is headed by the **accepted name** in agreement with the rules of The International Code of Nomenclature for algae, fungi, and plants (Mcneill *et al.* 2012) followed by the abbreviation of the author's name (according to Brummitt & Powell 1992) and the publication abbreviation according to BPH/S guidelines (Bridson & Smith 1991)[26]. For each accepted name a **list of synonyms** is presented with the author and publication abbreviations in accordance to the above. First the homotypic synonyms ("≡") are indicated, then the heterotypic synonyms ("=") and finally the invalid or misplaced names ("_"), all in chronological order.

Next comments on **typification** are provided (mainly concerning new typifications) followed by a **detailed description** of the *taxon* in question based on the studied material. The continuous quantitative characters, indicated in the description, correspond to minimum and maximum values (rare or unique measures among the observations conducted are given between brackets). The descriptions are complemented by SEM images and illustrations of the complete specimen (when possible) and the characters considered the most important.

After the detailed description of each *taxa*, **comments on taxonomy and nomenclature** are presented, including explanations concerning the synonymisation of heterotypic names and important aspects related to morphological and taxonomic variability.

Comments on taxonomy and nomenclature are followed by **karyology** with the indication of the number of chromosomes according to the consulted literature.

Afterward information on **ecology** (including vegetation associations) is provided accompanied by the **conservation status**, either indicated in the bibliography consulted or constituting new evaluations based on the IUCN Red List Categories and Criteria Version 3.1 (IUCN 2001; 2012).

Subsequently the **geographic distribution** is presented. In order to illustrate the distribution area for each *taxon* a map was elaborated representing the collection localities of the studied material (and in some cases the localities mentioned in the literature). The coordinates for each *taxon*, included in a database of specimens (FileMaker 5.0) were exported to a software application DIVA-GIS version 7.5.0.0., which allowed the construction of the maps. Coordinates were obtained by using the NGA GEOnet Names Server (GNS)[27] and the GeoNames geographical database[28]

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[26] Plant names, authors and publications as well as publication abbreviations may be consulted in The International Plant Names Index (IPNI) database in http://www.ipni.org/index.html

[27] http://geonames.nga.mil/gns/html/

[28] http://www.geonames.org/

Finally, the **list of studied material** is presented for each taxon, arranged alphabetically by countries or regions and in some cases by provinces, followed by collection locality, collection date, collector, collector number, herbarium and herbarium number. Specimens which were not assignable to any locality due to the lack of information or unintelligible characters on the herbarium labels were indicated, respectively, by ["Unkown locality"] and ["Loc incert.].

4.2 Systematics

Andryala L. was validly published by Linnaeus (1754: 351) in the fifth edition of *Genera Plantarum* where the author made reference to an earlier name (*Eriophorus* Vaill.) authored by the French botanist Vaillant (1721) who greatly contributed to the understanding of Asteraceae. Later Adanson (1763) considered the genus *Forneum* Adans. in section Lactucæ (Asteraceae), distinguishing it from other genera based on features that clearly fit *Andryala* L. (entire leaves, corymbose inflorescences, simple involucres, receptacles with hairs, and ligules with five teeth, sessile and denticulate pappus). Roth (1790) described the genus *Voigtia* Roth, including a single species (*Voigtia tomentosa* Roth). This author actually stated that he found no genus in the Linnaean System corresponding to *Voigtia* Roth. Probably having no knowledge of the recently described *Voigtia* Roth, Schreber (1791) described a new genus, *Rothia* Schreb., stressing its resemblance to *Andryala* L. Accordingly, Gaertner (1791) considered *Andryala* L. and *Rothia* Schreb. as two distinct genera, including them in two different plant groups: the first in "*Seminibus uniformibus*" and the latter in "*Seminibus difformibus*". Roth (1797) was grateful to Schreber for naming the genus after him, and agreed that *Rothia* Schreb. is close to *Andryala* L., differing essentially by receptacle characters (i.e. receptacle with straw like bracts at the circumference and pilose at the centre) and by seed characters (i.e. peripheral seeds devoid of pappus, unlike the inner ones exhibiting a pappus, plumose at the base). Much later, Steudel (1840) published a valuable work of synonyms in which *Forneon* Adans., *Voigtia* Roth and *Rothia* Schreb. are given as synonyms of the genus *Andryala* L.

Caballero (1916) described *Paua* Caball. as a new genus, naming it in honour of Carlos Pau (1857-1937), one of the most prominent botanists of his time. Caballero (op. cit) consulted Pau concerning a peculiar plant collected in North Africa, since he thought it could correspond to a new *Andryala* species. Nevertheless, Pau had a different opinion: "*Si fuese Andryala sería una especie notable; pero vea usted el receptáculo y los pelos del vilano que no son los del género éste ... se trata de una planta que no conozco, ni se conoce tal tipo o aire en las floras mediterrâneas*". Hence, Caballero (1916: 540) considered the new genus very close to *Andryala* L., differing mainly by the habit, receptacle, pappus and cypsela ("*Genus Andryala valde affine differt: habito, alveolis receptaculi breviter dentatis nec longius setosis, pappi pilis basi dentati nec sub-plumosis, apice achaeniae edentata nec coronata, etc.*"). However, Maire (1922) definitely placed *Paua* Caball. in *Andryala* L., when validly publishing *Andryala maroccana* (Caball.) Maire (≡ *Paua maroccana* Caball.)

Nyárády (1963) described as a new genus *Pietrosia* Nyár. Nevertheless, Sell (1975) did not recognise this genus, placing it in *Andryala* L. More recently, although Sennikov (1999) proposed to restore *Pietrosia* Nyár., Greuter (2003) maintained that it corresponds merely to a synonym of *Andryala* L.

The International Code of Nomenclature for algae, fungi, and plants (Mcneill *et al.* 2012) predicts that for any *taxon* from family to genus, inclusive, the correct name is the earliest legitimate one with the same rank (Art. 11.3).

The valid publication of names at ranks of genus and below for Spermatophyta, is treated as beginning at 1 May 1753 (Linnaeus, *Species plantarum*, ed. 1), according to Art. 13 of ICN (Mcneill *et al.* 2012). Hence, the valid name for the genus under study is *Andryala* L., while *Paua* Caball. and *Pietrosia* Nyár. ex Sennikov are to be considered as heterotypic synonyms.

***Andryala* L., Sp. Pl. 2: 808. 1753**

= *Forneum* Adans., Fam. Pl. (Adanson) 2: 112. 1763
= *Voigtia* Roth, in Roem. & Usteri, Mag. 10: 17. 1790.
= *Rothia* Schreb. Gen. Pl., ed. 8[a]. 2: 531. 1791
= *Paua* Caball. in Bol. Soc. Esp. Hist. Nat. 16: 541. 1916
= *Pietrosia* Nyár. ex Sennikov in Komarovia 1: 77. 1999

Typus: *A. integrifolia* L., designated by Green (1929)

4.2.1 Description of the genus

Annual to perennial herbaceous plants. Therophytes, hemicryptophytes or chamaephytes. Single-stemmed or multi-stemmed herbs, sometimes caespitose. STEMS 8–152 cm, simple or branched in the upper third, upper half or from the base, branches erecto-patent to ascending, puberulous to densely stellate-tomentose sometimes with glandular hairs at least in the upper part. LEAVES whitish grey, glaucous, apple green, pale green or deep green, puberulous to densely stellate-tomentose (especially the upper leaves) on both faces or sometimes the abaxial face more stellate-hairy than the adaxial face, sometimes with glandular hairs at least in the upper leaves; lower leaves occasionally crowded and arranged in rosettes, sometimes marcescent at anthesis, 22–260 x 5–13 mm, attenuate into a petiole 6–57 mm, sometimes winged, or semiamplexicaul, spatulate, oblanceolate, lanceolate, linear-lanceolate, ovate-lanceolate, obovate-lanceolate, obovate-oblong, obovate, oblong or elliptic, apex obtuse, acute or acuminate, and margin entire to pinnatisect; cauline leaves few to numerous, 7–180 x 1–71 mm, usually semiamplexicaul, sometimes sessile or amplexicaul, ovate-oblong, ovate-lanceolate, linear-lanceolate, lanceolate, oblong, or elliptic, base rounded or cordate, sometimes attenuate, auriculate, cuneate to subcuneate, or truncate, apex obtuse, acute, or acuminate, rarely retuse, and margin entire to pinnatisect; upper leaves 5–77 x 0.7–31.6 mm, usually amplexicaul, sometimes sessile or semiamplexicaul, ovate, ovate-lanceolate, elliptic, oblong, ovate-oblong, obovate-oblong, lanceolate, linear-lanceolate, linear-subulate, linear, bractiform, base rounded or cordate, sometimes attenuate, auriculate, cuneate to subcuneate, or truncate, apex obtuse, acute or acuminate and margin entire, sometimes subentire to pinnatipartite. INFLORESCENCE corymbose sometimes paniculate-corymbose, racemose or with solitary capitula. CAPITULA 7–38 mm in diameter; peduncles 5–79 mm stellate-hairy, sometimes with few or numerous glandular hairs 0.2–4 mm; involucre 4–20 x 4–31 mm, campanulate to hemispherical at anthesis, with involucral bracts in 2–6 rows; external involucral bracts 3.5–14 x 0.7–2.5 mm, lanceolate to linear-lanceolate, apex acuminate, sometimes acute or subulate, flat not enfolding a floret or involute enfolding a floret, not enclosing a cypsela or sometimes strongly involute enclosing a cypsela, the outer face stellate-tomentose sometimes with few or numerous glandular hairs 0.2–3.9 mm, yellow, black or yellowish at the apex and blackish towards the base; internal involucral bracts 3.6–11 x 0.6–2.7 mm, with narrow or broad scariose margins, sometimes almost completely scariose, receptacle convex, rarely ± flat, puberulous to villous, with short or long setose hairs 0.3–7.5

mm. FLORETS hermaphrodite, ligulate, often golden yellow, sometimes pale yellow, bright yellow, orange yellow, the external with a tube of 1.8–13 mm and ligule of 2.6–13 x 0.5–4.2 mm sometimes with a reddish stripe on the outer face. CYPSELAE 0.5–3.8 x 0.3–0.8 mm, oblong to obconical, usually dark brown or black, sometimes light-brown or brownish yellow, with white, light-brown or reddish brown ribs, apex with an inner ring more or less eroded or with more or less conspicuous teeth, disposed at a lower level than the prolongation of the ribs, at the same level or at a higher level, ribs extended at the apex or not, apex rarely with a 2-rimmed disc; pappus of white or dirty-white bristles 3–7.7 mm, deciduous, denticulate or pilose at the base.

4.3 Infra generic division

The taxonomy of the genus *Andryala* proposed herein is the corollary of the results obtained largely from the morphometric study performed as well as the numerical analysis. The latter allows inferring a segregation of *taxa* and groups of *taxa* and as a result a hierarchical structure is proposed. Molecular data were also taken into account to a certain extent inasmuch as in the phylogenetic study performed most of the species relationships remained unresolved.

The genus *Andryala* is here hierarchized in two sub-genera, subgen. *Andryala* and subgen. *Paua* (Caball.) Sennen, the first with six sections and the second with two sections. This taxonomic treatment will follow the proposal of Sennen (1936) of including *A. maroccana* Pau ex Caball in the sub-genus *Paua* (Cab.) Sennen. However, this sub-genus should also include *A. agardhii* Haens. ex DC., *A. laevitomentosa* (Nyár. ex Sennikov) Greuter and *A. ragusina* L., as suggested below. The diagnostic characters of each sub-division are summarily indicated, especially the ones concerning the plant habit, type of inflorescence, receptacle indumentum, external involucral bracts convolution, cypsela size and morphology, and pappus morphology.

subgen. *Andryala*

Often annual or biennial, sometimes perennial or perennating, single-stemmed to multi-stemmed, not caespitose. Stems sometimes woody at the base. Cypsela ribs usually extended at the apex forming a more or less prominent crown.

Typus: *A. integrifolia* L.

1. sect. *Integrifolia* M. Z. Ferreira sect. nov., including *A. integrifolia* L. and *A. atlanticola* H.Lindb.

Biennial to perennial. Involucre campanulate at anthesis, involucral bracts in 2–3 rows; external involucral bracts 5–8 x 1–2 mm, apex acute to acuminate, flat not enfolding a floret, the inner face not stellate-hairy. Receptacle villous with long setose hairs, (1.7-)2–4.7 mm.

Typus: *A. integrifolia* L.

2. sect. *Arenaria* M. Z. Ferreira sect. nov., including *A. arenaria* (DC.) Boiss. & Reut., *A. dentata* Sm. and *A. cossyrensis* Guss.

Annual. Involucre often campanulate at anthesis, involucral bracts in 2–3 rows; external involucral bracts 5–8 x 0.8–1.5 mm, apex sometimes purplish, usually acuminate, involute enfolding a floret. Receptacle puberulous to pubescent, with usually short setose hairs 0.3–2.5(-3) mm.

Typus: *A. arenaria* (DC.) Boiss. & Reut.

3. sect. *Rothia* M. Z. Ferreira sect. nov., including *A. rothia* Pers.

Annual. Involucre hemispherical at anthesis, involucral bracts in 4–6 rows; external involucral bracts 6–13 x 1–1.6 mm, apex subulate, strongly involute enclosing a cypsela. Receptacle pubescent-tomentose with tendentiously short setose hairs 0.7–3 mm.

Typus: *A. rothia* Pers.

4. sect. *Glandulosa* M. Z. Ferreira sect. nov., including *A. crithmifolia* Aiton, *A. sparsiflora* (Lowe) M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq., and *A. glandulosa* Lam.

Annual to perennial, sometimes perennating, often woody at the base. Involucre ± campanulate at anthesis or hemispherical, involucral bracts in 2–3 rows or 4–5 rows; external involucral bracts 3.5–14 x 1–2.5 mm, apex acuminate or subulate, involute enfolding a floret or strongly involute enclosing a cypsela. Receptacle villous with setose hairs 1-6 mm.

Typus: *A. crithmifolia* Aiton

5. sect. *Pinnatifida* M. Z. Ferreira sect. nov., including *A. pinnatifida* Aiton, *A. mogadorensis* Coss. ex Hook.f., *A. chevalierii* Barratte ex L. Chevall., and *A. perezii* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq.

Biennial to perennial. Stems often woody at the base. Involucre often ± hemispherical at anthesis, involucral bracts in 2–3 rows; external involucral bracts 3–10 x 0.8–1.6 mm, apex acuminate, sometimes subulate or rarely acute, often flat not enfolding a floret. Receptacle often villous with usually long setose hairs (0.4-)1–6.5 mm.

Typus: *A. pinnatifida* Aiton

6. sect. *Nigricans* M. Z. Ferreira sect. nov., including *A. nigricans* Poir.

Biennial, sometimes perennating. Involucre campanulate at anthesis, involucral bracts in 2–3 rows; external involucral bracts 5–6 x 0.8–1 mm, apex acuminate to subulate, involute to slightly involute enfolding a floret. Receptacule villous with long setose hairs 3–4 mm.

Typus: *A. nigricans* Poir.

subgen. Paua (Caball.) Sennen.

Perennial, single-stemmed to caespitose, with a dark woody stock, sometimes covered with persistent bases of petioles. Cypselae ribs usually not extended at the apex.

Typus: *A. agardhii* Haens. ex DC.

1. sect. *Agardhii* M. Z. Ferreira sect. nov., including *A. maroccana* Pau ex Caball, *A. agardhii* Haens. ex DC., and *A. laevitomentosa* (Nyár. ex Sennikov) Greuter

Perennial, caespitose, with a dark woody usually branched stock, covered with persistent bases of petioles. Stems (8-)12–24 cm, erect, simple often with a single capitulum. Inflorescence with a single capitulum. Receptacle puberulous with short setose hairs 0.3–2.2 mm, rarely villous with laciniate scales bearing long hairs 3.9–4.2 mm. Cypselae small (-0.5)1.3–1.5 x 0.4–0.5 mm, rarely large 2.5–3.8 x 0.5–0.8 mm, ribs not extended at the apex. Pappus denticulate at the base.

Typus: *A. agardhii* Haens. ex DC.

2. sect. *Ragusina* M. Z. Ferreira sect. nov., including *A. ragusina* L.

Perennial, single-stemmed to caespitose, with a dark woody stock. Stems 22–78 cm, branched from the middle or the base. Inflorescence with a single capitulum or paniculate-corymbose with ± 4 capitula. Receptacle often puberulous with short setose hairs 0.3–2 mm. Cypselae large 2–2.7 x 0.3–0.6 mm, apex with an inner ring of small teeth, ribs slightly extended at the apex forming a crown. Pappus usually pilose at the base.

Typus: *A. ragusina* L.

4.3.1 Key to the *Andryala* L. species

1a. Caespitose; leaves almost all basal, entire to lobate; stems with a single capitulum, rarely two. 2

1b. Single or multi-stemmed, rarely caespitose; leaves inserted along the stems, entire to pinnatisect; stems with numerous capitula. 4

2a. External involucral bracts long simple eglandular hairs; receptacle villous with laciniate scales extended into hairs ± 3 times longer than the cypselae; ligules 12–13 mm long, with 5-7 apical teeth 1.87-1.97 mm long. .... *A. laevitomentosa*

2b. External involucral bracts with no simple eglandular hairs, receptacle puberulous with setose hairs shorter than the cypselae, ligules 5.4–8.5 mm long with 5 apical teeth 0.26-0.7 mm long. 3

3a. Stems stellate-hairy with black glandular hairs at least above; lower and cauline leaves entire; external involucral bracts often flat, not enfolding a floret; cypsela apex with a broad eroded ring at the tip. .... *A. agardhii*

3b. Stems stellate-hairy with no glandular hairs; lower and cauline leaves lobate; external involucral bracts involute enfolding a floret; cypsela apex with an almost imperceptible ring at the tip. .... *A. maroccana*

4a. Single-stemmed to caespitose; with no glandular hairs, cypsela 2–2.7 mm long, light-brown with whitish ribs. .. *A. ragusina*

4b. Single or multi-stemmed, rarely caespitose; quite often with glandular hairs, cypsela 0.9–2 mm long, often dark brown or black with white or reddish brown ribs. 5

5a. Capitula 8-14 mm in diameter; ligules pale-yellow, slightly exceeding the involucre. .... *A. dentata*

5b. Capitula 14-37 mm in diameter, ligules pale-yellow or golden-yellow, largely exceeding the involucre. 6

6a. Involucral bracts arranged in 4 or more rows. 7

6b. Involucral bracts arranged in 2–3 rows. 8

7a. Stem glandular-hairy in the upper half, rarely with scarce glandular hairs below; upper leaves sometimes with few glandular hairs, cypsela apical ring with prominent thin teeth largely exceeding the prolongation of the ribs. .... *A. rothia*

7b. Stem glandular-hairy in all its extension; upper leaves with abundant glandular hairs mainly on the middle nerve of the abaxial face, cypsela apical ring ± equal to the prolongation of the ribs. .... *A. glandulosa*

8a. Annual, receptacle with setae shorter or only slightly exceeding the cypsela. .... *A. arenaria*

8b. Biennial or perennial, sometimes annual, receptacle with setae, often largely exceeding the cypsela. 9

9a. Leaves frequently more densely stellate-tomentose on the abaxial face; cypsela ribs largely extended at the apex forming a conspicuous crown. .... *A. pinnatifida*

9b. Leaves often equally stellate-tomentose on both faces, cypsela ribs not extended at the apex or only slightly so. 10

10a. External involucral bracts flat, not enfolding a floret. 11

10b. External involucral bracts involute, enfolding a floret. 13

11a. Involucre campanulate at anthesis, ligules pale yellow. .... *A. integrifolia*

11b. Involucre ± hemispherical at anthesis, ligules golden yellow or orange yellow. 12

12a. Upper leaves ovate to ovate-oblong, sometimes oblong to obovate-oblong, base rounded, subcordate or auriculate, apex often obtuse or rounded, sometimes acute; cypsela apex with a inner ring of teeth largely exceeding the almost imperceptible prolongation of the ribs. .... *A. mogadorensis*

12b. Upper leaves linear or narrowly ovate-lanceolate, base usually rounded, apex acute to acuminate; cypsela apex with a inner ring of teeth equalling or only slightly exceeding the conspicuous prolongation of the ribs. .... *A. chevallieri*

13a. Annual, external involucral bracts apex sometimes purplish, receptacle setae 0.8–2.5(-3) mm (± up to 2 times longer than the cypselae). .... *A. cossyrensis*

13b. Biennial or perennial, external involucral bracts apex not purplish, receptacle setae 3–7 mm (± 3 to 5 times longer than the cypselae). 14

14a. Stems 10–25 cm, leaves not sparse above; lower and cauline leaves deeply lobed to pinnatisect, segments or lobes not divided; involucre ± hemispherical at anthesis; peduncles with few glandular hairs. .... *A. perezii*

14b. Stems 41–152 cm; leaves sparse above; lower and cauline leaves often pinnatisect, segments sometimes divided, involucre ± campanulate at anthesis; peduncles usually with abundant glandular hairs. 15

15a. Lower leaves deeply pinnatisect, segments often filiform and divided; upper leaves ± linear-lanceolate; ligule teeth stellate-hairy in all florets. .... *A. crithmifolia*

15b. Lower leaves subentire to pinnatisect, segments neither filiform nor divided; upper leaves ovate-lanceolate to narrowly ovate-lanceolate, or linear-subulate, ligule teeth rarely stellate-hairy. 16

16a. Lower leaves subentire to pinnatipartite; external involucral bracts with glandular hairs 0.8–1.8 mm; florets golden yellow, ligules never with a reddish stripe on the outer face. .... *A. sparsiflora*

16b. Lower often pinnatisect; external involucral bracts with glandular hairs glandular hairs (0.3-)0.6–0.8 mm; florets orange yellow, ligules sometimes with a reddish stripe on the outer face. .... *A. nigricans*

4.4 *Andryala agardhii* Haens. ex DC., Prodr. 7(1): 244. 1838

≡ *Pietrosia agardhii* (Haens. ex DC.) Sennikov in Komarovia 1: 78. 1999
Ind. loc.: "in summis Sierra Tejeda frequens, et in Sierra Nevada Hisp. Granat. rara."
Typus: [Spain] "in summis Sierra Tejeda, 1837", *Boissier 136* – Lectotype (designated by Burdet *et al.* 1983): G00323917 (specimen on the left)

4.4.1 Description

Perennial herb, caespitose, with a dark woody sometimes branched stock, covered with persistent bases of petioles (Figure 4.1A). STEMS (8-)12–22 cm, erect, simple, pubescent to densely tomentose, mainly with stellate hairs and some black glandular hairs in the upper half (Figure 4.2A). LEAVES glaucous and stellate-tomentose on both faces (Figure 4.2B); lower leaves crowded and arranged in rosettes, 42–70 x 8–13 mm, attenuate at the base into a winged petiole 20–35 mm, spatulate to oblanceolate, apex obtuse to ± acute, and margin entire; cauline leaves few, 7–28 x 1–4(-6) mm, semiamplexicaul, elliptic, base ± truncate, apex acute and margin entire; upper leaves 5–9 x 0.7–1.6 mm, sessile to semiamplexicaul, linear-lanceolate, bractiform, base ± truncate, apex acute to acuminate and margin entire. INFLORESCENCE with solitary capitula. CAPITULA 16–22 mm in diameter (Figure 4.1B); involucre 10–14 x 11–15 mm, hemispherical at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 7–9 x 1.4–2 mm, lanceolate, apex ± acuminate, flat not enfolding a floret, the outer face stellate-tomentose with black glandular hairs 0.7–1.2 mm; internal involucral bracts 7–8 x 1.7–2 mm, with broad scariose margins, receptacle convex, puberulous with setose hairs 0.7–2.2 mm (± half the length of the cypselae). FLORETS ligulate, bright yellow, the external with a tube of 4–6.8 mm and ligule of 5.4–8.5 x 1.5–2.6 mm with a reddish stripe on the outer face (Figure 4.1C). CYPSELAE 2.5–3.8 x 0.5–0.8 mm (Figure 4.1D), oblong, brownish yellow with lighter ribs, apex with a ± broad eroded ring exceeding the ± anastomosed tips of the ribs (Figure 4.2C); pappus of whitish bristles 5.5–6.7 mm, denticulate at the base (Figure 4.2D).

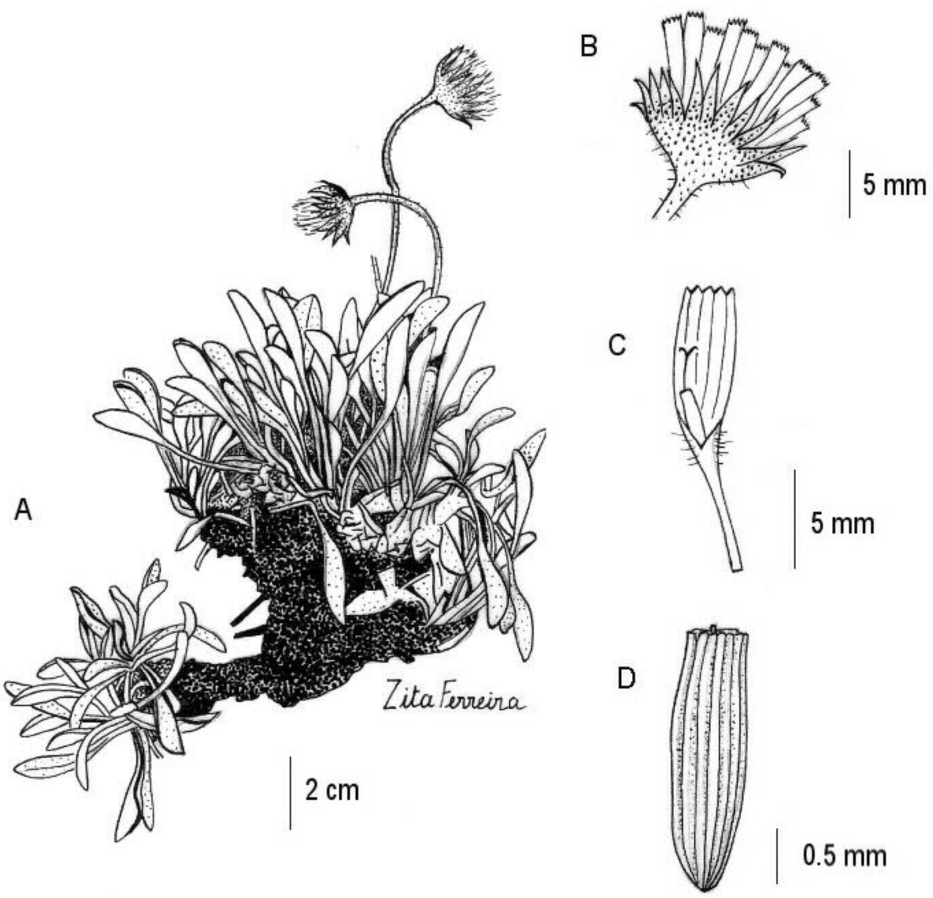

Figure 4.1 *Andryala agardhii* Haens. ex DC. A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

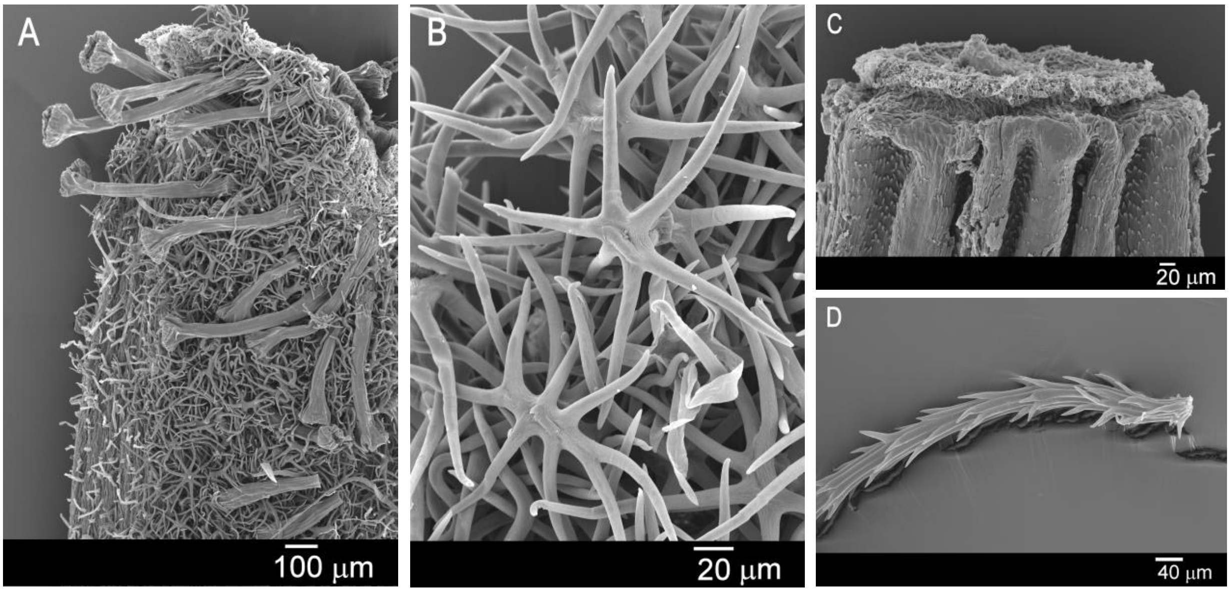

Figure 4.2 *Andryala agardhii* Haens. ex DC. A – Stem indumentum, B – Leaf indumentum, C – Cypsela apex, D – Pappus base.

4.4.2 Comments on taxonomy and nomenclature

Bossier (1841) provided a detailed description of *Andryala agardhii* Haens. ex DC. accompanied by a fairly good illustration (Figure 4.3). In the same publication, this author stressed that the specific name (*Andryala agardhii*) was given by Haenseler, who first collected it, in honour to the Swedish botanist Agardh, with whom he was in correspondence. Indeed, when De Candolle (1838) validly described this species, Haenseler was mentioned as the author of the name based on herbarium material collected by Boissier. Consequently and according to the Art. 46.5. of the ICBN, the correct name for this species is either *A. agardhii* Haens. ex DC. or *A. agardhii* DC.

Sennikov (1999) proposed the treatment of *Andryala* L. and *Pietrosia* Nyárády ex Sennik. as distinct genera and suggested the inclusion of *A. agardhii* Haens. ex DC. in the latter as *P. agardhii* (Haens. ex DC.) Sennikov. Nonetheless, Greuter (2003) was not convinced with Sennikov´s proposal to split *Pietrosia* from *Andryala* and, therefore, accepted the name *P. agardhii* (Haens. ex DC.) Sennikov as a homotypic synonym of *A. agardhii* Haens. ex DC.

4.4.3 Karyology

The somatic chromosome number of *Andryala agardhii* Haens. ex DC. is 2n = 18 (Stebbins *et al.* 1953). More recent counts performed on Spanish plants (from Sierra de Sagra and Sierra de Baza, Granada) confirmed this diploid number (Romero *et al.* 1985).

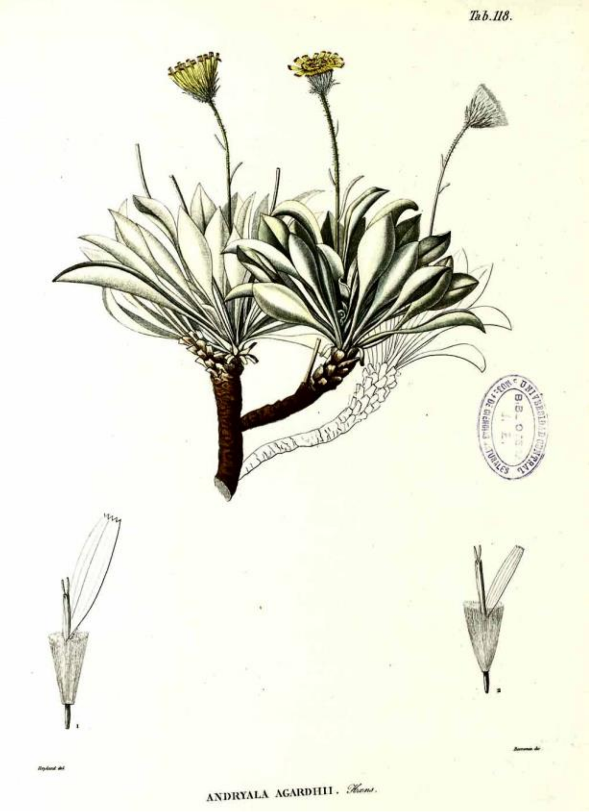

Figure 4.3 Reproduction of the icon representing *Andryala agardhii* Haens. ex DC., in Voy. Bot. Espagne (1841)

4.4.4 Ecology and conservation status

In Europe *A. agardhii* Haens. ex DC. occurs on mountain rocks and screes (Sell 1976). Specifically, it grows on calcareous rocky soils, limestone-dolomite sands, and sometimes in rock cracks and crevices, along with species also mostly whitish-tomentose to reflect the incident radiation and avoid excessive water loss, such as *Anthyllis tejedensis* Boiss., *Pterocephalus spathulatus* (Lag.) Coult., *Convolvulus boissieri* Steud., *Centaurea granatensis* Boiss ex DC., *Centaurea boissieri* DC. subsp. *funkii* (Schultz-Bip ex Willk.), *Santolina elegans* Boiss. ex DC., *Helianthemum pannosum* Boiss., *Erodium astragaloides* Boiss. & Reuter, *Erodium boissieri* Coss., *Scabiosa pulsatilloides* Boiss. subsp. *pulsatilloides, Thymus granatensis* Boiss. and *Rothmaleria granatensis* (Boiss.) Font Quer, at high altitudes between 1600 and 2100 m, on the supramediterranean and oromediteranean belts (Blanca *et al.* 2001). Likewise, in North West Africa *A. agardhii* Haens. ex DC. occurs on rocky high mountains peaks, particularly on sandstones and limestone rock, at 3000 - 3400 m (Jahandiez & Maire 1934; Emberger & Maire 1941).

In what concerns the conservation status, *A. agardhii* Haens. ex DC. is included in the threatened vascular flora of Sierra Nevada, where only two populations occur comprising less than 5000 individuals (Blanca *et al.* 1998; Blanca *et al.* 2001). Although, the rarity of this species can be attributed to specific ecological conditions and habitat discontinuity, the low number of individuals per population is mainly due to the influence of herbivorous mammals (mountain goats and domestic livestock) that graze on accessible plants, which almost never get to produce fruits (Blanca *et al.* 2001). Moreover, only the individuals that occur in more or less inaccessible crags develop normally, since such places constitute refuge areas (Blanca *et al.* 2001). Actually, *A. agardhii* Haens. ex DC. is listed as VU

C2a(i); D2 in the *Red List of Spain Vascular Flora 2008* (Moreno & Coord. 2008, 2011). In *Catalogue des plantes vasculaires rares, menacées ou endémiques du Maroc*, this species is also considered very rare (Fennane *et al.* 1998).

4.4.5 Geographic distribution

Andryala agardhii Haens. ex DC. is an ibero-maghrebian endemism, occurring only in Spain and Morocco (Carazo-Montijano & Fernández-López 2006). Indeed, Candolle (1838) assigned it to southern Spain (Province of Granada), considering it frequent on the summit of Sierra Tejeda, although rare in Sierra Nevada[29]. However, in Spain it occurs in the Baetic Mountains, encompassing the provinces of Granada, Málaga, Jaén, Almería and Murcia (Blanca *et al.* 2001). According to available herbarium data, it can be found from Sierra Tejeda eastwards to Sierra de Moratalla, including Sierra Nevada, Sierra Mágina, Sierra de Baza, Sierra María, Sierra de La Sagra, and Sierra de las Cabras (Figure 4.4). This species can also be found in certain Moroccan mountain ranges, more specifically in Mountain Bou Nacer, the highest point in the Middle Altas, and Seksaoua in the Western *High Atlas* (Jahandiez & Maire 1934; Emberger & Maire 1941).

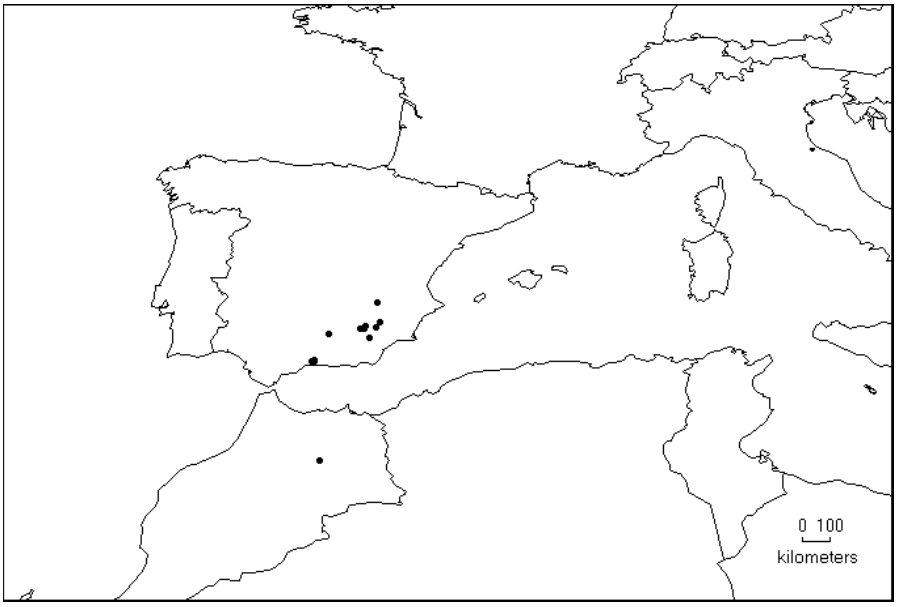

Figure 4.4 Distribution area of *Andryala agardhii* Haens. ex DC., according to studied material.

4.4.6 List of studied material

Morocco:
[Loc. incert.] : [?] 05-VIII-1933, MPU. Moyen Atlas, Eboulis Gréso-Calcaires du Dj. Bou Naceur (Guelb er Rahal), 21-VII-1929, Emberger L., RAB 078038.
Spain:
[Albacete]: Nérpio. Sierra de las Cabras. Collado entre el vértice y el Macalón 30SWH 5413, Claros del matorral-pastizal. Dolomias, 1993 m, 07-VII-2001, M.J. Martínez-Lirola & J.M. Herranz, s/ nº, MA 697075. Nérpio (AS) Sierra de las Cabras, 30 SWH5414, 1700 m en cascajares dolomiticos, 12-VII-1987, J. Herranz & A. Valdes, MA 478742.
[Almería]: Sierra María, umbria caliza rocosa, 1750 m, 05-VII-1980, A. Segura Zubizarreta, MA 351539. Sierra María, 1750 m, in calcareis lapidosis, cum *Scabiosa turolensis, Digitalis obscura, Lavandula latifolia, Vella spinosa, Festuca reverchoni, Alyssum altanticum, Cephalaria leucanta, Biscutella valentina, Erysimum linifolium ssp. - baeticum, Festuca pseudoskia, Helioctotrichon filifolium*, 05-VII-1980, A. Segura Zubizarreta, 19309, MA 238510.

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[29] According to Blanca (1998) *A. agardhii* Haens. ex DC. is a paleoendemic species from the Terciary flora which survived the last glaciation in favourable biotopes of Sierra Nevada that were little affected by the glaciations.

[Granada]: Pico de La Sagra, La Puebla de Don Fadrique, base del embudo de la ladera N, pedregales calcáreos, WH 3801, 1750 m, 14-VII-1993, V. J. Araís & Mª J. Tohá, MA 528235. El Serrata, picacho 1900 m alt. peñascoso y árido, 20-VII-1925, MA 139337. Huéscar, Sierra de La Sagra, 30 S WH 30, 2000 m, in glareosis calcareis, 19-VII-1977, Blanco, Castroviejo, Prada e Valdés, MA 422231. Sierra de La Sagra, pedregales, móviles calizos, alt. 1900 m, 13-VII-1978, E. Fuertes, M. Ladero et C. Navarro, MA 224615. Sierra de la Sagra, lieux arides, sur le calcaire, 1800 m, MA 139328. Sierra de La Sagra, pedregales móviles, alt. 1900 m, 13-VII-1978, E. Fuertes, M. Ladero et C. Navarro, MA 209556. Subida de La Sagra [30WG77], 2000 m, gleras, E. Valdés-Bermejo, P. Blanco, C. Prada, Gutierrez e S. Castroviejo, EV2486.

[Jaén]: Mancha Real, Sierra Mágina, barranco Covatillas, 30SVG5975, 1905 m, 13-VII-2000, A. Aparício, M. A, Carrasco, F. Martín & M. Velayos, 9892, MA 648474.

[Málaga]: Sierra Tejeda, 05-VII-1926, E. Gros, MA 701931. Sierra Tejeda, 29-VII-1919, Estramera, MA 139332. in summis Sierra Tejeda, alt. 6000', P 04308416.

[Múrcia]: Moratalla, Sierra de Moratalla, subida el Pico Revolcadores por la cara norte, 30 SWH6414, 1700 m, matorral seco, exposición norte, 22-VII-1997, A. Aparicio, M.A. Carrasco & Velayos, 8804 (1/3), MA 594049.

4.5 *Andryala arenaria* (DC.) Boiss. & Reut., Pugill. Pl. Afr. Bor. Hispan. 71. 1852

≡ *Andryala tenuifolia* DC. var. *arenaria* DC., Prodr. 7(1): 245. 1838, *basion.*
≡ *Andryala parviflora* Lam. var. *arenaria* (DC.) Boiss., Voy. Bot. Espagne 2(13): 394. 1841
≡ *Andryala integrifolia* L. var. *arenaria* (DC.) Ball. in J. Linn. Soc., Bot. 8 (93): 541. 1878
≡ *Andryala dentata* subsp. *arenaria* (DC.) Nyman, Consp. Fl. Eur.: 438. 1879
≡ *Andryala rothia* subsp. *arenaria* (DC.) var. *eu-arenaria* Maire in Emberger & Maire, Cat. Pl. Maroc.: 4: 1167. 1941
Ind. loc.: "in arenis maritimis circà Gibraltariam legit cl. Boissier."
Typus: [Spain] "in arenis maritimis Gibraltario, 1838", *Edm. Boissier* – Lectotype (designated by Ferreira *et al.* 2015b, see Appendix 4): G00319814.
= *Andryala arenaria* Boiss. & Reut. var. *pinnatifida* Lange, in Willkomm & Lange, Prodr. Fl. Hispan. 2: 272. 1865
Ind. Loc.: "In sabulosis et arenosis incultis regionis inferior. Hispaniae central, (in agro Madrit. ad Casa del Campo, REUT., CUT., BOURG.! LGE.! var. β.), orient. (Catal. ad fluv. Besós versus S. Adriá, CSTA.), regni Granat. (int. Estepona, S. Roque et Gibraltar, BSS.! int. Almuñecar et Salobreña, WK., pr. Granada, CAMPO, ad promont. Cabo de Gata, BOURG.! in monte Gibraltar. WK.) Apr.-Julio. Hab. etiam in Algarbiis (ad Faro, BOURG.!) et Sicilia."
Typus: [Spain] "Casa d Campo, 1852", *J. Lange s.n.* – Lectotype (designated here): C herbarium, no number (specimen on the left)
= *Andryala arenaria* (DC.) Boiss. & Reut. var. *ficalhiana* (Daveau) Cout. in Bol. Soc. Brot. 20: 95-121. 1920
Andryala ficalheana Daveau in Bol. Soc. Brot. 1: 42, 51. 1883, *basion.*
Ind. loc.: "Ile Berlenga, juillet et aout 1879."
Typus: [Portugal] "Insula Berlenga, Jul. 1882", *Julio Daveau 927* – Lectotype (designated here): P04308426! (specimen on the left); isolectotypes: P04308426! (remaining specimens); P04308425!, MPU019841
= *Andryala cossyrensis* Guss. var. *oligadena* Maire & Weiller in Bull. Soc. Hist. Nat. Afrique N. 30(5): 289. 1939
Ind. loc.: "Tripolitaine: sables de l'Ouadi Ganima (n° 1727)"
Typus: [Lybia] "sables de l'Ouadi Ganima, 15 Apr. 1938", *Maire & Weiller 1727* – Holotype: MPU004056.
= *Andryala arenaria* subsp. *parvipila* Franco, Nova Fl. Portugal 2: 543. 1984
Ind. loc.: "Pousios ou sítios áridos, ± arenosos, do interior. CW. Cintr., CE. Camp. CE. plist., SW. set. e SE."
Typus: [Portugal] "Loulé - Sales - sítio da Quinta, 5-VI-1964", *A.F. Leal de Oliveira, s.n.* – Lectotype (designated here): LISI16353.

4.5.1 Typification

The specimen G00319814 was designated as lectotype of *Andryala arenaria* (DC.) Boiss. & Reut. (Ferreira *et al.* 2015b, see Appendix 4). This specimen was most surely the basis of the original description of *A. tenuifolia* var. *arenaria* by De Candolle (1838) as the collector and collection locality both coincide with those in the protologue. According to Stafleu & Cowen (1976) the herbarium and types of Boissier are kept at G herbarium. This botanist was one of De Candolle's pupils at the school of systematic botany in Geneva who greatly contributed to the work *Prodromus systematis naturalis vegetabilis* (Sigrist & Bungener, 2008) in which *A. tenuifolia* var. *arenaria* was described. Boissier made his first botanical trip to Southern Spain in 1837 and some of the Asteraceae material collected by him constituted the basis of certain descriptions in this work (González Bueno, 2010). Boissier spent the last days of 1837 and the first months of 1838, studying his Spanish collections (González Bueno, 2010). The specimen designated as lectotype was originally identified in 1838 as "*Andryala arenaria*" (accompanied by the information: "*affinis Andr. tenuifolia DC.*"). In what seems to be a later label, handwritten by De Candolle, a new determination was added: "*Andryala tenuifolia* γ *arenaria* DC."

The original description of *Andryala arenaria* Boiss. & Reut. var. *pinnatifida* Lange was most likely based on material from the Copenhagen herbarium as the Lange collection and types are mostly deposited at this institution (Stafleu & Cowan 1979). Indeed, a specimen under the name "*Andryala arenaria* B.R. var. *pinnatifida* nob." from the Lange herbarium, perfectly matching the original description, was found in the C herbarium and is here designated as lectotype.

All type specimens of *Andryala arenaria* (DC.) Boiss. & Reut. var. *ficalhiana* (Daveau) Cout.[30] mentioned above were collected in 1882 by Daveau at the Berlenga Island. Although the collection date does not match the one in the protologue (i.e. 1879, possibly the date of the handwritten description by Daveau) most of them are labelled as "*Andryala Ficalheana Nob. Sp. nov.*", corresponding thus to original material. Some specimens under "*A. ficalhiana*" and bearing the date of the protologue were found, but the collection locality is not Berlenga Island. The specimen P04308426 is here designated as lectotype given that it corresponds to the best preserved one under the name "*Andryala Ficalheana Nob. Sp. nov.*" handwritten by Daveau.

A single specimen labelled as *Andryala cossyrensis* Guss. var. *oligadena* Maire & Weiller was found at MPU herbarium (MPU004056), corresponding to material collected by Maire & Weiller during a botanic trip to Lybia in April 1938. Since the Maire herbarium and types are hosted at MPU and seeing that collection locality and collector number match the ones in the protologue, this specimen is mostly likely the holotype.

Concerning *Andryala arenaria* subsp. *parvipila* Franco, several specimens originally under the name *Andryala arenaria* (DC.) Boiss & Reut., hosted at the LISI herbarium, show a later determination by J. Franco and L. M. Rocha Afonso (but prior to the publication date): *Andryala arenaria* subsp. *parvipila* Franco. Hence, these specimens are all potential candidates for lectotypification. The specimen LISI16353 was chosen as lectotype of *Andryala arenaria* subsp. *parvipila* Franco as it fits the original description and is well preserved.

4.5.2 Description

Annual herb, usually single-stemmed (Figure 4.5A). STEMS 8.5–40 cm, branched in the upper third or from the base, stellate-tomentose sometimes with some glandular hairs mainly in the upper part (Figure 4.6A). LEAVES pubescent-tomentose on both faces covered with stellate hairs and few glandular hairs, mainly on the middle nerve of the upper leaves when present (Figure 4.6B); lower leaves 33–126 x 8–31 mm, attenuate into a short petiole 7–20(-27) mm, oblanceolate, apex acute or less frequently obtuse, and margin subentire to pinnatipartite; cauline leaves (16-)23–79 x 6–30 mm, semiamplexicaul or amplexicaul, ovate-oblong to ovate-lanceolate, base frequently cordate, apex acute and margin entire to pinnatifid; upper leaves 11–38 x 4–10 mm, amplexicaul, ovate-oblong sometimes ovate-lanceolate, base frequently cordate, apex acute to acuminate and margin entire or rarely pinnatifid.

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[30] It is unclear whether the change of spelling from "*ficalheana*" to "*ficalhiana*" by Coutinho (1920) was deliberate or not.

INFLORESCENCE corymbiform with 3–8 capitula. CAPITULA 9–21 mm in diameter (Figure 4.5B); peduncles 9–19(-22) mm densely stellate-hairy, sometimes with few glandular hairs 0.3–1.7 mm (Figure 4.6C); involucre 7–12 x 7–14 mm, campanulate at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 5–8 x 1–1.5 mm, lanceolate, apex usually acuminate, involute enfolding a floret, the outer face densely stellate-tomentose usually with yellow or dark glandular hairs 0.7–2 mm mainly on the middle nerve; internal involucral bracts 5–8.7 x 1.2–2 mm, with scariose margins, receptacle convex, puberulous to pubescent with usually short setose hairs 0.3–2(-2.7) mm (shorter or more frequently slightly longer than the cypsela). FLORETS ligulate, golden yellow, the external with a tube of 2–9 mm and ligule of 4–10 x 1.2–3 mm sometimes with a reddish stripe on the outer face (Figure 4.5C). CYPSELAE 1–1.4 x 0.3–0.5 mm (Figure 4.5D), usually oblong, dark brown with white ribs, apex with a ring of thin teeth ± exceeding the conspicuous prolongation of the ribs (Figure 4.6D); pappus of whitish bristles 3.8–5.7 mm, pilose at the base (Figure 4.6E).

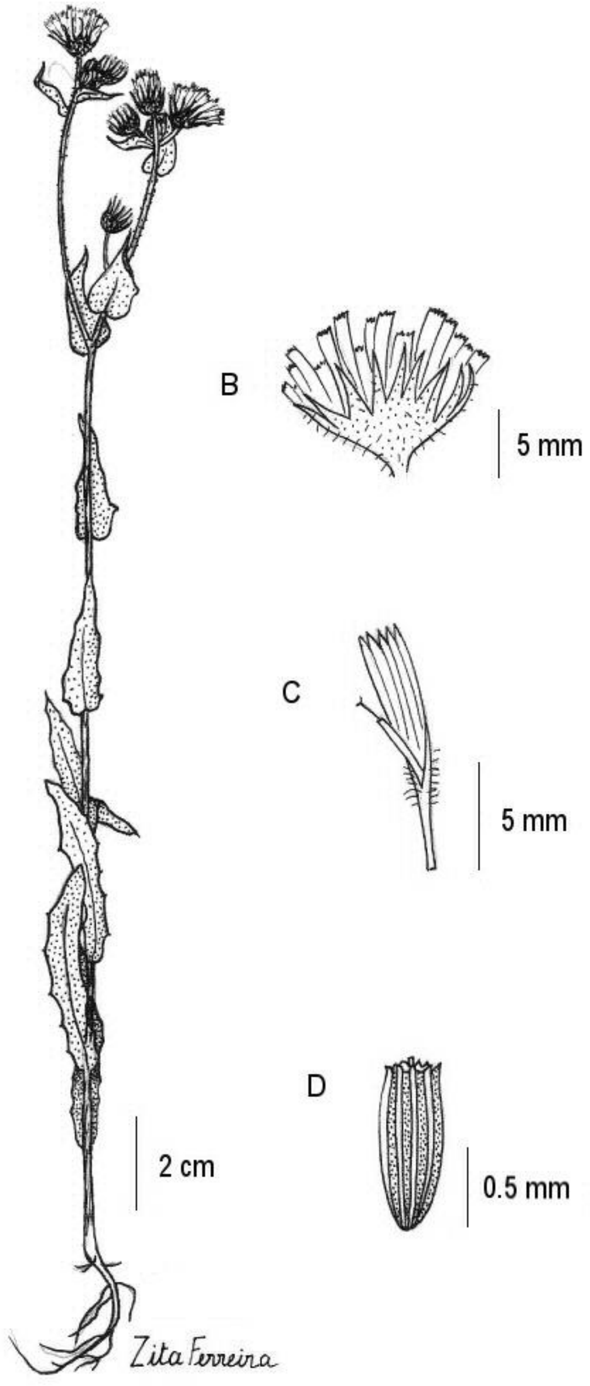

Figure 4.5 *Andryala arenaria* (DC.) Boiss. & Reut. A – Fertile habit, B – Capitulum, C – Floret, D – cypsela.

4.5.3 Comments on taxonomy and nomenclature

Boissier & Reuter (1852) described *Andryala arenaria* (DC.) Boiss. & Reut. as a distinct species, indicating two homotypic synonyms: *A. parviflora* Lam. β *arenaria* Boiss. and *A. tenuifolia* γ *arenaria* DC. Indeed, De Candolle (1838) briefly described *A. tenuifolia* γ *arenaria* DC. based on plant material collected by Boissier, as stated in the protologue. It appears that the epithet "*arenaria*" is of De Candolle's authority and, therefore, the correct name is *A. arenaria* (DC.) Boiss. & Reut. In this publication Boissier & Reuter (1852: 245) stressed that this species has been confounded in previous works with an oriental plant which these authors clearly distinguished from *A. arenaria* (DC.) Boiss. & Reut. by the inflorescences laxly corymbose or subracemose; cauline leaves linear-lanceolate slightly dilated at the base, involucres tenuously velvety and not densely lanate, ligules pale yellow and slightly exceeding the involucre and not largely exceeding. Although Boissier & Reuter (op. cit.) designated this oriental plant as *A. tenuifolia* Guss., it most surely corresponds to *A. dentata* Sm.

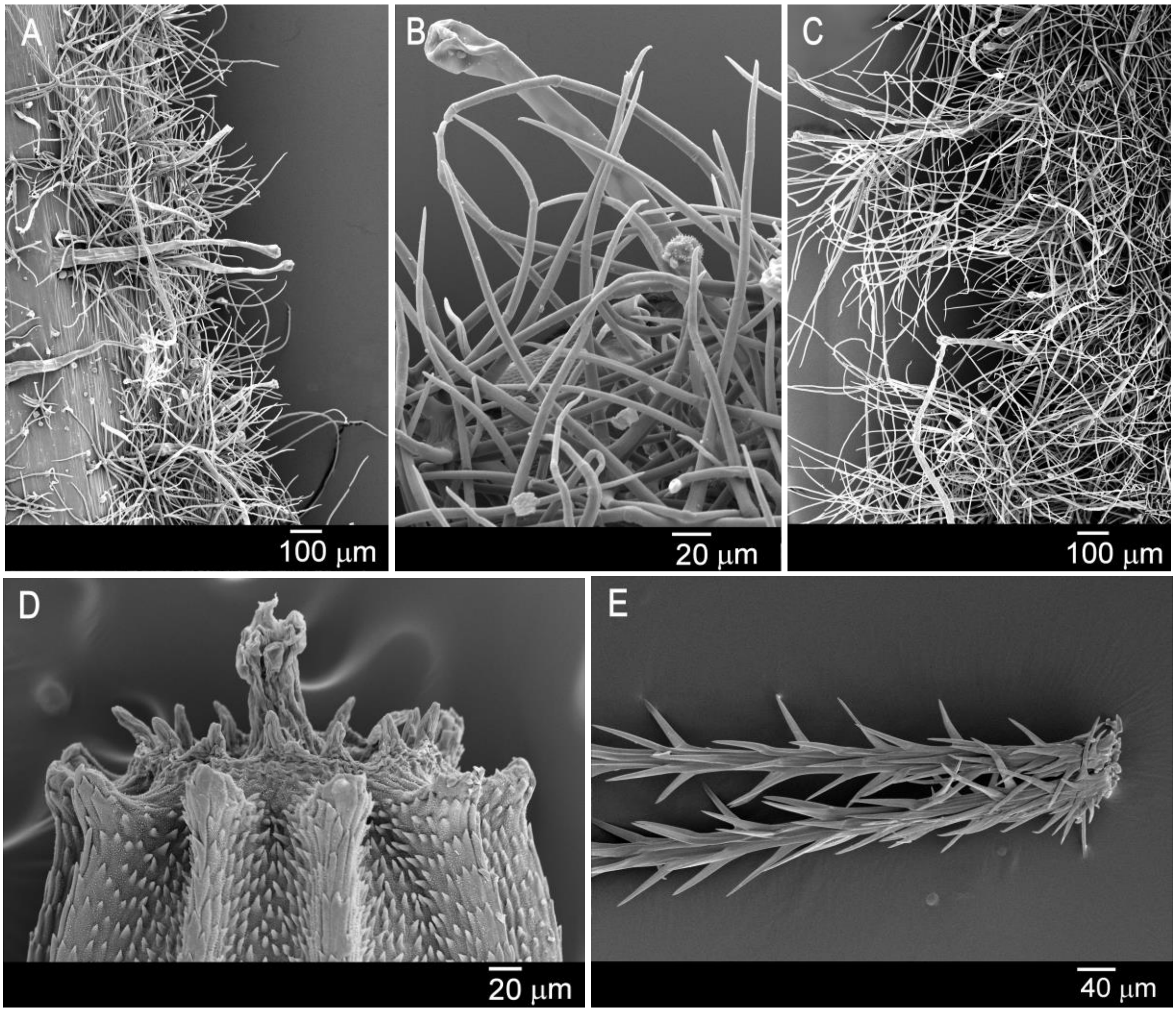

Figure 4.6 *Andryala arenaria* (DC.) Boiss. & Reut. A – Stem indumentum, B – Leaf indumentum, C – Peduncle indumentum, D – Cypsela apex, E – Pappus base.

Ball (1878) included *Andryala arenaria* (DC.) Boiss. & Reut. in *A. integrifolia* L. under the name *A. integrifolia* var. *arenaria* (DC.) Ball. This author stated *A. arenaria* (DC.) Boiss. & Reut. as a synonym, which makes *A. integrifolia* var. *arenaria* (DC.) Ball a homotypic synonym of *A. arenaria* (DC.) Boiss. & Reut. In the same publication Ball added that *A. integrifolia* L. is a very polymorphic species with a very intricate synonymy, which authors have divided in many false species and that it probably does not even differ much from *A. dentata* Sm. from the Eastern Mediterranean. Later authors, such as Barratte in Barratte (1896), recognised *A. integrifolia* L. var. *arenaria* (DC.) Ball. Nonetheless, *A. arenaria* (DC.) Boiss. & Reut. is worthy of a specific distinction since morphologically it is quite different from *A. integrifolia* (e.g. involucral bracts involute and not flat, receptacle hairs short and not largely exceeding the cypselae, ligules golden yellow and not pale yellow) and also from *A. dentata* Sm. as stated by Boissier & Reuter (1852).

Nyman (1879) erroneously included *Andryala arenaria* (DC.) Boiss. & Reut. in *A. dentata* Sm. as a subspecies, assigning it to the Iberian Peninsula, where indeed *A. arenaria* (DC.) Boiss. & Reut. occurs. Thus, *A. dentata* Sm. subsp. *arenaria* (DC.) is a homotypic synonym of *A. arenaria* (DC.) Boiss. & Reut. Similarly to Boissier & Reuter

(1852), Murbeck (1897) stressed that *A. arenaria* (DC.) Boiss. & Reut. differs from *A. dentata* Sm. by its ligules golden yellow and not lemon yellow, the outer ones considerably longer than the involucral bracts; by the involucral bracts indumentum a little more abundant and by the cauline leaves broader at the base. Nonetheless, Murbeck (1897) joined *A. arenaria* Boiss. & Reut. and *A. cossyrensis* Guss. in a single species (*A. arenaria*) since, according to the author, they agree on the essential morphological features, judging by the original description by Gussone. However, years later Murbeck (1905) recognised his misinterpretation and definitely distinguished *A. arenaria* (DC.) Boiss. & Reut. from *A. cossyrensis* Guss. by its cauline leaves cordate-amplexicaul, capitula with shorter peduncles and involucre densely tomentose. In agreement, Jahandiez & Maire (1934) recognised *A. arenaria* (DC.) Boiss. & Reut. and *A. cossyrensis* Guss. as two distinct species. Later, quite surprisingly, Emberger & Maire (1941) placed these two *taxa* in one single polymorphic species, *A. rothia* Pers., suggesting new combinations: *A. rothia* subsp. *cossyrensis* (Guss.) Maire and *A. rothia* Pers. subsp. *arenaria* (DC.) Maire. Additionally, within the latter subspecies, Emberger & Maire (1941) considered two varieties: *A. rothia* Pers. subsp. *arenaria* (DC.) Maire var. *eu-arenaria* Maire [the true *A. arenaria* (DC.) Boiss. & Reut.] and *A. rothia* Pers. subsp. *arenaria* (DC.) Maire var. *pinnatifida* (Lange) Maire. The specific epithet "*rothia*" was misapplied given that *A. rothia* Pers. corresponds to a very distinct species, traditionally known as *A. laxiflora* DC., and lead to incorrect nomenclature.

Willkomm & Lange (1865: 272) recognised a new variety, *A. arenaria* (DC.) Boiss. & Reut. var. *pinnatifida* Lange, differing from the typical one by the more divided leaves ("*foliis pinnatifidis v. pinnatipartitis*"). Many years later, Maire & Weiller (1939: 289) described *A. cossyrensis* Guss. var. *oligodena* Maire & Weiller as a new variety, stressing its similarity to *A. cossyrensis* Guss. var. *arenaria* (Boiss. & Reut.) Maire. The description of *A. cossyrensis* var. *oligodena* ("*Folia caulina plus minusve dentata l. basi sub-pinnatifida, basi dilatata, cordata, plus minusve amplexicaulia. Capitula breviter pedunculata, sine ligulis 10-12* ^{mm} *diam. Involucrum valde albo-tomentosum, sine phyllis internis brevioribus paleaceis. Ligulae aurantiacae involucro subduplo longiores. Indumentum herbae undique stellato-tomentosum, setis olivaceis glandulosis parcissimis in tomento albo immersis, lente acriore tantum perspicuis. Folia e tomento laxiore viridi-cinerascentia.*") fits *A. arenaria* Boiss. & Reut. quite well. In fact, Maire & Weiller (1939) highlighted that this taxon differs from *A. cossyrensis* Guss. var. *arenaria* (Boiss. & Reut.) Maire. mainly by the indumentum almost with no glandular hairs. Actually, the original material (MPU004056) resembles the earlier described *A. arenaria* var. *pinnatifida* Lange considering the more divided leaves. *Andryala arenaria* var. *pinnatifida* Lange is not herein recognised as a distinct taxon given that the only difference compared to *A. arenaria* (DC.) Boiss. & Reut. is the leaf margin.

4.5.4 Karyology

The somatic chromosome number of *Andryala arenaria* (DC.) Boiss. & Reut. is 2n = 18. This number was obtained from Portuguese plants identified as *A. arenaria* (DC.) Boiss. & Reut. var. *arenaria* (Fernandes & Queirós 1971) and confirmed on Spanish material from Granada (Romero *et al.* 1985) and Huelva (Pastor *et al.* 1990), both under the name *A. arenaria* (DC.) Boiss. & Reut.

4.5.5 Ecology and conservation status

As the name suggests, *Andryala arenaria* (DC.) Boiss. & Reut. occurs mainly on sandy sites, from coastal to inland areas. Indeed, Willkomm & Lange (1865) mentioned gravelly and sandy uncultivated lowlands as the habitat of this species. Coutinho (1939) stated that it grows on sandy soils of inland areas such as heathlands, vineyards, and pine forests and Sampaio (1949) highlighted the preference of this species for sandy and arid habitats. Likewise, Talavera (1987) and Blanca (2009, 2011) referred its occurrence in therophytic plant pastures, on sandy substrate, from 0–1200 m. Taking into account the occurrence area, Franco (1984) even admitted two distinct subspecies: the typical one being frequent on sands or dunes covering coastal rocks, and *A. arenaria* (DC.) Boiss. & Reut. subsp. *parvipila* Franco growing in sandy fallow or barren sites of inland areas[31]. In Morocco *A. arenaria* (DC.) Boiss. & Reut. can be found in similar habitats: sandy soils of oak forests as well as sandy and rocky pastures (Lindberg 1932; Jahandiez & Maire 1934).

In *Flora Vascular de Andalucía Oriental*, Blanca (2009, 2011) considered *Andryala arenaria* (DC.) Boiss. & Reut. as occasional (i.e. species observed in numerous locations but never abundant) and listed it as Least Concern (LC) according to the *IUCN Red List categories and criteria* (IUCN 2001; 2012). *Andryala arenaria* (DC.) Boiss. & Reut. is frequent in Portugal (Coutinho 1939) and seems to be less common in North Africa. Actually, for the Moroccan flora it is presumably rare (Fennane *et al.* 1998; Tattou 2001).

4.5.6 Geographic distribution

Andryala arenaria (DC.) Boiss. & Reut. is considered an Ibero-North African *taxon* (Tattou 2001). It was originally cited for Gibraltar, the most Southern end of Spain (although, under the name *A. tenuifolia* var. *arenaria* DC.). Boissier & Reuter (1852) assigned it to Central and Southern Spain as well as to North Africa, namely Algeria. Actually, in Spain it is mainly found in the South, specifically in Andalusia (Talavera 1987; Carazo-Montijano & Fernández-López 2006; Blanca 2009, 2011). Later Willkomm & Lange (1865) included Southern Portugal in the distribution area of this species, where it occurs almost throughout the country (Coutinho 1939; Sampaio 1949; Franco 1984). Likewise, Murbeck (1905) indicated the Iberian Peninsula and Algeria as the distribution area of *A. arenaria* (DC.) Boiss. & Reut., and later included Morocco (Murbeck 1923), as did Emberger & Maire (1941) and Carazo-Montijano & Fernández-López (2006).

Willkomm & Lange (1865: 272) assigned *Andryala arenaria* var. *pinnatifida* Lange to the Iberian Peninsula (Central and Southern Spain, and Southern Portugal). In the same publication Willkomm & Link incorrectly assigned it also to Sicily, probably confounding it with *Andryala cossyrensis* Guss. since the latter resembles *A. arenaria* (DC.) Boiss. & Reut., by the cauline lower leaves which are lyrate-pinnatifid. Much later, *A. arenaria* (DC.) Boiss. & Reut. var. *pinnatifida* Lange was reported for North Africa, namely Northern Morocco (Caballero 1917; Jahandiez & Maire 1934; Sennen & Mauricio 1934) and Northern Libya (Maire & Weiller 1939), although in the latter case under the name *A. cossyrensis* Guss. var. *oligodena* Maire & Weiller.

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[31] This subspecies are not here recognised as they only differ by the colour and length of the glandular indumentum of the involucre, according to Franco (1984).

According to available herbarium material, *Andryala arenaria* (DC.) Boiss. & Reut. is mainly found in central and southern regions of the Iberian Peninsula, as well as in Mediterranean regions of Morocco, Algeria, Tunisia, and Libya (Figure 4.7). In Portugal, it also occurs in the Berlenga Islands.

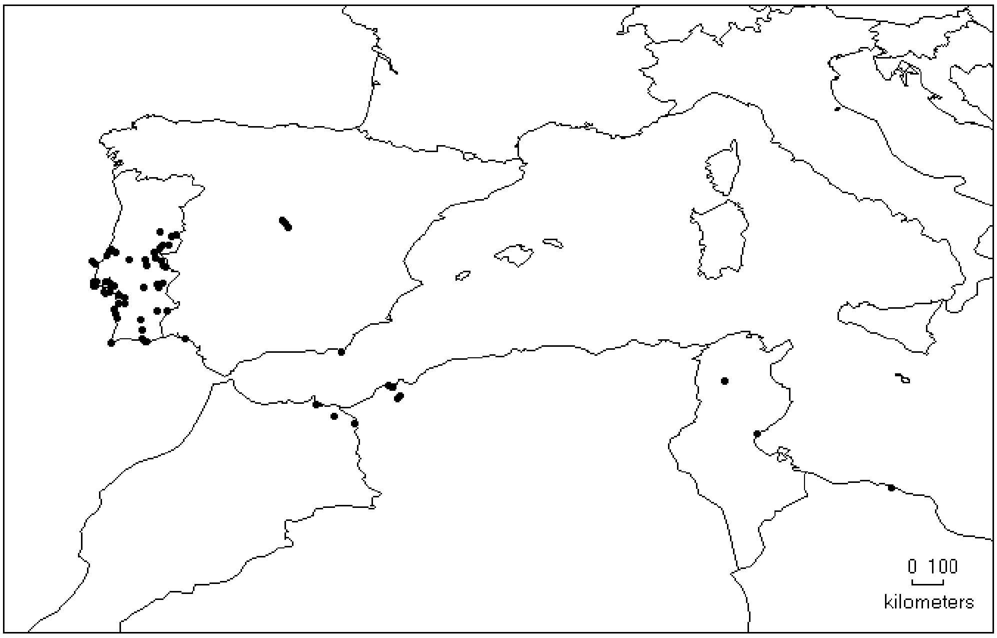

Figure 4.7 Distribution area of *Andryala arenaria* (DC.) Boiss. & Reut., according to studied material.

4.5.7 List of studied material

Algeria:
[Oran]: sables maritimes à la batterie espagnole, 13-V-1883, O. Debeaux [?], s/nº, LISU 55327. Les Lauriers Roses, Liewe incults prés la Gare, 25-V-1919, A. Faure, MPU-Maire. champs, MA 139307. Vallon de Noiseux, Broussailles, 23-V-1909, A. Faure, MA 176874. sables maritimes à la batterie espagnole, 05-V-1883, Debeaux, MA 139305. prop de Bou Tlétlis vers Aïn el Turk, 30-V-1989, C. Benedí, G. Montserrat Marti & J. M. Monserrat Martí, JMM-2240, MA 537488.
[Tlemcen]: Le Ghar-Rouban, Lieur pierreur 850 m, 03-VII-1935, A. Faure, MPU-Maire.
Libya: Tripolitania, nach Ganima, sables, 07-IV-1938, R. Maire & Weiller, M., 1727, MPU 004056.
Morocco:
[Berkane]: In ditione Beni-Snassen, prope Taforalt, 600 m, 02-V-1925, MPU-Maire.
[Nador]: Melilla, Mazuza, 26-V-1934, Sennen et Mauricio, MA 139294.
Portugal: Margens do Pico Chança, Dr. Palhinha, H. Navel e F. Mendes, s/nº, LISU 40259. [?], s/nº, LISU 55984.
[Algarve]: de Sagres ao Cabo de S. Vicente pelo interior [?], R. P., s/nº, LISU 139839. Arredores de Faro - Atalaia, [?], s/nº, LISU 55927. Loulé: Almanal, Garrão, 30-III-1964, J. Martins Farrajota, s/ nº, LISI 23593. Vila do Bispo: Sagres, a 2 Km da Ponta de sagres a caminho do Cabo de S. Vicente, Q. 974, 15-VI-1988, D. Espírito Santo, s/ nº, LISI 46595. Loulé, Sales, sítio da quinta, mancha geológica do carbónico inferior, exp. N, alt. 270m, 05-VI-1954, A.F. Leal de Oliveira, s/ nº, LISI 16353. Faro, Sables maritimes, 26-IV-1855, E. Bourgeau, P 03758384. Faro, Sables maritimes, 26-IV-1855, E. Bourgeau, P 03758389.
[Alto Alentejo]: (Estação da) Torre das Vargens, A.R. da Cunha, s/nº, LISU 40224. Sra. da Penha - Portalegre, A.R. da Cunha, s/nº, LISU 40219. Serra d´Ossa prés Estremoz, J. Daveau, s/nº, LISU 40221. Arieiro, Castello de Vide, A. R. da Cunha, s/nº, LISU 40255. Nisa, Freguesia do E. Santo, 20-V-1956, J. Fragoso de Almeida, s/ nº, LISI 19551. Vila Viçosa: Herdade da Capela, 31-V-1949, M. Calheiros Braga, s/ nº, LISI 12795. Portalegre: Alegrete, Serra do Pico, encosta das vinhas, Q. 574. Inv. 8, alt. 520, exp. S, num sobreiral ralo, 13-VI-1952, A. Rodrigues F. Raimundo, s/ nº, LISI 14226. Tapada Real de Vila Viçosa, 12-VI-1955, M. Sousa da Câmara, s/ nº, LISI 17721. Herdade da Contenda, Concelho do Redondo, alt. 400m, exposição Oeste solos esqueléticos de xisto, sob coberto de *Pinus pinaster* Q. 700 Inv. 7, 22-V-1956, José Francisco C.B. Cordovil, s/ nº, LISI 18719. Redondo, 23-V-1956, J.F.C.B. Cordovil, s/ nº, LISI. Évora, Graça do Divor, Herdade da Figueira, Q. 716/734 -inv. 23, alt. 240 m em solo fragoso com sobreiral denso, 05-VI-1956, João V. Saldanha O. e Sousa, s/ nº, LISI 19068.
[Baixo Alentejo]: Serra de Ficalho - vertente sul (Serra da Adiça), C. de Ficalho & J. Daveau, s/nº, LISU 40242. Entre Villa Nova de Milfontes et Cereal, J. Daveau, s/nº, LISU 40231. Entre Corte-Figueira et Mú, alt. 560m., J. Daveau, s/nº, LISU 40232. Entre Carregueiro e Castro Verde, J. Daveau, s/nº, LISU 40239. Dr. R. Palhinha e F. Mendes, s/nº, LISU 56537. Alcácer do Sal; Mata de Valverde, J. Q. Quita, s/ nº, LISI 15028. Sines, Porto Côvo, falésias, plataforma sobre os rochedos, a N. da povoação, erva anual erecta, tomentosa, flores amarelas, 30-V-1970, J. Gomes Pedro, 200, LISI 30593. Serpa, Prof. Dr. Azevedo Gomes & L. Melo, s/ nº, LISI 4688. Alcácer do Sal: Sta. Maria do Castelo, Açude da Murta, Q. 759, 25-V-1988, D. Espírito Santo, s/ nº, LISI 46237
[Beira Baixa]: Tapada do Tanque – Idanha-a-Nova, A. R. da Cunha, s/nº, LISU 40223. Alcains, F. Mendes, s/nº, LISU 40228. Monte

Lombardo - Castelo Branco, A.R. Cunha, s/nº, LISU 40241. Portas do Ródão - Villa Velha do Rodão, A. R. da Cunha, s/nº, LISU, 40251. (S. Sebastião) Covilhã, A. R. da Cunha, s/nº, LISU, 40254. Idanha-a-Nova, Freguesia da Aldeia de Sta. Margarida, num pousio, alt. 385m inv.9, 24-V-1956, A. A. Vaz da Silva, s/ nº, LISI 18763. Penamacor, Monsanta, espécie frequente no local, em floração, 07-VII-1987, M. Lousã, M. L. Rosa, J. P. Luz, LISI 44613, Penamacor, Qta do Major, espécie frequente no local, em floração, 14-VII-1987, M. Lousã, M. L. Rosa, J. P. Luz, LISI 44703.

[Beira Litoral]: Pinhal de Leiria, S. Pimentel, s/nº, LISU, 55991. Marinha Grande, Carlos de Sousa Pimentel, s/nº, LISU 40222. Marinha grande, Carlos de Sousa Pimentel, s/nº, LISU 40217. Litoral - Pederneira, A. R. da Cunha, s/nº, LISU 40253. Pinhal de Leiria - talhão 241, Q. 450 - alt. 75m, solo podzólico com surraipa, sob pinhal bravo, 20-V-1956, J. Estevão Mariano, s/ nº, LISI 18696. Azóia (Camarinheiras - p. geodésico), J.M. Carvalho & F.M. Flores, s/ nº, LISI 6870.

[Estremadura]: Mata Nacional dos Medos: Península de Setúbal, 15-V-1956, Rogério Lameiro, s/ nº, LISI 18496. Praia Grande vs. Rodísio, ad viam in pascuis marítimis solo arenoso, 28-V-1984, A. R. Pinto da Silva, Alexandra Silca Costa, R.H. Bacelar, 2054 ASC, LISU 147184. Praia das Maças, F. [?], s/nº, LISU. Flora da área de paisagem protegida Sintra-Cascais. Cascais, Ponta da Abelheira, Solos pedragosos. Erva bienal com ca. de 30 cm., corola amarelo torrado. Associada a *Ulex* Sp., *Lavandula stoechas, Cistus ladaniferus, Rosmarinus officinalis*, etc., M. Correia & J. Cardoso, 5418, LISU 151956. Arredores de cascais: de Oitavos a Cabo Raso, s/nº, LISU, 40244. Dunas da Lagoa de Albufeira, Dr.R. Palinha e Luis G. [?], s/nº, LISU 40237. Sesimbra, Lagoa de Albufeira, C. Romariz e E. J. Mendes, s/nº, LISU 65119. Cascais, arred. do Farol da Guia., Nas fendas dos rochedos junto ao farol associação de *Euphorbia paralias, Frankenia hirsuta, Arméria welwitschii, Herniaria maritima,* etc. erva anual, corola amarela., M.F. Correia, 4373, LISU 69397. Alcochete, vallados, caminhos, campos, A. X. Pereira Coutinho, 2198, LISU 40215. Ilha Berlenga (perto do Pharol), Julio Daveau, s/nº, LISU 40262. Ilha Berlenga, Dr. Palhinha e J.J. Barro, s/nº, LISU 40263. Cabo Carvoeiro, à [?] de Peniche, J. Daveau, s/nº, LISU 40266. Cascais; Ponta da Abelheira, Erva anual, corola amarelo-claro. Forma costeira complexa de Herb.-lenhosas Baix. com *Ulex* sp., *Lavandula stoechas, Cistus ladaniferus, Rosmarinus officinalis*. Solos pedregosos com cascalho, 07-VI-1983, M. Correia & J. Cardoso, 5402, LISU 151940. Ilha Berlenga, 14-VI-1979, T. Vasconcelos & J. D. Femandes, s/ nº, LISI 36779. Sesimbra: Santana, Herdade da Ferreira, Q. 723 - sob coberto de eucaliptal, 30-V-1956, F. Nobre Coutinho, s/ nº, LISI 18838. Grândola: sítio do Borbolegão, alt. 65 m, terreno do Pliocénico Q. 792, 22-V-1959, Filipe C. Vilhena, s/ nº, LISI 20283. Palmela, Rio Frio, Almocreves, alt. 25 m, terra Pliocénico horizontal, 28-V-1963, A. Cruz Marcelino, s/ nº, LISI 22912. Sintra: Rodísio, 09-V-1966, M. Lisete C.L. Caixinhas, s/ nº, LISI 25205. Cascais, arredores do farol da Guia, nas fendas dos rochedos junto ao farol associação de *Euphorbia paralias, Frankenia hirsuta, Arméria welwitschii, Herniaria maritima*, etc. erva anual, corola amarela, 11-V-1973, M. F. Correia, 4373, LISI 35436. Grândola, Melides, Carvalhal, entre a praia e a povoação, à Malhada Alta, médo com pinhal bravo, [?] bosque com *Stauracanttus* [?], *Santolina, Ulex, Lavandula,* terofito, lanoso, flores amarelas, 07-V-1977, J. Gomes Pedro, s/ nº, LISI 35822. Berlenga Grande. Ilha velha a caminho da Sereia, 14-V-1979, T. Vasconcelos & J. D. Femandes, s/ nº, LISI 36784. Camarate (Alcochete), 22-IV-1949, Ernesto Goes, s/ nº, LISI 12580. Herdade da Ferraria, Santana, Sezimbra Q. 724 - sob coberto de eucaliptal, 30-V-1956, F. Nobre Coutinho, s/ nº, LISI, 18837. Grândola, entre os lugares de pintos e Lagoso, alt. 65 m; terreno do Pliocénico Q. 791, inv 22, 05-V-1959, Filipe C. Vilhena, s/ nº, LISI 20351. Setúbal, S. Lourenço de Azeitão, Serra da Arrábida, morro de jaspe, vert. SE, arriba marítima; com *Lobularia maritima, Papaver, Cerinthe*, terófito lanoso, até 0, 8 m, flores amarelas, 29-V-1978, J. Gomes Pedro, s/ nº, LISI 36172. Cascais, Malveira, Biscaia, J. M. Carvalho, F. Flores. & E. Vales, s/ nº, LISI, 9323. Sintra: Colares, Cabo da Roca, zona do chorão queimado, 02-VI-1978, C.M. Baeta Neves, s/ nº, LISI 36262. Berlenga (perto do Pharol), Julio Daveau, s/nº, LISU 40265.

[Ribatejo]: Belver, prox. de Abrantes, D. Maria do C. Pereira Coutinho, 2199, LISU 40216. Barquinha, J. Daveau, s/nº, LISU 40250. Setubal?, Pinhal do Alfeite, A.R. da Cunha, s/nº, LISU 40230.

Spain:

[Almería]: Cabo de Gata, Coteaux incultes, 25-IV-1851, E. Bourgeau, P 03758388.

[Huelva]: Mazagon, laguna de las Pozas, 17-V-1979, S. Silvestre, S. Talavera et al., s/nº, LISU 163434.

[Madrid]: Monte del Pardo, in collibus arenosis, 20-V-1917, Carlos Vicioso14, 16, s/nº, LISU 55357. Casa del Campo, La Gasca, MA 139324. Hoyo de Manzanares, 14-VI-1947, S. Rivas Goday et E. F. Galiano, MA 165827. Casa del Campo, dans les champes incultes, 12-VI-1854, E. Bourgeau, P 03758385, Casa del Campo, 12-VI-1854, E. Bourgeau, P 03758383. Casa del Campo, 06-VI-1851, John Lange, P 03758364.

Tunisia: Gabes, Raz-el-Oued, in aridis, C. J. Pitard, MA 139310. Sfax, A. Roux Enc. Skira, A. Roux, MPU.

4.6 *Andryala chevallieri* Barratte ex L. Chevall. in Mem. Herb. Boiss. 7: 10. 1900

Ind. loc.: “In provincial Oranensi australi imperio Maroccano confine in aggeribus arenæ mobilis prope Aïn-Sefra (Chevallier, nº341, 29 maio 1899)”

Typus: [Algeria] “Ain-Sefra, in agger. arenae mobilis, 29 Maj. 1899”, *L. Chevallier 341* – Lectotype (designated by Ferreira *et al.* 2015b, see Appendix 4): P03290615!; isolectotypes: MA139351!, P03290786!, P02712789!, P02712787!, P03290614!, HBG504059, JE00010480, JE00010481, JE00010482, WAG0104953, W20110009296.

4.6.1 Typification

The specimen P03290615 was designated as lectotype for being the best developed, clearly showing the habit of the plant. Specimens from the herbaria P, MA, HBG, JE, WAG, and W are elected as isolectotypes given that Chevallier, the validating author, did not mention a particular specimen as holotype or the herbarium in which it was deposited (Ferreira *et al*. 2015b, see Appendix 4).

4.6.2 Description

Biennial herb, multi-stemmed. STEMS 47–72 cm, branched in the upper third (Figure 4.8), pubescent-tomentose with stellate hairs and sometimes with rare glandular hairs above (Figure 4.9A). LEAVES pubescent-tomentose on both faces covered with stellate hairs and few glandular hairs, mainly on the middle nerve of the upper leaves when present (Figure 4.9B); lower leaves 79–150 x 10–34 mm, attenuate into a long petiole 17–30(-55) mm, lanceolate to linear-lanceolate, apex obtuse or less frequently acute, and margin lobate to pinnatipartite; cauline leaves 43–87 x 6–15 mm, usually semiamplexicaul, lanceolate to ovate-lanceolate, base rounded, apex acute or less frequently obtuse, and margin entire to pinnatifid; upper leaves 18–38 x 2–11 mm, amplexicaul, linear or narrowly ovate-lanceolate, base frequently rounded, apex acute to acuminate and margin entire. INFLORESCENCE paniculate-corymbose with 4–7 capitula or more rarely solitary capitula. CAPITULA 15–24 mm in diameter (Figure 4.8B); peduncles 23–37 mm stellate-tomentose with some short glandular hairs 0.2–1 mm (Figure 4.9C); involucre 11–13 x 10–14 mm, ± hemispherical at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 8–10 x 1–1.3 mm, linear-lanceolate, apex acuminate to subulate, ± flat not enfolding a floret, the outer face pubescent-tomentose with stellate hairs and some glandular hairs 0.4–1.4 mm, yellow and blackish towards the base, mainly on the middle nerve; internal involucral bracts 7–10 x 1.7–2.7 mm, with broad scariose margins, receptacle convex, villous with long setose hairs 2–3.8 mm (± 2 times longer than the cypselae). FLORETS ligulate, golden yellow, the external with a tube of 3.5–5.5 mm and ligule of 6–8

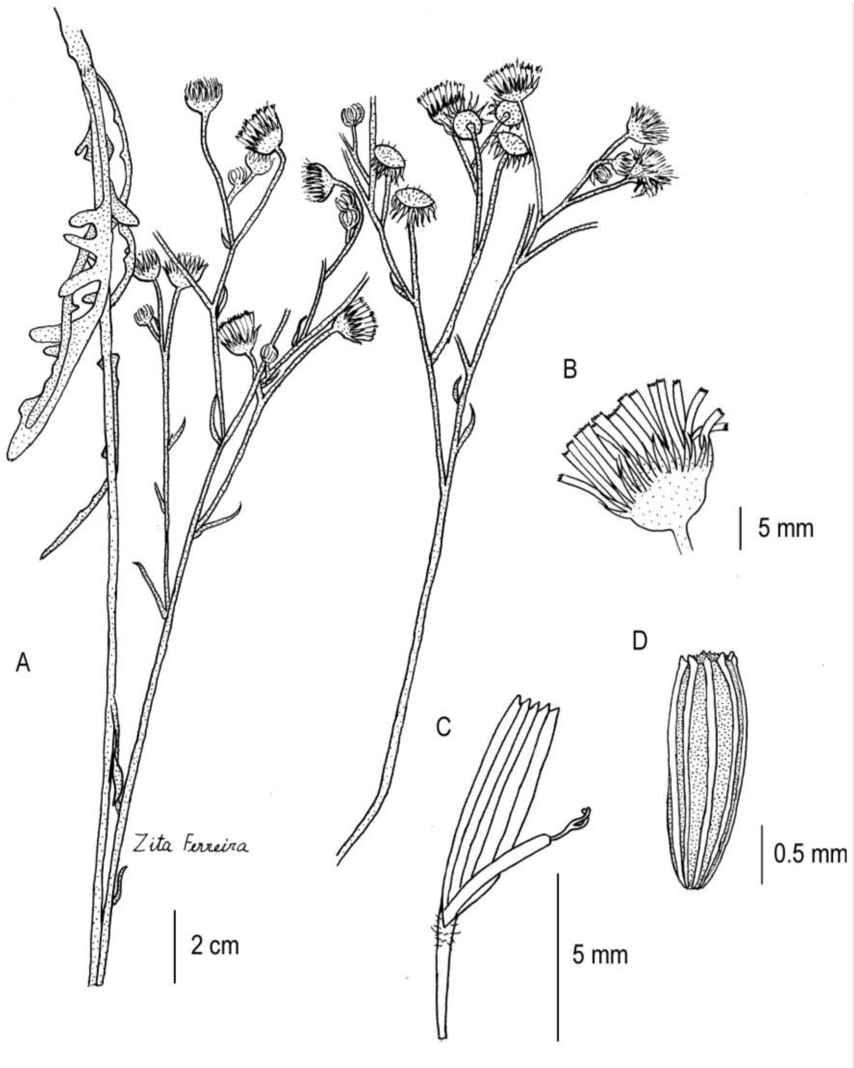

Figure 4.8 *Andryala chevallieri* Barratte ex L. Chevall. A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

x 1–2 mm (Figure 4.8C). CYPSELAE 1.5–2 x 0.4–0.5 mm (Figure 4.8D), obconical, dark brown with white ribs, apex with a ring of short teeth equalling or slightly exceeding the ± conspicuous prolongation of the ribs (Figure 4.9D); pappus of whitish bristles 6–7 mm, pilose at the base (Figure 4.9E).

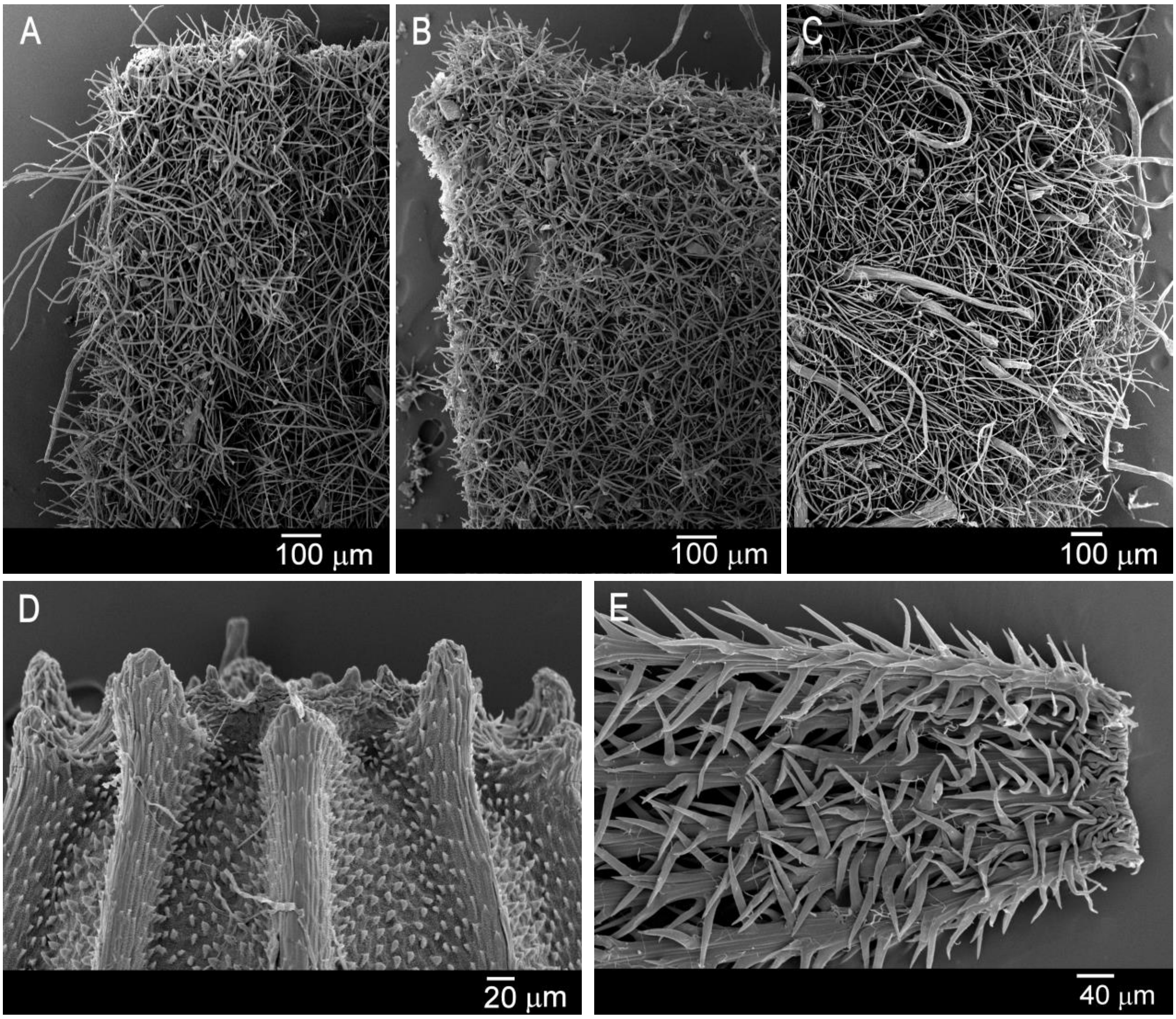

Figure 4.9 *Andryala chevallieri* Barratte ex L. Chevall. A – Stem indumentum, B – Leaf indumentum, C – Peduncle indumentum, D – Cypsela apex, E – Pappus base.

4.6.3 Comments on taxonomy and nomenclature

Andryala chevallieri Barratte ex L. Chevall. was validly described by Chevallier (1900). Although the original material was collected by Chevallier, the author of the name appears to be Barratte, according to the voucher information in the protologue: "*Andryala chevallieri* Barr. ap. Chevall. Pl. Sah. Alg. exs. nº 341". According to Chevallier (1900) it is closely related to *A. nigricans* Poir., differing mainly by the indumentum: "*Species nostra valde affinis A. nigricanti Poir. (Voy. II, 228; Desf. Fl. Atl. II, 236) sed praesertim differt habitu, facie ubique cinereo nec in parte superiore nigricante, indumento ramorum involucrorumque pulverulento pilis nonnullis simplicibus glanduliferis sparsis donato nec tomentoso pilis numerosis simplicibus glanduliferis confertis longis nigricantibus crebre glanduloso-piloso, indumento pulverulento etiam in parte inferiore caulis persistente nec tam evanescente ut caulis inferne pro caule glabro etiam glaberrimo habeatur.*" Nonetheless, *A. chevallieri* is quite different from *A. nigricans* Poir. considering other characters (e.g. longer peduncles, larger capitula, shorter receptacle setae, longer cypselae).

4.6.4 Karyology

The somatic chromosomes number 2n = 18 was determined by Stebbins *et al.* (1953) on material under the name *Andryala jahandiezii* Maire var. *microcarpa* Maire, collected in Saïdia by A. Faure. Several specimens collected by A. Faure in Saïdia (in Northeast Morocco) are hosted at the P herbarium and these correspond rather to *A. chevallieri* Barratte ex L. Chevall. than to *A. jahandiezii* Maire var. *microcarpa* Maire.

4.6.5 Ecology and conservation status

Andryala chevallieri Barratte ex L. Chevall. occurs in sandy sites, including pastures and dunes (Chevallier 1900; Jahandiez & Maire 1934). It can be found near large sand dunes created by the Sahara desert winds (Faure 1923). In what concerns the conservation status, in *Catalogue des plantes vasculaires rares, menacées ou endémiques du Maroc* this species is considered rare (Fennane *et al.* 1998).

4.6.6 Geographic distribution

Andryala chevallieri Barratte ex L. Chevall. is endemic to Morocco and Algeria (Fennane *et al.* 1998). Chevallier (1900) assigned this species to the province of Oran, in Northwest Algeria, near the border to Morocco ("*In provincia Oranensi australi, imperio Maroccano confini*"). Similarly Faure (1923) found this species in Aïn Sefra (South of Oran, Algeria). Although considering the Algerian Sahara as the distribution area of this species, Jahandiez & Maire (1934) also cited it for eastern Morocco. Indeed, according to available herbarium material, this *taxon* also occurs in Saïdia, a locality in the northeast Mediterranean coast of Morocco, at the Moroccan-Algerian border (Figure 4.10).

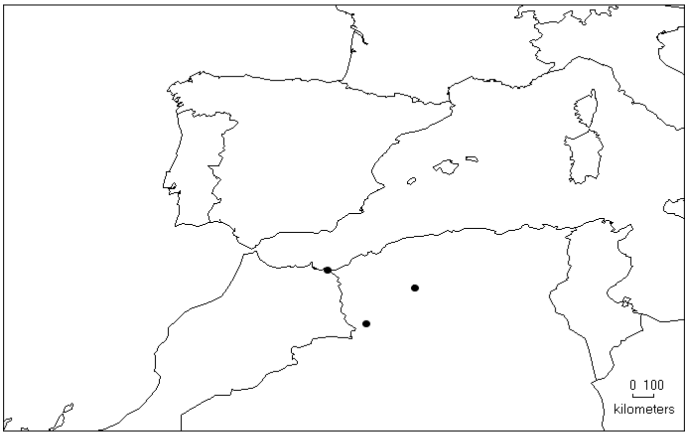

Figure 4.10 Distribution area of *Andryala chevallieri* Barratte ex L. Chevall., according to studied material.

4.6.7 List of studied material

Algeria:

[Loc. incert.] O. Cheddad (Hauts plateaux), Battandier, s/nº, MPU-Maire.

[Naama]: Sud. Oranais - Aïn-Sefra, [?] Grande dune, 20-V-1922, [?], s/nº, LISU 55330. Sud. Oranais, Environs d´Aïn-Sefra, Grande dune (1100 m), 01-VII-1934, A. Faure, s/nº, MPU. Sud-Oranais Environs de Ain-Sefra, Grande Dune, 1100 m, 01-VI-1934, A. Faure, MA 139352. Ain-Sefra, in agger arenae mobilis, 29-V-1899, L. Chevallier, MA 139351. Sud-Oranais, Ain-Sefra, 20-V-1922, MA 139350. Département d´Oran: Ain-Sefra, au pied de la grande dune, 1100 m, 10-V-1929, R. L. Cesve, MA 470223.

Morocco:

[Berkane]: Saïdia, prés de Martimprey-du-Kiss, sables maritimes, 09-V-1937, A. Faure, MPU-Maire. Berkane, Saïdia, Plage de Saidia, sables maritimes, 12-V-1929, A. Faure, MA, 139358. Saïdia, Plage de Saïdia, sables maritimes, 12-V-1929, A. Faure, MA 139359.

4.7 *Andryala cossyrensis* Guss. Fl. Sicul. Syn. 2(1): 407. 1843

≡ *Andryala tenuifolia* (Tineo) DC. var. *lyrata* Guss. ex DC. Prodr. 7(1): 245. 1838
≡ *Andryala sinuata* L. var. *cossyrensis* (Guss.) Arcang., Comp. Fl. Ital. 447. 1882
≡ *Andryala rothia* Pers. subsp. *cossyrensis* (Guss.) Maire in Emb. & Maire, Cat. Pl. Maroc 4: 1167. 1941
Ind. loc.: "in insulâ Pantellaria"
Typus: [Italy] "Isola Pantellaria, 1831", *M. Gussone* – Lectotype (designated by Ferreira *et al.* 2015b, see Appendix 4): G 00493395.
?= *Rothia tenuifolia* Tineo. Cat. Pl. Hort. Panorm. 280. 1827
Andryala tenuifolia (Tineo) Ten., Syll. Pl. Fl. Neapol. App. 5: 38. 1842
Ind. loc.: "Crescit in arvis prope Panormum; alli Ficarazzi"
Typus: [Italy] "Ficarazzii" – Lectotype (designated here): PAL11873 (specimen at the top).
= *Andryala gracilis* Pau in Bot. Soc. Arag. 17: 130. 1918
Andryala integrifolia L. subsp. *eu-integrifolia* Maire var. *gracilis* (Pau) Maire in Jahandiez & Maire, Cat. Pl. Maroc, 3: 841. 1934
Ind. loc.: "D. Angel Aterido, ayudante jardinero que fue del Jardín Botánico de Madrid y en la actualidad en el Museo de Ciencias Naturales de Barcelona, durante el servicio militar en el Rif recogió algunas plantas que he podido revisar durante mi corta estancia en la capital del Principado Catalán este año pasado. … Las etiquetas de las muestras solamente traen una localidad, Tifasor; y fueron recogidas desde el día 10 al 30 de Julio del año 1915…"
Typus: [Morocco] "Trifasor (Mellila), 22 July 1915", *Angel Aterido* – Lectotype (designated here): MA139218! (specimen on the upper left-hand corner); isolectotypes: MA139218! (remaining specimens).
_ *Andryala gracilis* Caball. in Bull. Soc. Hist. Nat. Afrique N. 28: 364. 1937. *nom. illeg.*

4.7.1 Typification

Candolle (1838) described *Andryala tenuifolia* β *lyrata* Guss. ex DC. stating that Gussone saw the specimen but did not validly publish the name ["*A. tenuifolia* β *lyrata* (Guss.! in litt.")]. Later Gussone (1843) validly published *A. cossyrensis*, citing *A. tenuifolia* β *lyrata* Guss. ex DC. as a synonym. Given that Gussone merely transferred *A. tenuifolia* β *lyrata* to species rank, the lectotype was chosen from herbarium material that was used as basis for the original description. Indeed, in the Candolle collection held at G there is a specimen under *Andryala tenuifolia* β *lyrata* DC., handwritten by Candolle, which fits the original description very well (G00493395). Besides, the collector and collection locality match those in the protologue. Therefore, this specimen was designated as lectotype (Ferreira *et al.* 2015b, see Appendix 4).

Concerning *Rothia tenuifolia* Tineo, material from the Vincenzo Tineo collection was located at the PAL herbarium. According to the curator Gianniantonio Domina (pers. comm.) there are no specimens labelled *Rothia*, but there are some under the name *A. tenuifolia* collected in Ficarazzii (locality mentioned in the protologue). In his opinion, the specimen PAL11874 should be original material as the label was handwritten by Tineo himself. Gianniantonio Domina (pers. comm.) also informed that the specimens on the herbarium sheet PAL11873 were labelled as *A. tenuifolia* by Todaro, pupil of Tineo. Thus, the probability of it corresponding to original material is quite high. Given the poor condition of PAL11874, the specimen at the top of the herbarium sheet PAL11873 could be designated as lectotype. However, it is not quite clear if *Andryala tenuifolia* (Tin.) Tenore (sub *Rothia tenuifolia* Tin.) corresponds to *A. cossyrensis* Guss. In fact, Gussone (1843) considered *A. tenuifolia* (Tin.) DC. and *A. cossyrensis* Guss. as distinct species. Although the specimens on sheet PAL11874 resemble *A. cossyrensis* Guss., the same can not be said for the specimen PAL11873 owing to its poor conservation state. Given the important nomenclatural implications, an observation in person of the type material will be necessary to further clarify this issue.

The lectotype of *Andryala gracilis* Pau was designated based on the collection date and locality as well as the collector. Pau (1918) stressed that the Moroccan specimens collected by D. Angel Aterido from the 10th to the 30th of July of 1915 are all from Tifasor. Indeed, the specimens on the herbarium sheet MA139218 are from this locality and both the collection date and collector are in agreement with the information in the protologue and, therefore, they are here considered as type specimens. A specimen from the Barcelona herbarium (BC36093) bears a label considering it type material. However, on the herbarium sheet we can read "*Andryala gracilis* Pau n. sp., Bisanor, Melilla (Tifasor?), Legit. Aterido, Jul. 1916" which means that it was collected after the publication of the name. Besides, the collection locality is dubious. Therefore, it is not fit for typification.

4.7.2 Description

Annual herb, single-stemmed or more rarely multi-stemmed. STEMS 12–34 cm, usually branched from the base or in the upper half (Figure 4.11A), stellate-tomentose sometimes with some glandular hairs above (Figure 4.12A). LEAVES puberulous to tomentose on both faces with stellate hairs and no glandular hairs (Figure 4.12B); lower leaves numerous, in rosette, 44–63(-78) x 5–16 mm, attenuate into a petiole 7–11 mm, usually lanceolate, apex obtuse or less frequently acute, and margin pinnatifid to pinnatipartite or rarely lobate; cauline leaves 22–46(-56) x 4–18 mm, usually semiamplexicaul, narrowly ovate-lanceolate, base rounded or rarely cordate, apex acute, and margin pinnatifid to pinnatipartite; upper leaves 11–22(-28) x 2–5.5 mm, amplexicaul, narrowly ovate-lanceolate to ± linear-lanceolate, base rounded or rarely ± cordate, apex acute to acuminate and margin entire or rarely ± pinnatifid at the base.

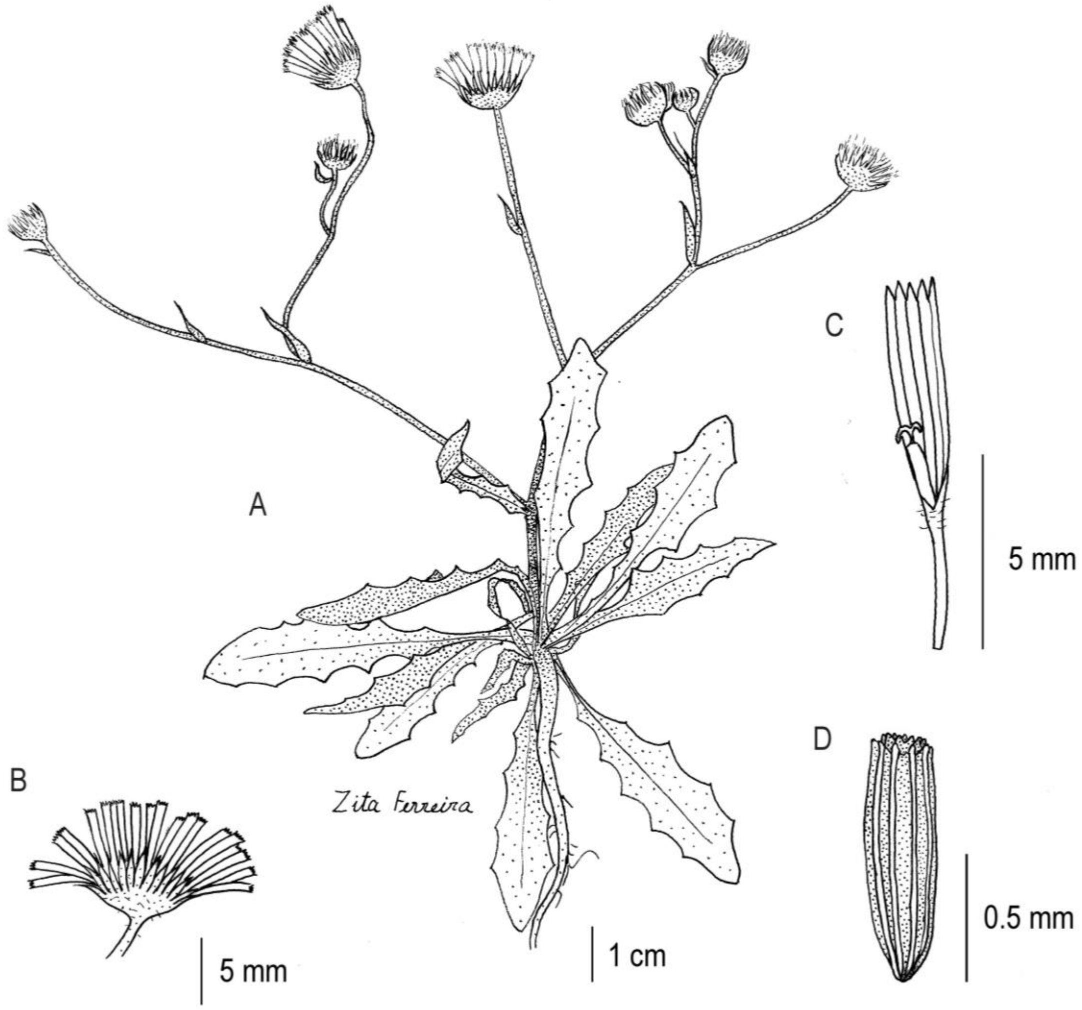

Figure 4.11 *Andryala cossyrensis* Guss. A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

INFLORESCENCE corymbiform with 3–7, sometimes with solitary capitula, longly pedunculate. CAPITULA 11–19 mm in diameter (Figure 4.11B); peduncles 18–36(-44) mm, stellate-tomentose with a few short glandular hairs 0.3–0.7 mm (Figure 4.12C); involucre 7–10 x 8–12 mm, campanulate at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 5–7 x 0.8–1.2 mm, lanceolate, apex sometimes purplish, usually acuminate or more rarely subulate, involute enfolding a floret, pubescent-tomentose with stellate hairs and few yellow glandular hairs 0.2–1.2 mm; internal involucral bracts 5–7 x 1–1.7 mm, with broad scariose margins, receptacle flat to slightly convex, ± pubescent with setose hairs 0.8–2.5(-3) mm (± up to 2 times longer than the cypselae). FLORETS ligulate, golden yellow, the external with a tube of 2–4 mm and ligule of 4–7 x 0.8–2.2 mm (Figure 4.11C). CYPSELAE 0.9–1.2 x 0.3–0.4 mm (Figure 4.11D), oblong, dark brown with white ribs, apex with a ring of thin teeth largely exceeding the prolongation of the ribs (Figure 4.12D); pappus of dirty-white bristles 3–5 mm, denticulate at the base (Figure 4.12E).

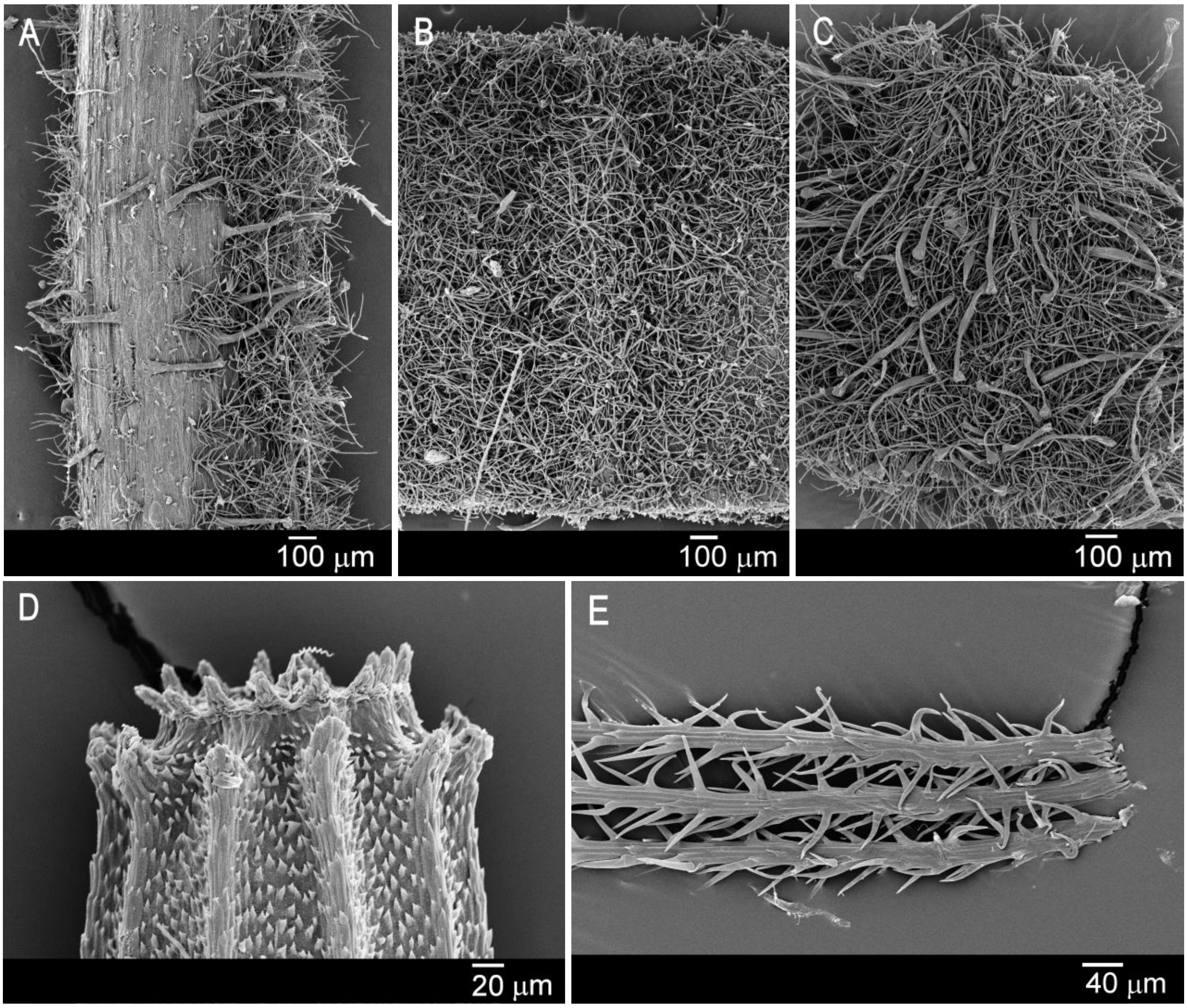

Figure 4.12 *Andryala cossyrensis* Guss. A – Stem indumentum, B – Leaf indumentum, C – Peduncle indumentum, D – Cypsela apex, E – Pappus base.

4.7.3 Comments on taxonomy and nomenclature

Tineo (1827: 280) provided a very brief description of the Italian *Rothia tenuifolia* Tineo ("*Laevissime lanuginosa. Caule basi ramosissimo, erecto, striato; foliis semi-amplexicaulibus, lanceolato-linearibus, inferné latiusculi, subintegerrimis; floribus corymbosis; calycibus pilosis, pilis nigricantibus.*"). This description is somewhat vague and could fit either *A. cossyrensis* Guss. or *A. dentata* Sm. Nonetheless, De Candolle (1838) recognised *A. dentata* Sm. and *Andryala tenuifolia* (Tineo) DC. as distinct species, indicating *Rothia tenuifolia* Tineo as the basionym of the latter. Moreover, De Candolle (1838: 245) admitted two varieties: *A. tenuifolia γ arenaria* [the basionym of *A. arenaria* (DC.) Boiss. & Reut.]. and *A. tenuifolia* β *lyrata* Guss. ex DC. However, De Candolle (op.cit.) expressed some doubts regarding the taxonomic position of the latter variety: "*An spec. forte distinguenda*?". Indeed, some years later Gussone (1843) transferred *A. tenuifolia* β *lyrata* Guss. ex DC. to a species rank and named it *A. cossyrensis* Guss. after an Italian island nowadays known as Pantelleria (ancient Cossyra). Curiously, a year before, Tenore (1842) transcribed the original description of *Rothia tenuifolia* Tineo, suggesting a new combination: *Andryala tenuifolia* (Tineo) Ten. In view of the foregoing, *Andryala tenuifolia* (Tineo) DC. does not correspond to *Andryala tenuifolia* (Tineo) Ten. as De Candolle (op.cit.) included two distinct *taxa* in *Andryala tenuifolia* (Tineo) DC.

Over the years *A. cossyrensis* Guss. has been confounded with different *Andryala* species by several authors. For instance, Arcangeli (1882) considered it as a mere variety of the very polymorphic *A. integrifolia* L., proposing the combination: *A. sinuata* L. var. *cossyrensis* (Guss.) Arcang. Gussone (1843) recognised for the flora of Sicily and adjacent islands *A. dentata* Sm. and *A. cossyrensis* Guss., among other *Andryala taxa*. However, the description of *A. dentata* by Gussone does not match *A. dentata* Sm. Actually, *A. dentata* sensu Guss. and *A. cossyrensis* Guss. share similar morphologically features (e.g. capitula twice as large, florets golden yellow, largely exceeding the involucral bracts) and differ mainly by the indumentum and leave margin. Therefore, *A. dentata* sensu Guss. should be included in *A. cossyrensis* Guss. One could argue that the description of *A. dentata* sensu Guss. reminds that of *A. arenaria* (DC.) Boiss. & Reut. ("*A. molliter tenueque cinereo-tomentosa, caule erecto basi simplici, foliis radiculibus oblong-lanceolatis dentato-subsinuatis subundulatis … pedunculis anthodiisque floccoso-tomentosis et setoso-glandulosis*") but there is no reference to cauline leaves with an expanded base rounded to cordate, a very good diagnostic character of this species. Besides, while *A. arenaria* (DC.) Boiss. & Reut. is found in the Iberian Peninsula and North Africa (Morocco and Algeria), *A. cossyrensis* Guss. grows in North Africa (Morocco, Algeria, Tunisia) and Italy.

As mentioned before, although Murbeck (1905) recognised *A. cossyrensis* Guss. and *A. arenaria* (DC.) Boiss. & Reut. as distinct species, Emberger & Maire (1941) placed these two *taxa* in *A. rothia* Pers. and suggested a new combination: *A. rothia* Pers. subsp. *cossyrensis* (Guss.) Maire.

Pau (1918: 130) described *Andryala gracilis* Pau as a new species, according to the following text: "*Annua, gracilis, párvula, ad summum 12 cm.; intricata-ramosissima, tomentosa, glabrescens et virescens, indumento deterso demum, caule basi ramoso; foliis lanceolato-linearibus, basilaribus sub-runcinatis, dentatis, ramealibus integris; pedunculis glandulosis, calathiis parvis, squamis linearibus cuspidatis, achaeniis nigricantibus, costis pallidioribus*." Nonetheless, it seems to correspond to a dwarfish form of *A. cossyrensis* Guss. Indeed, similarly to *A. gracilis* Pau, *A. cossyrensis* Guss. is slightly tomentose, stems sometimes branched, basal leaves in rosette, lower cauline lyrate-pinnatifid and upper narrow-linear, acuminate, entire, inflorescence subcorymbose, peduncles long and involucre slightly tomentose, ligules two times longer than the involucral bracts. Consequently, *A. gracilis* Pau can be considered a heterotypic synonym of *A. cossyrensis* Guss. Nonetheless, Jahandiez & Maire (1934) placed *A. gracilis* Pau in *A. integrifolia* L. as *A. integrifolia* L. subsp. *eu-integrifolia* Maire var. *gracilis* Pau. Caballero (1935) made reference to two specimens collected in a southwestern locality of Morocco which he identified as *A. gracilis* Pau.

However, according to Maire (1937) these specimens do not correspond to *A. gracilis* Pau. but to *A. cossyrensis* Guss. Maire (op. cit.) referred to this material as *A. gracilis* Caball. Thus, this name is a later homonym of the validly published *A. gracilis* Pau and is therefore illegitimate. However, it does indeed correspond to *A. cossyrensis* Guss. but not to the dwarfish form.

4.7.4 Karyology

The somatic chromosome number of *Andryala cossyrensis* is 2n = 18 (Pavone *et al.* 1981; Brullo *et al.* 1991). This number was first determined on plant material ascribed to *A. tenuifolia* (Tineo) DC. and collected in Sicily (Italy). Later chromosome counts were performed on material from Pantelleria and the voucher is currently deposited at CAT herbarium under *A. cossyrensis* Guss.

4.7.5 Ecology and conservation status

Andryala cossyrensis Guss. occurs on volcanic dry slopes (Gussone 1843; Pojero 1902). This species also grows in rocky pastures of arid regions as well as in planes and mountains of low and medium altitude (Lindberg 1932; Jahandiez & Maire 1934; Pottier-Alapetite 1981). Under the name *A. rothia* Pers. subsp. *cossyrensis* (Guss.) Maire, it was reported as occurring also in rocky or steppic pastures (Pottier-Alapetite 1981). According to available herbarium data, it can be found between 100-1200 m, on sandy and stony substrates, including sandy grasslands, stony river banks and coastal limestone rocks.

4.7.6 Geographic distribution

According to available herbarium data, *Andryala cossyrensis* Guss. is chiefly a Northwest African species, occurring in Morocco, Algeria, and Tunisia, although it also present in the Italian islands of Sicily and Pantelleria (Figure 4.13).

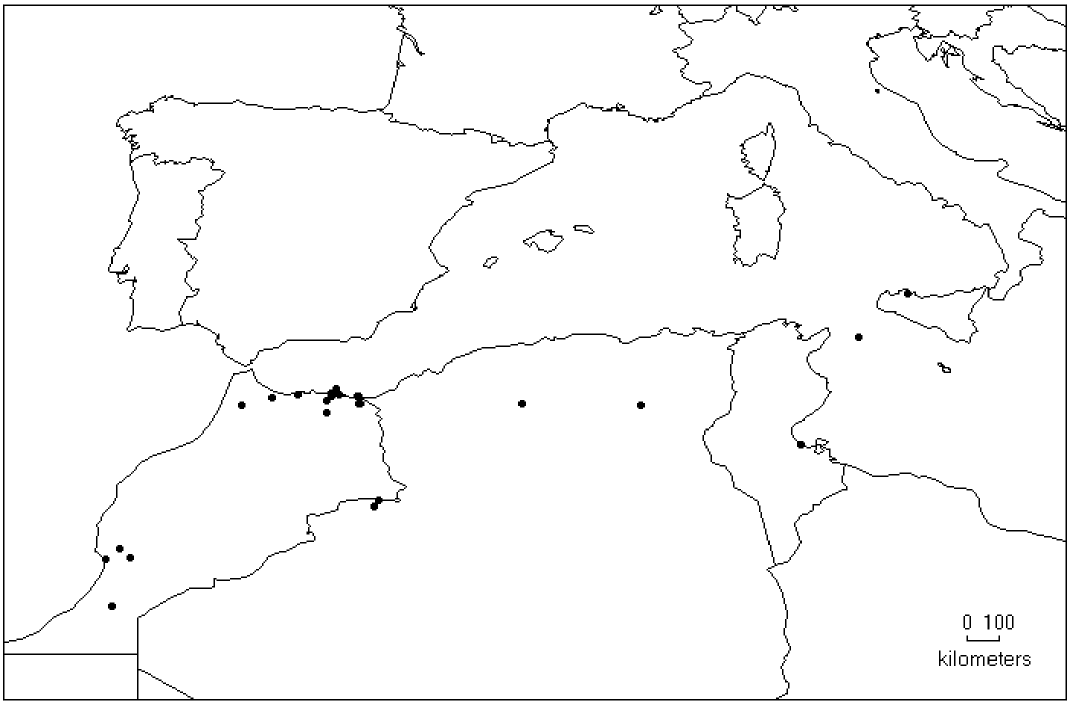

Figure 4.13 Distribution area of *Andryala cossyrensis* Guss., according to studied material.

Originally, it was assigned to the Island of Pantelleria, situated between Sicily and Tunisia (Gussone 1843). Years before, it had been cited exactly for the same locality by De Candolle (1838), under the name *A. tenuifolia* β *lyrata* Guss. Likewise, several later authors (e.g. Arcangeli 1882; Sommier 1922; Cattarini 1976; Pignatti 1982) assigned it for this island, although sometimes under different names. Pojero (1902) assigned *A. cossyrensis* Guss. not only to Pantelleria, but also to Sicily. Later a larger distribution area was indicated, including also Tunisia, Algeria and Morocco (Murbeck 1905; Jahandiez & Maire 1934). Several other authors cited *A. cossyrensis* Guss. for Morocco (e.g. Lindberg 1932; Sennen & Mauricio 1934).

4.7.7 List of studied material

Algeria:	
[Béchar]:	Sud Oranais: Ben-Zireg, Djebel Antar, H. Humbert, MPU-Maire,
[Biskra]:	Biskra, in petrosis fluviorum, 11-V-1904, L. Chevallier, MPU-Maire. Biskra, in petrosis fluviorum, 11-V-1904, L. Chevallier, MPU-Maire. Biskra, [?] ad Ain-Salabin, in glareosis, 13-VI-1902, L. Chevallier, MA 139306
Algeria:	
[Tamanghasset]:	In montibus Atakor-n-Ahaggar, in lapidosis vulcanicis montis Amezzeroni, 2400-2500 m, MPU-Maire.
Italy:	
[Palermo]:	Palermo, in cultis, H. Rofs., s/nº, MA 139355.
[Trapani, Sicily]:	Pantelleria, 1846, Guss., s/nº, P 03759996.
Marocco:	
[Al Hoceïma]:	Souk-el-Had Rouadi, In lapidosis calcareis litoris rifani, 300 m, 21-VI-1929, MPU-Maire.
[Agadir-Ida Ou Tanane]:	vallée d'Imouzzer des Ida-ou-Tanane, prés de Souk el Khemis d'Imouzzer, broussailles et pelouses thérophytiques sur sol pierreux calcaire, 1100 m, 10-VI-1988, J. Molero, A. M. Romo & A. Susanna, MA 537776.
[Berkane]:	Berkane, vallon d´Ouaklane, pelouses sablonneuses, 12-V-1933, A. Faure, MPU-Maire. Vallon de Zegzel, rocailles 400 m, 08-V-1928, A. Faure, MPU-Maire. Vallon d'Ouaklane, Pelouses sablonneuses, 12-V-1933, A. Faure, MA 139356. Alad, Sattut: Muluya, alluvions, 28-V-1935, F. Sennen et Mauricio, MA 162564. Vallon d´Ouaklane, Pelouses sablonneuses, 12-V-1933, A. Faure, MPU-Maire.
[Guelmin]:	prope Taghjicht, In lapidosis arenaceis Anti-Atlantis, 600 m, 06-IV-1935, Maire, MPU.
[Harare]:	M. Djebel Grouz, rocailles calcaires à Aïn-Yalou, 1200 m, 29-IX-1918, MPU-Maire.
[Nador]:	Beni Bu-lahi, Hab. in arenosis collis Cudia Arneb dicti, ad 550 m, 29-V-1929, MPU-Maire. Mellila, à Beni-Sicar, sites sablonneux, 18-V-1933, Sennen et Mauricio, MPU-Maire. Beni Sidel, 17-V-1934, F. Sennen et Hno. Mauricio, MA 139221. Tifasor, Mellila, 22-VII-1915, Angel Aterido, MA 139218. Kebdana, à Ulad-el-Hach, friches, 25-VII-1932, Sennen et Mauricio, MA, 139219. Beni Bu-lahi, in arenosis collis Cudia Arneb, ad 550 m alt., 19-V-1929, MA 139295. Beni-Bu-Yahi, Aguada de Afso, 07-V-1933, Sennen et Mauricio, MA 139296. Melilla, à Beni-Sicar, sites sablonneux, 18-V-1933, Sennen et Mauricio, MA, 139293. Beni Bu-lahi, in arenosis collis Cudia Arneb dicti, ad 550 m alt., 29-V-1929, Sennen et Mauricio, MA 139292. Segangane, escarpements de Atlaten (Beni-Sidel), 09-VII-1934, Sennen et Mauricio, MA 139309. Beni Ansar, Farkana, Cabo Tres Forcas, 100m, suelos pedregosos sobre subtrato volcanico, 03-V-2000, O. Fiz, V. Valcarcel, P Vargas, 204PV00, MA 657443. Cabo de Água, Melilla, F. Sennen, MA 139220. Melilla, Masusa, 08-VII-1932, Pardo & Martí, 402, MA 443610.
[Tarondant]:	Tarondant, arganietum zone de crue, 09-IV-1940, J. Gattefossé, MPU-Maire. Taroudant, M. Grand Altas, Bigoudine, gréves de l´Oued Massi, 600-700 m, 22-IV-1922, maire, MPU-Maire.
Tunisia:	
[Gabés]:	in arenosis palmetorum, prope Gabés, 1-V-1854, Kralik, P 02462497. Sebkhet Zarkin pr. Gabés, 04-IV-1912, H. Humbert, s/nº, MPU-Maire.

4.8 *Andryala crithmifolia* Aiton, Hort. Kew. 3: 129. 1789

Ind. loc.: “Nat. of Madeira, Mr. Francis Masson, Introd. 1778”
Typus: [Portugal, Madeira] “Madera, 1776”, *Fr. Masson s.n.* – Lectotype (designated by Ferreira *et al*. 2015b, see Appendix 4): BM000829762!

4.8.1 Typification

Aiton (1789) described several new species cultivated at the Royal Botanic Gardens, Kew, among them *A. crithmifolia*. According to the protologue, this species was collected by Francis Masson and introduced into the Royal

Botanic Gardens in 1778. Indeed, Masson was the first official plant collector of the Royal Botanic Gardens, Kew, who undertook extensive plant collecting on the Macaronesian archipelagos of Madeira, the Azores and the Canaries, between 1776 and 1779 (Francisco-Ortega *et al*., 2008). Furthermore, the specimens collected by Masson in Macaronesia, together with material grown from the introduced seeds, formed the basis for the description of many new species, mostly in the three volumes of the first edition of *Hortus Kewensis* (Francisco-Ortega *et al*., 2008). Considering that the core of the herbarium specimens collected by Masson in Macaronesia is currently deposited at BM (Francisco-Ortega *et al.,* 2008), the specimen BM000829762 was designated as lectotype (Ferreira *et al*. 2015b, see Appendix 4).

4.8.2 Description

Biennial herb, single or multi-stemmed. STEMS 52–152 cm, woody at the base, branched from the base or in the upper third, pubescent to tomentose below with stellate hairs and tomentose above with stellate hairs and glandular hairs. LEAVES glaucous, crowded towards the base, sparse above, tomentose on both faces with stellate hairs sometimes mixed with few glandular hairs on the upper leaves; lower leaves 94–205 x (18-)30–82 mm, with petiole 16–57 mm broader at the base, obovate-lanceolate to lanceolate, apex acute to acuminate, and margin deeply 1-2 pinnatisect, segments often filiform; cauline leaves 47–135 x 13–54(-66) mm, attenuate in petiole of 5–38 mm, oblong to lanceolate, apex acute to acuminate, and margin pinnatisect; upper leaves 10–30 x 1–7 mm, semiamplexicaul, ± linear-lanceolate, base ± rounded, apex frequently acuminate, and margin frequently entire. INFLORESCENCE corymbose with 5–12 capitula. CAPITULA 10–26 mm in diameter; peduncles 10–31 mm, with some stellate hairs and numerous short glandular hairs 0.4–0.9 mm; involucre 6–12 x 9–19 mm, ± campanulate at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 3.5–9.5 x 1–1.5 mm, lanceolate to linear-lanceolate, apex frequently acuminate, involute enfolding a floret, the outer face stellate-hairy with dense yellow glandular hairs 0.2–1.1 mm; internal involucral bracts 3.8–7.5 x 1–1.4 mm, with ± broad scariose margins, receptacle flat to slightly convex, villous with long setose hairs 3.5–7 mm (3 to 5 times longer than the cypselae). FLORETS ligulate, golden yellow, the external with a tube of 2–3.3 mm and ligule of 4.8–8 x 1.6–2.9 mm; ligule with all apical teeth stellate-hairy. CYPSELAE 1.2–1.9 x 0.4–0.6 mm, usually obconical, dark brown with reddish brown ribs, apex with an inner ring of teeth ± equalling the prolongation of the ribs; pappus of dirty-white bristles 4–5.5 mm, denticulate to pilose-denticulate at the base.

4.8.3 Karyology

According to available literature, there are no reports on the chromosome number of *Andryala crithmifolia.*

4.8.4 Geographic distribution

The typical subspecies occurs only in the south coast of Madeira and is restricted to a single locality to the east of Funchal (Pináculo, São Gonçalo) (Figure 4.14). In the past it was found in several sites to the east of Funchal, including Garajau where it grew abundantly (Lowe 1868; Menezes 1914).

Andryala crithmifolia subsp. *coronopifolia* is currently known from one population at Cabo Girão, the second highest cape in the world, to the west of Funchal (Figure 4.14). Based on herbarium material and earlier literature (Lowe 1868; Press 1994), this *taxon* possibly had a wider distribution in the past, having occurred to the west of Cabo Girão (Ferreira *et al.* 2014b, see Appendix 5).

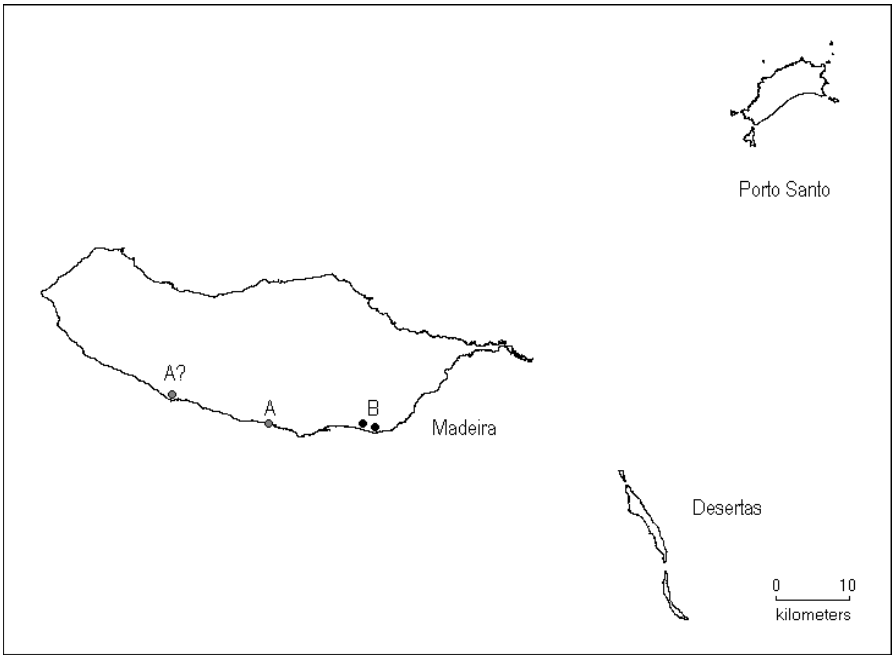

Figure 4.14 Distribution area of *Andryala crithmifolia* Aiton, according to studied material.

A – *A. crithmifolia* subsp. *coronopifolia* (Lowe) M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. (Cabo Girão)
A? – population not found (Ponta do Sol)
B – *A. crithmifolia* subsp. *crithmifolia* (Pináculo).

4.8.5 Key to the *Andryala crithmifolia* Aiton subspecies

1a. Leaf segments less than 2 mm wide; peduncles 10–18 mm; external involucral bracts with glandular hairs 0.2–0.5 mm; ligules 4.8–5.3 x 1.9–2.9 mm. .... *A. crithmifolia* subsp. *crithmifolia*

1b. Leaf segments 2–3 mm wide; peduncles 18–31 mm, external involucral bracts with glandular hairs 0.7–1.1 mm; ligules 5.8–8.0 x 1.6–2.4 mm. .... *A. crithmifolia* subsp. *coronopifolia*

4.8.6 *Andryala crithmifolia* Aiton subsp. *crithmifolia*

4.8.6.1 Description

Biennial herb, single or multi-stemmed. STEMS 52–152 cm, woody at the base, branched from the base or in the upper third (Figure 4.15A), pubescent to tomentose below with stellate hairs and tomentose above with stellate hairs and scarce glandular hairs (Figure 4.16A). LEAVES glaucous, crowded towards the base, sparse above, ± tomentose on both faces only with stellate hairs (Figure 4.16B); lower leaves 96–178 x 33–68 mm, with a petiole 16–26 mm broader at the base, obovate-lanceolate to lanceolate, apex acute to acuminate, and margin 1 to 2 pinnatisect with filiform segments less than 2 mm wide; cauline leaves 56–120 x 18–35(-66) mm, attenuate in petiole of 5–19 mm, oblong to lanceolate, apex usually acute, and margin pinnatisect; upper leaves 10–26 x 1–7 mm, semiamplexicaul, ± linear-lanceolate, base ± rounded, apex acute to acuminate and margin entire or pinnatisect. INFLORESCENCE corymbose, 5–12 capitula. CAPITULA 10–21 mm in diameter (Figure 4.15B); peduncles 10–18 mm, with some stellate hairs and abundant short glandular hairs 0.4–0.7 mm (Figure 4.16C); involucre 6–8 x 9–12(-

14) mm, ± campanulate at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 3.5–5.5 x 1–1.2 mm, lanceolate, apex acute to acuminate, involute enfolding a floret, the outer face stellate-hairy with dense yellow glandular hairs 0.2–0.5 mm; internal involucral bracts 3.8–5 x 1–1.4 mm, with ± broad scariose margins, receptacle usually ± flat, villous with long setose hairs 3.5–5 mm (3 to 4 times longer than the cypselae).

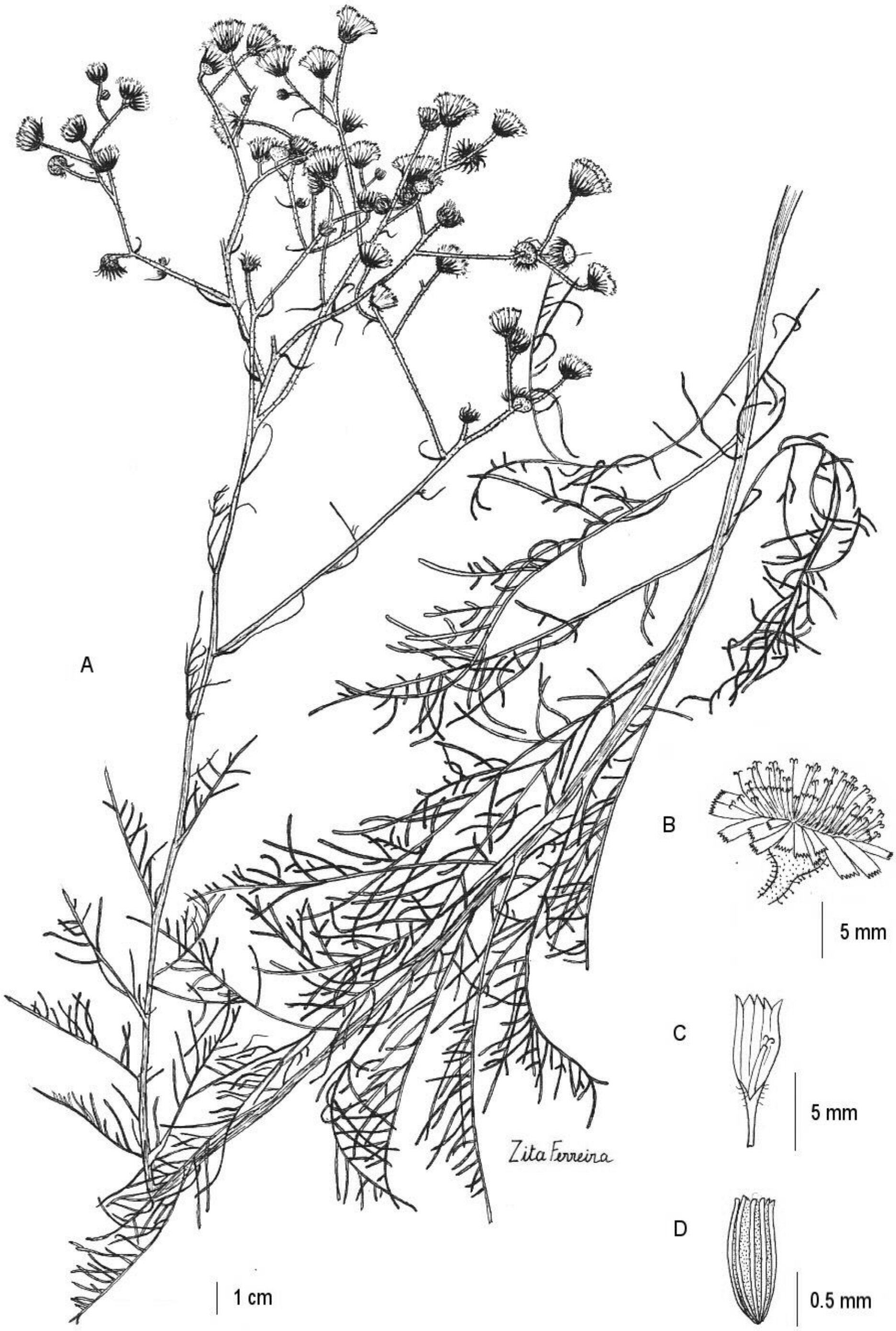

Figure 4.15 *Andryala crithmifolia* subsp. *crithmifolia* A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

FLORETS ligulate, golden yellow, the external with a tube of 2–3.3 mm and ligule of 4.8–5.3 x 1.9–2.9 mm (Figure 4.15C); ligule with all apical teeth stellate-hairy (Figure 4.16D). CYPSELAE 1.2–1.4 x 0.4–0.5 mm (Figure 4.15D), usually obconical, dark brown with reddish brown ribs, apex with an inner ring of teeth ± equalling the prolongation of the ribs (Figure 4.16E); pappus of dirty-white bristles 4–5 mm, denticulate to pilose-denticulate at the base (Figure 4.16F).

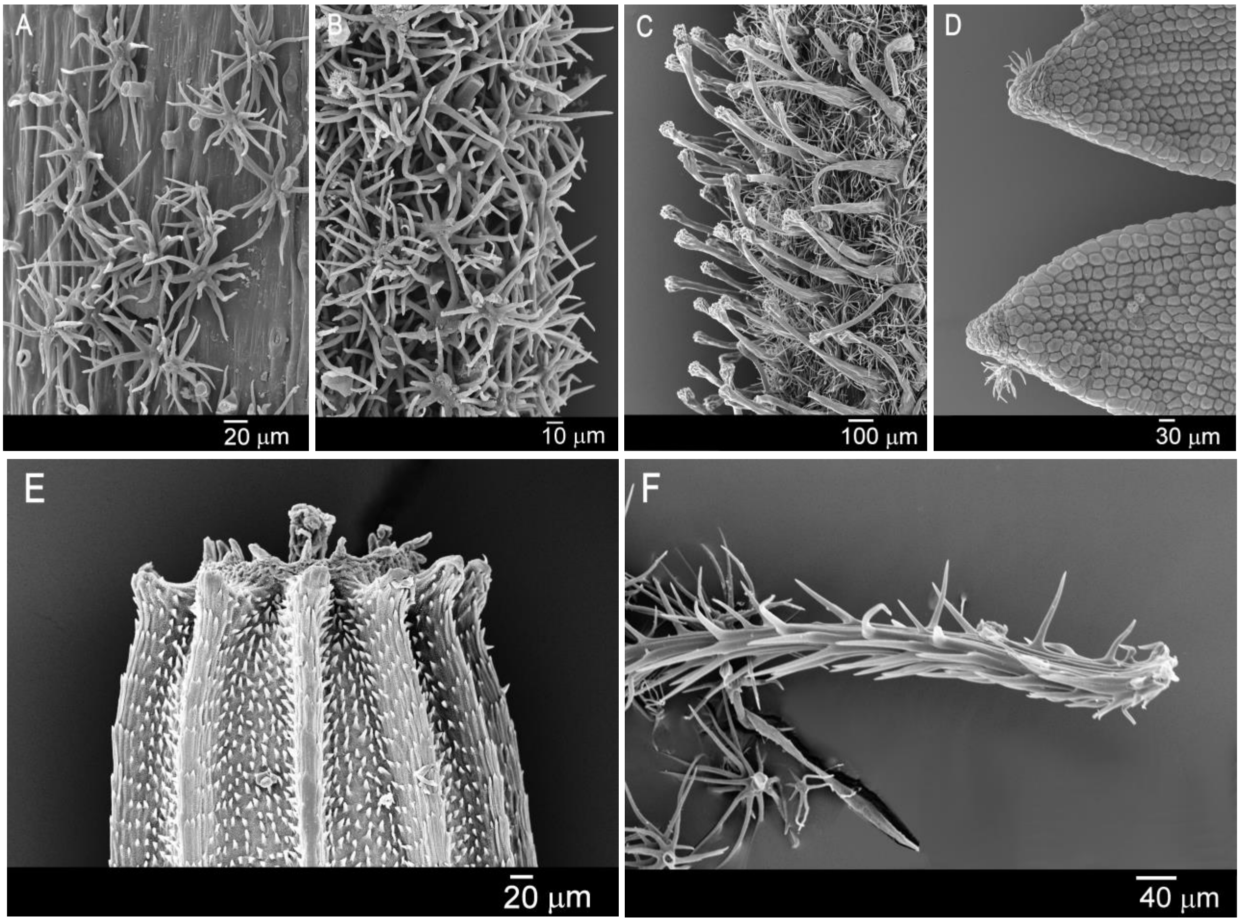

Figure 4.16 *Andryala crithmifolia* subsp. *crithmifolia.* A – Stem indumentum, B – Leaf indumentum, C – Peduncle indumentum, D – Ligule teeth, E – Cypsela apex, F – Pappus base.

4.8.6.2 Comments on taxonomy and nomenclature

Aiton (1789) described *Andryala crithmifolia* Aiton in the following terms: "*A. foliis pinnatis linearibus tomentosis*". Despite the very brief description, *A. crithmifolia* subsp. *crithmifolia* is a very distinct *taxon* within *Andryala* and, therefore, its taxonomic position and nomenclature have remained quite stable throughout the years.

4.8.6.3 Ecology and conservation status

Andryala crithmifolia susbp. *crithmifolia* can be found on rocky and steep sea cliffs in the vicinity of the low micro-forest of Madeiran Olive [Olea maderensis (Lowe) Rivas Mart. & del Arco], also known as Zambujal (Capelo *et al.* 2005). It grows in association with several *taxa*, including *Aeonium glutinosum* (Aiton) Webb & Berthel., *Olea maderensis* (Lowe) Rivas Mart. & del Arco, *Echium nervosum* Dryand., *Carlina salicifolia* (L.f.) Cav., *Globularia salicina* Lam., and *Musschia aurea* (L.f.) Dumort. This *taxon* is a rare endemic and is currently known from one small population. Indeed, the total number of mature individuals is estimated to be less than 50 individuals occurring in a protected area included in Natura 2000 Network. It is included in the Habitats Directive (Annex II) as well as the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention) (Jardim *et al.* 2006). Major threats are landslides, competition with invasive plants, urbanisation and road construction, damage by animals such as rats and rabbits (Jardim *et al.* 2006). Although in the *1997 IUCN Red list of threatened plants A. crithmifolia* Aiton was classified as endangered (Walter & Gillett 1998), it is currently assessed as Critically Endangered B2ac(iv); C2b ver 3.1 (IUCN 2013).

4.8.6.4 List of studied material

Portugal:
[Madeira]: rochas marítimas do Pico de S. Gonçalo, Menezes [?], s/nº, LISU 43557. Pináculo, São Gonçalo, 06-VI-1988, Nóbrega, s/nº, MADJ 06913. Pináculo, São Gonçalo, 10-III-1988, Nóbrega, s/nº, MADJ 05534. São Gonçalo, s/nº, MADJ 00792. Bei der Aussichtsterrasse an der Strasse São Gonçalo, Caniço, 280 m, 07-VII-1971, C. Simon, s/ nº, MADM. Funchal, São Gonçalo, Miradouro do Pináculo, ca. 210 m.s.m., 20-V-1954, J. Malato Beliz, 543, MA 239099. Pináculo, São Gonçalo, junto com *Opuntia tuna, Echium nervosum, Carlina salicifolia, Olea europeae, Foeniculum vulgare*, 30-VI-2006, Z. Ferreira, ZF138, UMad. Pináculo, S. Gonçalo, muito raro e só na falésia, abaixo do miradouro, 12-VIII-2009, Z. Ferreira, ZF260, UMad. Pináculo, S. Gonçalo, na falésia abaixo do miradouro, 12-VIII-2009, Z. Ferreira, ZF261, UMad. Pináculo, S. Gonçalo, na falésia abaixo do miradouro, 12-VIII-2009, Z. Ferreira, ZF262, UMad. Pináculo, caule 86 cm, 30-VI-2006, Z. Ferreira, ZF139.

4.8.7 *Andryala crithmifolia* Aiton subsp. *coronopifolia* (Lowe) M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. stat. & comb. nov. in Silva Lusitana nº Especial: 143-157. 2014 (See Appendix 5)

≡ *Andryala cheiranthifolia* L'Hér. var. *sparsiflora* Lowe subvar. *coronopifolia* Lowe, Man. Fl. Madeira 1(5): 564. 1868
Andryala cheiranthifolia L'Hér. subsp. *varia* ex DC. var. *coronopifolia* (Lowe) Bornm. in Bot. Jahrb. Syst. 33: 489. 1904
Andryala varia Lowe ex DC. subsp. *sparsiflora* Lowe f. *coronopifolia* (Lowe) Menezes, Fl. Madeira. 101. 1914
Andryala glandulosa Lam. subsp. *varia* var. *varia* f. *coronopifolia* (Lowe) R. Fern. in Anuário Soc. Brot. 25: 26. 1959
Ind. loc.: "Mad. in one or two spots only, sea-cliffs at Pta. do Sol at the E end of the beach, and at Magdalena at the tunneled part of the sea-cliff road to the westward beyond the Port." [Lowe, 1868]
Typus: [Portugal, Madeira] "Sea cliffs, Pta. do Sol, 20 July 1850", *Lowe 680* – Lectotype (designated by Ferreira *et al.* 2014b, see Appendix 5): BM000072526!
= *Andryala varia* Lowe ex DC. var. *crithmifolia* DC., Prodr. 7: 246. 1838 (non *A. crithmifolia* Aiton)
Ind. loc.: "In Maderæ rupibus maritimis valdés aridis."
Typus: Not designated.

4.8.7.1 Typification

Lowe (1868: 565) described *A. cheiranthifolia* L'Hér. var. *sparsiflora* subvar. *coronopifolia* (i.e. *A. crithmifolia* Aiton subsp. *coronopifolia*) stressing its limited distribution in Madeira (sea-cliffs of P^{ta} do Sol and at Magdalena). The specimen chosen as lectotype of this taxon (BM000072526) was indeed collected at P^{ta} do Sol and originally labelled in Lowe's handwriting as *A. crithmifolia* Aiton. Later the author attached another label with the name *A. cheiranthifolia* L'Hér. var. *sparsiflora* subvar. *coronopifolia* Lowe (Ferreira *et al.* 2014b, see Appendix 5).

4.8.7.2 Description

Biennial herb, STEMS 73–134 cm, woody at the base, branched from the base or in the upper third (Figure 4.17A), pubescent to tomentose below with stellate hairs and tomentose above with stellate and glandular hairs (Figure 4.18A). LEAVES glaucous, crowded towards the base, sparse above, tomentose on both surfaces, with stellate hairs (Figure 4.18B), sometimes mixed with glandular hairs on the upper leaves; lower leaves 94–210 x 18–65(-83) mm, with petiole 17–36(-57) mm broader at the base, obovate-lanceolate, apex acute to acuminate and margin 1 to 2 pinnatisect with segments less than 2–3 mm wide; cauline leaves 47–135 x 13–40(-54) mm, attenuate in petiole of 8–38 mm, obovate-lanceolate, apex acute to acuminate and margin pinnatisect; upper leaves 15–30 x 2–3 mm, semiamplexicaul, ± linear-lanceolate, base ± rounded, apex acuminate and margin frequently entire.

INFLORESCENCE corymbose with 5–10(-12) capitula. CAPITULA (11-)14–26 mm in diameter (Figure 4.17B), peduncles 18-31 mm with some stellate hairs and numerous short glandular hairs 0.5–0.9 mm (Figure 4.18C); involucre 9–12 x 12–19 mm, ± campanulate, with involucral bracts in 2–3 rows; external involucral bracts 7.7–9.5 x 1.0-1.5 mm, linear-lanceolate, apex acuminate, involute enfolding a floret, the outer face stellate-hairy with dense yellow glandular hairs 0.7–1.1 mm; internal involucral bracts 6–7.5 x 1–1.2 mm with ± broad scariose margins, receptacle flat to slightly convex, villous with setose hairs 4.3–5.5(-7.0) mm (3 to 5 times longer than the cypselae).

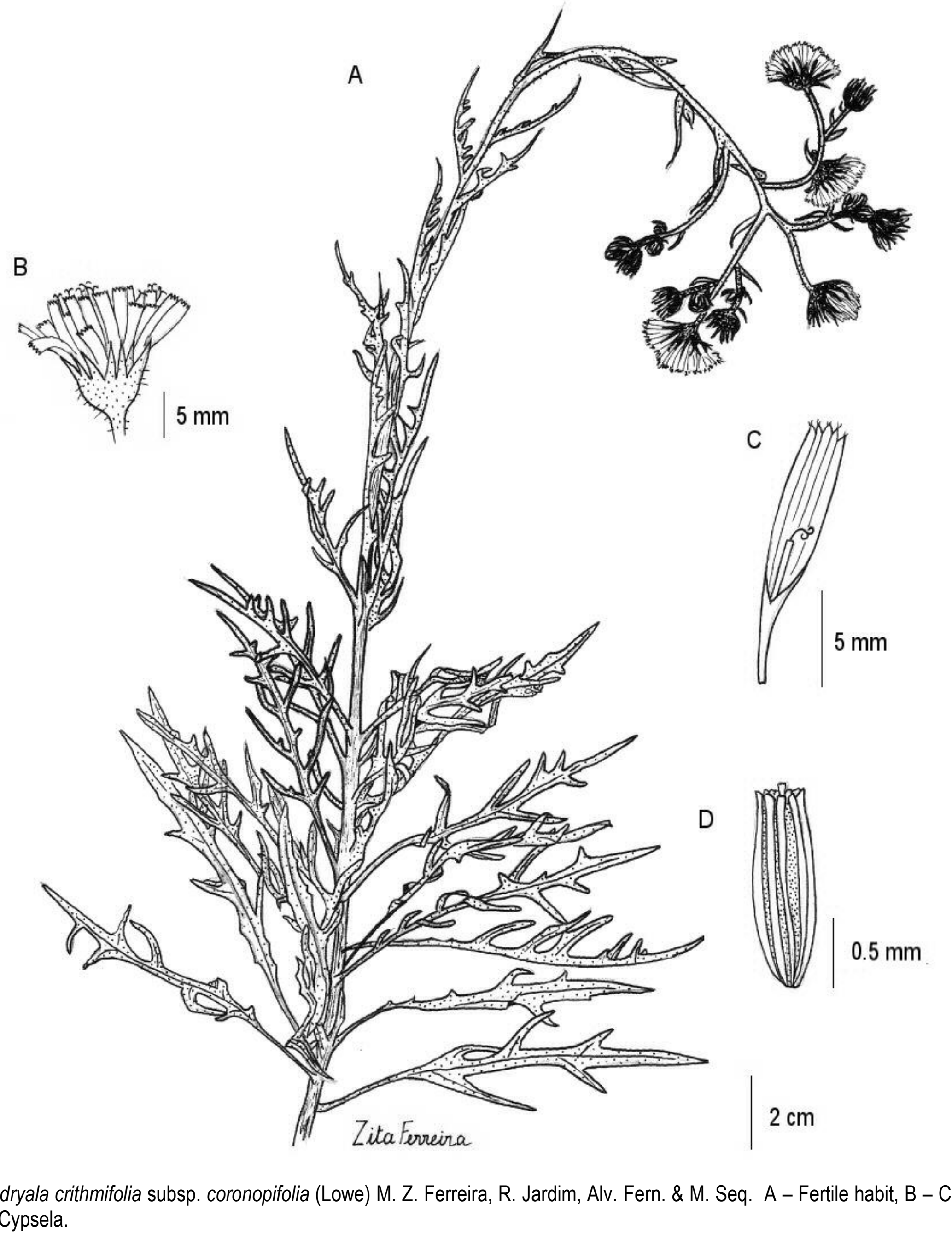

Figure 4.17 *Andryala crithmifolia* subsp. *coronopifolia* (Lowe) M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

FLORETS golden yellow, the external with a tube of tube 2.8–3.2 mm and ligule of 5.8–8.0 x 1.6–2.4 mm (Figure 4.17C); ligule with all apical teeth stellate-hairy (Figure 4.18D). CYPSELAE 1.4–1.9 x 0.4–0.6 mm (Figure 4.17D), usually obconical, dark brown with reddish brown ribs, apex with an inner ring of teeth ± equalling the prolongation of the ribs (Figure 4.18E); pappus of dirty-white bristles 4.7–5.5 mm, denticulate at the base (Figure 4.18F).

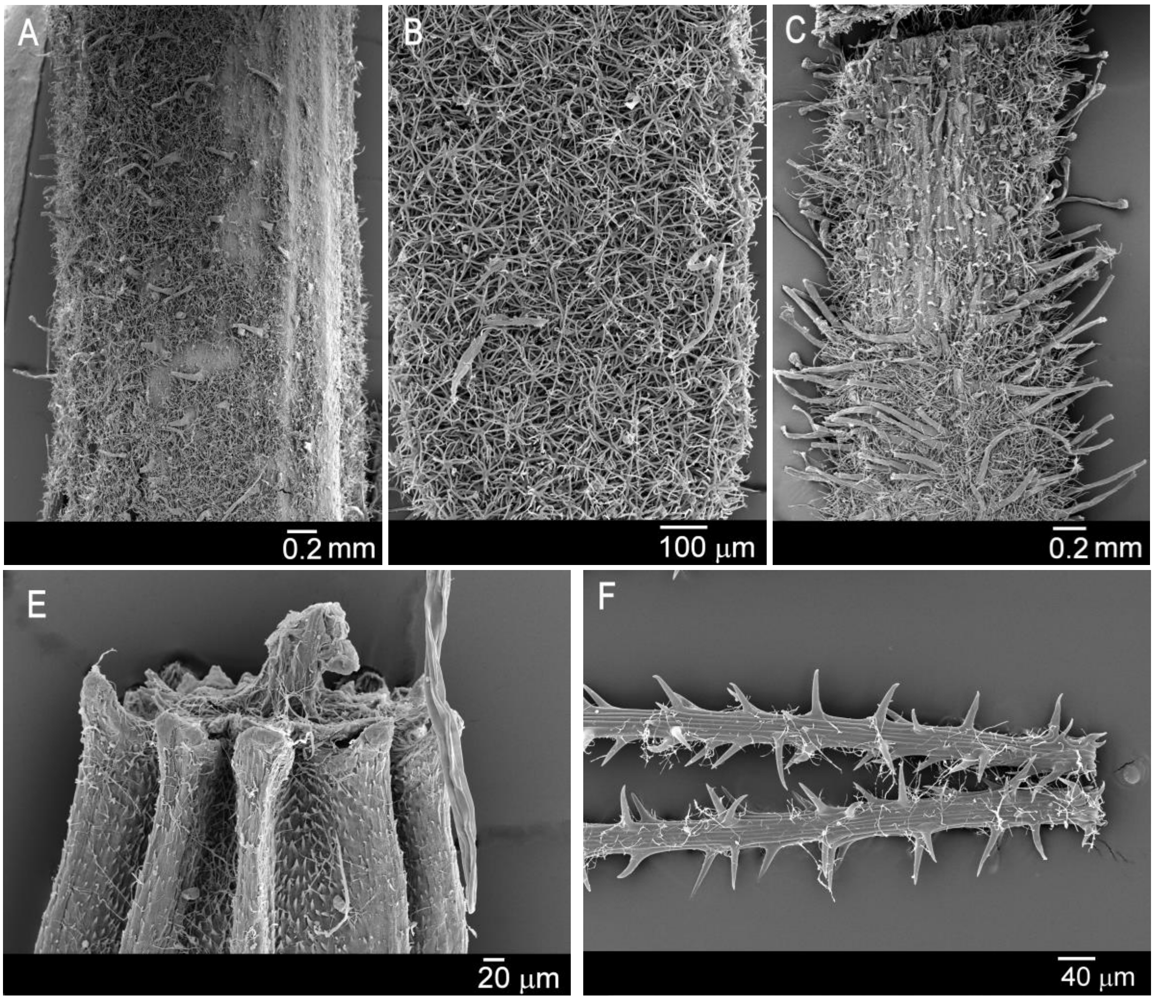

Figure 4.18 *Andryala crithmifolia* subsp. *coronopifolia* (Lowe) M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. A – Stem indumentum, B – Leaf indumentum, C – Peduncle indumentum, D – Ligule teeth, E – Cypsela apex, F – Pappus base.

4.8.7.3 Comments on taxonomy and nomenclature

De Candolle (1838) placed all Madeiran *Andryala taxa* in *A. varia* Lowe ex DC., describing several varieties. Among these, De Candolle recognised *A. varia* Lowe ex DC. var. *crithmifolia* (Aiton) DC., although with some doubts. In spite of mentioning *A. crithmifolia* Aiton as a synonym, De Candolle (1838) questioned if it did not instead correspond to *A. pinnatifida* from Madeira. Later Lowe (1868) admitted having sent a plant to De Candolle which did not correspond to the true *A. crithmifolia* Aiton, but to his *A. cheiranthifolia* L'Hér. var. *sparsiflora* Lowe subvar. *coronopifolia*. In fact, Lowe (1868: 565) described this *taxon* citing *A. varia* var. *crithmifolia* DC as a synonym, clearly excluding it from *A. crithmifolia* Aiton ["*A. varia ζ? crithmifolia DC! l. c. (excl. syn. Ait.). A. crithmifolia Novit. 1. c. (not Ait.)*"]. Lowe (op. cit.) considered this *taxon* as "*an extreme maritime form of A. cheiranthifolia var. β sparsiflora subvar. runcinata, with more divided tomentose canescent leaves, but not presenting the other peculiar characters of the true A. crithmifolia Aiton*". Nonetheless, Press (1994: 382), placed *A. cheiranthifolia* var. β *sparsiflora* subvar. *coronopifolia* again in *A. crithmifolia* Aiton, stressing that "*herbarium specimens show no discernible differences between the two taxa*" and that both *taxa* "*occur only on the south coast of Madeira*", conversely to the rest of the Madeiran *Andryala taxa* which are "*found in inland and northern, coastal sites*". Indeed, both *taxa* share a unique morphological feature in the genus *Andryala*: stellate hairs on the apex of the all teeth of the ligules. Although these *taxa* are morphological quite similar, they differ in a few morphological features (e.g. peduncle length, capitulum diameter, ligule size) and occur in two isolated populations about 13 km apart. Consequently, a new combination was recently proposed: *A. crithmifolia* Aiton subsp. *coronopifolia* (Lowe) M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. (Ferreira *et al.* 2014b, see Appendix 5).

4.8.7.4 Ecology and conservation status

Andryala crithmifolia subsp. *coronopifolia* occurs on rocky and steep sea cliffs as well as on xerophytic clearings of the low micro-forest of Madeiran Olive. Similarly to the typical subspecies, it is known from one small population that is Critically Endangered (B2ac(iv); C2b) according to the *IUCN Red List Categories and criteria* (IUCN 2012). It is threatened by invasive plants, exotic forest, agricultural activity, and human construction. However, this population does not occur in a legally protected area nor is it included in conservation projects (Ferreira *et al.* 2014b, see Appendix 5). Since both populations of *A. crithmifolia* are isolated and quite small, the risk of extinction is rather high (Ferreira *et al.* 2014b, see Appendix 5). Moreover, the probability of extinction may be increased by hybridisation with native and introduced congeners (Ferreira *et al.* 2011). These facts justify the urgent need for strong legal protection.

4.8.7.5 List of studied material

Portugal:

[Madeira]: Cabo Girão, Rochas do Cabo Girão, no chamado Poio do Capitão, descendo até cerca de 250 metros acima do nível do mar, muito perigosa a descida, espécie muito rara, 02-VI-1982, Nóbrega, s/nº, MADJ 02943. Rochas do Cabo Girão - Abaixo do Chão da Vigia, 15-V-1988, Nóbrega, s/nº, MADJ 06914. Cabo Girão, 10-IX-1997, R. Jardim e P. Gouveia, s/nº, MADJ 08669. Girão (base), 21-VII-1998, F. Fernandes, s/nº, MADJ 08953. Cabo Girão, 30-VI-2006, Z. Ferreira, ZF140, UMad. Cabo Girão, 26-VII-2002, S. Santa Clara Gomes, 5SSCG, UMad. Cabo Girão, base do Cabo Girão, 09-VIII-2009, Z. Ferreira, Irene Ferreira, 258ZF, MA 853265. Cabo Girão, base do Cabo Girão, 09-VIII-2009, Z. Ferreira, ZF259, UMad. Cabo Girão, base do Cabo Girão, 09-VIII-2009, Z. Ferreira, Irene Ferreira, ZF259, UMad.

4.9 *Andryala dentata* Sm. in Sibth. & Sm., Fl. Graec. Prodr. 2: 140. 1813

≡ *Andryala sinuata* subsp. *dentata* (Sm.) Arcang., Comp. Fl. Ital. 447. 1882
≡ *Andryala rothia* Pers. subsp. *dentata* (Sm.) Pignatti in Giorn. Bot. Ital. 111: 57. 1977
Ind. loc.: “In insulâ Milo”
Typus: [Greece, Milos] – Lectotype (designated by Ferreira *et al.* 2015b, see Appendix 4): OXF herbarium
= *Andryala undulata* C. Presl, Delic. Prag. 113. 1822
Andryala integrifolia L. var. *undulata* (C. Presl) DC. Prodr. 7(1): 246. 1838
Andryala integrifolia L. subsp. *undulata* (C. Presl) Brilli-Catt., Fl. Ital. [Zangheri]. 1976
Ind. loc.: “Hab. in arvis arenosis sterilibus prope Panormum Siciliae. Fl. Maj. Jun.”
Typus: [Italy, Sicily] “Arva sterilia ad pedem montis Pellegrini prope Panormum, May 1817” – Lectotype (designated here): PR254016A (upper right-hand corner); isolectotypes PR254016A (remaining specimens); PR254016B
= *Inula lesbiaca* P. Candargy in Rev. Méd.-Pharm. 5: 151. 1892
Ind. loc.: “Flore d´Ile de Lesbos (Mételin) … Habitat in locis siccis et superioribus”
Typus: [Greece] “Lesbos (Mitilini) Island, Apothikes, Kelpos, Kullonis, 9 June 1988”, *Hansen & Nielsen 5479* – Neotype (designated here): C10006911 (specimen on the right); isoneotype: C10006911 (specimen on the left).
_ *Andryala integrifolia* L. sensu Davis, Fl. Turkey 5: 763. 1975
_ *Andryala integrifolia* L. sensu Mouterde, Nouvelle flore du Liban et de la Syrie 3: 544. 1983
_ *Andryala integrifolia* L. sensu Tohmé & Tohmé, Illustrated Flora of Lebanon 2007

4.9.1 Typification

The illustration from *Flora Graeca Sibthorpiana* (*Icon. Fl Graec. t. 811*) referred in the protologue could have been considered as the holotype of *A. dentata* Sm. if no type specimens were located (Ferreira *et al.* 2015b, see Appendix

4). However, two specimens under the name "*Andryala dentata* nov. sp." (handwritten by Smith) can be found in the Sibthorpian Herbarium, deposited at the Fielding-Druce herbarium (hb. Sibthorp, OXF). Although the collector is not given, the herbarium sheet has a printed label indicating that they are from Sibthorp's collection. The collector could have been Sibthorp himself as he collected plants on two trips to the Mediterranean. Sibthorp died soon after the second trip and James Smith was appointed to continue Sibthorp's work (based on manuscripts, drawings and specimens from Sibthorp) and it was also this botanist who published *Flora Graeca* and *Prodromus F. Graeca* (Stafleu & Cowan, 1985). *Andryala dentata* was validly published in the latter work. Therefore, it seems possible that the specimens from Sibthorp's collection correspond to original material. The specimen on the left was designated lectotype as it represents *A. dentata* Sm. fairly well (Ferreira *et al*. 2015b, see Appendix 4).

The herbarium sheet PR254016A bears several specimens under the name "*Andryala undulata* Pr." According to the curator of the PR herbarium, Ota Sida (pers. comm.), the labels on this sheet are handwritten by C. Presl, but the specimens were collected by both brothers (J. Presl and C. Presl) during their journey to Sicily in 1817. Ota Sida (pers. comm.) stated that even though the specimens on the sheet PR254016B are from the same gathering they were separated during mounting, which is why only one label is presented. Hence, although the specimens from both sheets are all good candidates for lectotypification, the most complete and preserved one was chosen as lectotype of *Andryala undulata* Presl.

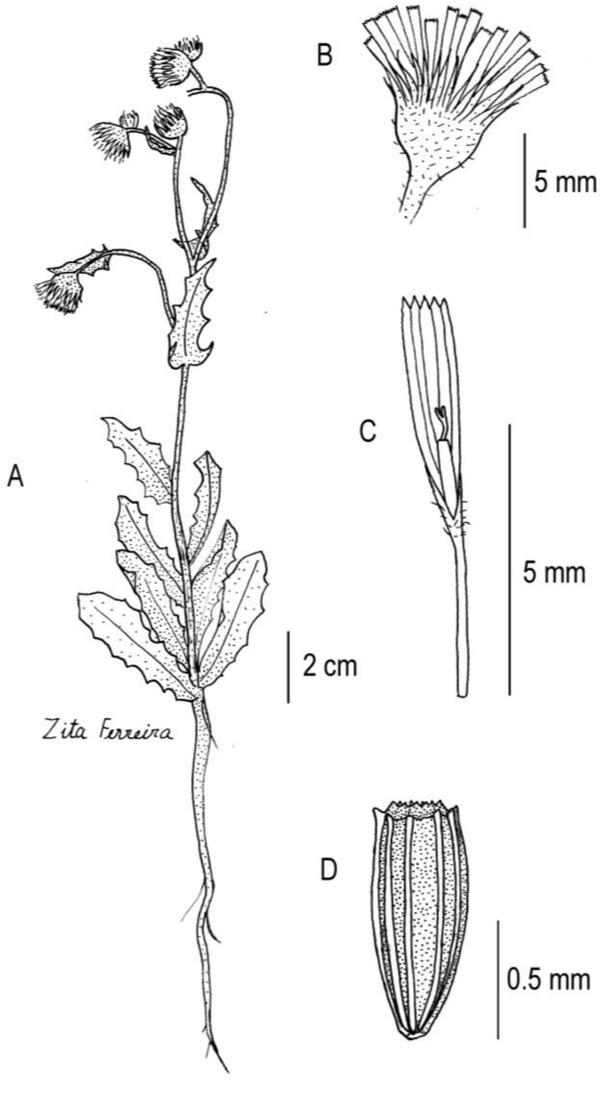

Figure 4.19 *Andryala dentata* Sm. A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

Regarding *Inula lesbiaca* P. Candargy, according to Stafleu & Cowan (1976) herbarium and types of P. Candargy are unknown. This fact may justify the choice of a neotype and indeed on the herbarium sheet C10006911 there is an annotation that reads: "*neotype of Inula lesbiaca*" by an anonymous. Since both specimens were collected in the locality mentioned in the protologue and fit the original description, they are equally good candidates for typification. Thus, the specimen on the right is here designated as neotype and the one on the left as isoneotype.

4.9.2 Description

Annual herb, single-stemmed rarely multi-stemmed (Figure 4.19A). STEMS 18–28 cm, usually branched in the upper half, ± stellate-tomentose to frequently puberulous in the upper half, sometimes with glandular hairs above (Figure 4.20A). LEAVES pubescent-tomentose on both faces with stellate hairs, very rarely with glandular hairs; lower leaves (26-)31–67 x 6–17(-21) mm, attenuate into a short petiole 7–11(-17) mm or semiamplexicaul, oblanceolate to lanceolate, apex obtuse to acute, and margin subentire to dentate; cauline leaves 20–52 x 6–21 mm, semiamplexicaul, ovate-oblong to ovate-lanceolate, base rounded to subcordate, apex acute to acuminate and margin dentate; upper leaves (9-)13–(-24)33 x 3–12 mm, amplexicaul, ovate-oblong to ovate-lanceolate, base rounded or subcordate, apex frequently acuminate and margin subpinnatifid to pinnatipartite at the base. INFLORESCENCE corymbiform with 4–6 capitula. CAPITULA 8–14 mm in diameter (Figure 4.19B); peduncles 6–19(-38) mm stellate-hairy, sometimes with few glandular hairs 0.3-1 mm (Figure 4.20B); involucre 7–10 x 7–11 mm, ± hemispherical at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 6–7 x 1–1.2 mm, linear-lanceolate, apex purpulish and usually acuminate, involute enfolding a floret, the outer face slightly stellate-tomentose with yellow or dark glandular hairs 0.5–1.6 mm mainly on the middle nerve; internal involucral bracts 5–8 x 1–1.6 mm, with scariose margins, receptacle ± flat, puberulous to pubescent with short setose hairs 0.4–2 mm (shorter or slightly longer than the cypselae). FLORETS ligulate, pale-yellow, the external with a tube of 2.6–4 mm and ligule of 2.6–3.6 x 0.5–0.9 mm sometimes with a reddish stripe on the outer face (Figure 4.19C). CYPSELAE 1–1.3 x 0.3–0.4 mm (Figure 4.19D), obconical dark brown with white ribs, apex with a ring of teeth exceeding the ± conspicuous prolongation of the ribs (Figure 4.20C); pappus of whitish bristles 4.5–5.5 mm, pilose at the base (Figure 4.20D).

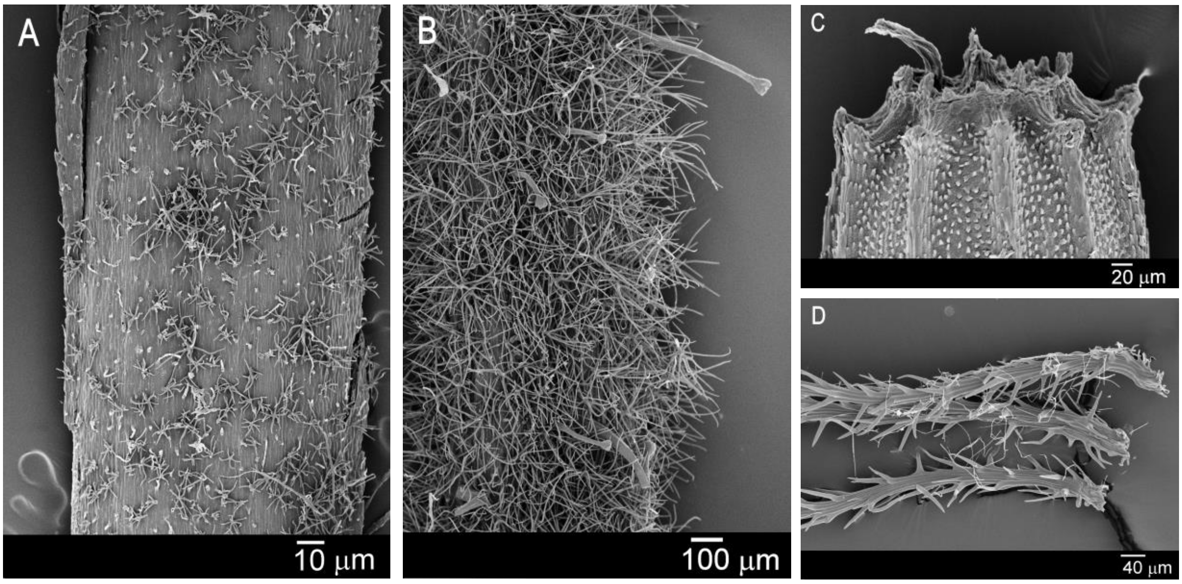

Figure 4.20 *Andryala dentata* Sm. A – Stem indumentum, B – Peduncle indumentum, C – Cypsela apex, D – Pappus base.

4.9.3 Comments on taxonomy and nomenclature

Andryala dentata Sm. was very briefly described by James Edward Smith in Sibthorp & Smith (1813), based upon plants collected by John Sibthorp. Indeed, the title of publication where the protologue appears clearly mentions Smith as the author of the descriptions, synonyms and notes. Thus, the correct name is *A. dentata* Sm. and not *A. dentata* Sibth. & Sm. Later, John Lindley in Sibthorp & Lindley (1837) described *Andryala dentata* Sm. in some detail ("*Herba pedalis et major, undique tomento brevi, canescente, molli obducta. Caulis erectus, striatus, apice cymosus. Folia oblongo-lanceolata, sessilia, dentata; suprema subpinnatifida; floralia angustissima, integra. Capitula multiflora, in pedunculis pilosis aequalibus racemosim dispositis solitaria. Involucrum hemisphaericum, post fructum reflexum,* *lanatum, polyphyllum; foliolis serie simplici dispositis, aequalibus, lineari-lanceolatis. Flosculi pallide flavi, involucro longiores. Receptaculum planum, vix alveolatum, fimbrilliferum. Achaenia conformia, turbinata, glabra, decagona, decem-dentata; pappo serie simplici, piliformi, aequali: setis apice scabris basi pilosis*."). Boissier (1875) acknowledged *A. dentata* Sm., stating *A. tenuifolia* DC. as a synonym, and correctly assigned it to the East Mediterranean, including Greece. However, Boissier (1875) also indicated Southern Italy, Sicily and Northern Africa as the geographic area of this species, which actually corresponds to the distribution area of *A. cossyrensis* Guss. [= *A. tenuifolia* (Tineo) DC. var. *lyrata* Guss. ex DC.]. Arcangeli (1882: 447) included both *A. dentata* Sm. and *A. cossyrensis* Guss. in *A. sinuata* L. (= *A. integrifolia* L.) as distinct varieties: *A. sinuata* L. subsp. β *dentata* Sm. with lower leaves laciniate, dentate or expanded, corymb very lax and capitula very small ("*fg. inf. laciniate, dentate od espanse: corimbo più lassù: capolini più piccoli*") and *A. sinuata* L. subsp. *cossyrensis* Guss. with basal leaves runcinate or pinnatifid and capitula in dichotomous panicle ("*fg. inf. ronchiate o pennatofesse: fi. in pannocchia dicótoma*"). However, *A. integrifolia* L. differs from both *taxa* by the long receptacle hairs, and flat involucral bracts. Although several other authors (e.g. Barratte 1896; Davis 1975; Sell 1976; Mouterde 1983; Tohmé & Tohmé 2007) have considered *A. dentata* Sm. as a synonym of *A. integrifolia* L., these *taxa* correspond in fact to two distinct species. Actually, *A. integrifolia* L. is a widespread Mediterranean species, also present in the Iberian Peninsula, whereas *A. dentata* Sm. is an East Mediterranean species, which can also be found in Southern Italy. Murbeck (1897) recognised *A. dentata* Sm. and *A. integrifolia* as distinct species, but did not distinguish *A. dentata* Sm. and *A. cossyrensis* Guss. (the author mentioned *Rothia tenuifolia* Tineo and "*Andryala tenuifolia DC. l. c; Guss. l. c. p. 406"* as synonyms of *A. dentata* Sm.). Later Murbeck (1905) having analysed authentic plant material of *A. cossyrensis* Guss., accurately recognised *A. dentata* Sm. as a distinct species from Sicily, Greece and Asia Minor, while the first occurs in the desert and sub desert regions of Algeria and Tunisia [and Morocco]. Gussone (1843) recognised for the Sicilian flora several *Andryala* species, including *A. undulata* Presl., *A. tenuifolia* (Tineo) DC., *A. dentata* Sm. and *A. cossyrensis* Guss. In this publication the descriptions of *A. undulata* Presl. and *A. tenuifolia* (Tineo) DC. seem to match *A. dentata* Sm. as they both include plants with pale-yellow florets, slightly exceeding the involucral bracts, whereas the description of *A. dentata* Sm. presented by Gussone does not fit the authentic *A. dentata* Sm. ("… *flores aurei … corollulis anthodium duplo excedentibus*"). In fact, this feature is shared with *A. cossyrensis* Guss. as the author himself pointed out ("*anthodio duplo longiores, ideoque magnitudine A. dentatae*"). Presl (1822: 114) described *A. undulata* Presl, stressing its similarity to *A. dentata* Sm., from which it differs by the leaf margin, inflorescence, and indumentum ("*foliis sinuato-dentatis, undulate-crispis, floribus corymbosis aggregatis, pedunculis calycibusque tomentosis pilosoque glandulosis*"). De Candolle (1838) correctly recognised *A. dentata* Sm. as a distinct species, but had a different opinion on the taxonomic position of *A. undulata* Presl. In effect, De Candolle (op. cit.) admitted *A. undulata* Presl. as a mere variety of *A. integrifolia* L. found in Sicily. In reality *A. undulata* Presl should be included in *A. dentata* Sm. since both have leaves oblong-lanceolate, more or less dentate, cauline sessile or semi-amplexicaul, capitula very small and with ligules pale-yellow, slightly exceeding the involucral bracts.

More recently Pignatti (1977) proposed the combination *Andryala rothii* Pers. subsp. *dentata* (Sibth. & Sm.) Pignatti. However, the author did not explain why he chose to treat *A. dentata* Sm. as a subspecies of *A. rothii* Pers. (correctly, *A. rothia* Pers.). One explanation would be that Pignatti (1977) used the name *A. rothia* Pers. in the same sense as Rouy (1888) who misapplied this name to *A. arenaria* (DC.) Boiss. & Reut. Indeed, Rouy (1888) admitted *A. arenaria* (DC.) Boiss. & Reut. and *A. ficalheana* Daveau [= *A. arenaria* (DC.) Boiss. & Reut.] as two subspecies of *A. rothia* Pers. However, in the same work Rouy excluded *A. dentata* Sm. from *A. rothia* Pers. and, therefore, it remains unclear why Pignatti suggested the combination *A. rothii* Pers. subsp. *dentata* (Sibth. & Sm.) Pignatti.

4.9.4 Karyology

Capineri *et al.* (1978a) determined the somatic chromosome number of 2n = 18 on Italian plant material from Sicily ascribed to *Andryala integrifolia* var. *undulata* (Presl) Fiori [a superfluous combination since De Candolle (1838) was the first author to suggest this name]. According to Capineri (op. cit.), the voucher specimen was deposited at CAT herbarium, but this material was not found. However, it could in fact correspond to *A. dentata* since De Candolle (1838) also assigned *Andryala integrifolia* var. *undulata* to Sicily.

4.9.5 Ecology and conservation status

Under the name *Andryala undulata* Presl., Gussone (1843) stated that *A. dentata* Sm. could be found in dry areas along the roads. In the same publication Gussone, also assigned it arid calcareous regions and slightly sandy places, although under the name *A. tenuifolia* Tin. According to Post (1896) *A. dentata* Sm. was found growing on sands along the coast. Pojero (1902) stated that *A. integrifolia* var. *undulata* Presl., that is *A. dentata* Sm., could be found on arid sandy slopes, roadsides, and shores, being common in Sicily.

Given that *A. dentata* Sm. is frequently mistaken with other *taxa*, there are no reliable data to establish its conservation status and, therefore, it should be considered “DD” according to *IUCN Red List of Threatened Species. Categories and Criteria, Version 3.1.* (IUCN 2001; 2012).

4.9.6 Geographic distribution

According to available herbarium data, *Andryala dentata* Sm. is a central and northeastern Mediterranean species, present in southern Italy (including also the islands of Sicily and Pantelleria), southern and eastern Greece (including islands), western Turkey and Lebanon (Figure 4.21).

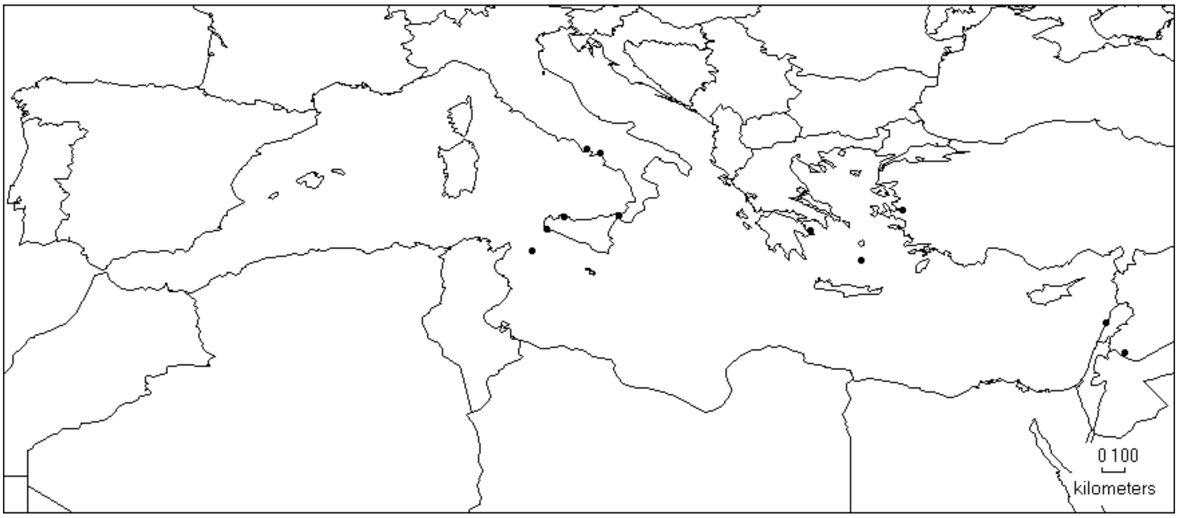

Figure 4.21 Distribution area of *Andryala dentata* Sm., according to studied material.

It was originally assigned to Greece, specifically to the Island of Milos (Sibthorp & Smith 1813). Later Presl (1822) cited *A. dentata* Sm. (under *A. undulata* Presl) for Sicily, and Arcangelli (1882) for southern Italy. Boissier (1875) assigned it not only to the Greek Aegean Islands and continental Greece, but also to Turkey and present-day Lebanon ("*Syriae maritimae circa Berythum*"). Post (1896) also cited *A. dentata* Sm. for "*Syria*" (Lebanon). Similarly to the previous authors, Murbeck (1897) assigned this species to Sicily, Greece, Minor Asia and Lebanon. Later Pojero (1902) extended the distribution area of *A. dentata* Sm. to Pantelleria. More recent floras assigned this species to central and southern Italy as well as Sardinia and Sicily (Cattarini 1976; Pignatti 1977).

4.9.7 List of studied material

Syrie:	Environs de Saïdia, 1854, P 03780641.
Greece:	
[Argolis]:	prope Vromolímni paeninsulae Methanaeae, in vinetis ad litora maris, solo trachytico, 25-V-1885, P 04296321, prope Vromolímni paeninsulae Methanaeae, in vinetis ad litora maris, solo trachytico, 25-V-1885, P 03759998. prope Vromolimni paeninsulae Methanaeae, in vinetis ad litora maris, solo trachytico, 25-V-1885, P 03759995. prope Vromolimni paeninsulae Methanaeae, in vinetis ad litora maris, solo trachytico, 25-V-1885, P 04296323. prope Vromolimni paeninsulae Methanaeae, in vinetis ad litora maris, solo trachytico, 25-V-1885, P 03692414. prope Vromolimni paeninsulae Methanaeae, in vinetis ad litora maris, solo trachytico, 25-V-1885, P 0362907774. prope Vromolimni paeninsulae Methanaeae, in vinetis ad litora maris, solo trachytico, 25-V-1885, P 03290774. Vromolimni paeninsulae Methanaeae, in vinetis ad litora maris, solo trachytico, 25-V-1885, P 03759999.
[Santorini]:	Volcan de Santorin, 1820, d'Urville, P 03276534.
Italy:	
[Messina, Sicily]:	in collibus, V-1898, G. Rigo, 217, P 03759987. in collibus, V-1898, G. Rigo, 217, P 04295361. in collibus, V-1898, G. Rigo, 217, P 03759986.
[Naples]:	bordes de chemins au pied du Vésure, 20-VII-1887, D. Luizet, P 03693510
[Palermo, Sicily]:	Marina di Palermo, in arvis maritimis, V-1879, M. Lojacono, P 03692415. Marina di Palermo, in arvis maritimis, V-1879 Lojacono, P 03759997. Palermo, Todaro, P 03759988. al Rocazzo, in glareosis rivulorum, 09-VII-1840, Heldreich, P 03759994.
[Salerno]:	Campania, M.
[Trapani, Sicily]:	Pantelleria, 17-V-2012, J. Zahradnícek et J. Chrtek, PRA.
Lebanon:	
[Beirut]:	sables au sud des pins de Beyrouth, 21-V-1816, C. Gaillardot, 2037, P 03780642. Beyrouth [Les Sables] (Liban), 10-V-1936, P. Mouterde, P 03288877
Turkey:	
[Loc. incert.]	Papasly, in litorali, 11-VI-1883, P. Sintenis, P. 796, P 03759993. Papasly, in litorali, 11-VI-1883, Sintenis, P 03780643
[Izmir]:	Calle Smyrne, V-1842, E. Boissier, P 04025762. Calle Smyrne, 1845, Boissier, P 03780642.

4.10 *Andryala glandulosa* Lam., Encycl. 1(1): 154. 1783

Ind. loc.: "On cultive cette plante au Jardin du Roi. Elle provient, je crois, de graines du voyage du Cook."
Typus: [Portugal, Madeira] "*Andryala glandulosa* H. R. P. Delamarck Diction." – Lectotype (designated by Ferreira *et al.* 2015b, see Appendix 4): P03772030!
= *Andryala cheiranthifolia* L'Hér., Stirp. Nov. 35. t. 18. 1785.
Andryala varia Lowe ex DC. var. *cheiranthifolia* (L'Hér.) DC., Prodr. (DC.) 7: 246. 1838
Ind. loc.: *"Habitat in Maderâ"*
Typus: [Portugal, Madeira] "*Andryala cheiranthifolia*" – Lectotype (designated here): G00470810
= *Andryala candidissima* Desf., Cat. Pl. Horti Paris. ed. 3, 399. 1829
Andryala varia Lowe ex DC. var. *candidissima* (Desf.) DC., Prodr. (DC.) 7: 245. 1838
Ind. loc.: sine, "H. p." (Hortus Parisiensis)
Typus: [France] "h. Paris" – Lectotype (designated here): FI-W110002
= *Andryala robusta* Lowe in Trans. Cambridge Philos. Soc. 6: 523-551.1838
Andryala cheiranthifolia L'Hér. subsp. *robusta* (Lowe) Bornm., in Bot. Jahrb. Syst. 33: 489. 1904
Ind. loc.: "Hab. in rupibus maritimis, praesertim orae septentrionalis Maderae et Insularum Desertarum: necnon in cacuminibus montium Insulae Portûs S^{ti}." [Lowe, 1838]
Typus: [Portugal, Madeira] "North side of the Pico do Castello in P^{to}. S^{to}. May 1828", *R. T. Lowe* 82 – Lectotype (designated here): K000251914!; isolectotypes: BM000829759! (all specimens); syntype: G00329630 ex herb. DC.

= *Andryala varia* Lowe ex DC. var. *angustifolia* DC., Prodr. (DC.) 7: 245. 1838
Andryala cheiranthifolia L'Hér. var. *congesta* Lowe subv. *angustifolia* (DC.) Lowe, Man. Fl. Madeira 1(5): 562. 1868
Andryala varia subsp. *congesta* (Lowe) Menezes f. *angustifolia* (Lowe) Menezes, Fl. Madeira. 101 (1914)
Ind. loc.: "part. ign. Sub nom. Andr. Ragusinæ in hortis vagat."
Typus: "Hort. Genev., 15 Oct. 1834" – Lectotype (designated here): G00326340
= *Andryala cheiranthifolia* L'Hér. var. *congesta* Lowe subv. *latifolia* Lowe, Man. Fl. Madeira 1(5): 561. 1868
Andryala varia subsp. *congesta* (Lowe) Menezes f. *latifolia* Lowe (Menezes), Fl. Madeira. 101 (1914)
Andryala glandulosa Lam. subsp. *glandulosa* var. *glandulosa* f. *latifolia* (Lowe) R. Fern. in Anuário Soc. Brot. 25: 27. 1959
Ind. loc.: "Mad. on P^{ta} de S. Lourenço, chiefly on the N. sea-cliffs. Ilheo dos Embarcadores and I. de Fora abundantly; S^{ta} Anna (S^{r} Moniz); P^{to} dos Frades in PS.; N., G. and S. Desertas, sea-cliffs."
Typus: [Portugal, Madeira] "Ilheo dos Embarcadores P^{ta}. de São Lourenço, 16 Apr.1868", *R. T. Lowe 296* – Lectotype (designated here): BM000829760! (specimen on the right); isolectotypes: BM000829760! (specimen on the left), BM000829757!; syntype: BM000753027!

4.10.1 Typification

Lamarck (1783) described *Andryala glandulosa* Lam. based on material cultivated at "Jardin du Roi" in Paris. There is only one specimen in Lamarck's herbarium under this name, but it does not fit the original description very well and no date is included. Nonetheless, the specimen P03772030 from the P herbarium, originally from the collection of Poiret (one of Lamarck's collaborators) matches the original description perfectly. This material includes the name *Andryala glandulosa* handwritten by Lamarck, and the letters: "H. R. P" (Hortus Regius Parisiensis), which means a plant cultivated at Jardin du Roi, just as mentioned in the protologue. This specimen was, therefore, designated lectotype of *A. glandulosa* Lam. (Ferreira *et al.* 2015b, see Appendix 4).

According to the protologue L'Héritier (1785) described *Andryala cheiranthifolia* L'Hér. based on a plant grown at "Hortus Regius Parisiensis", clearly assigning it to Madeira. The original description contains an illustration which could be accepted as the holotype. However, there is a specimen labelled as "Typus" included in the De Candolle collection, currently deposited at the Geneva herbarium (G00470810). Indeed, it is labelled as *Andryala cheiranthifolia* and belonged to L'Heritier's herbarium ("*ach. de l'herb. de L'Héritier*"). This information is handwritten by De Candolle as well as the following expression "*type l'espèce*". Besides, an additional label also handwritten by De Candolle contains synonyms of *Andryala cheiranthifolia* L'Hér. (i.e. *Andryala glandulosa* Lam. and *Andryala varia* ε *cheiranthifolia* DC.). Actually, when De Candolle (1838) recognised *A. varia* var. *cheiranthifolia* (L'Her.) DC., citing *A. cheiranthifolia* L'Hér. as the basionym, the author clearly stated that he had seen a specimen from L´Heritier's herbarium. This is not surprising as De Candolle acquired L'Heritier´s herbarium (containing plants collected by L´Héritier himself in the Paris Gardens) and made it the basis of his own herbarium, now deposited at G (Stafleu & Cowan 1981). Another type specimen was located at the British Natural History Museum herbarium (BM001124974). It exhibits a label indicating its provenance ("*Hort. Paris L'Héritier*"), handwritten by Joseph Banks with whom L'Héritier maintained correspondence. Moreover, an annotation in pencil reads "*Andryala cheiranthifolia L. Her.!*" In fact L'Héritier took a 15-month trip to London between 1786 and 1787 (Francisco-Ortega *et al.* 2008) having described 19 new Macaronesian endemics afterwards. It is possible that this specimen originally belonged to L'Heritier's herbarium. Although both specimens fit the original description quite well, the most complete specimen, G00470810, is herein designated as lectotype of *Andryala cheiranthifolia* L'Hér.

Desfontaines (1829) described *Andryala candidissima* Desf. based on a cultivated plant grown at "Hortus Parisiensis". In the protologue, the author stressed the morphological similarity to *A. cheiranthifolia* L'Hér., differing only by its greyish colour and its broad-lanceolate, entire and broader leaves. The Desfontaines collections are hosted at the Paris (P), Florence (FI), and Geneva (G) herbaria. The specimen FI-W110002 corresponds without any doubt to original material: it was cultivated at the Paris Garden, as we can deduce by the information on the herbarium label ("*h. Paris*") and is under the name *A. candidissima.* Moreover, it is quite clear that this specimen belonged to the Desfontaines herbarium (one of the labels reads "*Ex Herb. Desfontaines*"). The specimen G00329629 from the De Candolle collection is also original material given that on the label we can read "*Andryala candidissima Desf. Jardin de Paris, 1821*". In fact, years later De Candolle (1838) proposed a new combination: *A. varia* Lowe α *candidissima* (Desf.) DC., stressing that he saw a living plant as well as herbarium material, the latter most surely corresponding to the specimen G00329629. This specimen is not suitable for lectotypification due to the bad preservation state of the inflorescence. Thus, the specimen FI-W110002 is here designated as lectotype of *Andryala candidissima* Desf.

Lowe (1838) described *Andryala robusta* Lowe for Madeira, indicating the unpublished name *A. varia* var. *β* as the basionym. The specimen G00329630 ex herb. DC. is indeed labelled as "*Andryala varia* var. *β* nob." and was collected by Lowe in 1832. Thus, it corresponds to original material and is here considered a syntype. The lectotype was chosen among specimens collected by the author in Porto Santo in 1828 (also before the publication date of *Andryala robusta* Lowe) and in one of the localities mentioned in the protologue. The specimen here designated as lectotype, K000251914, is the best developed and fits the original description perfectly.

When describing *Andryala varia* Lowe ex DC. var. *angustifolia* DC., De Candolle (1838) mentioned a cultivated plant under the name "*Andr. Ragusinæ*" from unknown provenance ("part. ign."). This plant was most probably grown at the first botanical garden in Geneva, Jardin des Bastions, created in 1816 by De Candolle himself (Sigrist & Bungener 2008). Indeed, on the original label of the specimen G00326340 we can read "*Andryala ragusina*" and "*Hort. Genev*." (i.e. cultivated at the Geneva Botanical Garden). On a subsequent label the specimen was identified as *Andryala candidissima* var. *angustifolia* DC., but later the epithet "*candidissima"* was crossed out and replaced by *varia* in De Candolle's handwriting. Furthermore, given that it is from the De Candolle herbarium, currently deposited in the Geneva herbarium, it most surely corresponds to original material and is here designated as lectotype of *Andryala varia* Lowe ex DC. var. *angustifolia* DC.

The specimen BM000829760 (on the right) is here designated as lectotype of *Andryala cheiranthifolia* L'Hér. var. *congesta* Lowe subv. *latifolia* Lowe because is a complete specimen, fitting the original description better than the isolectotypes. Lowe (1868) most surely based the description on this material since it is accompanied by a label in the author's handwriting which reads "*Andryala cheiranthifolia L'Hér. α congesta Lowe subv. latifolia (A. robusta Lowe)*". Besides, it was collected by him in a locality mentioned in the protologue and the collection date is prior to publication. The specimen BM000753027 is here considered a syntype because it was mentioned in the protologue of *Andryala cheiranthifolia* L'Hér. var. *congesta* Lowe subv. *latifolia* Lowe.

4.10.2 Description

Chamaephyte, biennial to perennial, usually single-stemmed (Figure 4.22A). STEMS 16–112 cm, frequently woody at the base, branched in the upper half, more rarely from the base or in the upper third, stellate-tomentose to densely stellate-tomentose with glandular hairs all along the stem especially in the upper half (Figure 4.23A). LEAVES often apple green, usually densely stellate-tomentose on both faces with abundant glandular hairs at least on the cauline and upper leaves and mainly on the middle nerve of the abaxial face (Figure 4.23B); lower leaves arranged in a rosette, frequently marcescent at anthesis, sometimes slightly red, 73–260 x 15–76(-92) mm, semiamplexicaul, lanceolate to ovate-lanceolate, base ± attenuate, apex usually acute, and margin entire or subentire, sometimes lobate-pinnatifid; cauline leaves 49–180 x 9–57 mm, semiamplexicaul or amplexicaul, ovate-oblong to ovate-lanceolate, base rounded to subcordate, apex acute to acuminate, and margin entire, rarely subentire to lobate; upper leaves 16–67(-77) x (3-)8–27 mm, amplexicaul, usually ovate to ovate-oblong, base ± rounded to cuneate, apex acute or acuminate and margin entire.

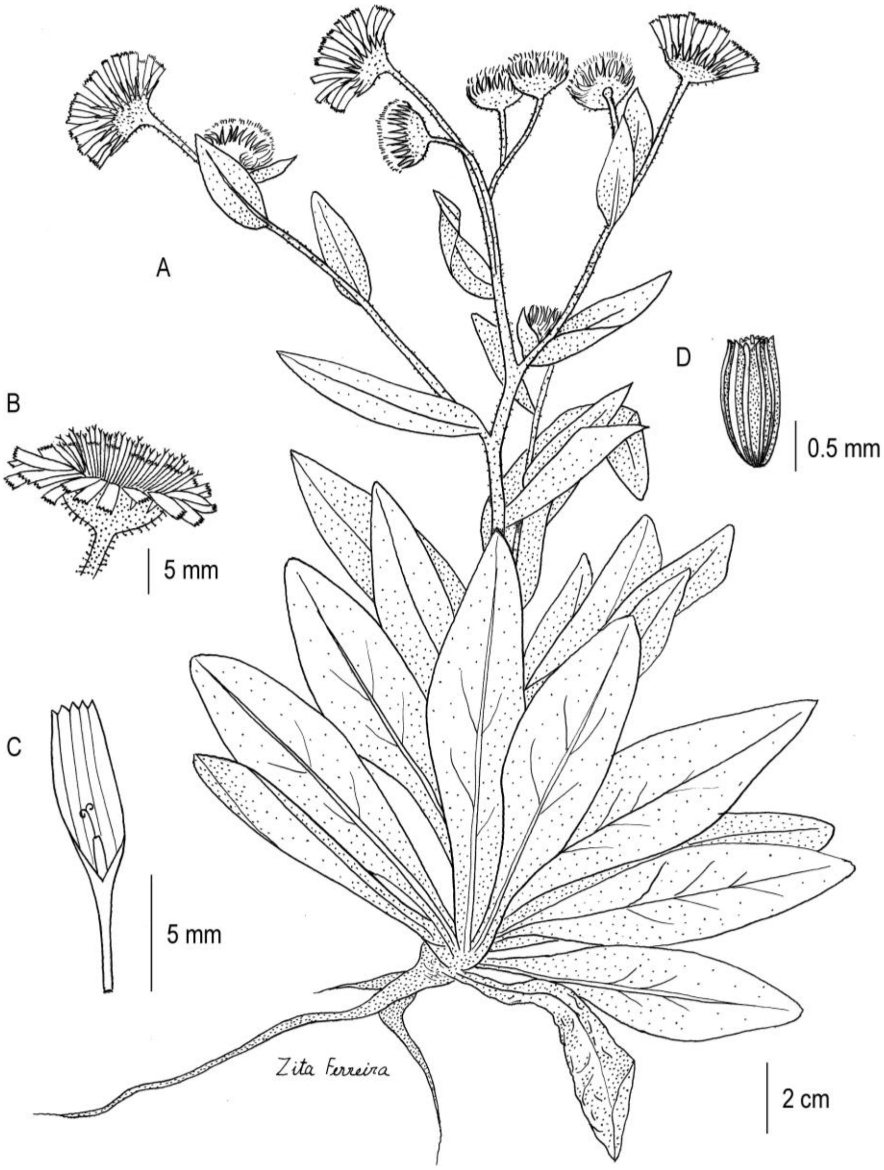

Figure 4.22 *Andryala glandulosa* Lam. A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

INFLORESCENCE corymbose or paniculate-corymbose, with 2–11 capitula, rarely with solitary and longly pedunculate capitula. CAPITULA 16–37 mm in diameter (Figure 4.22B); peduncles 19–79 mm with dense stellate hairs and long glandular hairs 1.3–4 mm (Figure 4.23C); involucre 11–20 x 14–31 mm, hemispherical at anthesis, with involucral bracts in 4(-5) rows; external involucral bracts 6.7–14 x 1.3–2.5 mm, lanceolate, apex acuminate to subulate, strongly involute enclosing a cypsela, the outer face densely stellate-tomentose with yellow glandular hairs

0.7–3 mm, the inner face stellate-hairy; internal involucral bracts 5–8 x 1–1.9 mm, with broad scariose margins to almost completely scariose, receptacle convex, usually villous with setose hairs 1–5 mm (up to 3 times longer than the cypselae). FLORETS ligulate, golden yellow, the external with a tube of 3–6 mm and ligule of 6–13 x 2–4.2 mm (Figure 4.22C). CYPSELAE 1–1.6 x 0.4–0.6 mm (Figure 4.22D), usually obconical dark brown or black with white or light-brown ribs, apex with a ring of teeth ± equalling the conspicuous prolongation of the ribs (Figure 4.23D); pappus of white or dirty-white bristles 5–6.7 mm, pilose at the base (Figure 4.23E).

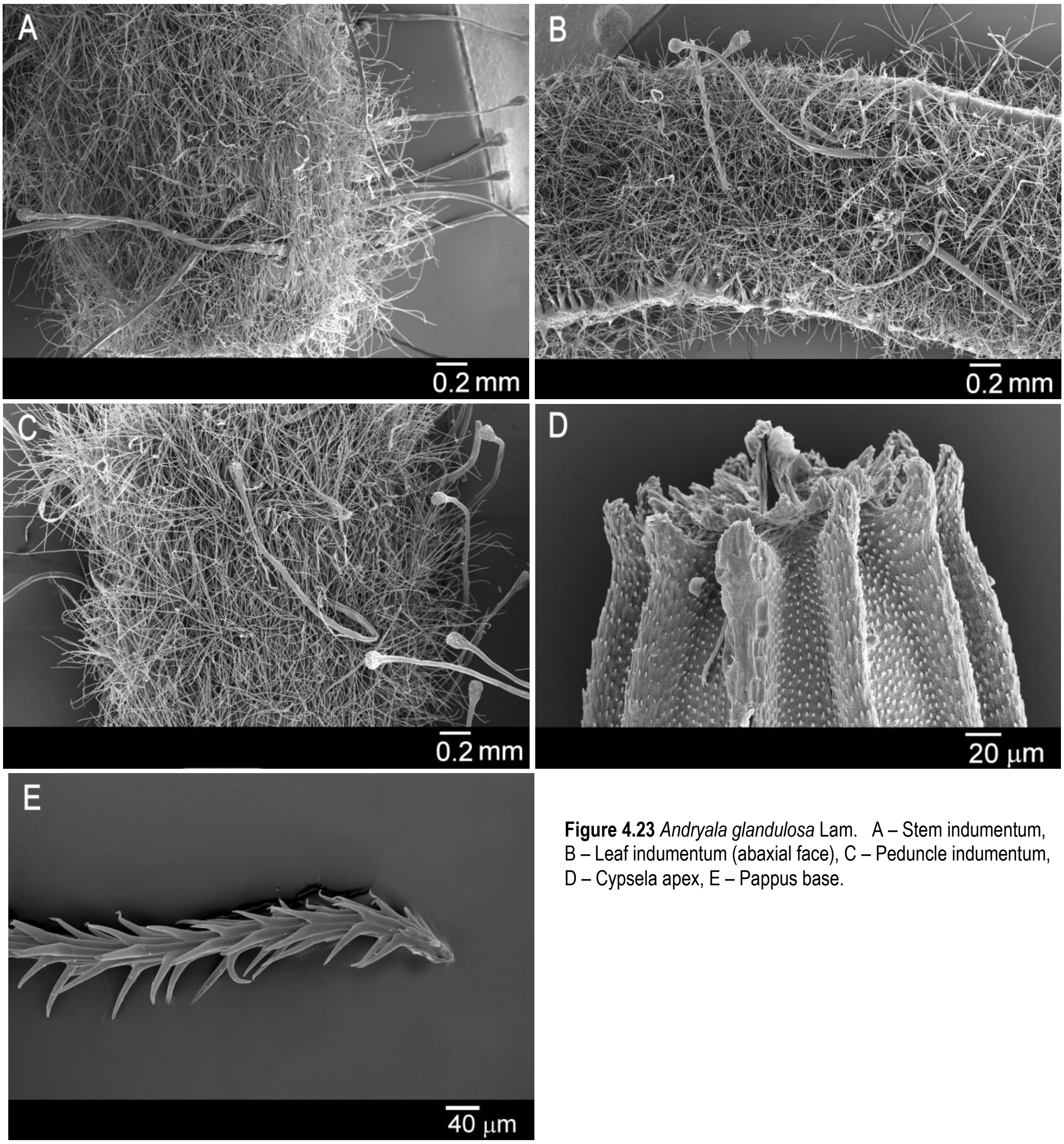

Figure 4.23 *Andryala glandulosa* Lam. A – Stem indumentum, B – Leaf indumentum (abaxial face), C – Peduncle indumentum, D – Cypsela apex, E – Pappus base.

4.10.3 Comments on taxonomy and nomenclature

Lamarck (1783) described *Andryala glandulosa* Lam. quite well from a living plant grown in the Paris Royal Botanical Garden, but of unknown origin. Later, L'Héritier (1785) described, from the same garden, *A. cheiranthifolia* L'Hér., assigning it exclusively to Madeira. The description of the latter fits *A. glandulosa* Lam. very well, although the lower leaves are runcinate, and not entire. Similarly to Lamarck (op. cit.), L'Héritier (1785: 35) mentioned the presence of yellow glandular hairs covering the entire plant ("*uti tota planta tomentosi hirsuti: villis apice glanduliferis; glandulis fulvis subviscosi*"). Indeed, the stems of *A. glandulosa* Lam. are covered with hispid, glandular-viscid, yellow hairs, especially in the upper part of the plant. Besides, *A. glandulosa* Lam. and *A. cheiranthifolia* L'Hér. exhibit chaffy-like bracts at the margin of the receptacle, which can be distinguished from the outer involucral bracts, as stated by Lamarck (1783: 154): " … *leur réceptacle est légérement velu dans son centre, & muni de quelques paillettes, à sa circonférence. Ces paillettes, quoique voisines du calice, sont tout-à-fait distinguées de ses folioles.*" as well as L'Héritier (1785: 36): "*RECEPTACULUM planum, villosum, cinctum paleis …".* Moreover, L'Heritier (1784: 36) mentioned the numerous involucral bracts present in *A. cheiranthifolia* ("*CALYX … squammis plurimis …*"). Actually, *A. glandulosa* Lam. exhibits 4(-5) rows of involucral bracts, the inner ones chaffy and glabrous and the outer densely stellate and glandular tomentose, completely involving a cypsela. Much later, Desfontaines (1829) also described plants from "*Horti Regii Parisiensis*", which he considered poorly known or even unknown, among them *A. candidissima* Desf. In fact, Desfontaines (1829: 399) considered it morphologically very similar to the Madeiran *A. cheiranthifolia* L'Hér., differing mainly by the greyish colour, and the leaf shape and margin: "*Differt canitie, foliis lato-lanceolatis, latioribus, integerrimis*." Actually, these features draw it closer to *A. glandulosa* Lam., which Lamarck (1783: 154) described in the following terms: "*Ses feuilles sont alternes, sessile, lancéolées & très entières*."). De Candolle (1838) placed all Madeira *Andryala taxa* in *A. varia* Lowe ex DC., recognising several varieties, between them *A. varia* Lowe ex DC. var. *candidissima* (Desf.) DC. and *A. varia* Lowe ex DC. var. *cheiranthifolia* (L'Hér.) DC. Interestingly, in the latter *taxon*, De Candolle (op. cit.) included both *A. glandulosa* Lam. and *A. cheiranthifolia* (L'Hér.). A month later, Lowe (1838) described *A. robusta* Lowe as a new species, also recognising *A. varia* Lowe, in which he included *A. cheiranthifolia* L'Hér. as a mere variety. Later Lowe (1868) reconsidered his taxonomic concept of *A. robusta* Lowe as an independent species and placed it in *A. cheiranthifolia* L'Her. var. *congesta* Lowe. Furthermore, Lowe (1868) recognised two sub varieties: *A. cheiranthifolia* L'Hér. var. *congesta* Lowe subv. *angustifolia* (DC.) Lowe, corresponding to *A. varia* Lowe ex DC. var. *candidissima* (Desf.) DC., and *A. cheiranthifolia* L'Hér. var. *congesta* Lowe subv. *latifolia* Lowe, including *A. varia* Lowe ex DC. var. *angustifolia* DC. and *A. glandulosa* Lam. This means that the author preferred the name *A. cheiranthifolia* L'Hér. over *A. varia* Lowe, probably because it is an earlier name. Nonetheless, the earliest validly published name is *A. glandulosa* Lam. and, therefore, both names are illegitimate due to superfluity. Bornmüller (1904) made a new combination, *A. cheiranthifolia* L'Hér. subsp. *robusta* (Lowe) Bornm., probably believing that the name *A. cheiranthifolia* L'Hér. var. *congesta* Lowe was invalid since the name *A. robusta* Lowe was suggested earlier in time. Subsequently, Menezes (1914) presented still another combination but also invalid: *A. varia* Lowe ex DC. subsp. *congesta* (Lowe) Menezes. More recently, Fernandes (1959), in agreement with the ICBN, restored the earliest validly published name, recognising two subspecies: *A. glandulosa* Lam. subsp. *glandulosa* and *A. glandulosa* subsp. *varia* (Lowe ex DC.) Fern. Actually, the first *taxon* corresponds to *A. glandulosa* Lam. (including *A. cheiranthifolia* L´Hér.) and the second to a distinct species herein proposed: *A. sparsiflora* (Lowe) M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. Curiously, in spite of following the taxonomic structure suggested by Lowe (1868) on the basis that this author was well acquainted with the Madeiran *Andryala taxa*, Fernandes (1959) highlighted that the observation of herbarium specimens seemed to support the distinction of two species: one from coastal areas, *A. glandulosa* Lam. (= *A.*

robusta Lowe) and another from the mountainous regions, *A. cheiranthifolia* L´Hér. (= *A. varia* Lowe ex DC. p.p.). The latter *taxon* is, indeed, recognised herein as a distinct species, *A. sparsiflora* (see p. 228).

4.10.4 Karyology

The first report on chromosome counts for *Andryala glandulosa* Lam. appears to be by Dalgaard (1985). This author determined both the haploid and diploid number of chromosomes (respectively, n = 9 and 2n = 18) on plant material under the name *A. glandulosa* subsp. *glandulosa* collected in Porto Santo (Madeira). Later Dalgaard (1986) confirmed the diploid number on plant material from Porto Moniz (north coast of Madeira).

4.10.5 Ecology and conservation status

Andryala glandulosa Lam. grows almost from sea level to 460 m (occasionally up to 1100 m). It occurs frequently on volcanic coastal rocks and cliffs, although, it can be found on volcanic and calcareous coastal sandy soils. Less frequently, *A. glandulosa* Lam. occurs in inland sites on rocky soils. It can be found on coastal rocky soils in association with *Plantago coronopus* L., *Lotus glaucus* Aiton, *Cynara cardunculus* L., *Tolpis succulenta* (Dryand. in Aiton) Lowe, *Calendula Maderensis* DC., *Helichrysum melaleucum* Rchb. ex Holl, *Echium nervosum* Dryand., *Sinapidendron gymnocalyx* (Lowe) Rustan, *Crithmum maritimum* L., and *Carlina salicifolia* (L.f.) Cav. It can integrate rupicolous plant communities of coastal areas, including other Madeiran endemics such as *Sonchus pinnatus* Aiton and *Aeonium glandulosum* (Aiton) Webb & Berthel. On sandy substrates it grows along with *Matthiola maderensis* Lowe, *Calendula maderensis* DC., *Argyranthemum pinnatifidum* (L.f.) Lowe subsp. *succulentum* (Lowe) Humphries, *Lotus glaucus* Aiton, etc. This *taxon* is frequently found in association with a parasitic plant of the genus *Orobanche* L. As is typical in coastal plants, *Andryala glandulosa* Lam. exhibits xerophytic adaptations, allowing it to grow in exposed areas with strong insolation and low water availability, such as a dense and whitish indumentum, which reflects sunlight and reduces evapotranspiration (Jardim & David 2005).

In what concerns the conservation status, this taxon is quite common and should be listed as Least Concern (LC) according to the *IUCN Red List categories and criteria* (IUCN 2001; 2012).

4.10.6 Geographic distribution

Andryala glandulosa Lam. is a Madeiran endemic that can be found on almost all islands of the archipelago (Figure 4.**24**). Indeed, Press (1994) cited this *taxon* for the islands of Madeira, Desertas and Porto Santo[32]. In Madeira Island *A. glandulosa* Lam. occurs mainly on the northern coast and eastwards to Ponta de São Lourenço. However, it can be found in western localities of the south coast with inflection to the north. Lowe (1868) assigned it to a locality in the south coast, east of Funchal, where no records are presently found. In Porto Santo it grows in inland sites, chiefly on the rocky peaks of Pico Castelo, Pico do Facho, Pico Branco and Pico Ana Ferreira, although it can be found in the northern coast of the island and surrounding islets. In Desertas it can be found on all three islands (Lowe 1868).

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[32] Records for the Canary Islands (e.g. Hansen & Sunding 1993) are not accurate since the *taxon* from this archipelago corresponds to a distinct species.

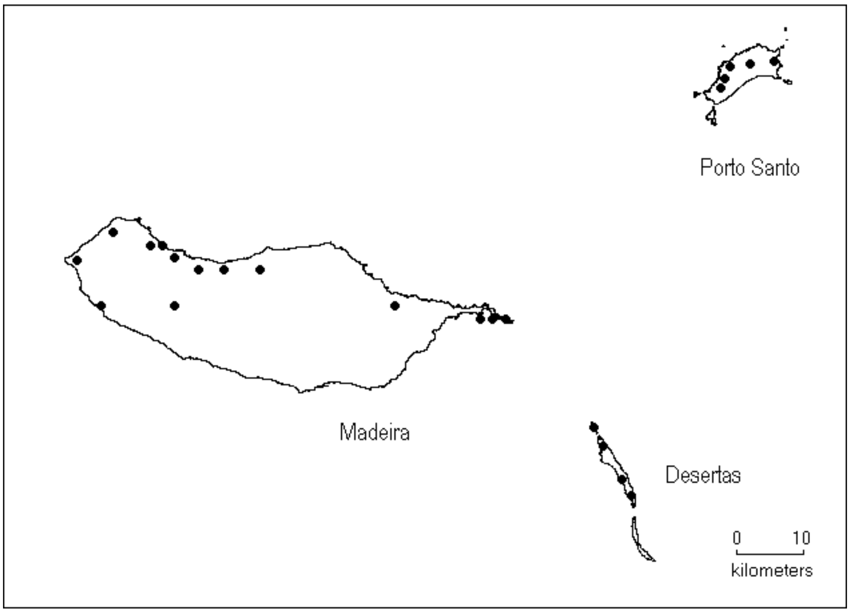

Figure 4.24 Distribution area of *Andryala glandulosa* Lam., according to studied material.

4.10.7 List of studied material

Portugal: [Madeira]: Porto Santo, Pico do Castelo, ca. 300 m. alt., 24-V-1952, Herman Persson, s/nº, LISU 64713. Ponta de S. Lourenço, Ilhéu dos Desembarcadouros, C. Menezes, s/nº, LISU 42688. entre Seixal e Ribeira Funda, rochas e cinzas vulcânicas húmidas em expos. N, C. Romariz, 787, LISU 43291. Prox. Furado Fajã da Areia, Rochas a pique em exp. N. Fendas das rochas húmidas, C. Romariz, 773, LISU 43288. Ponta de S. Lourenço, Ilhéu dos Desembarcadouros, C. Menezes, s/nº, LISU 42687. Ponta de S. Lourenço, C. Menezes, s/nº, LISU 43516. Baia d´Abra, Ponta de São Lourenço, 10-V-1991, Fontinha e José Carvalho, s/nº, MADJ 02738. Porto da Cruz. Maiata de Baixo à beira-mar, 19-XI-1991, Fontinha, J. Carvalho, Paulo Gouveia, s/nº, MADJ 02539. Ilhéu dos Desembarcadouros, 15-IV-1993, José Carvalho e Fontinha, s/nº, MADJ 07917. São Vicente, Ponta Delgada Vila, 30-V-1996, Fontinha e Baeta, s/nº, MADJ 09640. Entre Porto Moniz e Seixal, nos taludes rochosos da estrada, 08-VII-1957, Eng. Beliz, R. Santos, s/nº, MADJ 03551. São Vicente, rochas junto ao mar, 12-VII-1962, R. Santos, s/nº, MADJ 03554. São Vicente, rochas junto ao mar, 12-VII-1962, Eng. Rui Vieira, s/nº, MADJ 03555. Ribeira da Nogueira, Sul do Fanal na Ribeira da Janela, 01-IX-1987, Nóbrega, s/nº, MADJ 04735. Porto Santo, Marinhas, 26-V-1958, Rui Santos, s/nº, MADJ 05928. Porto Santo, Pico Branco, 17-IX-1960, Eng. Rui Vieira, s/nº, MADJ 05929. Porto Santo, Pico Branco, 08-IX-1962, Rui Santos, s/nº, MADJ 05930. Ribeira do Tristão, MADJ 00790. Ribeira do Tristão, MADJ 00791. Zwischen Porto Moniz und Seixal, 10 - 50 m, 19-VI-1971, C. Simon, s/nº, MADM. Vereda do Calvário, 17-VII-2000, Biscoito, s/nº, MADM. S. Vicente, entre a estrada e o mar, 05-VII-1977, Remane, s/nº, MADM. Ponta de São Lourenço, Ilhéu do Agostinho, 17-VI-1990, F. Zino, s/nº, MADM. Montado dos Pessegueiros, ca. 460 m.s.m., 12-VI-1954, J. Malato Beliz, 902, MA 239097. Levada do Rabaçal, 1100 m.s.m., R. Barreto, 9708, MA, 239100. Montado dos Pessegueiros, 26-IX-1991, C. Palmeira, s/nº, MADM. Ponta de São Lourenço, ao longo da vereda para a casa do Sardinha, 20-II-2006, CMSS (Lígia Carvalho, Magda Silva, Miguel Sequeira), UMad 966. Calhau Grosso, Santana, Alt. 10 m, Exp. NNE, Lígia Carvalho, Miguel Sequeira, Roberto Jardim, UMad 1020. Rocha das Cabras, Santana, Alt. 5 m, Exp. NW decl. 80º, 17-VII-2003, Lígia Carvalho, Emanuel Jesus, 9, UMad 1021. Deserta Grande, arredores da casa, Alt. 5 m, Exp. NW, 25-II-2006, Magda Silva, Lígia Carvalho, Dília Menezes, Isamberto, 416, UMad 1016. Deserta Grande, arredores da casa, Alt. 5 m, Exp. NW, 25-II-2006, Magda Silva, Lígia Carvalho, Dília Menezes, Isamberto, 468, UMad, 1017. Deserta Grande, zona Sul do topo, Alt. 305 m, 26-II-2006, Magda Silva, Lígia Carvalho, Dília Menezes, Luisa Oliveira, 501, UMad 1018. Grande, Vale da Castanheira, Alt. 350 m, Exp. SW, 02-III-2006, Magda Silva, Lígia Carvalho, Dília Menezes, Isamberto, João Paulo, 540, UMad 1019. Fonte da Areia, Porto Santo, solo arenoso, alt. 100 m, na descida para o antigo café, Zita Ferreira, ZF2, UMad. Porto Santo, Pico Branco, R. Jardim, MADJ. Pico Ana Ferreira, Porto Santo, R. Jardim, MADJ. Dunas da Piedade, Caniçal, Falésia do Norte, alt. 98 m, substrato arenoso, junto com *Matthiola maderensis, Calendula maderensis, Argyranthemum pinnatifidum* subsp. *succulentum, Orobanche,* 06-IV-2006, Z. Ferreira, ZF5. Porto da Cruz, base do Rochão junto à praia, alt. 13 m, solo pedregoso, junto com *Plantago coronopus, Lotus glaucus, Cynara cardunculus, Tolpis succulenta,* 28-IV-2006, Z. Ferreira, ZF6A, UMad. Porto da Cruz, Maiata de Baixo, Caminho dos muros, à beira-mar, alt. 10m, 28-IV-2006, Z. Ferreira, ZF7, UMad. Porto da Cruz, Maiata de Baixo, ao longo do Caminho dos Muros, solo pedregoso, alt. 19 m, 28-IV-2006, Z. Ferreira, ZF39, UMad. Foz da Ribeira do Faial, alt. 20m, solo de aterro, 04-V-2006, Z. Ferreira, ZF40, UMad. antiga estrada para o Seixal, solo pedregoso, alt. 42 m, 19-VI-2006, Z. Ferreira, M. Sequeira & A. Pupo Correia, ZF100, MA, 801899. Ilhéu Chão, Desertas, 09-V-2006, Lígia Carvalho, Magda Silva, Pedro Gouveia, CMSS 767, Umad 1489A. Deserta Grande, 06-V-2006, Lígia Carvalho, Magda Silva, Carlos Viveiros, CMSS 692, UMad 1414. Deserta Grande, 26-II-2006, Lígia Carvalho, Magda Silva, Dília Menezes, Luísa Oliveira, CMSS 501, UMad 1018. Ponta S. Lourenço, alt. 89 m, 13-VII-2009, Z. Ferreira, A. Correia, ZF212, UMad. Ponta S. Lourenço, alt. 89 m, 13-VII-2009, Z. Ferreira, A. Correia, ZF213, UMad. Ponta S. Lourenço, alt. 89 m, 13-VII-2009, Z. Ferreira, A. Correia, ZF214, UMad. Ponta S. Lourenço, alt. 89 m, 13-VII-2009, Z. Ferreira, A. Correia, ZF215, UMad. S. Lourenço, alt. 89 m, 13-VII-2009, Z. Ferreira, A. Correia, ZF217, UMad. Porto Santo, Fonte da Areia, solo arenoso, alt. 100 m, na rua que desce para a beira-mar, 08-V-2009, Z. Ferreira, ZF201, UMad. Porto da Cruz: Maiata, solo arenoso, alt. 100 m, na rua que desce para a beira-mar, 22-VII-2009, M. Sequeira, Z. Ferreira, A. Pupo, A. Figueiredo, ZF218, UMad. Porto da Cruz: Maiata, solo arenoso, alt. 100 m, na rua que desce para a beira-mar, 22-VII-2009, M. Sequeira, Z. Ferreira, A. Pupo, A. Figueiredo, ZF219, UMad. Porto da Cruz, Maiata, solo arenoso, alt. 100 m, na rua que desce para a beira-mar, 22-VII-2009, M. Sequeira, Z. Ferreira, A. Pupo, A. Figueiredo, ZF220, UMad. Porto da Cruz: Maiata, solo arenoso, alt. 100 m, na rua que desce para a beira-mar, 22-VII-2009, M. Sequeira, Z. Ferreira, A. Pupo, A. Figueiredo, ZF221, UMad. Faial, vereda na Fajã do Mar, solo pedregoso, 75 m, 22-VII-2009, M. Sequeira, Z. Ferreira, A. Pupo, A. Figueiredo, ZF222, UMad. Faial, vereda na Fajã do mar, solo pedregoso, 75 m, 22-VII-2009, M. Sequeira, Z. Ferreira, A. Pupo, A. Figueiredo, ZF223, UMad. Faial, Guindaste (Miradouro), 53 m, 22-VII-2009, M. Sequeira, Z. Ferreira, A. Pupo, A. Figueiredo, ZF224, UMad. Faial, Guindaste (Miradouro), 53 m, 22-VII-2009, M. Sequeira, Z. Ferreira, A. Pupo, A. Figueiredo, ZF225, UMad. Faial, Guindaste (Miradouro), 53 m, 22-VII-2009, M. Sequeira, Z. Ferreira, A. Pupo, A. Figueiredo, ZF226, UMad. S. Vicente, Fajã da Areia, para o lado de P. Delgada, 53 m, 24-VII-2009, M. Sequeira, Z. Ferreira, A. Pupo, A. Figueiredo, ZF227, UMad. S. Vicente, Fajã da Areia, para o lado de P. Delgada, 53 m, 24-VII-2009, M. Sequeira, Z. Ferreira, A. Pupo, A. Figueiredo, ZF228, UMad. Vicente, Fajã da Areia, para o lado de P. Delgada, 53 m, 24-VII-2009, M. Sequeira, Z. Ferreira, A. Pupo, A. Figueiredo, ZF229, UMad. S. Vicente, Fajã da Areia, para o lado de P. Delgada, 53 m, 24-VII-2009, M. Sequeira, Z. Ferreira, A. Pupo, A. Figueiredo, ZF230, UMad. S. Vicente, Fajã da Areia, para o lado de P. Delgada, 53 m, 24-VII-2009, M. Sequeira, Z. Ferreira, A. Pupo, A. Figueiredo, ZF231, UMad. Seixal, 24-VII-2009, M. Sequeira, Z. Ferreira, A. Pupo, A. Figueiredo, ZF232, UMad. Seixal, 24-VII-2009, M. Sequeira, Z. Ferreira, A. Pupo, A. Figueiredo, ZF233, UMad. Seixal, 24-VII-2009, M. Sequeira, Z. Ferreira, A. Pupo, A. Figueiredo, ZF234, UMad. S. Jorge, alt. 126 m, 26-VII-2009, M. Sequeira, Z. Ferreira, A. Pupo, A. Figueiredo, ZF249, UMad. S. Jorge, alt. 126 m, 26-VII-2009, M. Sequeira, Z. Ferreira, A. Pupo, A. Figueiredo, ZF250, UMad. S. Jorge, alt. 126 m, 26-VII-2009, M. Sequeira, Z. Ferreira, A. Pupo, A. Figueiredo, ZF251, UMad. S. Jorge, alt. 126 m., 26-VII-2009, M. Sequeira, Z. Ferreira, A. Pupo, A. Figueiredo, ZF252, UMad. S. Jorge, alt. 126 m, 26-VII-2009, M. Sequeira, Z. Ferreira, A. Pupo, A. Figueiredo, ZF252, UMad. Porto Santo, M. Sequeira, 6260, UMad. Porto Santo, M. Sequeira, 6267, UMad. Porto Santo, M. Sequeira, 6263A, UMad. Porto Santo, Norte da Camacha, Sítio das Alagoas, 149 m, 08-V-2009, Z. Ferreira, ZF202, UMad. entre São Vicente e Seixal, 10 m, parede cara el mar, 20-X-2010, S. Castroviejo & Miguel Sequeira, 181163SC, MA. Porto Santo, Pico Ana Ferreira, M. Sequeira, 4135, UMad. Porto Santo, M. Sequeira, MS 4140, UMad. Porto Moniz, após Ribeira do Inferno, 15-20 m, situação edafoxerofítica, com declive acentuado, litoral, 18-V-2009, M. Sequeira, M. Benedito, D. Henriques, 6154, MA. Ponta do Pargo, Floração tardia, 08-XII-2006, Leopoldo Medina, MA. Ponta do Pargo, Floração tardia, 08-XII-2006, Leopoldo Medina, MA. 08-XII-2006, MV 10857-2, MA. S. Jorge, 15-VII-2012, Z. Ferreira, ZF298, UMad. Porto Santo, Lagoa da Serra de Dentro, dentro da represa, seca, 27-V-2012, Roberto Jardim, 2943.

4.11 *Andryala integrifolia* L., Sp. Pl.: 808. 1753

Ind. loc.: "Habitat in Gallia, Sicilia"
Typus: Lectotype (designated by House in Jarvis *et al.* 1993): Herb. Burser VI: 57 (UPS)

4.11.1 Description

Hemicryptophyte, biennial or perennial herb, usually single-stemmed. STEMS 16–99 cm, frequently branched in the upper third, sometimes from the base or the upper half, pubescent to tomentose-lanate with stellate hairs combined with glandular hairs, particularly in the upper part. LEAVES puberulous to tomentose on both faces with stellate hairs and sometimes with glandular hairs, especially on the upper leaves, lower leaves sometimes marcescent, 38–140 x 6–49 mm, attenuate into a petiole (8–48 mm), oblanceolate to linear-lanceolate, sometimes obovate-lanceolate, apex obtuse to acute, and margin subentire to lobate, sometimes pinnatifid or pinnatipartite; cauline leaves 16–86 x 3–33 mm, semiamplexicaul or amplexicaul, oblong to linear-lanceolate, sometimes ovate-oblong to ovate-lanceolate, base frequently ± rounded, apex obtuse to acute and margin entire to pinnatipartite; upper leaves 9.6–42 x 1.7–13 mm, sessile, semiamplexicaul or amplexicaul, usually ovate-lanceolate or lanceolate, base rounded or cuneate, apex acute to acuminate and margin entire or rarely pinnatifid. INFLORESCENCE corymbose with few or numerous capitula. CAPITULA 7–20(-24) mm in diameter; peduncles 10–36 mm stellate-tomentose to densely stellate-tomentose sometimes with abundant glandular hairs 0.4–2 mm; involucre 7–12 x 7–14 mm, campanulate at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 5–8 x 1–2 mm, lanceolate to linear-lanceolate, apex acute to acuminate, flat not enfolding a floret, the outer face frequently stellate-tomentose with glandular hairs 0.4–4 mm, yellow or blackish towards the base, mainly on the lower half; internal involucral bracts 4.6–8 x 1.4–2.5 mm, with scariose margins, receptacle frequently convex, villous with long setose hairs (1.7-)2–4.7 mm (2 to 3 times longer than the cypselae). FLORETS ligulate, pale yellow, the external with a tube of 2.3–5.5 mm and ligule of 4.5–11 x 1–3.2 mm, sometimes with a reddish stripe on the outer face. CYPSELAE 1–1.5 x 0.3–0.5 mm, usually oblong, frequently dark brown with white ribs, apex with a ring of long thin teeth equalling or slightly exceeding the ± conspicuous prolongation of the ribs; pappus of usually dirty-white bristles 4–6 mm, ± pilose at the base.

4.11.2 Geographic distribution

Andryala integrifolia L. is a SW European and circum-Mediterranean species (Talavera 1987; Blanca 2009, 2011), although not present in the eastern part of the Mediterranean basin. According to available herbarium data, it occurs in the Iberian Peninsula, France, Tunisia, Algeria and Morocco. This species is also found in Italy, including Sardinia and Sicily (Cattarini 1976; Pignatti 1982). Furthermore, it occurs in Macaronesia, namely in the Canary Islands, the Azores and Madeira (Sunding 1979; Talavera 1987; Silva *et al.* 2005; Acebes Ginovés *et al.* 2010; Silva *et al.* 2010; Ferreira *et al.* 2011, see Appendix 1). Actually, it is the most widespread species in the genus. Distribution maps of the two subspecies of *A. integrifolia* here recognised will be presented ahead.

4.11.3 Key to the subspecies of *Andryala integrifolia* L.

1a. Stems ± slender, pubescent to tomentose with stellate hairs combined with glandular hairs; lower leaves lanceolate to linear-lanceolate, sometimes obovate-lanceolate, margin subentire to lobate, sometimes pinnatifid or pinnatipartite; cauline leaves oblong to linear-lanceolate, sometimes ovate-oblong or ovate-lanceolate; inflorescence laxly corymbose with 3–10 capitula; capitula 7–11 mm in diameter. ....*A. integrifolia* subsp. *integrifolia*
1b. Stems stout, pubescent to tomentose-lanate with dense stellate hairs combined with glandular hairs, lower leaves oblanceolate to lanceolate, margin subentire to lobate, cauline leaves oblong to lanceolate; inflorescence with numerous capitula arranged in dense terminal corymb; capitula 11–20(-24) mm in diameter. ....*A. integrifolia* subsp. *corymbosa*.

4.11.4 *Andryala integrifolia* subsp. *integrifolia*

= *Andryala sinuata* L., Sp. Pl. 2: 808. 1753
Andryala integrifolia var. *sinuata* (L.) Willk. in Willkomm & Lange, Prodr. Fl. Hispan. 2: 271. 1865.
Ind. loc.: “Habitat Monspelii, inque Sicilia.”
Typus: Lectotype (designated by House in Jarvis & Turland 1998): BM000646869 (Herb. Clifford: 387)
= *Andryala parviflora* Lam. Fl. Franç. (Lamarck) 2: 117. 1779
Andryala parviflora Lam. var. *sinuata* (L.) Boiss., Voy. Bot. Espagne 2(13): 394. 1841
Ind. loc.: [France] “On la trouve dans les lieux stériles des provinces médirionales.”
Typus: Not located.
= *Andryala mollis* Asso, Mant. Stirp. Arag. 175. 1781
Andryala integrifolia L. var. *angustifolia* DC., Prodr. 7(1): 246. 1838
Andryala parviflora Lam. var. *angustifolia* (DC.) Boiss., Voy. Bot. Espagne 2(13): 394. 1841
Ind. loc.: [Spain] “Provenit en Vicor, en el Monte de Herrera, circa Rodenas”
Typus: [Spain] “Mant. Arag. n. 1126” – Holotype: G00493548.
= *Rothia cheiranthifolia* Roth, Catal. Bot. fasc. 1: 105. 1797
Ind. loc.: “Habitat Monspelii”
Typus: sine loc. *A. W. Roth s.n.* – Lectotype (designated here): B-W14771-02 0
= *Rothia runcinata* Roth, Catal. Bot. fasc. 1: 107. 1797
Andryala runcinata Pers., Syn. Pl. [Persoon] 2(2): 378. 1807
Ind. loc.: “Habitat Monspelii”
Typus: *A. W. Roth s.n.* – Lectotype (designated here): B-W14772-01 0
= *Andryala allochroa* Hoffmanns. & Link, Fl. Portug. [Hoffmannsegg] 2: 154. 1825

Andryala integrifolia L. var. *allochroa* (Hoffmanns. & Link) Coutinho, Fl. Portugal ed. 2. 791. 1939

Ind. loc.: “Fréquent par tout le Royaume, le long des chemins et sur la lisière des champs.”

Typus: Holotype: illustration therein.

= *Andryala dissecta* Hoffmanns. & Link, Fl. Portug. [Hoffmannsegg] 2: 153. 1825

Ind. loc.: [Portugal] “Aux lieux sablonneux en-delà du Tage prés de Lisbonne, Setuval etc.”

Typus: Not located.

= *Andryala coronopifolia* Hoffmanns. & Link, Fl. Portug. [Hoffmannsegg] 2: 155. 1825

Ind. loc.: [Portugal] “Prés de Braga, sur les murs.”

Typus: Holotype: illustration therein.

= *Andryala integrifolia* L. var. *diffusa* DC., Prodr. 7: 246. 1838

Andryala diffusa Jan ex DC., Prodr. 7: 246. 1838.

Ind. loc.: “in Siciliâ (Jan.!), Corsicâ (Soleir.!)”

Typus: [France, Corsica] “Sartene”, *Soleirol s.n.* – Lectotype (designated here): G00493545; syntype: G00493404

= *Andryala reboudiana* Pomel, Nouv. Mat. Fl. Atl.: 259. 1874

Ind. loc.: “Région saharienne: Oued el-Arab (Reboud).”

Typus: Not located.

= *Andryala aestivalis* Pomel, Nouv. Mat. Fl. Atl. 259. 1874

Ind. loc.: “Terrains rocailleux, près Miliana.”

Typus: [Algeria] “Milianah, July 1874”, *A. N. Pomel s.n.* – Lectotype (designated here): MPU005677

= *Andryala minuta* Lojac., Fl. Sicul. 2(1): 223. 1902

Ind. loc.: “A. dentata strictissima Lojac. olim in sched. Colli Messina Zodda! Naso Reina! Tortorici Tod.! Magg.-Giugno.”

Typus: [Italy] “Prov. di Messina Zodda misit Ross” – Lectotype (designated by Aghababyan *et al.* 2008): PAL11870

= *Andryala integrifolia* L. var. *basaltica* Rouy, Fl. France 9: 454. 1905

Ind. loc.: “Ardèche: rochers basaltiques du Lignon à Jaujac (Rouy).”

Typus: [Spain] “Ardèche, Jaujac: rochers basaltiques du Lignon, 17 April 1897”, *G. Rouy s.n.* – Lectotype (designated here): LY179.

= *Andryala x faurei* Maire & Maire in Bull. Soc. Hist. Nat. Afrique N. 17: 121. 1926

Ind. loc.: “Hab. inter parentes in agro oranensi, prope «Les Lauriers-Roses» ubi leg. A. Faure maio et junio florentem.”

Typus: [Algeria] “Les Lauriers-Roses (Oran). Lieux incultes près de la gare entre les parents présumés, 29-5-1921”, *Faure* – Lectotype (designated here): MPU001670; syntype: P03290782.

= *Andryala antonii* Maire *in* Mém. Soc. Sci. Nat. Maroc 15: 47. 1927.

Andryala canariensis Lowe subsp. *antonii* (Maire) Maire in Jahandiez & Maire, Cat. Pl. Maroc. 3: 840. 1934

Andryala pinnatifida Aiton subsp. *antonii* (Maire) Dobignard in Willdenowia 37: 140. 2007

Ind. loc.: “Hab. in clivis argillaceis aridis ad radices Atlantis Majoris: in ditione Glaoua prope castellum Enzel, 700-800 m, ubi junio et julio floret.” [Maire, 1927]

Typus: [Marocco] “In Atlantis Majoris ditione Glaoua: Enzel in clivis argillaceis nec non in glareosis, 4 July 1924”, *Maire s.n.* – Lectotype (designated here): P00084243!; isolectotypes: MPU001820, RAB043321.

= *Andryala cedretorum* Maire in Mem. Soc. Sc. Not. Maroc 15: 45. 1927.

Andryala integrifolia L. subsp. *cedretorum* (Maire) Sauvage in Trav. Inst. Sci. Chérifien, Sér. Bot. 22: 203. 1961

Andryala integrifolia L. var. *cedretorum* (Maire) Dobignard in J. Bot. Soc. Bot. France 46-47: 85. 2009

Ind. loc.: “Hab. in cedretis et quercetis Atlantis Medii, solo calcareo nec non siliceo, ad alt. 1.500-2.200 m, junio et julio florens: in cedretis montis Hebbri, solo basaltico; in cedretis oropedii inter Aïn-Leuh et Ouiouane, nec non faucium amnis Senoual, solo calcareo; in quercetis prope Ouiouane et Bekrit, etc.”

Typus: [Morocco] “Moyen Atlas: Bekrit, Tizi-Ali ou Mansour, rocailles calcaires dans les forêts de Quercus ilex, 27 June 1923”, *Maire s.n.* – Lectotype (designated by Dobignard 2009): MPU001814; isolectotype: MPU001810; syntypes: P00084247, MPU001809, MPU001811, MPU001812, MPU001813

= *Andryala humilis* Pau ex Font Quer in Cavanillesia 1: 47. 1928

Andryala integrifolia subsp. *eu-integrifolia* Maire var. *typica* f. *humilis* (Pau) Jahan. & Maire, in Jahandiez & Maire, Cat. Pl. Maroc. 3: 841. 1934

Ind. loc.: [Morocco] “… plantas del Rif que el Dr. Font Quer há preparado durante su campaña de 1927.”

Typus: [Morocco] “Hab. in umbrosis Yebel Dahar, pr. Axdir (Beni Urriaguel), 9 May 1927”, *Font Quer 728* – Lectotype (designated here): MA139323 (specimen on the left); isolectotypes MA139323 (remaining specimens), MA139322, BC36140, MPU006365.

= *Andryala atlanticola* H. Lindb. in Itin. Mediterr. (Act. Soc. Sc. Fenn. n. s. B, i. No. 2) 151. 1932

Ind. loc.: “M., Atlas major, in convalle fluminis Aït Messane, in saxosis apricis prope pagum Tinitine, c. 1.400 m. In glareosis prope pagum Arround, c. 2000 m.”

Typus: [Morocco] *“Atlas magnum, in convalle fl. Aït Messane, in glareosis pr. pag. Arround, c. 2000 m, 12 June 1926”, Harald Lindberg 3926 – Lectotype (designated by Väre 2012): H1451861; isolectotypes: MPU009605 (Väre 2012),* K000251908!, LD1012165, S10-15684, B10-0093123*; lectoparatype* (designated by Väre 2012)*: H1451860.*

= *Andryala* × *caballeroi* Font Quer in Cavanillesia 8: 83. 1935

Ind. loc.: “Hab. in Imp. Maroccano, pr. Zinat, ditione Tingitana, inter parentes, ubi d. 28 maji 1930 legi.”

Typus: Morocco, “Hab. in Imp. Maroc., pr. Zinat, ditione Tingitana, inter parentes, 28 Maji 1930”, *Font Quer* – Holotype: BC141555

= *Andryala integrifolia* L. subsp. *perennans* Maire & Weiller in Bull. Soc. Hist. Nat. Afrique N. 31(1): 27. 1940

Ind. loc.: “Anti-Atlas: rocailles gréseuses près de Tifermit, 1200 m (Maire et Weiller, nº122); rocailles volcaniques de l'Amalou-n-Ou-Mansour dans les Monts Sargho, 2000-2300 m (M. et W., nº 421).

Typus: [Morocco] “In lapidosis arenaceis Anti-Atlantis, prope Tifermit, 16 June 1939”, *Maire & Weiller 122* – Lectotype (designated here): RAB043318; isolectotype: MPU004333.

4.11.4.1 Typification

Andryala mollis Asso is a heterotypic synonym of *A. integrifolia* subsp. *integrifolia.* The original description by Asso y del Rio (1781) is accompanied by an illustration which would be accepted as holotype if no herbarium material was located. Nonetheless, De Candolle (1838) described *Andryala integrifolia* var. *angustifolia* DC., citing *A. mollis* Asso. as a homotypic synonym. De Candolle (1838) based his description on plant material, presumably collected by Asso y del Rio, which was located at the G herbarium ex herb. De Candolle. This specimen was labelled *A. mollis* and is accompanied by the information “*Mant. Arag. n. 1126*” which also figures in the description of *A. integrifolia* var. *angustifolia* DC. Given that a specimen is preferable for typification rather than an illustration, the specimen in question (G00493548) is here accepted as holotype of *A. mollis* Asso.

Roth (1797) described *Rothia cheiranthifolia* Roth assigning it to Montpellier. Roth’s main collection was transferred to the B herbarium in 1925/1926, where it was incorporated in the main herbarium which was for the greater part destroyed in 1943 (Stafleu & Cowan 1983). However, the Roth material in the Willdenow herbarium, including several types, is still extant (Stafleu & Cowan 1983). Indeed, in the Willdenow herbarium hosted at B there are two specimens under the registration number B-W14771 identified as *Rothia cheiranthifolia*. Both correspond to original material but as the specimen B-W14771-02 0 fits the original description better it is here designated as lectotype. Later new determinations were made: *Andryala integrifolia* L. and *A. parviflora* Lam.

Roth (1797) also described *Rothia runcinata* Roth. Similarly, in the Willdenow collection hosted at the B herbarium two specimens under *Rothia runcinata* were found. Both have a handwritten label with the original description of *R. runcinata* taken from “Roth, Catal. Bot. 1 p. 107”. Hence, these must correspond to original material as well. The specimen B-W14772-01 0 is here elected as lectotype of *R. cheiranthifolia* as it matches the original description quite well and is in better condition.

According to Stafleu & Cowan (1979) the herbarium and types of Hoffmannsegg are deposited at several herbaria: B (partly in the Willdenow herbarium, extant), G, G-DC, H and HAL. Nevertheless, no original material of *Andryala allochroa* Hoffmanns. & Link was found in these institutions. In respect to Link’s personal herbarium, it was acquired by the B herbarium after his death but the greater part is now destroyed (Stafleu & Cowan 1981). Hence, the illustration in the protologue is here considered as holotype of *Andryala allochroa* Hoffmanns. & Link. Likewise, type material of *Andryala coronopifolia* Hoffmanns. & Link was not located and, therefore, the illustration in the protologue is here accepted as holotype. Regarding *Andryala dissecta* Hoffmanns. & Link, it was not depicted in the protologue and no original material was located.

De Candolle (1838) mentioned *Andryala diffusa* Jan. as the basionym of *A. integrifolia* var. *diffusa* Jan ex DC. and stated that it corresponds to a herbarium name (“pl. exs.”). De Candolle (1838) analysed herbarium specimens collected by Jan in Sicily and by Soleirol in Corsica. According to Stafleu & Cowan (1979) Jan’s herbarium and types are presumably found in Museo Civico di Storia Naturale di Milano (MSNM). However, Gabriele Galasso (pers.

comm.) stated that Jan's herbarium from MSNM was destroyed during the Second World War. Plant material collected by Jan and Soleirol was located in the De Candolle collection held at the G herbarium and it most surely constituted the basis of De Candolle's description. The specimen G00493545 is here designated as lectotype of *A. integrifolia* var. *diffusa* Jan ex DC. given that it was collected by Soleirol in Corsica (as mentioned in the protologue). Besides, it matches the original description quite well and is better preserved. The specimen G00493404 is considered a syntype seeing that it was mentioned in the protologue.

The Pomel herbarium and types were deposited at the AL herbarium (Stafleu & Cowan 1983). Judging by the herbarium label, the specimen MPU005677, here designated as lectotype of *Andryala aestivalis* Pomel, is originally from AL ex herb. Pomel. There is no doubt that it corresponds to original material because, besides bearing a handwritten version of the original description (most probably by Pomel himself) as well as a printed one, it is under the name *A. aestivalis* Pomel. On one of the labels we can read "*simple forme estivale de l' A. integrifolia L.*" Indeed, in the handwritten description attached to the herbarium sheet, *A. aestivalis* Pomel is compared with *A. integrifolia* L. based on the receptacle indumentum ("*… receptacle pileux, moins que dans integrifolia* ...") and with *A. sinuata* L. based on ligule, fruit, and pappus traits.

The lectotype of *A. minuta* Lojac, PAL11870, designated by Aghababyan *et al.* (2008) seems to have been well chosen as it matches the original description and is from a locality mentioned in the protologue. Besides, the name on the label (*Andryala stricta* Lojac) is similar to the one in the protologue: "*A. dentata strictissima Lojac. olim in sched.*"

Regarding *A. integrifolia* L. var. *basaltica* Rouy, the Rouy herbarium and types are kept at the LY herbarium (Stafleu & Cowan 1983). In this herbarium there is a specimen collected by the author himself at the locality indicated in the protologue (LY179). It also fits the original description and is, therefore, here designated as lectotype.

Any of the type specimens of *Andryala x faurei* Maire & Maire are good candidates for lectotypification, thus the specimen that best fits the original description is here designated as lectotype (MPU001670). Faure (1923) did not validly publish *Andryala* x *faurei* since no description was presented, but he clearly stated Maire as the author of the name. However, Faure (op. cit.) mentioned the locality of provenance: "*Lieux incultes prés des gares d'O.-Imbert et des Lauriers-Roses, au milieu des parents presumes; environs de Tlemcen, vers le pont des Cascades*". Indeed, in 1926 Maire mentioned in the protologue the same origin ("*Les Lauriers-Roses*"). Actually, this locality matches the one on the label of the lectotype and syntype herein designated.

Maire (1927) mentioned in the protologue of *A. antonii* Maire that the type specimens were deposited at the AL and RAB herbaria. However, after Maire's death his herbarium was transferred from the AL herbarium to the MPU herbarium and duplicates were passed on to the P herbarium. The specimens here indicated as type material were all collected by Maire in the same locality and on the same date. As Maire (op.cit.) did not mention a specific specimen as holotype, the specimen P00084243 is here designated as lectotype given its better state of preservation.

Dobignard (2009) designated the specimen MPU001814 as lectotype of *Andryala cedretorum* Maire and considered MPU001812 and P00084247 as "isotypes". However, the latter are syntypes (as well as MPU001809, MPU001811, and MPU001813) since they were collected in the localities mentioned in the protologue, but the collection date does not match the one in the lectotype.

The herbarium specimens here considered as type material of *Andryala humilis* Pau ex Font Quer are all labelled "*Andryala humilis* Pau sp. nov.; *Andryala integrifolia* L. var. *humilis* F.Q.". According to Font Quer (1928: 47), these specimens were collected during a botanic expedition made to Morocco in 1927: *"Se está procediendo a empaquetar la exsiccata de plantas del Rif que el Dr. Font Quer ha preparado durante su campaña de 1927.* In the same publication, Font Quer drew attention to the date of valid publication of the species described as new in printed labels of the exsiccata: "*Se expedirá el día 10 de marzo, que será la fecha válida de publicación de las especies que se describen como nuevas en las etiquetas impresas de la exsiccata*." Indeed, the specimens under "*A. humilis* Pau" are accompanied by a printed description authored by Pau. Thus, *A. humilis* Pau ex Font Quer was validly published in 10th Mar. 1928. Seeing that the specimen MA139323 (on the left) fits the original description quite well and is the best developed one, it is here designated as lectotype of *Andryala humilis* Pau ex Font Quer.

Font Quer (1935) described *Andryala* × *caballeroi* Font Quer. The Font Quer herbarium and types are hosted at the BC herbarium (Stafleu & Cowan 1976). Indeed, a single specimen with exactly the same collection information was found in this herbarium. Given that on the label we can read "*x Andryala caballeroi F. Q. typus*", handwritten by Font Quer, this specimen is to be considered the holotype.

In the protologue of *Andryala integrifolia* L. subsp. *perennans* Maire & Weiller two sets of specimens, differing by collector number and collection locality, were mentioned. However, insofar as the specimens under the collector number 421 were not found, the lectotype was chosen among the specimens with the collector number 122. Thus, the best preserved specimen, RAB043318, is here chosen as lectotype.

4.11.4.2 Description

Hemicryptophyte, biennial or perennial herb, single-stemmed or less frequently multi-stemmed (Figure 4.25A). STEMS 16–89 cm, ± slender, usually branched in the upper third, pubescent to tomentose with stellate hairs combined with glandular hairs, particularly in the upper part (Figure 4.26A). LEAVES puberulous to tomentose on both faces with stellate hairs and sometimes with glandular hairs, especially on the upper leaves (Figure 4.26B); lower leaves sometimes marcescent, 38–140 x 6–49 mm, attenuate into a petiole (8–47 mm), lanceolate to linear-lanceolate, sometimes obovate-lanceolate, apex acute or less frequently obtuse, and margin subentire to lobate, sometimes pinnatifid or pinnatipartite; cauline leaves 16–83 x 3–30 mm, usually semiamplexicaul, oblong to linear-lanceolate, sometimes ovate-oblong to ovate-lanceolate, base frequently ± rounded, apex usually acute and margin entire to pinnatipartite; upper leaves 9,6–36 x 1.7–9.8 mm, sessile, semiamplexicaul or amplexicaul, ovate-lanceolate or lanceolate, base rounded or sometimes cuneate, apex acute to acuminate and margin entire or rarely pinnatifid. INFLORESCENCE laxly corymbose with 3–10 capitula. CAPITULA 7–11 mm in diameter (Figure 4.25B); peduncles 10–36 mm stellate-hairy with some glandular hairs 0.4–2 mm (Figure 4.26C); involucre 7–11 x 7–13 mm, campanulate at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 5–8 x 1–2 mm, usually lanceolate, apex acute to acuminate, flat not enfolding a floret, the outer face frequently stellate-tomentose with glandular hairs 0.4–2.4 mm, yellow or blackish towards the base, mainly on the lower half; internal involucral bracts 4.6–8 x 1.4–2.5 mm, with scariose margins, receptacle frequently convex, villous with long setose hairs 2–4.7 –4.3 mm (2 to 3 times longer than the cypselae). FLORETS ligulate, pale-yellow, the external with a tube of 2.3–5.5 mm and ligule of 4.5–10 x 1–3.2 mm, sometimes with a reddish stripe on the outer face (Figure 4.25C). CYPSELAE 1–

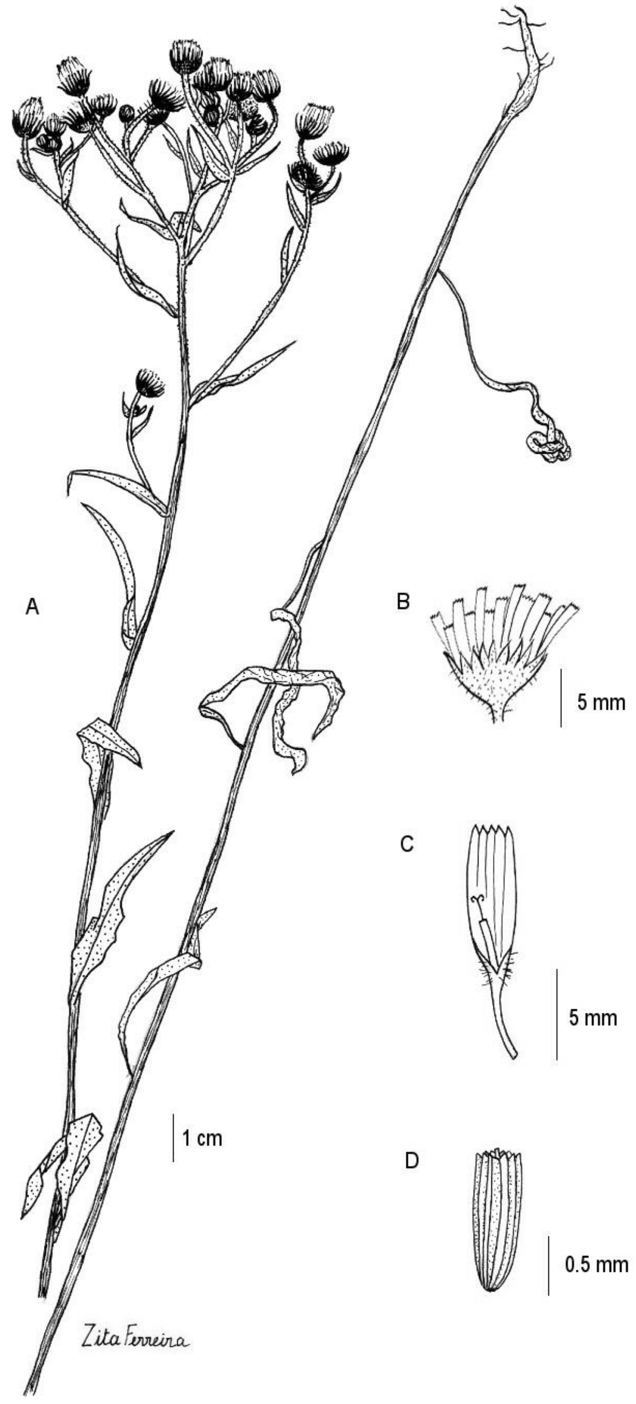

Figure 4.25 *Andryala integrifolia* subsp. *integrifolia* L. A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

1.4 x 0.3–0.5 mm (Figure 4.25D), usually oblong, frequently dark brown with white ribs, apex with a ring of long thin teeth equalling or slightly exceeding the ± conspicuous prolongation of the ribs (Figure 4.26D); pappus of dirty-white bristles 4–6 mm, ± pilose at the base (Figure 4.26E).

4.11.4.3 Comments on taxonomy and nomenclature

Linnaeus (1753: 808) validly published *Andryala integrifolia* L. and *A. sinuata* L. as distinct species, providing very vague descriptions: "*foliis integris*" and "*foliis sinuato-hastatis",* respectively. Later Linnaeus (1767) placed *A. sinuata* L. in *A. integrifolia* L., further describing the species according to the excerpt: "*fol. inferioribus runcinatis, superioribus ovato-oblongis, tomentosis"*. Lamarck (1795) also described *A. parviflora* Lam. that actually corresponds to *A. integrifolia* L.; the author cited *Sonchus villosus luteus minor* as a synonym, exactly the same polynomial that Linnaeus (1753, 1763) mentioned as a synonym of *A. sinuata* L. Indeed, later *A. parviflora* Lam. was combined as *A. parviflora* Lam. var. *sinuata* (L.) Boiss. In agreement, Willkomm (1865) recognised *A. integrifolia* var. *sinuata* (L.) Willk. describing it in the following terms: "*foliis angustis, inferioribus mediisque plus minus sinuato-dentatis, sinuato- v. runcinato-pinnatifidis*." Indeed, this description matches that of *A. sinuata* L. and, in fact, the author stated *A. sinuata* L. and *A. parviflora* Lam. var. *sinuata* (L.) Boiss. as synonyms. Furthermore, Willkomm (op. cit.) considered *A. integrifolia* var. *sinuata* (L.) Willk. morphologically close to *A. integrifolia* var. *angustifolia* DC. considering several features (e.g. plant indumentum, inflorescence type, capitula diameter, receptacle size) and distinguishing them based mainly on the leave margin [divided in the case of *A. integrifolia* var. *sinuata* (L.) Willk. instead of entire or sinuate-dentate]. Hence, both can be included in the typical subspecies: *A. integrifolia* subsp. *integrifolia*, despite the deeply divided leaves of some plants.

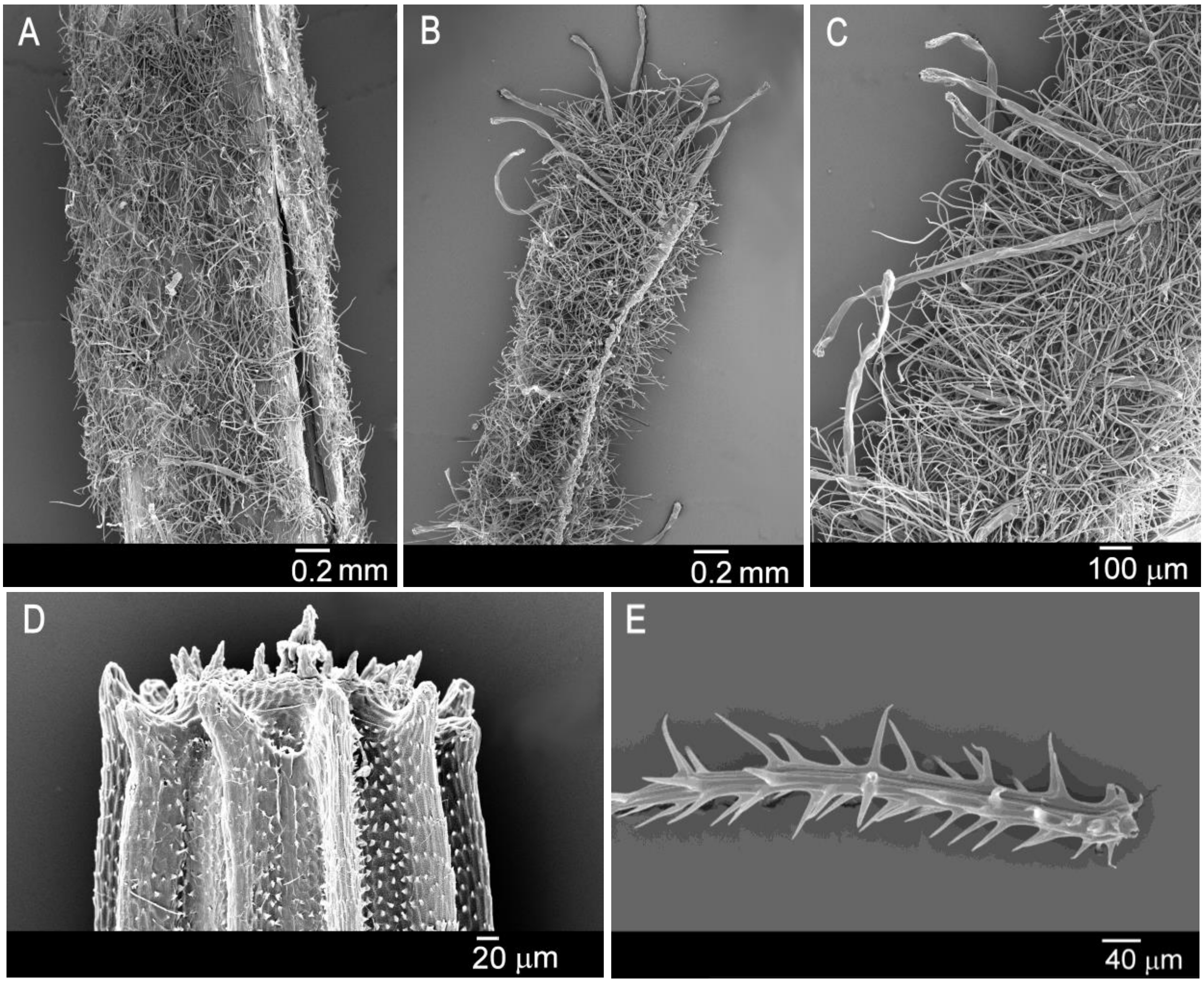

Figure 4.26 *Andryala integrifolia* subsp. *integrifolia* L. A – Stem indumentum, B – Leaf indumentum (abaxial face), C – Peduncle indumentum, D – Cypsela apex, E – Pappus base.

De Candolle (1838: 246) described *A. integrifolia* var. *angustifolia* DC. as follows: "*foliis omnibus subintegerrimis linearibus aut angustissimè lanceolatis*" and mentioned *A. mollis* Asso as a homotypic synonym. In the same publication, De Candolle distinguished it from other varieties mainly based on the leaf margin and shape. *Andryala mollis* Asso was depicted in the earlier work *Mantissa stirpium indigenarum Aragoniae* (

Figure **4.27**) and described in the following terms: "*foliis lanceolatis, versus petiolum atenuatis, dentatis, superioribus integerrimis*" (Asso y Del Río 1781).

Figure 4.27 Reproduction of the icon representing *Andryala mollis* Asso in Mant. Stirp. Arag. (1781)

Figure 4.28 Reproduction of the icon representing *Andryala allochroa* Hoffmanns. & Link in Fl. Portug. (1825)

Some years before Hoffmannsegg & Link (1825) published *A. allochroa* Hoffmanns. & Link describing its leaves in the following manner: "*Folia radicalia in petiolum angustata, dentato-sinuata, acuta, dente uno alterove aut integerrima, summa paullo latiora, integerrima*". This description as well as the illustration presented in this work (Figure 4.28) match quite well those of *A. mollis* Asso. Hence, *A. integrifolia* var. *angustifolia* DC. corresponds to *A. allochroa* Hoffmanns. & Link. Conversely to earlier authors (e.g. De Candolle 1838; Willkomm & Lange 1865; Amo y Mora 1872; Rouy 1905), Coutinho (1939) adopted the name *A. integrifolia* L. var. *allochroa* (Hoffmanns. & Link) Cout. instead of *A. integrifolia* var. *angustifolia* DC. Both seem to correspond to *Andryala integrifolia* L. plants with narrow leaves, linear to linear-lanceolate or oblong-linear, the lower dentate-lobate and the upper entire, and few capitula arranged in a lax corymb.

Hence, the correct name would be *A. integrifolia* L. var. *allochroa* (Hoffmanns. & Link) Cout. as the basionym was validly published much earlier than *A. integrifolia* var. *angustifolia* DC. Furthermore, *A. integrifolia* L. var. *allochroa* (Hoffmanns. & Link) Cout. and *A. integrifolia* var. *sinuata* (L.) Willk. are morphologically very close and are not herein recognised as distinct *taxa*. According to this taxonomic concept, both should be included in *A. integrifolia* subsp. *integrifolia.*

Roth (1797) described *Rothia cheiranthifolia* Roth and *Rothia runcinata* Roth., indicating different varieties of *A. integrifolia* L. as synonyms. Actually, both *R. cheiranthifolia* Roth and *R. runcinata* Roth. should be included in *A. integrifolia* L. Furthermore, Roth (op. cit.) correctly highlighted that *R. cheiranthifolia* Roth is not to be confounded with *A. cheiranthifolia* L'Hér. Actually, Hoffmannsegg & Link (1825) described *A. cheiranthifolia* Hoffmanns. & Link*, A. dissecta* Hoffmanns. & Link, and *A. coronopifolia* Hoffmanns. & Link, all later correctly placed in *A. integrifolia* L., together with *A. allochroa* Hoffmanns. & Link (Coutinho 1939). In fact, Hoffmannsegg & Link (op. cit.) underlined the similarity between these four *taxa*, residing the main differences on the plant indumentum and leaf margin. Steudel (1840) misinterpreted Hoffmannsegg & Link's work by considering *A. cheiranthifolia* Hoffmanns. & Link and *A. coronopifolia* Hoffmanns. & Link, clearly assigned to Portugal, as synonyms of *A. pinnatifida* Aiton from the Canary Islands. Although later authors followed this taxonomic point of view, the observation of the icon of *A. coronopifolia* Hoffmanns. & Link in this work (Figure 4.29) shows that it corresponds to *A. integrifolia* L., but with more profoundly divided leaves. Moreover, Hoffmannsegg & Link (1825) stressed its resemblance to *A. allochroa* Hoffmanns. & Link, a synonym of *A. integrifolia* L. Indeed, Coutinho (1939) transferred these *taxa* in rank, recognising *A. integrifolia* L. var. *allochroa* (Hoffmanns. & Link) Cout. and *A. integrifolia* L. var. *sinuata* (L.) Willk. (the latter including *A. dissecta* Hoffmanns. & Link and *A. coronopifolia* Hoffmanns. & Link as forms).

De Candolle (1838) described an additional variety, *A. integrifolia* var. *diffusa* Jan ex DC. based on *A. diffusa* Jan, an unpublished name of Jan's authority. Much later Rouy (1905: 454) recognised several varieties for *A. integrifolia* L. and presented a description for *A. integrifolia* var. *diffusa* Jan ex DC. similar to that of De Candolle's: "*Tige très rameuse dès la base, à rameaux étalés-diffus; feuilles linéaires, entières; calathides petites, long pédonculées.*" Apparently, *A. integrifolia* var. *diffusa* Jan ex DC resembles very much *A. integrifolia* L. var. *angustifolia* DC., except for the stem ramification as it is much branched from the base, with spreading branches. However, a detailed observation of the type material will be necessary to corroborate this taxonomic concept.

Figure 4.29 Reproduction of the icon representing *Andryala coronopifolia* Hoffmanns. & Link in Fl. Portug. (1825)

Rouy (1905: 454) described a new variety, *Andryala integrifolia* L. var. *basaltica* Rouy, according to the following text: "*Tige très grêle, de 20-25 cent., ± rameuse, à rameaux et pédoncules subfiliformes disposés en panicule lâche, racémiforme; feuilles petites, minces, linéaires-oblongues, entières ou les inf. denticulées; calathides très petites* (4-6 mill. de diam.)." As it is possible to note, this variety is again morphologically very close to *A. integrifolia* var. *angustifolia* DC., in spite of being more or less branched and exhibiting a paniculate inflorescence. These differences may be due to ecological conditions since *A. integrifolia* L. var. *basaltica* Rouy was found on an unusual substrate (basaltic rocks), as its own name suggests.

Several North African *taxa*, originally described as new species were later included by different authors in *A. integrifolia* L. For instance, Maire (1927) described *A. cedretorum* Maire, stressing its similarity to *A. integrifolia* L. var. *angustifolia* DC., and distinguishing it mainly by the habit (biannual or perennial) and tonality of the ligules (golden yellow). Sauvage (1961), although with some reservations, transferred this *taxon* to a subspecies rank, and later Dobignard (2009) combined it as *A. integrifolia* var. *cedretorum* (Maire) Dobignard, distinguishing it from the typical variety only by the colour of the ligules (pale yellow in the latter case). Although Dobignard (op. cit.) did not mention *A. integrifolia* var. *angustifolia* DC. as a synonym, the original description of *A. cedretorum* Maire (Maire 1927: 46) fits this *taxon* perfectly in what concerns leaf shape and margin ("*Folia basalia … oblonga l. oblongo-lanceolata, … superiora lineari-lanceolata, integra; suprema saepius linearia acuta.*"). Besides, it resembles *A. allochroa* Hoffmanns. & Link, by the base of the lower leaves and the inflorescence ("*Folia basalia … basi sensim in petiolum longiusculum attenuata, … in inflorescentiam laxiusculam … plus minusve paniculatam …*"). Likewise, *A. antonii* Maire, which was later erroneously placed in *A. pinnatifida* Aiton, corresponds to *A. integrifolia* L. (Ferreira *et al.* 2014c) and also resembles *A. integrifolia* var. *angustifolia* DC. Another example is the Moroccan *A. humilis* Pau ex Font Quer, which was validly published by Font Quer (1928) based on a description by Carlos Pau which can be seen on printed labels attached to an exsicata. Curiously, on the printed labels a synonym is indicated: *A. integrifolia* L. var. *humilis* F. Q., meaning that this *taxon* was transferred to a species rank. Thus, the correct name should be *A. humilis* Pau ex Font Quer. These specimens resemble very much *A. integrifolia* L. and as stated in the protologue they differ only by their smaller stature: "*Difiere … de la A. integrifolia por su tamaño menor*." In fact, Maire in Jahandiez & Maire (1934) included *A. humilis* Pau ex Font Quer in *A. integrifolia* as a form: *A. integrifolia* subsp. *eu-integrifolia* Maire var. *typica* Maire f. *humilis* Pau ex Font Quer.

Maire (1940) considered another subspecies, *A. integrifolia* L. subsp. *perennans* Maire & Weiller, morphologically approaching *A. integrifolia* var. *angustifolia* DC. (by the cauline leaves narrow and entire) and *A. cedretorum* Maire (by the habit, the only difference being the pale yellow tonality of the ligules). Additionally, Maire (op. cit) stressed that this subspecies differs from *A. integrifolia* L. subsp. *ampelusia* (Maire) by the narrow leaves and lax inflorescence. Thus, it appears that *A. integrifolia* L. subsp. *perennans* Maire & Weiller, *A. integrifolia* var. *angustifolia* DC. and *A. cedretorum* Maire correspond all to the same *taxon*.

Maire in Jahandiez & Maire (1934) suggested a more or less complex taxonomic structure for *Andryala integrifolia* L., recognising two subspecies: *A. integrifolia* subsp. *eu-integrifolia* Maire and *A. integrifolia* L. subsp. *ampelusia* (Maire) Maire, the first including several varieties [*A. integrifolia* subsp. *eu-integrifolia* Maire var. *typica, A. integrifolia subsp. eu-integrifolia* Maire *var. sinuata* (L.) Willk., *A. integrifolia* subsp. *eu-integrifolia* Maire var. *angustifolia* DC., *A. integrifolia* subsp. *eu-integrifolia* Maire var. *corymbosa* (Lam.) Willk. and *A. integrifolia* subsp. *eu-integrifolia* Maire var. *gracilis* Pau.]. Since the taxonomic delimitation between varieties is rather complicated and based mainly on leaf shape and margin, a more comprehensive *taxon* (*A. integrifolia* L. subsp. *integrifolia*) should be accepted, including all the ones proposed by Maire in Jahandiez & Maire (1934), except for *A. integrifolia* subsp. *eu-integrifolia* Maire var. *gracilis* Pau. (= *A. cossyrensis* Guss.) and *A. integrifolia* subsp. *eu-integrifolia* Maire var. *corymbosa* (Lam.) Willk. The latter as well as *A. integrifolia* L. subsp. *ampelusia* (Maire) Maire are here included in *A. integrifolia* subsp. *corymbosa* (Lam.) M. Z. Ferreira, Alv. Fern. & M. Seq. (see p. 141).

There are still some *taxa* whose inclusion in *A. integrifolia* L. is quite acceptable taking into account the original descriptions. These are *A. aestivalis* Pomel, *A. reboudiana* Pomel and *A. minuta* Lojac. The first seems to correspond to a summer form of *A. integrifolia* L. (as the name itself denotes) and, indeed, Pomel compared it to *A. sinuata* L. (= *A. integrifolia* L.) in his handwritten description attached to original herbarium material (MPU005677). *Andryala reboudiana* Pomel is in general considered as a synonym of *A. integrifolia* L. The analysis of type material would be enlightening as the vagueness of the original description hinders taxonomic delimitation; however, this material was not located. Likewise, *A. minuta* Lojac. is commonly accepted as a synonym of *Andryala integrifolia* L. (e.g. Aghababyan *et al.* 2008). Although expressing some uncertainty, Pojero (1902) described it as a new species, indicating the herbarium name *A. dentata strictissima* Lojac. as a synonym. The original description is not very elucidating since important diagnostic characters of *A. integrifolia* L. are not mentioned. Nevertheless, the observation of type material (PAL11870) supports its inclusion in *A. integrifolia*.

Lindberg (1932) described *Andryala atlanticola* H. Lindb. as a new species without comparing it to any *Andryala taxon* since he was not acquainted with anything similar. Indeed, Lindberg (op. cit), considering the difficult taxonomic delimitation within the genus, questioned whether it in reality corresponded to a distinct *taxon*. *Andryala atlanticola* H. Lindb. exhibits features that justify its inclusion in *A. integrifolia* L., the most polymorphic and wide spread species in *Andryala.* L. (e.g. involucral bracts flat and not involving a floret, receptacle setae long, cypsela with ribs only slightly extended at the apex).

Maire (1926) described *Andryala x faurei* Maire & Maire as a hybrid between *A. arenaria* (DC.) Boiss. & Reut. and *A. integrifolia* L. In the same publication, this author distinguished it from the parental species according to the excerpt: *"Ab A. arenaria D.C. differt radice crassiuscula, caule elatiore, inflorescentia plus minusve paniculata nec corymbosa, foliis caulinis mediis basi attenuatis nec rotundatis, foliis supremis integris nec plerisque dentatis, pedunculis nudis nec 1-foliatis; ab A. integrifolia L. foliis caulinis superioribus basi latitudinem maximam praebentibus, plus minusve amplexicaulibus, profunde dentatis dentibus angustis porrectis, ligulis aureis.",* highlighting that *Andryala x faurei* Maire & Maire is morphologically closer to *A. integrifolia*. However, the characters which the author mentioned to distinguish it from *A. integrifolia* L. can also be observed in this species. In fact, *Andryala x faurei* Maire & Maire resembles *A. integrifolia* even in the main diagnostic features of the species (e.g., flat involucral bracts and long receptacle setae). According to Maire (1926), although Faure collected a specimen with sterile cypselae he was able to gather fertile fruits on other specimens. These were sown to confirm the hybrid nature of *Andryala x faurei* Maire & Maire. Nevertheless, the results of these experiments (three plants morphologically closer to *A. integrifolia* L. with slight differences in the ligule colour and plant cycle duration) do not seem enough to support the hybrid nature of this *taxon*. Later Font Quer (1935) described *A. x caballeroi* Font Quer as a hybrid between the same parental species. Font Quer (1935) distinguished it from *A. arenaria* (DC.) Boiss. & Reut. and *A. integrifolia* L. according to the following text: "*Ab A. arenaria caule simpliciusculo a medio ad apicem ramoso, capitulis mediocre magnitudine, in corymbo densiore congestis, involucro flavescente, ligulis minoribus, differt. Ab A. integrifolia discrepat caule a medio ramoso, capitulis majoribus corymbum laxiorem formantibus, involucri phyllis magis elongatis acuminatisque sulphureis sed extus dilute purpuréis."* Again the features used to separate it from *A. integrifolia* L. are taxonomically very weak. Given that the hybrid nature of both *Andryala x faurei* Maire & Maire and *A. x caballeroi* Font Quer is very dubious, their inclusion in *A. integrifolia* subsp. *integrifolia* is proposed herein until further experimental work is carried out in order to clarifly the taxonomic position of these taxa.

4.11.4.4 Karyology

The first chromosome number reported for *Andryala integrifolia* (2n = 18) was determined on a cultivated plant from the Botanical Garden of Copenhagen (Stebbins *et al.* 1953). This somatic chromosome number was later confirmed on material collected in Spain (Björkqvist 1969; Izuzquiza 1988) and in Portugal, the latter provenance including plants ascribed to *A. integrifolia* L. var. *sinuata* (L.) Willk. (Fernandes & Queirós 1971). The same somatic chromosome number was obtained with plants from the French Oriental Pyrenees (Kliphuis & Wierffering 1972). The gametic chromosome number of n = 9 was determined on Italian material ascribed to *A. integrifolia* L. subsp. *integrifolia* (Capineri *et al.* 1978b) as well as to Spanish material (Pastor *et al.* 1990). The first chromosome count for plant material of Moroccan origin ("Plage des Nations", between Kenitra and Rabat) confirmed n = 9 as the basic chromosome number of *A. integrifolia* (Delay & Petit 1971) and later counts on material from several Moroccan provinces corroborated the diploid nature of this *taxon* (Vogt & Oberprieler 1993; Vogt & Oberprieler 1994; Parra *et al.* 1999).

4.11.4.5 Ecology and conservation status

Andryala integrifolia subsp. *integrifolia* can be found on disturbed lands and is frequent on roadsides, growing in localities between 0–2000 m (Talavera 1987; Blanca 2009, 2011) or even up to 2400 m (Jahandiez & Maire 1934). It grows on sandy, gravelly or barren lands, on uncultivated fields, and rocky walls (Willkomm & Lange 1865; Coutinho 1939; Franco 1984). It can be found growing on sandy-clay or clayish-sand soils at mountains bases (Sauvage 1961). It also occurs on volcanic slopes, above 1000 m (Ceballos & Ortuño 1976). This *taxon* can be found on calcareous and siliceous substrates, sandy pastures, scrublands, forests (e.g. oak and cedar forests as well as forest clearings), dunes, and sea-cliffs (Jahandiez & Maire 1934; Pottier-Alapetite 1981). According to available herbarium data, it can occur in pine forests, orchards and olive groves, and grows on acidic soils, limestone, quartzite, schist and granitic terrains, besides granitic outcrops. It occurs alongside with *Ulex* L. spp., *Lavandula stoechas* L., *Cistus* L. spp. *Rosmarinus officinalis* L., *Daphne gnidium* L., *Quercus* L. spp., *Olea europaea* L., *Pistacia lentiscus* L., *Andryala* L. spp.

In Southern Spain, it is quite common and is listed as Least Concern (LC) according to the *IUCN Red List categories and criteria* (IUCN 2001) (Talavera 1987; Blanca 2009, 2011). In mainland Portugal it is very frequent (Coutinho 1939). It is an introduced species in Madeira, the Azores and the Canary Islands (Silva *et al.* 2005; Ferreira *et al.* 2011; Ferreira *et al.* 2015a, see Chapter 5). This is cause of enormous concern because of the great capacity for hybridisation of *A. integrifolia* L. In fact, hybrids between different *Andryala* species and *A. integrifolia* have been recorded (e.g., Maire 1937; García Adá 1992) and the possibility of hybridisation with other *Andryala* species exists (Ferreira *et al.* 2011, see Appendix 1).

4.11.4.6 Geographic distribution

Andryala integrifolia subsp. *integrifolia* can be found in the Iberian Peninsula, France, and North Africa (Figure 4.30). Specifically, it occurs nearly in all of mainland Spain (Willkomm & Lange 1865; Amo y Mora 1872), where it is quite frequent in the South (Talavera 1987; Blanca 2009, 2011), and in most of mainland Portugal (Coutinho 1939; Sampaio 1949). It can be found in southern and central France and on the island of Corsica (Rouy 1905). This *taxon* has also been recorded for southern and central regions of Italy (occurring rarely in the North) as well as for the islands of Sicily and Sardinia (Cattarini 1976; Pignatti 1982).

Andryala integrifolia subsp. *integrifolia* occurs in Morocco, especially in the North, although it can also be found in southern and central regions (Ball 1878; Caballero 1917; Lindberg 1932; Sauvage 1961). It is also present in Algeria (Poiret 1789; Desfontaines 1799; Battandier 1889) and Tunisia, mainly in the North (Barratte 1896; Murbeck 1897; Lindberg 1932; Pottier-Alapetite 1981). Its presence in Libya is still in need of confirmation (Boulos 1979).

This *taxon* can also be found in Macaronesia, specifically on the Canary islands of Hierro (Lid & Lid 1967; Ceballos & Ortuño 1976) and La Palma (Santos-Guerra *et al.* 2013); on the Azorean islands of São Jorge, Faial and Santa Maria (Franco 1984; Silva *et al.* 2005; Silva *et al.* 2010); and on the Island of Madeira where it was recently introduced (Ferreira *et al.* 2011, see Appendix 1).

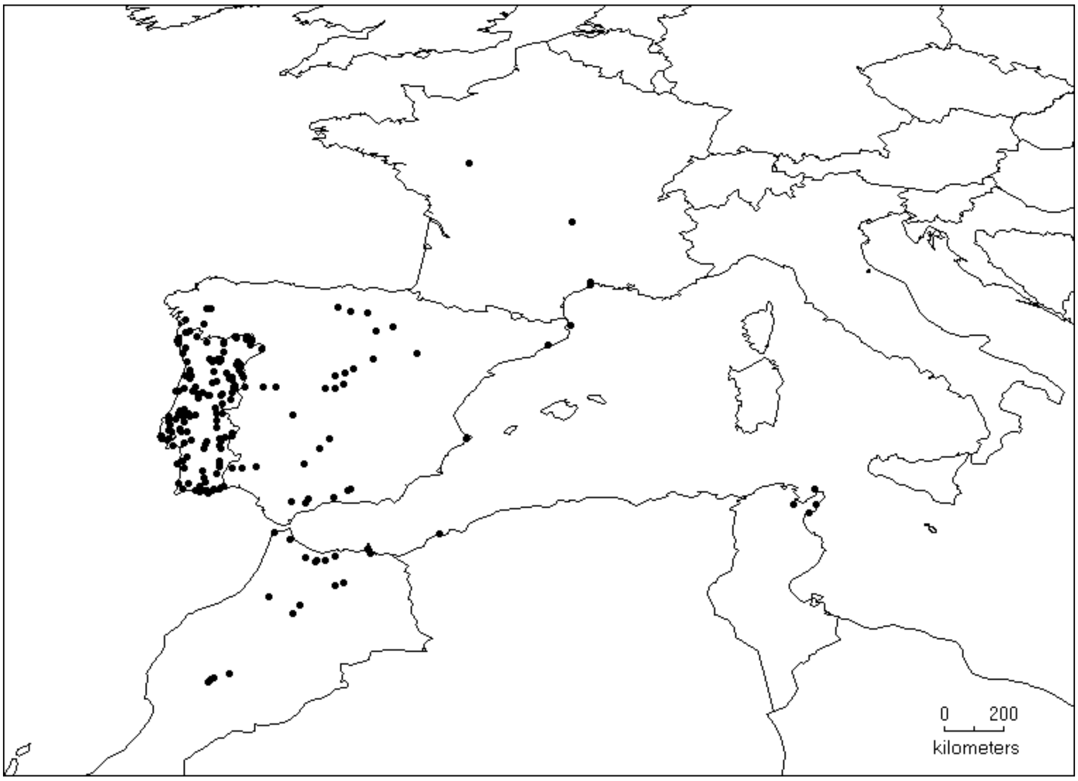

Figure 4.30 Distribution area of *Andryala integrifolia* L. subsp. *integrifolia*, according to studied material.

4.11.4.7 List of studied material

Algeria:

[loc. incert.]: 26-VI-1880, A. Roux, MPU-Maire.

[Oran]: prés de Oran, champs sablonneux du la plaine du cap Falcon, 07-VI-1932, MPU-Maire. à Gambetta, Pelouses et Broussailles, 11-VI-1911, A. Faure, MA 139186.

[Tlemcen]: Le Ghar-Rouban, 10-VI-2099, A. Pomel, MPU-Pomel.

France:

Guchen. Vallée d´Aures, 780 m, 26-VIII-1933, Dr. Ruy Palhinha, s/nº, LISU 55343, Montpellier, Grammont, 14-VII-1940, Licent, E., s/nº, P 04024359. St-Nicolas-de-Bourgueil, Espinay, L. d', s/nº, P 00707843. Maguelone, 13-VI-1941, Licent, E., s/nº, P 04024358. Puy de Dome, Le Saut du Loup, prés Issoire, alt. v. 428, 07-VIII-1932, MA 139143.

Morocco:

[Loc. incert.]: cedreto, c. 1600 m, 24-VI-1926, Harald Lindberg, MPU-Maire. Rif SW, massif du Khzana [?] du varzut SW, 1100 m, 14-VII-1958, Ch. Sauvage, MPU. Zaiane [?], 1000 m, 24-VI-1958, MPU-Maire. Zaiane, Tarmilete, rochus de da source froide, ligules orange, capitules en cone, plante vivace ou perenante, de rochus, 900 m, 07-VI-1961, MPU.

[Agadir-Ida Ou Tanane]: Región de Oukaimeden, Adrar Tizrag, 2580 m , 01-VII-2006, F. Cabezas & al, MA 746391.

[Al Hoceima]: Atlas Rifain, Telata de Ketama, 1340 m, 22-VII-1934, MPU-Maire. Rif SW: Ketama, nuberu d´Izaguene, lígules citrines, 1500 m, 10-VII-1959, Ch. Sauvage, MPU-Maire. Atlas Rifain, Telata de Ketama, 1340 m, 22-VI-1934, Sennen et Mauricio, MA, 139353. c. Targuist, Hab. in declivibus schitosis, 1100 m. alt., 22-V-1927, P. Merino, MA 139183.

[Béni-Mellal]: Just above El-Ksiba along road to Imilchil, 1000 m, ligules lemon yellow, 05-VII-1997, S.L. Jury, 17434, MA 616485.

[Chefchaouen]: Rif SW. J. Tizirène, versant SE, à la limite inferieure de la cédraie, Madame Suzanne Jovet-Ast, Paul Jovet et Ch. Sauvage, 13345, MA 169206.

[Ifrane]: MA central Statum de biologie d´Ifran, 1650 m, 18-VII-1941, M. Naudi, s/nº, MPU. In quercetis Atlantis Medii supra Aïn Leuh, solo calcareo, 1500 - 1700 m, flores aurei, 02-VII-1939, Harald Lindberg, MPU-Maire. Moyen Altas: Aïn-Leuh, cedraies sur calcaires 1750 m, fl. jaune d'or, P 00084247.

[Marrakech]: vallée de l'Ourika, 29RNQ73, talus rocailleux et au pied des falaises calcaires, 1240 m, 13-VI-1988, J. Molero, A. M. Romo & A. Susanna, R4337, MA 537777. Haut Atlas Mts. region Marrakech-Tensift-El-Haouz: Imlil, slopes near the road to Ansi, 2.5 km NNW of the village, 1585 m, 19-V-2010, J. Chrtek and Z. Dockalová, PRA, JC13. In Atlantis Majoris dictione Glaoua, enzel in clivis argillaceis nec non in glareosis 820 m, ligulae aurantiae, 04-VII-1924, P 00084243. Gd. altas central - Reraya, rochers dans la valleé de l´Acif Chisane, au dessus d´Arround, alt. 1950 m, 19-VII-1936, MPU-Maire, Altas: Arround, rocailles - 2000 m, 30-VI-1936, Balls, 2894, MPU-Maire.

[Nador]: Barranco del Lobo, Mazuza, 08-VII-1932, Pardo & Martí, 37, MA 443584. Gurugu, à Taquigriat, sites débroussailles, 960 m, Sennen et Mauricio, MA 139217. Barranco del Lobo, Masusa, 08-VI-1922, Pardo & Martí, MA 443599. region Taza-Al-Hoceima-Taounte, Tazzeka National Park: Ras el Ma, near the road above the restaurants, 10 km south of the railway station in the city of Taza, 1050 m, 16-V-2010, J. Chrtek and Z. Dockalová, PRA, JC7. Region Oriental, Beni Chiker, near the road 1.3 km SW of the village centre, 140 m alt., 16-V-2010, J. Chrtek and Z. Dockalová, PRA, JC4.

[Tanger-Asilah]: Djebel Kehir, C. Pau, MA 139102.

[Taza]: Rif. SW: env. de Rab. Taza. Marabout de Sidi Bou-Nouar, 830 m, 18-VII-1958, Ch. Sauvage, MPU-Maire.

[Tetouan]: Djebel Dersa, C. Pau, MA 139101.

Portugal:

[Loc. incert.]: [?] Abelheirinha, 05-VII-1948, [?] e Romariz, s/nº, LISU 968. Pereira, 9892, MA 576305. Alentejo, J. Daveau, s/nº, LISU 40308. Alentejo Litoral, S. Bartholomeu pr. S. Thiago Dela[?], J. Daveau , s/nº, LISU 40346.

[Algarve]: V. Real de Sto. António, Vila Nova da Cacela, solo coberto de sobreiro solo xistoso, Q. 958, 15-V-1991, M. Lousã & J.C. Costa, s/nº, LISI 48453. Sta. Catharina da fte. do Bispo, J. Daveau, s/nº, LISU 40208. Algarve, Villa Nova de Portimão, José Palhinha, 2402, LISU 40319. arredores de Faro [?], s/nº, LISU 56016. Monchique, Dr. R. Palhinha, s/nº, LISU, 40288. Vila Real de Santo António, Sesmarias em matos, espécie pouco frequente no local, solos xistosos, 21-04-1983, J. Martins e D. Duarte, s/nº, LISI 42349. Lagos: Bensafrim, 1 Km Sul de Espinhaço de Cão, Q. 948, 23-04-1988, D. Espirito Santo, s/nº, LISI 45644. Alcanena, Olhos de Água, 05-X-1959, M. Micaela da Fonseca, s/nº, LISI 20591. Castro Marim, Reserva, entre a povoação de Olhos de água e a pista de aviação, na encosta de um monte subcoberto muito esparso de pinheiros, planta pouco frequente no local. Q. 959, 09-V-1978, M. Lousã & J. Monjardino, s/nº, LISI 711. Aljezur: Barranco da Amoreira, Q. 920, 15-VI-1988, M. Dalila Espírito Santo, s/nº, LISI 46592. Monchique: Marmelete, na estrada para a barragem, Q. 934, 16-VII-1988, M. D. Espírito Santo, s/nº, LISI 46796. Loulé: Alte, Estivais de Moiros, solo calcário, alt. 125 m, Q. 953, mato alto de carrasco, pistaria e cistos, 11-VI-1988, D. Espírito Santo, s/nº, LISI 46928. Albufeira: Guia, entre Assomadas e Malhada Velha, Figueiras e amendoeiras, solo calcário, Q. 952, 11-V-1991, D. Espírito Santo, s/nº, LISI 48643. V. Real de Sto. António: Vila Nova da Cacela, perto de Silveira (a E de Montinho), Figueiras e mato, solo xistoso Q. 959, 15-V-1991, M. Lousã & J.C. Costa, s/nº, LISI 48952. Loulé: S. Sebastião, Campina de Baixo, 25-V-1991, M. D. Espírito Santo, s/nº, LISI 49171. Faro: Sta. Bárbara de Nexe, 800 m a N de Falfosa, olival, solo calcário, alt. 90m Q. 970, 25-V-1991, D. Espírito Santo, s/nº, LISI 49218. Tavira: Sto. Estevão, Monte Agudo, amendoeiras, alfarrobeiras, oliveiras e figueiras; solo calcário, Q. 957, 30-V-1991, M. Lousã, s/nº, LISI 49275. Vila Real de Sto. António: Vila Nova de Cacela, perto de Pocinho, mato sobre solo xistoso, 15-V-1991, M. Lousã, J. C. Costa, LISI 48924.

[Alto Alentejo]: Marvão, Prado, A.R. da Cunha, s/nº, LISU 40297. Casadas Meiadas, Povoa das Meiadas, A.R. da Cunha, s/nº, LISU 40299. Serra d´Ossa - Aldeia da Serra, J. Daveau, s/nº, LISU 40309. Crato, A. R. da Cunha, s/nº, LISU 40312. Fronteira, Ataleiros, J. de Vasconcellos, s/nº, LISI 6079. Vendas Novas, X. Basto, s/nº, LISI 4988. Vila Viçosa (Tapada das Vinhas das Casas Altas), 28-V-1949, M. C. Braga, s/nº, LISI 12773. Reguengos de Monsaraz, 20-V-1949, F. Xarro Guião, s/ .nº, LISI 12582. Tapada real da Vila Viçosa, 12-VI-1955, M.S. Câmara, s/nº, LISI 17722. Barroqueiras de Pero Crespo, Conc. do Redondo , alt. 400m, exp. sul, solos pardos não calcários de granito e afloramentos rochosos de granito, J.F.C.B. Cordovil, s/nº, LISI 19146. Redondo, Montoito - Herdade da Alcrovisca, 16-V-1956, J. Chicau, s/nº, LISI 19147. Évora, Graça do Divor, Herdade da Chaminé, 30-V-1956, J. V. de Saldanha O. e Sousa, s/nº, LISI 18840. Herdade das Fontes, Concelho do Redondo, alt. 300 m, Exp. sudeste, solos esqueléticos de xisto, 16-VI-1956, J.F. C.B. Cordovil, s/nº, LISI 19148. Nisa, 20-V-1957, J. Fragoso de Almeida, s/nº, LISI 19552. Monte Ruivo, a 300 m da estrada de S. Vicente - Sta Eulália (Elvas), 20-V-1957, J. T. A. Barradas, s/nº, LISI 19544. a 112 Km SW do Monte do Almeida (Elvas), 27-V-1957, J. T. Antunes Barradas, s/nº, LISI 19638. Nisa, Tapadas de Montalvão, 20-V-1957, J. F. Almeida, s/nº, LISI 19540. Marvão (San Mamede), Granitos, 16-V-1978, J. A. Devessa, J. Pastor, s/nº, SEV 129394. Nª. Sr.ª de Tarega, Valverde, Herdade da Mitra, sub bosque de montado, sob Quercus rotundifolius, ervedo seco, 24-VI-1985, J. Gomes Pedro, LISI, 43508

[Alto Douro]: Miranda do Douro. Duas igrejas, 05-VI-1954, Júlio Granjo, s/nº, LISI 16360. Chaves, Samaiões, Lamas do Olmo, no mato alt. c. de 500m, 21-IX-1966, J. de Vasconcellos, s/nº, LISI 25464. Bragança: Avelada, margem do rio de Ovar, a E de Codeçal, q. 18 -alt. 680m; solo xistoso-aluvial, 04-VII-1980, J. Franco & M. Lousã, s/nº, LISI, 39422. Bragança: Quintanilha, vertente sobre a margem do rio Mação, Q. 58 - alt. 540m; solo xistoso; na fronteira luso-espanhola, 05-VII-1980, J. Franco & M. Lousã, s/nº, LISI 39666. Miranda do Douro: Pazadela - Penha das Torres, solo de xisto, 16-VI-1988, C. Aguiar, s/nº, LISI 46806.

[Baixo Alentejo]: Entre Carregueiro et Castro Verde, J. Daveau, s/nº, LISU 40342. Entre Corte-Figueira et Mù, alt. 560m, J. Daveau, s/nº, LISU 40303. Distrito de setúbal, arredores de Sines, a caminho de Santo André, Erva anual, capítulos de flores amarelo-citrino, nas areias soltas e claras, 17-VI-1978, L.A. Grandvaux Barbosa, 12863, LISU 67168. Serpa, Prof. Dr. Azevedo Gomes e L. Mello, s/nº, LISI 4687. Serpa, Gleba da Mó, 30-V-1952, F. G. Palma, s/nº, LISI 14147. Almodôvar: Serra da Graça dos Padrões, Barranco do Amador, pto. de Samblana, alt. 220m, exp E., 29-VI-1982, D. Espirito Santo e M. Lousã, s/nº, LISI, 41853. Mértola: S. Miguel do Pinheiro, pto. do cruzamento da Ribeira de Carreiras com a estrada Alcaria Longa - S.M. do Pinheiro, alt. +/- 150 m Exp. N., 20-VII-1982, M. Lousã e A. P. Oliveira, s/nº, LISI 41974. Serpa: Prelo do Lobo, vertente do lado E, 17-VI-1970, J. Franco & M.M. Fonseca, s/nº, LISI 30759. Brinches, Herdade da Vargem de Cima, Q. 526 - num pousio, 17-VI-1970, J. Franco & M.M. Fonseca, s/nº, LISI 30758. Santiago do Cacém: Cercal, a 6Km a N de Fanganheira, 18-V-1972, J. Amaral Franco, s/nº, LISI 33040. Almodôvar: Senhora da Graça dos Padrões na margem direita da ribeira de oeiras +/- 2 Km com a estrada de Almodovar-Mértola, q. 901, alt. 230m, exp. W, 05-VI-1982, D. Espirito Santo e J. M. Lourenço, s/nº, LISI 41669.

[Beira Alta]: Muralhas, Almeida, A.R. da Cunha, s/nº, LISU 40358. Folha da Rasa, Villar Formoso, A. R. da Cunha, s/nº, LISU 40332. Castelo Melhor, proximidades, exp. S., 27-VI-1941, G. Pedro, s/nº, LISI 6728. Serra da Marofa, junto ao marco geodésico, J. Pedro, s/nº, LISI 6403. Guarda, junto ao castelo, G. Barbosa e F. Garcia, s/nº, LISI 7057. Lamego, F. Garcia e M. Myre, s/nº, LISI 9588. Trancoso, a cerca de 500 m da Cruz da Galega, junto à estrada para a Vila, alt. 719 m, pinhal, N. Menezes da Costa, s/nº, LISI 16281. Tapada; freguesia da Cunha Alta (Mangualde), alt. 575 m. mato e pinhal novo, 06-V-1955, F.S. Almeida, s/nº, LISI 17222. Gouveia: Cativelos, Q. 316, alt. c. 395 m, solo granítico, exp. S, 09-V-1980, J. Franco & M. Lousã, s/nº, LISI 38208. Guarda: Cavadoude, Quinta da Estrada, Q. 301, alt. 500 m, solo granítico, 09-V-1980, J. Franco & M. Lousã, s/nº, LISI 38203. Guarda: Arrifana, Outeiro de S. Miguel, Q. 302, alt. 900m, sítio plano, granítico, 10-V-1980, J. Franco & M. Lousã, s/nº, LISI 38410. Pinhel: Gouveias, sítio das Naves, Q. 285, alt.c. 750 m; solo granítico, 10-VI-1980, J. Franco & M. Lousã, s/nº, LISI 38419. Sabugal: Baraçal, a cerca de 1 Km a sul da Fonte Forgueira, Q. 339, alt. 800 m; exp. W; solo granítico, 11-VI-1980, J. Franco& M. Lousã, s/nº, LISI 38672. Sabugal: Aldeia de Santo António, prox. Cabeço das Alagoas, Q. 357, alt. 880 m; solo xistoso; flores amareladas, 11-VI-1980, J. Franco & M. Lousã, s/nº, LISI 38667. Vila Nova de Paiva: Queiriga, a norte do Cabeço da Abelha, Q. 246, alt 780 m; exp. NW; encosta granítica, 3-VII-1980, J. Franco & M. Lousã, s/nº, LISI 39257. Sabugal: Lageosa, Veiga Espinhosa, Q. 359, alt. c. 890m; exp. S., 15-VI-1981, Francisco Pires, s/nº, LISI 40827.

[Beira Baixa]: Penamacor: Meimão, Alísio, espécie frequente no local, em floração, 15-VII-1987, M. Lousã, M. L. Rosa, J. P. Luz, LISI 44747. Villa Velha do Ródão (Fonte das virtudes), A.R. da Cunha, s/nº, LISU 40302. Branco (Monte Brito), A.R. da Cunha, s/nº, LISU 40301. Barca d´ Alva, taludes do caminho-de-ferro, R. Palhinha e F. Mendes, s/nº, LISU 40310. Serra do Cabril, J. M. Carvalho e F. Flores, s/nº, LISI 11192. Serra da Gardunha: Santo da Estalagem, 23-VI-1952, João do Amaral Franco, s/nº, LISI 14271. Serra da Gardunha: Giralda, 26-VI-1952, J. do Amaral Franco, s/nº, LISI 14291. Fundão, Alcaide: Piçarra, alt. 600 m, 18-VII-1955, J. Amaral Franco, s/nº, LISI 17832. Idanha-a-Nova, Freguesia da Aldeia de Santa Margarida, 13-V-1955, A. A. Vaz da Silva, s/nº, LISI 18745. Pampilhosa da Serra: Barragem de Sta. Luzia, Casal do Cabril, 28-VIII-1971, João Rafael Monjardino, s/nº, LISI 32341. Penamacor: 2 Km a NW de Meimoa, vertente do Cabeção, Q. 374, alt. 550 m; exp. sul; solo xistoso revestido de regelação xerofítica, 11-VI-1980, J. Franco & M. Lousã, s/nº, LISI 38666. Penamacor, à saída W da vila, Q. 391, alt. 530 m; solo granítico, 11-VI-1980, J. Franco & M. Lousã, s/nº, LISI 38657.

[Beira Litoral]: Canto de Magos, Segadães, A. R. da Cunha, s/nº, LISU 40331. Coimbra, Villa Franca, Duarte L. Pereira da Silva, s/nº, LISU 40283. arredores de Coimbra, F. Miranda da C. Lobo, s/nº, LISU 40282. Lousã, Quinta da Alfrocheira, R. F. Palhinha, s/nº, LISU 40284. Matta do Bussaco, J. Daveau, s/nº, LISU 40276. Cabo Mondego, A. Moller, s/nº, LISU 40267. Gois, Baeta Neves, s/nº, LISI 7015. Oliveira de Azeméis, Vilar Perra10-04-1950, Franscisco Soares Pinheiro, s/nº, LISI 13110. Figueira da Foz, Quiaios entre esta povoação e a Lagoa dos Bracos, Q. 360J.C. Costa, M. Lousã e J. Franco, s/nº, LISI 45982. Vila Nova de Ourém. Fátima, Cova de Iria. Charneca, 3-VI-1955, A. Manuel da Cunha Lopes, s/nº, LISI 17746. Castanheira de Pêra, José Maria Duarte Mendes, s/nº, LISI 19249. Aveiro, Esgueiras, Paço, Q. 273, terreno arenoso, mais ou menos seco, circundando o sapal, 07-VI-1980, J. Franco & M. Lousã, s/nº, LISI 37951. Albergaria-a-Velha, Vale Maior, a 1 km a E de Sto António, Q. 274, alt. 55m, mato xerofítico em solo do complexo xisto-grauváquico, 08-V-1980, J. Franco & M. Lousã, s/nº, LISI 38069.

[Bragança]: Monte, Seixas, A. R. da Cunha, s/nº, LISU 40344. Bragança, Rebouço, França, tipo de rocha: xisto, alt. 765 m.s.m., mata de *Cistus ladanifer*, 01-VII-1985, Tjarda de Koe, LISI 43537.

[Douro Litoral]: Fonte da Moira ao Castello do Queijo (arredores do Porto), Dr. A. Ricardo Jorge, s/nº, LISU 40339.

[Estremadura] Caldas da Rainha (Charnecas), J. Daveau, s/nº, LISU, 40327. Arredores de Lisboa. Caparica, A. R. da Cunha, s/nº, LISU 40320. Arredores de Alenquer: Santa Quitéria de Meca, J. Gualberto de Barros e Cunha, s/nº, LISU 40320. Caparide (prox.de Cascais), Campos, caminhosA. X. Pereira Coutinho, 2195, LISU 40281. Cascais, Quinta do Marquês, Erva rizomatosa. Form. complexa herb. lenhosas baixas na encosta de um cabeço com *Quercus faginea, Quercus coccifera, Quercus lusitanica, Olea europea, Pistacia lentiscus*, 24-V-1983, M. Correia & Cardoso , 5324, LISU 151864. Arredores de Lisboa - Pinhal do Marechal Caparica, A.R. da Cunha, s/nº, LISU 40298. Algazarra, Champs quartzeux (Environs de Lisbonne), J. Daveau, s/nº, LISU 40307. Collines d´Obidos, J. Daveau, s/nº, LISU 40294. Setubal, Santiago do Cacém, à saída de Santiago do Cacém para a lagoa, Erva com a raiz +/- napiforme. Capitulos amarelo-citrino. Caules avermelhados na base. Abundante, 14-VII-1978, L. A. Grandvaux Barbosa, 13025, LISU 67169. Belas (Quinta da Senhora da Serra) Sintra, Em cenomaniano pedregoso fresco; mata espontânea. alt. 160 m exp. NNE, José M. de Carvalho e Francisco M. Flores, s/nº, LISI 6869. Sintra (Sabugo - Santa Cruz), José M. de Carvalho e Francisco M. Flores, s/nº, LISI 8764. Lisboa (Tapada da Ajuda), A. Veneno, s/nº, LISI 3934. Arredores de Alenquer: Sta Quitéria de Meca, J. Gualberto de Barros e Cunha, s/nº, LISI 3258. Bombarral: Carvalhal, Quinta dos [?], Q: 559, solo franco arenoso. alt. 50 m IF? 125, 23-VI-1983, M. D. Espírito Santo, s/nº, LISI 42674. Bombarral: à saída da vila, do lado direito da estrada para Peniche, Q: 559, solo argiloso-arenoso, alt. 40m IF 171, 01-VII-1983, M. D. Espírito Santo, s/nº, LISI 42714. Grândola, Herdade de Padrões, alt. 23 m, terreno de oligocénico inv. 11, 16-VI-1959, Filipe C. Vilhena, s/nº, LISI 20377. Conc. de Cascais, entre S. Domingos de Rana e Rebeloa, num inculto, 01-VI-1960, J. de Vasconcellos, s/nº, LISI 20733. Palmela, Marateca, Herdade do Zambujal, alt. 50 m Exp. W; terr. Pliocénico, 21-V-1963, A.Cruz Marcelino, s/nº, LISI 22864. Bombarral (freguesia Vale Covo - Urmal), 30-V-1968, F. Rebocho Lima, s/nº, LISI 27035. Porto de Mós: Mendiga, 23-V-1979, M. Lousã, s/nº, LISI 36831. Porto de Mós: Mira de Aire, Costa de Mira, sob as ventas do diabo, q. 506 alt. 425 m, 30-04-1980, Lousã, Esp. Santo, Moreira & Rosa, s/nº, LISI 37568. Miraflores. Freguesia de Carnaxide, Concelho de Oeiras, 05-V-1989, Maria Leonor Costa et al., s/nº, LISI 47641. Alenquer: Vila Verde dos Francos, a norte do Casal do chorão (Sº Montejunto), mato alto, alt. 370 m, exp. W, Q. 579, 06-VI-1989, D. Espírito Santo & J. C. Costa, s/nº, LISI 47943. Vila Franca de Xira, Calhandriz, J. Costa Mendonça, s/nº, LISI 15029. Sintra: Quinta da [?]enha Verde, 16-V-1953, J.T. Diniz, s/nº, LISI 15199. Sintra: Quinta de Monserrate, num pinhal queimado e cortado, 10-V-1968, Baeta Neves, s/nº, LISI 26886. Vila Nogueira, 25-V-1978, J. A. Devesa, J. Pastor e S. Talavera, 638/78, SEV 215138.

[Madeira]: Paul da Serra, talude rochoso junto à estrada, apenas um exemplar na zona, 24-VII-2009, M. Sequeira, A. Pupo Correia, A. Figueiredo, Z. Ferreira, ZF239, MA 801896. Estrada para os Prazeres, junto à rotunda, alt. 590 m, exp. WNW 301º, 29-VII-2009, Z. Ferreira, M. Benedito & M. Sequeira, MS6346B, MA 801898. Estrada para a os Prazeres, no talude da via rápida, exp. S, alt. 539 m, 29-VII-2009, Z. Ferreira, M. Benedito & M. Sequeira, MS6342, MA 801897. Prazeres, junto à rotunda, alt. 591 m, 03-VII-2011, Z. Ferreira, ZF273. Prazeres, logo abaixo da Vereda da Estacada, junto à estrada, alt. 630 m, 03-VII-2011, Z. Ferreira, ZF274. estrada para os Prazeres, no talude da via rápida, exp. S, 29-VII-2009, Z. Ferreira, M. Benedito & M. Sequeira, MS6342, MA 801897. Depois da Ponta do Pargo, para oeste, alt. 504 m, 23-VII-2011, Z. Ferreira, ZF290. Depois da Ponta do Pargo, para oeste, alt. 504 m, 23-VII-2011, Z. Ferreira, ZF291.

[Minho]: Lavandeira - Monsão, A. R. da Cunha, s/nº, LISU 40326. Pinhal Cabedello - Viana do Castelo, A. R. da Cunha, s/nº, LISU 40334. Souto - Barcellos, A. R. da Cunha, s/nº, LISU 40341. Pinhal - Ganfei, A.R. da Cunha, s/nº, LISU 40306. Praia d´Ancora, A.R. da Cunha, s/nº, LISU 40292. Cabedello, Caminha, A. R. da Cunha, s/nº, LISU 40289. Pinhal da Raposeira - Valença, A. R. da Cunha, s/nº, LISU 40314. Vila Verde - Guardizela, Guimarães, 16-V-1955, J.Dias Pereira, s/nº, LISI 17417. Serra da Peneda, Costa das Teixeiras, alt. 420 m. inclinação-exposição: 40º SER. Barreto, s/nº, LISI 19276. Vila Verde: Gondomar, q. 43, 28-VIII-1981, A. Saraiva, s/nº, LISI 40947.

[Ribatejo]: Golegã, Pomar de pereiras, 25-V-1979, T. Vasconcelos et al., s/nº, LISI 36584. Encosta de Santarém, A.R. da Cunha, s/nº, LISU 40305. Porto de Móz (Casais do Livramento), A.R. da Cunha, s/nº, LISU 40300. Pinhal de Sto. António, Torres Novas, A. R. da Cunha, s/nº, LISU 40290. Raposeira, Coruche, 05-V-1949, J. de Vasconcellos e E. Goes, s/nº, LISI 12697. Torres Novas, Casal do Valentão (Serra de Aires), 17-VI-1947, J. S. Gonçalves, s/nº, LISI 11906. Freguesia de Sta. Margarida da Coutada, Carvalhoso, Chã, 28-V-1954, L.F.A.V. Bairrão, s/nº, LISI 16263. Sta. Margarida da Coutada, Mariola, 06-VII-1954, L.F.A.V. Bairrão, s/nº, LISI 16504. Junto à estrada da Ribeira e Cruzamento Espanhol (Santarém), 06-VI-1956, Manuel Alfaiate, s/nº, LISI 19081. Vila Franca de Xira: Alverca do Ribatejo, montes acima de A. dos potes, Q. 6 Flores liguladas palido amarelas, 16-X-1976, J. Amaral Franco, s/nº, LISI 35612. Benavente: Barrosa, Monte da Parreira, Pomar de pessegueiros, 31-V-1979, T. Vasconcelos et al., s/nº, LISI 36635. Salvaterra de Magos, Pomar de pessegueiros, 31-V-1979, T. Vasconcelos, s/nº, LISI 36631. Almeirim, Pomar de pessegueiros, 31-V-1979, T. Vasconcelos, s/nº, LISI 36630. Torres Novas: Pedregoso, junto ao ponto mais alto da Serra de Aire, Q. 507 a 678 m de alt., 18-VI-1980, M. Lousã & D. Espírito Santo, s/nº, LISI 38973. Benavente: sto. Estevão, junto à E.N. 119 ao Km 25, Q.647, montado ralo de sobro em areia, 01-VI-1982, J. C. Costa e J. Monjardino, s/nº, LISI 41616. Fonte da Bica, Serra dos Candieiros, conc. de Rio Maior, alt. 230 m em terreno Jurássico sob estrato arbustivo xerófilo, 07-VI-1963, Catarina Trindade, LISI 23040. Rio Maior, Serra dos Candieiros, acerca de 500 m. de Alto da Serra, Exp. W, alt. 240 m, 15-V-1959, M. Lousã, M. L. Rosa, J. P. Luz, LISI 20235.

[Trás-os-Montes]: Nantes: Serra da Brunheira, Dr. R. Palhinha, H. Navel e F. Mendes, s/nº, LISU 40337. arredores de Miranda do Douro - Póvoa, J. de Mariz, s/nº, LISU 40340. Bragança, Dr. M. Paulino, s/nº, LISU 55926. Vilarinho de Freiras, talude do C. F. junto a Fírvida P. Lopes e G. Pedro, s/nº, LISI 6900. Entre vale de Mendiz e Pinhão, 02-VII-1942, G. Barbosa e M. Myres, s/nº, LISI 8793. Vilarinho de Freiras, Vale do Lorgo [?] Fírvida, P. Lopes e G. Pedro, s/nº, LISI 7137. Entre a Ribeira de Maçores e Paredo dos Castelhanos, G. Pedro, s/nº, LISI 6404. Pinhão (Qta. Sta. Bárbara) Casais do Douro, Pedro Bello, s/nº, LISI 5251. Gouvinhas, prox. de Sobreiral, G. Barbosa e F. Garcia, s/nº, LISI 8128. Geres (arredores) entre São Bento da Porta Aberta e Covelo, prox. ao caminho para Freitas, J. de Vasconcellos e M. Coutinho, s/nº, LISI 12126. Entre Casais do Douro e Ervadora a cerca de 3, 5 Km desta, 24-V-1945, G. Barbosa e F. Garcia, s/nº, LISI 8009. Trás-os-Montes, a jusante da Foz de Távora, G. Barbosa e F. Garcia, s/nº, LISI 7953. Murça, G. Barbosa e F. Garcia, s/nº, LISI 7222. entre Sedielos e Vinhós, F. Garcia e M. Myre, s/nº, LISI 9735. Tabuaço, no caminho para Plácido e vale Figueira, 10-VII-1942, G. Barbosa, M. Myre, G. Pedro, s/nº, LISI 8817. Bragança: França, aos Viveiros florestais, margem esquerda do rio Sabor, Q. 17 alt. 670 m, margens do caminho florestal, lígulas citrinas, 1-VII-1987, J.A. Franco e J. G. Pedro, s/nº, LISI 44875. Vinhais, a 3 km de Sobreiro de Cima, vindo de Chaves, 27-VIII-1971, J. de Vasconcellos, s/nº, LISI 32333. Bragança: Babe, Q. 36, alt 820 m; solo xistoso, 5-VII-1980, J. Franco & M. Lousã, s/nº, LISI 39665. Entre Casais do Douro e Ervadora a cerca de 3, 5 Km desta, 24-V-1945, G. Barbosa e F. Garcia, s/nº, LISI 8009A. Bragança: Aveleda, Varge, Alto da Portela, 04-VII-1980, J. Franco & M. Lousã, s/nº, LISI 39408. Vimioso: Argozelo, ao cimo do Vale de Madeiros, alt. 690 m. solo xistoso, nas sebes, 5-VII-1980, LISI 39684.

[Viana do Castelo]: Gandra, Monte Dôr, no pinhal próximo da praia, A. R. da Cunha, s/nº, LISU 40317.

Spain:

[Loc. incert.]: Galicia, escala [?], 20-V-1944, P. Merino, MA 139211. Galicia, abundantissima, 08-V-1933, P. Merino, MA 139180.

[Alicante]: Benissa, 226 m, cuneta en borde de cultivo, 27-VI-2009, Inés Alvarez & L. Medina, IA2023.

[Barcelona]: Montnegre, monte, 08-V-2049, Montserrat, MA 161644.

[Burgos]: 30TVN4434, cercanías de Huidobro, paramera caliza, 22-VII-1984, Galán Cela & A. Martín, 665, MA 639931. carretera entre Villamudria y Rábanos,19-VI-1976, E. Fuentes, MA 520218. Páramo de Masa, 30NTV4017, trigal, 01-VII-1986, Galán Cera & G. López, 2019, MA 639899.

[Cáceres]: Baños de Montemayor20-V-1944, A. Caballero, MA 139206. Guadalupe, Maribel, in collibus dumosis, 21-VI-1946, C. Vicioso, MA 139172. Las Mestas; Las Hurdes (Salamanca), 5-VII-1946, Caballero, MA 139129.

[Cádiz]: Entre Grazalema & el Puerto del Boyar, zona herbosa cerca del Arroyuelo. Caliza pie de la Sierracilla. Planta abundante, 4-VI-1978, A. Martínez, SEV 131363.

[Canary Islands]: La Palma. Immediaciones de Tagoja, 16-VI-1995, Pedro Luis Pérez de Paz, s/nº, TFC 38722. Hierro. San Andrés - El Pinar, borde carretera, 28-III-2004, Miguel António Padrón Mederos, s/nº, TFC 45089.

[Cantabria]: Valderredible: Ruijas, 30TVN2441, Cuneta, 780 m., 29-VI-2000, M. Pardo de Santayana, 1581MP, MA 726270.

[Catalonia]: Barranco del [?], Caballero, MA 139181.

[Ciudad Real]: Almodovar del campo, Sierra de los Bonales, cunetas, 620 m Ramiro García Río, MA 712245.

[Córdoba]: Rio Guadiato, orilla derecha, Cerro del Trigo. Esquisitos, J. A. Varela, SEV 129339. Conquista, bordes de la carretera granodioritas, 18-VI-1978, E. Dominguez; J. Munoz & J. A. Varela, SEV 129338. Trás-Sierra, margem derecha del Guadiato, desde Cerro del Trigo hasta el Pantano de la Brena. Esquisitos, 16-VI-1978, J. A. Varela, SEV 129340.

[Gerona]: Roses, Cap. Norfeu, borde de camino, 29-VI-2009, Inés Alvarez & L. Medina, IA2063.

[Granada]: Cuenca del Monachil, bajo, 24-V-1975, A. Soler. SEV. Barranco de las Gayombas, 20-VI-1973, MA 753015. Cincovillas, arenoso 1000 m, 24-VI-1972, A. Segura Zubizarreta, MA 351530.

[Guadalajara]: Valdelamusa15-V-1975, R. Murillo, SEV 131365. Higueras de la Sierra, 18-VI-1976, B. Cabezudo & J. García,

[Huelva]: SEV 131367. Santa Bárbara, in collibus dunosis, 13-V-1943, C. Vicioso, MA 139203.

[La Rioja]: Arnedillo, Logroño, cascajares del río, 580 m, 01-X-1974, A. Segura Zubizarreta, MA 351522.

[Logroño]: Castilla: Obarenes, monts, 8-VII-1908, H. Elias, s/nº, LISU 55351.

[Madrid]: Sierra de Guadarrama, Collado Mediano, 26-VI-1995, M. A. Carrasco & S. Pajarón, 1581MP, MA 582315. Villa del Prado, carretera al Encinar del Alberche, 30 T UK8859, pastos despejados entre jaras, en terreno silíceo pizarroso, a unos 500 m, 9-VII-1992, García Adá, G. López, 10517, MA 566054. Navalcarnero, in glareosis et pinguibus, C. Vicioso e F. Beltrán, MA 139195. Pontón de la Oliva, in arenosis glareosis, 29-V-1916, C. Vicioso, MA 139160. La Moncloa, in siccis arenosis, 5-VII-1916, C. Vicioso, MA 139161. Guadalix de la Sierra, rotonda de la ctra. a Miraflores, 850m, cuneta, 19-VI-2010, L. Medina & M. Sequeira, LM 5104, MA 809366.

[Málaga]: Sierra Tejeda, subiendo de Casillas de aceituno a la Casa das Nieves. Calizas y margas en Pinares 800 - 850 m.s.m., 21-VI-1974, S. Talavera & B. Valdés, SEV 129390. Entre Andales y Carratraca. Sierra de Alcaparaín, Calizas Roquedos 600-770 m.s.m, 4-VII-1970, B. Cabezudo & B. Valdés, SEV 129393. Yunquera, in collibus dunosis, 11-VII-1930, C. Vicioso, MA 139200.

[Ourense]: Castrelo de Miño, 19-VII-1935, A. Rodrigues, MA 139205.

[Pontevedra]: Cangas de Morrazo - Salgueirón, en borde de carretera, 21-VI-1970, S. Castroviejo, MA 196495.

[Saragossa]: Sierra de Vicort, in montanis, 14-VII-1907, C. Vicioso, MA 139167.

[Seville]: 30-XI-1975, D. Canete & E. Dominguez, SEV 131364. 15-V-1975, Murillo e Talavera, SEV 131360.

[Soria]: Montenegro de Cameros, silíceo nemoral, 30-X-1969, A. Segura Zubizarreta, MA 351537.

Tunisia:

[Loc. incert.]: Sidi Ben Hassen, 15-V-1888, Cosson, Barratte, Duval, P 02712847. Entre [?] et Hammamet, 29-V-1883, Cosson, Letourneux, Reboud, Barratte, Bonnet, P 02712847. Island Zembra, 05-VI-1888, Cosson, Barratte, Duval, P 02712847.

4.11.5 *Andryala integrifolia* subsp. *corymbosa* (Lam.) M. Z. Ferreira, Alv. Fern. & M. Seq. stat. nov.

≡ *Andryala corymbosa* Lam. Encycl. 1: 153. 1783, basion.
Andryala integrifolia var. *corymbosa* (Lam.) Willk., Prodr. Fl. Hispan. 2: 271. 1865
Andryala integrifolia subsp. *eu-integrifolia* Maire var. *corymbosa* (Lam.) Willk. in Jahandiez & Maire, Cat. Pl. Maroc. 3: 841. 1934
Ind. Loc.: "α. in regno Granat. ad alt. 5000´ usque (in agro Malacitano, BSS., Wk., FK.!, Sierra Nevada, WK.)" [Willkom & Lange, 1865]
Typus: [Spain] "Hab. in Sierra Nevada, 24 July 1844", *Willkomm 168* – Lectotype (designated here): COI41890.

= *Andryala cheiranthifolia* Hoffmanns. & Link, Fl. Portug. [Hoffmannsegg] 2: 152. 1825, *nom. illeg.*
Ind. Loc.: [Portugal] "Dans les terrains sablonneux en – delá du Tage, prés de Lisbonne, Setuval, etc."
Typus: Not located.

= *Andryala parviflora* Lam.var. *latifolia* Boiss., Voy. Bot. Espagne 2(13): 394. 1841
Ind. Loc.: [Spain] "In regione calidâ, var. a in pinguioribus ad culta, ..."
Typus: Not located.

= *Andryala ampelusia* Maire in Bull. Soc. Hist. Nat. Afrique N. 17: 120. 1926
Andryala integrifolia L. subsp. *ampelusia* (Maire) Maire in Jahandiez & Maire, Cat. Pl. Maroc. 3: 841. 1934
Andryala integrifolia L. var. *ampelusia* (Maire) Dobignard in J. Bot. Soc. Bot. France 46-47: 86. 2009
Ind. loc.: "Hab. in rupestribus arenaceis maritimis propre Tingidem, praecipue ad Promontorium Ampelusium, ubi julio floret"
Typus: [Morocco] "*Circa Tingidem: in rupestr. maritimis, promontorii Ampelusii,*11 July 1925", *Maire s.n.* – Lectotype (designated by Dobignard 2009): P00084244; isolectotypes: MPU001667 (designated by Dobignard 2009), MPU001668, RAB043320

= *Andryala integrifolia* L. var. *floccosa* Svent. in Index Seminum Hortus Acclim. Pl. Arautap. 50. 1969
Ind. loc.: "Habitat in clivibus humoso-herbosis versus 600 m alt. in Canaria magna; municipii Valleseco, ubi cum fructum 17 junii 1964 primum lecta fruit"
Typus: [Spain] "Gran Canaria: Valsendero; laderas humoso-herbosis e algo frescas, 17 June 1964.", *E. R. Sventenius s.n.* – Lectotype (designated here): ORT no number.

4.11.5.1 Typification

Lamarck (1783) described *Andryala corymbosa* from a living plant in "Jardin du Roi" in Paris and no specimen under this name was found in the author's own herbarium. Actually, some specimes ascribed to Lamarck were included in other collections (e.g. Jussieu herbarium at P, Moretti herbarium at FI, De Candolle herbarium at G, and Cambessedés herbarium at MPU). At the herbaria P, FI, and G no original material was found. In the protologue the author indicated *A. integrifolia* as a synonym. Much later Willkomm (1865) in Willkomm & Lange (1865) made a new combination, *A. integrifolia* var. *corymbosa*, recognising this variety for the Spanish flora. Indeed, Lamarck (1783) when describing *A. corymbosa* Lam. mentioned the distribution area, including France, Italy and Spain. Actually, Willkomm travelled in Spain and Portugal in 1844-1845 and the main collection and types of this trip are hosted at the COI herbarium (Stafleu & Cowan 1988). Thus, the lectotype of *A. integrifolia* subsp. *corymbosa* (Lam.) M. Z. Ferreira, Alv. Fern. & M. Seq. was chosen among original material deposited at this herbarium, taking into account the collection locality mentioned in the protologue of *A. integrifolia* var. *corymbosa* (Lam.) Willk.

Regarding *Andryala integrifolia* L. var. *floccosa* Svent., a specimen matching the original description of by Sventenius (1969) was located at ORT, although under the name *Andryala* sp. Accordingly, the indumentum is densely stellate-tomentose hairs with glandular hairs, the lower leaves are attenuate into a long petiole, margins sinuate-dentate and the inflorescence is a dense terminal corymb. Furthremore, as it was collected by the author himself and the collection date and locality coincide with those in the protologue, it is here designated as lectotype.

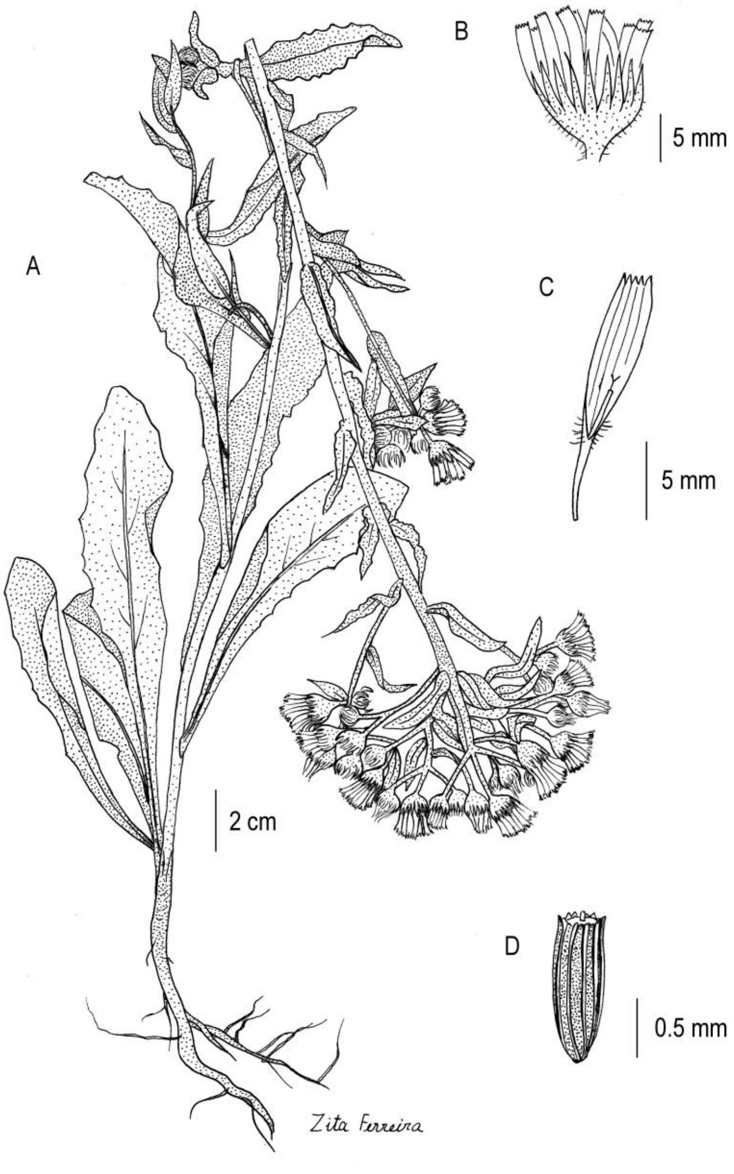

Figure 4.31 *Andryala integrifolia* subsp. *corymbosa* (Lam.) M. Z. Ferreira, Alv. Fern. & M. Seq.   A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

4.11.5.2 Description

Hemicryptophyte, biennial or perennial herb, frequently single-stemmed (Figure 4.31A). STEMS stout, 22–100 cm, usually branched in the upper third, pubescent to tomentose-lanate with dense stellate hairs combined with glandular hairs, mainly in the upper part (Figure 4.32A). LEAVES puberoulous to tomentose on both faces with stellate hairs and sometimes with glandular hairs, especially on the upper leaves (Figure 4.32B); lower leaves 90–130 x 20–32 mm, attenuate into a usually long petiole (23–48 mm), oblanceolate to lanceolate, apex usually obtuse, and margin subentire to lobate; cauline leaves 37–86 x 10–33 mm, frequently semiamplexicaul, oblong to lanceolate, base frequently rounded, apex obtuse to acute, and margin subentire to lobate; upper leaves 17–42 x 4–13 mm, semiamplexicaul or amplexicaul, usually ovate-lanceolate sometimes oblong to lanceolate, base rounded or rarely cuneate, apex usually acute, and margin entire. INFLORESCENCE with numerous capitula arranged in a dense terminal corymb. CAPITULA 11–20(-24) mm in diameter (Figure 4.31B); peduncles 11–23 mm, densely stellate-hairy with abundant glandular hairs 0.8–2 mm (Figure 4.32C); involucre 9–12 x 9–14 mm, campanulate at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 6–8 x 1–2 mm, lanceolate to linear-lanceolate, apex acute to acuminate, flat not enfolding a floret, the outer face stellate-tomentose with long glandular hairs 1–4 mm, yellow or blackish towards the base, mainly on the lower half; internal involucral bracts 6–8 x 1.5–2.3 mm, with scariose margins, receptacle frequently convex, villous with long setose hairs 2–4.7 mm (2 to 3 times longer than the cypselae). FLORETS ligulate, pale-yellow, the external with a tube of 3–5.5 mm and ligule of 6–11 x 1.5–3.2 mm, sometimes with a reddish stripe on the outer face (Figure 4.31C). CYPSELAE 1–1.5 x 0.3–0.5 mm (Figure 4.31D), oblong, frequently dark brown with white ribs, apex with a ring of long thin teeth equalling or slightly exceeding the conspicuous prolongation of the ribs (Figure 4.32D); pappus of usually dirty-white bristles 4.7–6 mm, pilose at the base (Figure 4.32E).

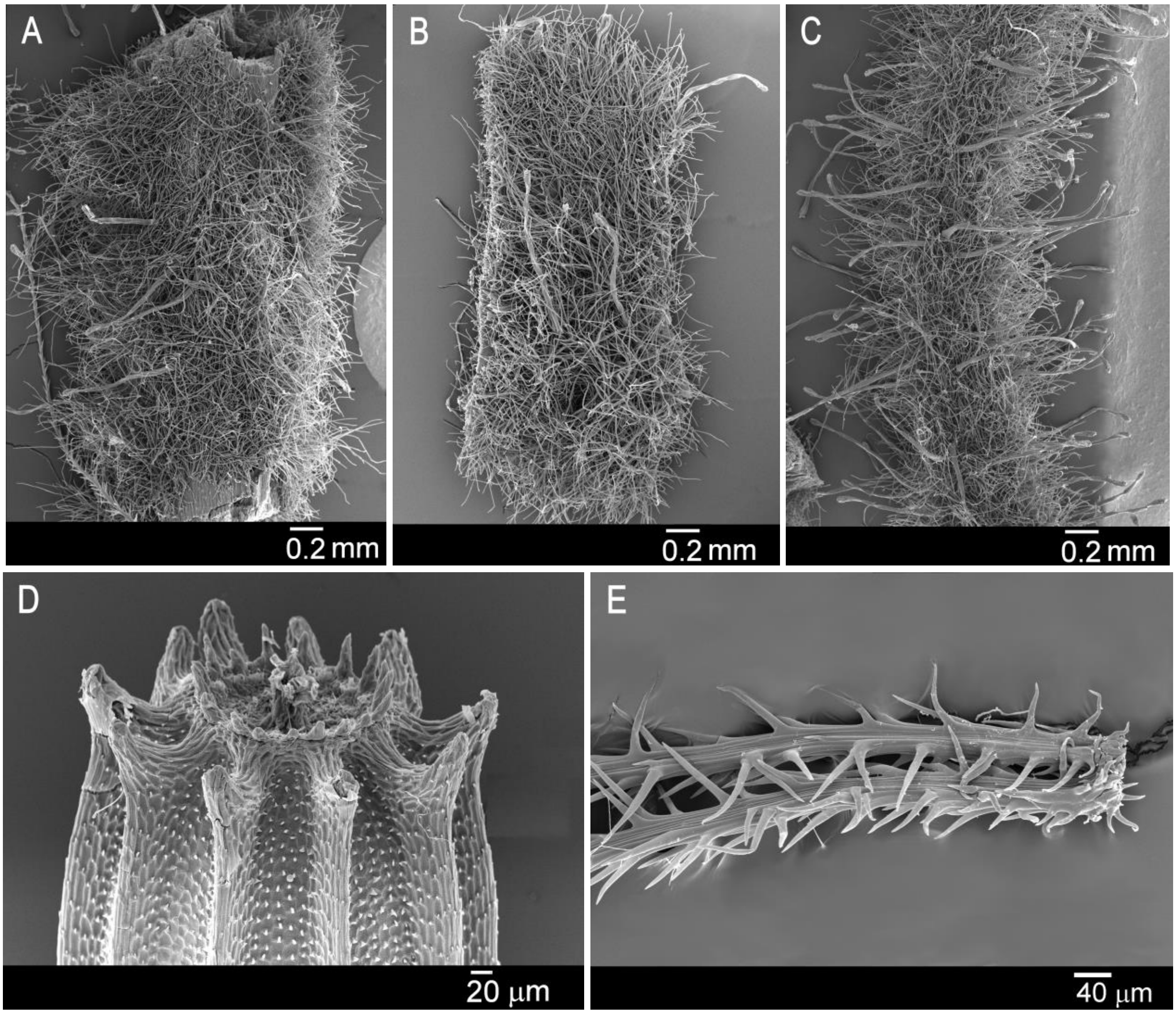

Figure 4.32 *Andryala integrifolia* subsp. *corymbosa* Lam. A – Stem indumentum, B – Leaf indumentum, C – Peduncle indumentum, D – Cypsela apex, E – Pappus base.

4.11.5.3 Comments on taxonomy and nomenclature

Lamarck (1783: 153) described *A. corymbosa* Lam. and cited *A. integrifolia* L. as a synonym. Judging by the description in the protologue ("*Andryala foliis inferioribus runcinatis, superioribus oblongis, integris; floribus corymbosis*."), it could be considered a homotypic synonym of *A. integrifolia* L. since Linneaus (1767) described *A. integrifolia* L. almost in the exact same words. ("*fol. inferioribus runcinatis, superioribus ovato-oblongis, tomentosis.*" However, Lamarck (1783: 153) referred morphological features which distinguish this *taxon* from *A. integrifolia* subsp. *integrifolia*, namely the indumentum ("*La partie superieure de cette tige est chargées, ainsi que les rameaux, les pedoncules & les calices, d´un coton jaunâtre ou ferrugineux très-remarquable. Les feuilles inférieures sont alongées, sinuées, dentées & rétrécies en pétiole vers leurs base; celles de la tige sont sessiles, oblongues & entrières. Les unes & les autres sont molles, trés-douces au toucher, cotonneuses & blanchâtres*.") and the inflorescence, which is a dense apical corymb ("*Les fleurs sont jaune, assez petite, & forment au sommet de la plante un corymbe feuille & paniculé.*"). The observation of original material would help clarify this taxonomic issue, but unfortunately it was not located. Nonetheless, in agreement with Willkomm & Lange (1865), *A. corymbosa* Lam. is herein considered as a variety of *A. integrifolia* L. Actually, Willkomm & Lange (op. cit.) described *A. integrifolia* var. *corymbosa* (Lam.) Willk., stating *A. corymbosa* Lam. as a synonym. Indeed, the original description ("*caule apice ramosissimo cymam corymbiformem satis compactam formante, foliis inferioribus sinuatis superioribus integerrimis, anthodio 4´´´l., florum disco 3/4´´diam. lato*.") matches that of *A. corymbosa* Lam. quite well. In fact, several later authors shared this point of view (e.g. Amo y Mora 1872; Rouy 1905; Coutinho 1939; Sampaio 1949) and Franco (1984) even considered *A. corymbosa* Lam. and *A. integrifolia* L. as distinct species.

Hoffmannsegg & Link (1825) described for the Portuguese mainland flora *Andryala cheiranthifolia* Hoffmanns. & Link, incorrectly citing *A. cheiranthifolia* L'Hér., *A. glandulosa* Lam. and *A. tomentosa* Scop. as synonyms (these correspond to Madeiran endemic *taxa*). In fact, *Andryala cheiranthifolia* Hoffmanns. & Link is illegitimate insofar as it is a later homonym. Nevertheless, Hoffmannsegg & Link (op. cit.) indicated an additional synonym, *A. corymbosa* Lam. from Brotero's *Flora Lusitanica*. Indeed, Brotero (1804) recognised *A. corymbosa* Lam., citing *A. integrifolia* L. and *A. sinuata* L. as synonyms. Noteworthy is that *A. corymbosa* Brot. in reality does not exist given that it corresponds to no more than *A. corymbosa* Lam., as stated by Brotero (op. cit.) himself: "ANDRYALA *corymbosa*. (La Marck)".

Bossier (1841: 394), improperly choosing the name *Andryala parviflora* Lam. over *A. integrifolia* L., recognised a new variety: *A. parviflora* Lam. var. α *latifolia* Boiss. and described it in the following terms: "*Folia oblonga, integra, dentata vel subruncinata*". Although this description is very vague, it might correspond to *A. corymbosa* Lam. Actually, in the protologue of *A. integrifolia* var. *corymbosa* (Lam.) Willk. the name *A. parviflora* Lam. var. α *latifolia* Boiss. was cited as a synonym (Willkomm & Lange 1865). The type material of *A. parviflora* Lam. var. α *latifolia* Boiss. could shed some light on this matter, however, it was not located.

Many years later Maire (1926) described *A. ampelusia* Maire for Northern Morocco, stressing its resemblance to *A. integrifolia* L. and the possibility of it corresponding to a subspecies or variety. Nevertheless, Maire (1926: 121) underlined some morphological differences: "... *differt radice crassa bienni (nec annua), foliis basalibus dense rosulatis cano-tomentosis sub anthesi persistentibus, inflorescentia corymbosa densiore, anthodii phyllis subcomplicatis achaenium amplectentibus*". Actually, these features can also be found in *A. integrifolia* L. subsp.

corymbosa except for the last. However, the inspection of type material showed that the involucral bracts are more or less flat, not really envolving a cypsela, a feature that is typical in *A. integrifolia* L. Rouy (1905: 454) provided quite a good description of *A. integrifolia* L. var. *corymbosa* (Lam.) Willk.: "*Tige très rameuse au sommet, à rameaux formant un ample corymbe ± dense; feuilles relativement larges, les inf. sinuées, les sup. entières; calathides assez grandes (12-14 mill. de diam.).*" *Andryala ampelusia* Maire and *A. integrifolia* L. var. *corymbosa* (Lam.) Willk. (here transferred to a subspecies rank) are indeed morphologically very similar since both exhibit a robust stem copiously branched above, densely tomentose; oblong-lanceolate to eliptic-lanceolate leaves, entire to lobate; and numerous capitula arranged in a dense apical corymb. Therefore, it seems reasonable to consider these as belonging to the same *taxon*. As mentioned before, Maire in Jahandiez & Maire (1934) recognised two subspecies within *A. integrifolia* L. However, due to a misinterpretation of earlier works, this author included *A. integrifolia* subsp. *eu-integrifolia* Maire var. *corymbosa* (Lam.) Willk. in the typical subspecies and considered *A. ampelusia* Maire as a distinct subspecies: *A. integrifolia* L. subsp. *ampelusia* (Maire) Maire. Indeed, Dobignard (2009) recognised it as a mere variety: *A. integrifolia* L. var. *ampelusia* (Maire) Dobignard and actually noted that the plants from coastal sands (referring to *A. ampelusia* Maire) have been attributed to *A. integrifolia* L. var. *corymbosa* (Lam.) Willk. growing under distinct ecological conditions.

Sventenius (1969) admitted a new variety for *Andryala integrifolia* L. in the Canary Islands, *A. integrifolia* L. var. *floccosa* Svent. and again the original description matches *A. integrifolia* subsp. *corymbosa* quite well, namely in what concerns the plant indumentum, stem ramification, leaf shape and margin, and inflorescence. In agreement, Kunkel (1980) recognised *A. integrifolia* L. var. *integrifolia* and *A. integrifolia* var. *floccosa* Svent.

4.11.5.4 Karyology

The somatic chromosome of *A. integrifolia* subsp. *corymbosa*, 2n = 18, was determined on material collected in Portugal under the name *A. integrifolia* var. *corymbosa* (Lam.) Willk. (Fernandes & Queirós 1971).

4.11.5.5 Ecology and conservation status

Andryala integrifolia subsp. *corymbosa* grows in barren sites, specifically on stone walls, roadsides, in fields, pastures, and stony places (Lamarck 1783; Brotero 1804; Hoffmannsegg & Link 1825; Rouy 1905). It can also occur on coastal sands and sandy sea cliffs as well as subcoastal sandy schrublands, cork oak woodlands, temporarily humid wastelands and degraded maquis of *Cistus* spp. (Maire 1926; Dobignard 2009). According to available herbarium material, this *taxon* occurs on acid soils, or on rocky soils along with *Cistus* spp., *Quercus coccifera* L., *Ulex* spp., *Daphne gnidium* L., etc. It can be found on dry calcareous lands, nearby roadsides, on rocky and dry basalt as well as on sandy substrates and lands with almond trees. In the Canary Islands it grows on abandoned croplands and pastures at medium elevations. Actually, it can be found at altitudes between 320 and 1300 m., ascending up to 1500 m (Willkomm & Lange 1865).

In what concerns the conservation status, this *taxon* is considered frequent in Portugal (Coutinho 1939) and should be listed as Least Concern (LC) according to the *IUCN Red List categories and criteria* (IUCN 2001; 2012).

4.11.5.6 Geographic distribution

Andryala integrifolia subsp. *corymbosa* has a wide distribution area, occurring, according to studied material, in the Iberian Peninsula, North Africa and Macaronesia (Figure 4.33). However, it can be also be found in France and Italy, including Sicily (Lamarck 1783). Specifically, it occurs in south-central France as well as in Corsica (Rouy 1905), Southern Spain (Willkomm & Lange 1865; Amo y Mora 1872) and several Italian islands (Fiori 1928). It was assigned to Portugal by several authors (Brotero 1804; Coutinho 1939; Sampaio 1949; Franco 1984). This *taxon* was cited for localities of NW Morocco (Maire 1926; Dobignard 2009), although under the names *Andryala ampelusia* Maire or *A. integrifolia var. ampelusia* Maire (Dobignard). In Macaronesia it occurs in Gran Canaria, corresponding to *Andryala integrifolia* L. var. *floccosa* Svent., as mentioned before (Sventenius 1969; Kunkel 1980).

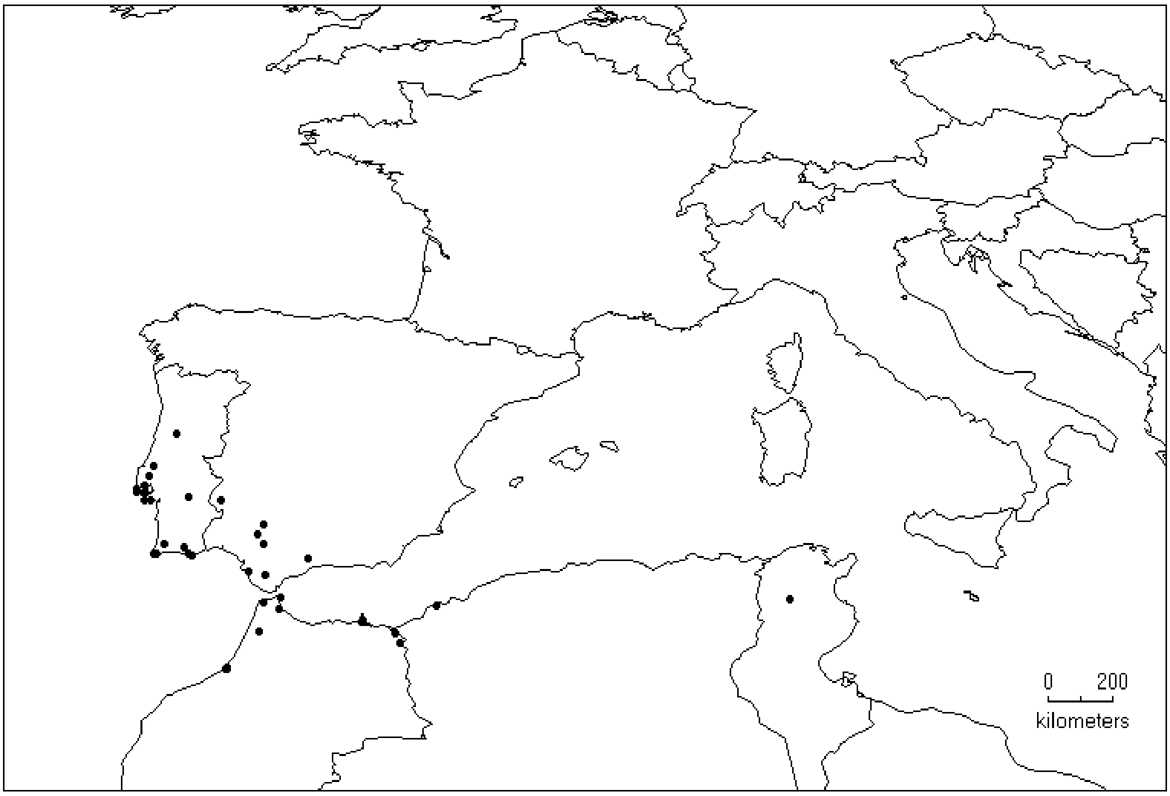

Figure 4.33 Distribution area of *Andryala integrifolia* L. subsp. *corymbosa* (Lam.) M. Z. Ferreira, Alv. Fern. & M. Seq., according to studied material. This taxon also occurs in Gran Canaria (Canary Islands, Macaronesia), according to studied material.

4.11.5.7 List of studied material

Unkown locality: 15-V-1975, R. Murillo, SEV 129397.

Algeria:

[Oran]: El-Ançor, prope del lloc anomenat Les Andalouses, 30-V-1989, C. Benedí, G. Montserrat Marti & J. M. Monserrat Martí, JMM2269, MA 537449.

Morocco:

[Azilal]: region Tadla-Azilal, Haut Atlas Mts. ,Demnate, along the road to Imi-n-Ifri, 2,7 km SE of the town centre, 1070 m,19-V-2010, J. Chrtek and Z. Dockalová, PRA, JC12.

[Berkane]: Monts Beni Snassen: Ahfir, near the main road to Oudja, near a parking place, 6 km SE of the village, 490 km alt.,14-V-2010, J. Chrtek and Z. Dockalová, PRA, JC2.

[Khemisset]: Khemisset, 400 m champs, 5-IV-1985, J. Lewalle, MA 521210. Khemisset, Tiflet, 300 m champs sableux, 23-V-1992, J. Lewalle, 13861, MA 563381.

[Larache]: pr. El Ksar-el-Quebir, in arenosis, 18-IV-1930, MA 139142.

[Marrakech]: Oukaïmedene, 2570 m laderas, bordos de arroyo y roquedos umbrosos, sobre areniscas rojizas,12-VII-1984, Lopéz & Muñoz Garmendia, MA 443015.

[Nador]: arredores de Mellila, 28-V-1915, Prof A. Caballero, MA 139098. Gurugú (Mellila), Prof. A. Caballero, MA

139308. Farkhana (SW) of Melilla, near the road S of the village, 15-V-2010, J. Chrtek and Z. Dockalová, PRA, JC5

[Oujda-Angad]: Oujda, entre Ahfir i Beni Drar, a la collada de Guerbouss, pinedes de pi blanc, 28-V-1989, G. Montserrat Marti & J. M. Monserrat Martí, JMM2223, MA 537494.

[Rabat] : Rabat, plant velouti glandulosum fleur jeun, 5-V-1987, J. Lewalle, 11691, MA 521103. Rabat, plant velouti glandulosum, fleur jeun, 5-V-1987, J. Lewalle, 11691, MA 521528. Rabat [?], plant velouti glandulosum fleur jeun, 5-V-1987, J. Lewalle, 11691, MA 510528.

[Tangier-Assilah]: Circa Tingidem, in rupestr. maritimis promontorii ampelusii, 11-VII-1925, P 00084244.

[Tétouan]: Tétouan, Mary Guindal, MA 139215.

Portugal:

[Algarve]: Valle de Sobreiros, [?] Villa do Bispo, Dr. B. Palhinha e F. Mendes, s/ nº, LISU 40335. S. João da Venda, [?], LISU 56015. Est[?] Coiro da Burra, [?] J. A. Guimarães, s/ nº, LISU 56011. Lagoão, estrada Olhão-Moncarapacho, Berma de caminho vicinal em terreno greso-calcareo, seco, 1-VII-1986, A. Moura, MA 420213. Vila do Bispo: Budens, encosta perto da confluência das Ribeiras de Vale Barão com a de Budens, Q. 962, Solo calcário, exp. W, 14-VI-1988, D. Espirito Santo, s/ nº, LISI 46446. Loulé (Salir - Cerro da Atalaia), Mancha geol. Carbónico inferior. Exp. Sul, 5-VI-1954, A. F. Leal de Oliveira, s/ nº, LISI 16359. Serra de Monchique, 29-V-1966, M. Micaela Fonseca, s/ nº, LISI 25198.

[Alto Alentejo]: Évora - S. Manços: Herdade S. da Espinheira, António Murteira, s/ nº, LISI 11761.

[Baixo Alentejo]: Beja, A. R. da Cunha, s/ nº, LISU 40273. Entre Almodovar e Ourique, J. Daveau, s/ nº, LISU 40274. Azeitão - Negreiros, 2-IV-1954, João da Maia Barbosa, s/ nº, LISI 15551.

[Beira Litoral]: Penacova, Ribeira, 24-IV-1956, A. Saúde Leitão, s/ nº, LISI 18085.

[Estremadura]: Cascais entre Zambujeiro e Murches, erva vivaz com ca. de 50 com., lígulas rosa velho Form.complexa herb.-lenhosas baix., pouco aberta com cerca de 50 cm., solos pedregosos com *Cistus monspeliensis, Cistus crispus, Quercus coccifer, Ulex* sp., *Daphne gnidium*, etc., 10-V-1983, M. Correia & J. Cardoso, 5163, LISU 151659. Cintra, J. de Sousa, s/ nº, LISU 40269. Cintra, Castello dos Moiros, J. dos Santos, s/ nº, LISU 40329. Península de Setúbal. Arrábida: Casais da Serra, erva anual, com cerca de 50cm; folhas onduladas, 6-VI-1979, João Paulo Lopes,42, LISU 139690. Serra de Sintra, 18-VI-1921, A. Mendonça, s/ nº, LISU 40271. Da Aldeia do Meio à Lagoa de Albufeira, F. Mendes, s/ nº, LISU 40268. Setúbal, na área da Quinta da estrelinha, na parte de baixo da encosta, num pousio; planta herbácea, erecta, com os capítulos de flores amarelo-enxofre terófito ou hemicriptófito bienal, 2-VI-1978, M. Myre & N. Rosa, s/ nº, LISI 36187. Lisboa, Tapada da Ajuda, J. de Vasconcellos, s/ nº, LISI 4116. Porto Brandão, Nunes de Sousa, s/ nº, LISI 4914. Monte Estoril, Pinto da Silva, s/ nº, LISI 5415. Sintra, J. Gomes Pedro, s/ nº, LISI 6757. Lisboa, Tapada da Ajuda, Francisco Rodrigues, s/ nº, LISI 6967. Montachique (ponto geodésico), em basalto pedregoso seco, inculto em pascigo. Alt. 350 m , Exp. a todos os quadrantes, J .M. Carvalho & F. M. Flores, s/ nº, LISI 6407. Montejunto (Cruz do Sabre, Rainha-Moinho do Moloico),em jurássico lusitaniano pedregoso seco, inculto em pascigo, Alt. 520 m, Exp. W, SW, J. M. Carvalho & F. M. Flores, s/ nº, LISI 6406. Quinta das Abelheiras, M.A. Gomes & C. Baeta Neves, s/ nº, LISI 6870.

[Minho]: Areosa, Litoral, A. R. da Cunha, s/ nº, LISU 40347.

[Ribatejo]: Pancas (840/B1), a sudoeste do espanadal, linha de água que termina no Mosqueteiro,sebe ao longo da linha de água. Na periferia. Erva anual com ca. de 80 cm, capítulos amarelos, 22-VII-1982, M. Correia & J. Cardoso, 4949, LISU150967. Rio Maior: Serra dos Candeeiros, pr. do Alto da Serra, alt. 320 m, 30-V-1962, M.Helena Dias et al., s/ nº, LISI 21795.

Spain:

[Alicante]: Moraira (Teulada), margens de los caminos, 31-V-1960, MA 368569.

[Cádiz]: Paterna de Ribeira: Baños de Gigonza margas, 2-VII-1975, S. Silvestre, s/ nº, LISU 163435. Cádiz, entre el Puente de la Nava e Algodonales,Terraplén de la carretera muy pendiente y bien poblado de vegetación expont.,18-VI-1978, A. Martínez, SEV 131362. Puerto de Santa Maria, 8-V-1933, C. Vicioso, MA 139201.

[Canary Islands]: Gran Canaria: Vega de S. Mateo, Matazano,1150 m. en eriales de cultivos abandonados y zonas de pastoreo de las medianías altas, 23-V-1999, A. Marrero, MA 632723. Osaro Moya, P. L. Pérez, C. Suárez, s/ nº, TFMC 880. Valsequillo, Alt. 564 m, 9-IV-2009, Z. Ferreira, ZF198, UMad. Valsequillo, Alt. 564 m, 9-IV-2009, Z. Ferreira, ZF196, UMad. Valsequillo, Alt. 564 m, 9-IV-2009, Z. Ferreira, ZF197, UMad. Valsequillo, alt. 628 (a crescer em jardim público), 9-IV-2009, Z. Ferreira, ZF195, UMad. Caminho los Eucaliptos (San José del Álamo, Teror), alt. 522 m, 8-IV-2009, Z. Ferreira, ZF190, UMad. Caminho los Eucaliptos (San José del Álamo, Teror), alt. 522 m, 8-IV-2009, Z. Ferreira, ZF191, UMad.

[Ceuta, North Africa]: in collibus, Vicioso, MA 139140.

[Jaén]: Sierra Morena, Santa Elena margenes, 1-V-1933, J. Cuatrecasas, s/ nº, MA 139202.

[Málaga]: Antequera. Torcal, 1150-1300, Hab. amongst calcareous rocks and stones, 14-VI-1988, B. Valdés, S. Talavera, G. Alziar, D. Jeanmonod, N. Gallan, U. Matthas, V. Stevanovic, P. Minissale, S. Fici, B. Foggi, M. Watson, P. Hinz, J. M. Romero, 70/88, SEV 135625.

[Seville]: Entre Castiblanco y El Pedroso, Hacienda de Los Melonares,Suelo ácido,09-VI-1975,B. Cabezudo, P. Murillo, S. Talavera & B. Valdés, s/ nº, LISU 163431. Burguillos, 9-VI-1975, B. Cabezudo, R. Murillo, S. Talavera, B. Valdés, SEV 131361. Carretera de Málaga. El Gandul, 22-V-1975, P. Candau, P. Murillo, A. Soler & S. Talavera, SEV 129395. Entre Castiblanco y El Pedroso, Hacienda de los Melonares. Suelo ácido, 9-VI-1975,B. Cabezudo, R. Murillo, S. Talavera, B. Valdés, SEV 129399. Entre Lora del Rio e Constantina, Bancales de Almendros,13-VI-1975, SEV 131366.

Tunisia: Siliana Dorsale, road C 77 between Hajeb el Ayoun and Makthar, c. 8 km S. Makthar, fields and road margins, 910 m ,18-V-1994, R. Vogt & Ch. Oberprieler, MA 586802.

4.12 *Andryala laevitomentosa* (Nyár. ex Sennikov) Greuter in Willdenowia 33(2): 232. 2003

≡ *Pietrosia laevitomentosa* Nyár. ex Sennikov in Komarovia 1: 78. 1999
Ind. loc.: Romania, "Moldavia, distr. Suceava, in montibus dictis "Pietrosul Brostenilor", parte nominata "Pietrosul Bogolin", supra limitem silvestrem, in gnaide porphiroidi, alt. 1600 - 1700 m"
Typus: [Romania] "Moldavia, distr. Suceava, in montibus dictis "Pietrosul Brostenilor", parte nominata "Pietrosul Bogolin", supra limitem silvestrem, in gnaide porphiroidi, alt. 1600 - 1700 m.s.m, 4 July 1973" *E. Topa, E. Marin, F. Diaconescu, s.n.* – Holotype: H1578347.
_ *Pietrosia levitomentosa* Nyár. in Rev. Biol. (Bucharest) n.s., 8: 252. 1963, *nom. inval.*
_ *Hieracium levitomentosum* (Nyár.) Soó in Acta Bot. Acad. Sci. Hung. 14: 153. 1968, *nom. inval.*
_ *Andryala levitomentosa* (Nyár.) P.D.Sell in Bot. J. Linn. Soc. 71(4): 256. 1976, *nom. inval.*

4.12.1 Typification

Sennikov (1999) validated the name *Pietrosia levitomentosa* Nyár., replacing it by *P. laevitomentosa* Nyár. ex Sennikov, based on the argument that Nyárády (1963) did not state the type specimen in the protologue, requisite of the International Code of Botanical Nomenclature (Art. 37). Indeed, Art. 37.1 of the Tokyo Code of 1993, the Saint Louis code of 1999 and the Vienna Code of 2005 postulate that "*Publication on or after 1 January 1958 of the name of a new taxon of the rank of genus or below is valid only when the type of the name is indicated*."[33] Later Negrean (2004) stressed that Sell (1975), not having noticed this detail, proposed an invalid combination: *Andryala levitomentosa* (Nyár.) Sell. Negrean (2004) also highlighted that Sennikov (1999) did not consult original material from the Cluj Botanical Garden for typification purposes. Indeed Sennikov (op. cit.) selected the specimen H1578347, collected years after the original description by Nyárády. For this reason, Negrean (2004) named as holotype CL433644, a specimen under the unpublished name "*Hieracium levitomentosa* Nyár sp. n.", as referred by Nyárády (1963) in the protologue. Sennikov´s selection of the type specimen could have been a bad choice, but as his name is from the nomenclatural point of view "a new name", his choice must be likely accepted.

4.12.2 Description

Perennial herb, caespitose, with a dark woody sometimes branched stock, covered with persistent bases of petioles. STEMS 12–20 cm, erect, simple with a single capitulum or rarely branched with two capitula (Figure 4.34A), pubescent to densely tomentose, mainly with stellate hairs and some black glandular hairs above (Figure 4.35A). LEAVES glaucous and densely stellate-tomentose on the abaxial face (Figure 4.35B) and stellate-tomentose on the adaxial face; lower leaves crowded and arranged in rosettes (Figure 4.34A), 49–96 x 20–31 mm, attenuate at the base into a winged petiole 18–47 mm, obovate to broadly elliptic, apex obtuse to ± acute, and margin entire to lobate; cauline leaves few, 74–71 x 11–13 mm, attenuate at the base, ovate-lanceolate, apex acute and margin entire to lobate; upper leaves 8–11 x 1.2–1.3 mm, semiamplexicaul, linear-lanceolate or linear, bractiform, base ± truncate, apex acute to acuminate and margin entire. INFLORESCENCE with solitary capitula. CAPITULA 17–23 mm in diameter (Figure 4.34B); involucre 12-14 x 12-15 mm, hemispherical at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 9.5–11.5 x 1.5–1.6 mm, linear-lanceolate, apex acuminate, usually flat not enfolding a floret, the outer face stellate-tomentose, with dense, long, simple eglandular hairs and few black glandular hairs 0.4-0.9 mm; internal involucral bracts 9.5–10.8 x 1.3–2 mm, with broad scariose margins; receptacle ± convex,

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[33] This rule corresponds to Article 40.1 of the current International Code of Botanical Nomenclature (Melbourne Code of 2011).

villous with laciniate scales bearing long hairs 3.9–4.2 mm (± 3 times longer than the cypselae). FLORETS ligulate, bright yellow, the external with a tube of 6.5–6.6 mm and ligule of 12–13 x 2.5 mm with 5–7 apical teeth (Figure 4.34C). CYPSELAE 1.3–1.4 x 0.4–0.5 mm (Figure 4.34D), obconical, brownish yellow with lighter ribs, apex with a broad eroded ring, overlying another prominent ring (Figure 4.35C)[34]; pappus of whitish bristles 7–7.7 mm, minutely denticulate at the base (Figure 4.35D).

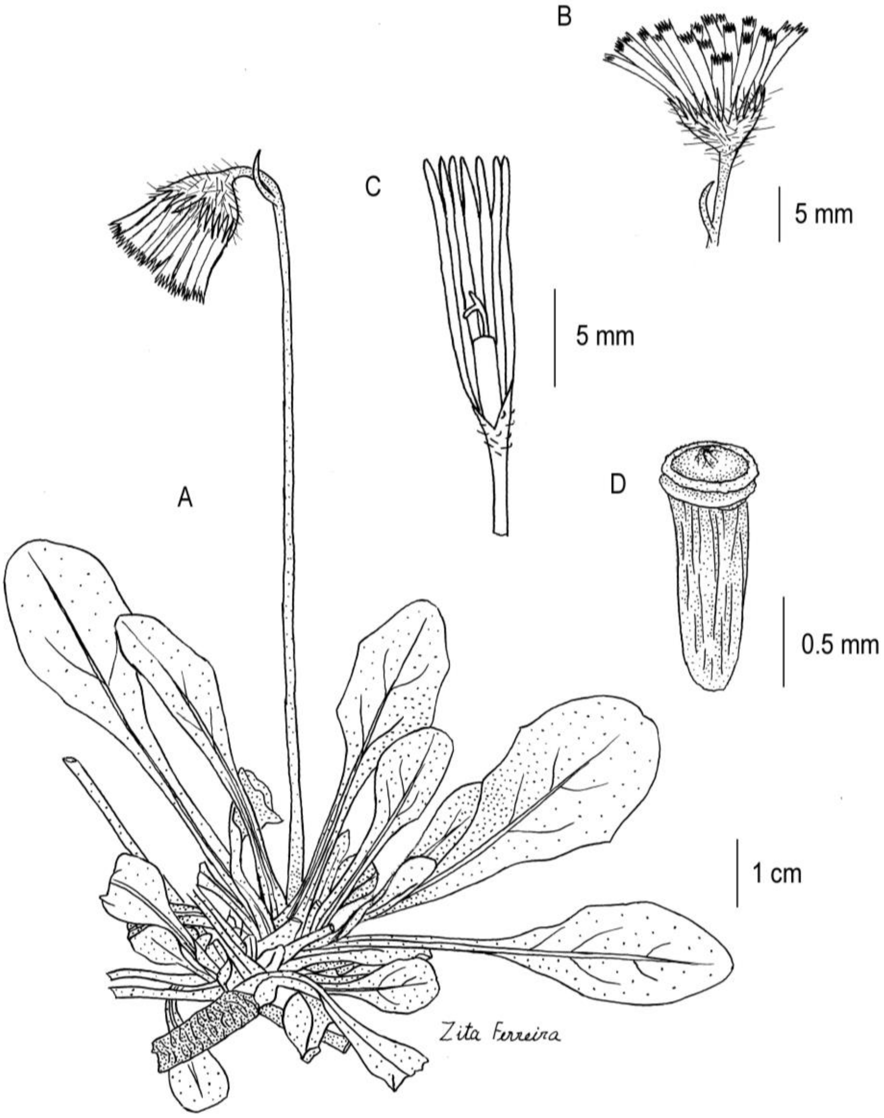

Figure 4.34 *Andryala laevitomentosa* (Nyár. ex Sennikov) Greuter A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

4.12.3 Comments on taxonomy and nomenclature

Nyárády (1963) described a new genus, *Pietrosia* Nyár., referring *Hieracium* sectio XIII Paleacina Nyár. as a synonym. As the only member of this genus, Nyárády (op.cit) described *P. levitomentosa* Nyár. based on herbarium material under the unpublished name *Hieracium levitomentosum* Nyár. The protologue included a very elucidative illustration of the new *taxon* (Figure 4.36), but Sennikov (1999) considered the name *P. levitomentosa* Nyár. as

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[34] According to Manole (2015), infertile cypsela are yellowish to light-brown and 1.5–1.8 mm in length while fertile fruits are dark-brown and mucher longer (3.9–4.3 mm). Moreover, in fertile fruits the subtending prominent ring is not observable; it is diminished in size compared to infertile fruits (Manole 2015).

invalid, as stated before. Sennikov (op.cit.) validated the name as "*Pietrosia laevitomentosa* Nyárady ex Sennik." (a deliberate spelling change) which, in what concerns author citation, should be *Pietrosia laevitomentosa* Nyár. ex Sennikov, according to Brummitt & Powell (1992).

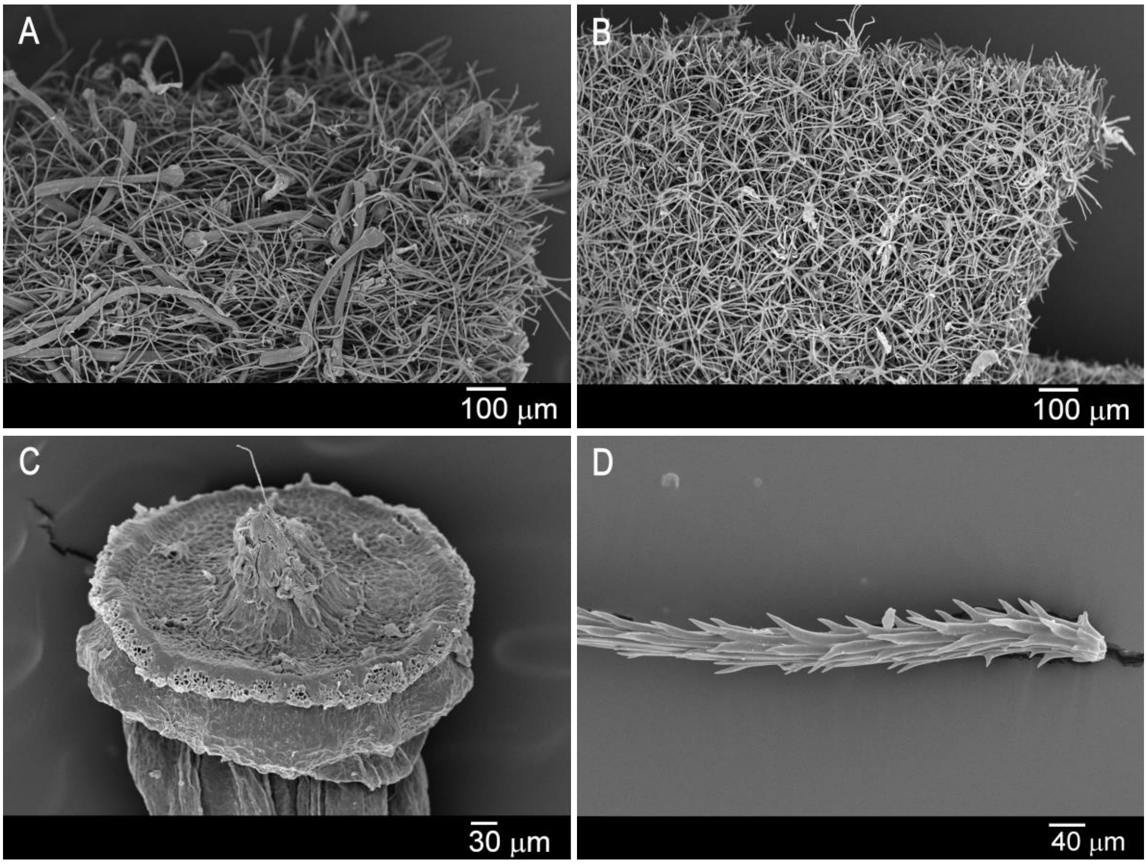
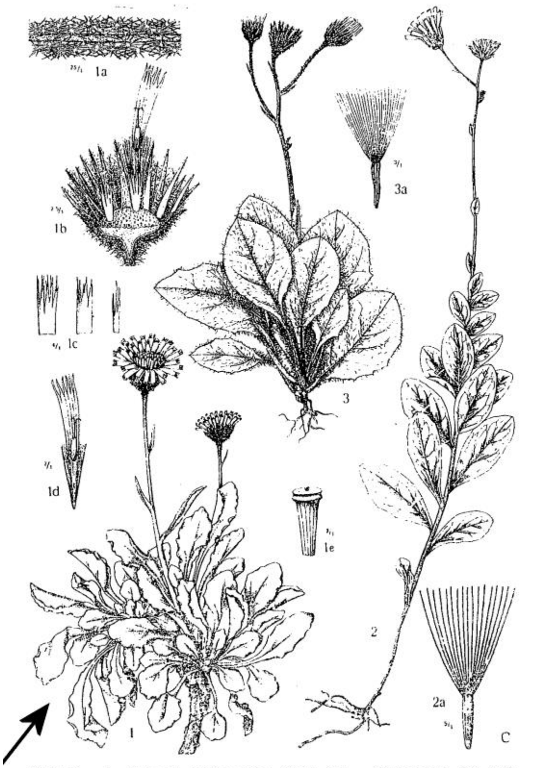


Figure 4.35 *Andryala laevitomentosa* (Nyár. ex Sennikov) Greuter A – Stem indumentum, B – Leaf indumentum: abaxial face, C – Cypsela apex, D – Pappus base.



Tafel I. — 1, *Pietrosia levitomentosa* Nyár. 1*a*. — Querschnitt des auf beiden Seiten mit Sternhaaren versehenen Blattes, 1*b*.— Längsschnitt des Blütenkörbchens mit einem Spreublatt und einer Blume mit Spreublatt auf dem Fruchtboden, 1*c*. — Fruchtbodenspreublätter, 1*d*.—Blüte, 1*e*.—junge Achäne. 2, *Hieracium orbiculare* Nyár. 2*a*.—Achäne mit Pappus. 3, *Crepis negoiensis* Räv. et Nyár., 3*a*.—Achäne mit Pappus. Die Verkleinerung der Pflanzen ist ${}^{2}/_{5}$

In the protologue Nyárády (1963) did not compare *Pietrosia* Nyár. to any genus. Nonetheless, some years later Soó (1968) proposed a new combination for *P. levitomentosa* Nyár.: *Hieracium levitomentosum* (Nyár.) Soó, incorrectly placing *P. levitomentosa* Nyár. in the genus *Hieracium* L. Conversely, Sell (1975) considered *P. levitomentosa* Nyár. very similar to *Andryala agardhii* Haens. ex DC. from Spain and, therefore, thought it reasonable to place *Pietrosia* Nyár. in the genus *Andryala* L. Thus, Sell (op. cit.) combined *P. levitomentosa* Nyár. as *A. levitomentosa* (Nyár.) P.D.Sell, an invalid name as the basionym was not validly published. Nevertheless, Sennikov (1999) did not agree with this taxonomic concept and restored the genus *Pietrosia* Nyár, proposing the treatment of *Pietrosia laevitomentosa* Nyár. ex Sennikov and *Andryala agardhii* Haens. ex DC. as the only members of an oligotypic genus. Sennikov

Figure 4.36 Reproduction of the icon of *Pietrosia levitomentosa* Nyár. in Rev. Biol. (Bucharest) (1963)

(1999) admitted within *Pietrosia* Nyár. two sections: Sect. 1. *Pietrosia* (Receptacle with long scales. Involucral bracts with long simple piles), including *P. laevitomentosa* Nyárády ex Sennik., and Sect. 2. *Andryalopsis* Sennik. sect. nov. (Receptacle without scales. Involucral bracts with short glandular piles), including *P. agardhii* (Haensel. ex DC.) Sennik. Nonetheless, Greuter (2003) was not convinced with Sennikov's proposal and suggested a new combination: *Andryala laevitomentosa* (Nyár. ex Sennikov) Greuter. Recently Manole (2015) also recognised *Pietrosia* as a separate genus (including *P. laevitomentosa* and *P. agardhii*) based on the morphology and anatomy of fertile fruits. Although these two species are morphologicaly similar, they share some features with *A. maroccana* (e.g. woody branched stock, covered with persistent bases of leaf petioles; several stems each usually bearing only one capitulum; basal leaves arranged in rosette, attenuate into winged petioles, cypsela ribs not extended at the apex). Hence, the proposal of a new genus is not justified neither on morphological nor molecular grounds (Ferreira *et al.* 2015a, see Chapter 5).

4.12.4 Karyology

Similarly to all chromosome counts performed on *Andryala taxa*, the number 2n = 18 was determined on plant material from Pietrosul Bogolini, Romania (Chrtek *et al.* 2009).

4.12.5 Ecology and conservation status

Andryala laevitomentosa (Nyár. ex Sennikov) Greuter occurs in rocky alpine grasslands, with leptosols fixed by *Festuca* sp. and other grasses and herbs as well as by scattered individuals of *Juniperus communis* L. var. *sibirica* Rydb. (Stefureac 1968; Negrea & Pricop 2009a). It can be found growing in soil pockets on steep slopes (35º–36º) or vertical mountain cliffs, facing south and south-east, at 1600–1700 m (Nyárády 1963; Sell 1976; Lucas & Synge 1978). The rocks are crystalline metamorphics (porphyritic gneisses), intruded by an acid dyke of schists outcropping at the summit of Mount Pietrosul and the soil is acid (pH 4.34–5.5), relatively rich in potassium and with a high proportion of organic material, which could be a reason for the very restricted habitat and distribution of the species (Stefureac 1968; Lucas & Synge 1978; Negrea & Pricop 2009a). The leaves also present a high potassium content (1.5%) and, therefore, *A. laevitomentosa* (Nyár. ex Sennikov) Greuter is a good indicator of soils with high potassium levels (Stefureac 1968; Lucas & Synge 1978). *Andryala laevitomentosa* (Nyár. ex Sennikov) Greuter occurs in association with several other species [e.g. *Campanula carpatica* L., *Campanula kladniana* (Schur.) Witasek, *Dianthus tenuifoius* Schur., *Juncus trifidus* L., *Juniperus communis* L. subsp. *alpina* (Gray) Celak., *Vaccinium vitis-idaea* L., *V. myrtillus* L., *Hypochoeris uniflora* Vill., and *Luzula luzuloides* (Lam.) Dandy & Wilmott], including also ferns, mosses and lichens characteristic of bare soil and rock (Lucas & Synge 1978; Negrea & Pricop 2009a).

In the *1997 IUCN Red list of threatened plants*, *Andryala laevitomentosa* (Nyár. ex Sennikov) Greuter was considered critically endangered (Walter & Gillett 1998) and according to the *Carpathian List of Endangered Species*, it is an endemic endangered species, strictly protected under the Bern Convention (Kukuła *et al.* 2003). Only six main populations were found in the Bistriței Mountains with an estimated total number of rosettes above 3000 (Negrea & Pricop 2009a). Previous studies lead to the conclusion that this species may have lost the ability to reproduce sexually as in natural populations the plants produce infertile seeds (Negrea & Pricop 2009a). Quite recently fertile fruits were discovered and, therefore, propagation by seeds, even though with very low frequency, could be a reasonable explanation for presence of a few populations within the distribution area of the species (Manole 2015). Given its clonal growth (although not exclusive, according to Manole 2015), the probability of a low genetic diversity is high, and consequently the long-term viability of the species is quite questionable (Negrea & Pricop 2009a). Fortunately, *A. laevitomentosa* (Nyár. ex Sennikov) Greuter occurs in an important plant area in Central and Eastern Europe (Pietrosul Brostenilor, Bogolin) which was proposed as a priority area for plant conservation (Anderson *et al.* 2005). Furthermore, based on recent studies a new conservation strategy was poposed: maximization in the collection of fertile fruits, followed by the proper growth of the plants *ex situ* and the transfer of the well-established plants into their natural habitat (Manole 2015).

4.12.6 Geographic distribution

Andryala laevitomentosa (Nyár. ex Sennikov) Greuter is geographically isolated from all the present day *Andryala* L. species (Figure 4.37). It can be found at the Bistrița Mountains, in Pietrosul Broştenilor, Bogolin (an area of about 400 ha in the Eastern Carpathians, Romania) (Nyárády 1963; Nyárády 1965; Lucas & Synge 1978; Negrea & Pricop 2009a). Although this species was also assigned to the Ukrainian Carpathians, its occurrence in this region needs to be confirmed (Kricsfalusy & Budnikov 2007).

Figure 4.37 Distribution area of *Andryala laevitomentosa* (Nyár. ex Sennikov) Greuter, according to studied material.

4.12.7 List of studied material

Romania:

Suceava: Bukovina: Vatra Dornei, Mt. Pietrosul Brostenilor, rocks near the summit, 1705 m alt., 05-VIII-2011, J. Chrtek et al., PRA, E8. Bukovina, Vatra Dornei: Mt. Pietrosul Bogolin, rocks near the top (northernmost population), 1680 m, 05-VIII-2011, J. Chrtek, P. Mráz, V. Mrázová and M. Puskás, PRA, site A. Pietrosul Bogolin, 05-VIII-2011, Jindrich Chteck, PRA, A 1. Pietrosul Bogolin, 05-VIII-2011, Jindrich Chteck, PRA, C10.

4.13 *Andryala maroccana* (Caball.) Maire. in: Bull. Soc. Hist. Nat. Afrique N. 13(6): 218. 1922

≡ *Paua maroccana* Caball. in Bol. Soc. Esp. Hist. Nat. 16: 541. 1916, basion.
Ind. loc.: “Habitat in arenosis maritimis, ad occidentem urbis Melilla, in loco dicto Calablanca prope promontorium Tresforcas, ubi legimus 6-VI-1915.”
Typus: [Morocco] “Hab. in arenosis maritimis – Calablanca, 6 June 1915”, *Caballero s.n*. – Lectotype (designated by Ferreira *et al*. 2015b, see Appendix 4): BC36157; isolectotype: BC868424.
= *Andryala calendula* Doum. in Bull. Trimestriel Géogr. Archéol. 41: 135. 1921
Andryala maroccana Pau var. *calendula* (Doum.) Maire in Bull. Soc. Hist. Nat. Afrique N. 13(5): 218. 1922
Ind. loc.: “In littore abrupto montis Lindlès (El-Ançor-Andalouses prov. d’Oran)”
Typus: [Algeria] “O. Falaises abrupt du Cap Lindlès, 20 May 1920”, *Doumergue s.n.* – Lectotype (designated here): MPU009726.
= *Andryala calendula* f. *arenosa* Doum. in Bull. Trimestriel Géogr. Archéol. 41: 136. 1921
Ind. loc.: “El Ançor (departement d´Oran, Algerie): falaises maritimes du djebel Lindlès… assez rare, sur le sable des dunes qui gagne le bord de falaises, Nid de l`Aigle. Avril-mai.”
Typus: [Algeria] “El Ançor Andalouses sables bordant la falaise du versant de Habibas (Nid d’Aigle), 20 Apr. 1920”, *Doumergue s.n.* – Lectotype (designated here): P00084245 (specimen on the left); isolectotypes: P00084245 (remaining specimens); syntype: MPU019842.
= *Andryala calendula* f. *rupina* Doum. in Bull. Trimestriel Géogr. Archéol. 41: 136. 1921
Ind. loc.: “El Ançor (departement d´Oran, Algerie): falaises maritimes du djebel Lindlès… sur les falaises abruptes quartzeuses, cap Lindlès au cap. Nègre.”
Typus: [Algeria] “El Ançor Andalouses falaises maritimes du dj. Lindlès, 10 May 1920”, *Doumergue s.n.* – Lectotype (designated here): MPU009727 (lower specimen); isolectotypes: MPU009727 (remaining specimens)
= *Andryala maroccana* Pau f. *suffrutescens* Sennen, Diagn. Nouv. 136: 1936
Ind. loc.: “Hab. Maroc: Melilla, Hidum, à la Aguada de la Palmera, derniers escarpements sablonneux de falaises en ruines, bords de lambeaux de cultures. Leg. Sennen et Mauricio. N.° 8076”
Typus: [Morocco] “Hidum, Aguada de la Palmera; coteaux sablonneux,10 May 1931”, *Sennen et Mauricio* 8076 – Lectotype (designated here): BC141567; isolectotypes: MPU008328, MPU008329, MPU008330.

4.13.1 Typification

Original material of *Andryala maroccana* (Caball.) Maire was located at the BC herbarium. The specimen BC36157 was designated as lectotype because it is complete (Ferreira *et al*. 2015b, see Appendix 4). Moreover, on both the lectotype and isolectotype the collector, collection date, and locality match the ones in the protologue.

The specimen MPU009726 was named *Andryala calendula* by Doumergue himself and given that the collection locality corresponds to the one in the protologue, it is here designated as lectotype. Although the protologue of *Andryala calendula* f. *arenosa* is accompanied by an icon (Pl. V), a lectotype is here designated as original material exists. The specimen P00084245 (on the left) was chosen as lectotype oweing to the fact that is complete and fits the original description quite well. The specimen MPU019842 can be considered as syntype as it was not collected on the same day as the lectotype. Nevertheless, it was obtained by Doumergue in El Ançor, locality mentioned in the protologue, and is under the name “*Andryala calendula (nov. sp.)*”. Similarly, in spite of the icon in the protologue representing *Andryala calendula* f. *rupina* (Pl. IV), a lectotype is here designated among original material. The lower specimen affixed on the herbarium sheet MPU009727 is the best preserved and is under the name *Andryala calendula* f. *rupina* handwritten by Doumergue. Hence, it is here designated as lectotype.

The specimens here considered as types of *Andryala maroccana* Pau f. *suffrutescens* Sennen are all from the same gathering and the collector number is identical to the one indicated in the protologue. However, since the author did not mention a particular specimen neither the herbarium where it was deposited, the specimen with the label “Typus” (BC141567), being the best preserved is here designated as lectotype.

4.13.2 Description

Perennial herb, caespitose, with a dark woody usually branched stock, covered with persistent bases of petioles. STEMS 11–24 cm, erect, simple with a single capitulum (Figure 4.38A), densely stellate-tomentose with no glandular hairs (Figure 4.39A). LEAVES glaucous and stellate-tomentose on both faces (Figure 4.39B); lower leaves crowded and arranged in rosettes, 22–30(-40) x 7–10 mm, attenuate at the base into a winged petiole 11–23 mm, spatulate or obovate-lanceolate, apex obtuse to ± acute, and margin lobate; cauline leaves few, 21–29 x 6–8 mm, sessile or semiamplexicaul, spatulate or ovate-lanceolate, base attenuate to truncate, apex obtuse to ± acute and margin lobate; upper leaves 11–17 x 4–7 mm, semiamplexicaul, lanceolate, bractiform, base ± truncate, apex ± acute, margin entire. INFLORESCENCE with solitary capitula. CAPITULA 12–20(-24) mm in diameter (Figure 4.38B); involucre 8.6-10 x 11-13.5 (-15) mm, ± campanulate at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 6–8 x 1.2–1.8 mm, lanceolate, apex acuminate, involute enfolding a floret, the outer face stellate-tomentose and with no glandular hairs; internal involucral bracts 6–8 x 1.5–2.5 mm, with broad scariose margins; receptacle convex, puberulous with setose hairs 0.3–1 mm (often shorter than the cypselae). FLORETS ligulate, golden yellow, the external with a tube of 2.5–5 mm and ligule of 7-8 x 1–2 mm with a reddish stripe on the outer face (Figure 4.39C). CYPSELAE (-0.5)1.3–1.5 x 0.4–0.5 mm (Figure 4.38D), ± oblong, black with brown ribs, apex with an almost imperceptible inner ring exceeding the inconspicuous tips of the ribs (Figure 4.39C); pappus of whitish bristles 4.4–4.5 mm, often denticulate at the base (Figure 4.39D).

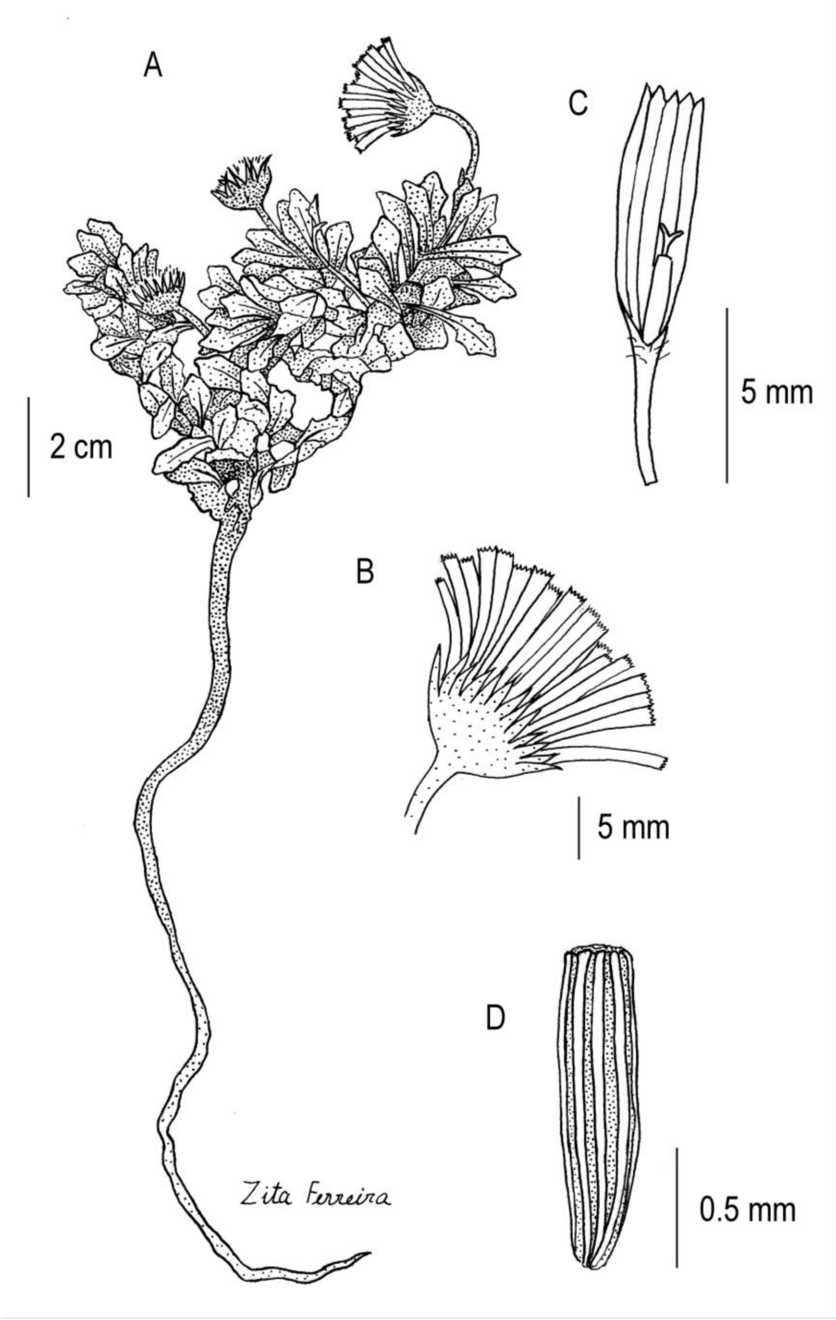


Figure 4.38 *Andryala maroccana* (Caball.) Maire A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

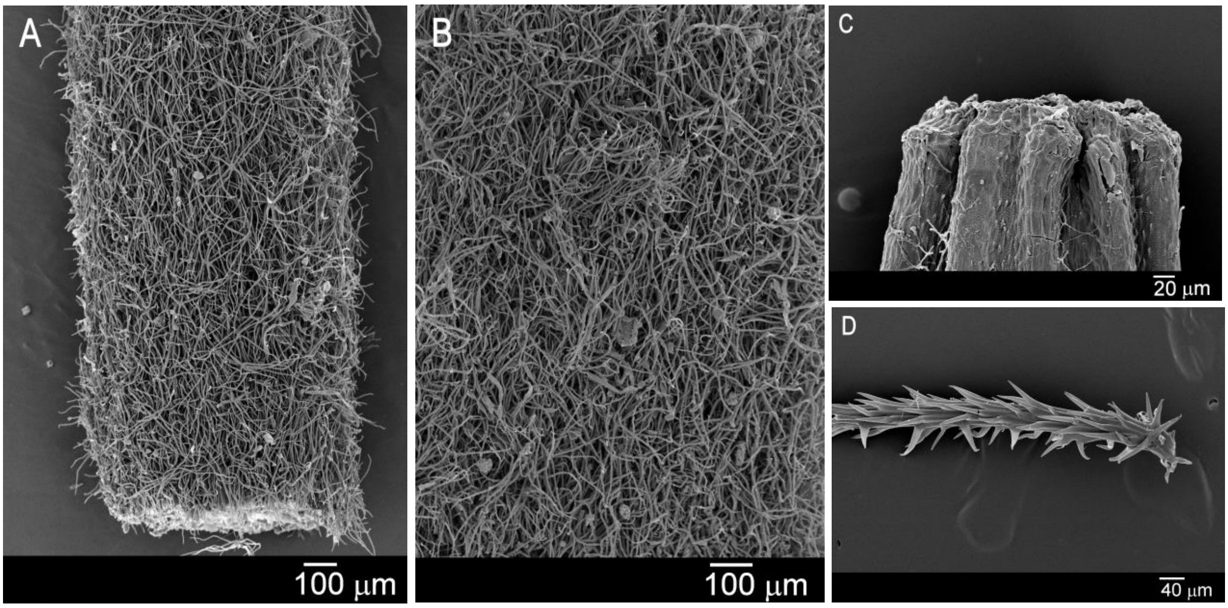


Figure 4.39 *Andryala maroccana* (Caball.) Maire A – Stem indumentum, B – Leaf indumentum, C – Cypsela apex, D – Pappus base.

4.13.3 Comments on taxonomy and nomenclature

Caballero (1916) described a single species, *Paua maroccana* Caball., for the also newly described genus *Paua* Caball, which was well illustrated in a later publication (Figure 4.40). In this publication, Caballero (1917) indicated *Andryala maroccana* Pau as a synonym of *Paua maroccana* Cab. ("*Paua maroccana* Cab. = *Andryala maroccana* Pau, In Littera."). It seems that the name *A. maroccana* Pau was stated in a letter exchanged between Pau and Caballero, and consequently it is not a validly published name. Doumergue (1921) described *A. calendula* Doum. for Algeria, most surely without any knowledge of the species described by Caballero for Morocco. Later Maire (1922) stated that the species discovered by Doumergue is extremely close to *Paua maroccana* Caball, although the pappus is plumose at the base, the receptacle setae can equal the length of the cypsela and sometimes the ribs form an inconspicuous crown at the apex of the cypsela. Consequently, Maire recognised a new variety: *A. maroccana* Pau var. *calendula* (Doum.) Maire, and definitely included *Paua maroccana* in *Andryala*, validly publishing *A. maroccana* (Caball.) Maire. Later Sennen (1936) recognised a new form: *A. maroccana* Pau f. *suffrutescens* Sennen, and, curiously, placed this *taxon* in a new sub genus, *Paua* (Cab.) Sennen. Actually, *A. maroccana* Pau ex Caball. resembles *A. laevitomentosa* (Nyár.

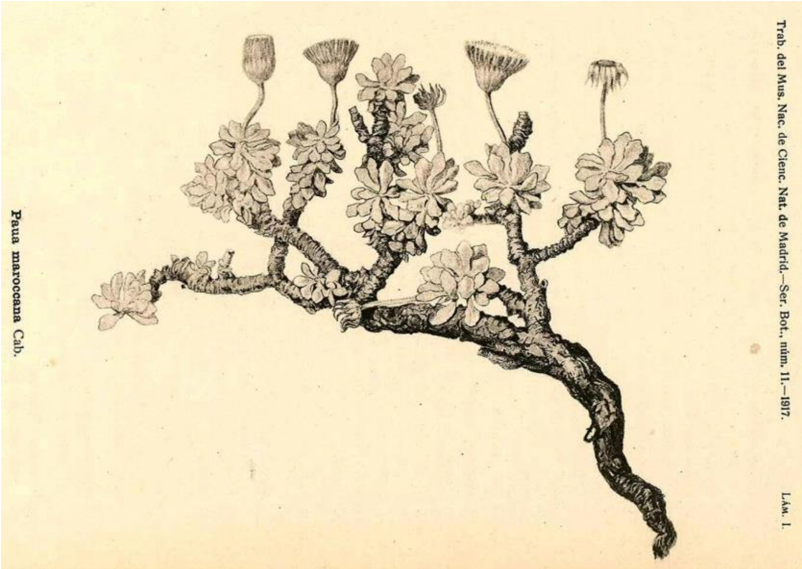


Figure 4.40 Reproduction of the icon of *Andryala maroccana* (Caball.) Maire in Trab. Mus. Nac. Ci. Nat., Ser. Bot. (1917)

ex Sennikov) Greuter, *A. agardhii* Haens. ex DC., and *A. ragusina* L. in what concerns the habit and, to some extent, the cypsela morphology and, thus, all four species should be included in the sub genus *Paua* (Cab.) Sennen.

4.13.4 Karyology

No chromosome numbers for *Andryala maroccana* (Caball.) Maire have been determined so far, according to the consulted bibliography.

4.13.5 Ecology and conservation status

Andryala maroccana Pau ex Caball. dwells in coastal sandy places, sandy soils of eroded cliffs and on the border of scraps of cultivated land (Caballero 1916; Sennen 1936). It can also be found on steep quartzite sea cliffs as well as on sand dunes on the edge of the sea cliffs (Doumergue 1921).

In what concerns the conservation status, in *Catalogue des plantes vasculaires rares, menacées ou endémiques du Maroc* this species is considered very rare (Fennane *et al.* 1998).

4.13.6 Geographic distribution

Andryala maroccana (Caball.) Maire occurs on the Mediterranean coast of Morocco and Algeria (Figure 4.42). Indeed, it can be found in Northern Morocco in Calablanca, a locality situated between the Cape Three Forks (a mountainous promontory on the Mediterranean coast) and the city of Melilla (Caballero 1916; Caballero 1917; Sennen 1936). It also grows in sites to the west of Cape Three Forks (Sennen 1936). Doumergue (1921) assigned it, under the name *Andryala calendula* Doum., to El Açor Andalouses (Province of Oran, Algeria).

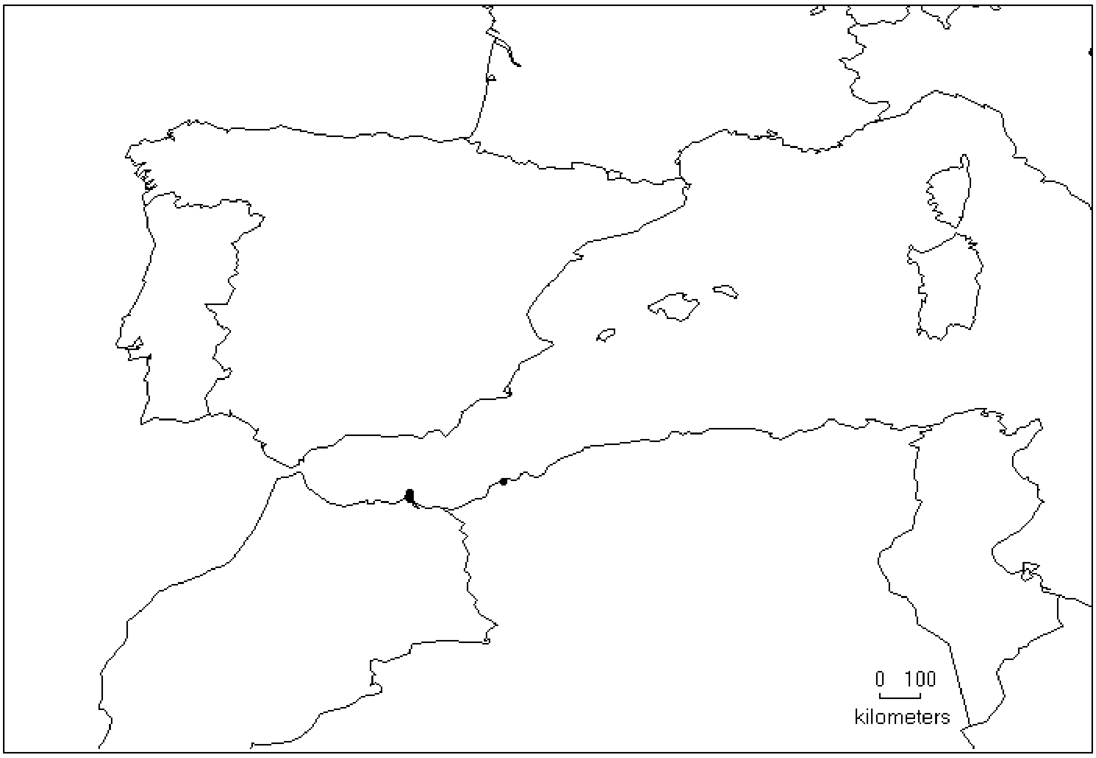


Figure 4.41 Distribution area of *Andryala maroccana* (Caball.) Maire, according to studied material.

4.13.7 List of studied material

Algeria:
[Oran]: El Ançor, Sables bordant les falaises du versant des Habibas (Nid de l'Aigle), 20-IV-1920, P 00084245.
Morocco:
[Nador]: Ismoar (Beni-Sicar), sables des falaises en ruines, 03-VI-1934, Sennen e Mauricio, MPU- Maire, Cala blanca (Melilla), arenosis maritimis, 06-VII-1915, A. Caballero, MA 139346. Cala Blanca d. pr. Mellila, Hab. in saxosis arenaceis littoris rhiphaei, 15 m. alt. fl. 7 aprillis, fr. 28 majii Loco clas., A. Caballero, MA 139344. Ismoar (Beni-Sicar), sables des falaises en ruines, 03-VI-1934, Sennen et Hno. Mauricio, MA 164210. Cala Blanca d. pr. Mellila, Hab. in saxosis arenaceis littoris rhiphaei, 15 m. alt. fl. 7 aprillis, fr. 28 majii Loco clas., 03-VI-1934, MA, 139347. Ismoar (Beni-Sicar), sables des falaises en ruines, 03-VII-1934, Sennen et Mauricio, 9447, MA 139345. Aguada de la Palmera, coteaux sablonneux, 10-V-1931, Sennen et Mauricio, 8076, MA 139348. Cabo Tres Forcas, Plages a l'oeste del cap. de les Tres Forques, 26-V-1989, C. Benedí, G. Montserrat Marti & J. M. Monserrat Martí, JMM-2212, MA 537496.
Spain (North Africa):
[Melilla]: dunes vers Yazanan, 16-IV-1932, H. Mauricio, MPU-Maire.

4.14 *Andryala mogadorensis* Coss. ex Hook.f. in Bot. Mag. 99: t. 6010. 1873 [January]

≡ *Andryala canariensis* Lowe subsp. *mogadorensis* (Coss. ex Hook.f.) Maire in Bull. Soc. Hist. Nat. Afrique N. 19: 59. 1928
≡ *Andryala pinnatifida* Aiton subsp. *mogadorensis* (Coss. ex Hook.f.) Greuter in Willdenowia 33(2): 232. 2003
Ind. loc.: "…on a little rocky islet in the bay of Mogadore, on the Western Marocco Coast, in lat. 31½º N, and has hitherto been found nowhere else. It was discovered by Balansa in 1868, and gathered by Messrs. Maw, Ball, and myself there in May, 1871. Mr. Maw was so fortunate as to transit a living plant to this garden at Benthal Hall, Broseley, which flowered in the following April, and is here figured."
Typus: Morocco, "*Isle de Mogador*", B. Balansa, 25-04-1867 – Lectotype (designated by Ferreira *et al.* 2014c): K000251901!; syntypes: P02462215! (specimen on the right), P02462221!, BM000949980!
= *Andryala mogadorensis* Coss. et Bal. ex Cosson in Bull. Soc. Bot. France. 20: 252. 1873 [November], *nom. illeg.*
Ind. loc.: "In maritimis insulae Mogador detexit cl. Balansa. 25 April. 1867 florifera et fructifera lecta."
Typus: *Andryala mogadorensis* sp. nov. (Coss.). Ile de Mogador. 25 avril. B. Balansa, pl. du Maroc, 1867 – Lectotype (designated by Ferreira *et al.* 2014c): P02462219! ex herb. Cosson; isolectotypes: P02462218! ex herb. Cosson, P02462215! ex herb. Cosson (specimen on the left)
= *Andryala ducellieri* Batt. in Bull. Soc. Hist. Nat. Afrique N. 9: 120. 1918, *basion.*
Andryala canariensis Lowe subsp. *ducellieri* (Batt.) Maire, in Jahandiez & Maire, Cat. Pl. Maroc. 3: 840. 1934
Andryala pinnatifida Aiton subsp. *ducellieri* (Batt.) Greuter in Willdenowia 33(2): 232. 2003
Ind. loc.: "… sur les falaises de Safi par M. Ducellier"
Typus: [Morocco], Falaises de Safi, Ducellier – Lectotype (designated by Ferreira *et al.* 2014c): MPU020221 (specimen on the left); isolectotype: MPU020221 (specimen on the right); syntype: MPU020220
= *Andryala canariensis* Lowe subsp. *maroccana* Maire in Bull. Soc. Hist. Nat. Afrique N. 19: 58. 1928.
Andryala pinnatifida Aiton subsp. *maroccana* (Maire) Greuter *in* Willdenowia 33: 232. 2003
Ind. loc.: "Hab. in arenosis litoris nec non in collibus aridis Imperii Maroccani austro-occidentalis, ubi a martio usque ad aestatem floret: in arenis prope Mogador copiosissime crescit." [Maire, 1928]
Typus: [Morocco], Dunes de Mogador, Jahandiez E., nº 368, 6-4-1920 – Lectotype (designated by Ferreira *et al.* 2014c): MPU001913; syntypes: MPU001906, MPU001907, MPU001909, MPU001910, MPU001911, MPU001912)
= *Andryala mogadorensis* Coss. et Bal. ex Cosson. f. *sinuatifolia* H. Lindb., Itin. Mediterr. (Act. Soc. Sc. Fenn. n. s. B, i. No. 2) 152. 1932
Andryala canariensis Lowe subsp. *mogadorensis* Coss. et Bal. ex Cosson f. *sinuatifolia* (H. Lindb.) Maire in Jahandiez & Maire, Cat. Pl. Maroc. 3: 840. 1934
Ind. loc.: "Mogador loco sterili in Insula Magna"
Typus: Morocco, occ., prope opp. Mogador, in sterilibus in Insula Magna, Harald Lindberg 2012, 11 May 1926 (H-1451919), designated by Väre in Phytotaxa 47: 15. 2012.
_ *Andryala pinnatifida* Aiton subsp. *maroccana* Maire in Mém. Soc. Sci. Nat. Maroc. 8 (1): 239. 1924, *nom. inval.*

4.14.1 Typification

In the protologue of *A. mogadorensis* several types were mentioned, including herbarium material from Balansa. Indeed, specimens gathered in 25 April 1867 and labelled by Balansa himself as "*Andryala Mogadorensis sp. nov. (Coss.)*" were found at the K, P and GOET herbaria. Hooker (1873) most likely based the original description on the specimen from the Kew herbarium given that he was one of the Directors of the Royal Botanic Gardens, Kew. For this reason the specimen K000251901 was designated lectotype of *Andryala mogadorensis* Coss. ex Hook.f. (Ferreira *et al.* 2014c, see Appendix 3). All the syntypes indicated here were collected on the rocky islet in the bay of Mogador to which Hooker (op.cit.) restricted *A. mogadorensis.* The specimen P02462215 (on the right), collected by Ball in April 1871 was considered a syntype, although the collection date (27 April 1871) does not exactly match with the one in the protologue (Ferreira *et al.* 2014c, see Appendix 3). The specimens P02462221 and BM000949980 correspond to plant material that was collected, respectively, by Hooker and Ball, as mentioned in the protologue.

Ernest Cosson (1873) described "*Andryala mogadorensis* Coss. et Bal.". based on specimens of *A. mogadorensis* also from Balansa, according to the information in the protologue "Bal. pl. Mar. (1867)" and the authority of the name. The description was based on specimens from the P herbarium ex Cosson that are labelled "B. Balansa, Pl. du Maroc, 1867": P02462219, P02462218 and P02462215. The specimen P02462219 was chosen as lectotype of *Andryala mogadorensis* Coss. et Bal. ex Cosson since it is the one that best fits the original description (Ferreira *et al.* 2014c, see Appendix 3).

Battandier (1918) described *Andryala ducellieri* Batt. stressing that plant material was collected at the cliffs of Safi by M. Ducellier. Indeed, three specimens collected by Ducellier in Safi were located at the MPU herbarium, all of them including a printed version of the protologue. Although they bear original labels with the name *Andryala mogadorensis,* these specimens were later identified as *Andryala ducellieri* Batt. The label of the herbarium sheet MPU020221 reads "*Andryala Ducellieri species nova, Safi*" and as there are two specimens on the same sheet, the one on the left, which is the best conserved, was designated as lectotype (Ferreira *et al.* 2014c, see Appendix 3). The labels on the specimens MPU020221 and MPU020220 by P. A. Schäfer, indicate the first as the holotype and the second as an isotype, but since no type designation was included in the protologue, a lectotype was designated.

Maire (1928) validly published *A. canariensis* subsp. *maroccana* Maire, highlighting its abundance on the dunes near Mogador. Additionally, Maire mentioned the herbarium where the type material was deposited: "*Typus in Herb. Univers. Algerensis*". Since all specimens from this herbarium were transferred to the P and MPU herbaria and Maire (op.cit.) did not mention a specific specimen as holotype, a lectotype was designated among the original material (Ferreira *et al.* 2014c, see Appendix 3) and the choice fell on a specimen matching quite well the original description (MPU001913). All the other type specimens of *A. canariensis* subsp. *maroccana* Maire mentioned above are syntypes. These belonged initially to the herbarium of the University of Algiers and most are labelled "*Andryala pinnatifida* Ait. ssp. *maroccana* Maire" and accompanied by a printed copy of the protologue (where *A. pinnatifida* subsp. *maroccana* Maire is cited as a *nomen nudum*). Furthermore, all were collected from the dunes of Mogador (Essaouira), except for the specimen MPU001907 which is from the dunes near Diabet (town to the south of Essaouira).

4.14.2 Description

Perennial herb, single or multi-stemmed. STEMS (11-)14–95 cm, ± woody at the base, stout, whitish, branched in the upper third or less frequently in the upper half or from the base, tomentose to tomentose-lanate with dense stellate hairs and sometimes with scarce glandular hairs in the upper part. LEAVES crowded or alternate, whitish-grey, tomentose to tomentose-lanate on both faces with dense stellate hairs; lower leaves 24–48 x 14–33 mm, marcescent at anthesis, attenuate into a short petiole 6–22 mm, obovate-oblong to obovate-lanceolate, apex usually obtuse, and margin entire to ± pinnatipartite; cauline leaves (14-)19–72 x 6–29 mm, frequently semiamplexicaul, usually oblong to obovate-oblong, base ± cordate or auriculate, sometimes base attenuate to ± rounded, apex obtuse or rounded, sometimes retuse or mucronate, and margin entire to ± pinnatipartite, sometimes undulate; upper leaves 8–27 x 4–16 mm, semiamplexicaul or amplexicaul, ovate to ovate-oblong, sometimes oblong to obovate-oblong, base rounded, subcordate, or auriculate, apex obtuse or rounded, sometimes acute, and margin entire or subentire, rarely lobate or pinnatifid. INFLORESCENCE densely or laxly corymbose, sometimes paniculate-corymbose, with 3–7 capitula. CAPITULA 10–30 mm in diameter; peduncles 9–27(-31) mm, densely stellate-hairy, occasionally with some glandular hairs 0.5–2.5 mm; involucre 8–13.5 x 8.5–17 mm, ± hemispherical at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 5–8.5 x 1–1.5 mm, linear-lanceolate, apex acuminate, flat not enfolding a floret, the outer face stellate-tomentose to densely stellate-tomentose, sometimes with yellowish or black glandular hairs 0.5–3.9 mm; internal involucral bracts 5–8.6 x 1.3–2.7 mm, with ± broad scariose margins, receptacle convex, villous with long setose hairs (1.8-)2.5–5 mm (± 2 to 3 times longer than the cypselae). FLORETS ligulate, orange yellow, the external with a tube of (2.5-)3.3–5.9 mm and ligule of 5.6–8 x 1–2 mm sometimes with a reddish stripe on the outer face. CYPSELAE 1–1.8 x 0.3–0.5 mm, obconical, dark brown or black with lighter ribs, apex with a ring of inconspicuous teeth exceeding the almost imperceptible prolongation of the ribs, pappus of white or dirty-white bristles 4–6.4 mm, pilose at the base.

4.14.3 Key to the *Andryala mogadorensis* Coss. ex Hook.f. subspecies

1a. Stems (11-)14–52 cm, leaves crowded; cauline leaves ± cordate or auriculate at the base, apex obtuse or rounded, sometimes retuse or mucronate, margin entire to ± pinnatipartite; peduncles usually with some glandular hairs; external involucral bracts with yellowish or black glandular hairs, mainly on the middle nerve. .... *A. mogadorensis* subsp. *mogadorensis*

1b. Stems ± 95 cm; leaves not crowded; cauline leaves attenuate to ± rounded at the base, apex obtuse, margin subentire to ± pinnatifid; peduncles usually with no glandular hairs; external involucral bracts sometimes with scarce yellowish or black glandular hairs at the apex. .... *A. mogadorensis* subsp. *jahandiezii*

4.14.4 *Andryala mogadorensis* subsp. *mogadorensis*

4.14.4.1 Description

Perennial herb, single or multi-stemmed (Figure 4.42A). STEMS (11-)14–52 cm, ± woody at the base, stout, whitish, branched in the upper third or less frequently in the upper half or from the base, tomentose-lanate with dense stellate hairs and sometimes with scarce glandular hairs in upper part (Figure 4.43A). LEAVES crowded, whitish grey, tomentose to tomentose-lanate on both faces with dense stellate hairs (Figure 4.43B); lower leaves 24–48 x 14–33 mm, marcescent at anthesis, attenuate into a short petiole 6–22 mm, obovate-oblong to obovate-lanceolate, apex usually obtuse, and margin entire to ± pinnatipartite; cauline leaves (14-)19–72 x 6–26 mm, semiamplexicaul, usually oblong to obovate-oblong, base ± cordate or auriculate, apex obtuse or rounded, sometimes retuse or mucronate, and margin entire to ± pinnatipartite, sometimes undulate; upper leaves 8–27 x 4–16 mm, semiamplexicaul or amplexicaul, ovate to ovate-oblong, sometimes oblong to obovate-oblong, base subcordate or auriculate, apex obtuse or rounded, sometimes acute, and margin entire, rarely lobate or pinnatifid.

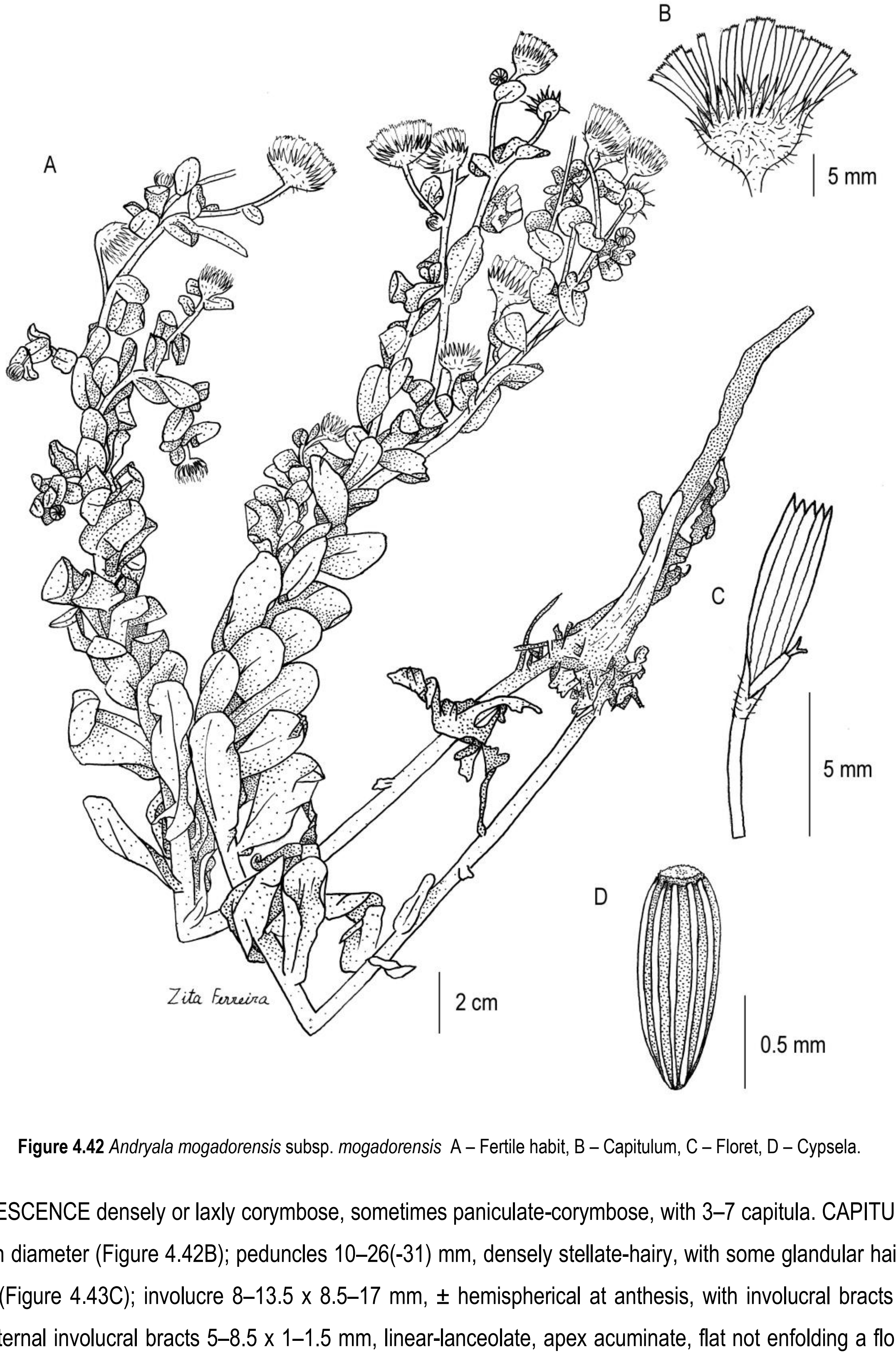


Figure 4.42 *Andryala mogadorensis* subsp. *mogadorensis* A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

INFLORESCENCE densely or laxly corymbose, sometimes paniculate-corymbose, with 3–7 capitula. CAPITULA 10–30 mm in diameter (Figure 4.42B); peduncles 10–26(-31) mm, densely stellate-hairy, with some glandular hairs 0.5–2.5 mm (Figure 4.43C); involucre 8–13.5 x 8.5–17 mm, ± hemispherical at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 5–8.5 x 1–1.5 mm, linear-lanceolate, apex acuminate, flat not enfolding a floret, the outer face stellate-tomentose, with yellowish or black glandular hairs 0.8–3.9 mm, mainly on the middle nerve; internal involucral bracts 5–8.6 x 1.3–2.7 mm, with ± broad scariose margins, receptacle convex, villous with long setose hairs (1.8-) 2.5–5 mm (2 to 3 times longer than the cypselae). FLORETS ligulate, orange yellow, the external with a tube of (2.5-) 3.3–5.9 mm and ligule of 5.6–7.6 x 1–2 mm frequently with a reddish stripe on the outer face (Figure 4.42C). CYPSELAE 1–1.8 x 0.3–0.5 mm (Figure 4.42D), obconical, dark brown or black with lighter ribs, apex with a ring of inconspicuous teeth exceeding the almost imperceptible prolongation of the ribs (Figure 4.43D); pappus of white or dirty-white bristles 4–6 mm, pilose at the base (Figure 4.43E).

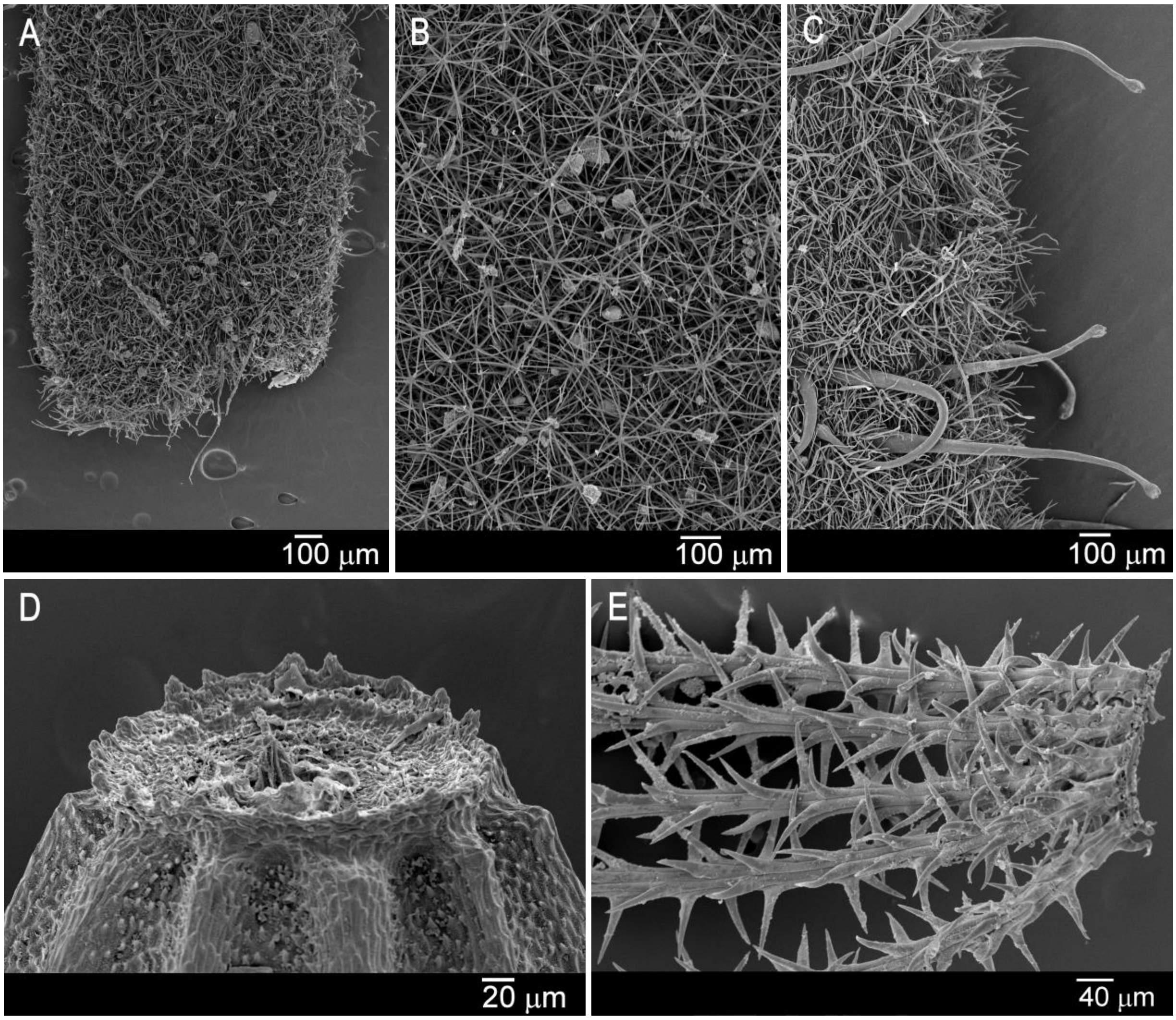


Figure 4.43 *Andryala mogadorensis* subsp. *mogadorensis* A – Stem indumentum, B – Leaf indumentum, C – Peduncle indumentum, D – Cypsela apex, E – Pappus base.

4.14.4.2 Comments on taxonomy and nomenclature

Andryala mogadorensis Coss. ex Hook.f. was validly published by Hooker in January of 1873. As stated before, in the protologue several types were mentioned, including an illustration (Figure 4.44) and specimens from Balansa (1867). According to the label information, these herbarium specimens were gathered precisely in 25 April 1867 and labelled by Balansa as "*Andryala Mogadorensis sp. nov. (Coss.)*". Apparently, the name is of Cosson's authority, but it was Hooker who first validly described the species. In fact, in November of 1873, Ernest Cosson published several new species for Morocco, including "*Andryala mogadorensis* Coss. et Bal.". It appears that Cosson (1873) described this species based on specimens of *A. mogadorensis* also from Balansa, according to the information in the protologue "*Bal. pl. Mar. (1867)*" and the authority of the name. While the description by Hooker was most surely based on material from the K herbarium, Cosson's description was based on specimens deposited in the P

Figure 4.44 Reproduction of the icon of *Andryala mogadorensis* Coss. ex Hook.f. in Bot. Mag. 99: t. 6010. (1873)

herbarium ex Cosson labelled "*B. Balansa, Pl. du Maroc, 1867*". In light of the above, *A. mogadorensis* Coss. et Bal. is an illegitimate name, because it is a later homonym.

Maire (1928) considered *A. mogadorensis* at a subspecies rank, designating it as *A. canariensis* subsp. *mogadorensis* (Coss. ex Hook. f.) Maire. Evidently, Maire (1928) adopted the name *A. canariensis* suggested by Lowe (1868: 564) for the Canarian *Andryala pinnatifida* Aiton. More recently, Greuter (2003) presented a new combination, *A. pinnatifida* subsp. *mogadorensis* (Coss. ex Hook. f.) Greuter, in order to restore the earliest validly published name, but but no typification was proposed.

Battandier (1918) described *Andryala ducellieri* Batt. as a Moroccan botanical novelty, collected from the cliffs of Safi by M. Ducellier. In the protologue, this author underlined its resemblance to *A. mogadorensis* ("*Par ses ligules et ses achaines, il se rapproche de l´A. Mogadorensis Cosson.*") and emphasized the morphological characters which differentiate it from *A. mogadorensis* ("*Il s'en distingue par sa couleur blanchâtre, par ses feuilles moins larges et non arrondies, obtuses au sommet, par ses inflorescences longuement hispides ainsi que les pédicelles et les capitules hérissés de poils blancs ou un peu jaunâtres, jamais noirs*."). Several years before, Ball (1878) made reference to *A. mogadorensis* plants growing along the coastline from the city Safi southwards, and distinguished them from the ones found on the Island of Mogador by their narrower, oblong and subsinuate leaves. Obviously, these plants correspond to *A. ducellieri* Batt. Much later Maire transferred *A. ducellieri* to a subspecies rank under the name *A. canariensis* subsp. *ducellieri* (Batt.) Maire (Jahandiez & Maire 1934). Restoring the earliest validly published name, Greuter (2003) proposed a new combination: *A. pinnatifida* subsp. *ducellieri* (Batt.) Greuter which is a synonym of *A. mogadorensis* subsp. *mogadorensis* (Ferreira *et al.* 2014c, see Appendix 3). Indeed, both are perennials exhibiting robust stems, covered with a dense whitish-lanate stellate indumentum, with long glandular hairs, especially in the upper part and inflorescence; crowded leaves, the lower ones petiolate, cauline semi-amplexicaul to amplexicaul, cordate or auriculate at the base, rounded or acute-obtuse at the apex; leafy inflorescence; densely glandular-hairy involucres, and receptacle bearing long setose hairs (Ferreira *et al.* 2014c, see Appendix 3).

Braun-Blanquet & Maire (1924) cited *A. pinnatifida* subsp. *maroccana* Maire for the first time, restricting it to "*Dunes de Mogador, dans le Retametum*", but no description was provided, which makes it an invalid name. Later Maire (1928) validly published the new *taxon* under the name *A. canariensis* subsp. *maroccana* Maire, stressing its abundance on the dunes near Mogador. Maire (1928) distinguished this subspecies from *A. canariensis* subsp. *mogadorensis* based on leaf characters ("*foliis plus minusve pinnatifidis apice acutiusculis*") and further stated that *A. canariensis* subsp. *maroccana* corresponds to a plant incorrectly cited by Ball (1878) as *A. ragusina* L. var. *lyrata* (Pourr.) DC. Indeed, Ball (1878) identified a specimen collected in the vicinity of Mogador based on leaf characters

(“*Folia in spec. nostris pinnatifida lobis oblongis obtusis.*”) as *A. ragusina* var. *lyrata.* Since this plant was not yet in anthesis, Ball (1878) revealed some uncertainty about its true identity and stressed that it could eventually correspond to the very polymorphic Macaronesian species, *A. pinnatifida* Aiton. However, there is no current evidence of the presence of *A. ragusina* near Mogador and the specimen could indeed correspond to *A. mogadorensis* subsp. *maroccana* (Ferreira *et al.* 2014c, see Appendix 3). Later, Greuter (2003) combined *A. canariensis* subsp. *maroccana* as *A. pinnatifida* subsp. *maroccana* (Maire) Greuter. The latter was synonymised with *A. mogadorensis* subsp. *mogadorensis* since it resembles this *taxon* in all morphological features, except for the leaf margin (Ferreira *et al.* 2014c, see Appendix 3).

4.14.4.3 Karyology

The gametic chromosome number of n = 9 for *Andryala mogadorensis* Coss. ex Hook.f. was determined on material collected in SW Morocco (Tamri, near Cap Ghir) and ascribed to *A. canariensis* Lowe subsp. *maroccana* (Coss. et Ball) Maire (Humphries *et al.* 1978). More recently, this chromosome count was confirmed on a sample from the Atlantic North of Morocco and considered as belonging to *A. pinnatifida* L. subsp. *maroccana* (Maire) Greuter (Kamari *et al.* 2009).

4.14.4.4 Ecology and conservation status

Andryala mogadorensis subsp. *mogadorensis* occurs on coastal rocks or cliffs as well as on sandy coastal areas (Barratte 1893; Battandier 1918; Jahandiez & Maire 1934). It can be found on coastal dunes among *Retama* Raf. broom bushes (Braun-Blanquet & Maire 1924). This *taxon* grows abundantly on the coastal dunes near Essaouira (Maire 1928), a city on the Atlantic coast of Morocco formerly known as Mogador, and less frequently on calcareous hills southwards of this locality. In what concerns the conservation status, in *Catalogue des plantes vasculaires rares, menacées ou endémiques du Maroc* this subspecies is considered as “suspected rare” (Fennane *et al.* 1998).

4.14.4.5 Geographic distribution

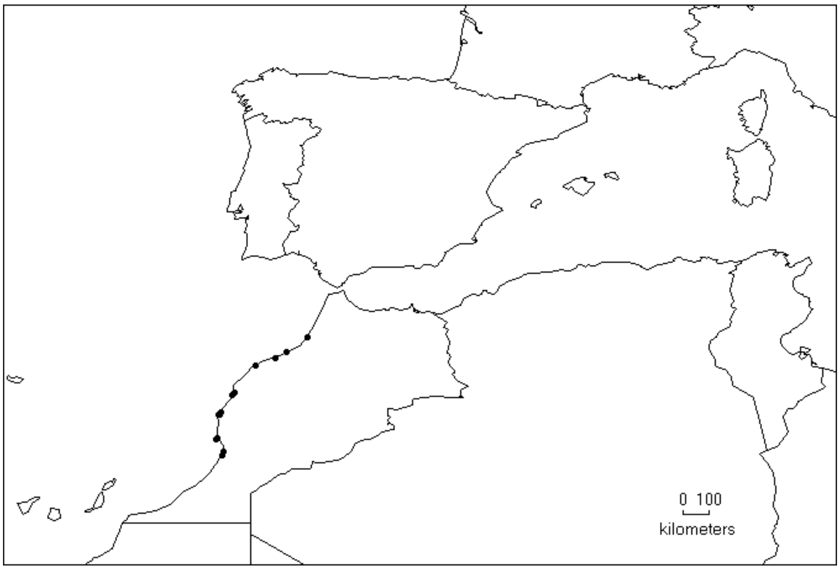


Figure 4.45 Distribution area of *Andryala mogadorensis* subsp. *mogadorensis,* according to studied material.

According to available herbarium data, *Andryala mogadorensis* subsp. *mogadorensis* can be found on the Western coast of Morocco, between the regions of Grand Casablanca and Souss-Massa-Drâa (Figure 4.45). This *taxon* was originally assigned to the islet of Mogador (Cosson 1873; Hooker 1873; Ball 1878) located near the bay of Essaouira, and later recorded for the western coast of Morocco, southwards from the city of Saffi (Ball 1878). Braun-Blanquet (1924) cited

A. mogadorensis not only to the islet of Mogador, but also for the dunes of Essaouira on the mainland, although under the name *A. pinnatifida* subsp. *maroccana* Maire. Maire (1928) assigned this *taxon* (under *A. canariensis* subsp. *maroccana* Maire) to SW Morocco, including Essauoira and Haha (a tribal region stretching along from the city of Essaouira south to the Souss Valley, mainly on the Atlantic coast).

4.14.4.6 List of studied material

Morocco:

[Agadir-Ida Ou Tanane]: Provinciae Haha, in arenosis prope castellum Tamri, 01-IV-1934, MPU-Maire. prov. Haha, Tamri, in arenosis prope castellum Tamri, 04-IV-1926, MPU-Maire. region Sous-Masa-Draâ: Tamri, near the main road along the Atlantic, 4, 7 km WSW of the village, 30 m alt., 22-V-2010, J. Chrtek and Z. Dockalová, PRA, JC15b. Cap Ghir, Souss-Massa-Drâa, junto à praia, substrato arenoso, alt. 2 m, Zita Ferreira, Inés A. Fernández, ZF267.

[Chtouka Ait Baha]: in rupestre maritimis prope Tifnit au merid. fluminis Sous, 03-IV-1934, MPU-Maire. litoral SW, Desembocadura Oued Massa, Dunas Litorales, 29RMD3527, 6 m, T. Buira & J. Calvo, s/ nº, MA 758357. Near Tifnit, dunas de praia arenosa, 5 m, Zita Ferreira, Inés A. Fernández, 268 ZF.

[El Jadida]: Doukahh litt. Dunes au S.-O de Mazagan, 12-VI-1950, Ch. Sauvage, MPU 8484. Mazagan, in rupestribus et arenosis maritimis prope Mazagan, 05-IV-1937, MPU-Maire.

[Essaouira]: prope opp. Mogador, in sterilibus, Insula Magna, 11-V-1926, Harald Lindberg, s/ nº, MPU-Maire 2014. Mogador, dunes maritimes vers Chicht, MA 139343. Mogador, Dunes north of the town Essaouira, Z. Ferreira & I. A. Fernández, ZF264, MA 870318. Dunas a Norte Essaouira, Zita Ferreira, Inés A. Fernández, ZF265. Essaouira, region Marrakech - Tensift-El-Haouz: Essaouira (Mogador), coastal dunes at the northern margin of the town, 8m alt., 22-V-2010, J. Chrtek and Z. Dockalová, PRA, JC16a. Region Marrakech - Tensift-El-Haouz: Essaouira (Mogador), coastal dunes at the northern margin of the town, 8m alt., 22-V-2010, J. Chrtek and Z. Dockalová, PRA, JC16b. Mogador, Broussonet, MA 139363. Mogador, Dunes north of the town Essaouira, Zita Ferreira, Inés A. Fernández, ZF263, MA 863328.

[Kénitra]: Mehdia [?], Dunes, 10-II-1949, Ch. Sauvage et J Vindt, MPU.

[Mohammedia]: Casablanca ad Fedhala (Bou Azria), ao mare, P. J. Pitard, 1869, MA 139349.

[Nouaceur]: Casablanca. Dar Bouazza (au SW de Casablanca), plage Oued Merzeg, Sables du Haut de la plage, 18-V-1944, J. Lambinon & Van Den Sande, MA, 554323.

[Safi]: Falaises de Saffi, 01-VIII-1917, Ducellier, MPU-Maire. Safi, region Doukkala-Abda: Sidi Rosia (S. of Safi), near the main road 3.4 km SSW of the village, 15 m alt., 22-V-2010, J. Chrtek and Z. Dockalová, PRA, JC17b.

4.14.5 *Andryala mogadorensis* subsp. *jahandiezii* (Maire) M. Z. Ferreira, Álv. Fern. & M. Seq. comb. nov. in Acta Bot. Malac. 39. 39: 283-293. 2014

≡ *Andryala jahandiezii* Maire *in* Mem. Soc. Sc. Nat. Maroc, 15: 46. 1927, *basion.*
Andryala canariensis Lowe subsp. *jahandiezii* (Maire) Maire in Jahandiez & Maire, Cat. Pl. Maroc, 3: 840. 1934
Andryala pinnatifida Aiton subsp. *jahandiezii* (Maire) Greuter in Willdenowia 33: 232. 2003
Ind. loc.: "In planitiebus arenosis inter flumina Sous et Massa (Maire, 1922)."
Typus: [Morocco], Sous, plaines sabloneuses entre l'Oued Sous et l'Oued Massa, Maire, 02-04-1922 – Lectotype (designated by Ferreira *et al.* 2014c): P00710614!; isolectotypes: RAB078016; MPU001815; syntypes: MPU001816, MPU001817, P04277958!

= *Andryala jahandiezii* Maire var. *microcarpa* Maire in Mem. Soc. Sc. Nat. Maroc, 15: 47. 1927
Ind. loc.: "In arenosis maritimis ad meridiem urbis Agadir-n-Ighir (Jahandiez, 1923; Maire, 1926)."
Typus: [Morocco], Agadir-n-Ighir, dunes, Jahandiez, nº 203, 28-04-1923 – Lectotype (designated by Ferreira *et al.* 2014c): MPU001818; isolectotypes: P02462208!, P04308378!

4.14.5.1 Typification

Maire (1927) described *Andryala jahandiezii* Maire from the province of Sous in Morocco. The protologue includes information on the location of the type specimens: "*Typi in Herb. Univers. Algeriensis et in Herb. Inst. Imper. Scient. Rabatensis*". The specimens from the University of Algiers were incorporated in the P and MPU herbaria, where indeed some type specimens of *A. jahandiezii* Maire were found. The author recognised two varieties based upon the size of the cypsela: *A. jahandiezii* var. *typica* Maire, occurring on sandy shores between the rivers Sous and Massa, and *A. jahandiezii* var. *microcarpa* Maire, found on sandy maritime shores near the city of Agadir-n-Ighir. According to the protologue, specimens representing the typical variety were collected by Maire in 1922. Three herbarium sheets from different herbaria (MPU, P and RAB) with the same collection date and collector (Maire, 2-4-1922) were found. The specimen MPU001815 was labelled by Muriel Durand and Caroline Loupe as the holotype, but Maire (op. cit.) made no reference to a particular specimen in the protologue and there are two type specimens (MPU001814 and MPU001815) labelled as "*Andryala jahandiezii* n.sp.". The best conserved specimen (P00710614) was designated as lectotype and the specimens MPU001815 and RAB078016 were considered as isolectotypes (Ferreira *et al.* 2014c, see Appendix 3). In the protologue, Maire (1927) made reference to specimens of *A. jahandiezii* var. *microcarpa* collected by Jahandiez in 1923. Actually, the specimen MPU001818 is labelled "*Andryala jahandiezii var. microcarpa n.sp.*" and was collected by Jahandiez on 24 April 1923, and therefore it was chosen as the lectotype. There are additional specimens (P02462208 and P04308378) collected by Jahandiez on the same day and locality, labelled "*Andryala mogadorensis Cosson*", for which reason these were considered as isolectotypes (Ferreira *et al.* 2014c, see Appendix 3). In the protologue, Maire referred to specimens of *A. jahandiezii* var. *microcarpa* Maire collected by himself in 1926. These were located in the herbaria MPU and P (MPU001816, MPU001817 and P04277958) under the name *Andryala jahandiezii* Maire, but since they were collected in a different locality from the one mentioned in the protologue ("*In arenosis ad ostium fluminis Sous*", where the typical variety is found), they could be considered as syntypes of *A. jahandiezii* Maire (Ferreira *et al.* 2014c, see Appendix 3).

4.14.5.2 Description

Perennial herb, single or multi-stemmed. STEMS ± 95 cm, ± woody at the base, stout (Figure 4.46A), whitish, branched in the upper third or less frequently in the upper half, tomentose to tomentose-lanate with dense stellate hairs and no glandular hairs (Figure 4.47A). LEAVES alternate, not crowded, whitish-grey, tomentose to tomentose-lanate on both faces with dense stellate hairs (Figure 4.47B); lower leaves marcescent at anthesis, attenuate into a short petiole, obovate-oblong to obovate-lanceolate, apex obtuse, and margin subentire to ± pinnatifid; cauline leaves 36–46.5 x 15–29 mm, frequently semiamplexicaul, oblong to obovate-oblong, base attenuate to ± rounded, apex obtuse, and margin entire to ± lobate, sometimes ± undulate; upper leaves 18–22 x 8–13 mm, semiamplexicaul or amplexicaul, ovate to ovate-oblong, sometimes oblong, base subcordate or rounded, apex obtuse or rounded, rarely acute, and margin entire or subentire. INFLORESCENCE laxly corymbose, sometimes paniculate-corymbose, with 3–6 capitula. CAPITULA 16–19 mm in diameter (Figure 4.46B); peduncles 9–27 mm, densely stellate-hairy with no glandular hairs (Figure 4.47C); involucre 10–11.5 x 9–14 mm, ± hemispherical at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 6–7 x 1–1.5 mm, linear-lanceolate, apex acuminate, flat not enfolding a floret, the outer face densely stellate-tomentose, sometimes with scarce yellowish or black glandular hairs 0.5–0.6 mm, mainly at the apex; internal involucral bracts 6–7 x 2–2.3 mm, with ± broad scariose margins, receptacle convex, villous with long setose hairs 2.6–4 mm (± 2 longer than the cypselae). FLORETS ligulate, orange yellow, the external with a tube of 4.2–4.3 mm and ligule of 6–8 x 1.3–1.8 mm (Figure 4.46C). CYPSELAE 1.3–1.7 x 0.4–0.5 mm (Figure 4.46D), obconical, dark brown with lighter ribs, apex with a ring of ± inconspicuous teeth exceeding the almost imperceptible prolongation of the ribs (Figure 4.47D); pappus of white or dirty-white bristles 5.7–6.4 mm, pilose at the base (Figure 4.47E).

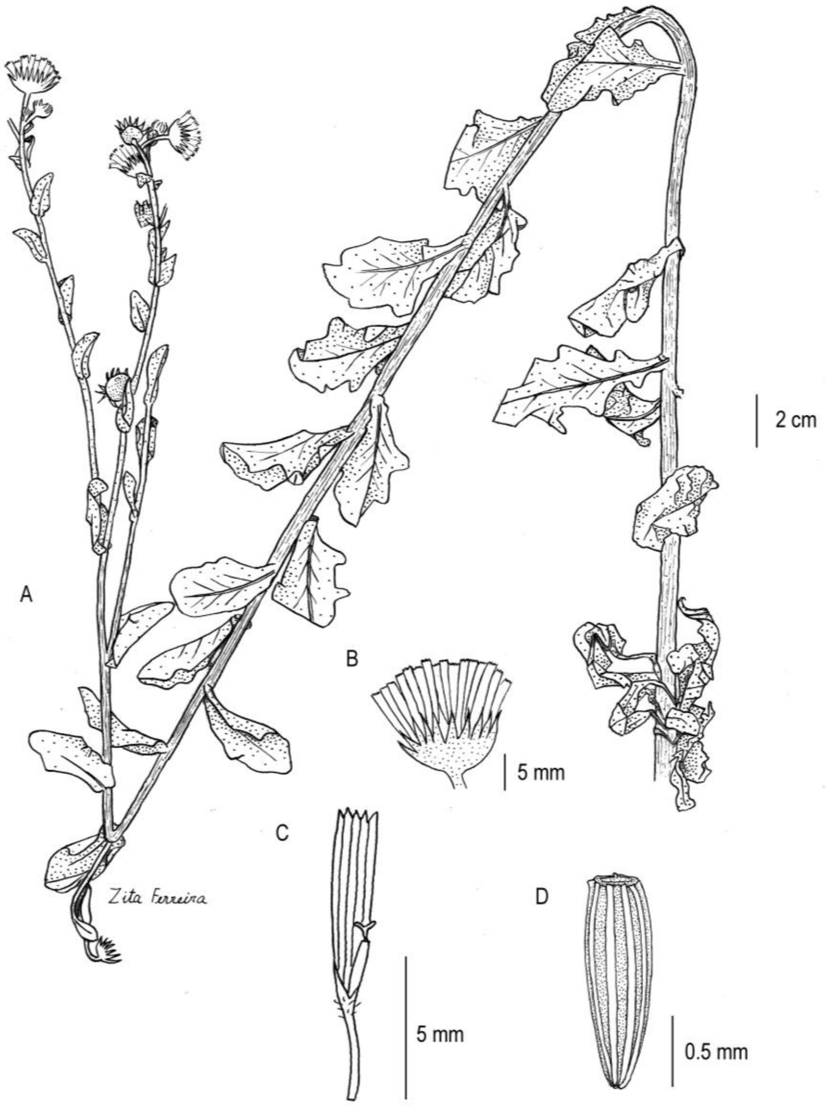


Figure 4.46 *Andryala mogadorensis* subsp. *jahandiezii* (Maire) M. Z. Ferreira, Álv. Fern. & M. Seq. A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

4.14.5.3 Comments on taxonomy and nomenclature

Maire (1927) described *Andryala jahandiezii* Maire, as a new species from the province of Sous in Morocco. The author recognised two varieties based on the size of the cypsela: *A. jahandiezii* var. *typica* Maire (2 x 0.7 mm) and *A. jahandiezii* var. *microcarpa* Maire (1.5 x 0.5 mm), occurring in different localities of this province. This taxonomic point of view is not warrantable as the length and width of the cypsela are characters with some intra-especific variation. In the same publication, Maire clearly distinguished *A. jahandiezii* Maire from *A. spartioides* Pomel by the indumentum and size of the capitula as well as from *A. ragusina* L., also by the indumentum, leaf margin and habit. Furthermore, Maire (1927: 47) emphasized that *A. jahandiezii* Maire differs from *A. pinnatifida* subsp. *maroccana* (Maire) Greuter only by the habit, leaf margin and indumentum ("*habitu magis virgato, foliis integris nec lobatis, pilis glanduliferis parcissimis*").

Years later Maire in Jahandiez & Maire (1934) transferred *A. jahandiezii* Maire to a subspecies rank under the name *A. canariensis* subsp. *jahandiezii* (Maire) Maire, which afterwards Greuter (2003) combined as *A. pinnatifida* subsp. *jahandiezii* (Maire) Greuter. Indeed, this *taxon* is worthy of distinction at a subspecies rank considering its morphological differences compared to *A. mogadorensis* subsp. *mogadorensis.* Besides, it is found in the Souss-Massa-Drâa region while the typical subspecies can be found northwards along the western coast of Morocco. However, a new combination was recently proposed as to place *A. pinnatifida* subsp. *jahandiezii* (Maire) Greuter [along with *A. pinnatifida* Aiton subsp. mogadorensis (Hook. f.) Greuter and *A. pinnatifida* Aiton subsp. *maroccana* (Maire) Greuter)] in *A. mogadorensis* Coss. ex Hook.f., on account of morphological differences compared to the Canarian *A. pinnatifida* Aiton (Ferreira *et al.* 2014c, see Appendix 3). The new combination, here recognised, is *A. mogadorensis* Coss. ex Hook.f. subsp. *jahandiezii* (Maire) M. Z. Ferreira, Álv. Fern. & M. Seq.

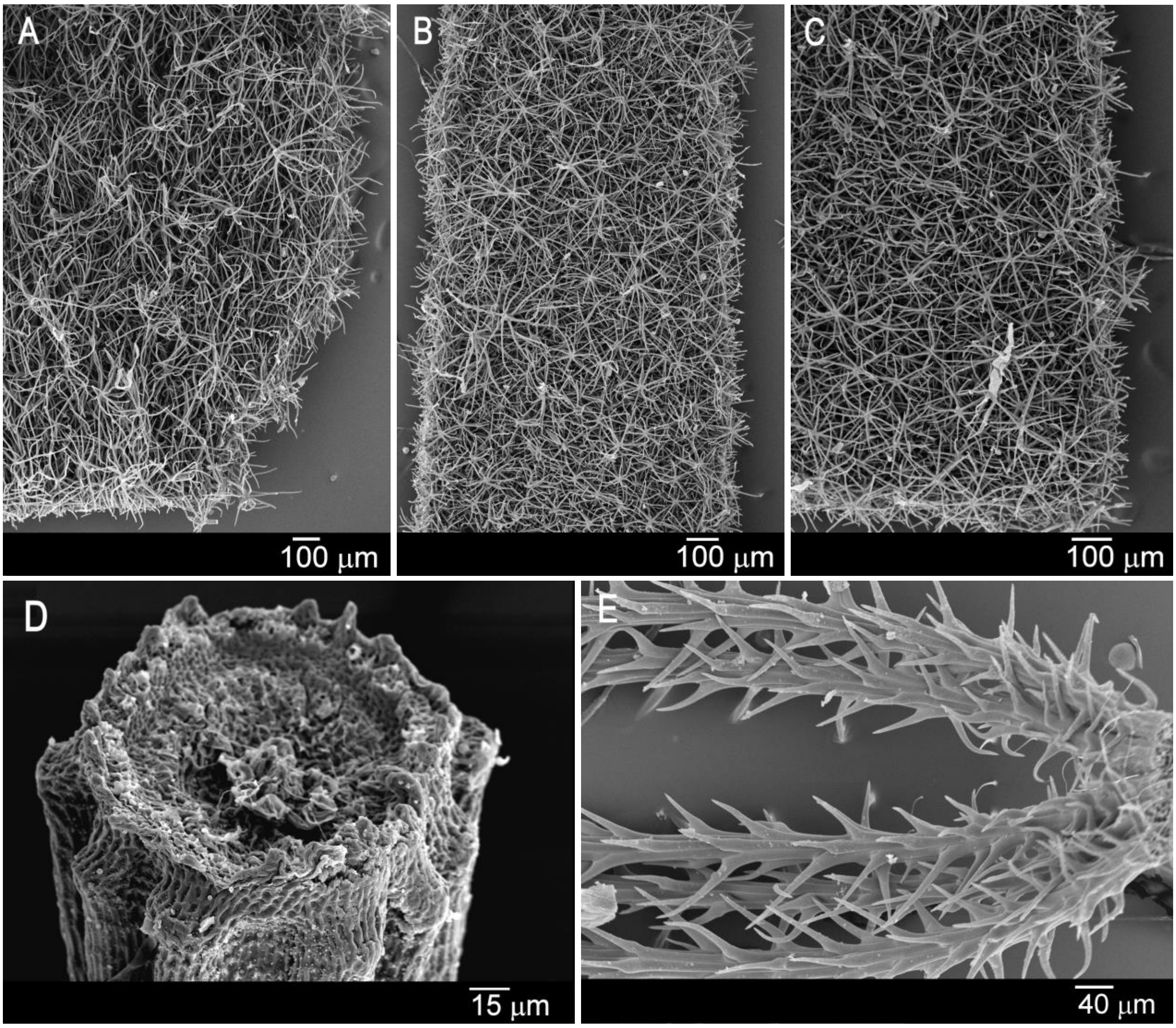


Figure 4.47 *Andryala mogadorensis* subsp. *jahandiezii* (Maire) M. Z. Ferreira, Álv. Fern. & M. Seq. A – Stem indumentum, B – Leaf indumentum, C – Peduncle indumentum, D – Cypsela apex © Muséum National D'Histoire Naturelle (MNHN) – Paris Herbarium (P), E – Pappus base.

4.14.5.4 Karyology

The somatic chromosomes number 2n = 18 was determined by Stebbins *et al.* (1953) on material under the name *Andryala jahandiezii* Maire var. *microcarpa* Maire, collected in Saïdia (Morocco) by A. Faure. Several specimens collected by A. Faure in Saïdia (in Northeast Morocco) are hosted at the P herbarium, however, these correspond to *A. chevallieri* Barratte ex L. Chevall.

4.14.5.5 Ecology and conservation status

Andryala mogadorensis Coss. ex Hook.f. subsp. *jahandiezii* (Maire) M. Z. Ferreira, Álv. Fern. & M. Seq. (originally described as *A. jahandiezii* Maire) occurs on coastal sands and dunes as well as sandy plains between rivers (Maire 1927; Quézel & Santa 1963).

In *Catalogue des plantes vasculaires rares, menacées ou endémiques du Maroc* this subspecies is listed as "very rare" (Fennane *et al.* 1998).

4.14.5.6 Geographic distribution

This *taxon* occurs mainly in Central Morocco, in the Souss-Massa-Drâa region (Figure 4.48). Specifically, it can be found between the rivers Sous and Massa as well as to the south of Agadir-n-Ighir (Maire 1927), a city on Moroccan Atlantic coast near the mouth of the Sous river valley.

Jahandiez & Maire (1934) assigned *A. canariensis* Lowe subsp. *jahandiezii* Maire to Southwest Morocco and further stated that, according to Faure, *Andryala canariensis* Lowe subsp. *jahandiezii* Maire var. *microcarpa* Maire is also found in Saïdia (Northeast Morocco, near the border to Algeria). Specimens from the Faure collection hosted at P herbarium collected in Saïdia resemble much more *A. chevallieri* Barratte ex L. Chevall. Further sampling will be necessary to clarify the presence of *A. mogadorensis* subsp. *jahandiezii* (Maire) M. Z. Ferreira, Álv. Fern. & M. Seq. in Northeast Morocco.

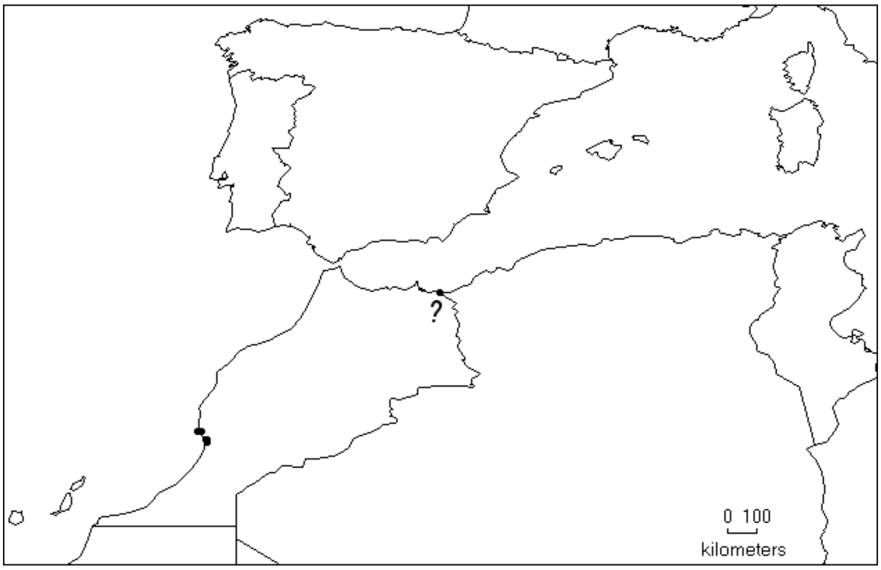


Figure 4.48 Distribution area of *Andryala mogadorensis* Coss. ex Hook.f. subsp. *jahandiezii* (Maire) M. Z. Ferreira, Álv. Fern. & M. Seq. according to studied material.

4.14.5.7 List of studied material

Morocco:

[Agadir-Ida ou Tanane]: Sous: Agadir, Dunes marítimes, 26-IV-1931, MA 139357. Tamri, dunes i penyasegats prop de Tamri, 50 m, matollars d'Euphorbia regis-jubae, 07-VI-1989, C. Benedí, G. Montserrat Marti & J. M. Monserrat Martí, JMM-2429, MA 537440. Sous, plaines sablonneuses entre l'oued Sous et l'oued Massa, 02-IV-1922, P 00710614. Agadir (Sous), dunes, grandes formations, 28-IV-1923, E. Jahandiez, LISU 55347.

[Inezgane-Aït Melloul]: region Sous-Masa-Draâ: Inezgane, near the road between the golf resort and King's Palace, near the river of Sous, 7 m alt., 22-V-2010, J. Chrtek and Z. Dockalová, PRA, JC14.

4.15 *Andryala nigricans* Poir., Voy. Barbarie 2: 228. 1789

≡ *Andryala integrifolia* L. var. β *nigricans* (Poir.) Barratte in Bonnet & Barratte, Expl. Sci. Tunisie, Cat. Pl. 1896
Ind. loc.: “Voyage en Barbarie … de l’ ancienne Numidie” [Poiret, 1789]
Typus: [Algeria] “Numidia”, *D. abbé Poiret s.n.* – Lectotype (designated here): P02462186
= *Andryala nigricans* Poir. var. *boitardii* R. Lit. & Maire in Bull. Soc. Hist. Nat. Afrique N. 25(2): 307. 1934
Ind. loc.: “Algérie: La Calle (Battandier, Maire); Cap Rosa (Maire), Tunisie: Tabarka (Cosson); Bizerte (Boitard); Tunis, La Marsa (Pomel, Cosson, Maire); etc.”
Typus: [Tunisia] “La Marsa, 29 May 1888”, *M. M. E Cosson, G. Barratte, Cl. Duval s.n.* – Lectotype (designated here): P02462187! (specimen on the left); isolectotypes: P02462187! (remaining specimens); syntypes: P04277942, MPU003327, P02462179!, P02462196!, P02462197!, P02462200!, P04119468!, MPU003325, MPU003326, MPU003327.

4.15.1 Typification

Poiret (1789) described *Andryala nigricans* Poir. from Numidia (now Algeria). The specimen P02462186 here designated as lectotype was collected by Poiret who, according to Stafleu & Cowan (1983), travelled in North Africa in 1785-1786, and was inserted in a Pourret collection, now deposited at P herbarium. Most of Pourret's collections were lost during various wars, but some came into the possession of Barbier (Stafleu & Cowan 1983). The specimen P02462186 from the Pourret collection was, indeed, extracted from the Barbier herbarium, according to the label data ("*Collection de l'Abbé Pourret, extraite de l'Herbier légué par M. le D^{r}. Barbier. 1848*"). Although under the name *Hieracium cheiranthoides* Pourr., it was later relabelled as *Andryala nigricans* Poir. in Pourret's handwriting. On the former label both the collection locality and collector are clearly indicated "*Numidia D. abbé Poiret*", allowing us to consider it as original material. Besides, it fits the original description quite well.

In the protologue Maire (1934) listed several localities and collectors of *Andryala nigricans* Poir. var. *boitardii* R. Lit. & Maire.: Algerie: La Calle (Battandier, Maire); Cap Rosa (Maire), Tunisie: Tabarka (Cosson); Bizerte (Boitard); Tunis, La Marsa (Pomel, Cosson, Maire). The choice of the lectotype fell on a specimen from La Marsa, P02462187 (on the left), considering that it is complete and fits the original description quite well. Based on the localities and collectors as well as on the collection dates (before publication date) several syntypes were found at the P and MPU herbaria, as listed above.

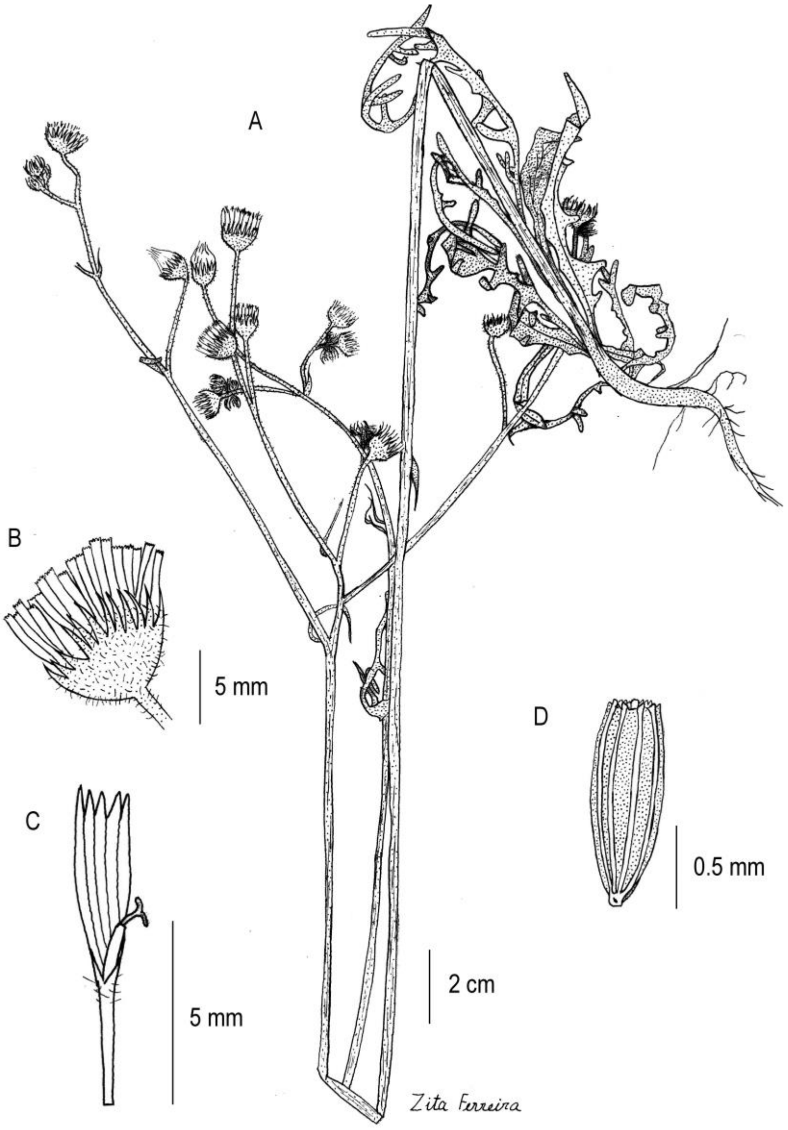


Figure 4.49 *Andryala nigricans* Poir. A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

4.15.2 Description

Hemicryptophyte, biennial or perennating herb, single-stemmed or multi-stemmed. STEMS 41–79 cm, branched in the upper half or upper third (Figure 4.49A), puberulous with some stellate hairs and a few glandular hairs, mainly in the upper part (Figure 4.50A). LEAVES puberulous on both faces with some stellate hairs, sometimes with scarce glandular hairs (Figure 4.50B); lower leaves arranged in a rosette, attenuate into a long and slightly winged petiole, oblanceolate to lanceolate, apex ± obtuse or acute, and margin frequently pinnatisect; cauline leaves few, 45–75 x 5–22(-34) mm, sessile, ovate-oblong to linear-lanceolate, base ± rounded, apex acute, and margin frequently pinnatisect; upper leaves 19–35 x 1–4 mm, semiamplexicaul or amplexicaul, narrowly ovate-lanceolate to linear-subulate, base ± rounded, apex acuminate to almost subulate, and margin entire or rarely ± pinnatifid. INFLORESCENCE corymbose with 5–7 capitula, rarely solitary. CAPITULA 10–14 mm in diameter (Figure 4.49B); peduncles 21–28(-38) mm stellate-hairy, usually with abundant glandular hairs 0.2–0.6 mm (Figure 4.50C); involucre 8.3–8.7 x 7–10 mm, campanulate at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 5–6 x 0.8–1 mm, linear-lanceolate, apex acuminate to subulate, involute to slightly involute enfolding a floret, the outer face stellate-tomentose with abundant glandular hairs (0.3-)0.6–0.8 mm, yellow and blackish towards the base; internal involucral bracts 4–6 x 0.9–1.2 mm, with broad scariose margins, receptacle convex, villous with long setose hairs 3–4 mm (± 3 times longer than the cypselae). FLORETS ligulate, orange yellow, the external with a tube of 2.6–4.5 mm and ligule of 5–7 x 1–2 mm, sometimes with a reddish stripe on the outer face (Figure 4.49C). CYPSELAE 1.3 x 0.4 mm (Figure 4.49D), obconical, dark brown with white ribs, apex with a ring of teeth equalling or slightly exceeding the prolongation of the ribs (Figure 4.50D); pappus of whitish bristles 4–5 mm, pilose at the base (Figure 4.50E).

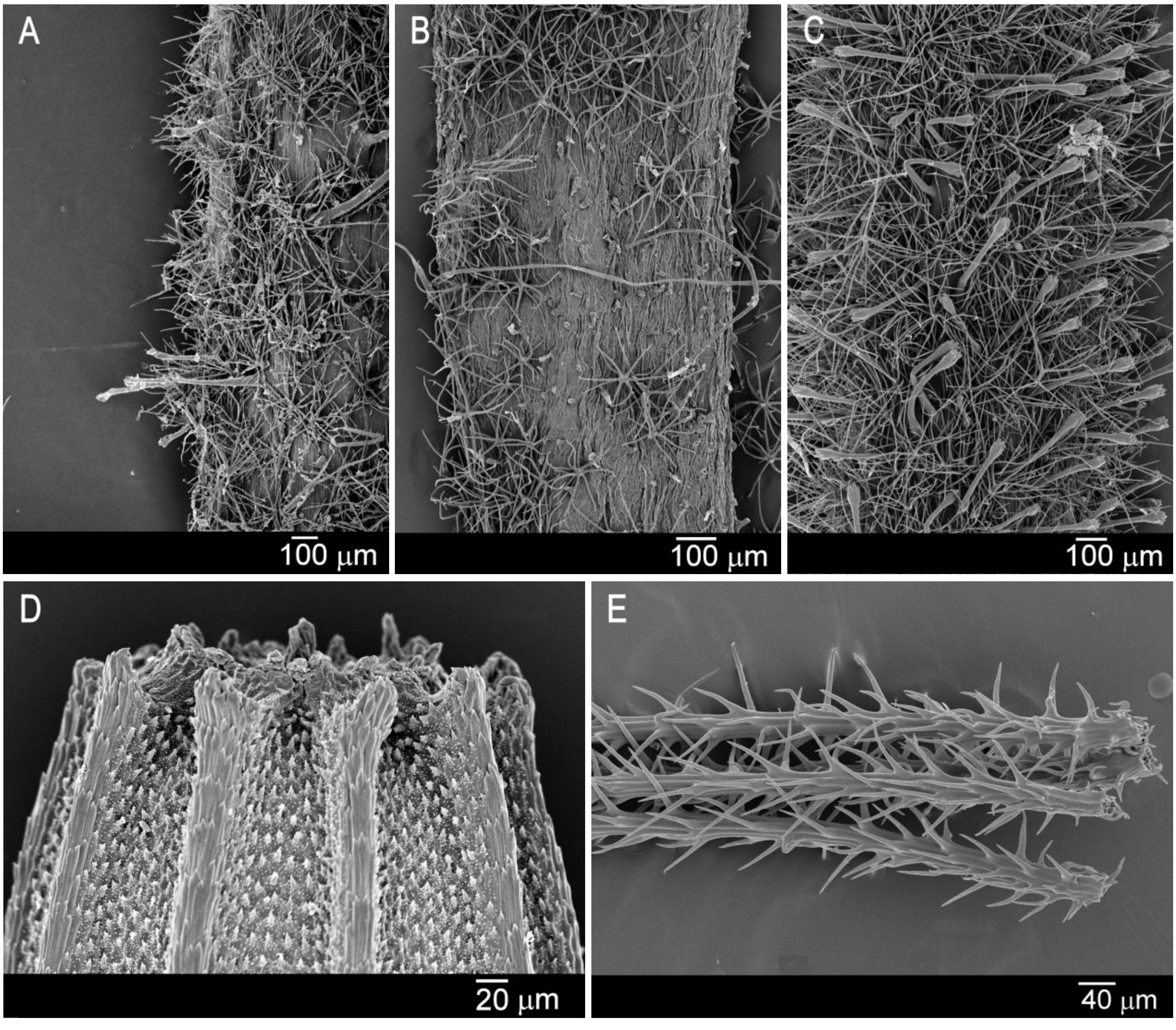


Figure 4.50 *Andryala nigricans* Poir. A – Stem indumentum, B – Leaf indumentum, C – Peduncle indumentum, D – Cypsela apex, E – Pappus base.

4.15.3 Comments on taxonomy and nomenclature

Poiret (1789) described *A. nigricans* Poir. very briefly: "*Foliis inferioribus lyrato-pinnatis, pedunculis ramosis, superiorum partum nigricante*". The specific epithet reflects the presence of almost black glandular hairs on the upper part of the plant, especially on the peduncles and involucre. Poiret (op. cit.) considered it distinct from *Andryala integrifolia* L. Later authors placed it in *A. integrifolia* L. as a mere variety: *A. integrifolia* var. *nigricans* (Poir.) Barratte (Barratte 1896; Battandier & Trabut 1905). However, Maire (1934) recognised this *taxon* at a species rank, admitting two varieties: *A. nigricans* Poiret var. *typica* Maire and *A. nigricans* Poiret var. *Boitardii* R. Lit. et Maire, corresponding the first to "*A. nigricans Poiret sensu stricto (e typo Poiretiano)*", as stated by the author. Maire (op. cit.) distinguished both varieties strictly based on the glandular indumentum: contrary to the typical variety, *A. nigricans* Poiret var. *Boitardii* R. Lit. et Maire exhibits short glandular hairs, only slightly exceeding the whitish indumentum, frequently not abundant, upper part of the plant not hirsute. Likewise, Pottier-Alapetite (1981) recognised *A. nigricans* Poir. and *A. integrifolia* L. as distinct species, distinguishing the latter by its dense corymb with pale yellow florets, conversely to *A. nigricans* Poir. that exhibits lax corymbs with orange yellow ligules. Actually, in *A. integrifolia* L. the corymbs may be more or less lax or quite dense, which means that, in this case, the number of capitula is a poor diagnostic feature. However, the ligules are indeed pale yellow. Besides, *A. integrifolia* exhibits flat involucral bracts not enfolding a floret, conversely to *A. nigricans*. Very recently Le Floc'h *et al.* (2010) recognised *A. nigricans* Poir. as a distinct species for the flora of Tunisia in the publication *Catalogue synonymique commenté de la Flore de Tunisie*, without mentioning any synonym.

4.15.4 Karyology

No chromosome number reports on *Andryala nigricans* Poir. were found in the reviewed literature.

4.15.5 Ecology and conservation status

Andryala nigricans Poir. occurs on hills among bushes (Poiret 1789). It grows in plains and river valleys and can be found in sites between 0-500 m (Murbeck 1905). It can also be found in sandy pastures, mountain scrublands, and roadsides (Pottier-Alapetite 1981), occurring also on dunes.

Pottier-Alapetite (op.cit.) considered it a fairly widespread species, but in the *1997 IUCN Red list of threatened plants* it was classified as vulnerable (Walter & Gillett 1998). No additional information on the conservation status of *A. nigricans* Poir. can be found in recent red lists. Nevertheless, this *taxon* is included in the list of protected uncultivated Algerian plant species (see: "Décret exécutif nº 12-03 du 10 Safar 1433 correspondant au 4 janvier 2012 fixant la liste des espèces végétales non cultivées protégées" 2012). Further studies will be necessary to better determine the actual conservation status of this species.

4.15.6 Geographic distribution

According to Pottier-Alapetite (1981) and available herbarium data, *Andryala nigricans* Poir. is an Algerian-Tunisian endemism (Figure 4.51). It was originally assigned to Algeria (Poiret 1789) and later Barratte (1896) included several Tunisian localities on the Mediterranean coast in the distribution area of this species. In agreement, several authors assigned *A. nigricans* Poir. to different localities in Northern Algeria (Desfontaines 1799; Sprengel 1826; De Candolle 1838) and Murbeck (1905) cited it for a few localities in northeastern Tunisia. Although Cavanilles (1801) cited this species for Morocco, the description by this author clearly fits *A. mogadorensis* Coss. ex Hook. f. Besides, Cavanilles (op.cit.) assigned it to the vicinity of Mogador (Essaouira), where *A. mogadorensis* Coss. ex Hook.f. occurs.

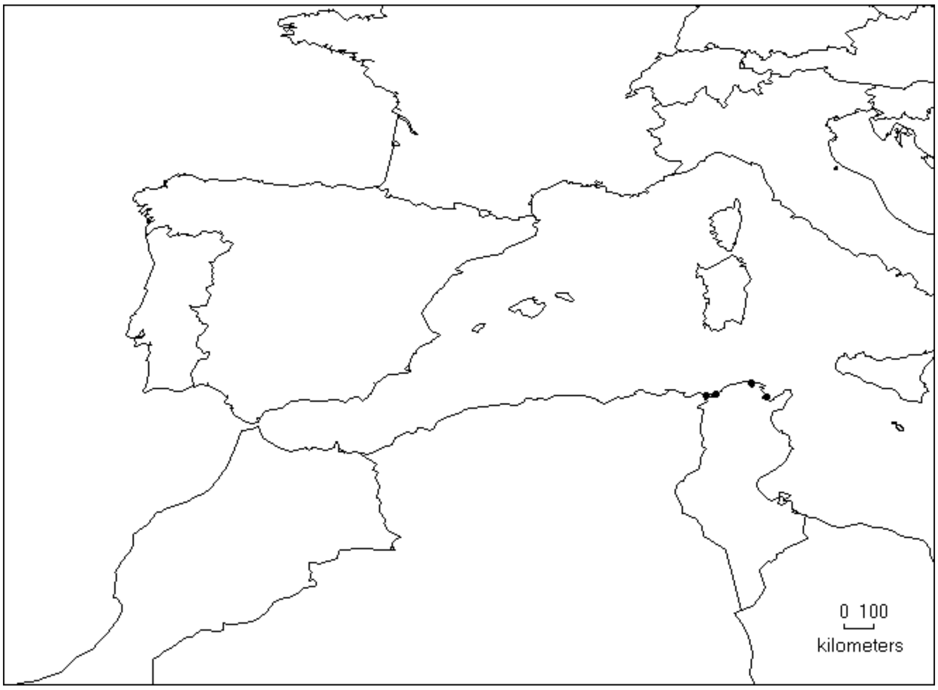


Figure 4.51 Distribution area of *Andryala nigricans* Poir., according to studied material.

4.15.7 List of studied material

Algeria :	[Loc. incert.], Pourret, P.A., s/ nº, P 02462186.
[El Taref]:	La Calle, 13-VI-1841, Durieu de Maisonneuve, M.C s/ nº, P 02462182.
Tunisia:	In arenosis prope promontorium Rosa ao occidentam Tunizae, 21-VI-1931, MPU-Maire. M. Sequeira, Tunisia 1, UMad. M. Sequeira, Tunisia 2, UMad.
[Bizerte]:	Harare, Dans les dunes à Bir-Icherba prés Bizerte, 22-X-1939, MPU-Maire.
[Jendouba]:	Tabarque, Dunes à l'Est de Tabarque, 06-VII-1883, Cosson, E. et Doumet-Adanson, A. Letourneux, V. Reboud, G. Barratte, E. Bonnet, s/ nº, P 02462179. Kroumirie orientale, Dune à Tabarque, 02-VII-1888, Cosson, E. et G. Barratte & C. Duval, s/ nº, P 02462196. Kroumirie orientale, Dune à Tabarque, 02-VII-1888, Cosson, E. et G. Barratte & C. Duval, s/ nº, P 02462197.
[Tunis]:	La Marsa, 29-V-1888, Cosson, E. et G. Barratte & C. Duval, s/ nº, P 02462187.

4.16 *Andryala perezii* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. sp. nov. in Novon, 23(2). 2014 (See Appendix 2)

Ind. loc.: “Fuerteventura and Lanzarote”
Typus: [Spain, Canary Islands] Lanzarote: Haría, altos del Bco de Chafarís, 23 Feb. 1994, *J. A. Reyes-Betancort*, *W. W. de la Torre & P. L. Pérez de Paz s.n.* – Holotype: TFC39728 (Ferreira *et al.* 2014a, see Appendix 2)
= *Andryala pinnatifida* Aiton f. *buchiana* Sch. Bip. Hist. Nat. Iles Canaries (Phytogr.). 2: 415. 1849. *p.p. quoad.*
Andryala pinnatifida Aiton subsp. *buchiana* (Sch. Bip.) Reyes-Bet. & A. Santos in *Willdenowia* 39: 328. 2010. *p.p. quoad.*

4.16.1 Description

Perennial, single or multi-stemmed. STEMS 10–25 cm, woody at the base, branched from the base or in the upper half (Figure 4.52A), densely tomentose with whitish stellate hairs very rarely with scarce glandular hairs (Figure 4.53A). LEAVES congested at base of stem; grayish white or glaucous, densely tomentose with stellate hairs (Figure

4.53B) on both surfaces, lower leaves 93–95 x 25–40 mm, attenuate into a winged petiole 21–24 mm, oblong to lanceolate, apex acute, and margin deeply lobate to pinnatisect, also crispate-undulate; cauline leaves 31–66(-92) x 12–29 mm, cordate at the base, semiamplexicaul or amplexicaul, oblong, and margin pinnatifid or deeply lobate, also crispate-undulate, apex obtuse; upper leaves 8.3(-13)–21.7 x 2.3–8.6 mm, amplexicaul, ovate-oblong to ovate-lanceolate, entire, cordate at the base, apex acute to acuminate. INFLORESCENCE corymbose with 3–8 capitula.

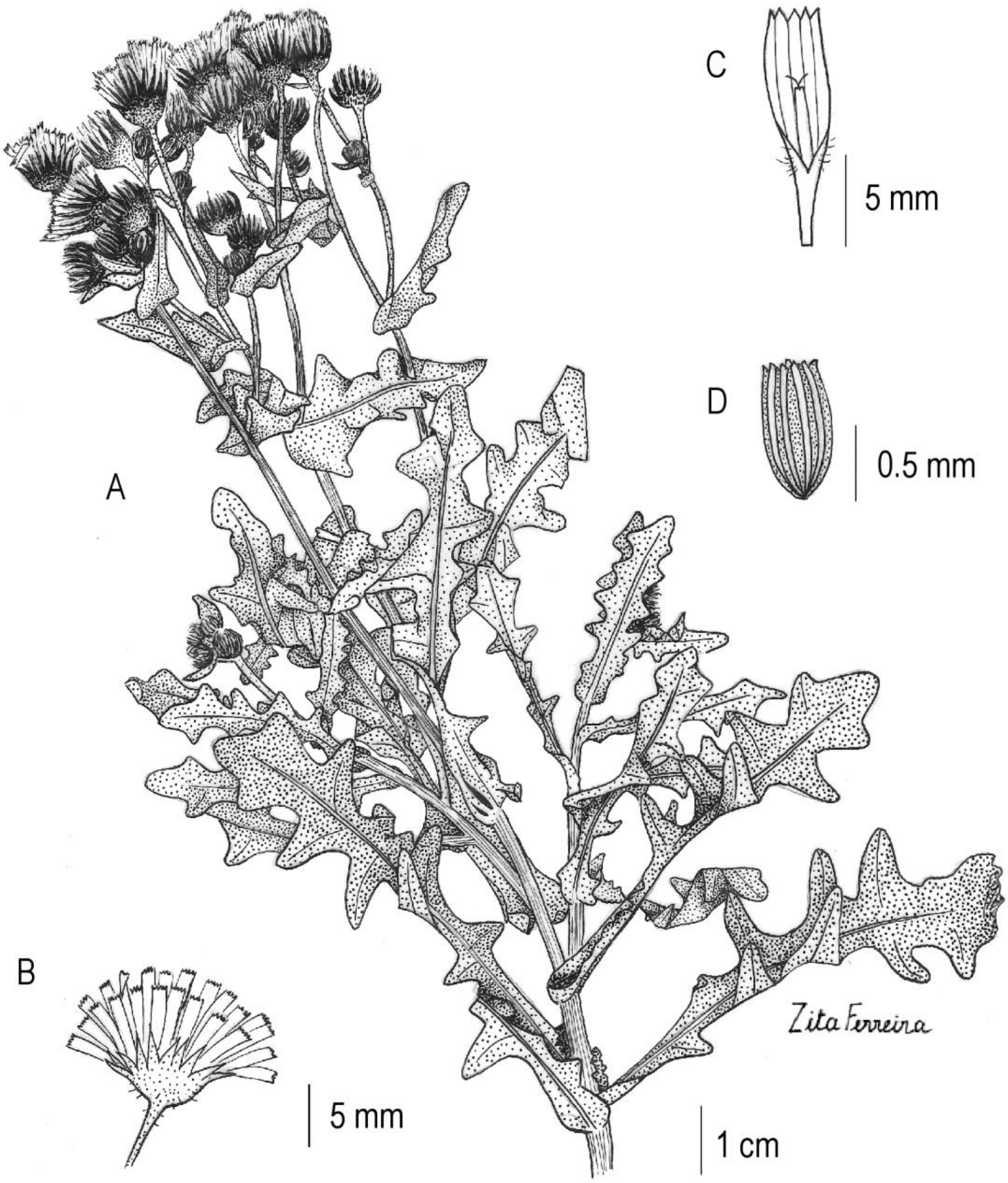


Figure 4.52 *Andryala perezii* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

CAPITULA 15–22 mm in diameter (Figure 4.52B); peduncles 26–43 mm, flattened and enlarged at the base of the capitulum, with dense stellate hairs and few glandular hairs (Figure 4.53C); involucre 10–12 x 11–18 mm, ± hemispherical with involucral bracts in 2–3 rows; external involucral bracts 7–7.5 x 1.2–1.6 mm, lanceolate to linear-lanceolate, apex acuminate to subulate, involute enfolding a floret, the outer face tomentose with dense stellate hairs and also abundant glandular hairs 1.2–1.9 mm, especially along the middle nerve, usually yellow at the apex and blackish towards the base; internal involucral bracts 6.5–8 x 1.5–2.3 mm, with narrow scariose margins; receptacle convex, puberulous to tomentose, with long setose hairs 3.3–4.2 mm (3 to 4 times longer than the cypselae). FLORETS ligulate, golden yellow, the external with a tube of 4–6.5 mm and ligule 7.4–10 x 1.9–3.1 mm (Figure 4.52C). CYPSELAE 0.9–1.1 x 0.4–0.5 mm (Figure 4.52D), oblong, dark brown with reddish brown ribs; the apex with a ring of short teeth, equaling the prolongation of the ribs (Figure 4.53D); pappus of white bristles 4.8–5.2 mm, pilose at the base (Figure 4.53E).

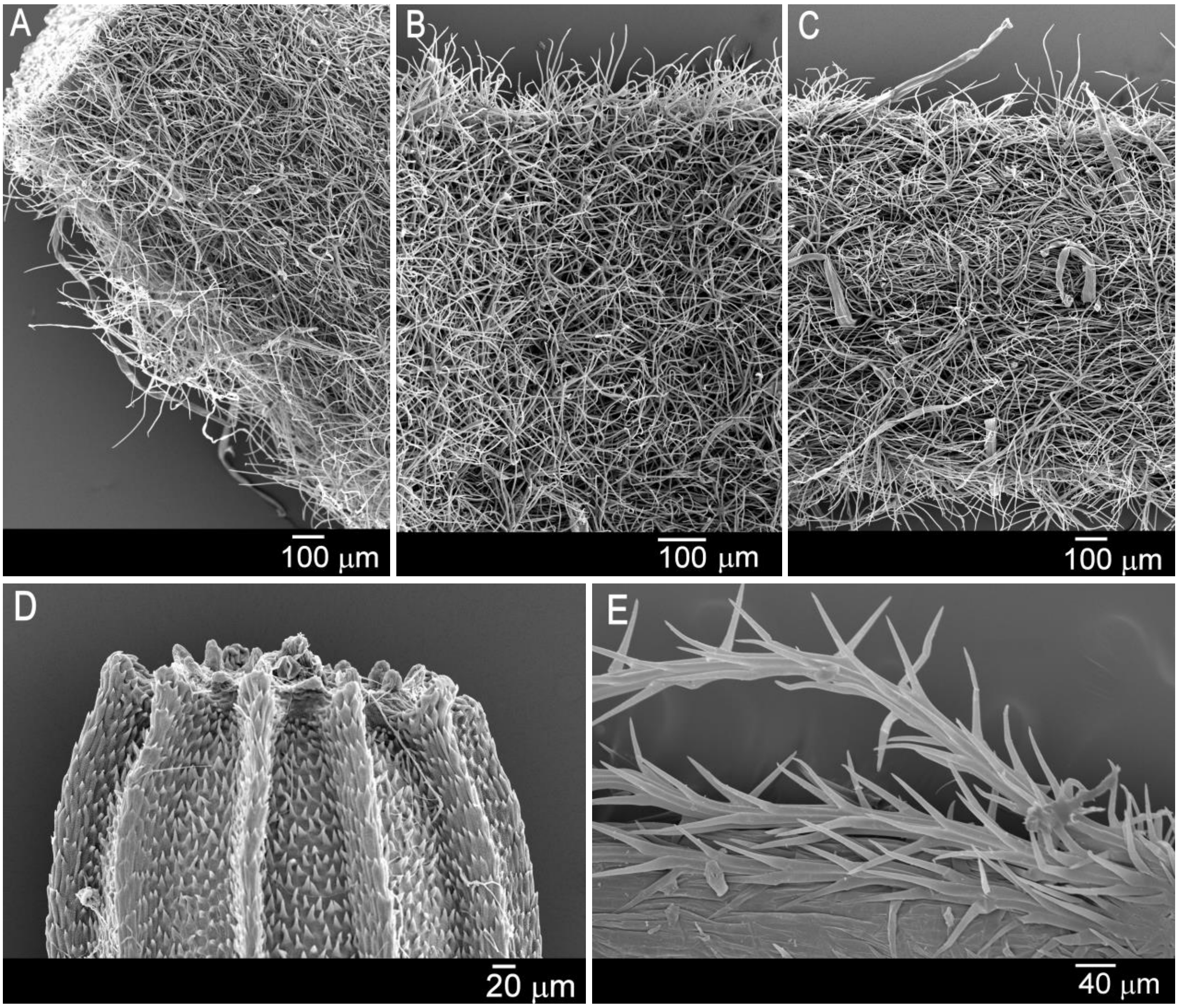


Figure 4.53 *Andryala perezii* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. A – Stem indumentum, B – Leaf indumentum, C – Peduncle indumentum, D – Cypsela apex, E – Pappus base.

4.16.2 Comments on taxonomy and nomenclature

Andryala perezii was for many years known as the *A. glandulosa* Lam. from the Canary Islands. Recent studies showed that this name has been misapplied for the Canarian populations by several authors (Kunkel 1977c; Kunkel 1982; Hansen & Sunding 1993; Bramwell & Bramwell 2001) which can be explained by the fact that in the protologue of *A. glandulosa* Lam. the only reference to its provenance is "*On cultive cette plant au Jardin du Roi. Elle provient, je crois, de graines du voyage de Cook*" (Lamarck 1783: 154). Thus, the origin of the species was unclear, since the seeds of the plants cultivated at the former Paris Royal Garden could either have come from the Canary Islands or the Madeira Archipelago. However, the likelyhood of a Madeiran origin is quite high (Ferreira *et al.* 2014a, see

Appendix 2). Actually, L'Héritier (1785) described *A. cheiranthifolia* L' Hér. (= *A. glandulosa* Lam.), which was explicitly assigned to Madeira. Many years later later, Lid & Lid (1967) accepted *A. cheiranthifolia* L'Hér. for the Canary flora, presenting an illustration which definitely represents *A. perezii*. Later, Kunkel (1978) admitted *A. glandulosa* Lam. as a Macaronesian endemic, indicating *A. varia* Lowe ex DC. and *A. cheiranthifolia* L'Hér. as synonyms, and in 1980 this author incorrectly assigned it to the Canary Islands and to Madeira. More recently, the former Canarian *A. glandulosa* Lam. was recognised as *A. pinnatifida* subsp. *buchiana* (Sch. Bip.) Reyes-Bet. & A. Santos and specifically assigned to Lanzarote and Fuerteventura (Greuter & von Raab-Straube, 2009). Apparently, *A. pinnatifida* f. *buchiana* Sch. Bip. was transferred in rank, but no typification was suggested. Actually, in the protologue Schultz Bipontinus (1849) included in this form both plants from Tenerife and Lanzarote, but only the latter belong to *A. perezii* (Ferreira *et al.* 2014a). Hence, the eastern Canary populations (from Lanzarote and Fuerteventura), formerly recognised as *A. glandulosa* Lam. and *A. cheiranthifolia* L'Hér. were very recently recognised as a new species. Indeed, *A. perezii* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. is morphologically quite distinct compared to the Canarian *A. pinnatifida* Aiton and the Madeiran *A. glandulosa* Lam. It differs from *A. pinnatifida* Aiton by the stem height, leaf indumentum and margin, peduncle length and indumentum, involucral bracts convolution, and cypsela morphology. Likewise, it can be distinguished from *A. glandulosa* Lam. by the stem height and indumentum; leaf colour, indumentum and margin; peduncle morphology and indumentum; and cypsela length (Ferreira *et al.* 2014a, see Appendix 2).

4.16.3 Karyology

The somatic chromosome number of 2n = 18 was reported for plant material collected in Lanzarote (Canary Islands) and originally identified as *Andryala cheiranthifolia* L'Hér. (Borgen 1970; Van Loon 1974). A careful observation of the herbarium voucher of the plant on which Borgen (op. cit) performed the chromosome counts made it clear that this specimen corresponds to the recently described *Andryala perezii* (Ferreira *et al.* 2014a, see Appendix 2).

4.16.4 Ecology and conservation status

Andryala perezii M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. is common on cliffs and rocky slopes of Lanzarote and Fuerteventura, growing also on roadsides and volcanic substrates, at elevations from 90 to 580(-800) m asl. Kunkel (1977a) considered the Canarian *A. glandulosa* (i.e. *A. perezii*) locally common in both islands, despite grazing by rabbits and goats, and did not regard it as a threatened *taxon*. *Andryala perezii* was evaluated under the name *A. glandulosa* for the Canary Islands and was not included in the Red Data Book of the Canarian Flora (Beltrán Tejera *et al.* 1999), nor was it mentioned in *Memoria de Evaluación de Especies Amenazadas de Canarias 2009* (Servicio de Biodiversidad del Gobierno de Canarias, 2009). Despite the restricted distribution in the Canary archipelago, this species is locally common in parts of its range and, therefore, according to the *IUCN Red List categories and criteria* (IUCN 2001; 2012), it should be listed as Least Concern (LC) (Ferreira *et al.* 2014a, see Appendix 2).

4.16.5 Geographic distribution

Andryala perezii can only be found on the eastern Canary Isands of Lanzarote and Fuerteventura (Figure 4.54). There are several records on the geographic distribution of this *taxon*, although under different names: *A. glandulosa* Lam. and *A. cheiranthifolia* L'Hér. (Lid & Lid 1967; Kunkel 1977c; Kunkel 1977a; Bramwell & Bramwell 2001). In Fuerteventura, this species occurs more abundantly in the southwestern part of the island, known as Peninsula of Jandía, in several localities (e.g. Pico de la Zarza, Pico del Fraile, Montaña del Cardón), in the central part (Riscos del Carnicero, Vega de Rio Palmas, Betancuria), and less frequently in the northern parts (e.g. Montaña de Vallebrón). In Lanzarote it occurs chiefly in the northeastern part of the island (Riscos de Famara, Risco de las Nieves, Peñas del Chache, Los Helechos, Haría, Malpaís de la Corona, Los Valles), and can also be found in central and southwestern localities (e.g. Montaña Blanca, Montaña Zonzamas, San Bartolomé, Timanfaya, Yaiza-Uga, Femés).

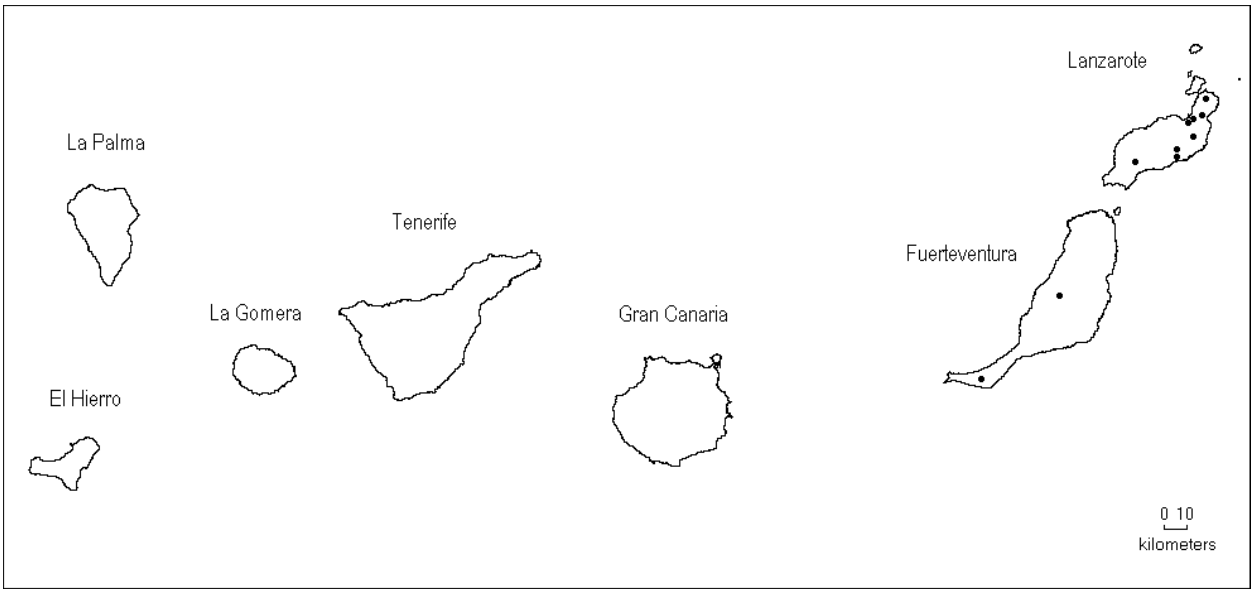


Figure 4.54 Distribution area of *Andryala perezii* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq., according to studied material.

4.16.6 List of studied material

Spain:

[Canary Islands]: Lanzarote. Haría, altos del Bco. de Chafarís UTM (28FT 449 227), 23-II-1994, J.A. Reyes-Betancort, Wolfredo Wildpret de la Torre & Pedro Luis Pérez de Paz, s/ nº, TFC 39728. Lanzarote. Montanã Blanca UTM (28RFT 6325 32065), 31-III-1994, J. A. Reyes-Betancort, s/ nº, TFC 37826. Risco de las Nieves, 19-I-1983, Marcelino del Arco Aguilar. Pedro Luis Pérez de Paz, Wolfredo Wildpret. dela Torre, s/ nº, TFC 28870. Lanzarote. Riscos de Famara., 25-III-1975, PL Pérez et J. R. Acebes, s/ nº, TFC 4794. Risco de Famara, Lanzarote, 25-III-1975, J. R. Acebes e P. L. Pérez, s/nº, TFMC 1770. Famara, Lanzarote, 10-V-1986, SSH, s/ nº, TFMC 2439. Lanzarote, Teguise, casas de Famara, 90 m, laderas pedregosas com *Euphorbia, Lycium* y *Launaea*, 04-IV-2006, C. Aedo, L. Medina & A, Quintanar, CA12532-1, MA, Haría, riscos de Famara, penas de Chache, 580 m, borde de camino e roquedos, 03-IV-2006, C. Aedo, L. Medina & A, Quintanar, CA12417-2, MA. Lanzarote, San Bartolomé, Monte Mina, 430 m, substrato vulcânico, 07-IV-2006, C. Aedo, L. Medina & A, Quintanar, AQ 1846-3, MA. Lanzarote, Montanã Famara, 500 m, 08-IX-1970, P Sunding, O. Lanzarote: Haría, Valle de Malpaso, 490 m.s.m. 28 R 6444873223480, 22-III-2011, J. A. Reyes-Betancort, ORT. Lanzarote, Yaiza, Atalaya de Femés, 565 m.s.m., 28 R 618577 3199734, 21-III-2011, J. A. Reyes-Betancort, ORT, 42331. Lanzarote, Haría, bajo el Mirador del Río, 340 m.s.m., 28 R 647220 3232398, 22-III-2011, J. A. Reyes- Betancort, ORT. Lanzarote, Yaiza, Atalaya de Femés, 565 m.s.m., 28 R 618577 3199734, 21-III-2011, J. A. Reyes-Betancort, ORT 42330. Fuerteventura. Pico del Fraile, 24-VII-1979, A. Banãres, s/ nº, TFC 21147. Fuerteventura, Pinar de Betancuria, 14-IV-1989, LSP e JMG, s/nº, TFMC 2416.

4.17 *Andryala pinnatifida* Aiton ex parte. Sch. Bip., Hist. Nat. Iles Canaries (Phytogr.). 2: 412. 1849

≡ *Andryala pinnatifida* Aiton var. *β.* Hortus Kew. 3: 129. 1789
Ind. loc.: “Canary Islands, Mr. Francis Masson, Introd. 1778”
Typus: [Spain, Canary Islands] “Tenerife, 1778”, *Fr. Masson s.n.* – Lectotype (designated by Ferreira *et al.* 2014a): BM000753022! (specimen on the right); isolectotype: BM000753022! (specimen on the left).
= *Andryala canariensis* Lowe, Man. Fl. Madeira 1: 564. 1868
Ind. loc.: “… Canarian. Tenerife, &c.”
Typus: [Spain, Canary Islands] “Ten. Rocks by the road above Realejo, 1 Jan. 1858”, *R. T. Lowe 126* – Lectotype (designated here): BM000072533a! (specimen on the right); isolectotype: BM000072533a! (specimen on the left); syntype: BM000072533b!
= *Andryala pinnatifida* Aiton f. *sprengeliana* Sch. Bip. in Webb & Berthel. Hist. Nat. Iles Canaries (Phytogr.) 2: 415. 1849
Andryala pinnatifida Aiton subsp. *preauxiana* var. *sprengeliana* (Sch. Bip.) G. Kunkel in Vieraea 8(2): 344. 1980
Ind. loc.: “Canaria, in collibus aridis argillosis Valsequillo, 25 Martio 1846: Bourgeau! n. 5 … Canaria, Barranco de la Vierge, 30 Martio 1846: Bourgeau! n. 6 … Canaria, in humidiusculis et convallium umbrosis, Martio 1846: Bourgeau! n. 10 … Canaria, Barranco de los Tiles, monte Doramas, 6 Apr. 1846: Bourgeau! n. 8; Teneriffa, Barranco de Ignoste, reg. Pini, Junio 1846: Bourgeau! n. 2.”
Typus: [Spain, Canary Islands] “Teneriffa: Bco. de Ignoste, région des pins, June 1846”, *E. Bourgeau 2* – Lectotype (designated here): P02462110!; syntypes: P02462106!, P02462107!, P02462111! (both specimens), FI-W109954 (specimen on the left); isosyntypes: P02462136!, P02462156!, P02462157!, P02462158!, FI-W109946, FI-W109949, FI-W109954 (specimen on the right).
= *Andryala pinnatifida* Aiton f. *philippiana* Sch. Bip. in Webb & Berthel. Hist. Nat. Iles Canaries (Phytogr.) 2: 415. 1849
Ind. loc.: “Teneriffa ad sylvæ marginem prope San Diego de Monte 26 Febr. 1845. Bourgeau!”
Typus: [Spain, Canary Islands] “Borde du bois a San Diego del Monte – Tenerife, 26 Feb. 1845”, *Bourgeau s.n.* – Holotype: P02462160!
= *Andryala pinnatifida* Aiton f. *fuerteventurensis* Sch. Bip. in Webb & Berthel. Hist. Nat. Iles Canaries (Phytogr.) 2: 415. 1849
Ind. loc.: “Fuerteventura, el Risco de Valdebron, 19 Febr. 1846; Bourgeau! n. 13. Iconem tab. 135.”
Typus: [Spain, Canary Islands] “En El Risco de Valdebron – Fuerteventura, 19 Feb. 1846”, *Bourgeau 13* – Holotype: P02462161!; syntype: illustration in the protologue (Iconem tab. 135).
= *Andryala pinnatifida* Aiton subsp. *preauxiana* (Sch. Bip.) G. Kunkel in Cuad. Bot. Canaria 14/15:54. 1972
Ind. loc.: “Localidades en Gran Canaria: El Caseron (Bco. la Virgen), 800 m. (Ku. 13327); El Tablero, Moya a Fontanales, 830 m. (Ku. 13603).
Typus: [Spain, Canary Islands] “Gran Canaria , 2 May 1970”, *G. Kunkel, 13327* – Lectotype (designated by Kunkel 1972): G00236905

4.17.1 Typification

Aiton (1789) described *A. pinnatifida* Aiton var. *β* from the Canary Islands based on material collected by Francis Masson and introduced in Kew Gardens in 1778. Two specimens with this name were found filed under the registration number BM000753022. Both were indeed collected in Tenerife by Fr. Masson in 1778, as mentioned in the protologue. They correspond most surely to original material, and since the one on the right better matches the original description (“*foliis profunde pinnatifidis: pinnis brevibus integris*”), it is was designated as lectotype of *A. pinnatifida* Aiton ex parte (Ferreira *et al.* 2014a, Appendix 2).

At the BM herbarium several specimens, collected in Tenerife by Lowe, are under the name *A. canariensis* Lowe (handwritten by Lowe himself). Therefore, these correspond to original material and the best conserved specimen (BM000072533a) is here designated as lectotype of *A. canariensis* Lowe.

Although the herbarium and types of Schultz Bipontinus are hosted at P herbarium, there are collections by others containing Schultz Bipontinus types e.g. FI, FR. (Stafleu & Cowan 1985). In the protologue Schultz Bipontinus (1849) mentioned several specimens under *Andryala pinnatifida* Aiton f. *sprengeliana* collected by E. Bourgeau in different localities of Gran Canaria and Tenerife which were located at the P and FI-W herbaria, including duplicates. Collection dates and collector numbers coincide exactly with the ones in the protologue. The specimen P02462110 is here designated as lectotype of *Andryala pinnatifida* Aiton f. *sprengeliana* Sch. Bip., given that it fits perfectly the original description.

A single specimen under *A. pinnatifida* Aiton f. *philippiana*, with collection date and collector number identical to the ones in the protologue, was found (P02462160). It matches the original description very well and is here accepted as holotype of *A. pinnatifida* Aiton f. *philippiana* Sch. Bip., considering that no other specimen was discovered. Likewise, the specimen P02462161 was the only one found under *A. pinnatifida* f. *fuerteventurensis* and is here considered as the holotype as the collection date and collector number coincide exactly with those in the protologue.

4.17.2 Description

Perennial herb, single or multi-stemmed. STEMS 15–81(-128) cm, woody at the base, branched in the upper third, sometimes from the base or in the upper half, pubescent-tomentose to densely tomentose, rarely puberulous, with stellate hairs sometimes with glandular hairs in the upper part. LEAVES glaucous to deep green, puberulous to densely tomentose, especially the cauline and upper leaves, with stellate hairs and rarely with scarce glandular hairs, the abaxial face frequently with stellate hairs denser on the abaxial face than on the adaxial face; lower leaves 42–140 x 18–64 mm, attenuate into a winged petiole (7-)14–56 mm, oblong to lanceolate, sometimes obovate, elliptic, or oblong, apex obtuse or acute, and margin lobate to pinnatisect; cauline leaves 24–129 x 8–64(-71) mm, sessile or semiamplexicaul, elliptic to lanceolate, sometimes oblong or obovate, base attenuate sometimes rounded, cuneate ou subcuneate, apex obtuse or acute, and margin subentire to pinnatisect; upper leaves 10–42(-51) x 2–31.6 mm, usually semiamplexicaul or amplexicaul, elliptic to lanceolate or ovate to ovate-lanceolate, base usually rounded, sometimes subcordate or ± cuneate, apex acute sometimes acuminate, and margin entire sometimes lobate to pinnatipartite. INFLORESCENCE corymbose to paniculate-corymbose or racemose with 3–12 capitula. CAPITULA 7–26 mm in diameter; peduncles 5–34 mm, with dense stellate hairs sometimes with hispid glandular hairs 0.2–2.8 mm; involucre 4–12 x 4–15.5 mm, hemispherical or campanulate at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 4.3–7.6 x 0.8–1.5 mm, lanceolate to linear-lanceolate, apex acuminate sometimes acute or subulate, frequently flat not enfolding a floret or rarely involute, the outer face puberulous to tomentose with stellate hairs sometimes with few to numerous glandular hairs (0.4-)0.7–2.7 mm; internal involucral bracts 3.6–7.4 x 1.2–2.5 mm, sometimes with broad scariose margins; receptacle convex, villous with setose hairs (0.4-)1–6.5 mm (2 to 5 times longer than the cypselae). FLORETS ligulate, bright yellow to golden yellow, the external with a tube of 2.5–6 mm and ligule of 5-11 x 0.8–3.7 mm, sometimes with a reddish stripe on the outer face. CYPSELAE 1–1.7 x 0.4–0.5 mm, oblong to obconical, dark brown or black with reddish brown ribs, apex with a ring of small teeth largely exceeded by the conspicuous prolongation of the ribs; pappus of white or sometimes dirty-white bristles 4–6 mm, ± denticulate at the base.

4.17.3 Comments on taxonomy and nomenclature

Andryala pinnatifida Aiton was validly published by Aiton (1789: 129) who recognised two varieties: *A. pinnatifida* Aiton var. *α*, endemic for Madeira, and *A. pinnatifida* Aiton var. *β,* endemic for the Canary Islands. The original description of the Canarian variety was very brief ("*foliis profunde pinnatifidis: pinnis brevibus integris*"). According to the protologue, it was based on plant material collected by Francis Masson and introduced in Kew Gardens around 1778. Much later Lowe (1868) cautioned that part of the herbarium material, hosted at the British Museum, under the name *A. pinnatifida* var. *β* came from Madeira and not from the Canary Islands. Actually, the observation of type material unveiled a specimen from Madeira, collected by Masson in 1777, which must have been initially identified as *A. pinnatifida* var. *β.* (currently under *A. pinnatifida* var. *α.* while Aiton's *A. pinnatifida* var. *α.* from Madeira is labelled *A. pinnatifida* var. *β*, fact that can be explained by some label switch). As this specimen exhibits profoundly divided leaves, even more than the specimen from the Canary Islands, Lowe (1868: 564) stated that *A. pinnatifida* var. *β* from the Canary Islands "*has indeed such small pretensions to the name of A. pinnatifida Ait., and so much confusion is attached to its reception, that the adoption for it even now of a new name, A. canariensis, might be warrantable.*" However, as suggested by earlier authors (e.g. Sprengel 1826; De Candolle 1838; Schultz Bipontinus 1849) the name *Andryala pinnatifida* Aiton was restricted to the Canarian *taxa*, and correctly prevailed over *A. canariensis* Lowe for several years. Actually, Schultz Bipontinus (1849) described in detail *A. pinnatifida* Aiton *ex parte*, that is, the author included in this species solely the Canarian *A. pinnatifida* Aiton var. *β.* Unfortunately, Ball (1878) extended the name *A. pinnatifida* Aiton to a North African *taxon*, which actually is worthy of specific distinction: *A. mogadorensis* Coss. ex Hook.f. (Ferreira *et al.* 2014c; see p. 157 and Appendix 3).

Hansen and Sunding (1993) cited *A. bourgeauii* Sch. Bip., *A. canariensis* Lowe, and *A. coronopifolia* Link in Buch as synonyms of *A. pinnatifida* Aiton. Indeed, Schultz Bipontinus (1849) described a Canarian form (*A. pinnatifida* Aiton f. *bourgæana* Sch. Bip.) citing the unpublished name *A. bourgeauii* Sch. Bip. from the Webb Herbarium as a synonym. The analysis of type material showed that *A. bourgeauii* Sch. Bip. belongs in fact to *A. pinnatifida* Aiton. Buch (1825) assigned *A. coronopifolia* Hoffmanns. & Link to the Canary Islands of Gran Canaria and Tenerife, stressing that this *taxon* is also present in Portugal. Actually, Hoffmannsegg & Link (1825) assigned *A. coronopifolia* Hoffmanns. & Link to mainland Portugal and, as mentioned previously, it corresponds to *A. integrifolia* L. (see p. 132). In fact, the latter species can be found in Gran Canaria, El Hierro and La Palma, although its presence in Tenerife is dubious due to the lack of current records (Santos-Guerra *et al.* 2013).

4.17.4 Karyology

Chromosome counts were performed on plant material from Orotava (Tenerife) and the somatic chromosome number obtained was 2n = 18 (Larsen 1963). Additional counts were made on specimens from Gran Canaria and the same number was obtained (Borgen 1969). This diploid number was more recently confirmed on material from Tenerife by Baltisberger & Widmer (2006). The material used in these determinations was simply identified as *A. pinnatifida* Aiton. Therefore, the observation of the specimens in question is in need to ascertain their infraspecific position.

4.17.5 Ecology and conservation status

Ceballos & Ortuño (1951) considered *Andryala pinnatifida* Aiton as an extremely polymorphic species due to its adaptation to localities with quite diverse ecological conditions. According to these authors, this species is more abundant on degraded soils of humid areas of the laurel forest, although its presence in both mountain and coastal areas has been noted. *Andryala pinnatifida* is rather common, ascending to 1000 m in Hierro, 1400 m in Gomera, 1500 m in La Palma, 1900 m in Tenerife and 1950 m in Gran Canaria (Lid & Lid 1967). This species grows in scrublands and forest clearings, occurring frequently on cliffs between 200 and more than 1500 m above the sea (Kunkel 1977a), roadsides (Kunkel 1977b), and vineyards (Bornmüller 1904). Since it is rather common, at least on the western islands, *A. pinnatifida* Aiton should be considered as Least Concern (LC), according to the *IUCN Red List categories and criteria* (IUCN 2001; 2012). In fact, *Andryala pinnatifida* Aiton is not listed neither in *Libro rojo de especies vegetales amenazadas de las Islas Canarias*" (Gómez-Campo 1996) nor in *Catalogue of endangered species of the Canary Islands* (see: "Ley del Catálogo Canario de Especies Protegidas" 2010).

4.17.6 Geographic distribution

Kunkel (1977a) considered *Andryala pinnatifida* Aiton as a Canarian endemism, expressing some doubts concerning its presence on all islands of the archipelago. *Andryala pinnatifida* Aiton is very common on all the five western Canary Islands (Córdoba & Ortuño Medina 1951; Lid & Lid 1967). According to some authors, it can be also be found on the eastern islands of Lanzarote and Fuerteventura (Hansen & Sunding 1993; Bramwell & Bramwell 2001). However, in conformity with available herbarium data, it is not present in Lanzarote.

4.17.7 Key to the *Andryala pinnatifida* Aiton subspecies

1a. Plants very rarely with scarce glandular hairs; stems 73–128 cm; cauline leaves pinnatipartite to pinnatisect with linear segments; inflorescence paniculate-corymbose or racemose. .... *A. pinnatifida* subsp. *teydensis*

1b. Plants usually with a few or abundant glandular hairs at least in the upper part; stems up to 15–77 cm; cauline leaves dentate to pinnatipartite with broader segments, never linear; inflorescence often corymbose. 2

2a. Stems stellate-pubescent to densely stellate-tomentose below; cauline leaves never obovate, pinnatifid to pinnatipartite; peduncles often with a few glandular hairs up to 1.6 mm long. 3

2b. Stems stellate-puberulous to slightly stellate-tomentose below; cauline sometimes obovate, dentate to pinnatifid; peduncles always with abundant hispid glandular hairs up to 2.8 mm long... 4

3a. Lower leaves 83–120 x 27–55 mm, elliptic to lanceolate, often pinnatipartite with divided lobes; peduncles 10–34 mm long. ... . *A. pinnatifida* subsp. *pinnatifida*

3b. Lower leaves 50–85 x 18–29 mm, oblanceolate, pinnatifid with entire lobes; peduncles 5–18 mm long. .... *A. pinnatifida* subsp. *preauxiana*

4a. Stems not purplish; leaves crowded, abaxial face stellate-lanate, cauline leaves cuneate to subcuneate, lobate to ± pinnatifid. .... *A. pinnatifida* subsp. *cuneifolia*

4b. Stems sometimes purplish; leaves not crowded, abaxial face stellate tomentose, cauline leaves attenuate or rounded, dentate. .... *A. pinnatifida* Aiton subsp. *webbiana*

4.17.7.1 *Andryala pinnatifida* subsp. *pinnatifida*

4.17.7.1.1 Description

Perennial herb, single or multi-stemmed. STEMS 15–57 cm, woody at the base, usually branched from the base or in the upper half (Figure 4.55A), pubescent to densely tomentose, especially below, with stellate hairs and usually with glandular hairs in the upper part (Figure 4.56A).

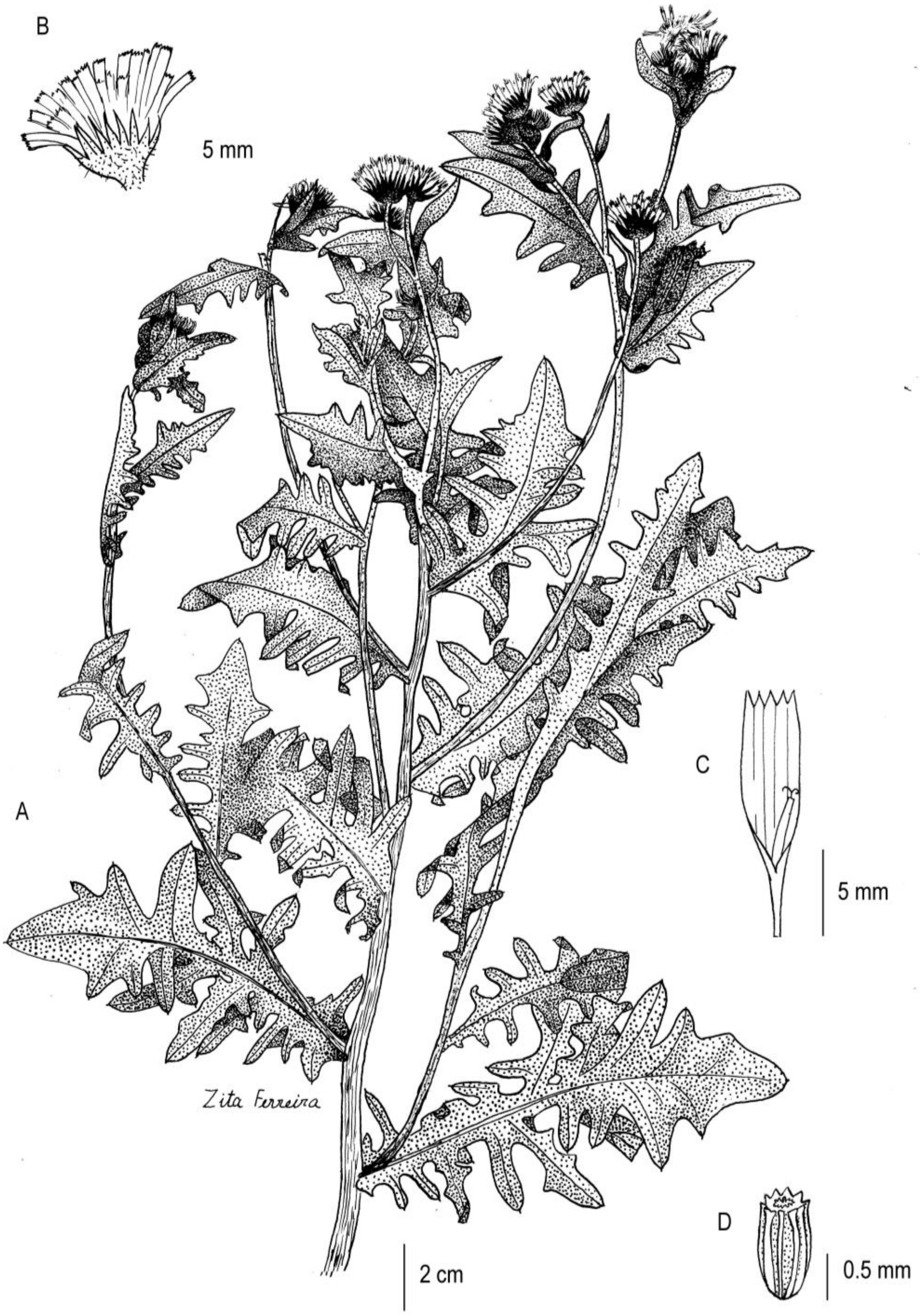


Figure 4.55 *Andryala pinnatifida* subsp. *pinnatifida* A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

LEAVES puberulous to tomentose, especially the upper leaves, with stellate hairs and rarely with scarce glandular hairs, the abaxial face more stellate-hairy than the adaxial face (Figure 4.56B); lower leaves 83–120 x 27–55 mm, attenuate into a winged petiole 14–28(-40) mm, elliptic to lanceolate, apex obtuse or acute, and margin pinnapartite or pinnatifid with divided lobes; cauline leaves 52–129 x 20–71 mm, sessile or semiamplexicaul, elliptic to lanceolate, base attenuate or rounded, apex obtuse, and margin pinnatifid to pinnatipartite with divided lobes; upper leaves 10–42 x 2–13 mm, semiamplexicaul or amplexicaul, ovate-oblong to ovate-lanceolate, base usually rounded, apex acute, and margin entire sometimes lobate to pinnatipartite. INFLORESCENCE usually corymbose with 5–12 capitula. CAPITULA 10–26 mm in diameter (Figure 4.55B); peduncles 10–34 mm, with dense stellate hairs frequently with a few glandular hairs 0.3–1.6 mm (Figure 4.56C); involucre 7.5–10.5 x 9–15.5 mm, hemispherical to campanulate at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 5–7.3 x 0.8–1.5 mm, lanceolate to linear-lanceolate, apex acuminate, flat not enfolding a floret or rarely involute, the outer face frequently tomentose with stellate hairs and sometimes with a few glandular hairs 0.8–1.6 mm; internal involucral bracts 4.3–7.2 x 1.2–2.5 mm, with scariose margins; receptacle convex, villous with long setose hairs (0.4-)2–5.4 mm (2 to 4 times longer than the cypselae). FLORETS ligulate, bright yellow, the external with a tube of 2.5–6 mm and ligule of 5-11 x 0.8–3.7 mm (Figure 4.55C). CYPSELAE 0.8–1.3 x 0.4–0.5 mm (Figure 4.55D), oblong, dark brown or black with reddish brown ribs, apex with a ring of small teeth largely exceeded by the quite conspicous prolongation of the ribs (Figure 4.56D); pappus of white or dirty-white bristles 4–5.4 mm, ± denticulate at the base (Figure 4.56E).

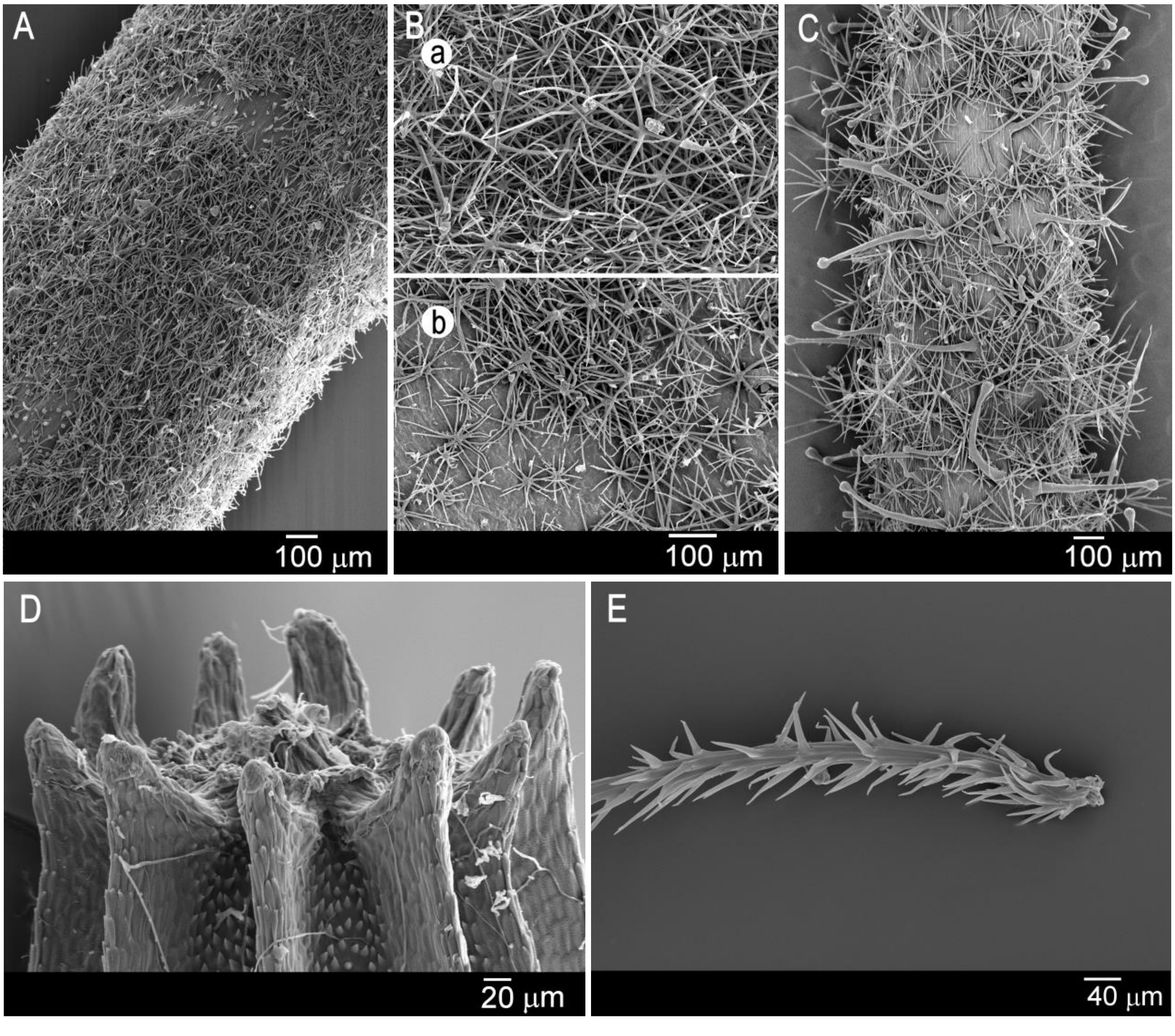


Figure 4.56 *Andryala pinnatifida* subsp. *pinnatifida* A – Stem indumentum, B – Leaf indumentum (a - abaxial face, b - adaxial face), C – Peduncle indumentum, D – Cypsela apex, E – Pappus base.

4.17.7.1.2 Comments on taxonomy and nomenclature

When describing *Andryala pinnatifida* var. *β* in *Hortus Kewensis*, Aiton (1789) mentioned that this *taxon* exhibits deeply pinnatifid leaves, with slightly divided lobes and this feature is quite evident on the type material observed (see p. 177). Kunkel (1977b) recognised *A. pinnatifida* subsp. *pinnatifida* with profoundly divided leaves or at least pinnatifid, but made no reference to the leaf lobes. Schultz Bipontinus (1849) described a considerable number of forms for *A. pinnatifid* Aiton from the Canary Islands. Among them the author recognised "*Forma genuina"* ("*Folia pinnatifida, pinnis integris*"), comprising *A. pinnatifida* f. *massoniana* Sch. Bip. (named after Masson, the collector of *A. pinnatifida* Aiton var. *β* described in *Hortus Kewensis*) and *A. pinnatifida* f. *preauxiana* Sch. Bip. Moreover, Schultz Bipontinus (1849: 414) described *A. pinnatifida* f. *massoniana* Sch. Bip. in the following terms: "*Caulis spithameus-pedalis, robustus v. gracilis, corymbosus; folia lanceolata ± profunde pinnatifida, 1/2-3/4 poll., ambitu metientia, plana, utrinque tomentosa vel supra glabrescentia; pinnae integrae, lineari-oblongae, obtusae.*" This description does not fit the lectotype of *Andryala pinnatifida* Aiton given that the leaves have linear-oblong and entire lobes. Schultz Bipontinus (1849) recognised an additional group, differing from "*Forma genuina*" by the leaves with divided lobes ("*Folia pinnatifida, pinnis dentatis-subpinnatifidis*"), in which he included *A. pinnatifida* f. *sprengeliana* Sch. Bip., *A. pinnatifida* f. *philippiana* Sch. Bip., and *A. pinnatifida* f. *fuerteventurensis* Sch. Bip. Schultz Bipontinus (1849) distinguished the first two forms only by the leave shape and inflorescence type. Furthermore, he emphasized the morphological similarity between *A. pinnatifida* f. *fuerteventurensis* Sch. Bip. and *A. pinnatifida* f. *sprengeliana* Sch. Bip. and, additionally, presented a hand drawing to illustrate both forms (Figure 4.57). Curiously, this illustration shows a caption that says "*Andryala pinnatifida Hort. Kew*" and, indeed, it resembles very much the type material of *A. pinnatifida* Aiton. Accordingly, the observation of type material of the Schultz Bipontinus collection deposited at the P herbarium showed that these three forms are morphologically very similar to the type specimens of *A. pinnatifida* Aiton. In view of the above findings, these forms should be included in *Andryala pinnatifida* subsp. *pinnatifida.*

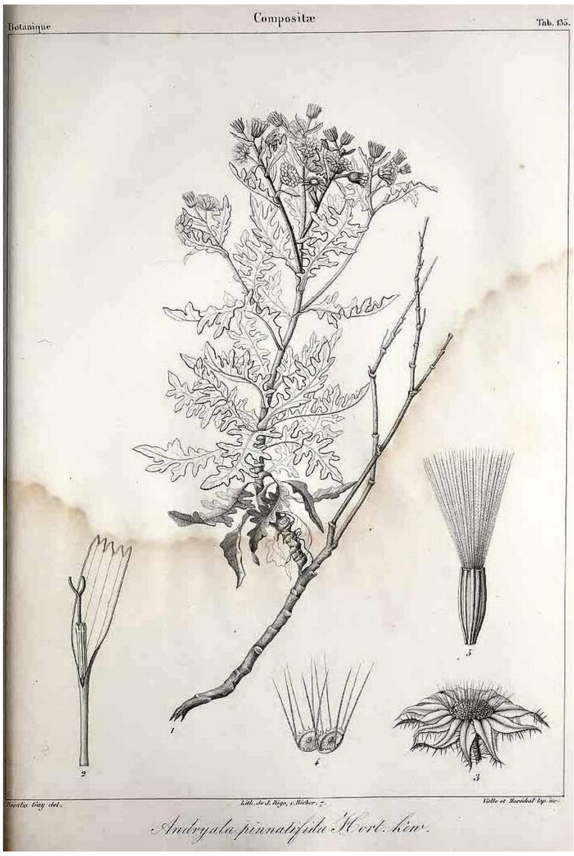


Figure 4.57 Reproduction of the icon representing *Andryala pinnatifida* f. *sprengeliana* Sch. Bip. in Webb & Berthel. Hist. Nat. Iles Canaries (1849)

Kunkel (1972) presented a new combination *A. pinnatifida* subsp. *preauxiana* (Sch. Bip.) Kunkel, citing *A. pinnatifida* f. *preauxiana* Sch. Bip. as the basionym. However, instead of selecting the lectotype among material from the Schultz Bipontinus herbarium, Kunkel (1972) designated a specimen from his own herbarium now deposited at G herbarium, G00236905, as lectotype. It is curious to note that morphologically this specimen resembles much more *A. pinnatifida* f. *sprengeliana* Sch. Bip. and *A. pinnatifida* f. *fuerteventurensis* Sch. Bip. than *A. pinnatifida*

f. *preauxiana* Sch. Bip. and, therefore, the inclusion of *A. pinnatifida* subsp. *preauxiana* (Sch. Bip.) G. Kunkel in *Andryala pinnatifida* subsp. *pinnatifida* seems quite reasonable. Later Kunkel (1980) described two varieties: *A. pinnatifida* subsp. *preauxiana* var. *preauxiana* (Sch. Bip.) G. Kunkel and *A. pinnatifida* subsp. *preauxiana* var. *sprengeliana* (Sch. Bip.) G. Kunkel, citing *A. pinnatifida* f. *sprengeliana* Sch. Bip. as the basionym of the latter. Again Kunkel (1980) did not select any type specimen from the Schultz Bipontinus collection, but he assigned *A. pinnatifida* subsp. *preauxiana* var. *sprengeliana* (Sch. Bip.) G. Kunkel, to Monte Doramas (Gran Canaria), the same locality cited for *A. pinnatifida* f. *sprengeliana* Sch. Bip. by Schultz Bipontinus (1849). Hence, also these putative varieties should be included in *A. pinnatifida* Aiton subsp. *pinnatifida.*

4.17.7.1.3 Ecology and conservation status

Andryala pinnatifida subsp*. pinnatifida* can be found in somewhat diverse habitats: clayish xerophytic slopes or humid and shady valleys and forest edges (Schultz Bipontinus 1849). According to available herbarium data, this *taxon* grows at altitudes between 550 – 1600 m, in thermophilous forests as well as laurisilva and pine forests, on cliffs and rocky slopes along roadsides. It seems to be locally common in some Canary Islands and so it should be listed as being of Least Concern (LC) according to *IUCN Red List Categories and Criteria, version 3.1* (IUCN 2001). In fact, it was placed in the category of Lower Risk (LR), according to the *1994 Red List Categories and Criteria, version 2.3* (Jardín Botánico Viera y Clavijo 2013).

4.17.7.1.4 Geographic distribution

Andryala pinnatifida subsp*. pinnatifida* is found mainly in Gran Canaria and Tenerife (Christ 1888; Kunkel 1980). In Fuerteventura it was recorded only for “Risco de Valdebrón” (Schultz Bipontinus 1849), probably meaning Vallebrón in the northeast of the island. However, its presence on this island needs to be confirmed. In Tenerife this *taxon* occurs in northern and northeastern localities (Icod, Pedro Álvarez, Orotava, San Diego and Santa Úrsula) and to a lesser extent in northwestern and eastern localities (El Tanque, Teno Alto, Ladera de Güimar). In Gran Canaria it grows in northern and central localties (Moya, Valsequillo, Bentaiga, Bco. de La Virgen, San Felipe, San Mateo, Tejeda) as well as northwestern localities (El Sao, Degollada de Tirma). It also occurs in La Gomera although in very few localities such as Monte Hermigua and Benchijiqua (Figure 4.58).

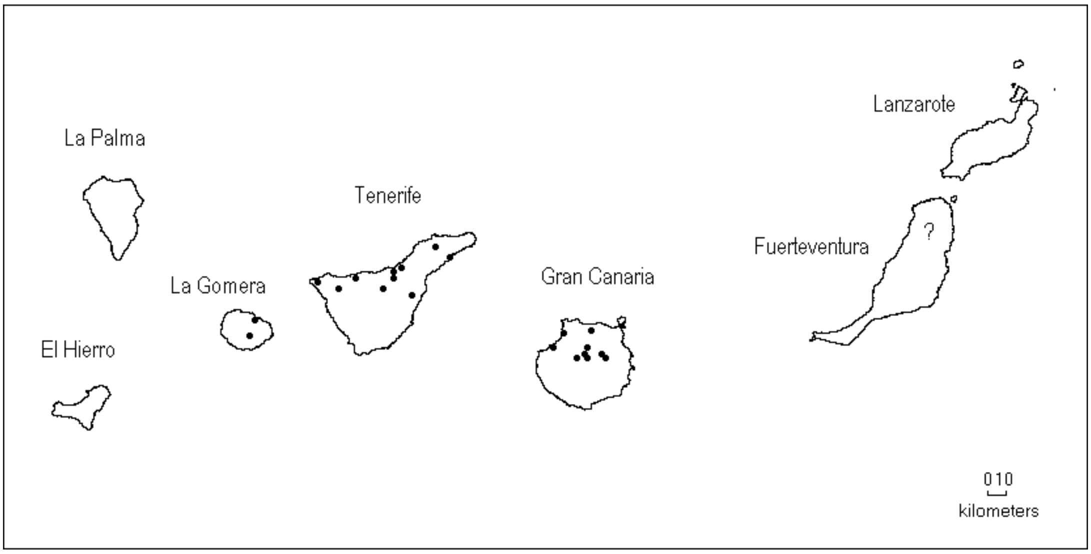


Figure 4.58 Distribution area of *Andryala pinnatifida* subsp. *pinnatifida,* according to studied material.

4.17.7.1.5 List of studied material

Spain: [Canary Islands]: Tenerife. Teno Alto, Degollada debajo Baracán al Norte, 850 m.s.m., 09-II-1995, Juan Ramón Acebes Ginovés, s/ nº, TFC 41141. Tenerife. El Tanque, 550 m.s.m., 27-V-1994, Enrique Montero Díaz, Marcelino del Arco Aguilar, Juan Ramón Acebes Ginovés, s/ nº, TFC 40493. Gran Canaria. Bco. del Agua, Valsequillo, 11-IV-1987, Carlos Suárez Rodríguez, s/ nº, TFC 31628. Lomo El Negro, Moya, 05-V-1986, Carlos Suárez Rodríguez, s/ nº, TFC 31589. Gran Canaria. Carretera de Tamadaba, Degollada de Tirma, 17-VI-1990, C. Suárez & G. Rodríguez, s/ nº, TFC 31801. Tenerife. Ladera de Güimar, Trajecto por el canal de los 1050-1000 msm. Fuga de los 4 reales. Cabeceras del Bco de Badajoz, 16-IV-1981, Pedro Luis Pérez de Paz. Wolfredo Wildpret., Marcelino del Arco Aguilar. s/ nº, TFC 32118. Tenerife. La Ladera (Carretera) Agache, 23-IV-1984, Octávio Rodríguez Delgado, s/ nº, TFC 27666. Gran Canaria. Ladera Izq. B. de los Laureles. Moya, 13-IV-1976, B. Méndez; J.R. Acebes, M. del Arco, s/ nº, TFC 6125. Gran Canaria. Bco. del Agua, Valsequillo, 11-IV-1987, Carlos Suárez Rodríguez, s/ nº, TFC 31632. Gran Canaria. Bentaiga, Cunetas (valas das bermas da estrada), 620 m, Rivas Goday, MA 504112. , Tenerife, Ladera de Guimar, 23-I-1993, Ricardo Mesa Coelho, s/nº, TFMC 4964. La Gomera, Arisel, Benchijiqua, 07-I-1995, Ricardo Mesa Coelho, s/nº, TFMC 4294. Tenerife, Bº Cueva del Siento, Icod, 600 m.s.m., 24-III-1984, S. Socorro, s/ nº, TFMC 1626. Gran Canaria, Bco. Osaro, Moya, P.L. Pérez e C. Suárez, s/nº, TFMC 894. Gran Canaria, El Sao, Agaete, 20-IV-1990, R. Mesa Coelho, s/ nº, TFMC 2784. Tenerife, Pedro Álvarez,12-IV-2006, L.M. Ferrero & E. Carrilo. La Gomera, Monte Hermigua, MA 139338. Gran Canaria, San Martín, 18-IV-1935, J. Cuatrecasas, MA 492687. Tenerife, reg. inferiore prope Orotava, MA 160714. Tenerife, San Diego, C. Sobrado, MA 139339. Tenerife, Santa Ursula, 3 km al WSW de la carretera dorsal sobre la carretera de tierra a Santa Ursula y zona recreativa de el Ricón. Hiebas perennes de 20-50 cm de alto, corollas amarillas. Bosque de pino. Ocasional 1600 m 282418.2162610.9, José Panero y Javier Fco. Ortega, 6937, MA 599506. Gran Canaria, Barranco de La Virgen, in rupestribus, H. de la Perraudiére, MA 160712. Gran Canaria, San Mateo, entre San Mateo e Teror, alt. 700 m, pentes finemente rocailleuses dominant la route, 29-IV-1982, B. Retz, 82933, MA 388368. Tenerife, Veremundo Cabrera y Agustín Cabrera, MA 157875. Gran Canaria, Tejeda, Degollada Becerra junto al Centro de Interpretación 1542 m de altitud, 06-IV-2009, Z. Ferreira, ZF186, UMad, Gran Canaria, Valleseco, 06-IV-2009, Z. Ferreira, ZF188, UMad.

4.17.7.2 *Andryala pinnatifida* subsp*. preauxiana* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq. comb. nov.

= *Andryala pinnatifida* Aiton f. *preauxiana* Sch. Bip. in Webb & Berthel. Hist. Nat. Iles Canaries (Phytogr.) 2: 414. 1849
Ind. loc.: "α Capitula corymbosa. In rupibus Teneriffæ cum forma Massoniana. β Racemoso-corymbosa parva longe pedicellata, folia angustiora, caulis gracilior. Canaria Despréaux! [*Andr. coronopifolia* Link. – An *A. pinnatifidae* var. ex Webb in Litt.])"
Typus: [Spain, Canary Islands] – Lectotype (designated here): P02462103! (specimen on the right); syntypes: P02462109! (specimen on the left), P02462103! (specimen on the left).

= *Andryala pinnatifida* Aiton f. *massoniana* Sch.Bip. in Webb & Berthel. Hist. Nat. Iles Canaries (Phytogr.) 2: 414. 1849
Ind. loc.: "In rupestribus Teneriffæ vulgaris: Webb!"
Typus: [Spain, Canary Islands] – Lectotype (designated here): P02462109! (specimen on the right)

= *Andryala pinnatifida* Aiton f. *palmensis* Sch. Bip. in Webb & Berthel. Hist. Nat. Iles Canaries (Phytogr.) 2: 416. 1849
Ind. loc.: "Palma, la Caldera, 2 Aug. 1845: Bourgeau n. 4 (*A. coronopifolia* C. H. Schultz Bip. olim), et unicum eodem loco te die a cl. Bourgeau lectum."
Typus: [Spain, Canary Islands] "Insul. Palma - la Caldera, 02 Aug. 1845", *Bourgeau 4* – Lectotype (designated here): P02462113! (specimen on the right); isolectotypes: P02462113 (specimen on the left), FI-W109930 (specimen on the left), FI-W109941.

= *Andryala pinnatifida* Aiton f. *multidentata* Sch. Bip. in Webb & Berthel. Hist. Nat. Iles Canaries (Phytogr.) 2: 416. 1849
Ind. loc.: "Teneriffa, ad pedem cataractæ in Barranco Tomodoya Arico, 29 Junio 1846: Bourgeau!"
Typus: [Spain, Canary Islands] "Barranco de Tomadoya, Arico, Tenerife, 29 June 1846", *Bourgeau s.n.* – Lectotype (designated here): FI000182.; isolectotype: P02462170!

= *Andryala pinnatifida* Aiton f. *cheiranthoides* Sch.Bip. in Webb & Berthel. Hist. Nat. Iles Canaries (Phytogr.) 2: 417. 1849
Ind. loc.: "Teneriffa, Barranco de Anavigo, Arafa, 17 Maio 1845: Bourgeau!"
Typus: [Spain, Canary Islands] "Tenerife: Bco. de Anavigo, Arafa, 17 May 1845", *Bourgeau s.n.* – Lectotype, (designated here): FI-W109930 (specimen one the right); isolectotype: P02462164!

4.17.7.2.1 Typification

Although there is no indication of the origin of the specimen P02462103 (on the right), it is here designated as lectotype of *Andryala pinnatifida* Aiton f. *preauxiana* Sch. Bip. since it corresponds to material from the P herbarium ex herb. Schultz Bipontinus. Indeed, it is labelled by Schultz Bipontinus himself as "*A. pinnatifida DC. A. fol. pinnatifida a. pinnis integris 2. invol. canum = f. preauxiana*". In spite of the specimen P02462109 bearing exactly the same information, it is not so well conserved and, consequently, is here considered a syntype. The specimen

P02462103 (on the left), collected by Despréaux in “insula Canaria”, is under the name *Andryala coronopifolia* Link, although the label also reads: “*an A. pinnatifidae var.*” Thus, it is likewise considered as a syntype.

As stated before, Schultz Bipontinus (1849) described *A. pinnatifida* f. *massoniana* indicating the Canarian *A. pinnatifida* described in Aiton’s *Hortus Kewensis* as a synonym. The name of this form alludes to Francis Masson, but it does not resemble the specimen collected by this botanist and described by Aiton in 1789 (leaves not crowded, pinnatifid and with entire lobes, contrary to Masson´s specimen which exhibits crowded and pinnatifid leaves with divided lobes). Schultz (1849) described *A. pinnatifida* f. *massoniana* stressing that the lobes are entire and, thus, it seems that the original description was based on material from Schultz and not from Masson. Indeed, the specimen P02462109 (on the right) here designated as lectotype is labelled “*A. pinnatifida DC. A. fol. pinnatifida a. pinnis integris – genuina 1. involu. glanduloso = forma massoniana*”, handwritten by Schultz himself. Although no indication of the collection locality and date is given, it corresponds to original material since it is from the Schultz herbarium (“*Herb. Car. Henr. Schultz, Bipont.*”).

The specimens here considered as type material of *A. pinnatifida* f. *palmensis* were collected by Bourgeau in the locality and date mentioned in the protologue (“Caldera de La Palma, 2 Aout. 1845”). The specimen P02462113 (on the right) is under the name *Andryala pinnatifida* f. *palmensis*, handwritten by Schultz Bipontinus himself, and was collected by Bourgeau according to the label “*E. Bourgeau, Plantæ Canariensis, nº. 4*”. Since it clearly matches the information in the protologue and is the best preserved specimen, it is here designated as lectotype. The specimen P02462113 (on the left), also identified as *A. pinnatifida* f. *palmensis*, was collected by Bourgeau, but no collector number was indicated. However, in an earlier label we can read “*Andryala coronopifolia* Link”, name that also figures in the protologue as unpublished. Likewise, the specimen FI-W109930 (on the left), under the name *Andryala pinnatifida* f. *palmensis*, bears no collector number. This specimen was considered in 2005 by A. Santos as type material, and is indeed considered as an isolectotype herein. In spite of the specimen FI-W1109941 also bearing the name “*A. coronopifolia* C. H. Schultz Bip.”, the collection number does not coincide with the one in the protologue (“*E. Bourgeau, Plantæ Canariensis, nº. 1163*”) and, therefore, is here considered as an isolectotype.

On both specimens here considered as original material of *A. pinnatifida* Aiton f. *multidentata* Sch. Bip. the collection data matches exactly the one in the protologue. The specimen FI000182 is here designated as lectotype as it fits the original description quite well. Actually, on the herbarium sheet FI000182 there is an annotation by A. Santos from 2005 considering it as a type specimen.

Two herbarium specimens under *Andryala pinnatifida* Aiton f. *cheiranthoides* Sch. Bip., handwritten by Schultz Bipontinus, with collection information (locality, date and collector) that matches the one in the protologue were found. However, the best developed specimen is here chosen as lectotype. Indeed, this specimen bears an annotation by A. Santos from 2005 considering it type material.

4.17.7.2.2 **Description**

Perennial herb, single or multi-stemmed. STEMS 36–63 cm, woody at the base, usually branched from the base or in the upper third (Figure 4.59A), pubescent to densely tomentose, especially below, with stellate hairs and sometimes with glandular hairs in the upper part (Figure 4.60A). LEAVES tomentose with stellate hairs only, the abaxial face with denser stellate hairs than the adaxial face (Figure 4.60B); lower leaves 50–85 x 18–29 mm, often marcescent at anthesis, attenuate into a winged petiole 7–23 mm, oblanceolate, apex ± acute, and margin pinnatifid with entire lobes; cauline leaves 24–91 x (8-)10.5–37 mm, sessile or semiamplexicaul, oblong to lanceolate, base attenuate, rounded or auriculate, apex acute to obtuse, and margin pinnatifid to pinnatipartite with entire lobes; upper leaves 12–42 x 2–13 mm, semiamplexicaul or amplexicaul, elliptic to lanceolate or ovate-oblong to ovate-lanceolate, base usually rounded, apex acute to acuminate, and margin entire sometimes pinnatifid.

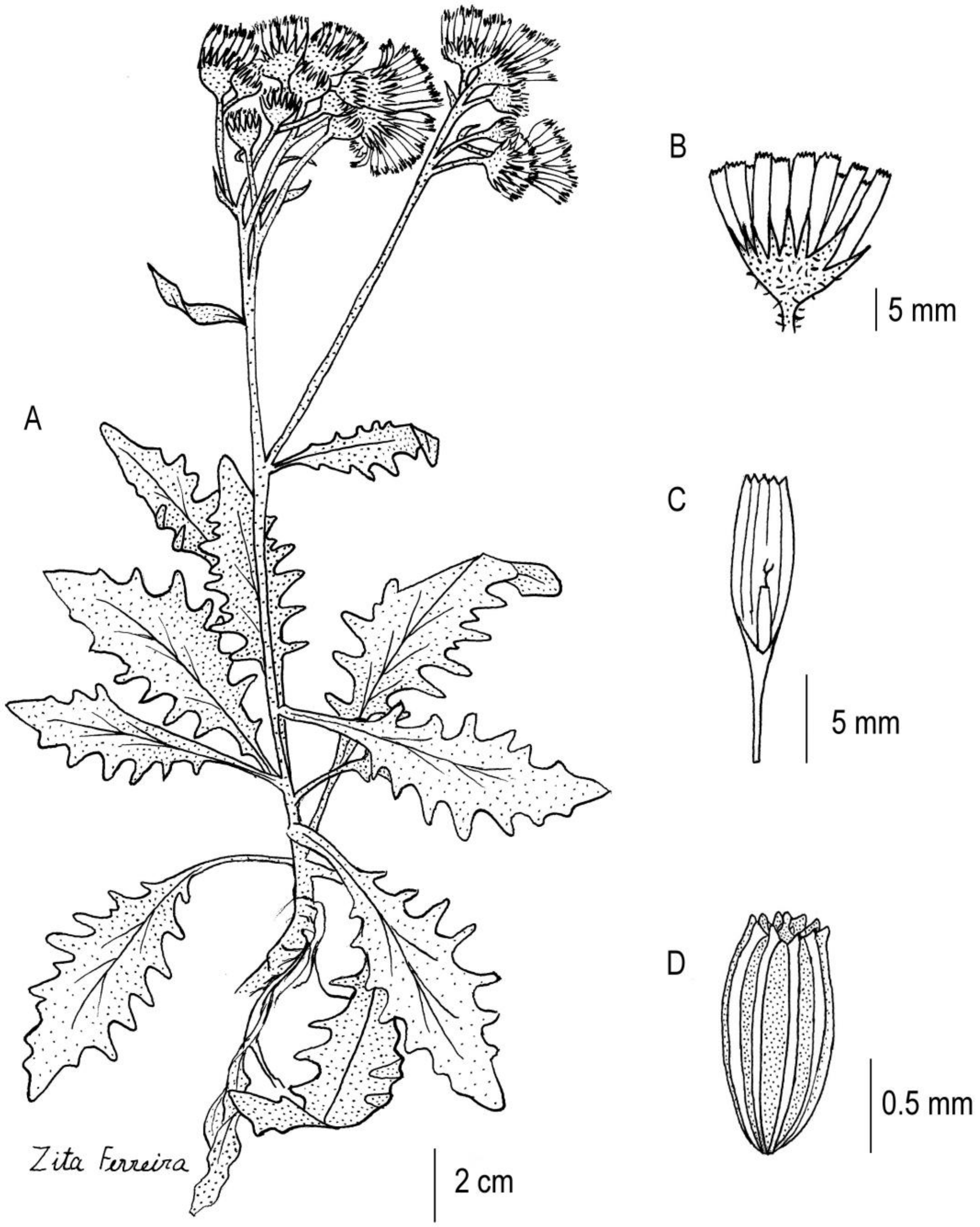


Figure 4.59 *Andryala pinnatifida* subsp. *preauxiana* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq. A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

INFLORESCENCE corymbose to racemose with (3-)5–9 capitula. CAPITULA 7–22 mm in diameter (Figure 4.59B); peduncles 5–18 mm, with dense stellate hairs frequently with some glandular hairs 0.2–1.3 mm (Figure 4.60C); involucre 4–10 x 4–13 mm, campanulate at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 4.3–6.3 x 0.8–1.5 mm, linear-lanceolate sometimes lanceolate, apex acuminate, flat not enfolding a floret, the outer face tomentose with stellate hairs sometimes with a few glandular hairs 0.4–1.4 mm; internal involucral bracts 4.3–6 x 1.2–2 mm, with broad scariose margins; receptacle convex, villous with usually long setose hairs (1.3-)2.7–5 mm (2 to 4 times longer than the cypselae). FLORETS ligulate, bright to golden yellow, the external with a tube of 2.8–5 mm and ligule of 5-11 x 1–3 mm (Figure 4.59C) sometimes with a reddish stripe on the outer face. CYPSELAE 1.2–1.5 x 0.4–0.5 mm (Figure 4.59D), oblong, black with reddish brown ribs, apex with a ring of small teeth largely exceeded by the conspicuous prolongation of the ribs (Figure 4.60D); pappus of white or dirty-white bristles 4–5.4 mm, ± denticulate at the base.

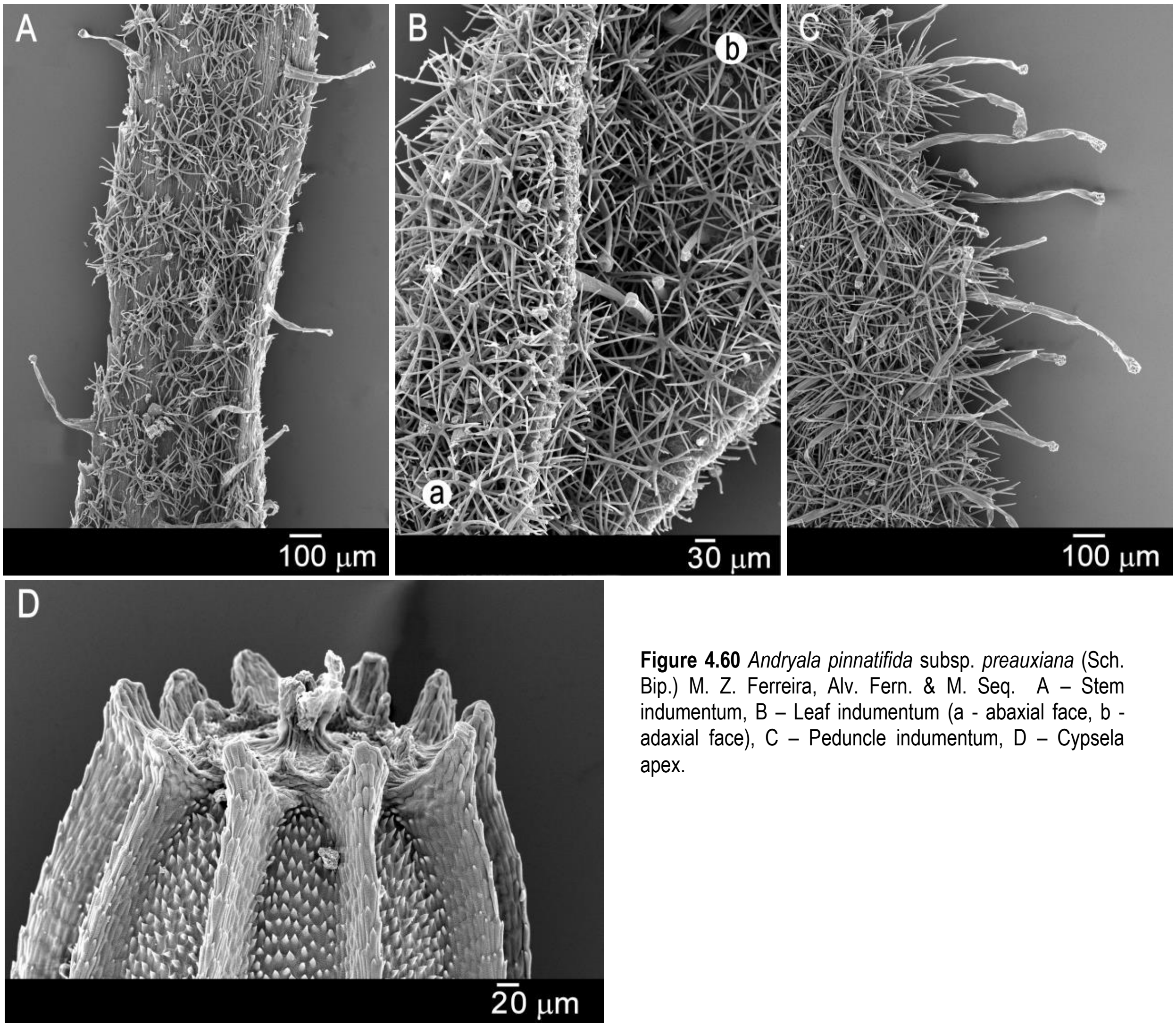


Figure 4.60 *Andryala pinnatifida* subsp. *preauxiana* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq. A – Stem indumentum, B – Leaf indumentum (a - abaxial face, b - adaxial face), C – Peduncle indumentum, D – Cypsela apex.

4.17.7.2.3 Comments on taxonomy and nomenclature

This *taxon* is traditionally known as *Andryala pinnatifida* subsp. *pinnatifida.* However, the name has been misapplied, probably because Schultz Bipontinus (1849) was not acquainted with the specimen on which Aiton (1789) based the original description, as mentioned previously. Schultz Bipontinus (op cit.) included *A. pinnatifida* f. *massoniana* Sch. Bip. and *A. pinnatifida* f. *preauxiana* Sch. Bip. in "*Forma genuina*", stating that the leaves of both forms are narrow-lanceolate, ± deeply pinnatifid, with entire linear-oblong lobes, being the only difference the presence/absence of glandular hairs on the involucre. When Kunkel (1972) considered *A. pinnatifida* subsp. *preauxiana* (Sch. Bip.) G. Kunkel as a new combination and status he also distinguished this subspecies from the typical one by its larger size, excessive ramification, smaller capitula, and the colour of its petals: the outer creamy white and the inner yellow. The specimen G00236905 designated by Kunkel (1972) as lectotype of *A. pinnatifida* subsp. *preauxiana* (Sch. Bip.) G. Kunkel resembles *A. pinnatifida* f. *preauxiana* Sch. Bip. by the narrow-lanceolate leaves, but the lobes are not quite entire as in the latter form. This feature draws it closer to *A. pinnatifida* f. *sprengeliana* Sch. Bip. whose leaves have dentate-subpinnatifid lobes, in spite of being broadly lanceolate. Furthermore, some collection localities of *A. pinnatifida* subsp. *preauxiana* (Sch. Bip.) G. Kunkel mentioned by Kunkel (op. cit.) coincide with those indicated for *A. pinnatifida* f. *sprengeliana* Sch. Bip. Hence, *A. pinnatifida* f. *preauxiana* Sch. Bip. and *A. pinnatifida* f. *massoniana* Sch. Bip. are here included in a subspecies and a new combination is suggested: *A. pinnatifida* subsp. *preauxiana* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq. [which does not correspond to *A. pinnatifida* subsp. *preauxiana* (Sch. Bip.) G. Kunkel]. Several forms described by Schultz Bipontinus (1849) are here included in *A. pinnatifida* subsp. *preauxiana* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq., namely *Andryala pinnatifida* Aiton f. *palmensis* Sch. Bip., *A. pinnatifida* f. *multidentata* Sch.Bip., and *Andryala pinnatifida* Aiton f. *cheiranthoides* Sch. Bip. All three forms exhibit leaves that are lanceolate, ± pinnatifid to sinuate-dentate with entire lobes.

4.17.7.2.4 **Ecology and conservation status**

This *taxon* occurs in rocky substrates, mostly in valleys (Schultz Bipontinus 1849). According to available herbarium data, it grows at altitudes between 700 m and 1500 m. It can be found in disturbed areas of Laurisilva forest where it seems to be occasional, although being somewhat frequent on rocky slopes along the roads. Although it is common in Fayal-Brezal woodlands, its ecology is not well known. Concerning the conservation status, it was placed in the category of Lower Risk (LR), according to the *1994 Red List Categories and Criteria, version 2.3* (Jardín Botánico Viera y Clavijo 2013). Indeed, given that it is frequent on some Canary Islands, it may be listed as being of Least Concern (LC) according to the *2001 IUCN Red List Categories and Criteria, version 3.1* (IUCN 2001).

4.17.7.2.5 **Geographic distribution**

This subspecies is frequent in Tenerife, but can also be found in Gran Canaria and in La Palma (Schultz Bipontinus 1849). According to available herbarium data, it is present in northern and northeastern localities of Tenerife (Aguamansa, Monte de los Realejos, Mesa Mota) as well as northwestern and eastern ones (Los Silos, San Tiago del Teide, Güimar). In Gran Canaria this *taxon* occurs mainly in north-central and northeastern localities (Valleseco, San Fernando, Moya, Las Palmas). While in La Gomera it can be found in northeastern localities (e.g. Hermigua), in La Palma it occurs in Volcan de S. Juan (Figure 4.61).

4.17.7.2.6 **List of studied material**

Spain:
[Canary Islands]: Tenerife. Charcos de Erjos UIM (28RCS2233), Los Silos, 27-V-1994, Vicente Lucía Sauquillo, C. Acosta, s/ nº, TFC 40786. Tenerife. Monte de los Realejos, 22-X-1972, J. R. Acebes, s/ nº, TFC 6764. Gran Canaria. Capellania, Utiaca, 900 m, 03-V-1986,Carlos Suárez Rodríguez, s/ nº, TFC 31591. La Gomera. Hermigua. Parque Nacional de Garajonay, cruce de las carreteras a Valle del Rey y San Sebastián por El Carmen y Roque Agando,Hierbas perenes de 30 a 60 cm de alto, corolas amarillo intenso. Laurisilva perturbado. Ocasional., José L. Panero, Javier Fco. Ortega y Arnold Santos, 7076, MA 595577. La Palma, Volcan de S. Juan, 24-VIII-1979, W. Wildpret, P. L. Pérez, M. del Arco, e I. la Se[?], s/nº, TFMC 764. Tenerife, Bco. Badajoz, Guimar, 800 m.s.m, 26-IV-1990, R. Mesa Coelho, s/nº, TFMC 3376. Tenerife, San Tiago del Teide, 06-IV-1976, P. Pérez, s/nº, TFMC 247. Tenerife, alto del puerto entre Santiago del Teide y Masca, 28R321163/3113745,11-IV-2006, L.M. Ferrero & E. Carrillo, MS-4. Tenerife, Agua Manza (Aguamansa),1200 m, common in Faya/Brezal woodland,17-X-1968, D. Bramwell, 241, SEV 13690. Tenerife, Mesa Mota, La Laguna. 18-V-1979, M del Arco, s/nº, TFMC 565. Gran Canaria, Bc. de San Felipe, ad rupes, J. C. Pitard, MA 139342. Unkown

locality, Ces. Sobrado, MA 502213. Las Palmas, C. Sobrado, MA 139340. Gran Canaria, estrada GC 21,alt. 1462 m, a crescer na rocha junto à estrada, abundante na descida para Moya, Z. Ferreira, ZF192, UMad. Gran Canaria, a caminho de Moya - Fontanales, alt. 1086 m, 08-IV-2009, Z. Ferreira, ZF193, UMad. Gran Canaria, San Fernando - Moya, alt. 695 m, abundante, 08-IV-2009, Z. Ferreira, ZF194, UMad. Gran Canaria, a caminho de Valleseco, alt. 1427 m, 06-IV-2009, Z. Ferreira, ZF187, UMad. Tenerife, Bco. Anavigo, Arafo, P 02462164.

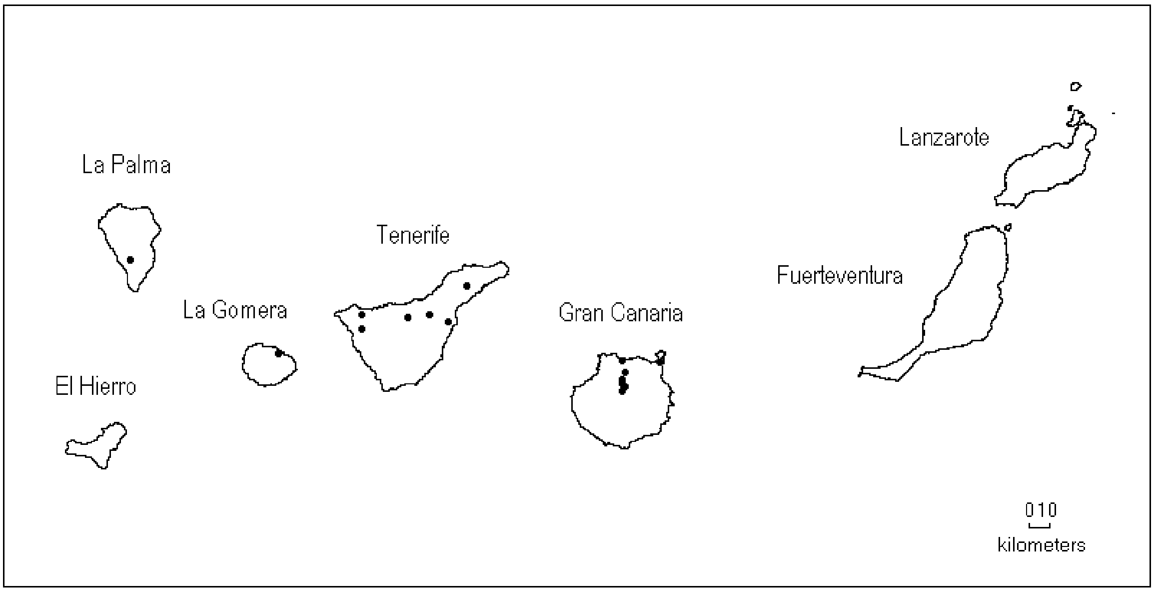


Figure 4.61 Distribution area of *Andryala pinnatifida* subsp. *preauxiana* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq., according to studied material.

4.17.7.3 *Andryala pinnatifida* Aiton subsp. *teydensis* (Sch.Bip.) S.Rivas-Martínez, Wildpret, del Arco, O. Rodr., P. Pérez, Garciá-Gallo, Acebes, T. E. Díaz & Fern. Gonz. in Itinera Geobot. 7: 350. 1993

≡ *Andryala pinnatifida* f. *teydensis* Sch. Bip. in Webb & Berthel. Hist. Nat. Iles Canaries (Phytogr.) 2: 416. 1849, *basion*.

Ind. loc.: "Teneriffa, prope pagum Chasna in rupibus aridis ad austrum montis alti (el Pico de Teyde) ad alt. 4800 ped. circiter super Oceanum. […] Eandem formam Teneriffa ad las Cañadas del Teyde die 9 Sept. 1845 legit Bourgeau! nº 3"

Typus: [Spain, Canary Islands] "Teneriffa - las Cañadas del Teyde, 09 Sept. 1845", *Bourgeau 3* – Lectotype (designated by Ferreira *et al.* 2015b, see Appendix 4): P02462114!; isolectotype: FI-W109939 (middle specimen); syntypes: P02462171!, FI-W109939 (specimen on the right).

4.17.7.3.1 Typification

The specimen P02462114 was designated as lectotype of *A. pinnatifida* Aiton subsp. *teydensis* based on the collector and number, date and locality which match exactly to the information in the protologue (Ferreira *et al.* 2015b, see Appendix 4). The label of herbarium sheet FI-W109939 referring to the middle specimen shows exactly the same information, but is without collector (although mostly likely the collector was again E. Bourgeau). Moreover, even though this specimen is better preserved, it is partially covered by the specimen on the right and, therefore it was designated as an isolectotype rather than lectotype (Ferreira *et al.* 2015b, see Appendix 4). In the protologue another collection locality was mentioned: "*Teneriffa, prope pagum Chasna in rupibus aridis ad austrum montis alti (el Pico de Teyde) ad alt. 4800 ped. circiter super Oceanum.*" Thus, the specimen P02462171, exhibiting precisely this information on the label, was considered as a syntype. As the specimen FI-W109939 (on the right) was also collected by Bourgeau at Chasna, but one year after the lectotype, it was also accepted as a syntype (Ferreira *et al.* 2015b, see Appendix 4).

4.17.7.3.2 Description

Perennial herb, single or multi-stemmed. STEMS 73–128 cm, woody at the base, branched from the base or in the upper half (Figure 4.62A), tomentose with stellate hairs very rarely with glandular hairs (Figure 4.63A).

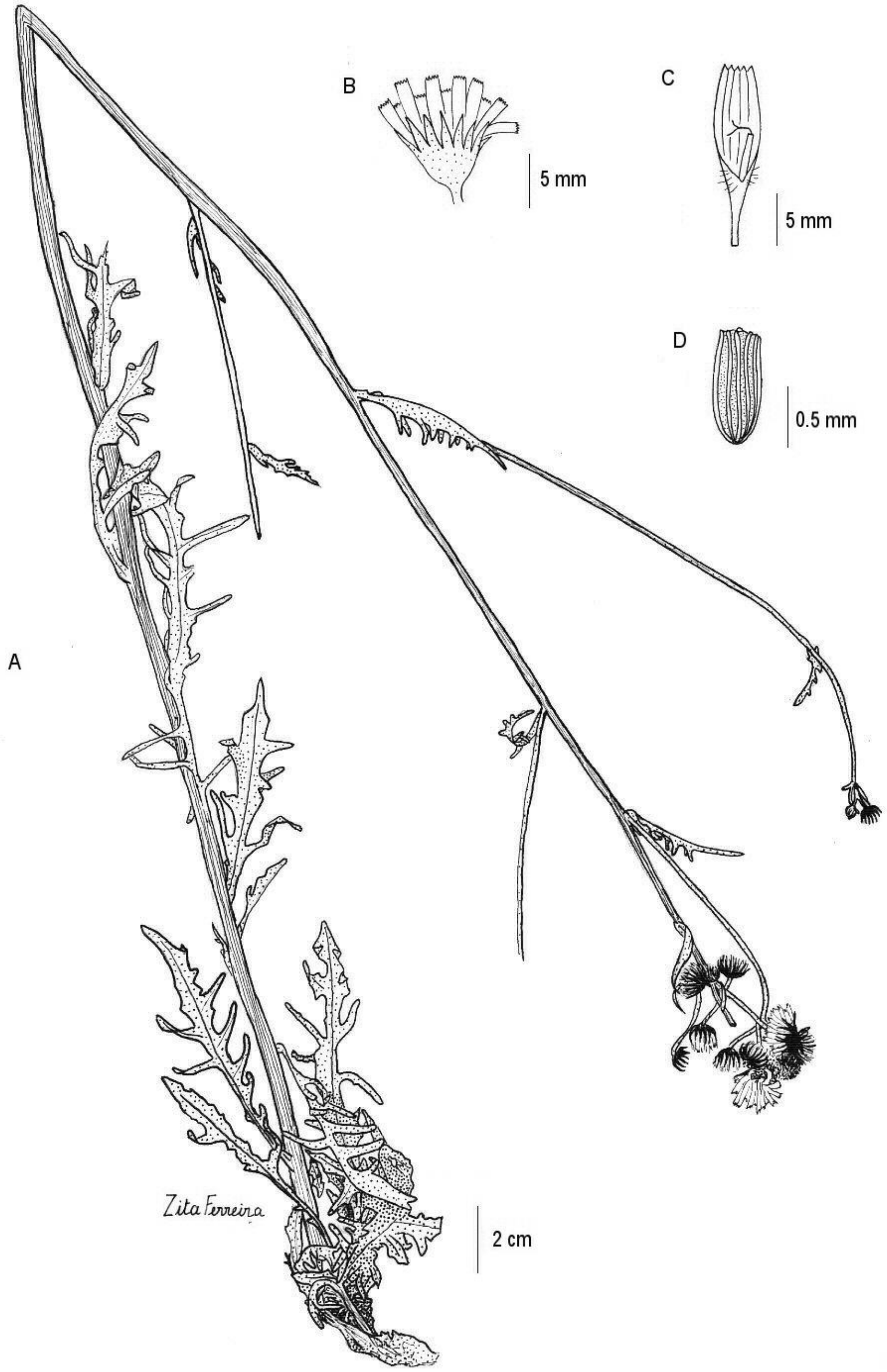


Figure 4.62 *Andryala pinnatifida* Aiton subsp. *teydensis* (Sch. Bip.) S. Rivas-Martínez, Wildpret, del Arco, O. Rodr., P. Pérez, Garciá-Gallo, Acebes, T. E. Díaz & Fern. Gonz. A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

LEAVES glaucous, tomentose with stellate hairs rarely with scarce glandular hairs, the abaxial face slightly more tomentose than the adaxial face (Figure 4.63B); lower leaves 135–140 x 25–36 mm, attenuate into a winged petiole 33–50 mm, lanceolate to linear-lanceolate, apex acute, and margin pinnatipartite to pinnatisect; cauline leaves 70–87 x 21–30 mm, sessile, oblong to lanceolate, base attenuate, apex acute, and margin pinnatipartite to pinnatisect with linear segments; upper leaves 14–25 x 3–5 mm, sessile or semiamplexicaul, narrowly ovate-lanceolate or lanceolate to linear-lanceolate, base rounded, apex acute to acuminate, and margin entire to pinnatifid. INFLORESCENCE paniculate-corymbose or racemose with 4–10 capitula. CAPITULA 11–18 mm in diameter (Figure 4.62B); peduncles 5–11 mm, with dense stellate hairs only (Figure 4.63C); involucre 7–10 x 8–14 mm, campanulate at anthesis, with involucral bracts in 2 rows; external involucral bracts 4.4–5 x 1.1–1.2 mm, lanceolate, apex acute, flat not enfolding a floret, the outer face pubescent-tomentose with stellate hairs only; internal involucral bracts 3.6–5 x 1.5–2 mm, with scariose margins; receptacle convex, villous with long setose hairs 3–5 mm (3 to 4 times longer than the cypselae). FLORETS ligulate, bright yellow, the external with a tube of 3–4.6 mm and ligule of 4.7–7.5 x 1.3–3 mm (Figure 4.62C) sometimes with a reddish stripe on the outer face. CYPSELAE 1.2–1.5 x 0.4–0.5 mm (Figure 4.62D), oblong to obconical, dark brown with reddish brown ribs, apex with a ring of small teeth largely exceeded by the conspicous prolongation of the ribs (Figure 4.63D); pappus of white bristles 4.7–5 mm, ± denticulate at the base.

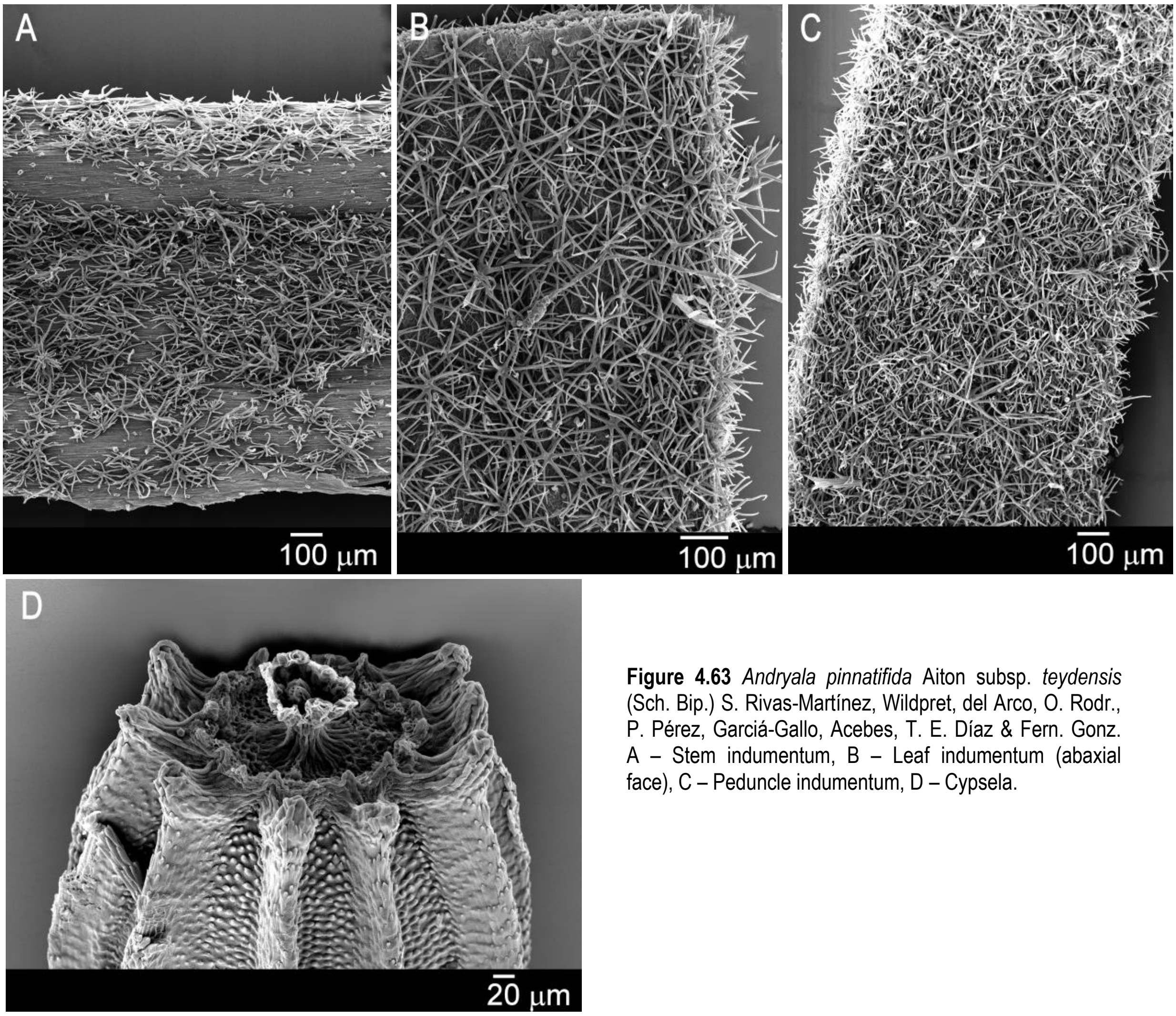


Figure 4.63 *Andryala pinnatifida* Aiton subsp. *teydensis* (Sch. Bip.) S. Rivas-Martínez, Wildpret, del Arco, O. Rodr., P. Pérez, Garciá-Gallo, Acebes, T. E. Díaz & Fern. Gonz. A – Stem indumentum, B – Leaf indumentum (abaxial face), C – Peduncle indumentum, D – Cypsela.

4.17.7.3.3 Comments on taxonomy and nomenclature

First described as *Andryala pinnatifida* Aiton f. *teydensis* Sch. Bip. by Schultz Bipontinus (1849: 416), the original description clealy shows that it corresponds to a morphologically quite distinct *taxon* when compared to the other *A. pinnatifida* Aiton *taxa* ("*pili s.d. glanduliferi desiderantur et plantæ canæ; caulis elongatus sesqui-bipedalis, folia adhuc angustiora , lineari-pinnatifido-dentata, capitula racemosa, racemo tantum 5-7-cephalo*"). Accordingly, Rivas-

Martinez *et al.* (1993) transferred it to a subspecies rank as *A. pinnatifida* Aiton subsp. *teydensis* (Sch. Bip.) S. Rivas-Martínez, Wildpret, del Arco, O. Rodr., P. Pérez, Garciá-Gallo, Acebes, T. E. Díaz & Fern. Gonz.

4.17.7.3.4 Ecology and conservation status

Andryala pinnatifida Aiton subsp. *teydensis* grows on dry rocks to the south of the volcanic peak, Pico del Teide, around 1463 m (Schultz Bipontinus 1849). According to available herbarium data it can ascend up to 3100 m asl (specimen MA239110). It also occurs on dry rocky slopes, disturbed areas and less frequently on volcanic dross. This subspecies is a characteristic *taxon* of the understory vegetation of *Pinus canariensis* C.Sm. ex DC. forests, (included in the *Cisto-Pinion canariensis* alliance) and grows on strongly acid soils (Rivas-Martínez *et al.* 2002; Tenerife 2008).

Andryala pinnatifida Aiton subsp. *teydensis* has a very limited distribution and grows in distinct ecological conditions; it is restricted to only one island out of seven encompassing the Canary Archipelago and occurs mainly at higher altitudes. Although this subspecies occurs in a protected area, the Teide National Park (Rosa *et al.* 2006), there are no records on its current conservation status. However, based on available data, it does not seem to be either widespread or abundant and, therefore, does not qualify for Least Concern (LC). Further research is in need to determine whether it is likely to qualify for a threatened category in the near future and, hence, by categorised as Near Threatened (NT).

4.17.7.3.5 Geographic distribution

Andryala pinnatifida Aiton subsp. *teydensis* is an endemic from Tenerife, an island with a central position in the Canary Archipelago. It is found near Chasna, lying to the south of Teide Peak, and the volcanic caldera Las Cañadas (Schultz Bipontinus 1849). Both the Teide Peak and the surrounding Las Cañadas, constitute a striking volcanic landscape in the centre of the island. According to available herbarium data, it occurs indeed in Vilaflora (former Chasna), Arafo (NE of the peak), and Topo de la Grieta (SE of Teide Peak and one of the peaks of Las Cañadas) (Figure 4.64).

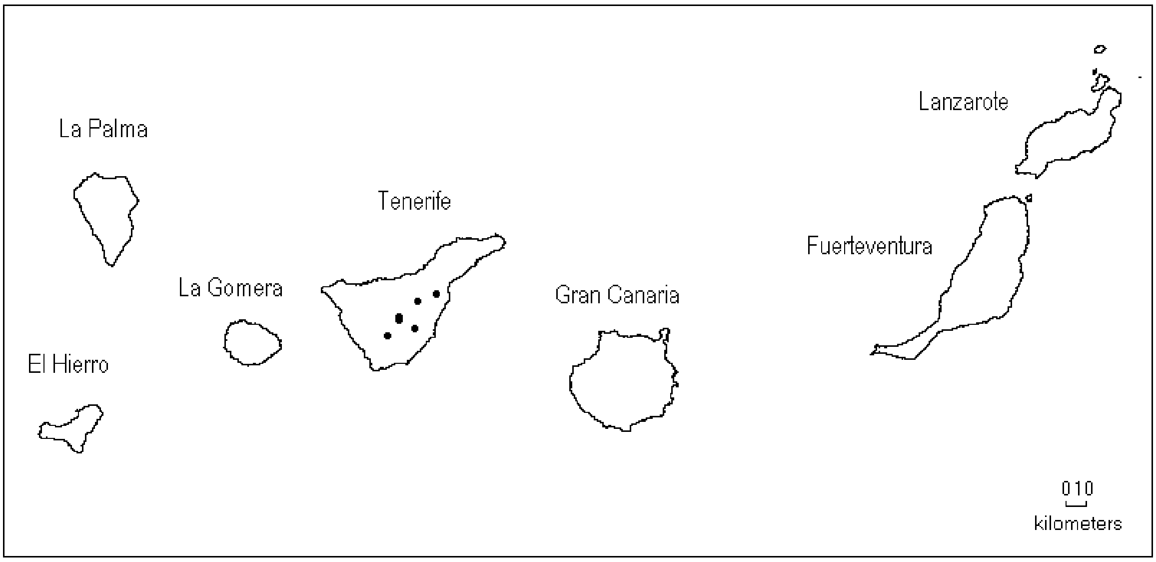


Figure 4.64 Distribution area of *Andryala pinnatifida* Aiton subsp. *teydensis* (Sch. Bip.) S. Rivas-Martínez, Wildpret, del Arco, O. Rodr., P. Pérez, Garciá-Gallo, Acebes, T. E. Díaz & Fern. Gonz., according to studied material.

4.17.7.3.6 List of studied material

Spain:

[Canary Islands]: Tenerife. Vilaflor, Pista de Lomo Blanco 1600 m, 13-V-1979, Pedro Luís Pérez de Paz, Consuelo Hernández Padrón, s/ nº, TFC 32410. Tenerife. Topo de la Grieta. Degollada Guajara, 20-VI-1985, Pedro Luis Pérez de Paz, Irene La Serna Ramos, Immaculada Medina Medina, s/ nº, TFC 24742. Tenerife. Arafo, Pista de las Arenas en el Lomo del Agua,1959 m, zonas removidas, 27-IX-2007, L. Medina e M. Sequeira, LM4248-5, MA. Tenerife. Arafo, Pista de las Arenas en el Lomo del Agua,1959 m, zonas removidas, 27-09-2007, L. Medina e M. Sequeira, LM4248-4, MA. Arafo, Pista de las Arenas en el Lomo del Agua,1959 m, zonas removidas, 27-IX-2007, L. Medina e M. Sequeira, LM 4248-3 ,MA. Arafo, Pista de las Arenas en el Lomo del Agua,1959 m, zonas removidas, 27-IX-2007, L. Medina Medina e M. Sequeira, LM4248-1, MA. Tenerife. Arafo, carretara de Izana a la Laguna, 2111 m, talud rocoso,27-IX-2007, L. Medina Medina e M. Sequeira, LM4246-1, MA. Tenerife. Arafo, carretara de Izana a la Laguna, 2111 m, talud rocoso, 27-IX-2007, L. Medina Medina e M. Sequeira, LM4246-3, MA. Tenerife. Arafo, carretara de Izana a la Laguna, 2111 m, talud rocoso, 27-IX-2007, L. Medina Medina e M. Sequeira, LM4246-4, MA. Tenerife. Arafo, carretara de Izana a la Laguna, 2111 m, talud rocoso, 27-IX-2007, L. Medina Medina e M. Sequeira, LM4246-5, MA. Tenerife. Topo de la Grieta-Parque Nacional del Teide. La Orotava, 2400 m, 18-IX-1987, P. Romero, MA 395935. Tenerife, Navaria: Las Canadas, prope Portillo, in rupibus aridis et in scoria vulcanica sat minusve pauca, 3100 m.s.m., 16-VIII-1950, MA 239110.

4.17.7.4 *Andryala pinnatifida* Aiton subsp. *cuneifolia* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq. *stat. nov. in* Novon 23(2). 2014 (See Appendix 2)

= *Andryala pinnatifida* Aiton f. *cuneifolia* Sch. Bip. in Webb & Berthel. Hist. Nat. Iles Canaries (Phytogr.) 2: 417. 1849.
Ind. loc.: “Ins. Hierro, monte de Savinosa, 18 Junii 1845: Bourgeau! n. 9”
Typus: [Spain, Canary Islands] “Insula Hierro, Monte de Savinosa, 18 June 1845”, *Bourgeau 9* – Lectotype (designated by Ferreira *et al.* 2014a): P02462115!

= *Andryala pinnatifida* Aiton f. *buchiana* Sch. Bip. in Webb & Berthel. Hist. Nat. Iles Canaries (Phytogr.) 2: 415. 1849. p.p. quoad.
Ind. loc.: “Teneriffa, as rupes atlas, de las Mercedes, 9 Junii 1846: Bourgeau! n.7”
Typus: [Spain, Canary Islands], “Teneriffa - contre les rochers élevés de las Mercedes, 9 June1846”, *Bourgeau 7* – Lectotype (designated by Ferreira *et al.* 2014a): P02462105!

= *Andryala pinnatifida* Aiton f. *gomeræa* Sch. Bip. in Webb & Berthel. Hist. Nat. Iles Canaries (Phytogr.) 2: 417. 1849
Ind. loc.: “Gomera, valle Hermoso, locis siccis, 16 Apr. 1845 Bourgeau!”
Typus: [Spain, Canary Islands] “Valle Hermoso – lieux secs La Gomera, 16 Apr. 1845”, *Bourgeau s.n.* – Lectotype (designated here): FI-W000183; isolectotype: P02462165!

= *Andryala pinnatifida* Aiton f. *bourgæana* Sch. Bip. in Webb & Berthel. Hist. Nat. Iles Canaries (Phytogr.) 2: 417. 1849
Andryala bourgeauii Sch. Bip. in Webb & Berthel. Hist. Nat. Iles Canaries (Phytogr.) 2: 417. 1849
Ind. loc.: “Gomera, Barranco Seco de Valhermoso, 16 Apr. 1845, Bourgeau!”
Typus: [Spain, Canary Islands] “Bco. Seco de Valhermoso - La Gomera, 16 Apr. 1845”, *Bourgeau s.n.* – Lectotype (designated here): FI-W109950; syntypes: P02462100!, FI-W109928 (bottom specimen).

= *Andryala pinnatifida* Aiton var. *latifolia* Bornm. in Bot. Jahrb. Syst. 33: 489. 1904, *basion*.
Andryala pinnatifida Aiton subsp*. latifolia* (Bornm.) G.Kunkel in Vieraea 8: 344. 1980
Ind. loc.: “Teneriffa: Montes Anaga, 7-900 m (n. 863). Hierro: supra Sabinosa, 6-700 m (n. 5621) et Risco Jinama (n. 2561b).”
Typus: [Spain, Canary Islands] “Teneriffa: Cumbre de Anaga, 27 June 1901”, *Bornmüller 863* – Lectotype (designated by Ferreira *et al.* 2014a): P02462137!; isolectotype: JE00013921: syntype P02462101!; isosyntype: JE00013922.

_ *Andryala pinnatifida* subsp. *webbii* Sch. Bip. ex Christ sensu G.Kunkel in Cuad. Bot. Canaria 25: 27. 1975. *nom. illeg.*

4.17.7.4.1 Typification

In order to typify *A. pinnatifida* Aiton subsp. *cuneifolia* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq., herbarium specimens under *A. pinnatifida* f. *cuneifolia* Sch. Bip were sought. The specimen P02462115 was designated as lectotype based on the fact that the collector number, collection date and locality match perfectly the collection data in the protologue.

The specimen FI-W000183 is here designated as lectotype of *Andryala pinnatifida* Aiton f. *gomeræa* Sch. Bip. since it is complete, conversely to the other specimen under this name (P02462165) which consists of a single leaf. The specimen FI-W000183 has an annotation by A. Santos from 2005 considering it as type material. Indeed, both specimens correspond to original material as the collector, collection locality and date, all coincide exactly with the information in the protologue.

The specimen FI-W109950 from the Webb collection is here designated as lectotype of *A. pinnatifida* Aiton f. *bourgæana* Sch. Bip. as it fits the original description of quite well and was originally labelled as "*Andryala bourgeæi* C. H. Schultz Bip." Indeed, in the protologue Schultz Bipontinus indicated as a synonym *A. bourgeauii* C. H. Schultz Bip., an unpublished name from the Webb Herbarium. Schultz Bipontinus (1849) mentioned plant material collected by Bourgeau in La Gomera in 16 April 1845 and, in fact, the lectotype is labelled with this information. Two other specimens with the same voucher information were found at the P and FI ex Webb herbaria and are, therefore, considered as syntypes (P02462100! and FI-W109928). In consonance, both the specimens FI-W109950 and FI-W109928 have an annotation by A. Santos from 2005 considering them type material.

In the protologue Bornmüller (1904) assigned *A. pinnatifida* var. *latifolia* Born. to Tenerife ("*Montes Anaga*") and Hierro ("*supra Sabinosa and Risco Jinama*") and mentioned type material for all three localities, indicating the collector number. The herbarium and type material of Bornmüller are hosted at the JE herbarium, although many duplicates were deposited in numerous herbaria (Stafleu & Cowan 1976). The type material of *A. pinnatifida* var. *latifolia* Born. (including duplicates) was located at the P and JE herbaria except for the specimen from Jinama (Bornmüller, n. 2561b). Robert Vogt (pers. comm.) from the B herbarium, where a Bornmüller collection is kept, believes it was destroyed in World War II. The specimen P02462137 is here designated as lectotype given that it is a complete and well preserved specimen. Besides, the collector number and collection locality match the information in the protologue.

4.17.7.4.2 **Description**

Perennial herb, single or multi-stemmed. STEMS 18–60(-74) cm, woody at the base, branched in the upper half, sometimes from the base or in the upper third (Figure 4.65A), puberulous to slightly tomentose below, densely tomentose above with stellate hairs sometimes with a few glandular hairs in the upper part (Figure 4.66A). LEAVES crowded, glaucous to deep green, puberulous to densely tomentose, especially the cauline and upper, with stellate hairs and rarely with scarce glandular hairs, the abaxial face tomentose-lanate with stellate hairs denser than the adaxial face which is sometimes puberulous (Figure 4.66B); lower leaves 42–135 x 19–56 mm, often marcescent at anthesis, attenuate into a winged petiole 14–41.5 mm, oblong or obovate, apex obtuse, and margin lobate to pinnatifid; cauline leaves 25–88 x 12–42 mm, sessile or semiamplexicaul, elliptic to oblong or obovate, base cuneate to subcuneate, apex obtuse sometimes obtuse to acute, and margin lobate to ± pinnatifid; upper leaves 14–51 x 4.5–31.6 mm, semiamplexicaul or amplexicaul, elliptic to oblong or ovate to ovate-lanceolate, base rounded, subcordate or cuneate, apex frequently acute, and margin entire sometimes lobate to pinnatifid. INFLORESCENCE corymbose or paniculate-corymbose with 4–10 capitula. CAPITULA 15–25 mm in diameter (Figure 4.65B); peduncles 8–21 mm, with dense stellate hairs and abundant hispid glandular hairs 0.5–2.8 mm (Figure 4.66C); involucre 7.6–12 x 8–13.6 mm, ± hemispherical at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 5–7.6 x 1–1.5 mm, lanceolate to linear-lanceolate, apex acuminate, flat not enfolding a floret, the outer face puberulous to tomentose with stellate hairs numerous hirsute glandular hairs 0.7–2.7 mm; internal involucral bracts 5–7.4 x 1.2–2.1 mm, with scariose margins; receptacle convex, villous usually with long setose hairs (1-)3.5–6.5 mm (about 3 to 5 times longer than the cypselae). FLORETS ligulate, bright to golden yellow, the external with a tube of 3–6 mm and ligule of 5.6-10 x 1.5–3.3 mm (Figure 4.65C), sometimes with a reddish stripe on the outer face. CYPSELAE 1–1.7 x 0.4–0.5 mm (Figure 4.65D), oblong to obconical, black with reddish brown ribs, apex with a ring of small teeth largely exceeded by the conspicuous prolongation of the ribs (Figure 4.66D); pappus of white or dirty-white bristles 4.4–5.7 mm, denticulate at the base (Figure 4.66E).

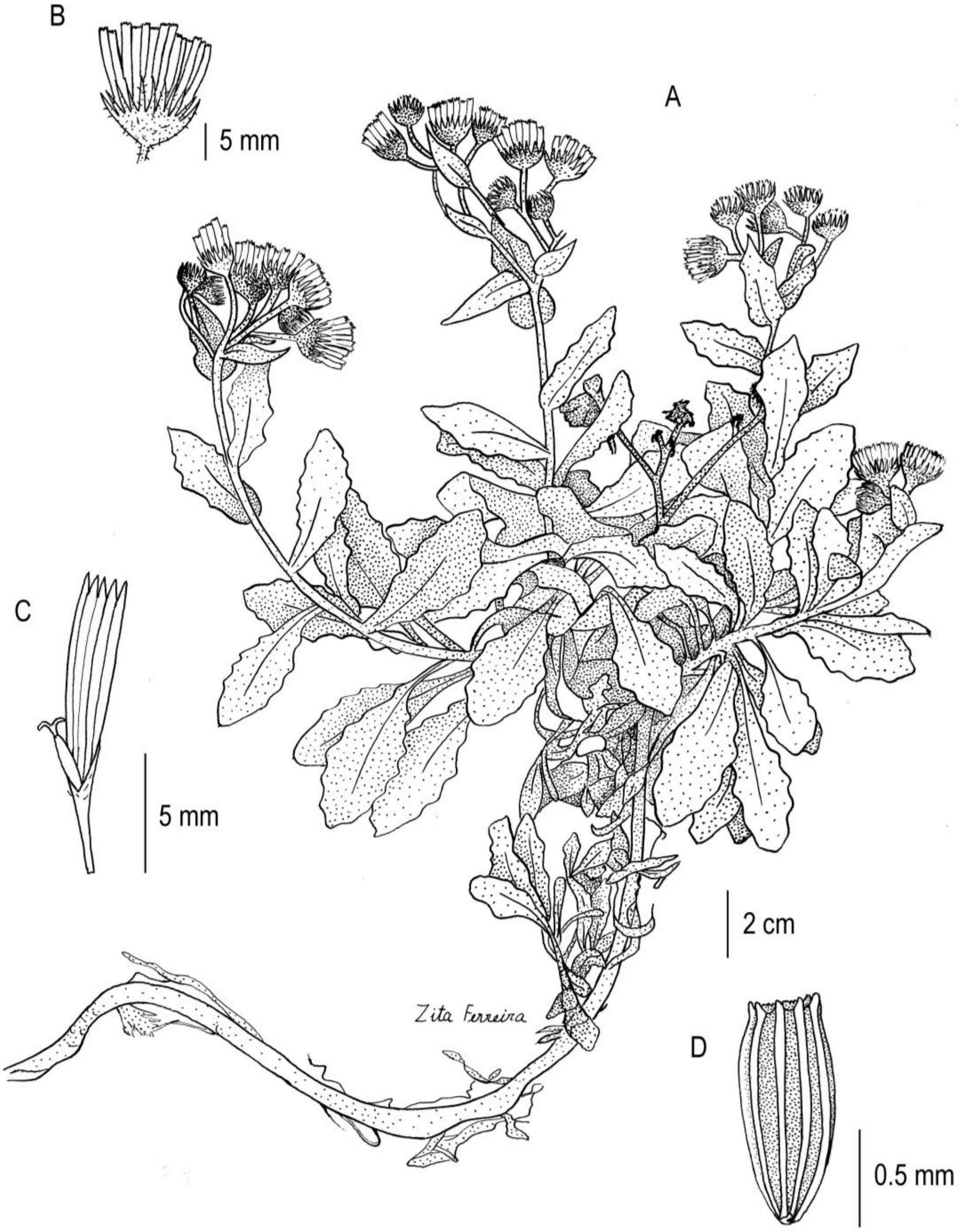


Figure 4.65 *Andryala pinnatifida* Aiton subsp. *cuneifolia* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq. A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

4.17.7.4.3 Comments on taxonomy and nomenclature

This subspecies includes several forms described by Schultz Bipontinus (1849): *Andryala pinnatifida* Aiton f. *cuneifolia* Sch. Bip. (the basionym), *A. pinnatifida* Aiton f. *gomeræa* Sch. Bip., and *A. pinnatifida* Aiton f. *bourgæana*

Sch. Bip., and *A. pinnatifida* Aiton f. *buchiana* Sch. Bip., the latter including only the plants from Tenerife [the ones from Lanzarote correspond to a distinct species, *A. perezii* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. (Ferreira *et al.* 2014a, see Appendix 2)]. All four forms are morphologically similar: leaves frequently broad, dentate-lobate, with abaxial face stellate-lanate, lower leaves attenuate in petiole, cauline and upper leaves semiamplexicaul, base subcuneate to cuneate, and inflorescences corymbose-racemose.

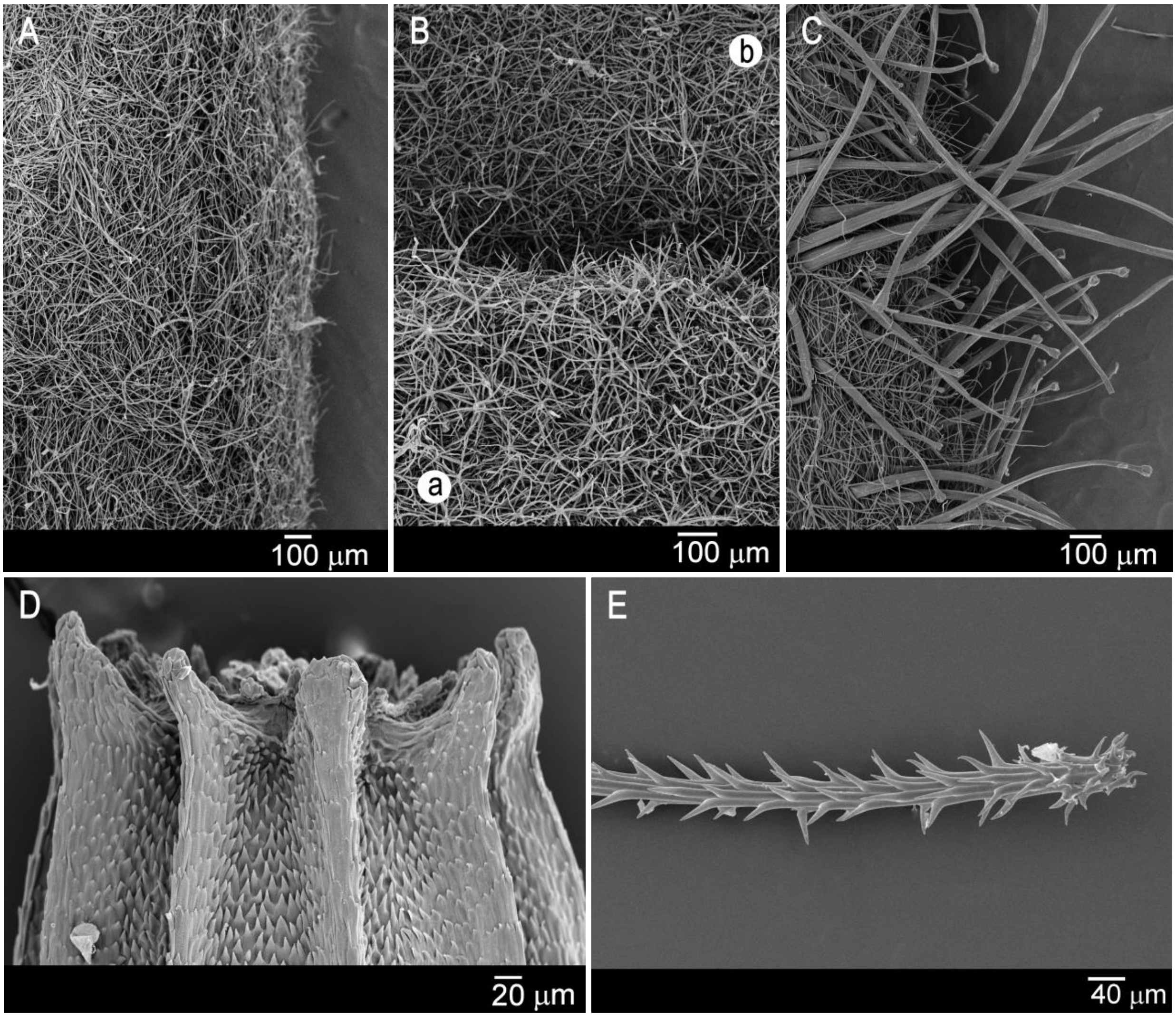


Figure 4.66 *Andryala pinnatifida* Aiton subsp. *cuneifolia* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq. A – Stem indumentum, B – Leaf indumentum (a - abaxial face, b - adaxial face), C – Peduncle indumentum, D – Cypsela apex, E – Pappus base.

Indeed, according to Schultz Bipontinus (1849) *A. pinnatifida* f. *cuneifolia* Sch. Bip. resembles *A. pinnatifida* f. *buchiana* Sch. Bip. (from Tenerife), which in turn exhibits some similarity to *A. pinnatifida* Aiton f. *gomeræa* Sch. Bip. Furthermore, Schultz Bipontinus (op. cit.) emphasized the resemblance of the latter with *A. pinnatifida* Aiton f. *bourgæana* Sch. Bip., namely in what concerns the stellate indumentum, despite the absence of glandular hairs and the leaf shape. Actually, even though the leaves are indeed narrower, *A. pinnatifida* Aiton f. *bourgæana* Sch. Bip reminds the other three forms by the leaf indumentum (abaxial face stellate-lanate), lower leaves petiolate, cauline and upper leaves dentate-lobate, semiamplexicaul and subcuneate at the base. The epithet "*cuneifolia*" was adopted as it corresponds to the first description in Schultz Bipontinus's publication of 1849, considering all four forms except for *A. pinnatifida* Aiton f. *buchiana* Sch. Bip. The epithet "*buchiana*" was employed in a subsequent name: *A.*

pinnatifida Aiton subsp. *buchiana* (Sch.Bip.) Reyes-Bet. & A.Santos [corresponding to the recently described *A. perezii* (Ferreira *et al.* 2014a, see Appendix 2) and, therefore, its use would result in an illegitimate later homonym.

Later Bornmüller (1904) described very briefly *Andryala pinnatifida* Aiton var. *latifolia* Bornm. for Tenerife and El Hierro ("*capitulis majusculis atro-glandulosissimis*"). This author clearly assigned this *taxon* to the Anaga peninsula, matching the collection locality of *A. pinnatifida* f. *buchiana* Sch. Bip. [this form was assigned to Monte de Las Mercedes in the Anaga peninsula (Schultz Bipontinus 1849)]. Furthermore, the original description of this form fits quite well the type material of *A. pinnatifida* Aiton var. *latifolia* Bornm. hosted at the P herbarium. Bornmüller (op. cit.) assigned *A. pinnatifida* Aiton var. *latifolia* Bornm. also to Sabinosa (El Hierro), the same locality mentioned in the protologue of *A. pinnatifida* f. *cuneifolia* Sch. Bip. Type material of *A. pinnatifida* Aiton var. *latifolia* Bornm. from El Hierro, deposited at the JE herbarium, also matches quite well the original description of this form. This variety was later transferred to a subspecies rank by Kunkel (1980). Likewise, *A. pinnatifida* Aiton subsp. *latifolia* (Bornm.) G. Kunkel. was assigned to the Anaga peninsula and the original description of *A. pinnatifida* f. *buchiana* Sch. Bip. from Tenerife fits the representative specimen indicated by Kunkel (op. cit.). Based on the above considerations, *A. pinnatifida* Aiton subsp. *latifolia* (Bornm.) G. Kunkel. should be included in *A. pinnatifida* Aiton subsp. *cuneifolia* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq.

Kunkel (1975: 27) proposed the name *A. pinnatifida* subsp. *webbii* (Sch. Bip. ex Christ) G. Kunkel. as a new combination and status, based on *A. pinnatifida* var. *webbii* Sch. Bip. ex Christ. In fact, Christ (1888) validly published *A. pinnatifida* var. *strictam* f. *webbii* Sch. Bip. ex Christ. This is an illegitimate name given that it is nomenclaturally superfluous. Indeed, it corresponds to a herbarium name (*A. webbii* Sch. Bip.) which Schultz Bipontinus (1849) validly published under *A. pinnatifida* f. *webbiana* Sch. Bip. Furthermore, Kunkel (Kunkel 1975, 1980) cited *A. pinnatifida* subsp. *webbii* (Sch. Bip. ex Christ) G. Kunkel for La Gomera, when Schultz Bip. clearly assigned *A. pinnatifida* f. *webbiana* Sch. Bip. to El Hierro [also existent in La Palma, according to Christ (1888) and to herbarium specimens from Webb's collection]. Actually, the representative specimen from Barranco del Cedro (La Gomera) indicated by Kunkel (1980) resembles much more *A. pinnatifida* subsp. *cuneifolia* (the earlier described *A. pinnatifida* var. *latifolia* Bornm.) than the *taxon* corresponding to *A. pinnatifida* f. *webbiana* Sch. Bip. In fact, some years before Kunkel (1975) indicated *A. pinnatifida* var. *latifolia* Bornm. as a synonym of *A. pinnatifida* Aiton subsp. *webbii* (Sch. Bip. ex Christ) G. Kunkel and only later considered them as two distinct subspecies: *A. pinnatifida* subsp. *latifolia* (Bornm.) G. Kunkel and *A. pinnatifida* Aiton subsp. *webbii* (Sch. Bip. ex Christ) G. Kunkel. Considering the above, *A. pinnatifida* subsp. *webbii* (Sch. Bip.) G. Kunkel is a misapplied name and as it is based on an illegitimate name (*A. pinnatifida* Aiton var. *strictam* f. *webbii* Sch. Bip. ex Christ) it is also illegitimate.

4.17.7.4.4 **Ecology and conservation status**

Andryala pinnatifida Aiton subsp. *cuneifolia* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq. can be found in Tenerife at high altitudes between 700 and 900 m asl (Kunkel 1980). According to herbarium data, on this island it also occurs at lower altitudes between 120 and 300 m, on coastal cliffs and thermophilous scrublands, where it is given as occasional. This subspecies is frequent in the Anaga peninsula, in the northeastern extreme of Tenerife and in the Teno peninsula, in the western extreme of the island. Both correspond to ancient volcanic edifices formed mainly by basaltic rock and deeply eroded (Ancochea *et al.* 1990) where the laurel forest occurs on Tenerife (Fernández-

Palacios & Arévalo 1998). In some northern localities of Tenerife it is considered common, occurring in *Cistus* L. maquis. In La Gomera it can also be found on the edges of trails in fayal-brezal forests as well as laurisilva areas. In El Hierro this *taxon* is also present in areas at lower altitudes (thermophilous woodlands) as well as higher elevations (fayal-brezal and laurisilva forests). In view of the foregoing, this subspecies may be listed as being of Least Concern (LC) according to *IUCN Red List Categories and Criteria, version 3.1* (IUCN 2001; 2012).

4.17.7.4.5 Geographic distribution

A. pinnatifida Aiton subsp. *cuneifolia* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq., occurs in Tenerife and on two of the westernmost islands of the Canary Archipelago, La Gomera and Hierro (Figure 4.67). According to herbarium data, in Tenerife it is present mainly in two very ancient areas: Anaga peninsula, the north-easternmost part of the island (in localities such as Anaga, Las Mercedes, El Bailadero, Igueste, and Taganana) and Teno peninsula, the westernmost part (in Buenavista del Norte, Roque del Fraile, and faro de Teno), besides a few northern localities (e.g., San José, La Guancha). In La Gomera this *taxon* grows in north-central and eastern localities (e.g., Monte del Cedro, Barranco de Fuel, Degollada de Peraza, San Sebastian, Las Rosas, Vallehermoso), whereas in Hierro it can be found in the El Golfo region, in localities such as Mirador de Bascos and Sabinosa, as well in San Andrés on the way to Frontera.

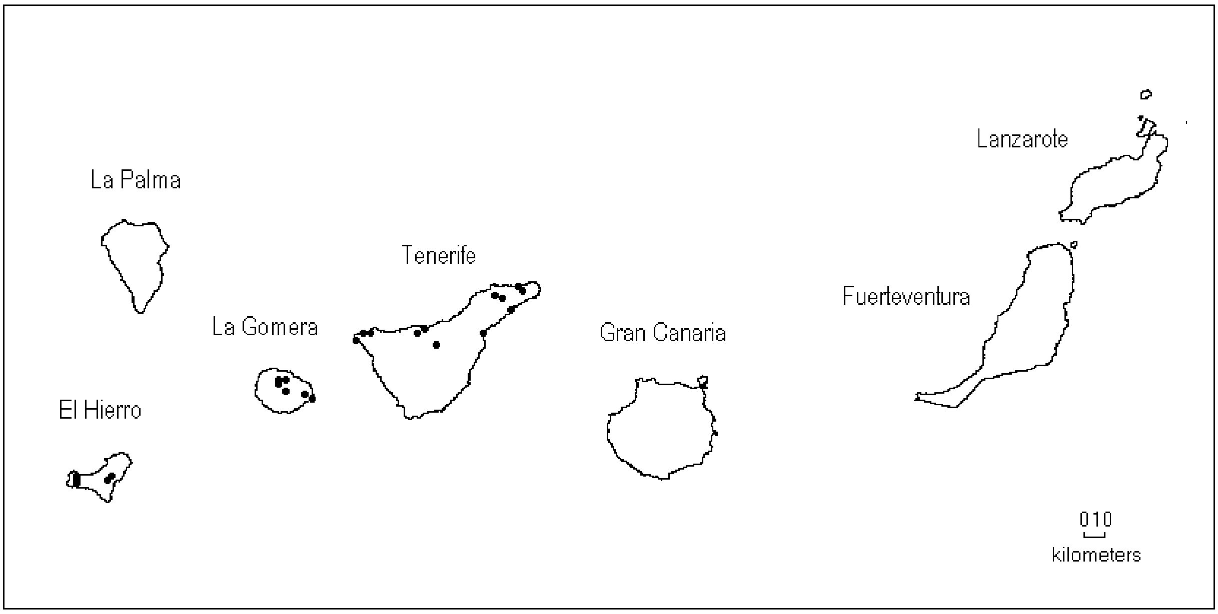


Figure 4.67 Distribution area of *Andryala pinnatifida* subsp. *cuneifolia* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq., according to studied material.

4.17.7.4.6 List of studied material

Spain:	
[Canary Islands]:	El Hierro. Mirador de Bascos, 21-III-1998, Pedro Luís Pérez de Paz & Gilberto Cruz Trujillo, s/ nº, TFC 42546. La Gomera. Monte del Cedro, 18-VII-1974, W. W; B. M; J. R. A., s/ nº, TFC 4531. Tenerife, Anaga, E. Valdés. Pedro Luis Pérez de Paz, alumnos, s/ nº, TFC 34935. Tenerife. El Bailadero, Anaga, 30-XI-1980, C. Hernández Padrón y P. L. Pérez, s/ nº, TFC 8797. La Gomera, Barranco de Fuel. Monte Verde, 15-IV-1988, Pedro Luís Pérez de Paz, Marcelino del Arco Aguilar, Vicente Luís Sauquillo, s/ nº, TFC 27492. La Gomera, Degollada de Peraza, 950m., 11-IV-1981, B. Méndez; J. R. Acebes, s/ nº, TFC 13595. Tenerife, Buenavista del Norte. Km 3-4 dela carretera Buenavista - Punta de Teno, Hierbas anuales de 20-40 cm de alto, corolas amarillo-naranja. Matorral termófilo. Ocasional. 300 m, José L. Panero, Javier Fco. Ortega y Arnold Santos, 7076, MA 595514. Fuerteventura, Riscos de Jandía, L. Sánchez-Pinto, s/nº, TFMC 4120. Tenerife, Roque del Fraile (Teno),150 m.s.m., 02-III-1984, S. Socorro, s/nº, TFMC 1618. Tenerife: faro de Teno, junto el boca del túnel por el lado del faro, 28R134714/3138798, 11-IV-2006, L. M. Ferrero & E. Carrillo, MS-6. Tenerife: San José above La Rambla, 50-60 m tall, in *Cistus* maquis.

Common. 150 m, 25-I-1969, D. Bramwell, 616, SEV 5117. Tenerife, Monte de las Mercedes, 21-III-1959, Bellot et Casaseca, MA 500536. Tenerife, Las Mercedes, ad juga montium, H. de la Perraudiére, MA 160713. Tenerife, Monte de las Mercedes, 21-III-1959, MA 504109. Tenerife, MA 139373. Tenerife, cabo frontal de Taganana, Brezal, 30-XI-1985, S. Castroviejo, MA 471788a. Tenerife, Las Mercedes,C. Gz. Campo & al., MA 619663. Tenerife, Igueste, acantilados del litoral, 120 m, 30-III-1979, E. Valdez-Bermejo, 5042EV, MA 238519. La Gomera, San Sebastián de La Gomera, camino de Enchered, 600 m, 15-IV-2005, A. Herrero & L. Medina, AH 2480, MA 733766. Tenerife, cabo frontal de Taganana, Brezal, 30-XI-1985, S. Castroviejo, MA 471788b. El Hierro, San Andrés 2 km WSW an der strabe nach Frontera, 1157 m.s.m., Brachland mit *Chamaecytisus proliferus*_Gebüsh, zusammen mit *Andryala integrifolia*, 22-V-2010, S. et E. Braütigam, PRA, H16. El Hierro, San Andrés 4 km WSW an der Strabe nach Frontera, 980 m.s.m., Gebüsh, vorherrschend *Chamaecytisus prolifeus*, 20-V-2010, PRA, H13/2. Hierro, Sabinosa 3 km SW, bei der Ermita Virgen de los Reyes, 720 m.s.m., felsige, beweidete Stelle angrenzend Euphorbia_Kleinia_ Sukkulentenbusch, 21-V-2010, S. et E. Braütigam, PRA, H14/2. La Gomera, Las Rosas, Ortsausgang an der Strabe zum Centro de Visitantes (ICONA), ca. 600 m.s.m., Rand eines Pfades im Fayal-Brezal (*Myrico fayae_Ericetum arboreae*), 09-V-2010, PRA, G6. La Gomera, Vallehermoso 3 km SSE an der Strabe von der Hochfläche nach Las Rochas,980 m.s.m., felsiger Strabenrand in Lorbeerwald, 11-V-2010, PRA, G9. Tenerife, Puerto de La Cruz 12 WSW, La Guancha, oberer Osrtrand,600 m.s.m., Feldsteimauer im terrassierten Brachland, 03-V-2010, S. et E. Braütigam, PRA, T1. El Hierro, Sabinosa, 2,5 km W, am Fahrweg von der Ermita Virgen de los Reyes nach El Sabinar, 660 m.s.m., schattiger Straenrand mit *Cupressus*, 21-V-2010, S. et E. Braütigam, PRA ,H14b. La Gomera, Vallehermoso 3 km SSE an der Strabe von der Hochfläche nach Las Rochas, 980 m.s.m., felsiger Straenrand in Lorbeerwald, 11-V-2010, PRA, G9B. El Hierro, San Andrés 4 km WSW an der Strabe nach Frontera, 980 m.s.m., Gebüsh, vorherrschend *Chamaecytisus prolifeus*, 20-V-2010, PRA, H13/1. La Gomera, Bco. Seco de Valhermoso, 16-IV-1865, Bourgeau, P 02462100.

4.17.7.5 *Andryala pinnatifida* Aiton subsp. *webbiana* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq. stat. nov.

≡ *Andryala pinnatifida* Aiton f. *webbiana* Sch. Bip. in Webb & Berthel. Hist. Nat. Iles Canaries (Phytogr.) 2: 417. 1849. *basion.*
Andryala webbii Sch. Bip. in Webb & Berthel. Hist. Nat. Iles Canaries (Phytogr.) 2: 417. 1849.
Ind. loc.: "Ins. Hierro, Intra de Inama, 8 Junii, Bourgeau!"
Typus: [Spain, Canary Islands] "Intra de Iñama, ins. Hierro, 08 June1845", *Bourgeau s.n.* – Lectotype (designated here): P02462116; syntypes: FI-W109925, P02462133, P02462135, P02462140, P02462141.
= *Andryala pinnatifida* Aiton f. *glabrescens* Sch. Bip. in Webb & Berthel. Hist. Nat. Iles Canaries (Phytogr.) 2: 417. 1849
Ind. loc.: "Palma in rupestribus et in sylvis circa Los Sauces, 17 Julie 1845 Bourgeau! n. 13."
Typus: [Spain, Canary Islands] "In rupestribus et in sylvis circa Los Sauces insulae Palmae, 17 July 1845", *Bourgeau 13* – Lectotype, (designated here): P02462163.
_ *Andryala pinnatifida* var. *stricta* f. *webbii* Sch. Bip ex Christ in Bot. Jahrb. Syst. 9: 150. 1888, *nom. illeg.*
_ *Andryala webbii* (Sch. Bip. ex Christ) A. Santos, Veg. Fl. La Palma. 275. 1983, *nom. illeg.*

4.17.7.5.1 Typification

Schultz Bipontinus (1849) indicated material collected by Bourgeau, on the 8th of June, in a locality named "*Intra de Iñama*" (El Hierro). A specimen with these references is kept at the P herbarium (P02462116) and since it fits perfectly the description of *Andryala pinnatifida* Aiton f. *webbiana* Sch. Bip., it is here designated as lectotype. In the protologue Schultz Bipontinus also indicated as a synonym "*Andryala webbii* C. H. Schultz Bip.", an unpublished name from the Webb collection. Indeed, this specimen was originally designated as "*Andryala webbii*" and later a new determination was made: *Andryala pinnatifida* f. *webbiana* Sch. Bip. by Schultz Bipontinus himself. Another morphologically identical specimen collected by Bourgeau, in 17 July 1845, is deposited in the FI Herbarium ex herb. Webb (FI-W109925). One of the labels reads "*Andryala webbii C. H. Schultz Bip.*", handwritten by Schultz Bipontinus. However, it is not from El Hierro, as expected from the collection data in protologue, but from La Palma. This means that this form is present on both islands. The specimen in question was incorrectly considered in 2005 by A. Santos as type material of *A. pinnatifida* f. *glabrescens* Sch. Bip., probably due to its provenance (Los Sauces in La Palma, exactly where the latter can be found) and the collector number on the label by Schultz Bipontinus (nº 13). Actually, this number refers to a *taxon* described in the protologue under the name *A. pinnatifida* f. *glabrescens* Sch. Bip. Nonetheless, morphologically the specimen FI-W109925 matches the original description of *A. pinnatifida* f. *webbiana* Sch. Bip. rather that of *A. pinnatifida* f. *glabrescens* Sch. Bip. Thus, it is here considered a syntype of the first. Several other specimens from La Palma fitting the description of *A. pinnatifida* f. *webbiana* Sch. Bip. were found (P02462133, P02462135, P02462140, P02462141). Although they are under the name *Andryala webbiana* Sch. Bip. in Schultz Bipontinus's own handwriting and not under the name *A. webbii*, they seem to correspond to original material and are therefore considered here as syntypes of *A. pinnatifida* f. *webbiana* Sch. Bip.

A specimen under the name *A. pinnatifida* Aiton f. *glabrescens* Sch. Bip., originally from the Schultz Bipontinus herbarium hosted at the P herbarium, exactly with the same information as the one in the protologue (collection date and locality, as well as collector and collector number) was found at the P herbarium (P02462163). Although the specimen was originally named by Schultz Bipontinus as "*Andryala Webbii* var. α", later the author renamed it as "*Andryala pinnatifida forma glabrescens C. H. S. Bip*." and, in fact, it fits the original description of this form quite well and is, therefore, designated here as lectotype.

4.17.7.5.2 **Description**

Perennial herb, frequently single-stemmed. STEMS 29–77 cm, usually branched in the upper third (Figure 4.68A), sometimes purplish, puberulous to slightly tomentose below, tomentose above with stellate hairs and abundant glandular hairs at least in the upper part (Figure 4.69A). LEAVES not crowded, puberulous to tomentose, especially the cauline and upper leaves, with stellate hairs and sometimes with scarce glandular hairs, the abaxial face more stellate-tomentose than the adaxial face which is sometimes puberulous (Figure 4.69B); lower leaves often marcescent at anthesis, attenuate into a winged petiole about 19 mm, elliptic, apex obtuse to acute, and margin lobate; cauline leaves 39–84 x 10–45 mm, sessile or semiamplexicaul, elliptic to lanceolate or obovate, base attenuate sometimes rounded, apex obtuse or acute, and margin dentate; upper leaves 14–39 x 3–9(-21) mm, semiamplexicaul or amplexicaul, lanceolate sometimes ovate-oblong to ovate-lanceolate or obovate, base rounded, apex acute or acuminate, and margin entire to dentate. INFLORESCENCE corymbose with 3–8 capitula. CAPITULA 11–22 mm in diameter (Figure 4.68B); peduncles 8–20 mm, with stellate hairs and abundant hispid glandular hairs 0.8–2 mm (Figure 4.69C); involucre 6.7–10 x 7–13 mm, ± campanulate at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 5.8–7 x 0.8–1.3 mm, usually linear-lanceolate, apex acuminate to subulate, flat not enfolding a floret, the outer face puberulous with few stellate hairs and numerous glandular hairs on the middle nerve, 0.7–1.7 mm; internal involucral bracts 5.5–7 x 1.2–2.2 mm, with usually broad scariose margins; receptacle convex, villous with long setose hairs 3–6.5 mm (2 to 5 times longer than the cypselae). FLORETS ligulate, bright yellow, the external with a tube of 3.4–4.5 mm and ligule of 6-8 x 1.2–2.7 mm (Figure 4.68C). CYPSELAE 1.3–1.7 x 0.4–0.5 mm (Figure 4.68D), usually oblong, dark brown frequently with reddish brown ribs, apex with a ring of small teeth largely exceeded by the conspicuous prolongation of the ribs (Figure 4.69D); pappus of usually white bristles 4.6–6 mm, denticulate at the base (Figure 4.69E).

4.17.7.5.3 **Comments on taxonomy and nomenclature**

Schultz Bipontinus (1849) described two *taxa* for *Andryala pinnatifida* Aiton, considering them morphologically quite close: *A. pinnatifida* Aiton f. *webbiana* Sch. Bip. and *A. pinnatifida* Aiton f. *glabrescens* Sch. Bip. Indeed, these forms have some features in common: leaves not crowded, alternate, obovate or elliptic, conspicuously dentate, abaxial face stellate tomentose, membranaceous, and the inflorescence is ± corymbose with large capitula.

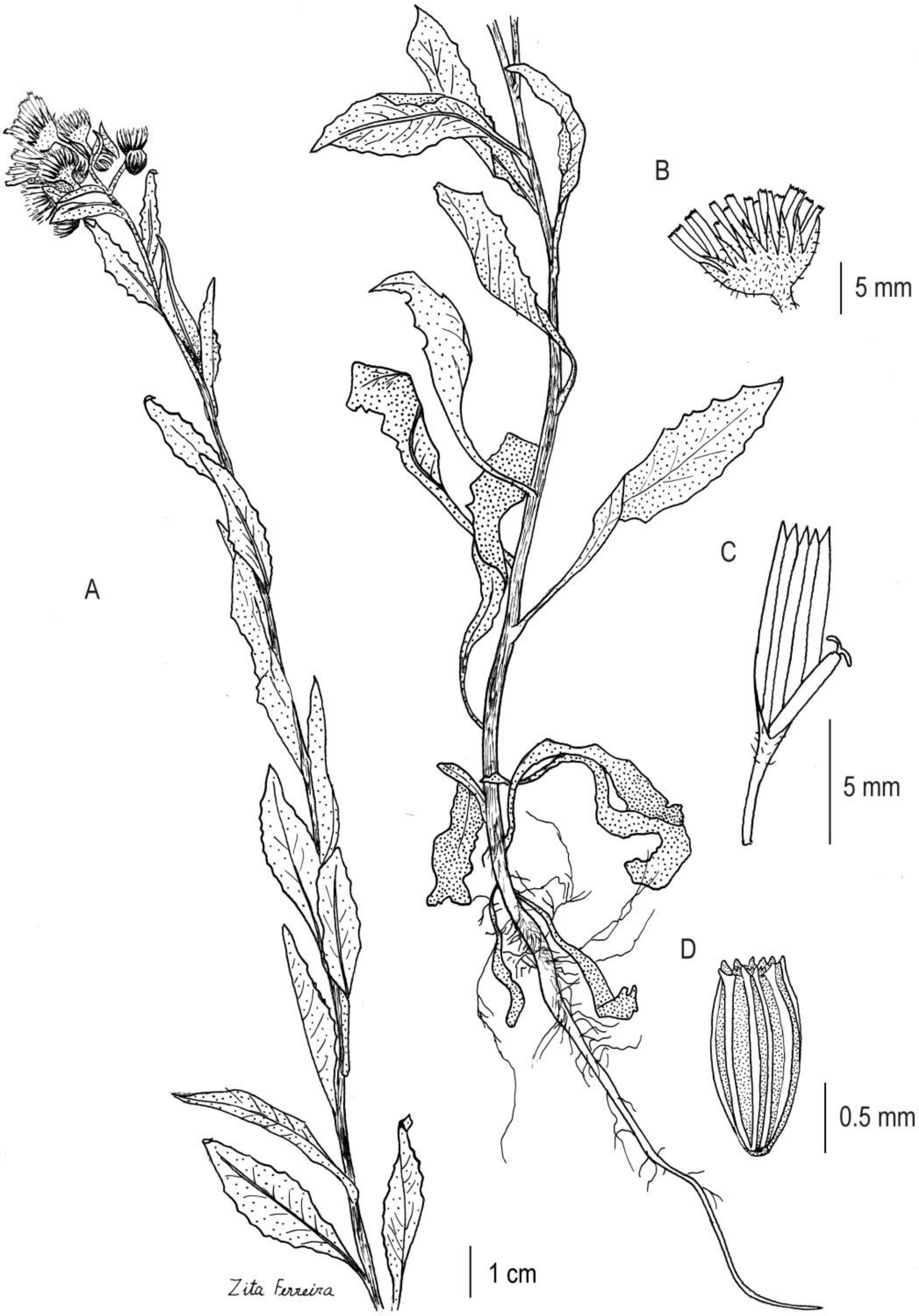


Figure 4.68 *Andryala pinnatifida* Aiton subsp. *webbiana* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq. A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

Later Christ (1888) recognised two varieties for *A. pinnatifida* Aiton, the typical one and *A. pinnatifida* var. *strictam.* For the latter, the author recognised three forms: *A. pinnatifida* var. *strictam* f. *teydensis* Sch. Bip., *A. pinnatifida* var. *strictam* f. *glabrescens* Sch. Bip. and *A. pinnatifida* var. *strictam* f. *webbii* Sch. Bip ex Christ. Incorrectly Christ (1888) preferred the epithet "*webbii"* (an herbarium name by Schultz Bipontinus: "*Webbii Schultz in Sched. Bourg. It. 1, 340*") over "*webbiana"* seeing that the name published by this author was in fact *A. pinnatida* f. *webbiana* Sch. Bip. Based on herbarium material collected by Bourgeau (collector number 340) in Los Sauces, Christ (1888: 149) presented a brief description of *A. pinnatifida* var. *strictam* f. *webbii* Sch. Bip ex Christ. ("*Foliis late ovatis indivisis leviter dentatis*"), which matches perfectly the original description of *A. pinnatida* f. *webbiana* Sch. Bip. Christ (1888) assigned this *taxon* to La Palma, whereas Schultz Bipontinus (1849) cited it for El Hierro. The observation of type material showed that this *taxon* is effectively present on both islands. This means that *A. pinnatifida strictam* f. *webbii* Sch. Bip ex Christ. is not in reality a new name [nor are *A. pinnatifida* var. *strictam* f. *teydensis* and *A. pinnatifida* var. *strictam* f. *glabrescens* since both correspond to forms earlier described by Schultz Bipontinus (1849) exactly with the same epithets]. Thus, *A. pinnatifida* var. *strictam* f. *webbii* Sch. Bip ex Christ is a superfluous name and, therefore, illegitimate.

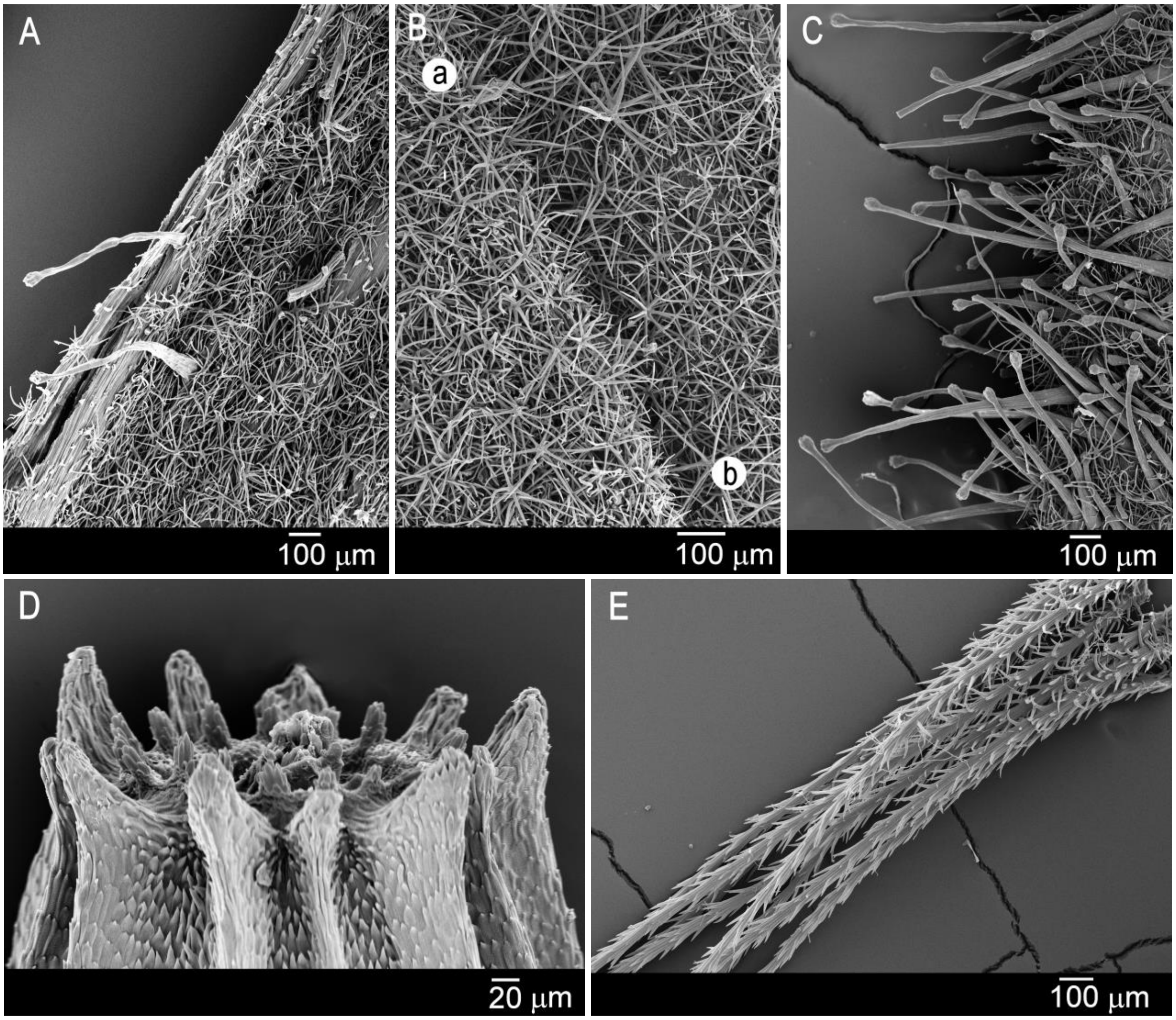


Figure 4.69 *Andryala pinnatifida* Aiton subsp. *webbiana* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq. A – Stem indumentum, B – Leaf indumentum (a - abaxial face, b - adaxial face), C – Peduncle indumentum, D – Cypsela apex, E – Pappus base.

More recently Ceballos & Ortuño (1976) recognised *A. webbii* Sch. Bip. ex Christ for La Palma but did not explicitly propose a new combination or status. Moreover, these authors assigned this *taxon* to several localities in La Palma based on information provided by A. Santos. This could mean that Ceballos & Ortuño (1976) misinterpreted Christ's work, raising *Andryala pinnatifida* var. *strictam* f. *webbii* to a species rank. Another possibility is that the herbarium specimens from A. Santos were labelled as *A. webbii* Sch. Bip. ex Christ. by the collector himself. Indeed, later Santos (1983) cited *A. webbii* Sch. Bip. ex Christ for the flora of La Palma and clearly mentioned voucher data including the collector number, collection date and locality, the latter matching exactly the same collection localities as those mentioned by Ceballos & Ortuño (1976). Actually Greuter (2006+) considered *A. webbii* (Sch. Bip. ex Christ) A. Santos as a homotypic synonym of *Andryala pinnatifida* subsp. *webbii* (Sch. Bip. ex Christ) G. Kunkel, an illegitimate combination insofar as it is based on the herbarium name *A. webbii* Sch. Bip. (*nom. nudum*). Santos (1983) stressed that the plants cited for La Gomera probably do not correspond to this *taxon*. This taxonomic point of view is in accordance with the placement of *A. pinnatifida* f. *gomeræa* Sch. Bip. in a distinct *taxon*, *A. pinnatifida* subsp. *cuneifolia* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq. In regard to *A. pinnatifida* Aiton f. *webbiana* Sch. Bip. and *A. pinnatifida* Aiton f. *glabrescens* Sch. Bip., both forms are here included in a single subspecies for which a new combination is suggested: *A. pinnatifida* Aiton subsp. *webbiana* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq. Indeed, despite the different leaf shape (broader and elliptic to obovate in *A. pinnatifida* Aiton f. *webbiana* and narrower and more elliptic in *A. pinnatifida* Aiton f. *glabrescens* Sch. Bip.), these two forms are morphologically close, as mentioned above.

4.17.7.5.4 Karyology

The somatic chromosome number of *Andryala pinnatifida* Aiton subsp. *webbiana* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq. (n = 9) was determined on plant material from La Palma identified as *Andryala pinnatifida* Ait. var. *webbii* (Sch. Bip.) Christ. (Ortega & Navarro 1977).

4.17.7.5.5 Ecology and conservation status

Andryala pinnatifida Aiton subsp. *webbiana* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq. occurs especially in Laurisilva areas and rocky cliffs (Schultz Bipontinus 1849; Bramwell & Bramwell 1974; Bramwell & Bramwell 2001). It is common in forest clearings or in cool sites of pine forests, growing at altitudes between 700 and 1350 m (Ceballos & Ortuño 1976). According to available herbarium data, it can also be found in fayal-brezal forests (as part of the *Myrico fayae-Ericetum arboreae* community). Additionally, it grows on roadsides as well as in more or less humid and shady places in the vicinity of the volcano San Juan Pinares (La Palma). In La Palm it is locally common, growing in association with species such as *Sideritis barbellata* Mend.-Heuer and *Orobanche* L. spp. (the latter are root parasitic herbaceous plants). In light of the above, this subspecies may be listed as being of Least Concern (LC) according to the *IUCN Red List Categories and Criteria, version 3.1* (IUCN 2001), although it was listed as rare in the *1997 IUCN Red List of Threatened Plants* (Walter & Gillett 1998).

4.17.7.5.6 Geographic distribution

Andryala pinnatifida Aiton subsp. *webbiana* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq. occurs in the western Canary Islands of La Palma and El Hierro (Figure 4.70), although less frequently in the latter. According to herbarium data, in La Palma it can be found in central and northern localities such as Cumbrecita (El Paso), La Caldera, Puntagorda, Los Sauces, Cueva de La Zarza, Roque del Faro, and Llano Negro (the latter three in Garafia), whilst in El Hierro it has a more restricted distribution occurring only in some localities of the El Golfo region.

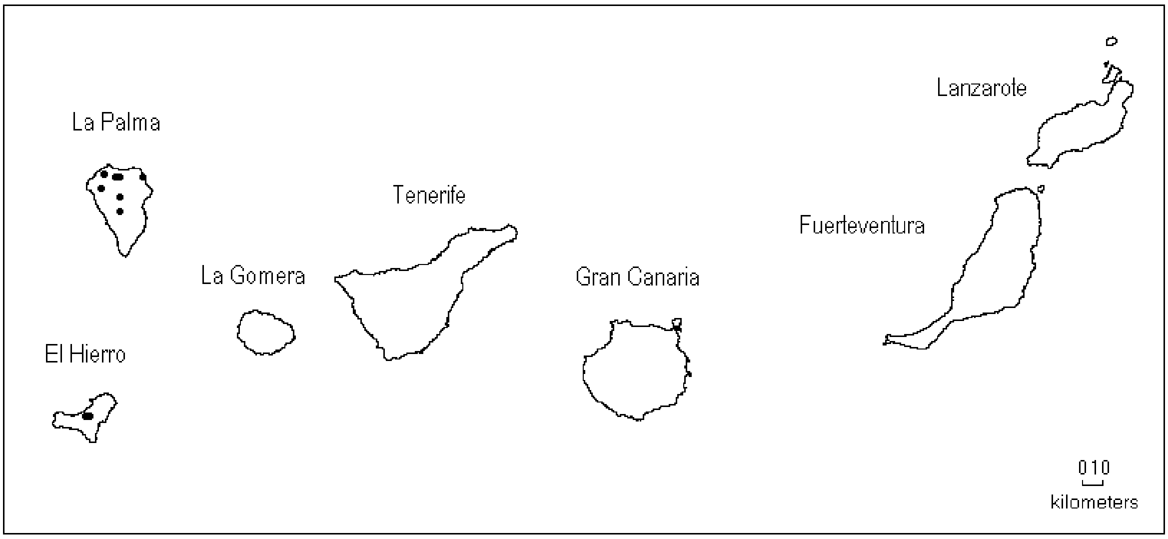


Figure 4.70 Distribution area of *Andryala pinnatifida* subsp. *webbiana* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq., according to studied material.

4.17.7.5.7 List of studied material

Spain:

[Canary Islands]: La Palma, Localmente frequente, en el cauce del Bco. de Izcagua (Puntagorda), com [?] canariense, *Sideritis barbelleta, Orobanche* spp., +/- 600 m, 20-V-2005, A. Santos e G. Bernadillo, ORT 39523. La Palma, Garafia, entrada en San Antonio, borde de pista, escasa en fayal brezal [?], +/- 1200 m, 27-V-2005, ORT 39531. La Palma, Los Sauces, in sylva, E. Bourgeau, 340, P 02462135. La Palma. El Riacho, Cumbrecita, El Paso, 07-VI-2005, Pedro Luís Pérez de Paz, s/ nº, TFC 45948. La Palma. La Farola, La Caldera, 05-V-1992, Pedro Luís Pérez de Paz, s/ nº, TFC 35193. El Hierro, Carretera Frontera. El Golfo 900m., 07-VII-1985, Pedro Luís Pérez de Paz., s/ nº, TFC 24653. La Palma. El Paso, Immediaciones del volcán de San Juan Pinares: en sitios más ou menos húmedos y sombrios, 24-VIII-1979, B. Méndez; J. R. Acebes, M. del Arco, s/ nº, TFC 20485. La Palma, Cueva de la Zarza, Garafia, 15-VII-1977, P. L. Pérez, s/nº, TFMC 1551. La Palma, Entre Llano Negro e la Mata, Garafia, 07-XII-1994, R. Mesa Coelho, s/nº, TFMC 4223. La Palma, 09-VI-2006, Aida Pupo Correia, s/nº, UMad. La Palma, 09-VI-2006, Aida Pupo Correia, s/nº, UMad. La Palma, 09-VI-2006, Aida Pupo Correia, s/nº, UMad. Hierro, El Golfo, Ces. Sobrado, MA 139341. La Palma, Strabe Barlovento - Puntagorda an der Abzweigung der strabe LP 9 bei Roque del Faro,1030 m.s.m., Strabenrand, angren Vegetatio Fayal-Brezal (Myrico fayae-Ericetum arboreae),14-V-2010, S. et E. Braütigam, PRA, P11/1.

4.18 *Andryala ragusina* L., Sp. Pl., ed. 2. 2: 1136. 1763

Ind. loc.: “Habitat in insulis Archipelagi”
Typus: Lectotype (designated by House in Jarvis & Turland 1998): LINN 956.4
= *Andryala laciniata* Lam., Encycl. 1(1): 153. 1783
Ind. loc.: “Cette plant croit en Espagne & dans les environs de Narbonne.”
Typus: Lectotype (designated here): P00355812 (specimen on the right); isolectoptype: P00355812 (specimen on the left); syntypes: specimens on the herbarium sheet P00355811
= *Andryala lyrata* Pourr. in Mem. Acad. Toul. 3: 308. 1788
Andryala ragusina L. var. *lyrata* (Pourr.) DC., Prodr. 7(1): 244. 1838
Andryala lyrata Pourr. var. α *lyrata*, Voy. Bot. Espagne. 2(13): 393. 1841
Ind. loc.: [France] “Cette superbe plante est très-commune sur les bordes des petits revieres des hauts Corbières, notammente à Pader, St. Paul de Fenouilhedes, …”
Typus: Lectotype (designated here): P03693513 (specimen on the upper right-hand corner); isolectotypes: P03693513 (remaning specimens)
= *Rothia argentea* Lapeyr., Hist. Pl. Pyrenées 485. 1813
Ind. loc.: [France] Abondamment sur les bords de la Gly à Saint-Paul, à Prades, à Perpignan.”
Typus: “Perpignan, Pader, St. Paul, lelong de la Riviera” – Lectotype (designated here): MHNT.BOT.2011.0.2769
= *Crepis incana* Lapeyr., Hist. Pl. Pyrenées 483. 1813. *basion.*
Andryala incana (Lapeyr.) DC., Fl. Franc. (DC.), ed. 3. 6: 445. 1815
Andryala ragusina L. var. *incana* (Lapeyr.) DC. Prodr. 7(1): 244. 1838
Ind. loc.: [France] “Dans les sables de la rivière de *Sin* et de *Plan.”*
Typus: “Vallée de Gistan ou de Plan au bord de la rivière sur le sable” – Neotype (designated here): G003296223
= *Andryala macrocephala* Boiss. ex DC., Prodr. 7(1): 244. 1838

Andryala lyrata Pourr. var. β *macrocephala* (Boiss. ex DC.) Boiss., Voy. Bot. Espagne. 2(13): 393. 1841
Andryala ragusina L. subsp. *macrocephala* (Boiss. ex DC.) Nyman, Consp. Fl. Eur. 2: 438. 1879
Ind. loc.: "ad.torrentès littorales regni Granatensis legit cl. E. Boissier."
Typus: [Spain] "in glareosis reg. Calidae Granat, May 1837" *Boissier s.n.* – Lectotype (designated by Burdet *et al.* 1983): GDC023651, isolectotypes (designated by Burdet *et al.* 1983): G00222222, G00222223.
= *Andryala ragusina* L. var. *minor* Lange in Willkomm & Lange, Prodr. Fl. Hispan. 2: 271. 1865
Ind. loc.: "in utraque Cast, (agro Salmanticensi, CLUS., Madrit., COLM., CUT., PROL.!), Extremad. (pr. Plasencia, BOURG.!) Aragon, (int. Borja et Bera, ad Pto. de S. Martin etc., WK., Desierto de Calanda, Puertos de Valderrobles, LOSC. PARD.), Catal. (c. Igualada, en el Vallès, Priorato, Espluga de Francoli, pr. Gerona, Figueras, Olot, CSTA.), regno Valent. (Sierra de Chiva, WK ., en el Maestrazgo, LOSC. PARD.), regno Murc. (GUIR.!), Granat. (Sierra de Gador, Bss., c. Granada, FK.!), Extremad. (Pto. de Miravete, BOURG.! ad fluv. Guadiana SCHOUSB.!)"
Typus: [Spain] "… Puerto de S. Martin pr. de Cariñena in Arragonia, July 1850" *Willkomm 445* – Lectotype (designated here): COI41919
_ *Andryala tomentosa* Salisb., Prodr. Stirp. Chap. Allerton 182. 1796, *nom. inval.*

4.18.1 Typification

The lectotype of *A. ragusina* L. was chosen by House among the herbarium material from the Linnaean Herbarium held by the Linnean Society of London (Jarvis & Turland 1998). Two other good candidates would be the specimens from the Linnaean herbarium kept at the S herbarium (microfiche numbers IDC 329.3 and IDC 329.5), filed under *A. ragusina* L. Indeed, both the lectotype and the specimen under IDC 329.3 fit the original description very well: "*foliis lanceolatis indivisis denticulatis acutis tomentosis, floribus solitariis*" (Linnaeus 1763). However, the third specimen does not qualify for type material as it exhibts pinnatid lower leaves.

Under the name *A. laciniata* Lam., handwritten by Lamarck, there are three specimens from Lamarck's collection hosted at the P herbarium (herbarium sheet P00355811). None of them bear any flowers and are, therefore, not good candidates for lectotypification. However, these can be considered syntypes given that the label also says: "*Chondrilla prior legitima Clus. hist. 2. p. 143*", matching the protologue data. However, two other specimens from the Lamarck collection qualify for type material (P00355812); they are under *Andryala incana* DC., a name that figures in the protologue as a synonym of *A. laciniata* Lam. The specimen on the right matches the original description of *A. laciniata* Lam. very well and is, therefore, here designated as lectotype.

In the Pourret collection several specimens under *A. lyrata* Pour., corresponding to original material, were found (P03693513, P03693514 and P03772106). The herbarium sheet P03772106 bears a label handwritten by Pourret that reads "*Andryala lacinata Lam. quae lyrata Pourr. aut totos*", possibly meaning that these are synonyms. Actually, Lamarck (1783: 154) highlighted that *A. laciniata* Lam. was made known to him by Pourret ("… *elle me été communiqué par M. l' Abbé Pourret*."). Interestingly, on the herbarium sheet P03693513 Pourret annotated his amazement before the fact that Lamarck did not adopt his designation (*A. lyrata*), seeing that he learned about the species through him. As the specimen on the upper right-hand corner of the herbarium sheet P03693513 fits the original description quite well, it is here designated as lectotype.

Lapeyrouse (1813) described *Rothia argentea* Lapeyr. indicating *Andryala lyrata* Pourr. as a synonym. The Lapeyrouse collection and types are mainly hosted at the TLJ herbarium, now part of the TL herbarium. Indeed, a specimen under "*Rothia argentea* Lapey.", handwritten by Lapeyrouse, was found (MHNT.BOT.2011.0.2769). It fits the original description very well and is here elected as lectotype.

Regarding *Crepis incana* Lapeyr., although the herbarium and types of Lapeyrouse are held at the TLJ, UPS and MPU herbaria (Stafleu & Cowan 1979), no specimen under this name was located at these institutions. Hence, the designation of a neotype is justified. The specimen G003296223 from the G ex De Candolle herb. is here elected as neotype based on the fact that De Candolle (1815) made a new combination (*Andryala incana* DC.) based on *Crepis incana* Lapeyr. Furthermore, he assigned it to the same localities as Lapeyrouse ("*Elle croît dans les Pyrénées, dans les vallées de Plan et de Gistan, au bord de la rivière sur le sable … et m'a été communiquée par M. Boileau"*). Actually, this information coincides exactly with the collection data on the label attached to the specimen G003296223.

The Willkomm collection and types were mainly deposited in the COI herbarium (Stafleu & Cowan 1988). In the protologue Willkomm (1865) mentioned a representative specimen of *A. ragusina* L. var. *minor* Lange collected by him ("*A. laciniata LAMK, A. sinuata WK. exsicc. 1850, n. 455!*") which was found precisely at this herbarium (COI41919). The collection locality matches one of the localities cited in the protologue ("…*ad Pto. de S. Martin etc., WK.*"). Thus, this specimen is original material and is here designated as lectotype.

4.18.2 Description

Perennial herb, single-stemmed to caespitose, with a dark woody stock. STEMS 22–78 cm, branched from the middle or the base, frequently tomentose with stellate hairs especially below and no glandular hairs. LEAVES glaucous, tomentose to densely tomentose especially on the abaxial face; lower leaves more or less crowded at the base, 38–163 x 10–40 mm, attenuate into a winged petiole (10-)17–53 mm, obovate-lanceolate or oblanceolate to lanceolate, more rarely linear-lanceolate, apex obtuse or acute, and margin dentate to pinnatipartite; cauline leaves 20–66 x 2.8–39 mm, sessile or semiamplexicaul, oblong to lanceolate, sometimes elliptic, linear-lanceolate or linear, base attenuate, apex acuminate sometimes acute, and margin dentate to pinnatipartite; upper leaves 8.6–42 x 1.3–28 mm, sessile or semiamplexicaul, ovate to narrowly ovate-lanceolate or elliptic to linear, base ± cuneate or rounded, sometimes truncate, apex acuminate or acute, and margin entire to pinnatifid. INFLORESCENCE paniculate-corymbose with ± 4 capitula or with solitary capitula longly pedunculate. CAPITULA 10–38 mm in diameter; peduncles 29–70 mm, with dense stellate hairs only; involucre 8–17 x 5.6–19 mm, ± campanulate at anthesis, with involucral bracts in 2–4 rows; external involucral bracts 3.7–11 x 0.7–1.5 mm, linear-lanceolate or linear, apex acuminate sometimes subulate, flat not enfolding a floret, the outer face stellate-tomentose with no glandular hairs; internal involucral bracts 3.6–11 x 1–1.8 mm, with broad scariose margins; receptacle convex, frequently puberulous with short setose hairs 0.3–2 mm (much shorter than the cypselae, rarely equalling them). FLORETS ligulate, golden yellow, the external with a tube of 2.6–8 mm and ligule of 3.6–12 x 0.8–3 mm, with a reddish stripe on the outer face or not. CYPSELAE 2–2.7 x 0.3–0.6 mm, oblong to obconical, light-brown with whitish ribs, apex with a inner ring of small teeth exceeding the inconspicuous prolongation of the ribs; pappus of white or dirty-white bristles 4–7.5 mm, pilose at the base, rarely denticulate.

4.18.3 Karyology

The somatic chromosome number of 2n = 18 was reported for *Andryala ragusina* L. and was determined on plant material collected in southern Spain (Löve & Kjellqvist 1974). Despite the voucher information and given that the specimen was not observed in person, it was not clear to which infraspecific *taxon* this number refers to.

4.18.4 Key to the *Andryala ragusina* L. *taxa*

1a. Stems often branched from the middle; cauline leaves ± crowded, (8-)11–39 mm wide, often oblong to oblanceolate; upper leaves 3 mm wide or more; capitula (13-)16.5–38 mm in diameter; involucre 9.3–17 x 8.6–19 mm; ligule up to 12 mm long. .... *A. ragusina* subsp. *ragusina*

1b. Stems profusely branched from the base; cauline leaves rather sparse, 8–9 mm wide, linear-lanceolate or linear; upper leaves less than 3 mm wide; capitula 10–17.5 in diameter; involucre 8–10.7(-12) x 5.6–10.4 mm; ligule up to 8 mm long. 2

2a. Stems densely stellate-tomentose; cauline leaves 8–9 mm wide, linear-lanceolate; capitula 15.6–17.5 mm in diameter; involucre 9.4–10.7(-12) x 9.3–10.4 mm; external involucral bracts 6–8.6 x 1–1.2; ligule 4.6–8 x 1.5–2 mm; cypsela 2.5 x 0.5 mm. .... *A. ragusina* subsp. *ramosissima*

2b. Stems stellate-tomentose; cauline leaves 2.8 mm wide, linear; capitula ± 10 mm in diameter; involucre 8 x 5.6 mm; external involucral bracts 3.7–4.8 x 0.7–1; ligule 3.6 x 0.8 mm; cypsela 2 x 0.3 mm. .... *A. ragusina* L. subsp. *spartioides*

4.18.5 *Andryala ragusina* L. subsp. *ragusina*

4.18.5.1 Description

Perennial herb, single or multi-stemmed, with a dark woody stock (Figure 4.71A). STEMS 22–60(-70) cm, branched in the upper half or upper third sometimes from the base, tomentose to densely tomentose especially below, with stellate hairs only. (Figure 4.72A). LEAVES glaucous, tomentose to densely tomentose especially on the abaxial face (Figure 4.72B); lower leaves often arranged in a rosette, 38–148(-163) x 10–40 mm, attenuate into a long winged petiole (10-)17–53 mm, obovate-lanceolate to lanceolate, sometimes oblanceolate, apex obtuse or acute, and margin dentate to pinnatipartite; cauline leaves 20–66 x (8-)11–39 mm, frequently semiamplexicaul, oblong to oblanceolate, rarely elliptic or linear-lanceolate, base attenuate or slightly cuneate, apex acute, and margin lobate to pinnatifid, rarely pinnatipartite; upper leaves 11.6–42 x 3–28 mm, frequently semiamplexicaul sometimes sessile, elliptic to lanceolate or ovate to ovate-lanceolate, base ± cuneate or rounded, sometimes truncate, apex usually acuminate, and margin entire or lobate to pinnatifid. INFLORESCENCE paniculate-corymbose with ± 4 capitula or more frequently with solitary capitula longly pedunculate. CAPITULA (13-)16.5–38 mm in diameter (Figure 4.71B); peduncles 29–70 mm, with dense stellate hairs only (Figure 4.72C); involucre 9.3–17 x 8.6–19 mm, ± campanulate at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 6.5–11 x 0.9–1.5 mm, linear-lanceolate to linear-subulate, apex acuminate to subulate, flat not enfolding a floret, the outer face tomentose to densely stellate-tomentose with no glandular hairs; internal involucral bracts 6.7–11 x 1–1.8 mm, with broad scariose margins; receptacle convex, puberulous with short setose hairs 0.3–2 mm (much shorter than the cypselae, rarely equalling them). FLORETS ligulate, golden yellow, the external with a tube of 2.6–8 mm and ligule of 6.2–12 x 1–3 mm (Figure 4.71C), frequently with a reddish stripe on the outer face. CYPSELAE 2–2.7 x 0.3–0.6 mm (Figure 4.71D), oblong to obconical, light-brown with whitish ribs, apex with a ring of small teeth exceeding the inconspicuous prolongation of the ribs (Figure 4.72D); pappus of usually white bristles 4–7.5 mm, pilose at the base (Figure 4.72E).

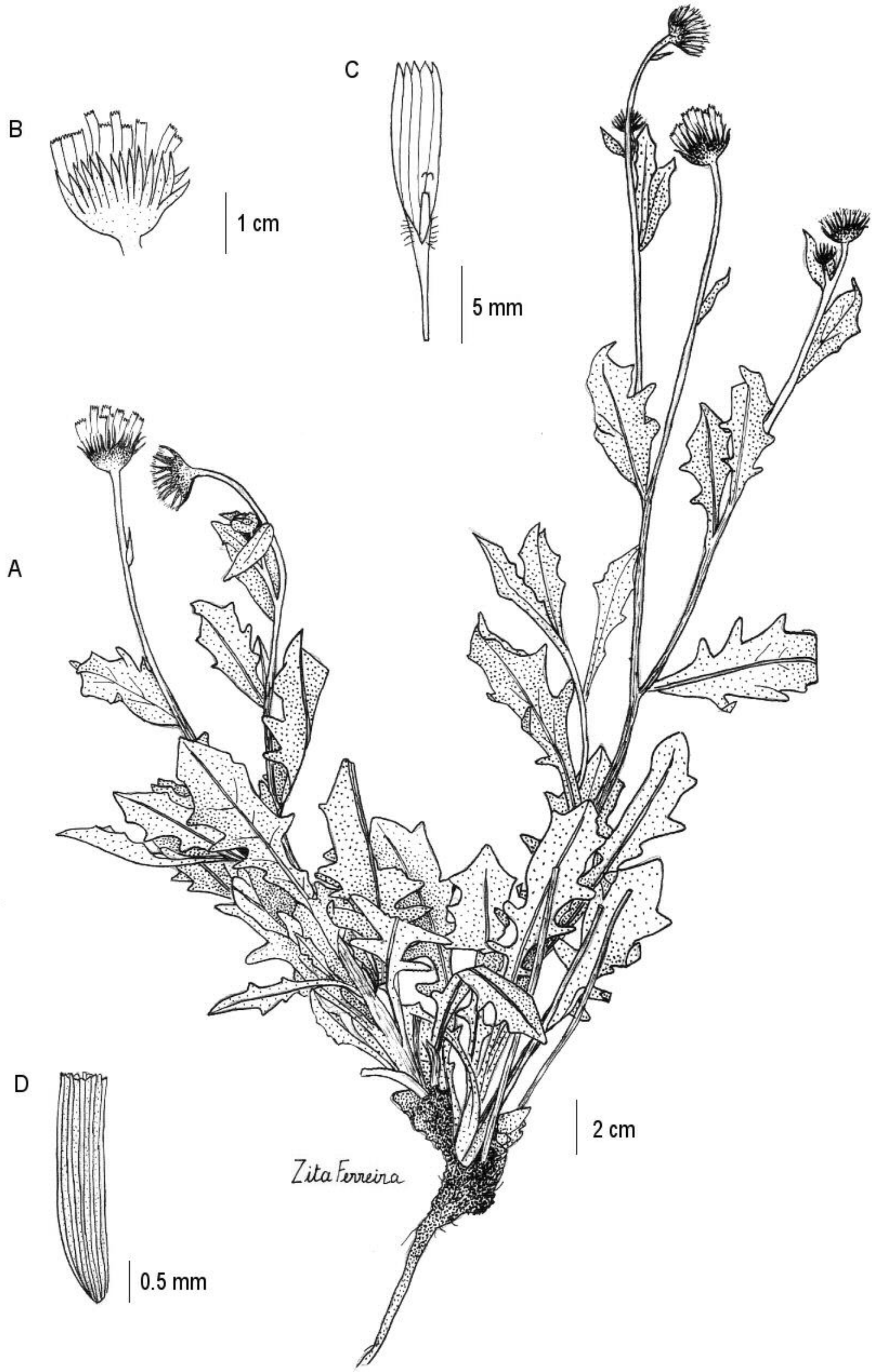


Figure 4.71 *Andryala ragusina* L. subsp. *ragusina* A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

4.18.5.2 Comments on taxonomy and nomenclature

Despite having recognised *Andryala ragusina* L., validly published by Linnaeus (1763), Lamarck (1783) described *A. laciniata* Lam. as a distinct species. In the protologue, Lamarck assigned *A. laciniata* Lam. to Spain and the vicinity of Narbonne (South of France), while the first was cited for the islands of the Aegean Sea ("*Isles de l'Archipel*") in accordance with Linnaeus. This disjunct geographic distribution may have had some influence in Lamarck's decision to consider both as distinct species.

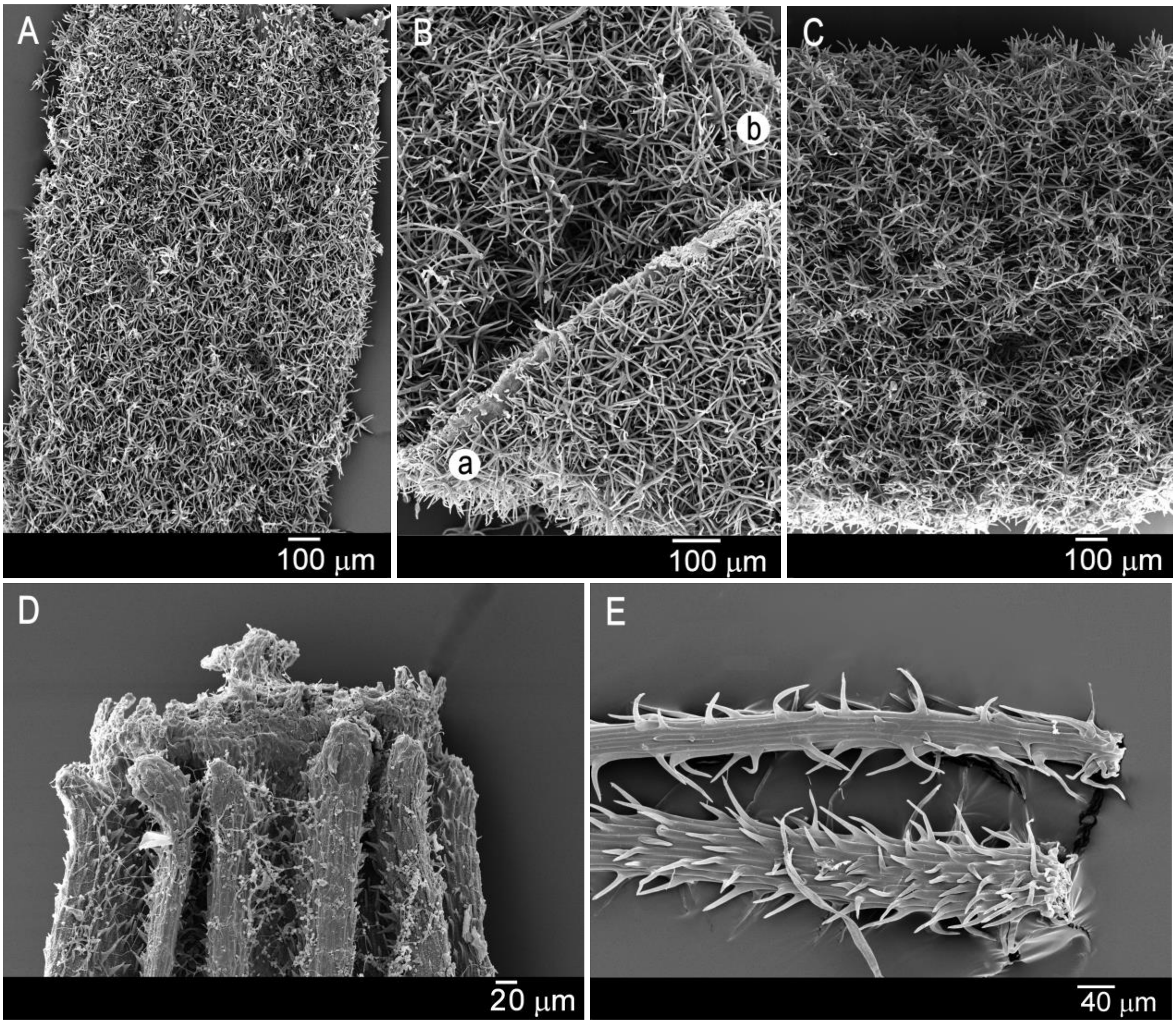


Figure 4.72 *Andryala ragusina* L. subsp. *ragusina* A – Stem indumentum, B – Leaf indumentum (a - abaxial face; b - adaxial face), C – Peduncle indumentum, D – Cypsela apex, E – Pappus base.

Some years later Pourret (1788) described *A. lyrata* Pourr. also for Narbonne. Since Lamarck (op. cit.) stated himself that *A. laciniata* Lam. was reported to him by Pourret, it seems that *A. laciniata* Lam. and *A. lyrata* Pourr. are no more than synonyms. Indeed, De Candolle (1838) recognised the variety *A. ragusina* var. *lyrata* (Pourr.) DC., indicating as synonyms *A. laciniata* Lam. and *A. lyrata* Pourr., besides *Rothia argentea* Lapeyr.

De Candolle (1838) also recognised *A. ragusina* L. var. *incana* (Lapeyr.) DC., citing as homotypic synonyms *A. incana* (Lapeyr.) DC. and *Crepis incana* Lapeyr. Some years before De Candolle (1815) had indeed made a new combination, *A. incana* (Lapeyr.) DC., citing *Crepis incana* Lapeyr. as the basionym. Candolle (1838: 244) distinguished the above varieties mainly based by leaf characters: *A. ragusina* var. *lyrata* Pourr. (DC.) ("*foliis infer. obtuse lyrato-pinnatifidis, caulinis obtusiusculè dentatis*") and *A. ragusina* L. var. *incana* (Lapeyr.) DC. ("*foliis infer. dentatis, caulinis ferè omnibus integerrimis acutissimis, capitulis minoribus*")[35]. The latter approaches quite well the original description of *A. ragusina* L. by Linnaeus (1763: 1136): "*foliis lanceolatis indivisis denticulatis acutis tomentosis, floribus solitariis*". In the protologue of *Crepis incana* Lapeyr. Lapeyrouse (1813: 483) also mentioned these features: *"… feuilles difformes sessile linéaires acuminées ou obtuse, entières avec une ou deux dents*

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[35] Besides *A. ragusina* var. *lyrata* Pourr. (DC.) and *A. ragusina* L. var. *incana* (Lapeyr.) DC., De Candolle (1838) acknowledged a third variety: *A. ragusina* var. *ramosissima* Boiss. ex DC. (see p. 213).

placées dant le haut, dans le bas ou dans le milieu de la feuille, … fleurs solitaires petits…". Given that *A. ragusina* var. *lyrata* Pourr. (DC.) and *A. ragusina* L. var. *incana* (Lapeyr.) DC. differ mainly by the margin of the lower and cauline leaves, both are here included in *A. ragusina* subsp. *ragusina.*

Boissier (1841) recognised *A. lyrata* Pourr., indicating *A. ragusina* L. and *A. laciniata* Lam. as synonyms. This author did not adopt the earliest validly published name, explaining that although name *A. lyrata* Pourr. is not very suitable for the species due to the variability in leaf shape, it is preferable to that of Linnaeus', given the error regarding to the provenance of the species. Actually, Boissier (1841) clearly assigned *A. ragusina* L. to France and Spain, refuting the origin stated by several authors in earlier literature (i.e. Dalmatia, an historical region of Croatia, and the islands of the Aegean Sea). Indeed, this species seems to have been inaccurately named after the Republic of Ragusa, a maritime republic centred on the city of Ragusa, currently known as Dubrovnik, Croatia).

Boissier (1841) recognised *A. lyrata* Pourr. var. *macrocephala* (Boiss. ex DC.) Boiss. Years before De Candolle (1838) described *A. macrocephala* Boiss. ex DC. as a distinct species, but Boissier (1838) considered it as a mere variety of *A. ragusina* L. growing in fertile soils. Furthermore, Boissier (1841: 393) distinguished *A. lyrata* Pourr. var. *macrocephala* (Boiss. ex DC.) Boiss. from *A. lyrata* Pourr. var. *lyrata* [= *A. ragusina var. lyrata* (Pourr.) DC.] mainly by the size of the plant, leaf shape, and size of the capitula ("*Major, folia latiora oblonga acuta semipinnatifendida lobis paucis. Capitula magna*."). In fact, the morphological similarities (e.g. perennial, stellate-tomentose with no glandular hairs; capitula few, solitary and usually longly pedunculate; involucral bracts linear-lanceolate and flat, not enfolding a floret) justify the inclusion of *A. macrocephala* Boiss. ex DC. in *A. ragusina* L. Accordingly, Nyman (1879) transferred it to a subspecies rank [*A. ragusina* L. subsp. *macrocephala* (Boiss. ex DC.) Nyman], probably also based on the geographical distribution since this author limited it to ancient Roman province in Southern Spain ("Baetica"). Nevertheless, this *taxon* has a wider distribution area in Spain, occurring also in Central and Northeastern localities. In light of the above, *A. ragusina* L. subsp. *macrocephala* (Boiss. ex DC.) Nyman is likewise here included in *A. ragusina* subsp. *ragusina.*

4.18.5.3 Ecology and conservation status

According to Hoffmannsegg & Link (1825), *A. ragusina* L. occurs on river shores and maritime fields. Likewise, De Candolle (1838) mentioned sandy river banks as the habitat of *A. ragusina* var. *lyrata* (Pourr.) DC. (here included in *A. ragusina* subsp. *ragusina*). Also referring to the species as whole, Willkomm & Lange (1865) stressed that it grows in sandy, gravelly, barren, and cultivated areas, from lower altitudes to mountainous regions reaching about 1700 m asl. In agreement Coutinho (1939) mentioned that *A. ragusina* L. can be found in stony or sandy, barren or dry places, including river banks. According to available herbarium data this *taxon* can also be found in vineyards, rocks, and scrublands. Talavera (1987) mentioned that *A. ragusina* L. can be found on slopes and pastures, growing chiefly on alkaline soils. In fact, Blanca (2009, 2011) indicated nitrophilous perennial pastures and thyme fields as its habitat, considering it still a ruderal and roadside species. In the same publications, Blanca also highlighted the wide altitudinal range of *A. ragusina* L. (0-2200 m). *Andryala ragusina* subsp. *ragusina* grows on thermo to supramediterranean dry and subhumid gravel, pebble and block slopes as part of plant communities included in the vegetation classe *Thlaspietea rotundifolii* Br.-Bl. (Rivas-Martínez *et al.* 2002).

Andryala ragusina L. is frequent, at least for Eastern Andalusia (Blanca 2009, 2011), and could be listed as Least Concern (LC) according to the *IUCN Red List categories and criteria* (IUCN 2001; 2012), as suggested by this author. Nevertheless, in Portugal *A. ragusina* L. is considered rare (Franco 1984).

4.18.5.4 Geographic distribution

A. ragusina subsp. *ragusina* occurs in SW Europe (Figure 4.73). Willkomm & Lange (1865) assigned *A. ragusina* L. to Spain (including Central, Oriental and Southern localities), as well as to Portugal, Southern France and Corsica. Sell (1976), Talavera (1987) and Blanca (2009, 2011) mentioned the same distribution area for *A. ragusina* L. , and extended it to the Balearic Islands. The reference of *Andryala ragusina* L. in several Italian floras (Arcangeli 1882; Fiori 1928; Cattarini 1976; Pignatti 1982) relates to its presence in Corsica. Indeed, Conti *et al.* (2005) do not cite it for Italy in the recent publication *An annotated checklist of the Italian vascular flora*. In Portugal *A. ragusina* L. is distributed in the central and southern parts, occurring only a in few localities in the North (Coutinho 1939; Sampaio 1949).

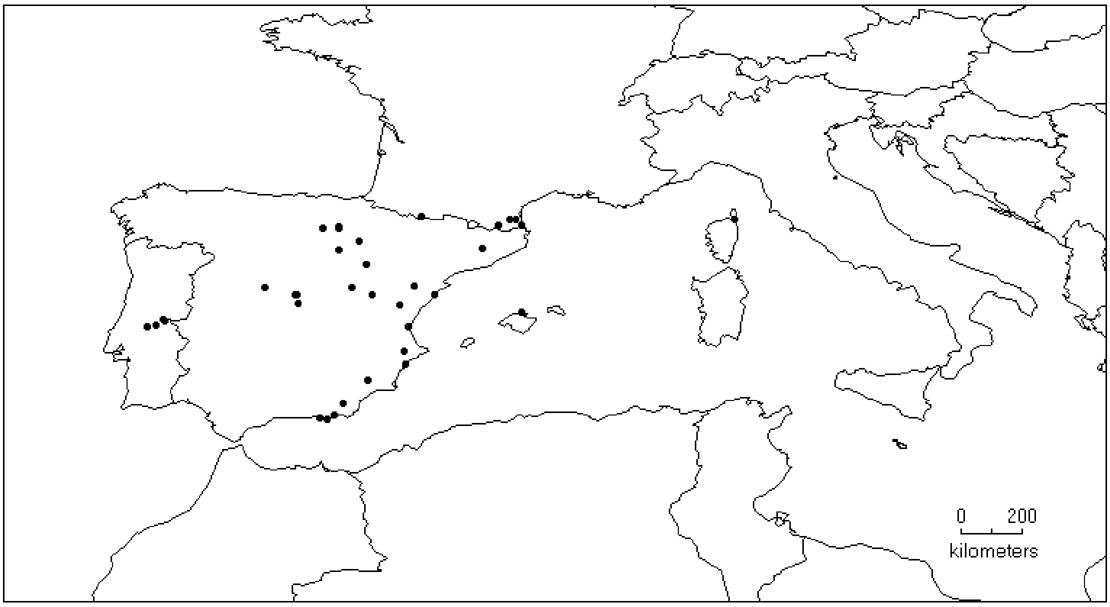

Figure 4.73 Distribution area of *Andryala ragusina* subsp. *ragusina*, according to studied material.

4.18.5.5 List of studied material

France: Gèdre, Pyrenees, Bordère, P 03692446. Argelès-sur-Mer, Pyrenees, sables de la plage, 01-VI-1851, Penchinat, P 03758444. Perpignan, Pyrénées orientales, Jude, P 04122284. Gèdre, Haut-Pyrenees, Bordère, P 03290755. Bord de la Têt, entre Ille et Millas (Pyrénées orientales), Pons-Simon, P 03277160. Bastia [Corsica], Bords de chemins, 21-VI-1849, P 03758445.
Portugal:
[Alto Alentejo]: Margens do Tejo: Belver, J. M. Zuqte d´O. Simões, s/ nº, LISU 40209.
[Beira Baixa]: Villa Velha de Rodão (fonte das virtudes), A. R. da Cunha, s/ nº, LISU 40203. Portas do Ródão: areaes do Tejo, J. da Silva Tavares., s/ nº, LISU 40212.
[Ribatejo]: Abrantes - Sto. António. Margem do Rio Tejo, A. R. da Cunha, s/ nº, LISU 40207.
[Trás-os-Montes]: pr. Bemposta, herbazales sobre arenas en la orilla del río, bordes de camino, roquedos, y matorrales, 13-VI-2010, C. Aedo & al., 17728.
Spain:
[Loc. incert.]: L. Née, MA 139364.
[Alicante]: Sra. de [?] Julian, [?] algo nitrofila, 28-IV-2053, MA 368584. Sierra Mariola, 10-VI-1896, MA 139043.
[Almería]: Seron Margas, 800 m.s.m., 20-V-1976, B. Cabezudo, S. Talavera & B. Valdés, s/ nº, LISU 163428. Sierra de Gador, por le encima de la Envía, Felix, 300 m, calizas, matorral de *Anthyllis cytisoides*, C. Aedo & al., CA3988, MA 591561. Adra, 19-VII-1929, E. Gros., MA 139073. Almerimar, arenas marítimas, 24-VI-1984, MA 352029.
[Ávila]: Ávila, río Adaja en laderas del pinar, Barrera, Carrasco, Sanchez & Velayos, MA 313299.
[Catalonia] : Cabanas, Friches, Sennen, MA 139045.

[Guadalajara]: Penãlen, los Callejones, 30 0574093 4503225, 1350 m, calizas, 08-VII-2010, L. M. Ferrero, L. Medina & A. Vela, LM 5128, MA.
[Ibiza]: Cala Molins, 24-V-1918, Gros, BC 36082.
[La Rioja]: Logroño, cerca del molina del Camposanto, en el Sotillo, MA 139018. Logroño, Ribera Del Ebro e Irezna, MA 139019. Logroño, Santo Domingo de la Calzada, Saludo, 76, MA 139363.
[Madrid]: Cerro Negro, in collibus aridis, Vicioso, MA 139066. Valdemoro, in collibus aridis, Vicioso C. et F. Beltran, MA 139063. Casa de Campo, 25-V-1852, Isern, MA 139005. La Moncloa, in marginibus camporum cerro negro, MA 139003. Guadalix de la Sierra, rotonda de la ctra. a Miraflores, 30T 0440371 4515490GEWGS84, 850 m, cuneta, 19-VI-2010, L. Medina & M. Sequeira, LM 5103, MA 809365.
[Múrcia]: Sierra de Espuña, in dumetis, 21-VI-1747, C. Vicioso, MA 139067.
[Navarre]: Euskal Herria, Navarra, Fitero, Barranco Blancares, 500 m, Aizpuru & Catalán, MA 704607.
[Saragossa]: Calatayud, sables stériles, 18-VII-1910, C. Vicioso, MA 139055. Calatayud, in aridis, Vicioso B. et C., MA 139015. Calatayud, frequens in vineis, B. Vicioso, 329, MA 139094.
[Soria]: Numancia, 06-VII-1955, MPU.
[Tarragona]: Pista de Fredes al Monte Caro, barranco de Millers, 1000 m, C. Aedo, I. Aizpuru, J Aldasoro, S. Castroviejo, R. Tavera & M. Velayos, MA 626748.
[Teruel]: Cueva Santa, S. Agustin, Olba, In vineis, MA 139095. Val de Gabriel (Sierra de Albarracín), Blanca, MA 139093.
[Valencia]: Segorbe, in collibus arenosis, 22-VI-1923, Dr. C. Pau?, s/ nº, LISU 55355. Benicarló, graviers du Rio Seco, 06-VI-1909, MA 139084.

4.18.6 ***Andryala ragusina*** **L. subsp.** ***ramosissima*** **(Boiss. ex DC.) M. Z. Ferreira, Alv. Fern. & M. Seq. stat. nov.**

≡ *Andryala ragusina* L. var. *ramosissima* Boiss. ex DC., Prodr. 7(1): 244. 1838 [late Apr 1838], *basion.*
Andryala ramosissima (Boiss. ex DC.) Boiss., Elench. Pl. Nov. 63. 1838 [Jun 1838]
Andryala lyrata Pourr. var. γ *ramosissima* (Boiss. ex DC.) Boiss., Voy. Bot. Espagne. 2(13): 393. 1841
Ind. loc.: “in collibus siccis et calcareis maritimis regni Granatensis usque ad 5000 ped. altit. legit cl. Boissier.”
Typus: [Spain] “In montanis arenosis Regn. Granat. Alt. 2000´-5000´, Jun. 1837”, *Boissier 137* – Lectotype (designated by Burdet *et al.* 1983): G00222221 (middle specimen of sheet 1); isolectotypes: G00222221 (remaining specimens); GDC023652 (designated by Burdet *et al.* 1983), MPU019275, MPU019276, MPU019277, P03772091, P03772080, P03772129, G00223888, NY00158200, NY00158201, HAL 0113308, GH0000849.

4.18.6.1 Typification

Several specimens filed under the registration number G00222221 are kept at the G ex herb. Boissier. Although distributed on eight herbarium sheets, all are clearly part of the same gathering (the labels show identical collection date and collector number). Burdet *et al.* (1983) designated the middle specimen of sheet 1 as lectotype, believing that it was the basis of the illustration (Tab. 118a) presented in the first volume of *Voyage botanique dans le midi de l'Espagne pendant l'année 1837* by Boissier (1841). However, this *taxon* was first described by De Candolle (1838) under *A. ragusina* var. *ramosissima* Boiss. ex DC. and not by Boissier. Hence, the specimen from the De Candolle collection on which the author most likely based his description (GDC023652) could have been a better choice. Indeed, it is under the names “*Andryala ramosissima Boiss.”* and “*Andryala ragusina var. ramosissima DC.*” handwritten by De Candolle. Burdet *et al.* (1983) elected this specimen as isolectotype, just as the remaining specimens of all eight sheets filed under G00222221. Additional isolectotypes were found in different herbaria, including P, MPU, NY, HAL, and GH.

4.18.6.2 Description

Perennial herb, multi-stemmed or caespitose, with a dark woody stock (Figure 4.74A). STEMS 36–65 cm, profusely branched from the base, densely tomentose with stellate hairs only (Figure 4.75A). LEAVES glaucous, tomentose on both faces (Figure 4.75B); lower leaves persistent or sometimes marcescent at anthesis, 85 x 12 mm, attenuate into a winged petiole 32 mm, lanceolate to linear-lanceolate, apex acute, and margin lobate to pinnatifid; cauline leaves 52–58 x 8–9 mm, scarce, sessile or semiamplexicaul, linear-lanceolate, base attenuate, apex acute, and margin ±

pinnatifid; upper leaves 15–19.4 x 1.3–2.9 mm, semiamplexicaul, narrowly ovate-lanceolate or linear-subulate, base truncate, apex acuminate, and margin entire. INFLORESCENCE with solitary capitula longly pedunculate. CAPITULA 15.6–17.5 mm in diameter (Figure 4.75B); peduncles about 68 mm, with dense stellate hairs only (Figure 4.75C); involucre 9.4–10.7(-12) x 9.3–10.4 mm, ± campanulate at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 6–8.6 x 1–1.2 mm, linear-lanceolate, apex acuminate to subulate, flat not enfolding a floret, the outer face stellate-tomentose with no glandular hairs; internal involucral bracts 6.3–7.7 x 1–1.8 mm, with broad scariose margins; receptacle convex, puberulous with short setose hairs 1.9 mm (shorter than the cypselae).

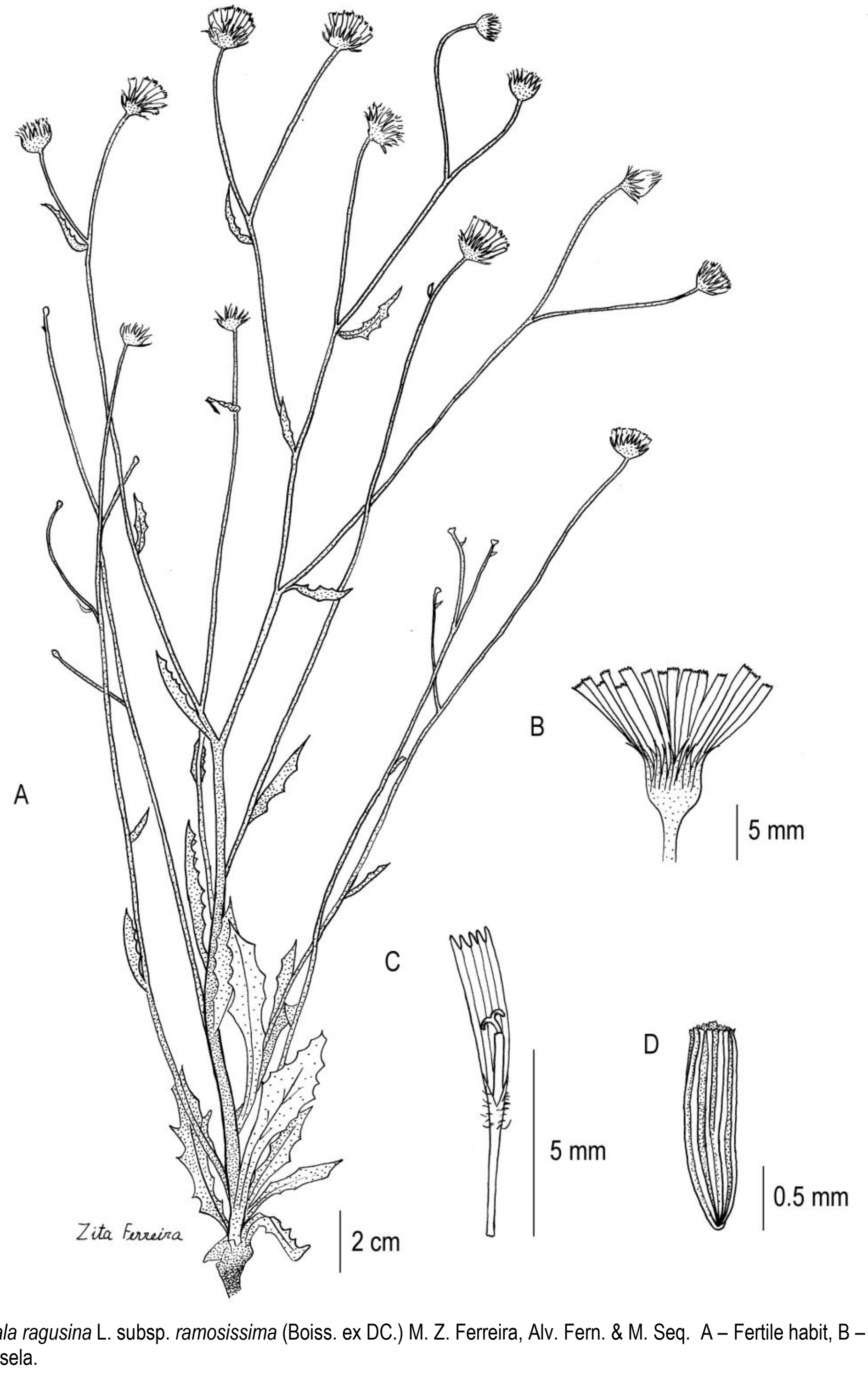

Figure 4.74 *Andryala ragusina* L. subsp. *ramosissima* (Boiss. ex DC.) M. Z. Ferreira, Alv. Fern. & M. Seq. A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

FLORETS ligulate, golden yellow, the external with a tube of 3.3–5 mm and ligule of 4.6–8 x 1.5–2 mm (Figure 4.74C), frequently with a reddish stripe on the outer face. CYPSELAE 2.5 x 0.5 mm (Figure 4.74D), oblong to obconical, light-brown with whitish ribs, apex with a ring of small teeth exceeding the inconspicuous prolongation of the ribs (Figure 4.75D); pappus of dirty-white bristles 5.5–6 mm, ± pilose at the base (Figure 4.75E).

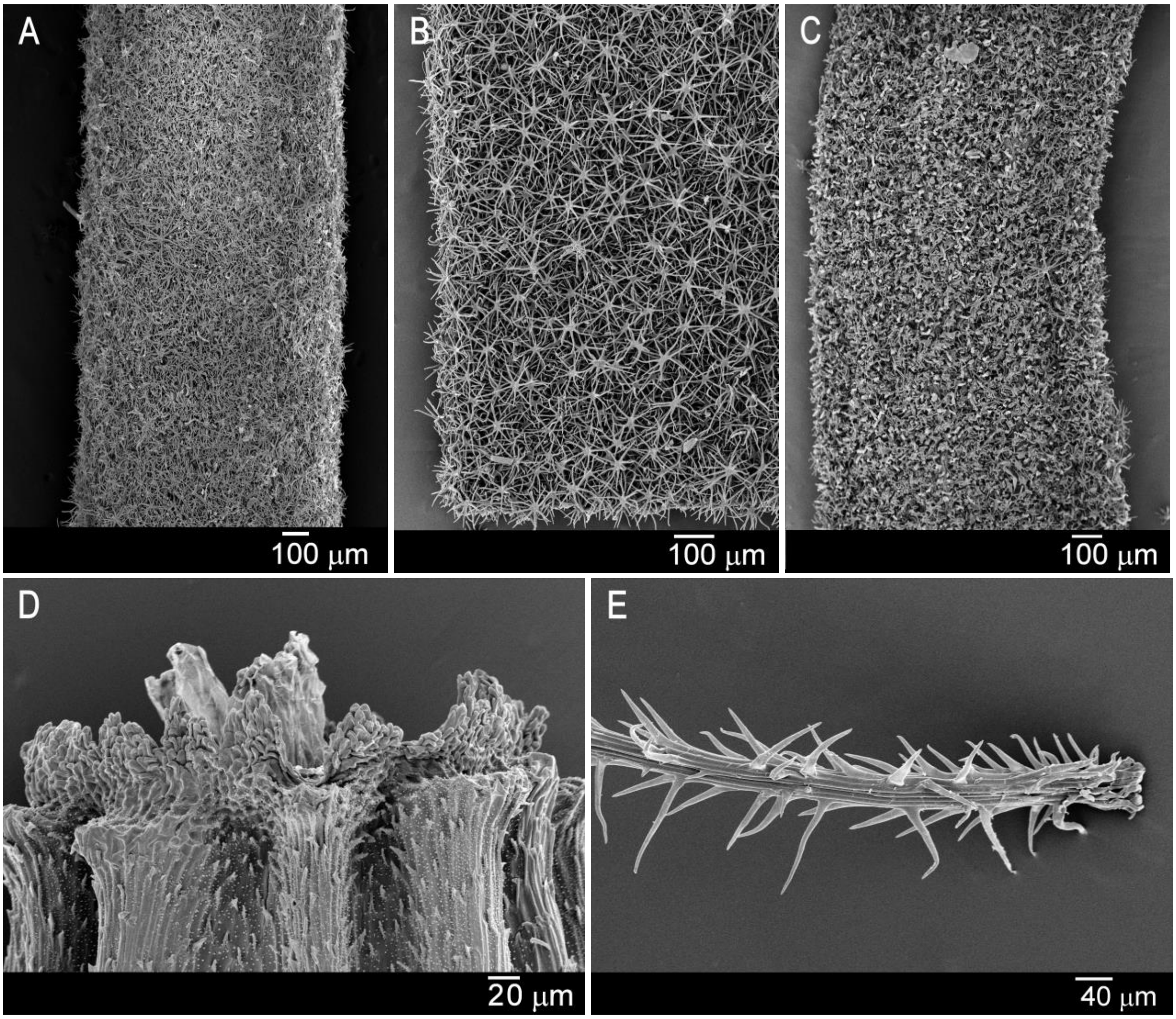

Figure 4.75 *Andryala ragusina* L. subsp. *ramosissima* (Boiss. ex DC.) M. Z. Ferreira, Alv. Fern. & M. Seq. A – Stem indumentum, B – Leaf indumentum, C – Peduncle indumentum, D – Cypsela apex, E – Pappus base.

4.18.6.3 Comments on taxonomy and nomenclature

De Candolle (1838) described *Andryala ragusina* var. *ramosissima* Boiss. ex DC., using the unpublished epithet "*ramosissima"* of Boissier's authority, as stated by the author himself. Only some months later Boissier (1838) transferred this *taxon* to a species rank, indicating *A. ragusina* var. *ramosissima* Boiss. ex DC. as the basionym, and considered it morphologically distinct from *A. ragusina* L., as illustrated by the following text: "*Ab A. ragusina bene distinguitur caulibus simplicibus strictis fragilibus unifloris, involucri squamis latioribus margine late membranaceis nec subulatis, flosculis multò brevioribus*." Later, Boissier (1841) combined it under *A. lyrata* Pour. var. *ramosissima* (Boiss. ex DC.) Boiss. and provided a very good illustration of this *taxon* (Figure 4.76). Several later authors recognised *A. ragusina* var. *ramosissima* Boiss. ex DC. (e.g. Willkomm & Lange 1865; Amo y Mora 1872; Franco 1984; Blanca 2009, 2011). In particular, Blanca (2009, 2011) distinguished *A. ragusina* var. *ramosissima* Boiss. ex

DC. from the typical variety based on stem ramification, leaf width, and capitula size ["*var. ragusina … generalmente ramificada en el tercio superior, hojas más anchas y capítulos mayores (involucro 9–15 x 7–15 mm), y var. ramosissima Boiss., profusamente ramificada desde la base, hojas más estrechas y capítulos menores (involucro 7–8 x 5–6 mm)*"]. Similarly, Sell (1976: 358) differentiated these two varieties based on the same characters and further emphasized that they may deserve the rank of subspecies. According to Sell (op.cit.) both appear to occur throughout the range of the species and their ecology is not clearly understood. However, *A. ragusina* subsp. *ramosissima* definitely occurs in mountain chains, while the typical subspecies has high altitudinal range. Thus, it seems quite reasonable to follow Sell's taxonomic point of view of attributing a subspecies rank to *A. ragusina* var. *ramosissima*. Actually, some authors recognise this *taxon* and *A. ragusina* L. subsp. *ragusina* as distinct species, including them in different plant communities (Rivas-Martínez *et al.* 2002).

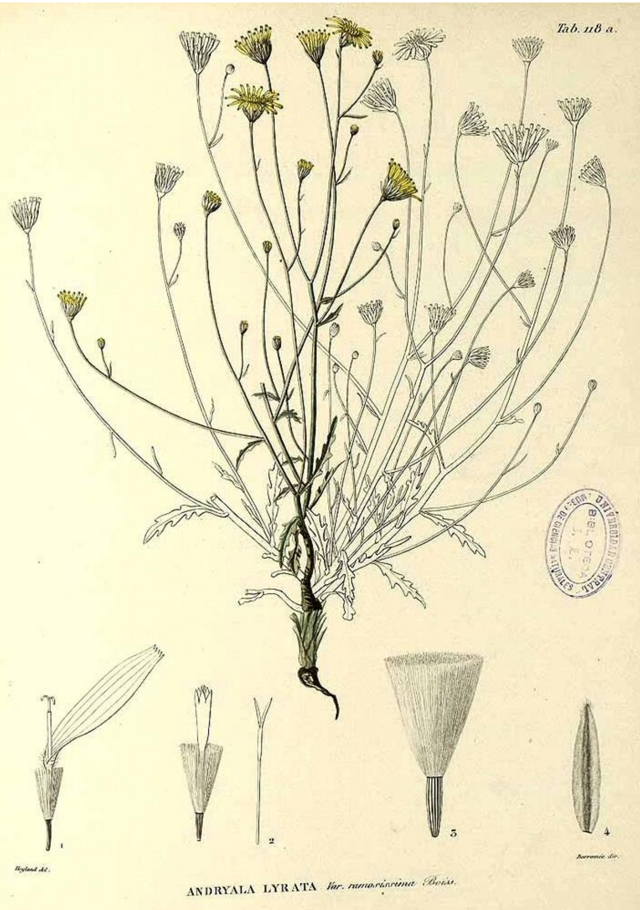

Figure 4.76 Reproduction of the icon of *Andryala lyrata* Pourr. var. γ *ramosissima* (Boiss. ex DC.) Boiss., Voy. Bot. Espagne. 2(13): 393 (1841)

4.18.6.4 Ecology and conservation status

Although De Candolle (1838) stressed the occurrence of *A. ragusina* var. *ramosissima* Boiss. ex DC. on dry calcareous coastal slopes ascending up to 1500 m asl., Bossier (1838: 63) specifically stated that this *taxon* grows on sandy mountains and not on gravelly shores where the typical variety thrives ("*Hab. in montanis arenosis totius regni Granatensis usque ad 5000´, nunquám verô in glareosis litoralibus ubi A. ragusina viget."*). Later Bossier (1841) further elucidated that it ocurrs in calcareous barren sands, in mountainous regions from ± 300 to 1400 m ("*in arenis calcareis mobilibus sterilissimis regionis calidae superioris et montanae… Alt. 1000´ - 4500´*"). Blanca (2009, 2011) stated that this *taxon* can be found in the crystalline dolomites in mountain chains. In fact, it grows in the dolomitic Betic Mountains as part of the dwarf perennial chasmo-comophyte rupestrian plant communities included in the vegetation classe *Phagnalo-rumicetea indurati* (Rivas Goday & Esteve 1972) Rivas-Martínez, Izco & Costa, (Rivas-Martínez *et al.* 2002). According to available herbarium data, *A. ragusina* L. subsp. *ramosissima* (Boiss. ex DC.) M. Z. Ferreira, Alv. Fern. & M. Seq. occurs on dolomite sands and rocks at high altitudes, on roadsides and scrublands. In what concerns the conservation status, Blanca (2009, 2011) highlighted that this *taxon* is less frequent than the typical one. However, it can be listed as Least Concern (LC) according to the *IUCN Red List categories and criteria* (IUCN 2001; 2012).

4.18.6.5 Geographic distribution

Andryala ragusina L. subsp. *ramosissima* (Boiss. ex DC.) M. Z. Ferreira, Alv. Fern. & M. Seq. can be found in Eastern Andalusia (Spain) and the neighbouring region of Murcia in the southeast of the country (Boissier 1838; Boissier 1841; Willkomm & Lange 1865; Amo y Mora 1872). According to available herbarium data, it occurs in the Andalusian provinces of Granada, Málaga and Córdoba (Figure 4.77) and is possibly found in the Pyrenees in South and Southwestern France. Its presence in Portugal is dubious because it was only cited by Franco (1984) to the central-east part of the country. More sampling will be necessary to enhance the knowledge on the distribution area of this *taxon*.

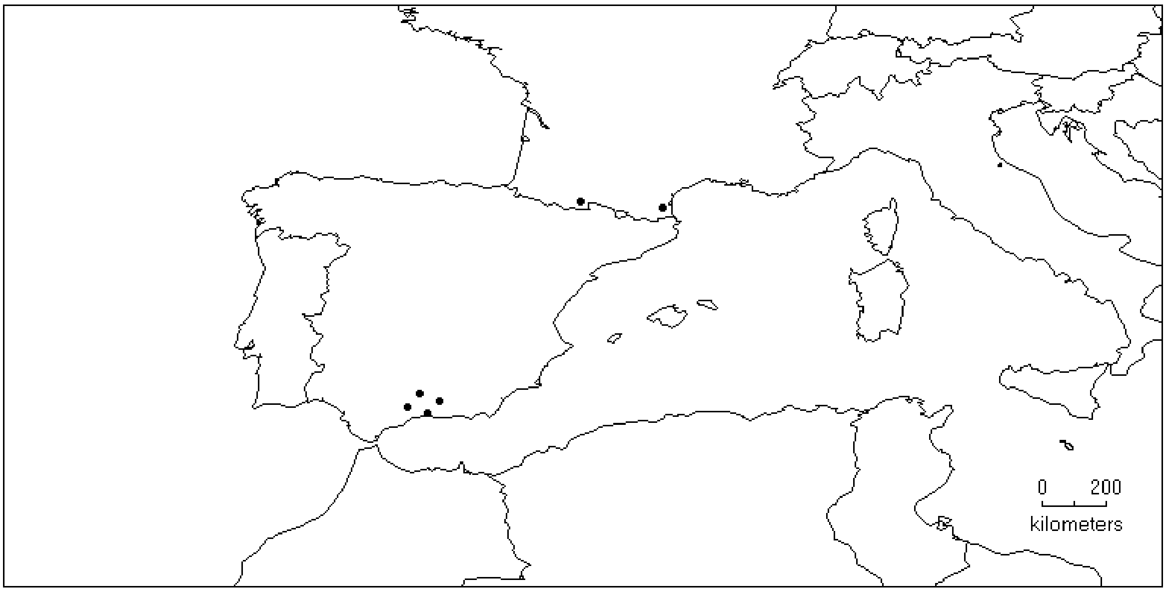

Figure 4.77 Distribution area of *Andryala ragusina* subsp. *ramosissima* (Boiss. ex DC.) M. Z. Ferreira, Alv. Fern. & M. Seq., according to studied material.

4.18.6.6 List of studied material

France: lit de la Têt, à Perpignan, 12-VII-1870, P 03289023. Environ de Ille (Pyrénées orientales), gravieres au bord de la Têt, 25-VII-1891, Pons-Simon, P 03692444.
Spain: Sierra Halconera, Priego, Matorrales, bordes de caminos, J. Borja, MA 182140.
[Córdoba]: In montanis arenosis Regn. Granat. Alt. 2000-5000 ft, Boissier, P. E., El. 137, P 03772091.
[Granada]: Sierra de Competa., arena y rocas dolomiticas, 850-900 m.s.m., 07-VII-1973, B. Cabezudo & B. Valdés, s/ nº, LISU
[Málaga]: 163430. pr. Antequera, Bordes de caminos, 25-V-1965, J. Borja et Rivas Goday, MA 187208.

4.18.7 *Andryala ragusina* L. subsp. *spartioides* Pomel ex Batt. in Batt. & Trab. Fl. Alger. 566. 1890

≡ *Andryala spartioides* (Pomel ex Batt.) Barratte, Ill. Fl. Atlant. 2(6): 74, t. 145. 1893

Ind. loc.: "Djelfa, El-Outaïa, El-Kantara, etc. Maroc (Cosson)."

Typus: [Algeria] "El Outaïa", *Battandier s.n.* – Lectotype (designated by Ferreira *et al*. 2015b, see Appendix 4): MPU019886, syntypes: MPU019883, MPU019884, MPU019885, P02462509, P02462513, P02462535, MPU019280; P02462508, P02462510, P02462511, P02462514, P02462520, P02462521, P02462522, P02462540, P04119461, P04119462, MPU020477.

_ *Andryala ragusina* var. *virgata* Coss. in Batt. & Trab. Fl. Alger. 566. 1890, *nom. nud.*

4.18.7.1 Typification

Battandier (1890: 566) described *A. ragusina* subsp. *spartioides* based on specimens under the herbarium names *A. spartioides* Pomel (from the Pomel herbarium, as mentioned in the protologue) and *A. ragusina* var. *virgata* Cosson (presumably from the Cosson herbarium). The specimen MPU019886, designated as lectotype, is originally from

Battandier's herbarium (included in the Maire collection now at MPU) and is labelled as *Andryala spartioides* in Pomel's hand. Moreover, it was collected in a locality mentioned in the protologue and matches the original description quite well (Ferreira *et al*. 2015b, see Appendix 4). Although a few other specimens under the name *A. spartioides* Pomel were found (MPU 019884 and MPU 019885 - fragments of the same plant - and MPU 019883 - a duplicate), they are not suitable for lectotypification given their poor preservation state. However, they are syntypes, just as are all specimens under the herbarium name *A. ragusina* var. *virgata* from the Cosson herbarium, held at the P and MPU herbaria (Ferreira *et al*. 2015b, see Appendix 4).

4.18.7.2 Description

Perennial herb, caespitose, with a dark woody stock (Figure 4.78A). STEMS about 78 cm, profusely branched from the base, tomentose with stellate hairs only (Figure 4.79A). LEAVES tomentose on both faces only with stellate hairs (Figure 4.79B); lower leaves numerous, marcescent at anthesis, usually not persistent, attenuate into a winged petiole, lanceolate to linear-lanceolate, apex acute, and margin lobate to pinnatifid; cauline leaves scarce, 41 x 2.8 mm, semiamplexicaul, linear, base truncate, apex acute, and margin entire; upper leaves scarce, 8.6 x 2.2 mm, semiamplexicaul, narrowly ovate-lanceolate or linear, base truncate, apex acute, and margin entire. INFLORESCENCE paniculate-corymbose or with solitary capitula longly pedunculate. CAPITULA about 10 mm in diameter (Figure 4.78B); peduncles about 65 mm, stellate-tomentose with no glandular hairs (Figure 4.79C); involucre 8 x 5.6 mm, campanulate at anthesis, with involucral bracts in 3–4 rows; external involucral bracts 3.7–4.8 x 0.7–1 mm, lanceolate to linear-lanceolate, apex acuminate, flat not enfolding a floret, the outer face thinly stellate-tomentose with no glandular hairs; internal involucral bracts 3.6–4.8 x 1–1.4 mm, with broad scariose margins; receptacle convex, puberulous with short setose hairs 0.5–0.7 mm (much shorter than the cypselae). FLORETS ligulate, golden yellow, the external with a tube of 2.6–3.6 mm and ligule of 3.6 x 0.8 mm (Figure 4.78C). CYPSELAE 2 x 0.3 mm (Figure 4.78D), oblong, light-brown with whitish ribs, apex with a ring of small teeth exceeding the inconspicuous prolongation of the ribs; pappus of whitish bristles about 4 mm, ± pilose at the base (Figure 4.79E).

4.18.7.3 Comments on taxonomy and nomenclature

Battandier (1889) described *Andryala ragusina* subsp. *spartioides* Pomel ex Batt. and later Barratte (1893) transferred it to a species rank. Nonetheless, Barratte (1893: 75) highlighted that it shares some features with *A. ragusina* L., namely the habit, indumentum and the inflorescence: "*A. spartioides caudice perenni lignoso superne pluricipite, indumento stellato pilis simplicibus glanduliferis intermixtis omnino destituto, capitulis apice ramorum pedunculorumque solitariis …*". In the same publication, this author still emphasized that this *taxon* is morphologically very closely related to *A. ramosissima* Boiss., in spite of some differences: "*A. ramosissima* Boiss. *Elench. 63 valde affinis, sed differi indumento pulverulento etiam in herbariis viridi-flavescente, non plus minus floccoso primum incano demum valde rufescente, habitu, foliis jam sub anthesi emarcidis ad petiolorum vestigia redactis, non persistentibus, ramis gracilibus elongatis virgatis subaphyllis, non saepissime robustis, capitulis minoribus, involucri foliolis 3-4 seriatis, non 2-seriatis, pappo achaenium duplo non 5-plo aequante.*" Indeed, *A. ragusina* subsp. *ramosissima* exhibits stems densely stellate-tomentose, basal leaves persistent at anthesis, branches often less slender and more leafy, capitula larger, and involucral bracts arranged in 2-3 rows. Given the morphological similarities to *A. ragusina* L. as well as the differences compared to *A. ragusina* subsp. *ramosissima* and since this *taxon* occurs in a geographic area entirely apart from the other *A. ragusina taxa* herein accepted, it is worth of a subspecies rank.

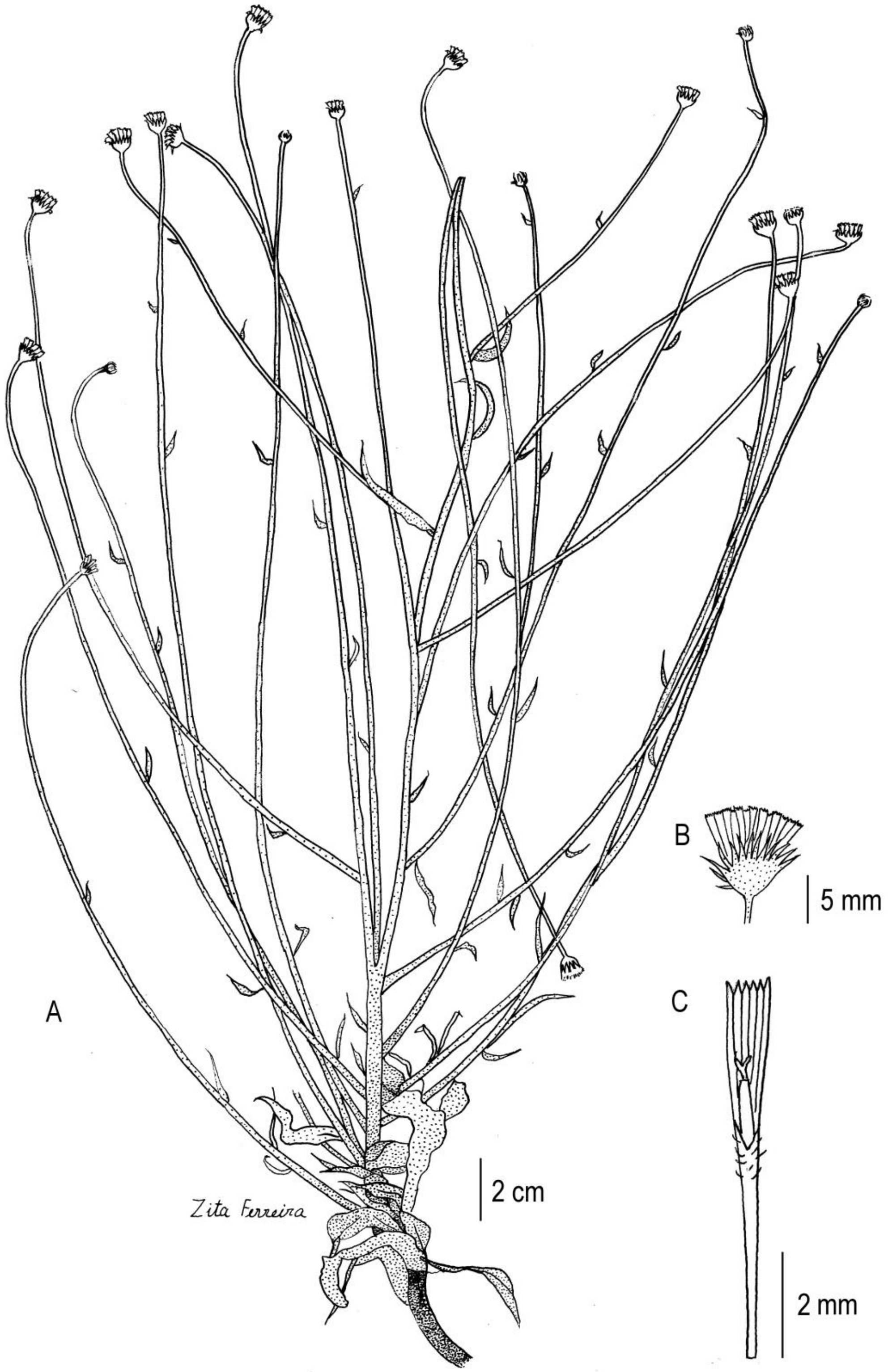

Figure 4.78 *Andryala ragusina* L. subsp. *spartioides* Pomel ex Batt. A – Fertile habit, B – Capitulum, C – Floret.

4.18.7.4 Ecology and conservation status

Andryala ragusina L. subsp. *spartioides* Pomel ex Batt. occurs in sandy uncultivated places and dunes (Barratte 1896; Pottier-Alapetite 1981). It can be found in sandy pastures and mountain slopes, dry water channels in the sub-Saharan region, and more rarely in plains with high temperatures (Barratte 1893). In accordance with available herbarium data, this *taxon* also grows on dry gravelly places. In what concerns the conservation status, literature on this matter is quite scarce, however, *Andryala ragusina* L. subsp. *spartioides* Pomel ex Batt., is found in the list of protected uncultivated Algerian plant species (see: "Décret exécutif nº 12-03 du 10 Safar 1433 correspondant au 4 janvier 2012 fixant la liste des espèces végétales non cultivées protégées" 2012).

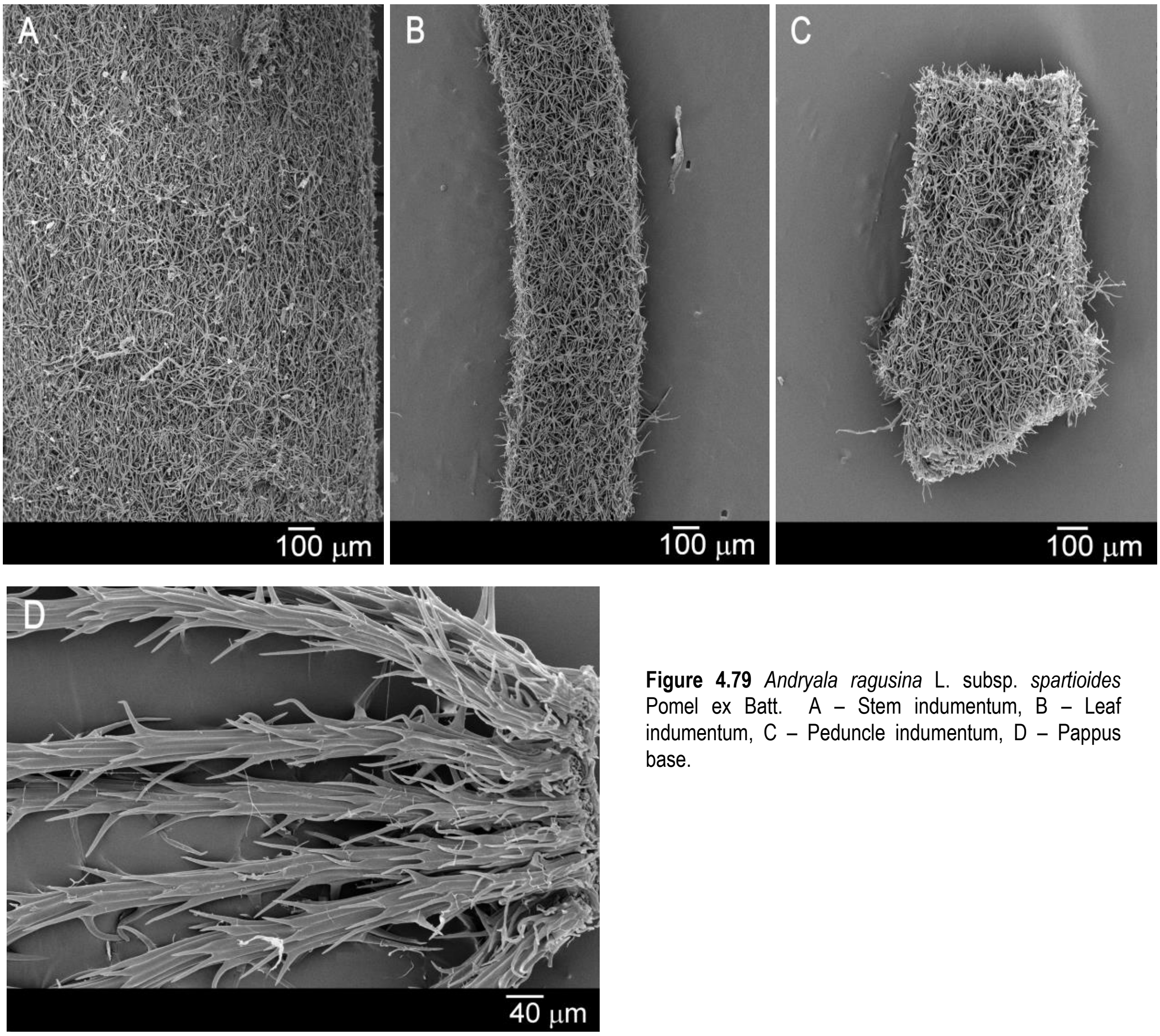

Figure 4.79 *Andryala ragusina* L. subsp. *spartioides* Pomel ex Batt. A – Stem indumentum, B – Leaf indumentum, C – Peduncle indumentum, D – Pappus base.

4.18.7.5 Geographic distribution

Andryala ragusina subsp. *spartioides* Pomel ex Batt. is endemic for Tunisia and Algeria (Pottier-Alapetite 1981) (Figure 4.80). According to Barratte (1896), it occurs in southern Tunisia. In *Checklist des endémiques et spécimens types de la flore vasculaire de l'Afrique du Nord* it was assigned not only to Tunisia and Algeria, but also to Libya (El Oualidi *et al.* 2012). However, the presence of this *taxon* in Libya still needs verification as stated by Boulos (1979).

Figure 4.80 Distribution area of *Andryala ragusina* subsp. *spartioides* Pomel ex Batt., according to studied material.

4.18.7.6 List of studied material

Algeria:	
[Biskra]:	El Kantara, in aridis glareosis, 08-VII-1902, L. Chevallier, MA 139052. El Outaïa, Battandier, J.A., s/ nº, MPU 019886.
[Djelfa]:	Environs de Djelfa, Oued Melah, 1856, Reboud V.C., P 04122241.
Tunisia:	
[Harare]:	Oued Zitoum, 21-VI-1884, Letourneux, A., s/ nº, P 02462508.
[Kairouan]:	Aïn-Cherichira, Ouest de Kairouan, 20-VI-1883, Cosson, E., Doumet-Adanson, A. Letourneux, V. Reboud, G. Barratte, E. Bonnet, s/ nº, P 00723595. Aïn Cherichira, 20-VI-1883, MPU-Maire 34223. Nord-este d'Ain-Cherichira, 19-VI-1883, Cosson, E., Doumet-Adanson, A. Letourneux, V. Reboud, G. Barratte, E. Bonnet, s/ nº, P 02462511.
[Kasserine]:	Feriana, VI-1884, Robert, J. F., 317, P 02462520.

4.19 *Andryala rothia* Pers., Syn. Pl. [Persoon] 2(2): 378. 1807

≡ *Voigtia tomentosa* Roth in Roem. & Usteri, Mag. 10: 17. 1790. *syn. subst.*
Rothia andryaloides Gaertn., Fruct. Sem. Pl. 2: 371. 1791, *nom. illeg. nom. superfl.*
Andryala rosea Steud., Nomencl. Bot., ed. 2. 2: 779 in syn., sphalm. 1841, *nom. illeg. nom. superfl.*
Ind. loc.: sine (Roth, 1790)
Typus: *A. W. Roth s.n.* – Lectotype (designated by Ferreira *et al.* 2015b, see Appendix 4): M0031113.

= *Andryala laxiflora* DC., Prodr. 7(1): 246. 1838, *nom. illeg. nom. superfl.*
Rothia laxiflora Salzm., in De Candolle, Prodr. 7(1): 247. 1838.
Andryala sinuata L. subsp. *laxiflora* (DC.) Nyman, Consp. Fl. Eur.: 438. 1879
Ind. loc.: "in Mauritania circà Tanger legit cl. Salzmann et circà Malagam cl. Boissier.
Typus: [Morocco] "Tanger 1825", *Salzmann s.n.* – Lectotype (designated here): G00493574; isolectotypes: K000251903, K000251906, K000251907, E00239945; syntypes: HAL0113310, MPU001365, MPU001366, MPU001367, MPU001524, MPU001525, MPU001526, MPU001527, MPU001528, MPU001529, M0109464.

= *Andryala floccosa* Pomel, Nouv. Mat. Fl. Atl. 3. 1874
Rothia floccosa Pomel, Nouv. Mat. Fl. Atl. 3. 1874, *nom. alt.*
Andryala laxiflora var. *floccosa* (Pomel) Batt. & Trab., Fl. Algerie Tunisie 218. 1905
Ind. loc.: [Algeria] "Terrains argilo-gypseux: Dahra."
Typus: Algeria, "Beni Zerovals O. Dahra, 05-1867", *Pomel s.n.* – Lectotype (designated here): P04119456 (specimen on the lower left-hand corner); isolectotypes: P04119456 (remaining specimens).

= *Andryala laxiflora* DC. var. *candicans* Maire in Jahandiez & Maire, Cat. Pl. Maroc. 3: 843. 1934
Ind. loc.: "*Andryala laxiflora* (Salzm.) DC. var. *candicans* Maire, Contr. 608 - MA. Mont Tazzeka (Emb. et Maire)"
Typus: [Morocco] "In Atlantis medii montibus supra urbem Taza in rupestribus schistaceis, 1300 m, 18 June 1925", *Maire s.n.* – Lectotype (designated here): MPU002123 (specimen on the left), isolectotypes: MPU002123 (remaining specimens), P00710612!; syntypes: MPU002122, RAB043317.

= *Andryala arenaria* subsp. *mariana* Rivas Goday & Bellot in Bol. Soc. Esp. Hist. Nat. 40, Biol: 64. 1942

Ind. Loc.: [Spain] "Hab: in rupestribus apricis, loco dicto Valdeazores, circa Despeñaperros, Montium Marianorum: 650 alt. ubi d. 12 junii 1941, invenimus."

Typus: Spain, "in rupestribus apricis, loco dicto Valdeazores (Despeñaperros) Montium Marianorum, 12-06-41", *S. Rivas Goday & F. Bellot s.n.* – Holotype: MAF09056; isotype: MAF09056.

_ *Andryala malacitana* Haens. in Willkomm & Lange, Prodr. Fl. Hispan. 2: 272. 1865, *nom. nud. in sched.*

4.19.1 Typification

Roth (1790) described the genus *Voigtia* Roth, comprising a single species: *Voigtia tomentosa* Roth. Later, Gaertner (1791) combined *Voigtia tomentosa* into *Rothia* Schreb. under the name *Rothia andryaloides*, which is illegitimate, because the epithet "*tomentosa"* should have instead been used according to Art. 7.4 of the ICN (McNeill *et al*., 2012). Much later Persoon (1807) included *Voigtia tomentosa* in the genus *Andryala*, but under the name *A. rothia* given that *A. tomentosa* Scop. (Scopoli 1787) already existed. There is one specimen at the M herbarium accompanied by the original description of *V. tomentosa* handwritten on the sheet by Roth; this sheet also includes the name *R. andryaloides* lately added by him. There is another specimen at B-W herbarium (B-W14770-01 0) under the same name handwritten by Roth as well, but no reference to the name *V. tomentosa* is included. For this reason, the specimen hosted at the M herbarium (M0031113) was designated as lectotype of *Voigtia tomentosa* Roth (Ferreira *et al*. 2015b, see Appendix 4).

In the protologue of *A. laxiflora* DC. De Candolle (1838) made reference to herbarium material collected in Tangier and Málaga, respectively, by Salzmann and Boissier. In particular, the author indicated a specimen under "*Rothia laxiflora Salzm.! pl. exs. 1825*". Indeed, a specimen labelled *"Rothia laxiflora mihi"* in Salzmann's handwriting was located in the De Candolle collection held at the G herbarium. The collection data on the label is identical to the one mentioned in the protologue. In a later label De Candolle renamed the specimen as *Andryala laxiflora* DC. In view of the foregoing, this specimen (G00493574) is here designated as lectotype. A few specimens with the same collection data, originally under the name *Rothia laxiflora* Salzm., handwritten by Salzmann, were found at the K and E herbaria and are, therefore, isolectotypes. The Salzmann herbarium and types are deposited mainly at the MPU herbarium (Stafleu & Cowan 1985) and, in fact, several specimens collected by Salzmann in Tangier are kept at this herbarium. Insofar as the collection date does not match the one in the protologue, these are here considered as syntypes. The specimen M0109464 is also a syntype as the collection date is unknown date, despite having been collected by Salzmann in Tangier.

In what concerns *Andryala floccosa* Pomel, according to the annotation on the label, the specimens affixed on the herbarium sheet P04119456 correspond to original material inasmuch as they belong to the Pomel collection ("Herbier Pomel"). Besides, the name *Rothia floccosa* Pomel also figures on the label as a synonym. All were collected exactly in the locality mentioned in the protologue and are equally good candidates for lectotypification. Hence, the best developed specimen (on the lower left-hand corner) is here designated as lectotype.

Regarding *Andryala laxiflora* DC. var. *candicans* Maire, on the herbarium sheet MPU002123 there are several specimens under this name, handwritten by Maire. A printed version of the original description is attached to this sheet as well and is accompanied by the number 608 which is mentioned in the protologue. These specimens were collected in a mountain near the city of Taza (Tazzeka Mountain, which corresponds to the locality mentioned in the protologue) and correspond, therefore, to original material. The left-hand specimen on the sheet MPU002123 is here elected as lectotype seeing that it is the best developed specimen. Likewise, the specimens affixed on the sheet P00710612 correspond to original material, considering that the collection data coincides exactly with the one on the lectotype. However, the label in not handwritten by Maire and, therefore, they are here considered as isolectotypes. The specimen MPU002122 was collected by Maire in the same locality and also has a printed version of the protologue. However, its collection date is different from that of the lectotype and given its poor condition it is not a good candidate for lectotypification. Nevertheless, it can be considered a syntype as it is accompanied by a printed version of the original description, also numbered 680. The specimens on sheet RAB043317 were also collected by Maire near Taza, but not on the same date as the lectotype and, therefore, they are here considered as syntypes.

There are two herbarium sheets under the registration number MAF09056, both bearing a specimen identified as *Andryala arenaria* subsp. *mariana* Rivas Goday & Bellot. One is accompanied by a copy of an image representing the *taxon* in the protologue and the annotation “Holotypus”. The other has no image but bears the annotation “Isotypus”. According to Stafleu & Cowan (1983), the herbarium and types of Rivas Goday are only kept at the Universidad Complutense herbarium (MAF) which means that these specimens constitute the only existent original material and can be indeed accepted as holotype and isotype. Furthermore, the collection locality and date match exactly the information in the protologue and the collectors are the authors themselves.

4.19.2 Description

Annual herb, usually single-stemmed (Figure 4.81A). STEMS 15–80 cm, frequently branched in the upper third or from the base, pubescent to densely stellate-tomentose and sometimes with glandular hairs, mostly in the upper half (Figure 4.82A). LEAVES pale green or glaucous, puberulous to densely stellate-tomentose in the upper, slightly denser on the abaxial face than on the adaxial face sometimes with few glandular hairs on the

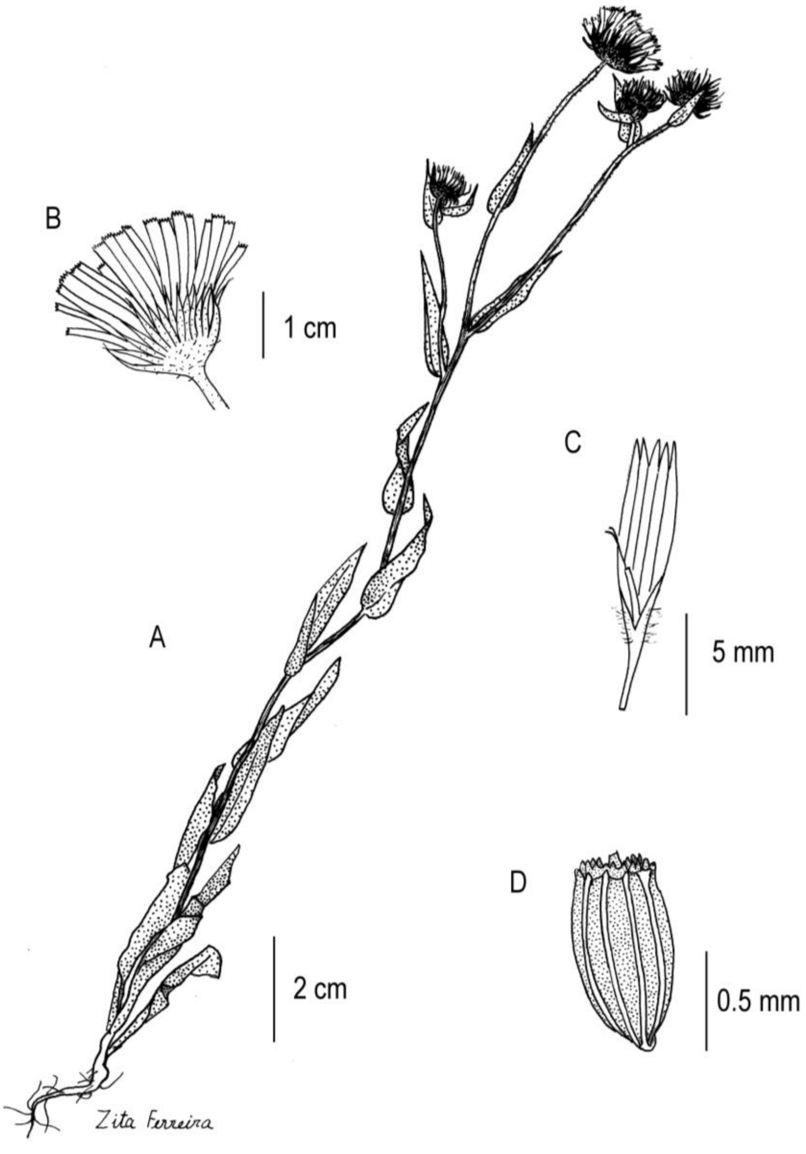

Figure 4.81 *Andryala rothia* Pers. A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

upper leaves (Figure 4.82B); lower leaves often marcescent at anthesis, 40–68(-104) x 8–15(-23) mm, attenuate into a short winged petiole 11-18(-31) mm, lanceolate, apex obtuse to acute, and margin subentire to dentate-lobate, cauline leaves 27–73 x 5–25 mm, semiamplexicaul or amplexicaul, ovate-lanceolate to lanceolate, base usually rounded, apex frequently acute, and margin entire to dentate-lobate, rarely pinnatifid; upper leaves 10(-14)–31 x 2.5–12.5 mm, usually amplexicaul, frequently ovate-lanceolate to narrowly ovate-lanceolate, base ± rounded to cuneate, apex acuminate, and margin usually entire. INFLORESCENCE laxly corymbose with 2–6 capitula or with solitary and longly pedunculate capitula. CAPITULA 14–33 mm in diameter (Figure 4.81B); peduncles 23–60 mm, pubescent-tomentose with stellate hairs and few glandular hairs 0.4–1.4 mm (Figure 4.82C); involucre 8.4–15 x 12–23 mm, hemispherical at anthesis, with involucral bracts in 4–6 rows; external involucral bracts 6–13 x 1–1.6 mm, linear-lanceolate, apex usually subulate, strongly involute enclosing a cypsela, the outer face tomentose-lanate with dense stellate hairs and abundant yellow glandular hairs 0.5–1.8 mm, the inner face stellate-hairy; internal involucral bracts 4–6.5 x 0.6–1.3 mm, with broad scariose margins to almost completely scariose, receptacle convex, pubescent-tomentose with setose hairs 0.7–3 mm (up to ± 2 times longer than the cypselae, although tendentiously short). FLORETS ligulate, pale yellow, the external with a tube of (1.8-)3–6 mm and ligule of 5–12 x 0.8–3.4 mm (Figure 4.81C) with a reddish stripe on the outer face. CYPSELAE 1–1.4 x 0.3–0.5 mm (Figure 4.81D), oblong dark brown with white ribs, apex with a ring of prominent thin teeth largely exceeding the prolongation of the ribs (Figure 4.82D); pappus of usually white bristles 4–6 mm, pilose at the base (Figure 4.82E).

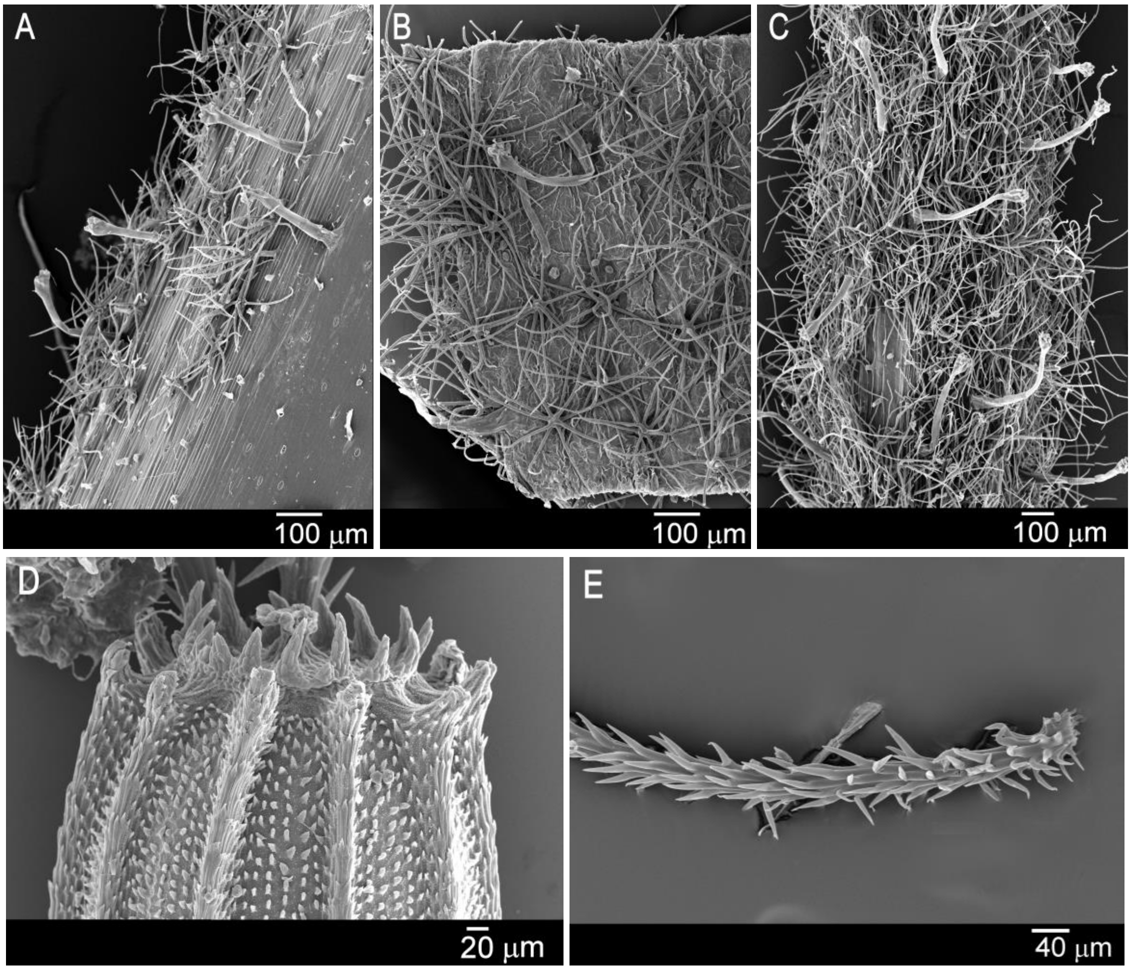

Figure 4.82 *Andryala rothia* Pers. A – Stem indumentum, B – Leaf indumentum (abaxial face), C – Peduncle indumentum, D – Cypsela apex, E – Pappus base

4.19.3 Comments on taxonomy and nomenclature

Roth (1790) described the genus *Voigtia* Roth including a single species, *Voigtia tomentosa* Roth. A year later, Schreber (1791) described the genus *Rothia* Schreb., considering it very similar to *Andryala* L. Gaertner (1791) recognised both genera and described *Rothia andryaloides* Gaertn. Roth (1797) admitted that *Voigtia* Roth actually corresponds to *Rothia* Schreb., thanking Schreber for naming it after him. In the same publication Roth also stressed that *Rothia* Screb. differed from *Andryala* L. by the receptacle with chaffy bracts at its circumference and setae at the centre, by the outer seeds enclosed in the bracts and without pappus, and inner ones with pappus. Additionally, Roth (1797) recognised three species: *Rothia andryaloides* Gaertn., *Rothia cheiranthifolia* Roth and *Rothia runcinata* Roth.

Persoon (1807) joined both genera, *Rothia* Screb. and *Andryala* L., under the earlier name (*Andryala* L.) admitting two sections: "*seminibus omnibus paposis*" and "*seminibus marginalibus nudis*" (i.e. *Rothia* Schreb.). In the latter section Persoon (1807) included *A. rothia* Pers., *A. sinuata* Pers., and *A. runcinata* Pers. Furthermore, Persoon (op. cit.) combined *Rothia andryaloides* Gaertn. as *A. rothia* Pers. Likewise, De Candolle (1838) classified *Andryala* L. in two sections: sect. I – *Euandryala* (corresponding to *Andryala* L.) and and sect. II - *Voigtia* Roth (i.e. *Rothia* Screb.). In the latter, the author included several species, namely, *A. rothia* Pers., *A. varia* Lowe ex DC., *A. sinuata* L. (= *Rothia cheiranthifolia* Roth), *A. integrifolia* L. (= *Rothia runcinata* Roth) and *A. laxiflora* DC. Herbarium specimens from Roth (namely M0031113 and B-W14770-01 0) showed that *Rothia andryaloides* Gaertn. (basionym of *A. rothia* Pers.) is morphologically identical to *A. laxiflora* DC., which De Candolle (1838) described as a new species based on herbarium species under *Rothia laxiflora* Salzm. In view of the foregoing, the earlier name for *A. laxiflora* is indeed *A. rothia* Pers. (which De Candolle, in the same publication, considered a distinct species). In agreement, Amo y Mora (1872) stressed that the species published under the name *Voigtia tomentosa* Roth, which several later authors referred to, was never found in Spain. Thus, these authors suspected that this species could correspond to some variety of *A. laxiflora* DC., if not *A. laxiflora* DC. itself. Accordingly, Blanca (2009, 2011) has already adopted the name *A. rothia* Pers., indicating *A. laxiflora* DC. as a heterotypic synonym. Thus, although currently the accepted name is *A. laxiflora* DC, the correct name is clearly *A. rothia* Pers.

Pomel (1874) described *Rothia floccosa* Pomel, stating the unpublished name *Andryala floccosa* Pomel as a synonym. The description fits *A. laxiflora* DC. and, interestingly, Pomel highlighted that *A. floccosa* is very similar to this species, but can be distinguished by the cypsela with a inner ring of very prominent teeth; by the indumentum more floccose, with no glandular hairs; and involucral bracts longer and more arcuate. However, the observation of herbarium specimens showed that these features are not sufficient to consider two distinct species. In fact, Battandier & Trabut (1905) recognised *A. laxiflora* var. *floccosa* (Pomel) Batt. & Trab. Later Maire in Jahandiez & Maire (1934) considered a new variety, *A. laxiflora* var. *candicans* Maire, which he distinguished from the typical variety by its dense whitish tomentose indumentum (according to the printed label of the type specimens). Furthermore, Maire stated that the new variety is very similar to *A. floccosa* Pomel, differing mainly by the inflorescence indumentum which is densely glandular-hairy.

4.19.4 Karyology

The somatic chromosome number of 2n = 18 was first determined on material from Portugal under the name *Andryala laxiflora* DC. (Fernandes & Queirós 1971; Queirós 1973). This number was confirmed by the gametic number n = 9 obtained with plants from Western Andalusia, Spain (Luque & Mejías 1986; Pastor *et al.* 1990).

4.19.5 Ecology and conservation status

According to Willkomm & Lange (1865), *Andryala rothia* Pers. (= *A. laxiflora* DC.) grows on sandy, barren, rocky and sunny lower regions. Jahandiez & Maire (1934) stated it that can be found in rocky pastures, sandy fields of plains and of low mountains. Coutinho (1939) cited pine forests, heaths, barren and sandy places as habitats of this *taxon*. Likewise, Franco (1984) stressed that this species occurs in heathlands and other dry sandy sites. Pottier-Alapetit (1981) mentioned that this species grows in arid pastures, woods, scrublands, sandy places, and rocky coastal areas. *Andryala rothia* Pers. flourishes on acid soils (Talavera 1987) and also grows on siliceous substrates, occurring from sea level to 700 m (Blanca 2009, 2011).

Andryala rothia Pers. is not included in *Catalogue des plantes vasculaires rares, menacées ou endémiques du Maroc* (Fennane *et al.* 1998). In fact, it seems quite common in North Africa and the Iberian Peninsula and should, therefore, be listed as Least Concern (LC) according to the *IUCN Red List categories and criteria* (IUCN 2001). Actually, for Eastern Andalusia, Blanca (2009, 2011) considered *A. rothia* Pers. as occasional and also as Least Concern (LC).

4.19.6 Geographic distribution

According to available herbarium data, *Andryala rothia* Pers. occurs mainly in the Iberian Peninsula and can also be found in North Africa, namely in Morocco, Algeria, and to a lesser extent in Tunisia (Figure 4.83). As an introduced species, it occurs in the Canary Islands (Tenerife), as mentioned by Hansen & Sunding (1993) and Acebes Ginovés *et al.* (2010). This species was first assigned by Roth (1797) to Spain under the name *Voigtia tomentosa* Roth. Based on this publication, several authors cited *A. rothia* Pers. [= *Voigtia tomentosa* Roth] for the same country (e.g. Persoon 1807; De Candolle 1838; Willkomm & Lange 1865; Amo y Mora 1872). Although under the name *A. laxiflora* DC., this species was cited for Spain and Morocco (De Candolle 1838; Willkomm & Lange 1865; Amo y Mora 1872; Ball 1878) as well as Algeria (Battandier 1889; Chevallier 1900), for which country *A. floccosa* Pomel (a synonym) was originally cited (Pomel 1874). Barratte (1896) extended the North African distribution area of *A. laxiflora* DC. to Tunisia, where it was considered very rare, and limited to the Northern part of the country (Murbeck 1897). In agreement with earlier literature, Maire in Jahandiez & Maire (1934) and Nègre (1962) assigned this species to North Africa and the Iberian Peninsula. Indeed, Talavera (1987) cited it for the southern half of the Iberian Peninsula, in accordance with Sell (1976). Actually, in Portugal it occurs mainly in the southeastern part of the country (Coutinho 1939; Sampaio 1949; Franco 1984).

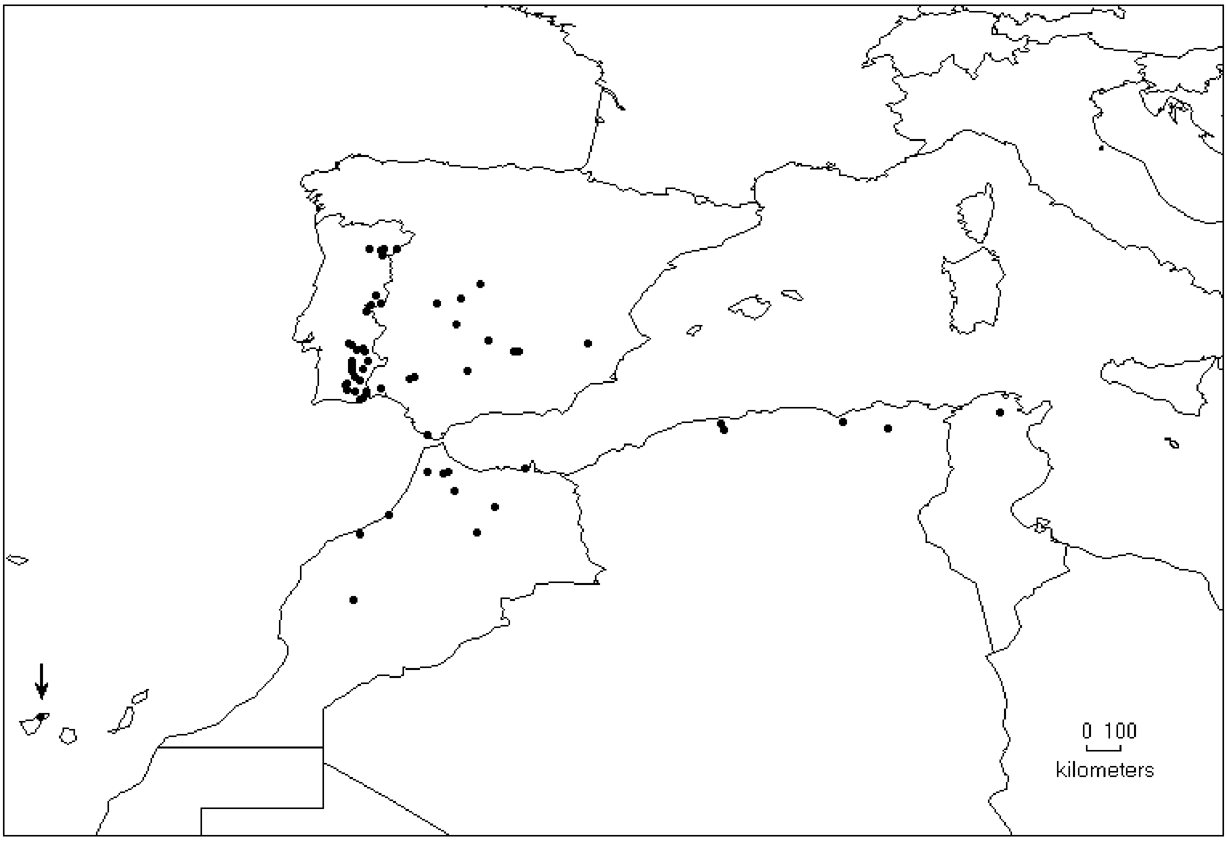

Figure 4.83 Distribution area of *Andryala rothia* Pers., according to studied material.

4.19.7 List of studied material

Algeria:

[Aïn Defla]: infra Miliana, in clivis argillaceis, 300-500 m, 10-V-1936, MPU-Maire.

[Chlef]: Beni Rache[?], MPU-Maire.

[Constantine]: Constantine - Sidi Mecid, 1884, MPU.

[Setif]: Mont Babor, Lieux arides, sur le calcaire, 1700 m, MA 139354.

[Tipaza] : Djebel Bou-Maad, sommet rocailles [?] du versant Sud, 1400 m, 29-VI-1917, R. Maire, MPU.

Morocco:

[Loc. incert.]: [?] Moyen Altas Oriental, 1650 m, 06-VII-1935, MPU-Maire. [?], VI-1925, MA 139360.

[Chefchaouen]: ad pedem Yebel Sugna (Yebala), in arenosis, 500 m, 01-VI-1928, Sennen et Mauricio, MA 139321.

[Marrakech]: Moyen Atlas: Aoudine, rocailles calcaires 1000 m, MA 139319.

[Larache]: Larache, 19-VII-1923, A. Caballero, MA 162593.

[Nador]: Xanen, 15-V-1921, M. Vidal Lopez, MA 139320.

[Nouaceur]: Oued Bou Skoura, in aridis, C. J. Pitard, MA 139100.

[Rabat]: [?] Rabat, 19-V-1941, Ch. Sauvage, MPU.

[Taza-Al Hoceima-Taounate]: Ouergha: El Mzader, moissons, 20-V-1929, MA 139318. Taza, In Atlantis Medii montilres supra urbem Taza, in rupestribus schistaceis 1300m, ligulae aureae, 18-VI-1925, R. Maire, P 00710612.

[Tétouan]: sur Chechaouene, pinède à pin d'Alep, sol sablonneux, 700 m, 20-IV-1988, J. Molero, A. M. Romo & A. Susanna, R4640, MA 537677.

Portugal:

[Algarve]: Cachopo, F. Mendes, s/ nº, LISU 40220. Castro Marim, Odeleite, num mato perto da margem direita da ribeira de Odeleite, 20-VI-1985, M. Lousã & P. Oliveira Paes, s/ nº, LISI 43498. Tavira: Santa Maria, perto de Ricota, Q. 619 - Matos xerofílicos em Serra Xistosa, 27-V-1969, J. P. Horta Correia, s/ nº, LISI 28874. Castro Marim, Odeleite, num mato muito ralo perto da margem esquerda da ribeira de Odeleite, a montante da segunda daquelas localidades, solo derivado de xisto com 30% de declive, espécie frequente no local, 20-VI-1985, M. Lousã & P. Oliveira Paes, s/ nº, LISI 43500. V. Real de Sto. António: Vila Nova da Cacela, 1 Km a Sul de Sesmarias, sob coberto de sobreiros, solo xistoso Q. 958, 15-V-1991, Lousã & J. C. Costa, s/ nº, LISI 48955. Real de Sto. António, Vila Nova da Cacela, perto da Ribeira de Álamo, sob coberto de sobreiros, solo xistoso Q. 959, 15-V-1991, M. Lousã & J.C. Costa, s/ nº, LISI 48954.

[Alto Alentejo]: Possés entre la gare e la ville. Évora, J. Daveau, s/ nº, LISU 40193. Pr. da ribeira de vide, Povoa das Meiadas, A. R. da Cunha, s/ nº, LISU 40194. Reguengos Monsaraz - Castelo de Monsaraz, 20-V-1949, F. X. Guião, s/ nº, LISI 12754. Redondo, Montoito - Herdade da Alcrovisca, 16-V-1956, J. Chicau, s/ nº, LISI 18579. Évora, Graça do Divor - Herdade da Sempre Noiva, 29-V-1956, J. V. S. O. Sousa, s/ nº, LISI 18804. Évora, Herdade dos pinheiros, J. Crespo Ascenso, s/ nº, LISI 19732. Alta, Montoito, Redondo, cultura: trigo, 03-VI-1987, A. P. Leitão, s/ nº, LISI 380. Monte do Gavião, S. Manços, Évora, 06-V-1987, J. M. Martins, s/ nº, LISI 379.

[Baixo Alentejo]: Entre Corte-Figueira et Mù, Alt. 560 m, J. Daveau, s/ nº, LISU 40202. Charneca da Rata - Beja, A. R da Cunha, s/ nº, LISU 40200. Senhora das Neves- Beja, A. R. da Cunha, s/ nº, LISU 40192. Mértola: S. João dos Caldeireiros Cerros Altos, junto à Ribeira de Oeiras, Q: 890, Alt. 180 m, exp. N., 24-VII-1982, M. Lousã e J. Monjardino, s/ nº, LISI 42030. Serpa: Herdade do Pexoto, prox. da E.N. 265, Q. 555, 18-VI-1970, J. Franco & M. M. Fonseca, s/ nº, LISI 30927. Moura, margem esquerda do rio Guadiana, 07-VI-1944, Carlos U. Cansado, s/ nº, LISI sem número. Mértola: Alcaria Ruiva, Q. 564/575 - Matos xerofílicos em terreno xistoso, J. P. Horta Correia, s/ nº, LISI 28736. Serpa: Herdade da Lapa, margem da ribeira de Limas, 17-VI-1970, J. Franco & M. M. Fonseca, s/ nº, LISI 30766. Serpa: Pulo do lobo, vertente do lado E., 17-VI-1970, J. Franco & M. M. Fonseca, s/ nº, LISI 30767. Beja: Trindade, na estrada nº 391, Q. 552, 06-VI-1972, A. Leitão, s/ nº, LISI 33823. Moura: Póvoa, Q. 514 - terreno xistoso seco, 31-V-1972, A. Leitão, s/ nº, LISI 33679. Cuba: a 2 Km de Cuba na estrada para Faro do Alentejo, Q. 524, 02-VI-1972, A. Leitão, s/ nº, LISI 33749. Almodôvar: Sra. da Graça dos Padrões; Cerro do Lobo, junto à confluência do Barranco do Pires com o Barranco das Lages, Q. 902, alt. +/- 230m, 10-VI-1982, M. Lousã & A.P. Oliveira, s/ nº, LISI 41724. Almodôvar: Senhora da Graça dos Padrões, Horta da Revesa, na linha de água a jusante desta, Q. 902, alt. +/- 200 m, 25-VI-1982, M. Lousã & J. Monjardino, s/ nº, LISI 41827.

[Beira Alta]: prox. da estação C. F de Castelo Melhor, G. Barbosa & M. Myre, s/ nº, LISI 8594.

[Beira Baixa]: Margem do Tejo - Malpica (Castelo branco), A. R. da Cunha, s/ nº, LISU 40198. Beira Baixa, Vale da Cova, Ladoeiro, Idanha-a-Nova, Pomar de pereiras, 22-VII-1981, J. M. Martins, s/ nº, LISI 40831. Rosmarinhal – Serra (ou Rosmaninhal), 09-V-1956, J. C. Folgato, s/ nº, LISI 18341.

[Trás-os-Montes]: Vale do Sabor; Silhares, Moncorvo, Nas areias da margem, 18-VI-1941, G. Pedro, s/ nº, LISI 6646. Moncorvo, Larinho, margem do Sabor, Pido, 05-VI-1944, G. Barbosa & F. Garcia, s/ nº, LISI 6976. Entre Tua e Alegria, vertente para o Douro, G. Barbosa & F. Garcia, s/ nº, LISI 8184

Spain:

[Badajoz]: Finca de las Navas: Herrera del Duque, 22-VI-1969, M. Ladero, MA 202383.

[Caceres]: Campillo de Deleitosa, 20-V-1982, D. Belmonte, MA, 341308.

[Cadiz]: Road to Zahara de los Atunes, in dry pacth by roadside mixed with *A. integrifolia, Medicago* sp., *Centarium tenuiflorum, Galium parisiense, G. setacium Trifolium, lappceum.* Road to Zahara de los Atunes: Tarifa Dest. (more or less sea level), 18-VI-1975, B. Molesworth Allen, 9752, SEV 36634

[Canary Islands]: Tenerife. Aeropuerto de los Rodeos. La Laguna, 24-V-1994, Marcelino del Arco Aguilar, s/ nº, TFC 36 568. Tenerife. La Laguna Cabecera de los Rodeos, 28-IV-1994, Juan Ramón Acebes Ginovés, s/ nº, TFC, 36 440. Tenerife. La Laguna, 28-IV-1994, Wolfredo Wildpret de la Torre, António Garcia Gallo, Isabel Zaldivar, s/ nº, TFC 22038. Tenerife, La Laguna, 03-V-2000, R. Mesa Coelho, s/ nº, TFMC 5039

[Ciudad Real]: Ciudad Real, Almodovar del campo, La Garganta, Navarrillo, 840 m. restos de alcomocales [?], 22-VI-1997, Ramiro García Río, MA 596824.

[Córdoba]: Córdoba, 19-VI-1927, C. Lacaite, MA 139325.

[Huelva]: Entre San Bartolomé de la Torre y Alonso, suelo pizarroso, 20-VI-1978, S. Talavera & B. Valdés, MA 467401.

[Jaén]: Puerto de Despeñaperros, matorrales acidófilos, pedregosos, J. Borja, MA 182139. Las Correderas. Aldeaquemada, 21-VI-1978, M. Ladero, MA 224623.

[Madrid]: Entre Almorox e Cenicientos, 510m, pastizales, terófitos sobre suelos areno-limosos en superficie (Tuberarion guttattae), 29-VI-1984, D. Sánchez-Mata, MA 366430.

[Málaga]: Sierra Parda - Zolox, 14-VI-1932, L. Ceballos, MA 139317

[Salamanca]: Presa de Aldeadávila, 29TPF9463, 400m, nemoral en bosquetes de hojaranzos, 23-VI-1988, Amich y Sánchez Rodríguez, MA 456635.

[Seville]: El Ronquillo, encinar, 17-VI-1969, S. Silvestre & B. Valdés, s/ nº, LISU 163426. Castillo de los Guardas, Fragoso, MA 139312

[Toledo]: Las Herencias, cultivo arenoso, 380, 01-VII-1979, A. Segura Zubizarreta, MA 351538.

Tunisia:

[Bizerte]: roux Bordj Toumi, MPU-Maire.

4.20 *Andryala sparsiflora* (Lowe) M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. stat. & comb. nov.

≡ *Andryala cheiranthifolia* L'Hér. var. *sparsiflora* Lowe, Man. Fl. Madeira 1(5): 563. 1868
Ind. loc.: "Mad. reg. 1-4, chiefly 2-4".
Typus: [Portugal] "Madeira, 1777", *Fr. Masson s.n.* – Lectotype (designated here): BM000829755!; syntype: BM000829754!

= *Andryala tomentosa* Scop. Delic. Fl. Faun. Insubr. 2: 12. 1787, non *Andryala tomentosa* Chaix
Ind. loc.: sine
Typus: Holotype: illustration therein.

= *Andryala varia* Lowe ex DC. var. *subglabrata* DC., Prodr. (DC.) 7: 246. 1838
Ind. loc.: "in rupibus subumbrosis convallium Maderæ ad alt. 2000-5000 ped. ubique vulgatissima. *Andryala varia* var α Lowe! in litt."

Typus: [Portugal] "Hab. in rupibus subumbrosis convallium Maderæ ad alt. 2000-5000 ped. ubique vulg., 1832", *M. Low. 399* – Holotype: G00326360 ex herb. DC.

= *Andryala varia* Lowe ex DC. var. *aprica* DC., Prodr. (DC.) 7: 246. 1838

Ind. loc.: "In convallibus Maderæ ad altit. 3000 ad 5000 ped. locis rupestribus apricis siccis. *A. varia* var. α subvar. 2. Lowe! in litt."

Typus: [Portugal, Madeira] "hab. in Mad.æ ad altit. 3000-5000 ped. in locis rupibus apricis siccis, magis quam quibus subv. 1 nascitur, 1832", *M. Low. 388* – Holotype: G00326377 ex herb. DC. (specimen on the left)

= *Andryala cheiranthifolia* L'Hér. var. *sparsiflora* Lowe subv. *integrifolia* Lowe, Man. Fl. Madeira 1(5): 563. 1868

Andryala cheiranthifolia L'Hér. subsp. *varia* Lowe ex DC. var. *integrifolia* (Lowe) Bornm. in Bot. Jahrb. Syst. 33: 489. 1904

Andryala varia Lowe ex DC. subsp. *sparsiflora* Lowe f. *integrifolia* (Lowe) Menezes, Fl. Madeira. 101. 1914

Andryala glandulosa Lam. subsp. *varia* var. *varia* f. *varia* sensu R. Fern., in Anuário Soc. Brot. 25: 28. 1959

Ind. loc.: "Rocks and dry rocky banks in Mad. everywhere, especially from 1500 to 5000 ft.; about and above the Mount, in chestnut-woods about the Jardim, above P^{to}. da Cruz, in the Serra d'Agua, Rib. de S^{ta} Luzia, Rib. Frio, da Metade, de S. Jorge, &c.; S. Vicente from the beach or sea-cliffs upwards; at "Jardim do Mar and Rabaçal" S^{r} Moniz. June-Sept."

Typus: [Portugal, Madeira] "Rocks in Ribeiro Frio, 29 June 1827", *Lowe 130* – Lectotype (designated here): K000251909!; syntypes: BM000072528!, BM000072530a!, BM000072530b!, BM000072530b! BM000829754!

= *Andryala cheiranthifolia* L'Hér. var. *sparsiflora* Lowe subv. *runcinata* Lowe, Man. Fl. Madeira 1(5): 564. 1868

Andryala cheiranthifolia L'Hér. subsp. *varia* Lowe ex DC. var. *runcinata* (Lowe) Bornm. in Bot. Jahrb. Syst. 3: 489. 1904

Andryala varia Lowe ex DC. subsp. *sparsiflora* Lowe f. *runcinata* (Lowe) Menezes, Fl. Madeira. 101. 1914

Andryala glandulosa Lam. subsp. *varia* var. *varia* f. *runcinata* (Lowe) R. Fern., in Anuário Soc. Brot. 25: 28. 1959

Ind. loc.: "Mad. here and there occasionally with subv. 1; rocky banks about and above the Mount up to the Arrebentão, Rib. de S^{ta} Luzia, R. dos Soccorridos near São Martinho, and in the N. on a rock at the head of Rib. Fundo above the Lagoa or Fanal, &c."

Typus: [Portugal] "Rock at the head of the Rib^{a}. Funda above the Lagoa or Fanal, 18 July 1855", *R. T. Lowe 400^{XX}* – Lectotype (designated here): BM000072531a!; isolectotype: K000251919! syntypes: BM001125621!, BM000829755!, BM000829756!

_ *Andryala pinnatifida* Aiton var. *α* sensu Aiton, Hortus Kew. 3: 129. 1789

_ *Andryala denudata* Sol. in Lowe, Man. Fl. Madeira 1(5): 563. 1868, *nom. nud. in sched.*

_ *Andryala glandulosa* Lam. subsp. *cheiranthifolia* sensu Greuter in Willdenowia. 33: 232. 2003

4.20.1 Typification

In the protologue of *Andryala cheiranthifolia* L'Hér. var. *sparsiflora* Lowe specimens from the BM herbarium were mentioned as synonyms: "*A. pinnatifida and A. denudata Sol.! in BH*". The specimen BM000829755, under the name *Andryala pinnatifida* α, is here designated as lectotype since it fits the original description quite well and is better preserved than the specimen BM000829754 that, being under the herbarium name *A. denudata* Sol. and, therefore, unpublished, is here considered as a syntype.

Scopoli (1787) provided a fairly good description of *Andryala tomentosa* Scop., although its provenance is unclear ("*Semina communicavit Dom. Thuin*"). Apparently, the plants on which the author based is description were obtained from seeds sent by André Thouin, a French botanist from Jardin du Roi (Paris). Insofar as no type material was traced, the illustration in the protologue is here accepted as holotype.

De Candolle (1838) described *Andryala varia* Lowe ex DC. var. *subglabrata* DC. based on a herbarium specimen from Lowe, considering the information in the protologue: "*Andryala varia var. α Lowe! in litt. (v.s.)*". Indeed, De Candolle's collection held at the G herbarium includes a single specimen with a collection locality handwritten by Lowe that matches perfectly the one in the protologue (G00326360). Besides, the specimen is under the name "*Andryala varia var. α subvar. 1*" and, according to the label, it was collected by Lowe in 1832. Hence, it is here accepted as the holotype.

Similarly, De Candolle (1838) described *Andryala varia* Lowe ex DC. var. *aprica* DC. based on a Madeiran plant collected by Lowe, deducing by the information in the protologue: "*Andryala varia var. α subvar. 2 Lowe! in litt. (v.s.)*" In fact, the De Candolle collection kept at the G herbarium hosts only one specimen labelled in Lowe's handwriting as "*Andryala varia var. α subvar. 2*" (G00326377). The collection locality, also handwritten by Lowe, coincides exactly with the information in the protologue. Thus, it is here accepted as the holotype.

Concerning, *Andryala cheiranthifolia* L'Hér. var. *sparsiflora* Lowe subv. *integrifolia* Lowe, in the protologue Lowe (1868) mentioned several localities in Madeira where it can be found. Indeed, specimens from these localities collected by the author himself were located at the BM herbarium and are, therefore, considered as syntypes. In particular, the specimen BM000829754 is a syntype insofar as Lowe (op. cit.) mentioned it in the protologue: "*Madeira Fr. Masson 1777*". Nevertheless, the specimen K000251909 is here selected as lectotype since it fits the original description very well and was collected by Lowe himself precisely in one of the localities cited in the protologue. On the original label handwritten by Lowe we can read "*Andryala lanata* Hook var. *α* subv. 1." where "*lanata Hook*" appears crossed out. In a later label, Lowe renamed the specimen as "*Andr. cheiranthifolia Herit. var. β sparsiflora subv. 1 integrifolia Lowe*". Actually, *Andryala lanata* Hook is an unpublished name and to present knowlegde it is not cited in any publication.

The provenance of the specimens designated here as lectotype (BM000072531a) and isolectotype (K000251919) of *Andryala cheiranthifolia* L'Hér. var. *sparsiflora* Lowe subv. *runcinata* Lowe is mentioned on the label in Lowe's handwritting and matches exactly the localities in the protologue. Moreover, these specimens were collected by Lowe himself and fit the original description quite well. Furthermore, they were later relabelled as "*Andryala cheiranthifolia Herit. var. β sparsiflora subv. 2 runcinata Lowe*" by the author himself. As the specimens BM001125621, BM000829755, and BM000829756 were mentioned in the protologue: "*Madeira Fr. Masson 1777*" and "*Hort. Kew. 1778*", they are considered as syntypes.

4.20.2 Description

Annual to biennial herbs, sometimes perennating, single-stemmed (Figure 4.84A). STEMS 37–94(-105) cm, branched in the upper half, less frequently from the base or in the upper third, puberulous to tomentose with stellate hairs and numerous glandular hairs at least in the upper part (Figure 4.85A). LEAVES glaucous to deep green, puberulous to tomentose on both faces with stellate hairs mixed with ± abundant glandular hairs on the upper leaves (Figure 4.85B); lower leaves arranged in a rosette, often marcescent at anthesis, 83–223 x 9–47(-68) mm, attenuate into a winged petiole 16-50 mm, usually lanceolate, apex acute, and margin subentire to pinnatipartite with lobes more than 3 mm wide (Figure 4.84B); cauline leaves 55–130(-152) x 5–41 mm, semiamplexicaul, lanceolate to linear-lanceolate, base ± rounded sometimes attenuate, apex acute sometimes acuminate, and margin subentire to pinnatipartite; upper leaves 14–44 x 2–10 mm, semiamplexicaul or amplexicaul, ovate-lanceolate to narrowly ovate-lanceolate, base ± rounded sometimes cuneate, apex acuminate, and margin entire, rarely subentire to dentate. INFLORESCENCE corymbose or paniculate-corymbose, with 5–12 capitula. CAPITULA (12-)16–30 mm in diameter (Figure 4.84C); peduncles 23–65(-77) mm with stellate hairs and some glandular hairs 0.9–1.8 mm (Figure 4.85C); involucre 8–12 x 9–18 mm, campanulate at anthesis, with involucral bracts in 2–3 rows; external involucral bracts 5–9 x 0.7–1.5 mm, lanceolate to linear-lanceolate, apex frequently acuminate, involute enfolding a floret, the outer face pubescent-tomentose with stellate hairs and glandular hairs 0.8–1.8 mm, yellowish at the apex and blackish at the base, the inner face glabrous; internal involucral bracts 4–7 x 1–2 mm, with broad scariose margins or almost completely scariose, receptacle convex, villous with long setose hairs 3–6 mm (2 to 4 times longer than the cypselae). FLORETS ligulate, golden yellow, the external with a tube of 2.5–5 mm and ligule of 6–12 x 1.5–4.5 mm (Figure 4.84D). CYPSELAE 1–1.7 x 0.4–0.6 mm (Figure 4.84E), usually obconical dark brown with white ribs, apex with an inner ring of teeth equalling or slightly exceeding the prolongation of the ribs (Figure 4.85D); pappus of white bristles 4–6 mm, denticulate at the base (Figure 4.85E).

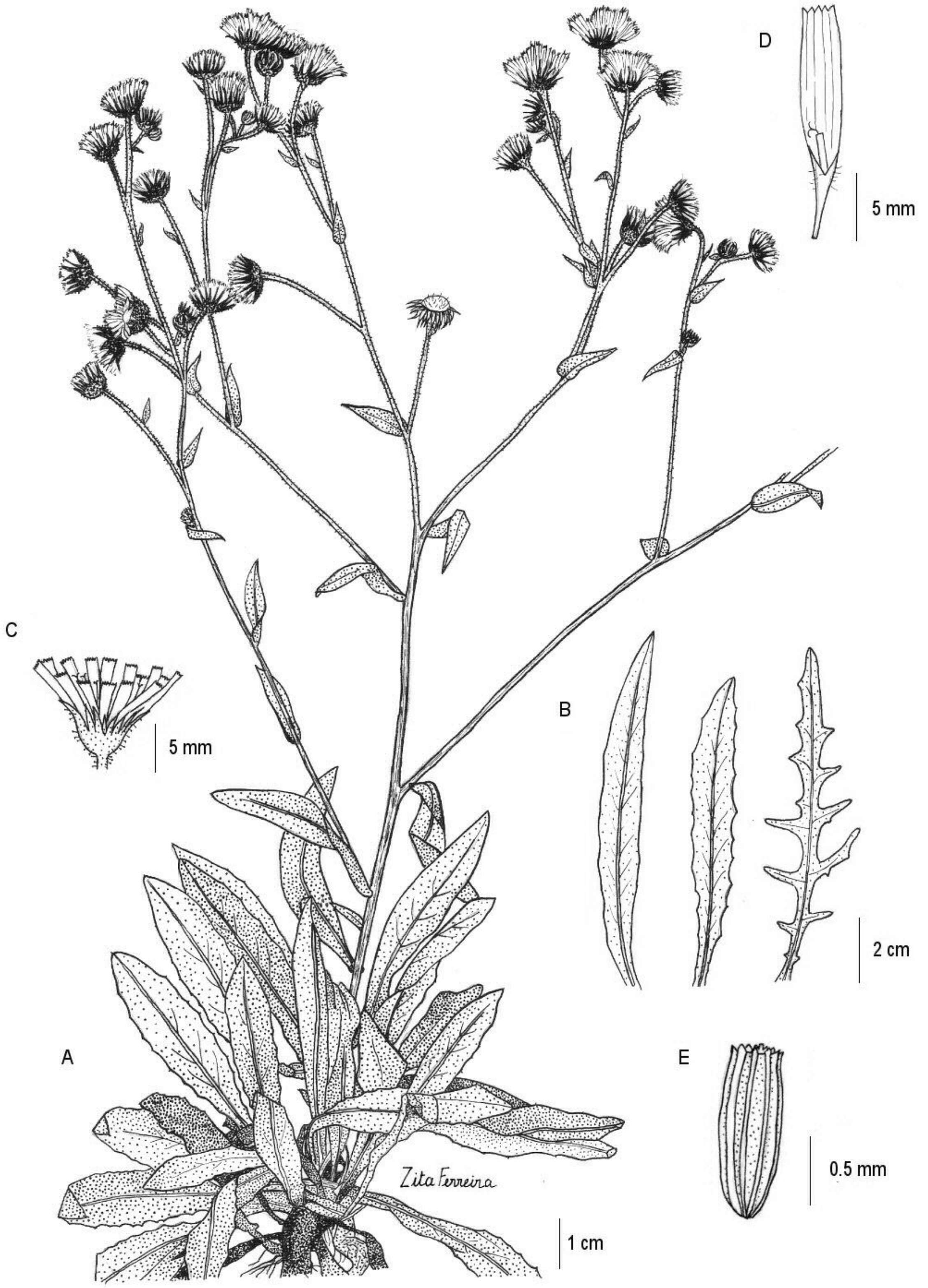

Figure 4.84 *Andryala sparsiflora* (Lowe) M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. A – Fertile habit, B – Lower leaf margin, C - Capitulum, D – Floret, E – Cypsela.

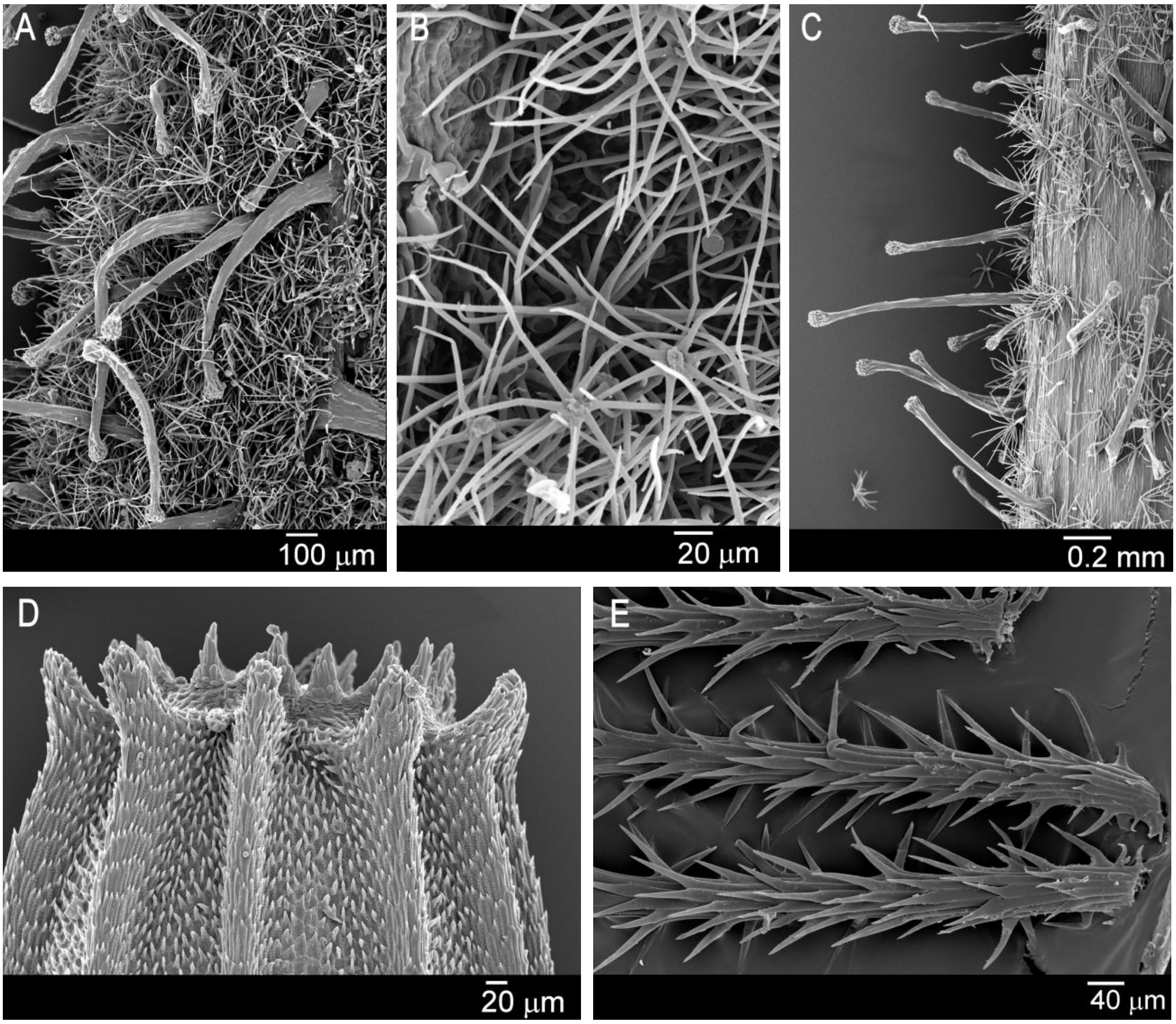

Figure 4.85 *Andryala sparsiflora* (Lowe) M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. A – Stem indumentum, B – Leaf indumentum, C – Peduncle indumentum, D – Cypsela apex, E – Pappus base.

4.20.3 Comments on taxonomy and nomenclature

De Candolle (1838) included all Madeiran *Andryala taxa* in *A. varia* Lowe ex DC. and recognised six varieties. Two of these (*A. varia* Lowe ex DC. var. *subglabrata* DC. and *A. varia* Lowe ex DC. var. *aprica* DC.) are synonyms of *A. cheiranthifolia* L´Hér. var. *sparsiflora* Lowe subv. *integrifolia* Lowe, as indicated by Lowe (1868). Thus, they can also be synonymised with *A. sparsiflora* (Lowe) M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. Noteworthy is the fact that De Candolle (1838) included both *A. glandulosa* Lam. and *A. cheiranthifolia* L'Hér. (= *A. sparsiflora*) in a single variety: *A. varia* Lowe ex DC. var. *cheiranthifolia* (L´Hér.) DC. This author was well acquainted with *A. cheiranthifolia* L'Hér. through herbarium material, as mentioned in the protologue, conversely to Lowe, who had knowledge of this *taxon* only from the protologue and illustration therein. Therefore, it seems reasonable to include *A. varia* Lowe ex DC. var. *cheiranthifolia* (L´Hér.) DC., along with *A. varia* Lowe ex DC. var. *candidissima* (Desf.) DC. and *A. varia* Lowe ex DC. var. *angustifolia* DC., in the earlier described *A. glandulosa* Lam. As mentioned before, according to the protologues of *A. glandulosa* Lam. and *A. cheiranthifolia* L'Hér., these share an interesting feature: numerous involucral bracts arranged in several rows, being the inner chaffy-like and glabrous. Curiously in the past, this feature was seen as a good reason to consider a separate genus from *Andryala*, *Rothia* Schreb. (Gaertner 1791; Schreber 1791). Indeed, Lowe (1868: 562, 563) mentioned this feature to distinguish *A. cheiranthifolia* L´Hér. var. *congesta* Lowe (= *A. glandulosa* Lam.) from *A. cheiranthifolia* L´Hér. var. *sparsiflora* Lowe (= *A. sparsiflora*), stating that the first exhibits "*outer scales of inv. linear lanceolate herbaceous thickly tomentose and fulvo-glandulose, the inner chaffy naked*", while the latter presents "*scales of inv. fewer or more remote and distinct* …". Lowe (1868: 565) highlighted that, although in the past he treated *A. robusta* Lowe (= *A. glandulosa* Lam.) as a separate Madeiran species, it is not really worthy of a specific distinction, and should be included in *A. cheiranthifolia* L´Hér. var. *congesta* Lowe. Nevertheless, the characters mentioned by Lowe himself to distinguish *A. cheiranthifolia* L´Hér. var. *sparsiflora* Lowe from *A. cheiranthifolia* L´Hér. var. *congesta* Lowe are of great taxonomic value (e.g. stem and leaf indumentum, leaf thickness, capitula diameter, involucre size, number of involucral bracts). Thus, although Lowe (op. cit.) referred *A. cheiranthifolia* L´Hér. as a synonym of his *A. cheiranthifolia* L´Hér. var. *sparsiflora* Lowe subv. *runcinata* Lowe, these belong to distinct *taxa*, respectively *A. glandulosa* Lam. and *A. sparsiflora*. Consequently, the name *A. cheiranthifolia* L´Hér. was misapplied when the combination *A. glandulosa* subsp. *cheiranthifolia* (L'Hér.) Greuter was suggested (Greuter 2003). In view of the foregoing, this *taxon* is here recognised as *A. sparsiflora*. The choice of the name is related to the fact that *A. varia* Lowe ex DC. was used indiscriminately for all Madeiran *taxa* (including *A. glandulosa* Lam.), except for *A. crithmifolia* Aiton. Another option would be *A. tomentosa* Scop. since Scopoli (1787: 12) described the involucre basically with two rows of involucral bracts, making no reference to a inner series of chaffy-like bracts ("*Calyx communis subrotundus, constans unica serie foliolorum linearium, ad cuius basim foliolum aliud pariter lineare, calyce non longius occurrit.*"). Besides, Scopoli (op. cit.) stressed that the leaves are diverse concerning the margin (*"Folia diversa; nunc enim quae ex radice oriuntur profunde pinnatifida, segmentis lanceolatis, patulis, flexuosis, obtusis; nunc vero omnia sunt lanceolata; imis tamen sinuato-dentatis: superioribus autem integris*."), contrary to *A. glandulosa* Lam. that exhibits mostly quite entire leaves or only the lower ones divided but never profoundly. Nonetheless, *A. tomentosa* Scop. is a later homonym and, therefore, illegitimate. Indeed, *A. tomentosa* Chaix. was validly published a year before *A. tomentosa* Scop., despite being a misapplied name[36]. Thus, a new combination is proposed: *Andryala sparsiflora* (Lowe) M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq.

4.20.4 Karyology

The first report on chromosome counts for Madeiran *Andryala taxa* was presented by Ortega & Navarro (1977), authors that determined the gametic number of n = 9 on plant material collected at Pico do Areeiro. Although this material was ascribed to *A. glandulosa* subsp. *glandulosa* it most probably corresponds to *A. sparsiflora* since the latter *taxon* occurs indeed at Pico do Areeiro, contrary to the first.

4.20.5 Ecology and conservation status

Press (1994) stated that *A. glandulosa* Lam. subsp. *varia* (Lowe ex DC.) Fern. (most surely referring to *A. sparsiflora*) occurs everywhere in Madeira up to 1500 m, almost always at inland sites, usually on dry rocks and

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[36] Chaix in Villars (1786) cited *A. lanata* L. as a synonym of *A. tomentosa* Chaix. However, *A. lanata* L. is a superfluous name and, therefore, illegimate (replaced synonym: *Hieracium tomentosum* L.).

banks. In fact, *A. sparsiflora* occurs especially between 590 – 1500 m, although it can also be found in high mountain peaks up to 1786 m asl. At the higher altitudes, this species occurs on dry rocky-soil slopes and rocky soils, in association with different species (e.g. *Echium candicans* L.f., *Rumex bucephalophorus* L. and *Crepis vesicaria* L.). At lower altitudes on the South face of Madeira, in areas quite disturbed by human intervention and where the potential vegetation corresponds to the barbusano-tree [*Apollonias barbujana* (Cav.) Bornm.] and the stink-laurel [*Ocotea foetens* (Aiton) Baill.] forests, this species dwells on rocky slopes along the roads, in association with other rupicolous species, such *Aeonium glutinosum* (Aiton) Webb & Berthel. Although it occurs mainly in inland sites, it can also be found in locatities nearer to the coast but at relatively high altitudes, in moist and shady places. When growing on hot exposed dry rocks, it may exhibit a more densely stellate-tomentose indumentum and whitish-green hue, contrary to the plants growing in humid slopes and valleys which bear thin and herbaceous leaves, less tomentose or glabrescent and intensely green. On the North face of the island, this species occurs in areas belonging to the stink laurel forest, growing on rocky slopes, in shady and humid places, along with other species, such as *Sibthorpia peregrina* L.

In what concerns the conservation status, this *taxon* is quite common in Madeira Island and should be listed as Least Concern (LC) according to the *IUCN Red List categories and criteria* (IUCN 2001; 2012).

4.20.6 Geographic distribution

Although not present in Desertas and Porto Santo, *Andryala sparsiflora* (Lowe) M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. occurs throughout the island of Madeira, mostly in inland areas such as Serra d'Água, São Vicente (especially in the vicinities of Encumeada), Paul da Serra, Rabaçal, Curral das Feiras, Camacha, and Pico do Areeiro (Figure 4.86). However, it can be found in localities near the southwest coast of Madeira (namely Prazeres and Fajã da Ovelha), sometimes coexisting with *A. glandulosa* Lam. or both *A. glandulosa* Lam. and *A. integrifolia* L. (Ferreira *et al.* 2011).

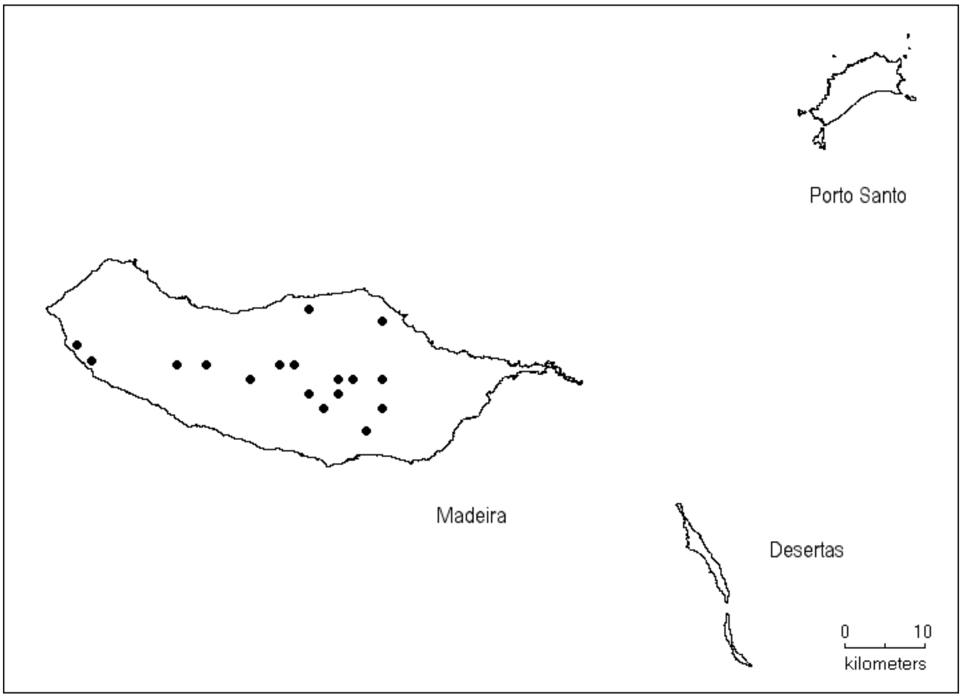

Figure 4.86 Distribution area of *Andryala sparsiflora* (Lowe) M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq., according to studied material.

4.20.7 List of studied material

Portugal:

[Madeira]: Rabaçal, Próx. da casa dos guardas [?] ao caminho das levadas [?] 1100 m, 05-VII-1951, C. Romariz, 775/978, LISU 43592. Prox. do Pº Jorge, Taludes rochosos terrosos, alt. 1500 m, 26-VI-1951, C. Romariz, 747/644, LISU 64742. Prox. do Pico Jorge, Taludes rochosos-terrosos húmidos, alt.1500 m, 26-VI-1951, C. Romariz, 751, LISU 43289. Prox. Pico Jorge, Taludes rochosos-terrosos, alt. 1500, 26-VI-1951, C. Romariz, 751, LISU 43287. Prox. do Pico Jorge, Taludes terroso-rochosos húmidos, alt. 1500 m, 26-VI-1951, C. Romariz, 751, LISU 43271. Ribeira de Santa Luzia, Menezes[?], s/ nº, LISU 42693. Próx. do Pico das Mós, Taludes terrosos húmidos, alt. 900 m, C.Romariz, 794, LISU 43272. Ribeira de Santa Luzia, C. Menezes, s/ nº, LISU 42692. Caldeirão Verde; Queimadas aos túneis, Taludes rochosos escorrentes, 930 m de alt., C. Romariz, 762, LISU 43247. Levada junto à Casa do Arieiro, Taludes húmidos junto à levada, 23-VI-1951, C. Romariz, 747/643, LISU 43246. Ribeira das Cales, 1.200 - 1.300 m alt., s/ nº, LISU 64712. Vereda entre Pico do Gato e Pico das Torres, 16 -V-1991, Fontinha, José Carvalho, Paulo, s/ nº, MADJ 02745. Descida pela vereda dos Prazeres para o Paúl do Mar, 22 -VI-1991, Fontinha, s/ nº, MADJ 02625. Encumeada - São Vicente, 30 -V-1996, Fontinha e Baeta, s/ nº, MADJ 09641. Estrada entre o Funchal e a Eira do Serrado, taludes rochosos, 22 -VII-1957, Eng. Beliz, R. Santos, s/ nº, MADJ 03552. Rabaçal, 16 -VI-1958, Eng. Rui Vieira, s/ nº, MADJ 03547. Pico do Arieiro, 18 -VI-1960, Eng. Rui Vieira e R. Santos, s/ nº, MADJ 03548. Rabaçal - Vinte e Cinco Fontes, 26 -VII-1960, Eng. Rui Vieira e R. Santos, s/ nº, MADJ 03549. Rabaçal - Vinte e Cinco Fontes, 26 -VIII-1960, Eng. Rui Vieira e R. Santos, s/ nº, MADJ 03553. Levada dos Balcões, 02 -VIII-1962, Nóbrega, s/ nº, MADJ 03556. Estrada da Encumeada para o Paúl da Serra, no Lombo do Mouro, 16 -VI-1988, Nóbrega, s/ nº, MADJ 06912. Pico Ferreiro - lado de São Vicente, ao longo do Poio da azeda na estrada para este poio a cerca de 1300 metros, é abundante, 09 -VIII-1988, Nóbrega, s/ nº, MADJ 06392. Ribeira da Ponte dos Ganchos em Boaventura, 30 -VIII-1988, Nóbrega, s/ nº, MADJ 06526. Ribeira de S. Luzia, MADJ 00788. Fanal, MADM. Santo António - Curral, Major Pickering, s/ nº, MADM. An der estrada des Carreiras de Camacha nach Poiso, 1100 m, 14 -VIII-1972, C. Simon, s/ nº, MADM. Encumeada ou Levada SW, 05 -VII-1977, Remane, s/ nº, MADM. Encumeada, Levada do Norte, 1200 m, 25-VI-2000, C. Navarro, G. Nieto Feliner, F. Pando, M. T. Tellería, P. Vargas & M. Velayos, 9708, MA 655297. Levada do Rabaçal, 1100 m.s.m., R. Barreto, MA 239102. Levada do Rabaçal, 1100 m, R. Barreto, 1581MP, MA 239101. Acima da Pousada dos Vinháticos, 27-VII-1980, F. Zino, 465, MADM. Meia Serra (Estação de Tratamento Selada), 800-900 m de altitude, no aterro, 30/11/2005, Miguel Sequeira, 4647, UMad 1022. Abaixo da Encumeada (acima da pousada dos Vinháticos), talude rochoso junto à estrada, alt. 806 m, 11-V-2006, Z. Ferreira, ZF67C, UMad. Pico do Areeiro, solo pedregoso, estrada abaixo da casa do Areeiro, alt. 1786, 22-VI-2006, Z. Ferreira, ZF114, UMad. Pico do Areeiro - Ninho da Manta, 21 -V-2006, Ligia Carvalho, Magda Silva, CMSS 930, UMad, 1650. Fajã da Ovelha, Lombo dos Cedros, 590-600 m.s.m. Exp. Sul. Ecologia: vale húmido edafohigrófilo, 23-IV-2009, M. Sequeira, M. Benedito & D. Henriques, MS 6015, UMad. Fajã da Ovelha, Lombo dos Cedros, 590-600 m.s.m. Exp. Sul. Ecologia: vale húmido edafohigrófilo, 23-IV-2009, M. Sequeira, M. Benedito & D. Henriques, MS 6015, UMad. Vereda da Boca da Corrida, em local rochoso exposto ao calor e à seca, 14-IX-2008, Z. Ferreira, ZF182, UMad. Vereda da Boca da Corrida, em local rochoso exposto ao calor e à seca, 14-IX-2008, Z. Ferreira, ZF183, UMad. Vereda da Boca da Corrida, em local rochoso exposto ao calor e à seca, 14-IX-2008, Z. Ferreira, ZF184, UMad. Vereda da Boca da Corrida, 14-IX-2008, Z. Ferreira, 185ZF, UMad. Paul da Serra, 24-VII-2009, M. Sequeira, Z. Ferreira, A. Correia, A. Figueiredo, ZF235, UMad. Paul da Serra, 24-VII-2009, M. Sequeira, Z. Ferreira, A. Correia, A. Figueiredo, ZF236, UMad. Paul da Serra, 24-VII-2009, M. Sequeira, Z. Ferreira, A. Correia, A. Figueiredo, ZF238, UMad. Serra d’Água - abaixo da Pousada dos Vinháticos, 24-VII-2009, M. Sequeira, Z. Ferreira, A. Correia, A. Figueiredo, 240ZF, UMad. Serra d’Água - abaixo da Pousada dos Vinháticos, 24-VII-2009, M. Sequeira, Z. Ferreira, A. Correia, A. Figueiredo, 241ZF, UMad. Serra d’Água - abaixo da Pousada dos Vinháticos, 24-VII-2009, M. Sequeira, Z. Ferreira, A. Correia, A. Figueiredo, ZF242, UMad. Carreiras (Camacha), alt. 1070 m, 26-VII-2009, M. Sequeira, Z. Ferreira, A. Correia, A. Figueiredo, ZF244, UMad. Carreiras (Camacha), alt. 1070 m, 26-VII-2009, M. Sequeira, Z. Ferreira, A. Correia, A. Figueiredo, 245ZF, UMad. Pico do Areeiro, 26-VII-2009, M. Sequeira, Z. Ferreira, A. Correia, A. Figueiredo, ZF246, UMad. Pico do Areeiro, 26-VII-2009, M. Sequeira, Z. Ferreira, A. Correia, A. Figueiredo, ZF247, UMad. Pico do Areeiro, 26-VII-2009, M. Sequeira, Z. Ferreira, A. Correia, A. Figueiredo, 248ZF, UMad. Fajã da Ovelha, 625 m, 29-VII-2009, M. Sequeira, Z. Ferreira, M. Benedito, 256ZF, UMad. Fajã da Ovelha, alt. 625 m, 29-VII-2009, M. Sequeira, Z. Ferreira, M. Benedito, ZF257, UMad. Fajã da Ovelha, 26-VII-2007, Licínia Ramos, UMad. Levada dos Prazeres, Berma da Levada, 646 m, 05-X-2009, João Bruno, António Branco, 7, UMad. Estrada para os Prazeres, alt. 590 m, exp. WNW 301º, 23-IV-2009, M. Sequeira, M. Benedito & Z. Ferreira, MS 6346, MA 801898. Abaixo da Encumeada (acima da pousada dos Vinháticos), talude rochoso junto à estrada, alt. 806 m, 11-05-2006, Z. Ferreira, ZF67D, UMad. Abaixo da Encumeada (acima da pousada dos Vinháticos) , talude rochoso junto à estrada, alt. 806 m, 11-05-2006, Z. Ferreira, M. Sequeira & A. Pupo Correia, ZF67B, MA 863325. Terreiro da Luta, 26-VI-2012, Roberto Jardim, 3048. Pico do Areeiro, 1818 m, 26-VI-2012, Roberto Jardim, 3039. Rochão Camacha - Caminho da Portela, alt. 947, 22-VI-2006, Z. Ferreira, ZF115, UMad.

4.21 Recognised hybrids

4.21.1 *Andryala* x *brievaensis* García Adá in Acta Bot. Malac. 17: 259. 1992

Ind. loc.: “Segovia: Brieva, 30TVL1244, 1040 m, tomillar pedregoso sobre calizas contiguas a terrenos silíceos, 21-VII-1989, leg. R. García Adá y G. López, 6546 RG. Holotype: MA 503134, Isotype: MA 503135.”
Typus: Spain, “Segovia, Brieva, VL1244, 1040 m, tomillar calizo pedregoso, 21-7-1989”, *R. García & G. López, 6546 RG* – Holotype: MA648908; isotype: MA503135 (García Adá 1992).

4.21.1.1 Description

Perennial herb, with a dark woody stock, multi-stemmed (Figure 4.87A). STEMS 37-57 cm, branched in the upper third or from the base, tomentose with stellate hairs only. LEAVES glaucous, tomentose; lower leaves lanceolate, apex acute, and margin dentate or ± pinnatifid, attenuate into a petiole; cauline leaves 77 x 21 mm, semiamplexicaul, ± lanceolate, base attenuate, apex acute, and margin dentate or ± pinnatifid; upper leaves 15.7 x 3.8 mm, semiamplexicaul, ovate-lanceolate, base rounded, apex acuminate, and margin entire. INFLORESCENCE corymbose with 2–5 capitula. CAPITULA (10-)13–15 mm in diameter (Figure 4.87B); peduncles ± 32 mm with stellate hairs only; involucre 12 x 10 mm, campanulate at anthesis, with involucral bracts in 3 rows; external involucral bracts 8–8.8 x 1–1.2 mm, linear-lanceolate, apex acuminate to subulate, flat not enfolding a floret, the outer face stellate-tomentose with no glandular hairs; internal involucral bracts 8–8.6 x 1–1.6 mm, with broad scariose margins; receptacle convex, puberulous to pubescent with setose hairs 1–2 mm (longer than the cypselae). FLORETS ligulate, golden yellow, the external with a tube of 3.8–4.7 mm and ligule of 7–8 x 1–1.2 mm (Figure 4.87C). CYPSELAE 1.5 x 0.3 mm, sterile, obconical, light-brown with whitish ribs, apex with a ring of small teeth ± equalling (not exceeding) the conspicuous prolongation of the ribs; pappus of dirty-white bristles 5.6–6.3 mm, pilose at the base.

4.21.1.2 Comments on taxonomy and nomenclature

Andryala x *brievaensis* García Adá is a putative hybrid between *A. integrifolia* L. x *A. ragusina* L. (García Adá 1992). It is a perennial plant that differs from *A. ragusina* L. by the length of the receptacle setae and width of the leaves as well as from *A. integrifolia* L. by the woody base and lack of glandular hairs, as stated in the protologue: “*Planta perennis, a A. ragusinae habito, foliis angustioribus, indumento et praecipue receptaculi setae cypselis perspicue longioribus differt; a A. integrifoliae caulibus ad bases lignosis, pedunculis et phyllis involucrorum pills glanduliferis destitutis recedit.*” According to García Adá (1992), the remarkable differences between the parental species and the clear morphological characters of the hybrid, make it unnecessary to consider other studies to confirm the origin this *taxon*. In fact, this hybrid resembles *A. ragusina* L. in habit, exhibiting a dark woody stock, an indumentum with no glandular hairs, a paniculate-corymbose inflorescence or longly pedunculate solitary capitula. However, its shares some features with *A. integrifolia* L. (e.g., receptacle hairs longer than the cypsela, short cypsela). García Adá (1992) also alluded to the hybrid sterility stressing that the cypselae appear to be empty.

4.21.1.3 Karyology

No chromosome counts are known for this hybrid.

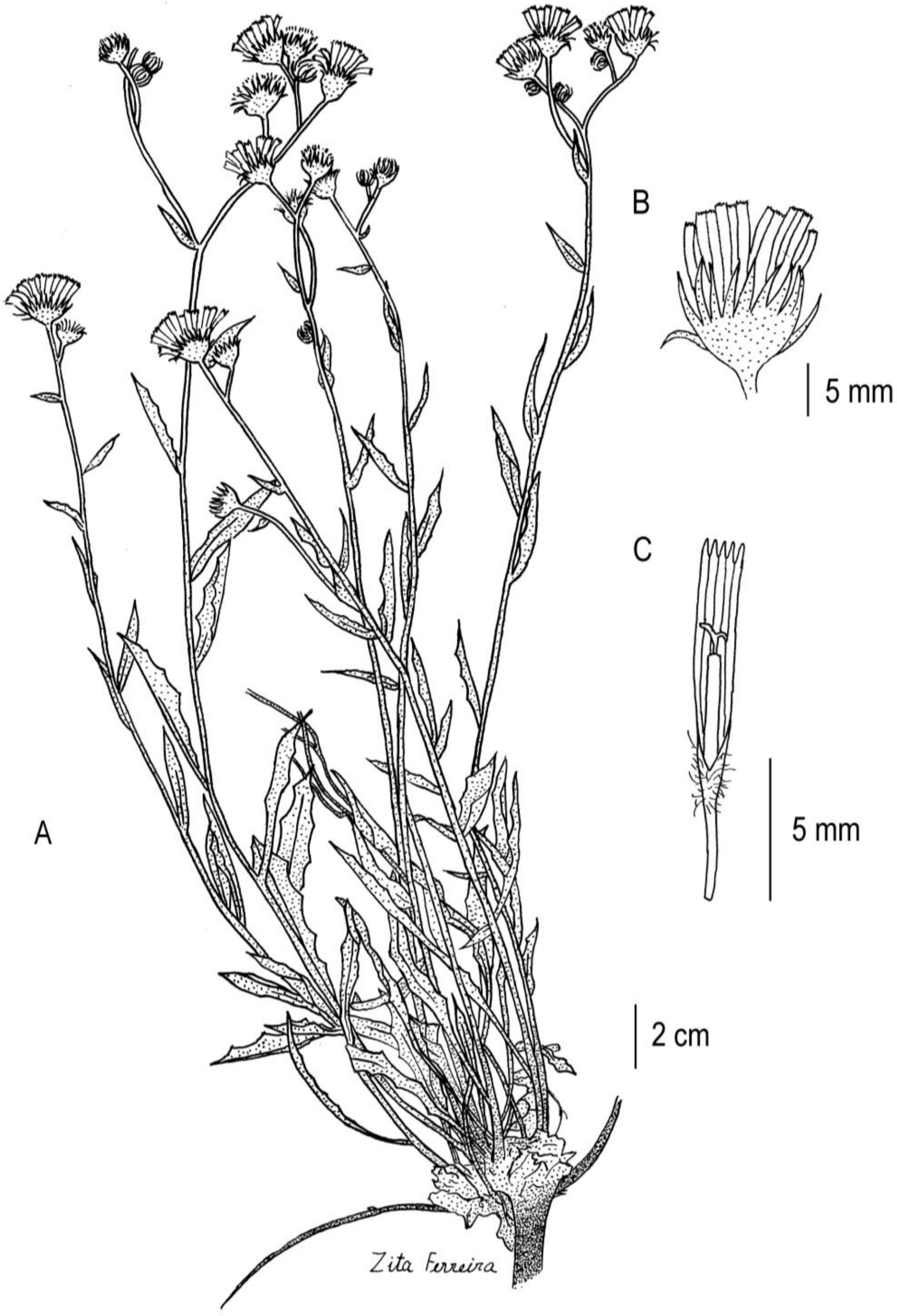

Figure 4.87 *Andryala* x *brievaensis* García Adá A – Fertile habit, B – Capitulum, C – Floret.

4.21.1.4 Ecology and conservation status

Andryala x *brievaensis* García Adá is found growing among its parental species in siliceous-calcareous transition fields, where other *taxa* characteristic of both types of substrate are settled (García Adá 1992). According to available herbarium data, it also occurs in rocky limestone thyme fields, at altitudes around 1040 m asl, as well as in pine forests and sandy coastal sites.

The available data are insufficient to assign an IUCN category and, therefore, the DD ("Data deficient") category should be applied to this *taxon*.

4.21.1.5 Geographic distribution

This hybrid can be found in Spain, more specifically, in the provinces of Segovia (García Adá 1992) and Valladolid, according to available herbarium data (Figure 4.88).

Figure 4.88 Distribution area of *Andryala* x *brievaensis* García Adá, according to studied material.

4.21.1.6 List of studied material

Spain:	
[Segovia]:	Brieva,1040 meters, tomillar calizo pedregoso, 21-VII-1989, R. García & G. López, 6546RG, MA 648908. Brieva, hacia Adrada de Pirón, 1040 meters, tomillar calizo pedregoso, 21-VII-1989, R. García & G. López, 6546RG, MA 503135.
[Valladolid]:	Castille, pinede, 1906, Fre. Sennen, MA 139096.

4.21.2 *Andryala* x *dichroa* Maire in Bull. Soc. Hist. Nat. Afrique 28(5): 364. 1937

Ind. loc.: "Alger, né des semences d'un pied d'*Andryala laxiflora* Salzm. élevé d'akènes récoltés à Jemmapes, au milieu des *A. integrifolia* spontanés."

Typus: [Algeria] "Alger: issu de semenses d'*A. laxiflora*, cultivé au milieu des *A. integrifolia*, 06-06-1936", *R. Maire 3151* – Lectotype (designated here): P04124214; isolectotypes: P02712781, P03891300, MPU004363.

4.21.2.1 Typification

According to Stafleu & Cowan (1981) the Maire herbarium and type specimens are kept at MPU herbarium, although important sets of duplicates can be found in other institutions including P herbarium. Thus, the specimen P04124214 is here designated as lectotype since it is the best developed and, comparatively to the specimen from MPU, it is better preserved.

4.21.2.2 Description

Annual herb, single-stemmed (Figure 4.89A). STEMS 30–54 cm, branched in the upper half or from the base sometimes in the upper third, pubescent to densely stellate-tomentose and sometimes with glandular hairs, especially in the upper third (Figure 4.90A).

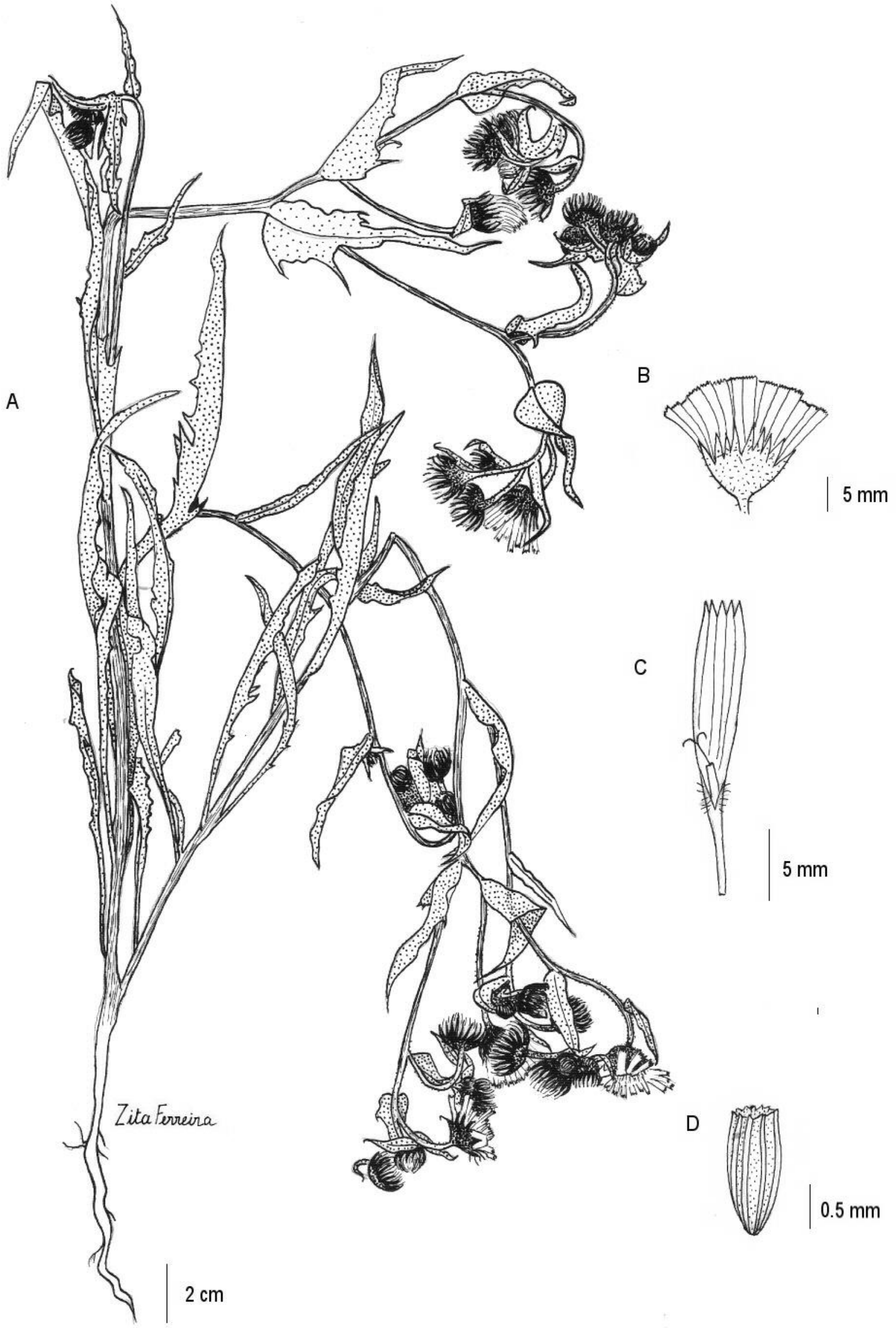

Figure 4.89 *Andryala* x *dichroa* Maire A – Fertile habit, B – Capitulum, C – Floret, D – Cypsela.

LEAVES glaucous to deep green, puberulous to tomentose on both faces with stellate hairs (Figure 4.89B), especially on the upper leaves, and sometimes with few glandular hairs; lower leaves marcescent at anthesis, 64 x 11 mm, attenuate into a short winged petiole 14 mm, ± lanceolate, apex acute, and margin dentate-lobate, cauline leaves 30–70(-90) x 7–14 mm, usually semiamplexicaul, linear-lanceolate to ovate-lanceolate or ovate-oblong, base attenuate to ± cuneate, apex acute to acuminate, and margin entire or ± pinnatifid; upper leaves 19–34 x 3.5–9 mm, amplexicaul, ovate-oblong to narrowly ovate-lanceolate, base ± rounded to subcordate, apex acuminate, and margin entire. INFLORESCENCE laxly corymbose or paniculate-corymbose with 2–7 capitula. CAPITULA 19–25 mm in diameter (Figure 4.90B); peduncles 24–42(-51) mm, pubescent-tomentose with stellate hairs and few glandular hairs 0.3–1.4 mm (Figure 4.90C); involucre 8–13 x 10–19 mm, campanulate to ± hemispherical at anthesis, with involucral bracts in 2–4 rows; external involucral bracts 5–11 x 1.2–1.6 mm, lanceolate to linear-lanceolate, apex acute to acuminate, involute to strongly involute enfolding a floret, the outer face tomentose with dense stellate hairs and abundant yellow glandular hairs 0.5–1.5 mm, the inner face sometimes stellate-hairy; internal involucral bracts 5–7.5 x 1.3–2.2 mm, with broad scariose margins, receptacle ± convex, frequently villous with setose hairs 2–4.6 mm (2 to 4 times longer than the cypselae). FLORETS ligulate, pale-yellow, the external with a tube of 3–4.8 mm and ligule of 5–10 x 1.6–2.5 mm (Figure 4.89C) sometimes with a reddish stripe on the outer face. CYPSELAE 1–1.5 x 0.3–0.5 mm (Figure 4.89D), many sterile, fertile oblong dark brown with white ribs, apex with a ring of prominent thin teeth exceeding the prolongation of the ribs (Figure 4.90D); pappus of white bristles 4.4–5.5 mm, pilose at the base (Figure 4.90E).

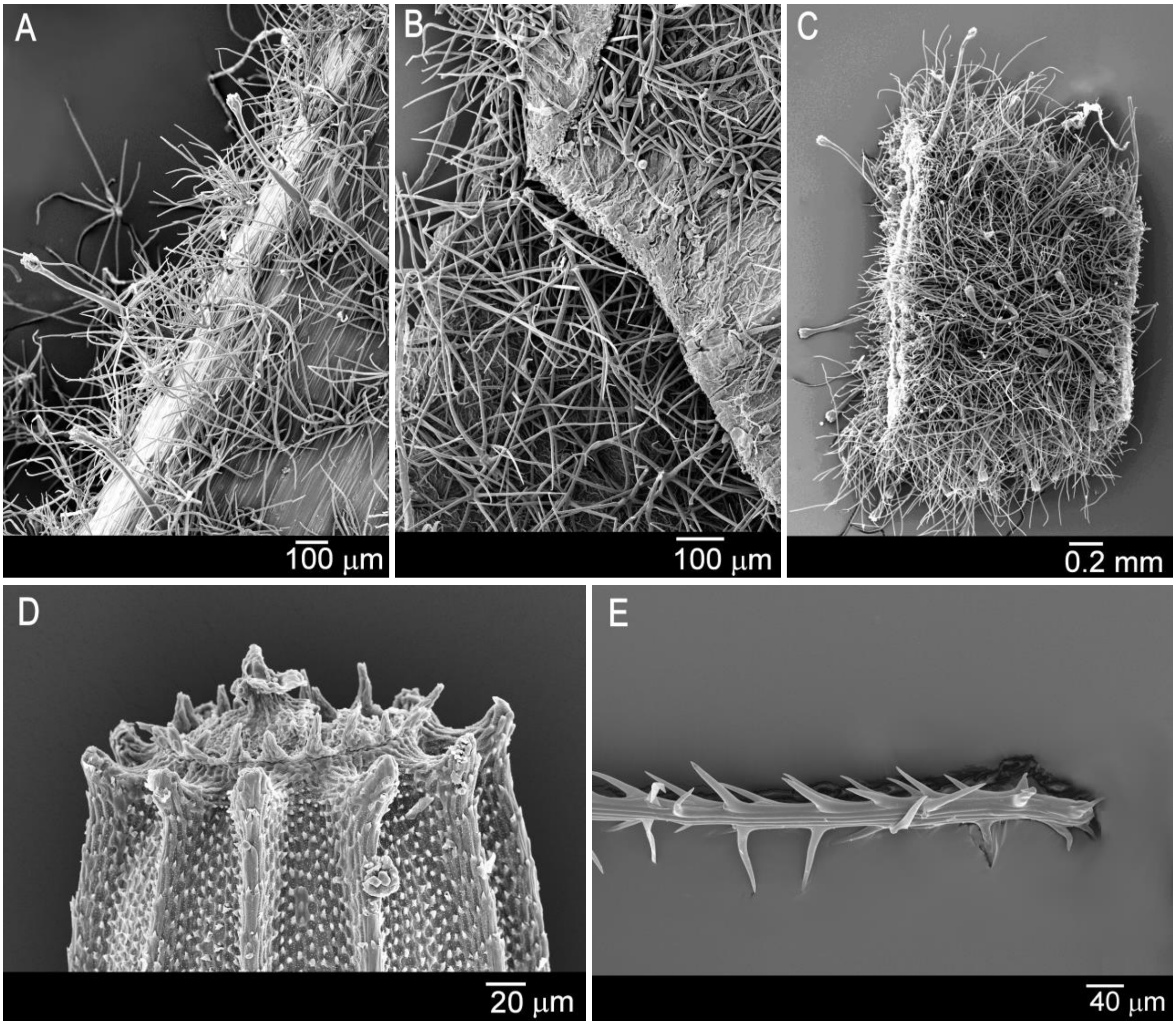

Figure 4.90 *Andryala* x *dichroa* Maire A – Stem indumentum, B – Leaf indumentum, C – Peduncle indumentum, D – Cypsela apex, E – Pappus base.

4.21.2.3 Comments on taxonomy and nomenclature

Andryala x *dichroa* Maire is a putatitive hybrid between *A. integrifolia* L. and *A. rothia* Pers. (= *A. laxiflora* DC.). In the original description, Maire (1937: 364) stressed its similarity to *A. laxiflora*, differing by the leaf margin, the stem and inflorescence indumentums as well as the colour of the external ligules: “*Par son port et la plupart de ses caractères cet hybrid se rapproche surtout de l'A. laxiflora; il en diffère par ses feuilles entières, sa tige sans glandes au dessous de l'inflorescence, l'indument de l'inflorescence plus épais, à poils glanduleux plus jaunes et plus longs, ses ligules externes très pâles*.” Indeed, the upper and cauline leaves are entire, although the latter are sometimes more or less pinnatifid. The author stated the absence of glandular hairs on the stem beneath the inflorescence. Nonetheless, these are usually scarce in the upper half of the stem and indeed absent in the lower part. Moreover, in *Andryala* x *dichroa* Maire the involucral bracts are not as strongly involute as in *A. rothia* Pers. and these exhibit an acute to acuminate apex and not subulate. Contrarily to *A. integrifolia* L. the external involucral bracts are involute enfolding a floret and the inner face is sometimes stellate-hairy. Maire (1937) stressed that this hybrid was obtained from seeds collected from an *Andryala laxiflora* Salzm. plant raised from cypselae collected in the field amongst *A. integrifolia* plants growing spontaneously. Furthermore, Maire (1937: 364) underlined that the cypselae of *Andryala* x *dichroa* Maire are almost all sterile.

4.21.2.4 Karyology

No chromosome counts are known for this hybrid.

4.21.2.5 Ecology and conservation status

According to available herbarium data, this hybrid can be found in localities between 280–1520 m asl, growing in vineyards on granitic soils. It also occurs in sparce and dry shrublands on limestone substrates. However, its ecology is not yet clearly undertood. The available data are insufficient to assign an IUCN category and, therefore, the DD (“Data deficient”) category should be applied to this *taxon*.

4.21.2.6 Geographic distribution

Andryala x *dichroa* Maire was first reported for Jemmapes in Algeria (Maire 1937), but it can also be found in central and southern Spain as well as central Morocco, according to available herbarium data (Figure 4.91).

4.21.2.7 List of studied material

Morocco:	
[Tiznit]:	Monte Buhalam (Ifni), 13-06-1934, Prof A. Caballero, MA 139216.
[Azilal]:	Cerca de Azilal, en las gargantas de Oued-El-Abid, 670 m, en matorral seco sobre calizas,13-06-1982, J. Fdez Casas, F. Muñoz Garmendia, A. Susanna & M. T. Telleria, MA 633473.
[Ouarzazate]:	cerca de Ait Bou-Ktir,1520 m, en matorral muy ralo, desertico,14-06-1982, J. Fdez Casas, F. Muñoz Garmendia, A. Susanna & M. T. Telleria, FC 6899, MA 446400.
Spain:	
[Ciudad Real]:	Solana del Rio, Sierra Madrona, Garganta de los Haces, 1000 m, 01-VI-1996, R. Garcia Rio, MA 596822.
[Códoba]:	Andalusia, Hornachuelos,280 m, J. Chrtek, PRA 1930/11.
[Madrid]:	Cadalso de los Vidrios, carretera de El Elcinar de Alberche a Cadalso, junto al limite provincial con Toledo, 30T UK8261, a unos 600 metros, viñedos en terrenos graníticos, 09-VII-1992, Garcia Adá, G. Lopéz González,10523, MA 566056. Cadalso de los Vidrios, carretera de El Elcinar de Alberche a Cadalso, junto al limite provincial con Toledo, 30T UK8261, a unos 600 metros, viñedos en terrenos graníticos, 09-VII-1992, Garcia Adá, G. Lopéz González,10524, MA 566053.

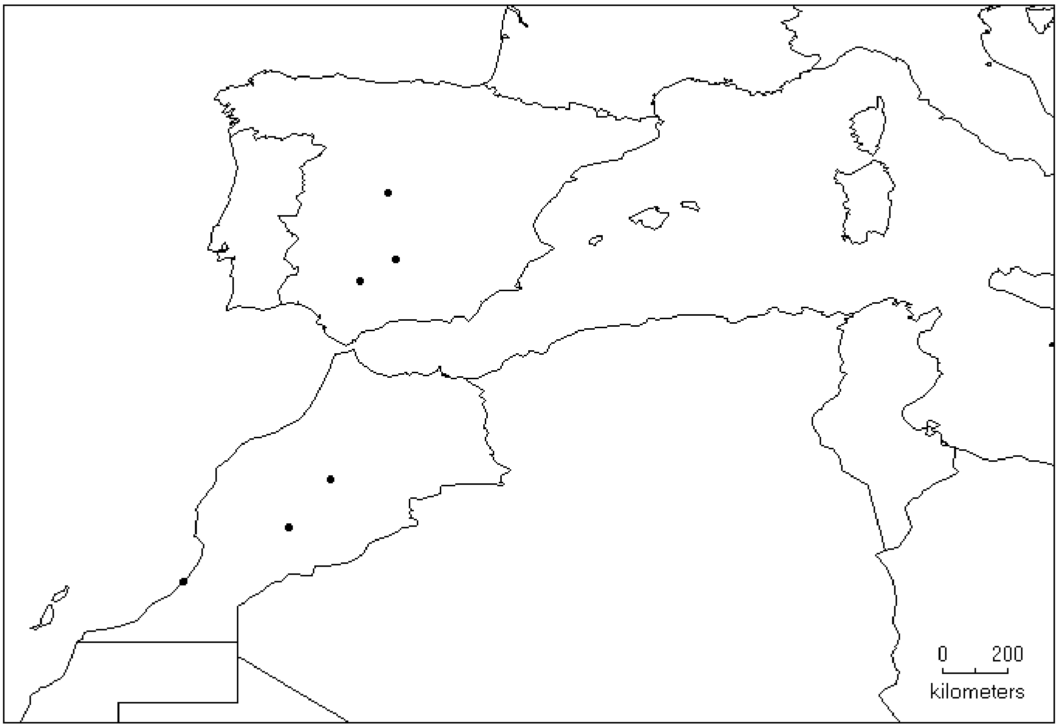

Figure 4.91 Distribution area of *Andryala* x *dichroa* Maire, according to studied material.

4.21.3 *Andryala* x *dansereauoi* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. hyb. nov.

Typus: Portugal: Madeira, Jardim do Mar, 32°44'20" N 17°12'41" W, 19 m, rocky coastal soil, 14-VI-2009, *Z. Ferreira 203* – Holoptype: MA 890187

4.21.3.1 Description

Chamaephyte, single-stemmed more rarey multi-stemmed (Figure 4.92A). STEMS 45–89 cm, frequently woody at the base, branched in the upper third or from the base, stellate-tomentose sometimes densely stellate-tomentose in the upper third, with abundant glandular hairs only above (Figure 4.93A). LEAVES glaucous or pale green, usually densely stellate-tomentose on both faces often with glandular hairs on the upper leaves (Figure 4.93B); lower leaves arranged in a rosette, frequently marcescent, 107–240 x 11–87 mm, attenuate into a winged petiole 15–35 mm, oblong to lanceolate, apex acute, and margin subentire to pinnatipartite, cauline leaves 58–145 x 6–55 mm, semiamplexicaul, oblong to linear-lanceolate, base attenuate sometimes ± rounded, apex acute, and margin entire to pinnatipartite; upper leaves 19–43 x 4–11 mm, semiamplexicaul or amplexicaul, ovate-lanceolate, base ± rounded to cuneate, apex acuminate and margin entire. INFLORESCENCE ± paniculate-corymbose or corymbose, with 6–10 capitula, sometimes with solitary and longly pedunculate capitula. CAPITULA 16–34 mm in diameter (Figure 4.92B); peduncles 19–50 mm with stellate and glandular hairs 1.3–1.7 mm (Figure 4.93C); involucre 9–13 x 11–20 mm, ± hemispherical at anthesis, with involucral bracts arranged in (3-)4 rows; external involucral bracts 8–10 x 1–2 mm, linear-lanceolate, apex acuminate, strongly involute completely enfolding a cypsela, the outer face often densely stellate-tomentose with abundant yellow glandular hairs 1.3–1.9 mm, the inner face stellate-hairy; internal involucral bracts 7–9 x 1.2–1.8 mm, with broad scariose margins to almost completely scariose, receptacle convex, villous with setose hairs 5–7.5 mm (3 to 5 times longer than the cypselae). FLORETS ligulate, golden yellow, the external with a tube of 3–4 mm and ligule of 7–11 x 1.4–4 mm (Figure 4.93C). CYPSELAE 1.5–1.7 x 0.5–0.6 mm (Figure 4.93D), usually obconical dark brown with white ribs, apex with a ring of teeth ± equalling the prolongation of the ribs (Figure 4.93D); pappus of dirty-white bristles 4.5–6.5 mm, ± denticulate at the base.

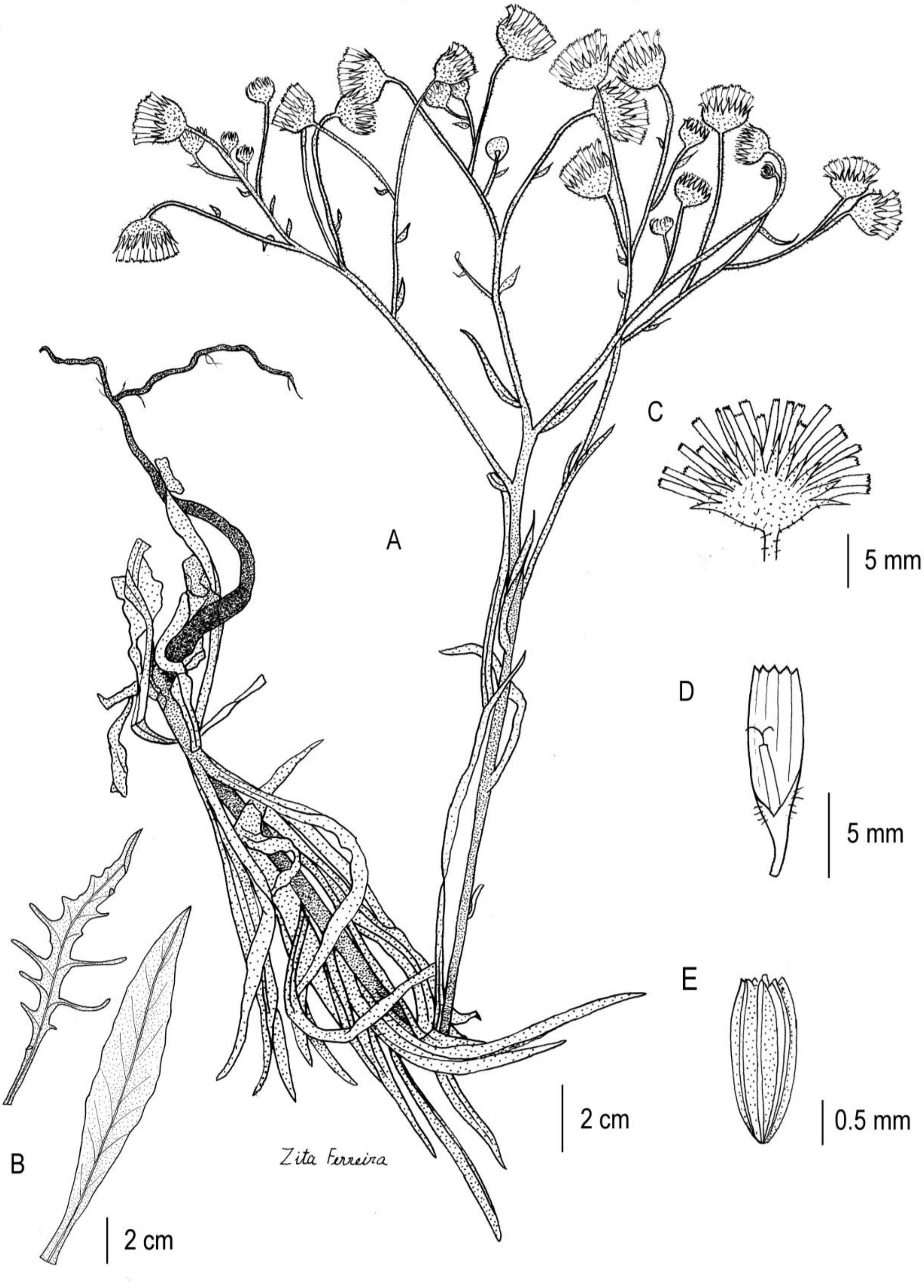

Figure 4.92 *Andryala* x *dansereauoi* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. A – Fertile habit, B – Lower leaf margin, C – Capitulum, D – Floret, E – Cypsela.

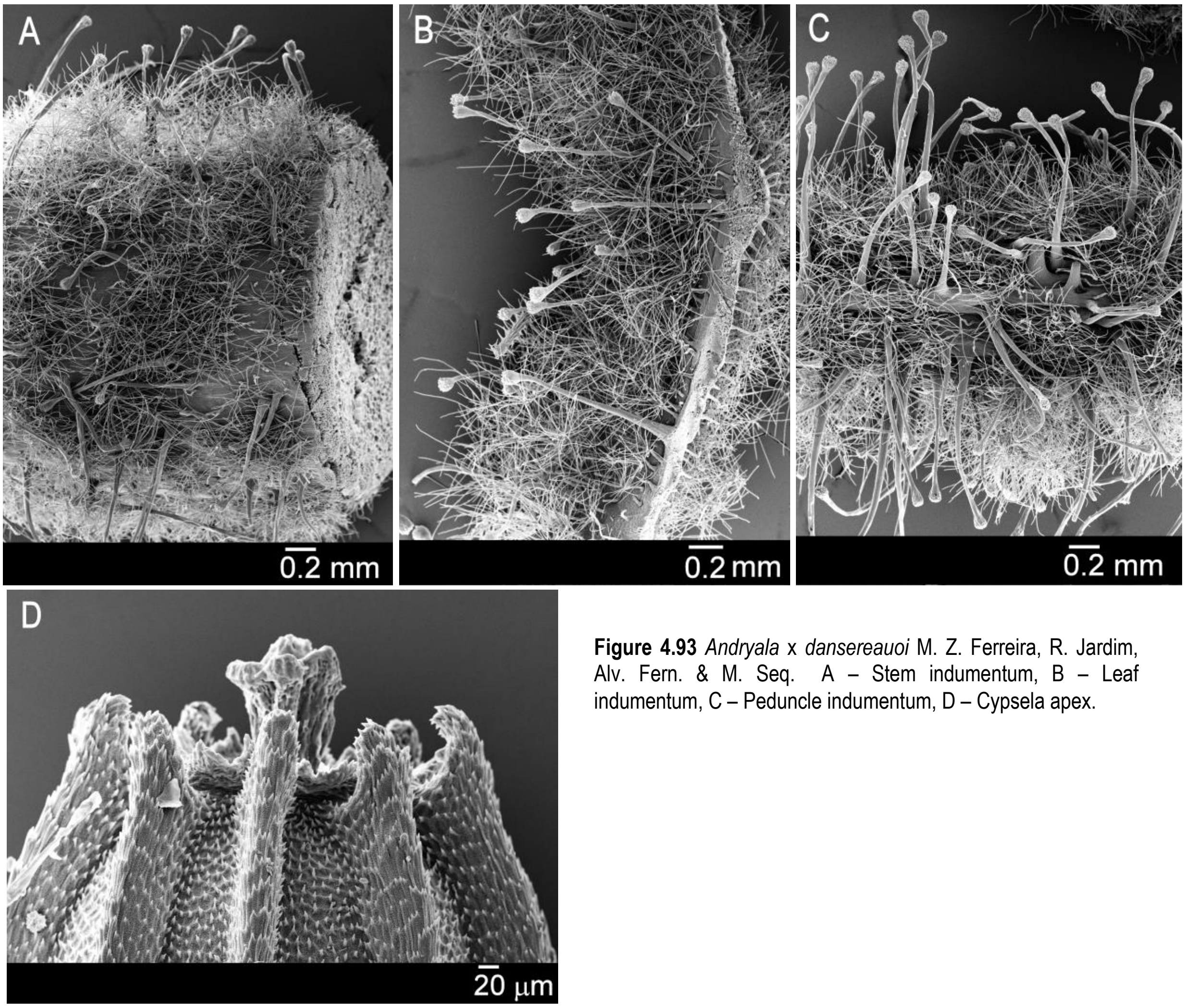

Figure 4.93 *Andryala* x *dansereauoi* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. A – Stem indumentum, B – Leaf indumentum, C – Peduncle indumentum, D – Cypsela apex.

4.21.3.2 Comments on taxonomy and nomenclature

Andryala x *dansereauoi* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. is dedicated and named after Pierre Dansereau (1911-2011), a Canadian ecologist known as one of the "fathers of ecology". Prof. Dansereau wrote a report on the foundation of Botanical Garden in Madeira, entitled *Un Jardin Botanique à Madère* which was included, along with other important works, in *Criação (a) do Jardim Botânico da Madeira*, published in 1960. The putative parents are *A. glandulosa* Lam. and *A. sparsiflora* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. and the possible hybrid nature of this taxon is suggested based on morphological grounds. It differs from *A. glandulosa* Lam. by the stem glandular-hairy only above, lower leaves attenuate into a petiole, oblong to lanceolate, usually pinnatipartite, and cauline leaves pinnatifid to pinnatipartite, less frequently entire and from *A. sparsiflora* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. by the involucre which is ± hemispherical at anthesis, external involucral bracts often arranged in 4 rows, strongly involute enfolding completely a cypsela, the outer face densely stellate-tomentose with abundant yellow glandular hairs, the inner face often stellate-hairy. However, further experimental work (molecular and karyological studies) will be necessary to confirm the hybrid nature of this *taxon*.

4.21.3.3 Karyology

No chromosome counts are known for this hybrid.

4.21.3.4 Ecology and conservation status

This *taxon* can be found on coastal rocky soils, at 5–19 m asl, among species such as *Euphorbia piscatoria* Aiton and *Matthiola maderensis* Lowe, and *Crithmum maritimum* L.

The available data are insufficient to assign an IUCN category and, therefore, the DD ("Data deficient") category should be applied to this *taxon*.

4.21.3.5 Geographic distribution

This *taxon* occurs in a few western localities of Madeira (Madalena do Mar, Calheta, Jardim do Mar and Paúl do Mar), rather near to localities where *A. glandulosa* and *A. sparsiflora* (its putative parents) co-occur. (Figure 4.94).

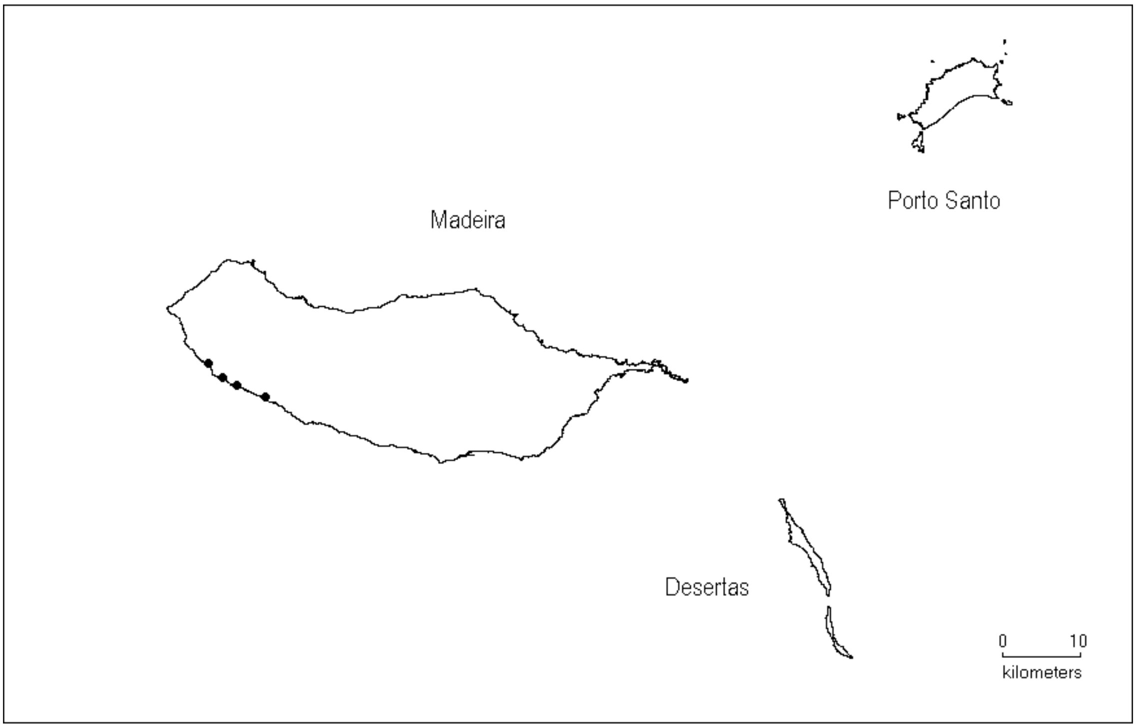

Figure 4.94 Distribution area of *Andryala* x *dansereauoi* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq., according to studied material.

4.21.3.6 List of studied material

Portugal:

[Madeira]: Paúl do Mar, Alt. 16 m, solo pedregoso à beira-mar (para este do Porto), junto com *Euphorbia piscatória, Matthiola maderensis*, 14-V-2006, Z. Ferreira, ZF83, UMad. Calheta (abaixo da EEM), nos taludes rochosos, na estrada junto ao mar, alt. 5 m., 15-VI-2006, Z. Ferreira, ZF99, UMad. Entre o Jardim do Mar e Paúl do Mar, 10-20 m.s.m.,13-IV-2009, M. Sequeira, M. Benedito & D. Henriques, MS 5913, UMad. Jardim do Mar, 19 m.s.m., rocky coastal soil, 14-VI-2009, Z. Ferreira, ZF203, MA 890187. Jardim do Mar, 19 m.s.m., rocky coastal soil, 14-VI-2009, Z. Ferreira, ZF204, UMad. Jardim do Mar, 19 m.s.m., 14-VI-2009, Z. Ferreira, ZF205, UMad. Calhau do Paul do Mar, 14-VI-2009, Z. Ferreira, ZF207, UMad. Calhau do Paul do Mar, 14-VI-2009, Z. Ferreira, ZF208, UMad. Calheta (Perto da Empresa de Electricidade), nos taludes rochosos, na estrada junto ao mar, alt. 5 m. 29-VII-2009, M. Sequeira, Z. Ferreira, M. Benedito, ZF253, UMad. Calheta (Perto da Empresa de Electricidade), nos taludes rochosos, na estrada junto ao mar, alt. 5 m, 29-VII-2009, M. Sequeira, Z. Ferreira, M. Benedito, ZF254, UMad. UMad. Calheta (Perto da Empresa de Electricidade), nos taludes rochosos na estrada junto ao mar, alt. 5 m, 29-VII-2009, M. Sequeira, Z. Ferreira, M. Benedito, ZF255, Madalena do Mar, à beira-mar, em substrato rochoso seco, 03-VII-2015, Z. Ferreira, R. Jardim, ZF303, UMad. Jardim do Mar, à beira-mar, em substrato rochoso seco, 03-VII-2015, Z. Ferreira, R. Jardim, ZF304, UMad.

5 Phylogenetic analysis

This chapter includes a published paper entitled “Tracing the evolutionary history of the little-known Mediterranean Macaronesian genus *Andryala* (Asteraceae) by multigene sequencing”. It is the output of phylogenetic analyses conducted on a taxonomically and geographically fairly comprehensive set of *Andryala* samples. This analysis was performed with nucleotide sequences of the internal transcribed spacers (ITS) and the external transcribed spacer (ETS) of nuclear ribosomal DNA (nrDNA), two chloroplast (cpDNA) markers (trnT–trnL and trnV–ndhC intergenic spacers), and part of the highly variable low-copy nuclear marker squalene synthase (sqs), by using Bayesian and Maximum Parsimony methods of inference. Page numbers in brackets correspond to the pagination of the present thesis.

Tracing the evolutionary history of the little-known Mediterranean-Macaronesian genus *Andryala* (Asteraceae) by multigene sequencing

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Abstract *Andryala* (Asteraceae: Cichorieae) is a little-known Mediterranean-Macaronesian genus whose taxonomy is much in need of revision. In order to elucidate species relationships in the genus, we performed phylogenetic analyses of nucleotide sequences of the internal transcribed spacers (ITS) and the external transcribed spacer (ETS) of nuclear ribosomal DNA (nrDNA), two chloroplast (cpDNA) markers (*trnT-trnL* and *trnV-ndhC* intergenic spacers), and one single-copy nuclear gene (*sqs*) using Bayesian and maximum parsimony methods of inference. While cpDNA analysis confirmed a previously inferred chloroplast capture event with the sister genus *Pilosella*, all nuclear markers supported the monophyletic origin of *Andryala*. However, determining accurate phylogenetic relationships within the genus was quite challenging due to very low levels of nucleotide divergence of all nrDNA and cpDNA markers and a high degree of homoplasy and incomplete lineage sorting in the variable *sqs* marker. Although none of the phylogenies were well resolved, all markers identified two well-supported basal lineages corresponding to the relict species *A. agardhii* (Spain, Morocco) and *A. laevitomentosa* (Romania). The remaining *Andryala* taxa under study, whose relationships were largely unresolved, formed a well-supported clade (“Major Radiation Group”). The capacity of the markers to resolve taxonomic entities within this group varied. While congruent genetic evidence was found for some taxa, several morphologically unambiguous species could not be distinguished at all with most or even all markers. The extremely low level of genetic divergence among most of the species, in spite of high morphological diversity, along with a basal polytomy found with all markers, suggests their relatively recent and rapid speciation. Phylogenetic analyses of the single-copy marker advocate for a single colonization event of the common ancestor of two endemic species (*A. glandulosa*, *A. crithmifolia*) from the Mediterranean region to Madeira and that of two other endemics (*A. perezii*, *A. pinnatifida*) to the Canary Islands. The frequently observed evolutionary pattern of continental dispersion followed by insular speciation also holds for *Andryala*.

Keywords *Andryala*; colonization; Macaronesia; Mediterranean Basin; molecular phylogeny; speciation

Supplementary Material Electronic Supplement (Table S1; Figs. S1–S5) and alignment are available in the Supplementary Data section of the online version of this article at http://www.ingentaconnect.com/content/iapt/tax

■ INTRODUCTION

The Mediterranean Basin is one of the world’s major biodiversity hotspots (Médail & Myers, 2004). This region comprises two major centers of biodiversity: one in the west that includes the Iberian Peninsula and Morocco, and one in the east comprising Turkey and Greece (Médail & Quézel, 1997). Considerable plant biodiversity, as well as endemism, in the Mediterranean region, are the result of the interaction of complex historical geological and environmental factors (Médail & Quézel, 1997; Thompson, 2005).

Macaronesia is an Atlantic region widely considered to comprise five volcanic archipelagos (Azores, Madeira, Selvagens, Canaries, Cape Verde), located at distances varying from 96 to 1500 km off the Iberian Peninsula and North Africa (Fernández-Palacios & al., 2011). This region also contains high plant diversity, where levels of endemic taxa reach 16.2% in Madeira and 67.8% in the Canary Islands (Jardim & Sequeira, 2008). The Macaronesian islands exhibit a wide range of geological ages, varying from 0.8 to 21 million years (Carracedo & al., 2002). Besides the presently emerged archipelagos, Macaronesia includes several seamount archipelagos that constitute Palaeo-Macaronesia. These seamount archipelagos, serving as “stepping stones” during glacial periods, might have facilitated dispersal and colonization from the European or African mainland to Macaronesia and occasionally in the opposite direction as well as inter-archipelago dispersal (García-Talavera, 1999; Carine & al., 2004; Fernández-Palacios & al., 2011).

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The Macaronesian islands have lately become the subject of several phylogenetic studies to clarify origin and diversification of various vascular plant groups. While very few of these studies have identified species endemic to Macaronesia as relicts of Tertiary origin, for example, *Lavatera phoenicea* Vent. (Fuertes-Aguilar & al., 2002), the majority of molecular studies suggested a general pattern of dispersal from the continent followed by insular speciation. In effect, molecular data have revealed single or multiple colonizations of Macaronesia from the Mediterranean region in several plant groups, such as the *Olea europaea* L. complex (Hess & al., 2000), *Lavatera* L. (Fuertes-Aguilar & al., 2002), *Hedera* L. (Valcárcel & al., 2003), *Cheirolophus* Cass. (Garnatje & al., 2007), *Festuca* L. (Díaz-Pérez & al., 2008), and *Echium* L. (Mansion & al., 2009). The Macaronesian islands show considerable habitat diversity, which most likely promoted adaptive radiation. One of the most spectacular cases of rapid speciation of Macaronesian endemics is *Argyranthemum* Webb ex Sch.Bip. (Asteraceae), a morphologically highly variable genus. Molecular studies supported the Mediterranean origin of this genus and revealed low levels of nucleotide divergence among species (Francisco-Ortega & al., 1997). The lack of sequence divergence in cpDNA and nrDNA has been an obstacle to achieve phylogenetic resolution in various groups of island plants. The pace of diversification in some insular groups has apparently been too rapid for fixation of sufficiently many shared mutations to allow robust phylogenetic reconstruction using a limited number of cpDNA and nrDNA characters (Baldwin & al., 1998).

Both the Mediterranean and Macaronesian regions host a little-known genus, *Andryala* L. This plant group is a member of tribe Cichorieae (Asteraceae), included in subtribe Hieraciinae, along with *Hieracium* L., *Hispidella* Barnad. ex Lam., *Pilosella* Vaill. (Fehrer & al., 2007a; Krak & Mráz, 2008) and *Schlagintweitia* Griseb., a segregate of *Hieracium*, including *S. intybacea* (All.) Griseb. (also known as *Hieracium intybaceum* All.), and two of its hybridogeneous derivates (Bräutigam & Greuter, 2007; Kilian & al., 2009). According to a divergence time estimate of tribe Cichorieae (Tremetsberger & al., 2013), the split of *Andryala* from other genera of the Hieraciinae occurred in the late Tertiary (Pliocene). *Andryala* (in its present circumscription, including *Paua* Caball., *Rothia* Schreb., and *Pietrosia* Nyár. ex Sennikov) comprises ca. 17 (Greuter, 2006–; Blanca, 2011; Ferreira & al., 2014a, b) perennial, less often annual or biennial, diploid (2*n* = 18) species distributed mainly in the Mediterranean Basin and Macaronesia with centers of diversity in NW Africa, the Iberian Peninsula and Macaronesia. Thus, *Andryala* is an excellent model system for Mediterranean and Macaronesian biogeography, as its diversity centers are located in these regions. Far apart from the present-day distribution center of this genus, few populations of the endemic relict species *Andryala laevitomentosa* (Nyár. ex Sennikov) Greuter can be found (Kukuła & al., 2003; Negrea & Pricop, 2009) in the Romanian Carpathians, that are known as a glacial refuge (Zhang & al., 2001; Petit & al., 2003). Since it survived outside the present distribution center of the genus, probably the distribution area of *Andryala* was wider in the past (Fehrer & al., 2007b). A morphologically similar species, *Andryala agardhii* DC., occurs in high-altitude regions of southeastern Spain and Morocco and has been considered a Tertiary relict and paleoendemic species (Blanca & al., 1998). According to these authors, *A. agardhii* survived the last glacial persisting in the Iberian Peninsula, a Pleistocene refugium (Taberlet & al., 1998).

No taxonomic revision of the genus *Andryala* as a whole has ever been performed, which accounts for its poorly known taxonomy. The numerous taxonomic studies in *Andryala* include both splitting and lumping approaches (the first recognizing small but consistent variation at species level and the latter emphasizing the close relationship among variants) as it comprises many morphologically highly variable and unclearly delimited taxa. For instance, according to some authors, *Andryala integrifolia* L., an extremely variable species, should probably be divided into many closely related taxa (e.g., Sell, 1976; Greuter, 2006–). Many new names were proposed (Greuter, 2003; Greuter & Raab-Straube, 2007) based on erroneous taxonomy or misidentified specimens (e.g., Ball, 1878; Jahandiez & Maire, 1934; for further details see Ferreira & al., 2014b). Taxonomic treatments of *Andryala* suffer from a lack of molecular data showing relationships among intrageneric taxa. So far, only one or few *Andryala* species were included as outgroup for phylogenetic studies of other genera of tribe Cichorieae (Fehrer & al., 2007a, 2009; Tremetsberger & al., 2013). Fehrer & al. (2007a) suggested that an ancient chloroplast capture event occurred between *Pilosella* and *Andryala*. In the same publication, nuclear (ITS) sequence data clearly revealed the monophyly of *Andryala* and showed three main lineages, i.e., two relict species *A. agardhii* and *A. laevitomentosa* as separate lineages and a well-supported clade including the Macaronesian and Mediterranean taxa.

In the present study, a taxonomically and geographically fairly comprehensive set of *Andryala* samples was analysed (see Electr. Suppl.: Table S1), using the ITS and ETS regions of nrDNA as multi-copy nuclear markers, the intergenic spacers *trnT-trnL* and *trnV-ndhC* as chloroplast markers, and part of squalene synthase (*sqs*) as a highly variable low-copy nuclear marker (Krak & al., 2012). The last has recently been used in a phylogenetic analysis of *Hieracium* (Krak & al., 2013), one of the sister genera of *Andryala*. Phylogenetic analyses were performed to (1) elucidate species relationships in the genus, (2) investigate whether the current classification of *Andryala* is consistent with molecular data, and (3) examine colonization patterns in the Macaronesian region.

■ MATERIALS AND METHODS

Plant material. — Living plants or seeds were collected during field trips between 2010 and 2012 or provided by international collaborators and were cultivated in the experimental garden of the Institute of Botany (Průhonice). Almost all European, North African, and Macaronesian *Andryala* species were included (ca. 90%). Due to difficulties in collecting new material in some countries/regions or inadequate documentation of localities on herbarium labels, three currently recognized North African species could not be included: *A. chevallieri*

Barratte ex L.Chevall., *A. nigricans* Poir., and *A. spartioides* (Pomel ex Batt. & Trab.) Barratte. Although recognized as distinct species (Greuter, 2006–), morphological studies support the inclusion of *A. floccosa* Pomel in *A. laxiflora* DC. as a mere variety (Battandier & Trabut, 1905; Ferreira & al., unpub. data), and in recent Floras *A. rothia* Pers. was synonymized with *A. laxiflora* (Blanca, 2009, 2011), the latter included in this study. For a comparison of the treatment of *Andryala* in the Euro+Med PlantBase (Greuter, 2006–) with the updated nomenclature and species concept we are applying in the present paper, see Electr. Suppl.: Table S1. For molecular analyses, we attempted to cover the range of morphological variation within a species as far as possible in order to assess its intraspecific genetic variation and correspondence to species boundaries. Therefore, morphologically variable taxa were represented by several accessions from different populations as far as possible. To avoid confusion with improperly identified material, plants of unclear taxonomic position or intermediate morphology and obvious hybrid individuals co-occurring with their parental species were excluded from molecular analyses. Altogether, a total of 49 accessions was analyzed. Based on previous studies (Fehrer & al., 2007a; Krak & Mráz, 2008), 12–16 samples of 10–11 species of the most closely related genera of Hieraciinae were chosen as outgroup for the phylogenetic analysis: these were species of *Pilosella* (Bräutigam & Greuter, 2007; formerly treated as a subgenus of *Hieracium*), *Hieracium*, *Hispidella* as well as *Schlagintweitia intybacea* (Fehrer & al., 2007a). Voucher specimens were deposited at PRA and MA. The taxa examined in this study are listed in Appendix 1, along with voucher data.

Molecular procedures. — Total genomic DNA was isolated from CTAB-preserved or silica-gel dried material, as well as from fresh or herbarium material, either by sorbitol extraction (Štorchová & al., 2000) or by use of the DNeasy Plant Mini kit (Qiagen, Hilden, Germany). Modifications to the sorbitol extraction were introduced: fresh samples were frozen in liquid nitrogen and crushed in a porcelain mortar, and poly(vinylpolypyrrolidone) (P 6755, Sigma-Aldrich, Prague, Czech Republic) as well as 1 µl of EDTA (ethylenediamine tetraacetic acid disodium salt dihydrate, 0.5 M, pH 8.19) were added between two additions of 650 µl of extraction buffer. DNA quality was checked through electrophoresis and its quantity measured using a spectrophotometer. PCR amplifications of the *trnT-trnL* intergenic spacer were performed as in Fehrer & al. (2007a). For ITS amplification, primers ITS-A and ITS-B (Blattner, 1999) were used with the same PCR conditions. The ETS region was PCR-amplified using primers Ast-8 and 18 S (Baldwin & Markos, 1998) as described in Fehrer & al. (2009). The chloroplast *trnV-ndhC* intergenic spacer and the part of the low-copy nuclear *sqs* gene spanning exon 4 through intron 8 were amplified following Krak & al. (2013). PCR products were purified and sequenced as described in Fehrer & al. (2009). All DNA regions under study were directly sequenced in both directions using the PCR primers; for *trnV-ndhC* and *sqs*, additional internal sequencing primers were utilized as described in Krak & al. (2013). Samples that were heterozygous for *sqs* were cloned as described in Fehrer & al. (2009). Cloned *sqs* sequences were also often sequenced with several primers due to the length of the amplification product and difficulties with polynucleotide runs. Correction of polymerase errors, elimination of recombinant clones and allelic interpretation were done as described in Krak & al. (2013). Four samples showed a single polymorphism in direct sequencing and were represented by two sequences with the alternative character states, designated as alleles A or B. No more than two alleles per plant were found, no extraordinary branch lengths occurred (i.e., individual lineages with strongly accelerated rates of molecular evolution which may be indicative of paralogs or pseudogenes), variation in exon regions was very low, and despite a number of outliers (see below), alleles of the same individual or species most often grouped together. Taken together, this indicates that the low-copy nuclear marker *sqs* is a functional single-copy gene in *Andryala* as it is in the closely related *Hieracium* (Krak & al., 2013). However, the proportion of homozygous plants was much higher in *Andryala*. GenBank accession numbers for each sequence are listed in Appendix 1.

Sequence and phylogenetic analysis. — Chromatograms were edited manually using Chromas v.1.45 or Chromas Lite v.2.01 (http://technelysium.com.au/) and aligned using the Bioedit Sequence Alignment Editor v.7.0.9.0 (Hall, 1999). For the multicopy nuclear markers ITS and ETS, both directions of sequence reads were checked for polymorphisms. Ribotypes of two accessions showed additive polymorphisms of other species indicative of introgression. The parental ribotypes (i.e., their specific character states) were present in unequal amounts (respective peak heights in electropherograms) and were sorted into major and minor ribotypes, respectively. Polymorphisms in other samples were treated as described in Fehrer & al. (2009). ITS and ETS polymorphic sequences grouped together with major ribotypes in preliminary analyses and thus, the last were used for final nrDNA tree reconstruction.

Phylogenetic analyses were conducted using maximum parsimony and Bayesian inference applying the same parameters for each marker (ITS, ETS, *trnT-trnL*, *trnV-ndhC*, *sqs*) unless stated otherwise. The datasets at first were analyzed separately. The topologies of the individual trees were in many respects conflicting between the nuclear ribosomal and plastid data (see Electr. Suppl.: Figs. S1–S4). Therefore, only the two nrDNA and the two cpDNA datasets, respectively, were combined, concatenating ITS+ETS and *trnT-trnL*+*trnV-ndhC* sequences. Many samples were heterozygous for *sqs*, sometimes with strongly divergent alleles, and the *sqs* tree topology was in conflict with the other trees as well. Therefore, this dataset was also analyzed separately. Parsimony analyses were performed with PAUP* v.4.0b10 (Swofford, 2002). Heuristic searches were done with 1000 random sequence addition replicates, saving no more than 1000 trees of length greater than or equal to 1 per replicate and TBR branch swapping. Gaps were coded using simple gap coding (Simmons & Ochoterena, 2000) as implemented in SeqState v.1.4.1 (Müller, 2005). Support for internal nodes was assessed using bootstrap analyses (Felsenstein, 1978) with 1000 replicates and the same settings as above. Bayesian analyses were carried out using MrBayes v.3.1.2 (Ronquist & Huelsenbeck, 2003). For these analyses, at first, the model best fitting the presumed molecular evolution of the respective datasets was determined using MrModeltest v.2.3 (Nylander, 2004). The best models found under the Akaike information criterion were used: GTR+G for ITS, ETS and the combined nrDNA dataset; GTR+I for *trnV-ndhC*; GTR for *trnT-trnL*; GTR+G for the combined cpDNA dataset; and GTR+I+G for the *sqs* dataset. Two replicate analyses with four chains each were performed with the default parameters and computed for 1.5 million generations, sampling every 1000th tree. All statistical parameters indicated that convergence was reached. The first 25% of the trees per run were discarded as burn-in, and the remaining trees were summarized. Multiple sequence alignments on which Figs. 1–3 are based are provided as supplementary data.

To assess the degree of interspecific variation for all markers, mean and maximum sequence divergences were calculated with MEGA v.5 (Tamura & al., 2011) using *P*-distances. To visualize character conflict observed in the alignment of *sqs* sequences, this dataset was also subjected to Neighbor Net analysis as implemented in SplitsTree v.4.11.3 (Huson & Bryant, 2006) using the default settings.

To assess the potential of combining the largely unresolved and incongruent ITS, ETS, *trnV-ndhC*, *trnT-trnL* and *sqs* datasets for species tree inference under coalescence, we used *BEAST v.1.8.1 (Drummond & al., 2012). This analysis was reduced to the ingroup due to the difficulty in aligning outgroup sequences for the low-copy marker. Individuals for which introgression was inferred (*A. laxiflora* JC 19/2 and *A. ragusina* L. JC 2011/2) were excluded. As the analysis requires at least two individuals per species, taxa represented by only one individual were combined: *A. atlanticola* H.Lindb.

Table 1. Species diagnosability by each molecular marker used in this study.

	Molecular marker				
	ETS	ITS	*trnV-ndhC*	*trnT-trnL*	*sqs*
A. laevitomentosa (Nyár. ex Sennikov) Greuter	+	+	+	+	+
A. agardhii DC.	+	+	+	+	+
A. maroccana (Caball.) Maire	+	+	+	+	+
A. ragusina L.	+ (JC 2011/2/1 introgressed)	+ (JC 2011/2/1 introgressed)	+	+ (weak support)	+ (except introgressed JC 2011/2/1)
A. dentata Sm.	+ (weak support)	+	+ (weak support)	–	+
A. perezii M.Z.Ferreira & al.	–	–	+	+ (weak support)	+ (paraphyletic)
A. pinnatifida Aiton	+ (weak support)	–	–	–	+
A. laxiflora DC.	–	+ (JC 19/2 introgressed)	–	–	–
A. arenaria (DC.) Boiss. & Reut.	+	–	–	–	–
A. mogadorensis Coss. ex Hook.f.	– (only shared polymorphisms)	– (only shared polymorphisms)	+ (except subspecies *jahandiezii*)	–	+ (comprising one allele of *A. atlanticola* 10JZ 08/1)
A. crithmifolia Aiton	–	–	–	–	+ (comprising one allele of *A. glandulosa* ZF 233)
A. glandulosa Lam.	–	–	–	–	+ (lacking one allele of *A. glandulosa* ZF 233)
A. cossyrensis Guss.	– (only shared polymorphisms)	–	–	–	–
A. integrifolia L.	–	– (partly shared polymorphisms, comprising *A. atlanticola* 10JZ 08/1)	–	–	–
A. atlanticola H. Lindb.	–	–	–	–	–

Notes: Branches with significant support for Bayesian and maximum parsimony analysis in the individual phylogenetic analyses (Electr. Suppl.: Figs. S1–S4; Fig. 3) are represented by "+"; "weak support" refers to bootstrap values <70% and posterior probabilities <0.95; markers that fail to identify species are represented by "–"; shared polymorphisms in nrDNA: the same double peaks or length variations (shifts) occur in different samples.

was included in *A. integrifolia* of which it may be only a variant (see below), *A. mogadorensis* subsp. *jahandiezii* (Maire) M.Z.Ferreira & al. was included in *A. mogadorensis* Coss. ex Hook.f., and the two subspecies of *A. glandulosa* Lam. were not distinguished. Models of molecular evolution were determined as above for each dataset, and GTR+I was used for *trnV-ndhC* and ITS; GTR for *trnT-trnL*; HKY+G for ETS and GTR+I+G for *sqs*. We applied the following parameters to the *BEAST analysis of each dataset: Yule tree prior, uncorrelated relaxed clock using a randomly generated starting tree; 0/1s representing the coded gaps were transformed to A/Cs. Two independent MCMC analyses were run for 50 million generations, sampling every 1000th tree. To check the stabilization of the analysis, ESS values of parameters were evaluated in Tracer v.1.6 (Rambaut & al., 2014). The two independent runs were merged by LogCombiner v.1.8 and the Maximum clade credibility tree was created with a burn-in period of 25% and a posterior probability limit of 0.5 with Treeannotator (both programs are included in the *BEAST package).

■ RESULTS

Altogether, 49 individuals of 15 species of *Andryala* (Table 1) and 12–16 outgroup samples belonging to 10–11 species of closely related genera were used for each sequence dataset. Two samples, *A. laxiflora* JC 19/2 and *A. ragusina* JC 2011/2, whose ITS and/or ETS sequences showed signs of introgression, were deleted from the nrDNA combined dataset prior to final phylogenetic analyses. According to character additivity, both were introgressed by *A. integrifolia* (Electr. Suppl.: Figs. S1–S2), the most widespread and common species of *Andryala*. These putative hybrids were, however, included in the cpDNA analyses to determine their maternal origin, and also in the phylogenetic analyses based on the nuclear *sqs* marker for which they were homozygous.

Nuclear ribosomal markers showed that all *Andryala* taxa formed a well-supported monophyletic group (Fig. 1). Chloroplast DNA analyses expectedly showed haplotypes of outgroup species that belong to the *Pilosella* II lineage in basal positions

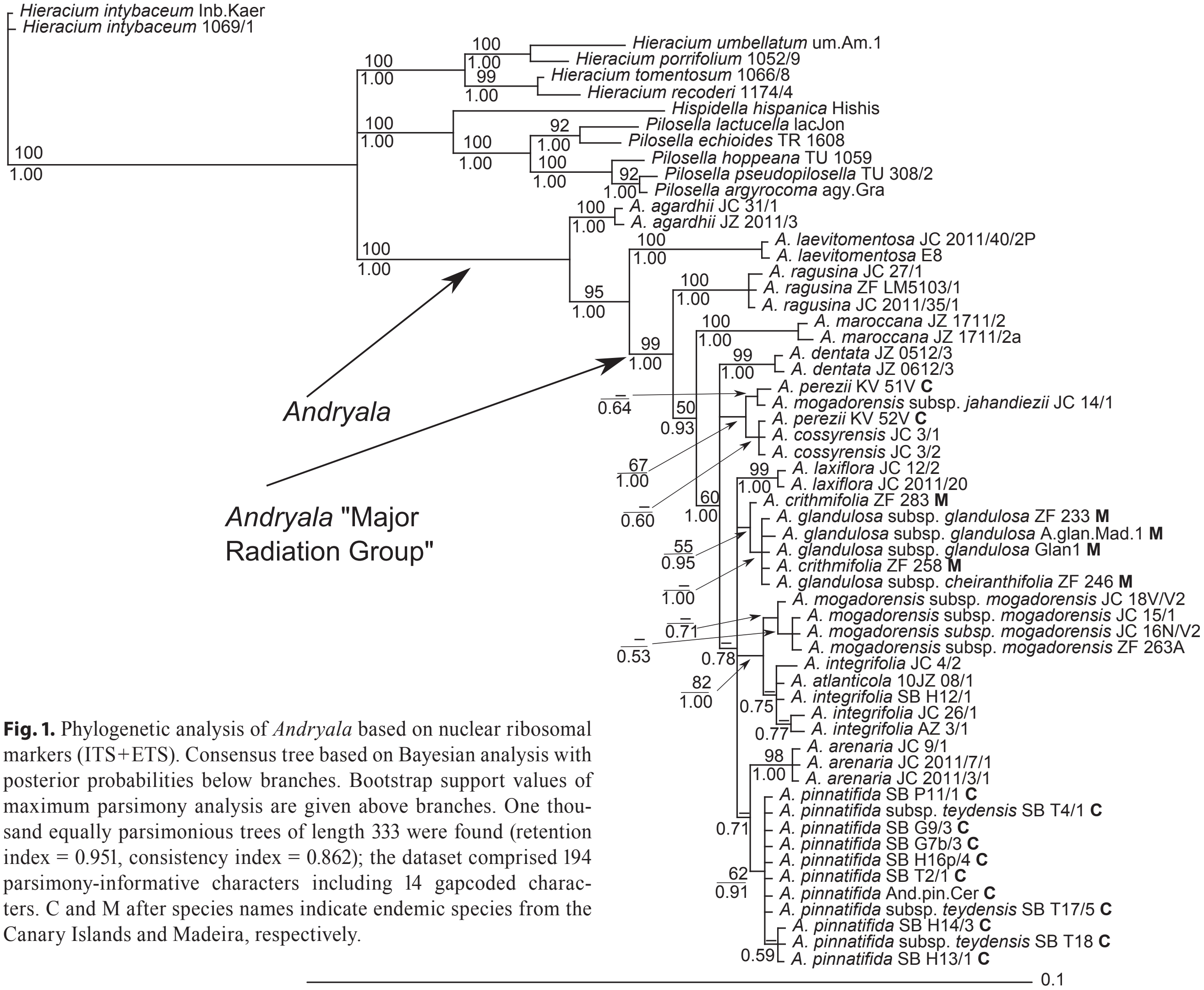


Fig. 1. Phylogenetic analysis of *Andryala* based on nuclear ribosomal markers (ITS+ETS). Consensus tree based on Bayesian analysis with posterior probabilities below branches. Bootstrap support values of maximum parsimony analysis are given above branches. One thousand equally parsimonious trees of length 333 were found (retention index = 0.951, consistency index = 0.862); the dataset comprised 194 parsimony-informative characters including 14 gapcoded characters. C and M after species names indicate endemic species from the Canary Islands and Madeira, respectively.

of the *Andryala* clade (Fig. 2), confirming a previously inferred ancestral chloroplast capture event (Fehrer & al., 2007a, b). The nrDNA and cpDNA markers revealed very low levels of sequence divergence within *Andryala* (mean/maximum *P*-distance including coded gaps: ETS, 0.9%/3.3%; ITS, 0.7%/2.2%; *trnV-ndhC*, 0.3%/2.0%; *trnT-trnL*, 0.5%/2.3%). The single-copy nuclear marker *sqs* had high genetic variation within *Andryala* (mean/maximum *P*-distance including coded gaps 3.9%/6.0%, mostly in intron regions), in contrast to the other four markers; the genus was also monophyletic according to *sqs* (Fig. 3).

All trees showed three main lineages in *Andryala*, namely the two relict species, *A. laevitomentosa* and *A. agardhii*, and a clade comprising all other taxa whose relationships were largely unresolved. Genetic variation within this clade was extremely low for the nrDNA and cpDNA markers (mean/maximum *P*-distance 0.1%–0.6%/1.0%–2.2%). We refer to these taxa as the "Major Radiation Group" (MRG) as they constitute the majority of the species and were monophyletic in all analyses. Although genetic variation in *sqs* for the MRG was relatively high (mean/maximum *P*-distance 3%/5.7%), relationships were mostly unresolved due to character conflict within the dataset (Electr. Suppl.: Fig. S5). PCR or cloning artifacts can be excluded, because most of the alleles that appeared in odd positions in the tree (Fig. 3) were from direct sequences of homozygous samples.

Within the MRG, the North African *A. maroccana* (Caball.) Maire was well distinguished from the other taxa and occurred in a basal position in all trees, along with *A. ragusina* in the nrDNA tree (Fig. 1). No other interspecific relationships within the MRG were supported (considering only bootstrap support [BS] of ≥70% and posterior probabilities [PP] of ≥0.95 as well-supported; Hillis & Bull, 1993; Larget & Simon, 1999) with the exception of a group consisting of *A. integrifolia*, *A. atlanticola* and *A. mogadorensis* subsp. *mogadorensis* (without *A. mogadorensis* subsp. *jahandiezii*) in the nrDNA tree (PP = 1.00, BS = 82%, Fig. 1). A group comprising *A. cossyrensis* Guss., *A. perezii* M.Z.Ferreira & al. and *A. mogadorensis* subsp. *jahandiezii* (North Africa and eastern Canary Islands)

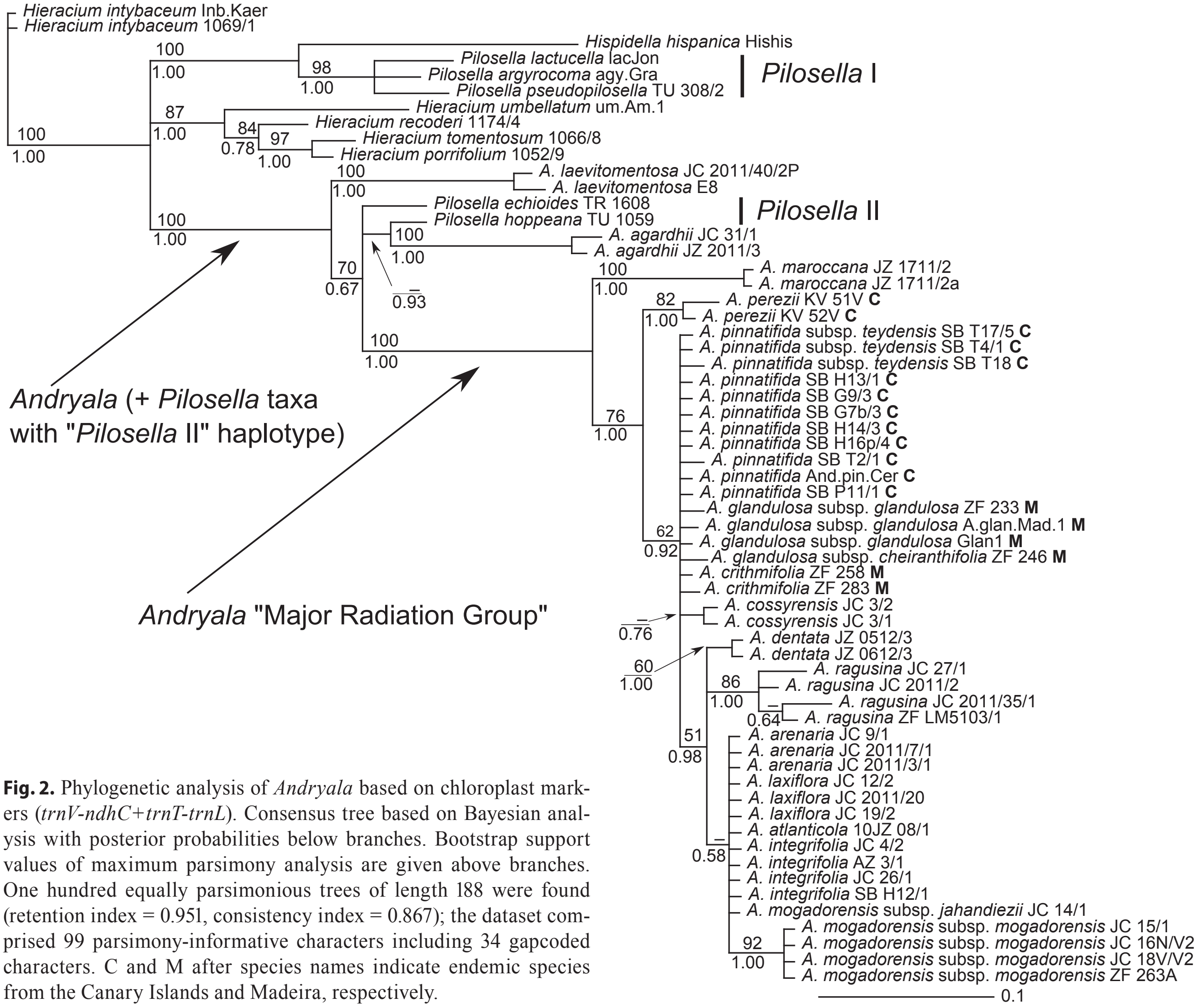


Fig. 2. Phylogenetic analysis of *Andryala* based on chloroplast markers (*trnV-ndhC+trnT-trnL*). Consensus tree based on Bayesian analysis with posterior probabilities below branches. Bootstrap support values of maximum parsimony analysis are given above branches. One hundred equally parsimonious trees of length 188 were found (retention index = 0.951, consistency index = 0.867); the dataset comprised 99 parsimony-informative characters including 34 gapcoded characters. C and M after species names indicate endemic species from the Canary Islands and Madeira, respectively.

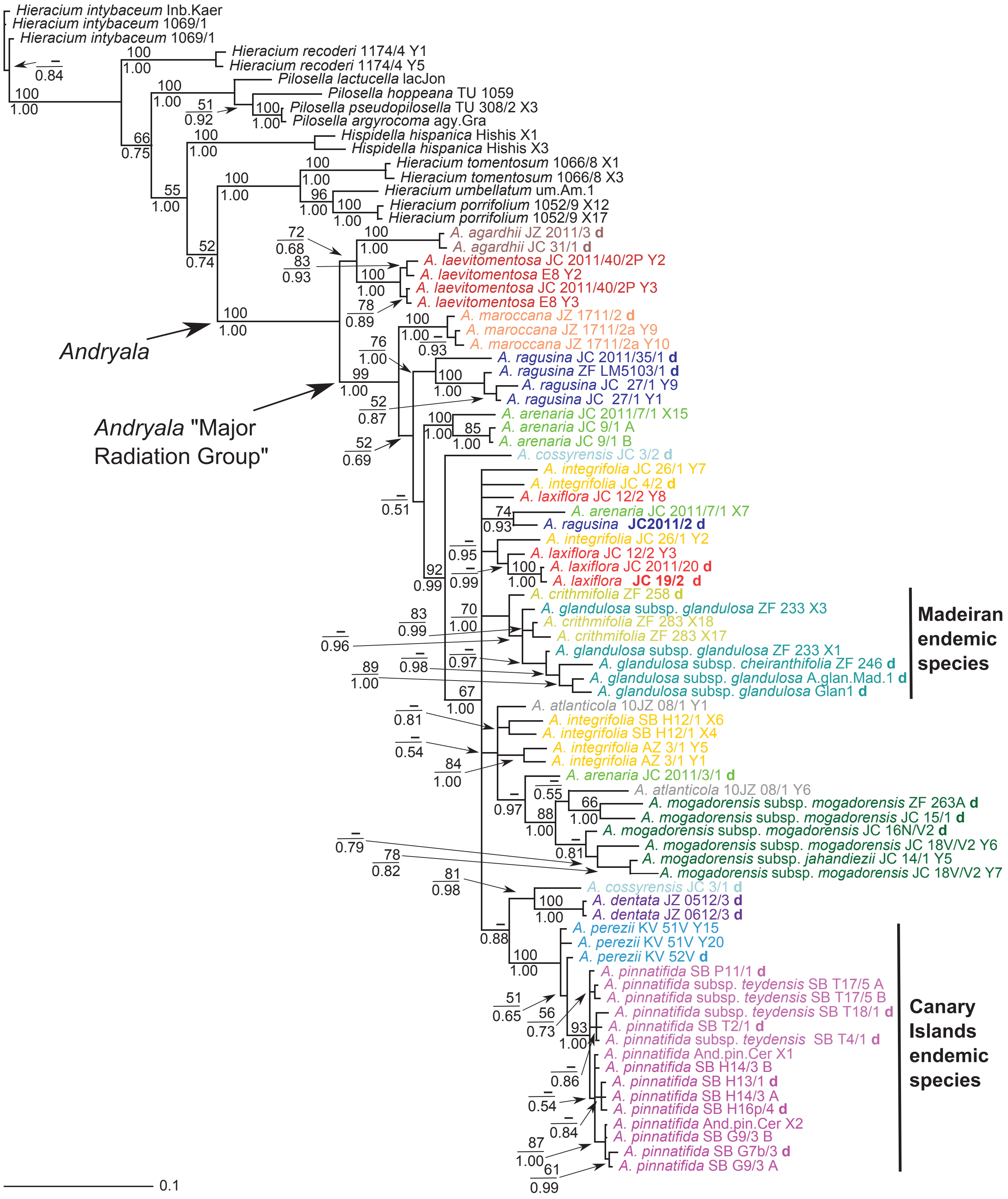


Fig. 3. Phylogenetic analysis of *Andryala* based on the single-copy nuclear marker *sqs*. Consensus tree based on Bayesian analysis with posterior probabilities below branches. Bootstrap support values of maximum parsimony analysis are given above branches. Four hundred equally parsimonious trees of length 1372 were found (retention index = 0.823, consistency index = 0.532); the dataset comprised 474 parsimony-informative characters including 169 gapcoded characters. Heterozygous individuals are represented by clones (X or Y plus number) or by alleles (A and B) if they differed only by a single polymorphism; direct sequences (i.e., homozygous individuals) are labeled with "d" after the taxon identifier. The direct sequences of the introgressed samples *A. ragusina* JC 2011/2 and *A. laxiflora* JC 19/2 are shown in bold. Colours of *Andryala* species are for easier visualization of the taxa.

(PP = 1.00, BS = 67%, Fig. 1) and a branch formed by *A. crithmifolia* Aiton and *A. glandulosa* from Madeira (PP = 0.95, BS = 55%, Fig. 1) were well-supported only in the Bayesian analysis of this dataset. The only well-supported group in the cpDNA data (also Bayesian analysis only) comprised the predominantly Iberian taxa *A. ragusina*, *A. laxiflora* and *A. arenaria* (DC.) Boiss. & Reut., the eastern Mediterranean *A. dentata* Sm., the widespread *A. integrifolia* and the North African taxa *A. atlanticola* and *A. mogadorensis* including both subspecies (PP = 0.98, BS = 51%, Fig. 2). According to the *sqs* tree (Fig. 3), many taxa within the MRG were not monophyletic (e.g., *A. arenaria*, *A. cossyrensis*). In addition, some of the samples that were heterozygous for this marker showed two strongly divergent alleles (e.g., *A. atlanticola*, *A. arenaria* JC 2011/7/1, *A. integrifolia* JC 26/1, *A. laxiflora* JC 12/2, *A. glandulosa* ZF 233). Consequently, species relationships within this group remain unclear with two notable exceptions: the Madeiran endemics *A. crithmifolia* and *A. glandulosa* (PP = 1.00, BS = 70%) and also the Canary Island endemics *A. perezii* and *A. pinnatifida* Aiton (PP = 1.00, BS = 100%) formed two well-supported groups. Of these, only the alleles of the accessions of *A. pinnatifida* were monophyletic.

Despite the failure to resolve species relationships in *Andryala*, individuals assigned morphologically to the same taxon often formed recognizable entities with one or several markers (Table 1). The potential of different markers to show species-specific features varied: the most divergent species *A. laevitomentosa*, *A. agardhii* and *A. maroccana* were unequivocally distinguishable with all markers; *A. ragusina* and *A. dentata* were distinguished by most markers, *A. perezii*, *A. pinnatifida*, *A. laxiflora* and *A. arenaria* by one or few markers. Some species, however, showed only shared polymorphisms or their accessions were not monophyletic (*A. mogadorensis*, *A. crithmifolia*, *A. glandulosa*, *A. cossyrensis*, *A. integrifolia*); one species did not show any diagnostic feature with any of the markers (*A. atlanticola*).

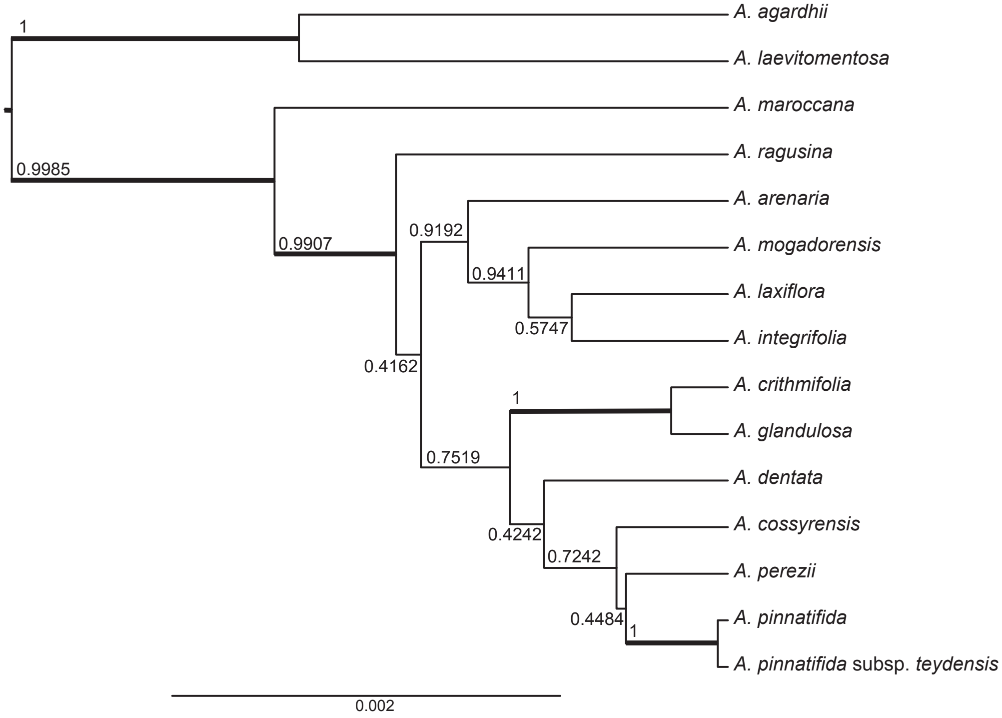
Species tree inference under coalescence based on all five datasets also resulted in mostly unresolved relationships. As before, *A. agardhii* and *A. laevitomentosa* formed separate lineages and *A. maroccana* occurred in an early branching position within the MRG (Fig. 4). The backbone of the rest of that group was again unsupported. The only species relationships within the MRG that were supported were between the Madeiran species *A. glandulosa* and *A. crithmifolia* as already found in the nuclear datasets (Figs. 1, 3).

■ DISCUSSION

Species relationships of the little-known Mediterranean-Macaronesian genus *Andryala* (Asteraceae), the exclusively sexually reproducing sister genus of the predominantly apomictic *Hieracium* and *Pilosella*, were investigated here for the first time with molecular markers, using a multigene approach based on two nuclear ribosomal regions, two chloroplast intergenic spacers and one single-copy nuclear gene marker. The most comprehensive and representative sampling possible was used to trace the evolutionary history of *Andryala*.

***Andryala* is a well-defined genus. —** Phylogenetic analyses of the nuclear markers showed that *Andryala* forms a well-supported monophyletic group (PP = 1.00, BS = 100%, Figs. 1, 3). However, cpDNA haplotypes of some species of

Fig. 4. Phylogenetic analysis of *Andryala* based on coalescence analysis of five datasets. Consensus tree based on Bayesian analysis as implemented in *BEAST with posterior probabilities at branches. Well-supported branches are shown in bold.



Pilosella were nested in *Andryala* (Fig. 2). This is the result of ancient wide hybridization as suggested by a previous molecular study that included only few species of *Andryala* (Fehrer & al., 2007a). The monophyly of *Andryala* (except in the cpDNA analysis) along with the non-monophyly of the two basal-most species, *A. agardhii* and *A. laevitomentosa*, contradicts the taxonomic placement of these two species in the genus *Pietrosia* as proposed by Sennikov (1999), although morphologically they are more similar to each other than to the remaining *Andryala* species (Sell, 1975, 1976). Thus, our data support the inclusion of these two species in *Andryala*, as recently suggested by Greuter (2003). Both *A. agardhii* and *A. laevitomentosa* can be regarded as relict species; they branched off earliest in the history of the genus, and sufficient time has elapsed for molecular divergence to occur. Likewise, our molecular data also strongly support the inclusion of the North African *A. maroccana* in *Andryala*, and not in a separate genus, *Paua*, as done by Caballero (1916). *Andryala maroccana* is morphologically more similar to *A. laevitomentosa* and *A. agardhii* than to the rest of *Andryala* in habit and cypsela morphology. Indeed, *A. maroccana* shares some features with *A. agardhii* and *A. laevitomentosa* (e.g., woody branched stock, covered with persistent bases of leaf petioles; several stems each usually bearing only one capitulum). Sell (1975) also highlighted the similarity of *A. agardhii* and *A. laevitomentosa* to North African species of *Andryala*, referring most likely to *A. maroccana.* This Moroccan-Algerian species branched off later than *A. agardhii* and *A. laevitomentosa.* It can probably be considered as a potential relict, as it seems to represent a relatively old lineage according to all molecular markers employed here (Fig. 4). Both *A. agardhii* and *A. laevitomentosa* are endangered species confined to mountain summits with similar ecological conditions. *Andryala agardhii* grows on calcareous rocky soils, screes and limestone-dolomite sands, and sometimes in rock crevices, at altitudes between 1600 and 3400 m (Jahandiez & Maire, 1934; Emberger & Maire, 1941; Blanca & al., 2001), while *A. laevitomentosa* occurs on metamorphic rocky alpine grasslands as well as in soil pockets on steep slopes or vertical cliffs, at 1600–1700 m (Lucas & Synge, 1978; Negrea & Pricop, 2009). Conversely, *A. maroccana* dwells on coastal sands as well as on steep quartzite sea cliffs (Caballero, 1916; Doumergue, 1921).

The major radiation of *Andryala*. — Despite high morphological and ecological diversity, all species of *Andryala*, except for *A. laevitomentosa*, *A. agardhii*, and, to a lower extent, also *A. maroccana*, showed very low nucleotide sequence divergence in all nuclear ribosomal and chloroplast datasets. Consequently, species relationships of the *Andryala* taxa designated as the “Major Radiation Group” remained almost completely unresolved (Figs. 1–2). Given that the nrDNA and cpDNA markers consisted mostly of non-coding sequences that are supposed to provide reasonably good resolution of interspecific relationships (Baldwin & Markos, 1998; Shaw & al., 2007), their extremely low overall genetic variation suggests that the majority of the *Andryala* taxa have undergone a very recent speciation. Despite higher interspecific sequence variation of *sqs*, the structure of the *sqs* tree (Fig. 3) revealed an almost complete lack of support of the basal nodes, which is consistent with a rapid divergence of the respective taxa (Fehrer, 1996; Stanley & al., 2011). The same lack of resolution was obtained using the five combined datasets in a coalescent approach (Fig. 4).

Similarly, the Mediterranean-Macaronesian *Cheirolophus* (Asteraceae: Cynareae) originated and radiated recently, an inference which was also based on low levels of nucleotide divergence (Garnatje & al., 2007). Unresolved phylogenetic groupings are suggestive of rapid diversification, as shown in the Mediterranean species of *Senecio* L. sect. *Senecio* (Asteraceae: Senecioneae; Comes & Abbott, 2001). These results are also consistent with molecular phylogenetic studies on Macaronesian genera of tribe Cichorieae (Asteraceae) such as the *Sonchus* L. alliance (Kim & al., 1996, 1999) and *Tolpis* Adans. (Gruenstaeudl & al., 2013). Likewise, the silversword alliance (Asteraceae: Madiinae) from Hawaii, as well as *Tetramolopium* Nees from the Hawaiian and Cook Islands, showed little genetic differentiation in spite of phenotypic and ecological diversity, supporting the hypothesis of a recent origin and rapid diversification on these islands (Baldwin & al., 1990; Okada & al., 1997). Thus, the example of *Andryala* fits the often observed evolutionary pattern of recent radiations that are characterized by a combination of low genetic diversity and large morphological differentiation.

Molecular evidence for introgressions. — Two samples, *A. laxiflora* JC 19/2 and *A. ragusina* JC 2011/2, showed additive patterns in nrDNA sequences that suggested a contribution of *A. integrifolia*. In the few *Andryala* hybrids described until now on the basis of morphology, *A. integrifolia* has repeatedly been reported as one of the parental species (e.g., Maire, 1937; García Adá, 1992). Indeed, re-inspection of cultivated plants or their herbarium vouchers revealed some morphological evidence of introgression that would have been overlooked without the molecular data. For *A. laxiflora* JC 19/2, only ITS indicated the influence of a second species (Table 1). The *A. integrifolia*–specific character states were consistently present only as smaller peaks at additive positions in sequence electropherograms, corresponding to the minor ribotype (PCRs were repeated in triplicate and pooled to ensure that this did not result from amplification bias), which may, along with its closer resemblance to *A. laxiflora*, indicate a later generation backcross. In contrast, the major ITS and ETS ribotypes of *A. ragusina* JC 2011/2 did not belong to this species, but to *A. integrifolia* (as indicated by ITS; ETS was equivocal due to a lack of species-specific characters). The nuclear *sqs* gene was homozygous in this sample and grouped near *A. integrifolia*, i.e., the sample had apparently lost its *A. ragusina*–specific allele. However, the chloroplast DNA belonged to *A. ragusina*. Thus, this sample may also represent a later generation backcross to *A. integrifolia*. The contrasting influence of hybridizations on various molecular markers observed in these two cases suggests an apparently random loss of at least some genetic evidence of these hybridization events. Differences in intraspecific genome size of *A. ragusina* of up to 50% (the usual level of intraspecific variation in other species of *Andryala* is below 5%; Zahradníček & al., unpublished data) may indicate that even morphologically well-defined species of *Andryala* (see also below) could have a complex past whose genetic and morphological traces may be largely erased.

Character conflict within and among datasets. — The nrDNA (Fig. 1) and cpDNA (Fig. 2) data resulted in an almost complete lack of resolution within the MRG, indicating stochastic variation because of low levels of genetic divergence of these markers. This is most probably the reason why weakly supported relationships do not correspond well between nuclear ribosomal and chloroplast data (e.g., the positions of *A. dentata*, *A. perezii*, or *A. ragusina*). Theoretically, also hybridization could be responsible for incongruence between these datasets. However, apart from the two individuals of *Andryala* discussed above and the chloroplast capture event involving *Pilosella*, there is no further indication of additional cases of introgression (such as, for example, individuals of a particular species with the cpDNA of another species). The character conflict in the *sqs* data (visualized in Electr. Suppl.: Fig. S5) is not caused by too low variation, however, but by a high degree of homoplasy as observed in the multiple sequence alignment (see alignment file in the online supplementary data and explanations therein). Patterns in the MRG across all trees and a failure of individual or all markers to identify even a morphologically unambiguous species such as *A. integrifolia* (Table 1) suggest that taxa in the MRG are not yet well differentiated genetically. Thus, the taxa that seem to have evolved very recently may be situated between a process of differentiation at the population level (characterized by a reticulate pattern of relationships) and a completed speciation process with reproductive or at least geographic isolation (characterized by bifurcating patterns). Both, incomplete lineage sorting and hybridization are typical phenomena at this level (Comes & Abbott, 2001; Trewick & al., 2004; Richardson & al., 2012; Vitales & al., 2014). The lack of resolution at the backbone of the MRG in the species tree inferred under coalescence (Fig. 4) can also be interpreted in terms of incomplete lineage sorting (Degnan & Rosenberg, 2009; Wielstra & al., 2014). As hybrids age they become historical genome mosaics, therefore, it is almost impossible to distinguish (ancient) hybridization from ancestral polymorphism with deep coalescense. In addition, the ease with which alleles of a single-copy marker can get lost in cases of introgression that are still traceable with nuclear ribosomal markers, as discussed above, may suggest that at least partly unrecognized hybridization events that have occurred after speciation (i.e., much more recently) could be responsible for alleles that occur in odd positions within the MRG (Fig. 3). These findings also confirm the susceptibility of this kind of marker to population genetic processes (Sang, 2002). While this is a handicap for the establishment of species relationships, it does allow the inference of gene drift and population bottlenecks as will be shown in the next section.

Macaronesian colonization and insular speciation. — The nuclear *sqs* gene, specifically developed as a low-copy marker for phylogenetic studies at low taxonomic level in Asteraceae (Krak & al., 2012), showed the highest variation among the markers employed. It revealed sister relationships and monophyly for the two pairs of endemic species occurring on the Canary Islands and Madeira, respectively (Fig. 3). This can be interpreted as evidence for single colonization events by the respective ancestors, followed by insular speciation. Due to the lack of tree node resolution, the continental sister species could not be identified. In Madeira, geographic separation may have facilitated speciation of *A. glandulosa* and *A. crithmifolia*. Indeed, *A. glandulosa* subsp. *glandulosa* occurs mainly along the northern coast of Madeira Island, Porto Santo and Desertas Islands and *A. glandulosa* subsp. *cheiranthifolia* (L'Hér.) Greuter grows almost everywhere in Madeira Island, chiefly in inland sites, whereas *A. crithmifolia* is found in only a few sites along the southern coast of Madeira Island (Press, 1994; Ferreira & al., in press). The occurrence of one allele of the heterozygous sample *A. glandulosa* subsp. *glandulosa* ZF 233 among *A. crithmifolia* sequences (Fig. 3) can be either explained by introgression or by incomplete lineage sorting. Similarly, the Canary Island endemic *A. perezii*, a recently described species (Ferreira & al., 2014a), is confined to the easternmost islands Lanzarote and Fuerteventura that are closest to the African Atlantic coast (Fuerteventura is only 100 km from the African continent), whereas *A. pinnatifida* occurs mostly on the central and western islands (Gran Canaria, Tenerife, La Palma, La Gomera, El Hierro). The *sqs* alleles of *A. perezii* are paraphyletic (Fig. 3) with *A. pinnatifida* sequences appearing as a single well-supported lineage emerging basal to these. This is consistent with an ancestor that may have colonized the Canaries from the nearby continent, followed by diversification proceeding from East to West.

There are several well-documented examples of biogeographic connections between northwest Africa and Macaronesia. Molecular studies unequivocally identified northwestern Africa as the likely place of origin of Canarian *Lotus* L. (Fabaceae; Allan & al., 2004) and supported a recent colonization of the Macaronesian islands by the *Asteriscus* (L.) Less. alliance (Asteraceae) from northern Africa (Francisco-Ortega & al., 1999). Another interesting example is *Tolpis* (distributed in Macaronesia, Mediterranean Europe and North Africa), which originated from at least three independent dispersal events from the European and North African mainland to the islands (Gruenstaeudl & al., 2013), in which the north–east trade winds seem to have played an important role (Moore & al., 2002; Gruenstaeudl & al., 2013). It seems possible that in *Andryala* the seamount archipelagos between continental areas and Macaronesia emerged during glacial periods (i.e., Palaeo-Macaronesia, according to Fernández-Palacios & al., 2011) could have served as colonization stepping stones in the dispersal process, since the deciduous pappus does not seem suitable for long-distance wind dispersal.

The populations of Madeiran *A. glandulosa* and Canarian *A. pinnatifida* exhibit high morphological variation, which can be explained by the considerable habitat diversity on oceanic islands, created by topology and humidity gradients, which, combined with their isolation, results in lower competition and empty ecological niches. This provides a template for the evolution of species radiations (Juan & al., 2000).

The most widely distributed species, *A. integrifolia*, also occurs on Macaronesian islands. It is considered introduced in Madeira and the Azores (Silva & al., 2005; Ferreira & al., 2011), but in the Canary Islands, it was thought to be probably native (Acebes Ginovés & al., 2010). Kunkel (1980) considered the species as originally Mediterranean, and probably introduced to the Canary Islands El Hierro and Gran Canaria, and the species has very recently been recorded for La Palma (Santos-Guerra & al., 2013). However, our results suggest a neophyte status of *A. integrifolia* also for the Canary Islands: a sample from El Hierro (SB H12/1) was most similar to plants of that species from the Iberian Peninsula and northern Africa and did not group with the Canary Island endemic species with any of the markers. As in Madeira, it can be found growing in roadside communities, as well as abandoned fields and pastures, and it has never been seen in more or less natural habitats (S. Bräutigam, pers. comm.). The occurrence of this species in habitats with strong anthropogenic influence corroborates the notion of its neophyte nature.

Species delimitation and taxonomy of *Andryala*. — Despite the low sequence divergence of the nrDNA and cpDNA markers and the extensive homoplasy of the *sqs* gene for taxa in the MRG, all five datasets showed some resolution at species level (summarized in Table 1). In all phylogenetic trees, both accessions of *A. maroccana* grouped together (PP = 1.00, BS = 100%, Fig. 1–3). Likewise, the three non-hybrid accessions of *A. ragusina* formed a strongly supported group (PP = 1.00, BS = 76%–100%, Figs. 1–3), which is in agreement with morphological data. Indeed, both are morphologically very distinct and generally accepted species.

The capacity of the markers to recognize further taxonomic entities within this group varied strongly. A good example for this is *A. integrifolia* and morphologically similar Mediterranean taxa with rather confusing taxonomy and unresolved nomenclature (Table 2; Electr. Suppl.: Table S1): *A. cossyrensis*, *A. arenaria*, and *A. dentata*. Accessions of *A. dentata* and *A. laxiflora* are well supported in the nrDNA tree (both PP = 1.00, BS = 99%, Fig. 1), in the latter case also supported by consistent diagnostic morphological characters. Indeed, *A. laxiflora* can easily be identified and is accepted at species level in the majority of recent Floras (e.g., Coutinho, 1939; Nègre, 1962; Pottier-Alapetite, 1981; Talavera, 1987; Blanca, 2009, 2011); it was even placed in a separate genus, *Rothia*, by earlier authors (e.g., Gaertner, 1791; Schreber, 1791; Roth, 1797). The same cannot be said regarding *A. dentata*, *A. cossyrensis*, and *A. arenaria*. The taxonomic delimitation of *A. dentata* has been very unclear; several authors suggested inclusion in *A. integrifolia* (Davis, 1975; Sell, 1976; Mouterde, 1983; Tohmé & Tohmé, 2007). Although *A. integrifolia* is a very common Mediterranean species, it is replaced by *A. dentata* in the East Mediterranean (Table 3). The contact zone of the two species is located in continental Italy and on Sicily and Pantelleria (Ferreira, unpub. results). Nonetheless, *A. dentata* is morphologically distinct from *A. integrifolia* (Table 2), and the present phylogenetic study supports this taxonomic point of view since *A. dentata* did not group with any *Andryala* species, including *A. integrifolia*, and was distinguished by most markers (Table 1). Similarly, accessions of *A. arenaria* are strongly supported in the nrDNA tree (PP = 1.00, BS = 98%, Fig. 1), but not by other markers (Table 1). *Andryala arenaria* has either been treated as a distinct species (Amo y Mora, 1872; Coutinho, 1939; Talavera, 1987; Blanca, 2009, 2011) or included in *A. integrifolia* (Ball, 1878; Barratte, 1896; Sell, 1976; Greuter, 2006–). In addition to the present molecular results (Fig. 1), its distinctive morphological features (Table 2) and a well-defined geographical range (distribution center in sandy habitats of the southwestern Iberian Peninsula and, to a lesser extent, in northwestern Africa) seem to justify

Table 2. Species distinction based on morphological features.

Species	Diagnostic characters
A. integrifolia L.	Upper leaves ovate-lanceolate or lanceolate, base rounded to cuneate Involucre usually stellate-tomentose All involucral bracts flat, not enfolding a floret Receptacle with usually long setae (1.7–)2–4.7 mm Ligules usually pale yellow, greatly exceeding involucral bracts
A. dentata Sm.	Upper leaves ovate-oblong to ovate-lanceolate, base rounded or subcordate Involucre slightly stellate-tomentose External involucral bracts involute, enfolding a floret, and purplish at the apex Receptacle with short setae 0.4–2 mm Ligules pale yellow, slightly exceeding involucral bracts
A. arenaria (DC.) Boiss. & Reut.	Upper leaves usually ovate-oblong, base cordate Involucre densely stellate-tomentose External involucral bracts involute, enfolding a floret Receptacle with usually short setae 0.3–2(–2.7) mm Ligules golden yellow, greatly exceeding involucral bracts
A. cossyrensis Guss.	Upper leaves narrowly ovate-lanceolate or ± linear-lanceolate, base rounded or rarely cordate Involucre slightly stellate-tomentose External involucral bracts involute, enfolding a floret, sometimes purplish at the apex Receptacle with usually short setae 0.8–2.5(–3) mm Ligules golden yellow, greatly exceeding involucral bracts

Note: Only species with traditionally controversial taxonomic delimitation are compared.

species status. On the other hand, *A. cossyrensis* showed almost no distinct molecular features (Table 1). Following our concept, it is a morphologically distinct species (Table 2), occurring predominantly in northwest Africa and on Sicily and Pantelleria, of which the latter island is situated only 60 km east of the Tunisian coast. In summary, our results show that *A. integrifolia*, *A. laxiflora*, *A. arenaria*, *A. cossyrensis*, and *A. dentata* do not form a monophyletic group and that the evaluation of the latter three at subspecific level proposed by some authors (e.g., Emberger & Maire, 1941; Pignatti, 1982) is not supported. Furthermore, their morphological distinctness (Table 2) and distinct distributions (Table 3) provide further support for their species status.

In all phylogenetic trees (Figs. 1–3) there was no resolution within *A. integrifolia*. The ancestor of the MRG may have survived the last glacial and then rapidly colonized the entire Mediterranean Basin, diversifying into several species, including *A. integrifolia*. This extremely polymorphic species seems to have successfully occupied different habitats, currently occurring in almost the entire distribution area of the genus (Table 3). In addition, there are several records of new species published in the past which actually correspond

Table 3. Geographical distribution of taxa used in this study.

Taxon	Distribution	Biogeographic region
Andryala agardhii DC.	southern Spain (few mountains of the Baetic System), Morocco (Atlas Mts., very rare)	CD
A. arenaria (DC.) Boiss. & Reut	mainly Iberian Peninsula, Morocco and Algeria	CD
A. cossyrensis Guss.	SW Italy (incl. Sicily and Pantelleria islands), Tunisia, Algeria and Morocco	DF[a]
A. crithmifolia Aiton	Madeira (southern coast, rare)	A
A. dentata Sm.	S and SW Italy (incl. Sicily and Pantelleria islands), S and E Greece, W Turkey and Lebanon (disjunct occurrences, rare)	F
A. glandulosa Lam. subsp. *glandulosa*	Madeira (mainly northern coast), Porto Santo and Desertas Islands	A
A. glandulosa subsp. *cheiranthifolia* (L'Hér.) Greuter	Madeira (mainly inland)	A
A. integrifolia L. (incl. *A. atlanticola* H.Lindb.)	Iberian Peninsula, France, Italy (incl. Sardinia and Sicily islands), Morocco, Algeria, Tunisia, Canary Islands, Madeira, Azores	CDEF[a,b]
A. laevitomentosa (Nyár. ex Sennikov) Greuter	Romanian Eastern Carpathians, very rare	G
A. laxiflora DC.	mainly Iberian Peninsula, Morocco, Algeria, Tunisia, Canary Islands (Tenerife)	CD[c]
A. maroccana (Caball.) Maire	Morocco and Algeria, very rare	D
A. mogadorensis Hook.f. subsp. *mogadorensis*	Morocco (between the regions of Grand Casablanca and Souss-Massa-Drâa)	E
A. mogadorensis subsp. *jahandiezii* (Maire) M.Z.Ferreira & al.	Morocco (Souss-Massa-Drâa Region)	E
A. perezii M.Z.Ferreira & al.	eastern Canary Islands (Fuerteventura, Lanzarote)	B
A. pinnatifida Aiton (excl. subsp. *teydensis*)	central and western Canary Islands (Gran Canaria, Tenerife, La Palma, La Gomera, El Hierro)	B
A. pinnatifida subsp. *teydensis* (Sch.Bip.) Rivas Mart. & al.	Canary Islands (Tenerife)	B
A. ragusina L.	Iberian Peninsula, southernmost France, Balearic Islands, (Algeria and Tunisia)[d]	C(D)[d]

Biogeographic regions: A, Madeira; B, Canary Islands; C, Mediterranean SW Europe (mainly Iberian Peninsula); D, Mediterranean N Africa; E, Atlantic NW Africa; F, Central and NE Mediterranean Basin; G, Romanian Eastern Carpathians.

[a] excluding the NE Mediterranean Basin; [b] neophytic occurrences on the Canary Islands, Madeira and the Azores; [c] neophytic occurrences in the Canary Islands; [d] the very rare *A. spartioides* (Pomel ex Batt. & Trab.) Barratte (not included here) occurring in Algeria and Tunisia might be a synonym of *A. ragusina* L.

to putative varieties of *A. integrifolia* (e.g., Coutinho, 1939; Dobignard, 2009). This seems to be also the case for *A. atlanticola* which morphologically resembles *A. integrifolia* when considering taxonomically important reproductive characters such as involucral bract convolution, receptacle indumentum, and ligule colour (Table 2).

Accessions of the northwest African *A. mogadorensis* form a well-supported clade in the cpDNA tree (PP = 1.00, BS = 92%, Fig. 2) and are clearly distinct from the Canarian *A. pinnatifida* according to all markers (Figs. 1–3). Although *A. mogadorensis* was traditionally recognized as a subspecies of *A. pinnatifida* (Jahandiez & Maire, 1934; Greuter, 2003), molecular data of the present study suggest to rank it at species level, which is in agreement with a recent morphological re-evaluation (Ferreira & al., 2014b).

Regarding the Macaronesian species, although the Canarian *A. perezii* was mistaken for *A. glandulosa* by earlier authors (e.g., Kunkel, 1980; Bramwell & Bramwell, 2001) and later recognized as a subspecies of *A. pinnatifida* (Greuter & Raab-Straube, 2009), morphological data support the distinction of these three taxa at species level (Ferreira & al., 2014a), which is also in accordance with the present molecular data. As for the Madeiran *A. glandulosa* and *A. crithmifolia*, although the molecular markers did not separate them completely (see above), these are morphologically distinct species with well-defined distribution areas (Menezes, 1914; Press, 1994; Ferreira & al., in press).

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Appendix 1. Accessions used for the molecular analyses and GenBank accession numbers.

Taxon name and authority, sample identifier: country: voucher collection records, altitude, *collector's name*, *collection number* (herbarium acronym), ITS accession number(s) / ETS accession number(s) / *trnT-trnL* accession number / *trnV-ndhC* accession number / *sqs* accession number(s) [sequences new for this study are marked by an asterisk].

Andryala agardhii DC., **JZ 2011/3:** Spain: Andalusia, province Jaén, Sierra Mágina, road to Pico Mágina, 1806 m, *Zahradníček & al.*, *1937/11* (PRA), KM372007*, KM372008* / KM371903*, KM371904* / KM371732* / KM386663* / KM371831*; **JC 2011/31/1:** Spain: Andalusia, province Granada, Sierra Baza, Calar del Desabezedo, 1195 m, *Chrtek & Dočkalová*, *1924/11* (PRA), KM372009*, KM372010* / KM371905*, KM371906* / KM371733* / KM371781* / KM371832*; ***A. arenaria*** (DC.) Boiss. & Reut., **JC 2011/9/1:** Spain: Andalusia, province Huelva, Almonte, 55 m, *Chrtek & Dočkalová*, *1931/11* (PRA), KM372011*, KM372012* / KM371907*, KM371908* / KM371734* / KM371782* / KM371833*, KM371898*; **JC 2011/3/1:** Spain: Andalusia, province Málaga, Artola near Marbella, 25 m, *Chrtek & Dočkalová*, *1929/11* (PRA), KM372013*, KM372014* / KM371909*, KM371910* / KM371735* / KM371783* / KM371834*; **JC 2011/7/1:** Spain: Andalusia, province Cádiz, Bornos, 237 m, *Chrtek & Dočkalová*, *1932/11* (PRA), KM372015*, KM372016* / KM371911*, KM371912* / KM371736* / KM371784* / KM371835*, KM371836*; ***A. atlanticola*** H.Lindb., **10JZ 08/1:** Morocco: region Marrakech-Tensift-El-Haouz, High Atlas, Imlil, 1960 m, *J. Zahradníček, 2012/10* (PRA), KM372017*, KM372018* / KM371913*, KM371914* / KM371737* / KM371785* / KM371837*, KM371838*; ***A. cossyrensis*** Guss., **JC 3/1:** Morocco: region Oriental, province Berkane, Berkane, Zegzal (Zegzel) valley, 260 m, *Chrtek & Dočkalová, 2016/10* (PRA), KM372019*, KM372020* / KM371915*, KM371916* / KM371738* / KM371786* / KM371839*; **JC 3/2:** Morocco: region Oriental, province Berkane, Berkane, Zegzal (Zegzel) valley, 260 m, *Chrtek & Dočkalová, 2017/10* (PRA), KM372021*, KM372022* / KM371917*, KM371918* / KM371739* / KM371787* / KM371840*; ***A. crithmifolia*** Aiton, **ZF 258:** Portugal: Madeira, Cabo Girão, base of the sea cliff, *Ferreira & Ferreira,* 258 (MA), KM372023*, KM372024* / KM371919*, KM371920* / KM371740* / KM371788* / KM371841*; **ZF 283:** Portugal: Madeira, São Gonçalo, Pináculo, 238 m, *Sequeira & Ferreira, 283* (MA), KM372025*, KM372026* / KM371921*, KM371922* / KM371741* / KM371789* / KM371842*, KM371843*; ***A. dentata*** Sm., **JZ 0512/3:** Italy: Isola di Pantelleria, Tracimo, 220 m, *Zahradníček & Chrtek, 689/12* (PRA), KM372027*, KM372028* / KM371923*, KM371924* / KM371742* / KM371790* / KM371844*; **JZ 0612/3:** Italy: Isola di Pantelleria, Siba-Roncone, 450 m, *Zahradníček & Chrtek, 691/12* (PRA), KM372029*, KM372030* / KM371925*, KM371926* / KM371743* / KM371791* / KM371845*; ***A. glandulosa*** Lam. subsp. ***glandulosa*****, A.glan.Mad.1:** Portugal: Madeira, Ponta do Pargo, ca. 312 m, *Bräutigam*, *148659* (GLM), KM372033*, KM372034* / KM371929*, KM371930* / AY573356 / KM371793* / KM371847*; **Glan1 (ZF 292):** Portugal: Madeira, Porto Moniz, 263 m, *Ferreira*, *292* (MA), KM372035*, KM372036* / KM371931*, KM371932* / KM371745* / KM371794* / KM371848*; **ZF 233:** Portugal: Madeira, Seixal, ca. 42 m, *Ferreira*, *233* (MA), KM372037*, KM372038* / KM371933*, KM371934* / KM371746* / KM371795* / KM371849*, KM371850*; ***A. glandulosa*** subsp. ***cheiranthifolia*** (L'Hér.) Greuter, **ZF 246:** Portugal: Madeira, Pico do Areeiro, 1542 m, *Ferreira & al., 246* (MA), KM372031*, KM372032* / KM371927*, KM371928* / KM371744* / KM371792* / KM371846*; ***A. integrifolia*** L., **JC 4/2:** Morocco: region Oriental, province Nador, Beni Chiker (Beni Sikar), 140 m, *Chrtek & Dočkalová*, *2020/10* (PRA), KM372039*, KM372040* / KM371935*, KM371936* / KM371747* / KM371796* / KM371851*; **SB H12/1:** Spain: Canary Islands, El Hierro, Valverde near Tinor, 980 m, *Bräutigam & Bräutigam*, *2046/10* (PRA), KM372041*, KM372042* / KM371937*, KM371938* / KM371748* / KM371797* / KM371852*, KM371853*; **JC 26/1:** Spain: Andalusia, province Granada, Guadix, 1075 m, *Chrtek & Dočkalová*, *1928/11* (PRA),

Appendix 1. Continued.

KM372043*, KM372044* / KM371939*, KM371940* / KM371749* / KM371798* / KM371854*, KM371855*; **AZ 3/1:** Algeria: Algiers, Kouba town district, 90 m, *Abida Zeddam*, *678/12* (PRA), KM372045*, KM372046* / KM371941*, KM371942* / KM371750* / KM371799* / KM371856*, KM371857*; ***A. laevitomentosa*** (Nyár. ex Sennikov) Greuter, **JC 2011/40/2P:** Romania: Judeţul Suceava, Munţii Bistriţei,Vatra Dornei, Pietrosul Bogolin, 1740 m, *Chrtek & al.*, *970/11* (PRA), KM372047*, KM372048* / KM371943*, KM371944* / KM371751* / KM371800* / KM371858*, KM371859*; **E8:** Romania: Judeţul Suceava, Munţii Bistriţei,Vatra Dornei, Pietrosul Bogolin, 1740 m, *Chrtek & al.*, *971/11* (PRA), KM372049*, KM372050* / KM371945*, KM371946* / KM371752* / KM371801* / KM371860*, KM371861*; ***A. laxiflora*** DC., **JC 2011/12/2:** Spain: Andalusia, province Huelva, Niebla, 40 m, *Chrtek & Dočkalová*, *1934/11* (PRA), KM372051*, KM372052* / KM371947*, KM371948* / KM371753* / KM371802* / KM371862*, KM371863*; **JC 2011/19/2:** Spain: Andalusia, province Córdoba, Hornachuelos, 280 m, *Chrtek & Dočkalová*, *1930/11* (PRA), KM372053*, KM372054* KM372055* / KM371949*, KM371950* / KM371754* / KM371803* / KM371864*; **JC 2011/20/1:** Spain: Andalusia, province Jaén, Linares, 405 m, *Chrtek & Dočkalová*, *1926/11* (PRA), KM372056*, KM372057* / KM371951*, KM371952* / KM371755* / KM371804* / KM371865*; ***A. maroccana*** (Caball.) Maire, **JZ 1711/2:** Morocco: region Oriental, province Nador, Ifrin-Dounacht, 74 m, *Zahradníček & Krak*, *2011/10* (PRA), KM372058*, KM372059* / KM371953*, KM371954* / KM371756* / KM371805* / KM371866*; **JZ 1711/2a:** Morocco: region Oriental, province Nador, Ifrin-Dounacht, 74 m, *Zahradníček & Krak*, *2010/10* (PRA), KM372060*, KM372061* / KM371955*, KM371956* / KM371757* / KM371806* / KM371867*, KM371868*; ***A. mogadorensis*** Coss. ex Hook.f. subsp. ***mogadorensis***, **ZF 263A:** Morocco: region Marrakech-Tensift-El-Haouz, province Essaouira, Essaouira (Mogador), 8 m, *Ferreira & Alvarez Fernández*, *263* (MA), KM372062*, KM372063* / KM371957*, KM371958* / KM371758* / KM371807* / KM371869*; **JC 16N/V2:** Morocco: region Marrakech-Tensift-El-Haouz, province Essaouira, Essaouira (Mogador), 8 m, *Chrtek & Dočkalová*, *2013/10* (PRA), KM372064*, KM372065* / KM371959*, KM371960* / KM371759* / KM371808* / KM371870*; **JC 15/1:** Morocco: region Souss-Massa-Drâa, prefecture Agadir-Ida ou Tanane, Tamri, 30 m, *Chrtek & Dočkalová*, *2019/10* (PRA), KM372066*, KM372067* / KM371961*, KM371962* / KM371760* / KM371809* / KM371871*; **JC 18V/V2:** Morocco: region Doukkala-Abda, province El Jadida, Moulay Abdallah, 12 m, *Chrtek & Dočkalová*, *2014/10* (PRA), KM372068*, KM372069* / KM371963*, KM371964* / KM371761* / KM371810* / KM371872*, KM371873*; ***A. mogadorensis*** subsp. ***jahandiezii*** (Maire) M.Z.Ferreira, **JC 14/1:** Morocco: region Souss-Massa-Drâa, prefecture Inezgane-Aït Melloul, Inezgane, 7 m, *Chrtek & Dočkalová*, *2018/10* (PRA), KM372070*, KM372071* / KM371965*, KM371966* / KM371762* / KM371811* / KM371874*; ***A. perezii*** M.Z.Ferreira & al., **KV 51V:** Spain: Canary Islands, Lanzarote, Mirador de Haría, 380 m, *Vazačová*, *838/10* (PRA), KM372072*, KM372073* / KM371967*, KM371968* / KM371763* / KM371812* / KM371875*, KM371876*; **KV 52V**: Spain: Canary Islands, Lanzarote, El Jurado, Guinate, 440 m, *Vazačová*, *839/10* (PRA), KM372074*, KM372075* / KM371969*, KM371970* / KM371764* / KM371813* / KM371877*; ***A. pinnatifida*** Aiton, **And.pin.Cer:** Spain: Canary Islands, La Gomera, El Cercado, 1000 m, *Bräutigam*, *158131* (GLM), KM372076*, KM372077* / KM371971*, KM371972* / AY573358 / KM371814* / KM371878*, KM371879*; **SB H16p/4:** Spain: Canary Islands, El Hierro, San Andrés, 1175 m, *Bräutigam & Bräutigam*, *2049/10* (PRA), KM372078*, KM372079* / KM371973*, KM371974* / KM371765* / KM371815* / KM371880*; **SB H13/1:** Spain: Canary Islands, El Hierro, San Andrés, 980 m, *Bräutigam & Bräutigam*, *2041/10* (PRA), KM372080*, KM372081* / KM371975*, KM371976* / KM371766* / KM371816* / KM371881*; **SB P11/1:** Spain: Canary Islands, Isla de la Palma, Roque del Faro, 1030 m, *Bräutigam & Bräutigam*, *2043/10* (PRA), KM372082*, KM372083* / KM371977*, KM371978* / KM371767* / KM371817* / KM371882*; **SB H14/3:** Spain: Canary Islands, El Hierro, Sabinosa, 720 m, *Bräutigam & Bräutigam*, *2051/10* (PRA), KM372084*, KM372085* / KM371979*, KM371980* / KM371768* / KM371818* / KM371883*, KM371884*; **SB T2/1:** Spain: Canary Islands, Tenerife, Puerto de la Cruz, 780 m, *Bräutigam & Bräutigam*, *2045/10* (PRA), KM372086*, KM372087* / KM371981*, KM371982* / KM371769* / KM371819* / KM371885*; **SB G7b/3:** Spain: Canary Islands, La Gomera, Arures, 940 m, *Bräutigam & Bräutigam*, *2050/10* (PRA), KM372088*, KM372089* / KM371983*, KM371984* / KM371770* / KM371820* / KM371886*; **SB G9/3/1:** Spain: Canary Islands, La Gomera, Las Rosas, 980 m, *Bräutigam & Bräutigam*, *2042/10* (PRA), KM372090*, KM372091* / KM371985*, KM371986* / KM371771* / KM371821* / KM371887*, KM371888*; **SB T17/5:** Spain: Canary Islands, Tenerife, Montañas de Anaga, Cruz de Carmen, 800 m, *Bräutigam & Bräutigam*, *2044/10* (PRA), KM372096*, KM372097* / KM371990*, KM371991* / KM371774* / KM371824* / KM371891*, KM371892*; ***A. pinnatifida*** subsp. ***teydensis*** (Sch.Bip.) Rivas Mart. & al., **SB T18/1:** Spain: Canary Islands, Tenerife, Cañadas, El Portilla, 1950 m, *Bräutigam & Bräutigam*, *2047/10* (PRA), KM372092*, KM372093* / KM371987*, KM371988* / KM371772* / KM371822* / KM371889*; **SB T4/1:** Spain: Canary Islands, Tenerife, Cañadas, La Escalona, 1190 m, *Bräutigam & Bräutigam*, *2103/10* (PRA), KM372094*, KM372095* / KM371989* / KM371773* / KM371823* / KM371890*; ***A. ragusina*** L., **JC 27/1:** Spain: Andalusia, province Granada, Guadix, 1075 m, *Chrtek & Dočkalová*, *1935/11* (PRA), KM372098*, KM372099* / KM371992*, KM371993* / KM371775* / KM371825* / KM371893*, KM371894*; **JC 2011/2/1:** Spain: Andalusia, province Málaga, Alhaurín el Grande, 230 m, *Chrtek & Dočkalová*, *1925/11* (PRA), KM372100*, KM372101*, KM372102* / KM371994*, KM371995*, KM371996* / KM371776* / KM371826* / KM371895*; **ZF LM5103/1:** Spain: Madrid, Guadalix de la Sierra, 850 m, *Sequeira & Medina*, *LM5103* (MA), KM372103*, KM372104* / KM371997*, KM371998* / KM371777* / KM371827* / KM371896*; **JC 2011/35/1:** Spain: Comunitat Valenciana, province Alicante, Sax, 610 m, *Chrtek & Dočkalová*, *1933/11* (PRA), KM372105*, KM372106* / KM371999*, KM372000* / KM371778* / KM371828* / KM371897*; ***Hispidella hispanica*** Barnades ex Lam., **His.his.2:** Spain: Sierra de Guadarrama, *Pizarro & Navarro*, *CN 2460* (M), KM372107* / EU821365 / AY573355 / JX129534 / JX129601, JX129602; ***Pilosella argyrocoma*** (Fr.) F.W.Schultz & Sch.Bip., **agy.Gra:** Spain: Province Granada, plant cultivated in Botanic Garden Munich, *Merxmüller & Gleisner, culture H11* (M), KM372108* / KM372001* / AY573320 / JX129536 / JX129605; ***P. lactucella*** (Wallr.) P.D.Sell & C.West, **lac.Jon.1:** Germany: Oberlausitz, Jonsdorf, *Bräutigam*, *140619* (GLM), KM372109* / KM372002* / AY192669 / JX129535 / JX129603; ***P. pseudopilosella*** (Ten.) Soják, **TU308/2:** Spain: Sierra Nevada, between Granada and Pradollano, *Urfus, 308/2* (PRA), KM372110* / KM372003* / JX129599 / JX129537 / KM371899*; ***P. hoppeana*** subsp. ***macrantha*** (Ten.) S.Bräut. & Greuter, **TU1059:** Romania: Banat, Gârnic, pastures on karst plateau SW of village, near the road to S. Helena, *Skála & Skálová*, *1059* (PRA), KM372111* / KM372004* / KM371779* / KM371829* / KM371900*; ***P. echioides*** (Lumn.) F.W.Schultz & Sch.Bip., **TR1608:** Czech Republic: Central Bohemia, Trubín, *Chrtek*, *258/2013* (PRA), KM372112* / KM372005* / KM371780* / KM371830* / -; ***Hieracium intybaceum*** All., **inb.Kaer:** Austria: Kärnten, *S. Jagalski*, *4* (M), KM372113* / EU821370 / AY573323 / JX129561 / JX129745; **1069/1:** Italy: Trentino-Alto Adige, Passo del Tonale, *Chrtek & Mráz*, *1069/2005* (PRA), HQ131821 / KM372006* / JX129600 / JX129560 / HQ131846, HQ131847; ***H. porrifolium*** L., **1052/9:** Austria: Carinthia, Karawanken Mts., Bad Eisenkappel, near the road to Bad Vellach, *Chrtek & Mráz*, *1052/2005* (PRA), HQ131823 / EU867631 / EU867730 / JX129578 / HQ131843, JX129701; ***H. recoderi*** De Retz, **1174/4:** Spain: Catalunya, province Barcelona: Berga, monastery of Queralt, *Chrtek*, *1174/2006* (PRA), KM372114* / EU867603 / EU867721 / JX129584 / KM371901*, KM371902*; ***H. tomentosum*** L., **1066/8:** France: dépt. Alpes Maritimes, valley of la Roya, Tende, *Chrtek & Mráz*, *1066/2005* (PRA), KM372115* / EU867596 / EU867731 / JX129590 / JX129726, JX129727; ***H. umbellatum*** L., **um.AM.1:** Germany: Upper Lusatia, SE Schönau-Berzdorf, *Bräutigam*, *46889* (GLM), KM372116* / EU867644 / AY573335 / JX129594 / JX129732

6 Paleobiogeography and speciation

Andryala L. is included in the subfamily Cichorioideae Chevall. which contains ca. 35% of the species in Asteraceae (Funk *et al.* 2009). It is part of a group of ca. 93 genera belonging to Tribe Cichorieae Lam. & DC. (Kilian *et al.* 2009) and is included in subtribe Hieraciinae. Cichorieae are mainly distributed in the temperate zone of the northern hemisphere, both in the Old and New Worlds, with centers of diversity in Central to Eastern Asia, the Mediterranean Basin and western North America (Kilian *et al.* 2009). Recently, Tremetsberger *et al.* (2013), based on available fossil evidence and DNA sequences, estimated the age of Cichorieae no later than Oligocene or Early Miocene while its subtribes diversified no later than Middle/Late Miocene or Early Pliocene. According to these authors, the split of *Andryala* from other genera of subtribe Hieraciinae occurred around 4.6 Ma ago in the Tertiary (Pliocene: 5.3–2.6 Ma). This implies a Middle/Late Pliocene divergence of the oldest lineages within *Andryala*, i.e. *A. agardhii* Haens. Ex DC. and *A. laevitomentosa* (Nyár. ex Sennikov) Greuter according to Ferreira *et al.* (2015a). Actually, *Andryala agardhii* is considered a paleo-endemic species of the Tertiary flora which was saved from extinction when the ice retreated after the last glaciation of the Quaternary. It survived on the summits of mountains chains in Southern Spain and Morocco (Jahandiez & Maire 1934; Blanca *et al.* 2001). Likewise, due to its morphological and reproductive particularities *A. laevitomentosa* is regarded as an orophyte, Carpathian endemism, which appeared probably during the Tertiary period (Stefureac 1968; Negrea & Pricop 2009b). Compared to these, the major radiation in *Andryala* must be much younger; indeed the extremely low overall genetic variation of highly variable DNA regions (Shaw *et al.* 2005; Shaw *et al.* 2007) suggests that the majority of the *Andryala taxa* have undergone a very recent speciation (Ferreira *et al*. 2015a, see Chapter 5).

6.1 The oldest lineages

Phylogenetic studies showed that *Andryala* L. is a monophyletic genus in which three main lineages occur: two separate ones for *A. laevitomentosa* and *A. agardhii* and another including Mediterranean and Macaronesian *taxa* (Fehrer *et al.* 2007a; Ferreira *et al.* 2015a, see Chapter 5). As mentioned before, *A. laevitomentosa* and *A. agardhii,* the two oldest lineages, show a geographically discontinuous distribution: the first occurs in the Romanian Carpathians and the second in high mountain peaks of Southern Spain and Morocco. Two alternative explanations have been proposed for this disjunct distribution pattern: dispersal across a pre-existing geographical barrier (for example, a mountain chain); or vicariance, the fragmentation of a widespread ancestral distribution by the appearance of a new barrier (e.g. Jong 1998; Coleman *et al.* 2003; Sanmartín 2003). Both biogeographical processes result in the isolation of a population by a geographic barrier, followed by differentiation of a new *taxon* by allopatric (geographically separated) speciation. It is plausible that *A. laevitomentosa* and *A. agardhii* have undergone a vicariance phenomenon caused by the last Pleistocene ice age. The fragmented distribution of these two species is further encouraged by the fact that they are high mountain plants. A certain level of genetic differentiation (depending on the time since the areas were isolated) and low gene flow between populations are evidence that vicariance is responsible for disjunct distribution (Šingliarová *et al.* 2008; Collevatti *et al*. 2009). Indeed, *A. laevitomentosa* and *A. agardhii* are genetically distinct lineages and long-distance gene flow is most unlikely due to restricted seed dispersal[37]. Nonetheless, the long-distance dispersal hypothesis, although remote, should not be disregarded. The ability to distinguish between these two possibilities has been greatly increased by use of a molecular clock approach (Kroph *et al.* 2006). Hence, phylogeographical analyses including molecular dating are necessary for a better understanding of the origin of the disjunct geographical distribution in question. This east–west cleavage in species distribution has been observed in many other plant groups such as *Viola cazorlensis* Gand. (Herrera 1990 and references therein), *Soldanella* L. (Zhang *et al.* 2001), *Holcus* L. (Menezes De Sequeira 2004), *Buxus balearica* Lam. (Rosselló *et al.* 2007), *Posidonia oceanica* Delile (Arnaud-Haond *et al.* 2007), *Erophaca* Boiss. (Casimiro-Soriguer *et al.* 2010), and *Convolvulus* L. (Salmerón-Sánchez *et al.* 2014). *Andryala agardhii* and *A. laevitomentosa* are linked, respectively, to the Iberian and Carpathian refugia where they remained stranded on high mountain summits after the last Quaternary ice age. It is often assumed in the biogeography of the Mediterranean flora that 'eastern' is equivalent to ancestral and, indeed, in very few cases western taxa have been demonstrated to be ancestral (Casimiro-Soriguer *et al.* 2010). Molecular studies have shown that the origin of *Andryala* is related to an ancient hybridisation event between Pilosella *II* haplotype and the *Andryala* ancestor. Moreover, the majority of *Pilosella* II species, especially diploids, occur in central and eastern Europe (Fehrer *et al.* 2007b). Accordingly, the western *Andryala agardhii* could have derived from eastern Europe ancestral *Andryala* populations. The Quaternary Period has been dominated by ice ages, which involved repeated global cooling. As interglacial times were relatively short, for most of the time the majority of the European species distributions would be oscillating in southern Europe in the longer glacial periods (Hewitt 1996; 1999). Populations with new adaptations to northern latitudes acquired in interglacials were also likely to be eliminated by the readvance of colder conditions, with more southerly genomes surviving and spreading south where possible. The survival of populations in southern refugia (peninsulas of Iberia, Italy and the Balkans), as well as in some in parts of the eastern Carpathians, over few to many Ice Ages, allowed their lineages to diverge and accumulate genetic differences, and they may ultimately have become species (Zhang *et al.* 2001, Hewitt 2004). Several characteristics, including morphological traits, may have evolved as adaptations to these refugia (Hewitt 1996). Following this pattern, ancestral *Andryala* populations, being cold-adapted, may have survived in the high mountains peaks of the Carpathians during interglacial times, expanding to the West during glacial periods. While the populations from the Romanian Carpathians gave rise to the probably oldest lineage in the genus, the populations from Southern Spain, isolated during interglacial periods from the ancestral populations, became genetically distinct and a new species emerged. Indeed, disjunct populations, originated during contraction periods, were potentially submitted to divergence processes driven by reproductive isolation due to geographical barriers, and genetic drift, which are key mechanisms for plant evolution and speciation (Martín-Bravo *et al.* 2010). In effect, *A. agardhii* differs in a range of morphological characters from *A. laevitomentosa*, some of which may well have evolved as adaptations to a new environment. Indeed, this species evolved in distinct ecological conditions compared to the populations of *A. laevitomentosa* from the Romanian Carpathians (see Chapter 4, pp. 85, 151).

During each of the Pleistocene glaciations, the sea level in the western Mediterranean region was lower than today, thereby reducing the distance between European and African coasts (Ortiz *et al.* 2007 and references therein). Moreover, emergent islands that were present periodically during succesive glacial periods in the extreme

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[37] In *A. laevitomentosa* reproduction is predominantly vegetative and propagation by seeds has a very low frequency (Manole 2015).

west of the Mediterranean, in the Strait of Gibraltar area, must have favoured contact between the two continents (Collina-Girard 2001). The Strait of Gibraltar, therefore, would not have been a major geographical barrier as it is at present (Ortiz *et al.* 2007). Geographical ranges of species have expanded and contracted in a cyclical manner according to the climatic changes of the Quaternary (Hewitt 1996). Actually, Quaternary refugia correspond to geographical region or regions that a species inhabits during the period of a glacial/interglacial cycle that represents the species' maximum contraction in geographical range. Furthermore, in general, cold-adapted species have a larger distribution during cold stages than during periods of warm climate (Stewart *et al.* 2010). Hence, it is possible that one of the glaciations of the Pleistocene facilitated the expansion of populations of *Andryala agardhii* (a cold-adapted species) across the Strait of Gibraltar into Morocco, assuming that the species originated in the Iberian Peninsula. Actually, it was postulated that high rates of endemism in combination with relatively moderate species numbers are typical of a refugial region only functioning as a source of colonisation, but not as a receptor from other areas (Husemann *et al.* 2014). In Morocco, *A. agardhii* is currently confined to very few high mountain peaks in the Middle and High Atlas. Quaternary glacial and periglacial features are present throughout the Atlas Mountains (Hughes *et al.* 2006) which means that *A. agardhii* found favourable ecological conditions during glacial periods in these mountains systems. However, it is possible that geographical isolation during interglacial cycles may have been too short to foster divergence, and glacial recolonisation frequently enabled secondary contacts between these disjunct populations, preventing from speciation (Comes & Kadereit 1998). On the other hand, if expansions are more recent (i.e. dating back to the Pliocene or early Pleistocene), it is possible that not enough time has gone by as to originate allopatric species (Husemann *et al.* 2014). Nevertheless, in respect to *A. agardhii* the hypothesis that this species may have evolved in North Africa and later expanded to Europe must not be discarded. The question of the direction of colonisation has been studied in a variety of organisms. In general, two criteria, especially if applied in combination, may help to detect refugial areas using molecular tools: (1) the level and structure of genetic differentiation between populations; and (2) a comparison of the genetic diversity (alleles and haplotypes) among respective regions. Moreover, the structures of gene trees often help resolve the question of source and receptor regions (Husemann *et al.* 2014 and references therein). Nonetheless, the hypothesis of a widespread Iberian-North African ancestor giving raise to *A. agardhii* should also be taken into consideration. More research is required to investigate the source and receptor regions of *Andryala* and the direction of colonisation as well as to evaluate the latter hypothesis.

So far only one phylogenetic study has been performed on *Andryala* in order to trace the evolutionary history of this genus (Ferreira *et al.* 2015a, see Chapter 5). Results support the relict nature of both *A. agardhii* and *A. laevitomentosa* (lineages that branched off earliest in the history of the genus) and the potential relict nature of *A. maroccana* (a relatively old lineage that branched of later). Furthermore, they suggest that the majority of the *Andryala taxa* have undergone a very recent speciation and rapid divergence. However, dating analysis in this group was not possible due to the lack of appropriate data; the only available fossils are Cichorieae-type pollen by which genera within the tribe cannot be distinguished (at least not in the lineage leading to *Andryala*). Knowing the age of lineages is key to understanding their biogeographic history. Indeed, DNA sequence data are increasingly being used in conjunction with relaxed molecular clock models and fossil calibration to estimate the age of ancestral lineages. Regarding *Andryala*, future research based on an adequate fossil-calibrated relaxed molecular clock will be necessary to estimate the timing of the major divergence events in the genus.

6.2 Major radiation of *Andryala* and more recent speciation

Apart from *A. agardhii* and *A. laevitomentosa,* in *Andryala* a third lineage occurs. It includes the majority of the *Andryala taxa* which has undergone a relatively recent speciation. Within this monophyletic group, *A. maroccana* (Pau ex Caball.) Maire seems to have branched off much earlier than the remaining species. Indeed, it shares some plesiomorphic features with the two oldest lineages in the genus (Ferreira *et al.* 2015a, see Chapter 5). The last opening of the Strait of Gibraltar occurred ca. 4.5 Ma, and the water that refilled the Mediterranean basin fragmented the distributions of the extant land species. Since then several plant groups have had the opportunity to evolve into different species on the Iberian and African plates (Rodríguez-Sánchez *et al.* 2008). *Andryala. maroccana* may have originated from a long-distance dispersal event, possibly from Iberian ancestral populations. As this Moroccan-Algerian species showed a lower nucleotide sequence divergence compared to the two oldest lineages (coupled possibly with a with low genetic diversity) it could have arose by a founder event or originated from an ancestral population that experienced a prolonged or severe bottleneck *in situ* (Kropf *et al.* 2006). A new lineage entering a novel niche or adaptive zone, or undergoing bottleneck situations, may diverge rapidly from the parental lineage and even new characters may appear (Hörandl 2006). In fact, *A. maroccana*, conversely to the older lineages, dwells on sandy coastal areas or steep quartzite sea cliffs of the Mediterranean Sea. After the colonisation event, the Strait of Gibraltar probably acted as a barrier to gene flow, as described for other Iberian–northern African plant lineages (reviewed in Rodríguez-Sánchez *et al.* 2008).

Despite high morphological diversity, most of *Andryala* species have an extremely low level of genetic divergence which suggests their relatively recent and rapid speciation (Ferreira *et al.* 2015a, see Chapter 5). Similarly to other plant groups as, for example, *Reseda* L. sect. *Glaucoreseda* (Martín-Bravo *et al.* 2010), speciation within *Andryala* in the Iberian Peninsula could be related to range shifts induced by Pleistocene climatic oscillations. The Iberian Peninsula was one of the most important Pleistocene glacial refugia in Europe (Taberlet *et al.* 1998). During the Pleistocene glacial periods vast medium-altitude areas in the central Iberian Peninsula were covered by cold steppe/tundra vegetation, providing suitable habitats for mountain plants (Martín-Bravo *et al.* 2010). Actually, the Iberian Peninsula constituted one of the southernmost limits of the steppe-tundra expanse during the Pleistocene (Álvarez-Lao & García 2010). The Pyrenees were the only extensively glaciated range, although patches of permanent ice sheet were also found in many high mountains areas of the Iberian Peninsula (Hughes *et al.* 2006). Interglacial warming probably forced populations to retreat to disjunct, high elevated mountain ranges or plateaus (Kropf *et al.,* 2008). Allopatric divergence of the resulting isolated populations may have occurred subsequently, leading to the appearance of new *taxa*. Therefore, vicariance driven by Pleistocene glaciations seems to be the most plausible scenario for the diversification of some plant groups in the Iberian Peninsula, as for some other European mountain plant groups (Zhang *et al.* 2001; Martín-Bravo *et al.* 2010; Kropf *et al.* 2006; 2008). Low genetic differentiation and lack of complete concerted evolution may be also the result of recent vicariance due to interglacial isolation. Likewise, incomplete lineage sorting has been suggested to be especially likely in recently diverged or rapidly radiating species groups (Pleines *et al.* 2009). The vicariance hypothesis for population disjunctions within the Iberian Peninsula, in which an ancestral, widespread species could have undergone differentiation by Quaternary interglacial fragmentation, may also hold for *Andryala*. *Andryala ragusina* L. is more or less widely distributed in the Iberian Peninsula and has a rather high altitudinal range, occurring from the thermo-Mediterranean to the oro-Meditarranean bioclimatic zone (Blanca 2009, 2011). The Iberian *A. ragusina* populations may have served as source for the colonisation of the Pyrenees and southern France, similarly to other plant groups such as *Juniperus thurifera* L. (Terrab *et al.* 2008). Moreover, a relatively recent long-distance dispersal may explain the colonisation of Corsica, as in *Juniperus thurifera.* The Algerian population (*A. ragusina* subsp. *spartioides* Pomel ex Batt.) may have derived from Iberian populations, presumably via long-distance dispersals, expanding later to Tunisia. However, this possibility is quite remote since the Mediterranean Sea served as a barrier to dispersal. Dispersal through the Strait of Gibraltar could be another possibility, but *A. ragusina* does not occur in Morocco (Carazo-Montijano & Fernández-López 2006; Ferreira *et al.* 2014c).

Concerning *Andryala arenaria* and *A. rothia* (= *A. laxiflora*), these species are mainly present in the Iberian Peninsula, but they also occur in North Africa. They were not originated from the same ancestor population (Ferreira *et al.* 2015a, see Chapter 5) but they could be recent Iberian species that reached North Africa through long-distance dispersal across the Strait of Gibraltar[38]. This strait should be particularly favourable for wind and vertebrate dispersal, as it regularly experiences very strong winds and is crossed every year by many migrant birds, some of them frugivorous (Rodríguez-Sánchez *et al.* 2008; Lavergne *et al.* 2013). In *Andryala* the fruit is a cypsela and, therefore, seed dispersal via ingestion by vertebrate animals (endozoochory), usually associated with fleshy fruits, does not seem very feasible. Nonetheless, species with a short life cycle and propagules dispersed by wind (anemochory) or externally on animals (ectozoochory) have apparently been most likely to cross the Strait of Gibraltar (Lavergne *et al.* 2013 and references therein). Both *A. laxiflora* and *A. arenaria* are annual species, having probably experienced migration across the Strait of Gibraltar, although long-distance dispersal by wind can be quite limited in *Andryala* owing to the deciduous pappus (Figure 6.1). It is possible that an allometric relationship between plant size and diaspore size may determine that annual plants have smaller seeds; hence crossing the Strait would be easier. Besides, annual *taxa* have fewer requirements for their establishment given their short life cycle (Arroyo 1997). Intercontinental colonisation has been proven possible despite the absence of specific mechanisms for long-distance dispersal (Fernández-Mazuecos & Vargas 2011). The small size of the seeds and the abundance of open and sandy habitats in the Mediterranean region may favour long-distance colonisation events (Fernández-Mazuecos & Vargas 2011).

Complete isolation by the Strait of Gibraltar could have permitted speciation through gradual genetic divergence of *taxa* (allopatric speciation). On the other hand, limited migration across the strait could have caused rare founder events that favoured speciation (peripatric speciation) (Lavergne *et al.* 2013). The latter could have been the case of *A. chevallieri* and *A. cossyrensis* which are predominantly Northwest African species. *Andryala chevallieri* is Moroccan-Algerian endemic with a rather narrow distribution, while *A. cossyrensis* has a wider distribution (Magherb and some islands in southern Italy).

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[38] A North African origin of these species with expansion to the Iberian Peninsula should not be discarded until further research is performed.

The three southern European peninsulas (the Iberian, Italian and Balkan peninsulas) played a major role as glacial refugia during the Quaternary cold periods (Taberlet *et al.* 1998). Many temperate species in Europe had their ranges reduced to at least one of these peninsulas during glacial periods (where mild conditions remained), whereas populations outside these areas went extinct. During interglacials they could expand their distributions again from these glacial refugia. Taking into account present-day *Andryala* distribution, during the Pleistocene cold periods the temperate *taxa* took shelter, not only in the Iberian refugium but also in the other two refuge areas mentioned above. *Andryala dentata* Sm. is the only east Mediterranean *Andryala*, occurring from central and southern Italy (including Sardinia and Sicily) to the southern part of the Balkan Peninsula, Western Turkey and Lebanon. The ancestor of this species may have gone through many contraction/expansion of geographical range during the Pleistocene climatic fluctuations. During glaciations northern populations may have gone extinct while southern populations could have been repeatedly and predominantly restricted to the Italian and Balkan refugia. During range expansion periods the Alps could have served as barrier to this species movement northwards, as suggested in previous studies (Taberlet *et al.* 1998; Hewitt 2004), whereby this species is not currently found beyond this mountain range system. The presence of *A. dentata* in both Italian and Balkan refugia can be explained by their geographical proximity and to the connection across the Adriatic Sea between these two refuge areas when the sea level was lower during cold periods (Hewitt 2004).

Strong affinities between Europe and North Africa are detectable for the Strait of Sicily, despite the over-seas distance of 140 km. Several studies have demonstrated strong genetic cohesiveness of some species between Sicily and Tunisia. This might have been fostered by the lower sea level during the glacial phases, reducing the distance between the two continents and causing the emergence of potential stepping-stone islands (Husemann *et al.* 2014). Actually, long-distance dispersal over the Strait of Sicily has been documented for *Cistus salviifolius* L. (Fernández Mazuecos & Vargas 2010), *Linaria* Mill. sect. *Versicolores* (Bentham) Wettst. (Fernández-Mazuecos & Vargas 2011), and the *Anthemis secundiramea* Biv. group (Lo Presti & Oberprieler 2011). *Andryala cossyrensis* Guss. is a Northwest African species, occurring from Morocco to Tunisia, and can also be found in Pantelleria and Sicily. This species may also have reached these Italian islands by long-distance dispersal across the Strait of Sicily (Figure 6.1). In view of the foregoing, *Andryala cossyrensis* and *A. dentata* were probably originated in different continents (Ferreira *et al.* 2015a, see Chapter 5).

The Maghreb was an important differentiation and speciation centre for warm-adapted organisms during the Pliocene and Pleistocene with high relevance as a colonisation source for Europe. The regions around the sea straits of Gibraltar and Sicily have acted as important biogeographical links between North Africa and Europe at different times. Furthermore, the Atlas Mountains (comprising the highest elevations of North Africa) provide strong orographic barriers that made large range shifts impossible. Instead of latitudinal shifts, cold-adapted species expanded their distributions to lower elevations during cooler phases and shifted to higher elevations during the drier and hotter interglacial phases (Husemann *et al.* 2014). While providing prolonged habitat stability, the strong barriers

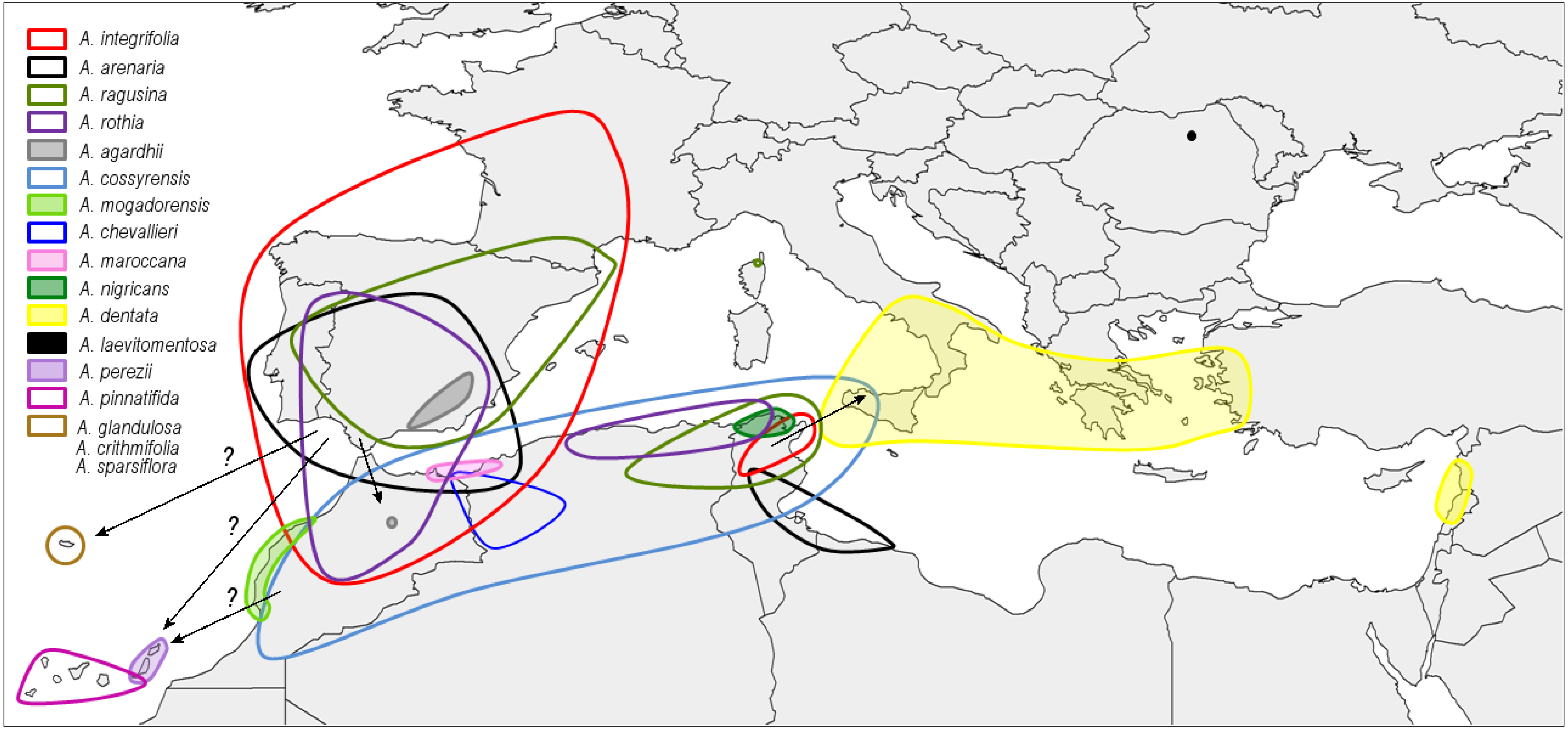

Figure 6.1 Distribution, dispersal routes and the Iberian Peninsula as a centre of diversification of *Andryala* sp.

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represented by high mountain ranges also played a major role in separating local populations of species, leading to strong genetic divergence among North African populations and high rates of micro-endemism (Habel *et al.*, 2012). Indeed, *A. mogadorensis* is a Moroccan endemic whose origin might have had a similar pattern as the one described above. This species is mainly found in western Morocco, growing on coastal rocky cliffs, coastal sands and dunes as well as on sandy rivers banks. As it is a warm-adapted species it could be hypothesized that it may have evolved due to an altitudinal descent of its ancestor during the cold periods of the Pleistocene. The resulting western populations may have adapted to new ecological conditions and become geographically and attitudinally isolated from the ancestral populations. Furthermore, in *Andryala* the cypselae shed their pappus readily at maturity and, therefore, this structure is not particularly effective in long-distance dispersal. This limited dispersal ability of the cypselae may present a natural barrier to gene flow that has also favoured divergence to some extent.

6.3 Macaronesia and insular colonisations

Although divergences times of the Madeiran and Canarian *Andryala* endemics are still unknown, a potential Pleistocene colonisation of these archipelagos by their respective ancestors can be deduced based on the age estimation of Cichorieae by Tremetsberger *et al.* (2013) using a fossil-calibrated relaxed molecular clock. The seamount archipelagos between continental areas and Macaronesia (i.e. Palaeo-Macaronesia) emerged during the glacial periods of the Pleistocene and could have served as colonisation stepping stones in the dispersal process of *Andryala*, given that the deciduous pappus does not seem suitable for long-distance wind dispersal (Ferreira *et al.* 2015a, see Chapter 5). Phylogenetic analysis supports single colonisation events of Madeira and the Canary Islands from the Mediterranean region, followed by extensive radiation. Hence, the frequently observed evolutionary pattern of continental dispersion and subsequent insular speciation (for examples see Chapter 5, pp. 250, 258) also applies to *Andryala.* It may be possible that the Madeiran *Andryala taxa* are related to the continental *A. rothia* (predominantly Iberian) as phylogenetic analysis showed a sister relationship between the Madeiran taxa and this species, although with very little support (Ferreira *et al.* 2015a, see Chapter 5). Curiously, this species and the Madeiran *A. glandulosa* share a unique feature in the genus (involucral bracts arranged in 4 or more rows instead of the usual number of 2-3). Phylogenetic analysis of the nrDNA showed a well-supported group comprising *A. mogadorensis* subsp. *jahandiezii*, *A. cossyrensis,* and the Canarian *A. perezii*, (Ferreira *et al.* 2015a, see Chapter 5). Furthermore, this analysis indicated a sister group relationship between *A. arenaria* and the Canarian *A. pinnatifida*, but almost with no support (Ferreira *et al.* 2015a, see Chapter 5). Nonetheless, it is plausible that the continental sister species of the Canarian *Andryala taxa* could be either *A. arenaria* or *A. cossyrensis*. Both are annual herbaceous species and plants with such a habit have a greater capacity of long-distance dispersal, colonising islands from nearby continents more easily (Carlquist 1974). Accordingly, several molecular studies have demonstrated that many Macaronesian groups are recently derived from herbaceous continental ancestors (e.g. Böhle *et al.* 1996; Kim *et al.* 1996; Helfgott *et al.* 2000; Barber *et al.* 2002; Mort *et al.* 2002). Moreover, *A. cossyrensis* and *A. arenaria* occur in Morocco and the latter is also present in the Iberian Peninsula and these are, indeed, potential continental source areas regarding *Andryala*. Nevertheless, additional research based on molecular data will be necessary to clearly identify the continental sister species of the Madeiran and Canarian *Andryala taxa*

(Ferreira *et al.* 2015a, see Chapter 5). Moreover, the estimation of time divergence of the Macaronesian and Mediterranean *Andryala taxa* could help clarify this issue. Overall genetic diversity among the endemic *Andryala taxa* from the Madeiran and Canarian archipelagos is quite low (Ferreira *et al.* 2015a, see Chapter 5). In general, island plant populations are less variable genetically than mainland ones. Several molecular studies showed low genetic variation and this has been attributed to genetic bottlenecks associated with long-distance dispersal and subsequent establishment on islands. Within an island archipelago, additional founder events and genetic drift in small populations could likewise reduce genetic variation by loss of alleles. Furthermore, inbreeding in small populations could also be an important factor involved in keeping diversity low (Kim *et al.* 1999 and references therein).

Although the archipelago of Madeira is quite recent, it was formed before the split of *Andryala* from other genera of subtribe Hieraciinae[39]. In Madeira, geographic barriers linked to a complex orographic pattern and ecology may have facilitated speciation of the endemic *Andryala* species. In effect, *A. glandulosa* Lam. occurs predominantly along the northern coast of Madeira Island, Desertas and Porto Santo, while *A. sparsiflora and A. crithmifolia* can be found only in Madeira Island, the first mainly in inland sites and the second in two sites along the southern coast (see Chapter 4).

The Canary Islands are composed of seven islands of different geological ages, being the easternmost islands (Lanzarote and Fuerteventura) the oldest in the archipelago[40]. *Andryala perezii* is found only in the latter islands, whereas *A. pinnatifida* occurs mostly on the central and western islands of the archipelago. Although phylogenetic analysis supports the monophyly of the Canarian *Andryala taxa*, the sqs alleles of *A. perezii* are paraphyletic with *A. pinnatifida* sequences which can be interpreted as evidence of diversification proceeding from East to West in the Canary archipelago (Ferreira *et al.* 2015a, see Chapter 5). Indeed, a number of studies have showed that many species groups in the Canary Islands follow an east to west colonisation direction, from Lanzarote and Fuerteventura, towards the younger western islands according to a stepping stone model, as suggested by several authors (e.g. Juan *et al.* 2000; Silvertown *et al.* 2005; Talavera *et al.* 2013).

Similarly to the oldest lineages in *Andryala*, the Canarian endemics exhibit a perennial habit. The habit of the Madeiran endemics varies from annual to perennial, although perennating plants were found among annual/biennial species. The perennial habit is a typical trait in the Tertiary relicts, *A. agardhii* and *A. laevitomentosa,* and in the potential relict *A. maroccana* also. Species that originated more recently are mostly annuals or biennials. Several studies of Macaronesian endemics showed that perennial insular woodiness is a derived trait rather than ancestral and suggested that their ancestors were herbaceous (e.g. Böhle *et al.* 1996; Kim *et al.* 1996; Panero *et al.* 1999; Emerson 2002). The *Andryala* endemic *taxa* from Macaronesia are mostly herbaceous perennials and, although they not really exhibit true insular woodiness, the root and stem base are somewhat woody. Even so, it is plausible that their continental ancestors were annual herbaceous generalists capable of colonizing many of the open or marginal habitats of the islands and that insular evolution gave rise to the perennial habit (or is still leading to this growth form). Therefore, it seems that in *Andryala* woodiness is an archaic feature, but in what concerns the Macaronesian *taxa* it is also a derived trait. Several reasons have been suggested for perennial growth and the insular woodiness, namely, competitive advantage through higher stature, increased longevity enhancing the chance of sexual

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[39] The Madeira-Desertas complex emerged around 7.0–5.6 Ma ago and Porto Santo about 11–14 Ma ago (Ramalho *et al.* 2015).

[40] Lanzarote and Fuerteventura have an estimated age of 15.5 Ma and 20.6 Ma, respectively (Carracedo *et al.* 1998).

reproduction in an environment where pollinators are scarce, moderate insular climates, promotion of sexual out-crossing, specialisation and selection in competitive environments with scarce resources (Whittaker & Fernández-Palacios 2007 and references therein).

6.4 Current distribution

The native distribution of *Andryala* L. is exclusive from the Old World, being chiefly a Mediterranean genus with larger specific diversity in the Iberian Peninsula and Northwest Africa (Figure 6.1). In Romania *A. laevitomentosa* occurs as an isolated species (Kukuła *et al.* 2003; Negrea & Pricop 2009b). In view of the above considerations, the present-day distribution of the genus *Andryala* L. can be explained by geographic isolation between Iberian-Northern African populations and Eastern European populations (resulting from the Quaternary glaciations) and events of long-distance dispersal over sea barriers. According to available data, the Iberian Peninsula is an important centre of diversification of the genus (Figure 6.1).

Some *Andryala* species are predominantly Southwest European (*A. agardhii*, *A. arenaria, A. rothia, and A. ragusina*), occurring all in the Iberian Peninsula and the latter also in France. Others are found only in Northwest Africa: *A. mogadorensis* in Morocco*, A. maroccana* and *A. chevallieri* in Morocco and Algeria, and *A. nigricans* in Algeria and Tunisia. In the East Mediterranean (including Greece, Turkey and Lebanon) solely one species can be found: *A. dentata*. The Central Mediterranean region (including Italy, Sicily, Sardinia, Corsica, Pantelleria and Tunisia) seems to constitute a contact zone between western and the eastern Mediterranean species. Indeed, in this area several *Andryala* species can be found: *A. cossyrensis* (also present in Morocco and Algeria), *A. ragusina* (i.e. *A. ragusina* subsp. *spartioides), A. arenaria, A. rothia*, and *A. dentata. Andryala integrifolia* is the most widespread and common species in the genus; it occurs in almost all the distribution area of the genus, except for the East Mediterranean. This species shows great capacity of hybridisation; DNA analysis showed that *A. ragusina* and *A. rothia* (i.e. *A. laxiflora*) have suffered introgression by *A. integrifolia* (Ferreira *et al.* 2015a, see Chapter 5), also supported by morphological data.

The Macaronesian *Andryala* endemisms correspond to neo-endemics with possible origin in the Iberian Peninsula or even Northwest Africa, as mentioned before (Figure 6.1). Indeed, the Madeira archipelago hosts three neo-endemic *Andryala* species: *A. glandulosa*, *A. sparsiflora* (formerly known as *A. glandulosa* subsp. *cheiranthifolia*), and *A. crithmifolia*, while the Canary Islands hosts two neo-endemics: *A. perezii* and *A. pinnatifida*. According to the model proposed (Figure 6.1), dispersal seems to have been the principal biogeographic mechanism for the Macaronesian endemics speciation. This region also includes *taxa* with a neophyte status (*A. integrifolia* and *A. rothia*). As mentioned in chapter 4, *A. integrifolia* is an introduced and fully naturalised species in the Canary Islands, the Azores and Madeira (Silva *et al.* 2010; Ferreira *et al.* 2011; Ferreira *et al.* 2015a). It was assigned to the Canary islands of El Hierro and Gran Canaria (Acebes Ginovés *et al.* 2010) and was recently cited for La Palma (Santos-Guerra *et al.* 2013). Likewise, in the Azores it was initially cited for Faial and S. Jorge (Hansen & Sunding 1993) and later for Santa Maria (Silva *et al.* 2010).

7 Conclusions and futures research perspectives

The present biosystematic study of the genus *Andryala* (Asteraceae: Cichorieae) was based on the revision of 1066 specimens from 13 herbaria and additional plant material collected during fieldwork as well as on phylogenetic analyses of nucleotide sequences of nuclear (nrDNA) and chloroplast (cpDNA) markers.

The morphometric study and subsequent numerical analysis was focused on 105 morphological characters (including quantitative, multistate and binary characters). The analyses performed by using exploratory methods (ordination and clustering methods) support the taxonomical treatment here proposed. Different analyses performed with ordination and clustering methods using all characters or subsets of these are coherent regarding the delimitation of the *Andryala* species here recognised. The numerical analysis carried out support:

1. an infra-generic division in two sub genera: subgen. *Andryala* L. comprising 6 sections and subgen. *Paua* (Caball.) Sennen. comprising 2 sections.
2. the inclusion of *A. agardhii* and *A. laevitomentosa* in *Andryala* under the subgen. *Paua* (Caball.) Sennen, along with *A. maroccana* and *A. ragusina*;
3. the distinction at a species rank of *Andryala taxa* traditionally with an unclear taxonomy: *A. integrifolia*, *A. arenaria, A. dentata, A. cossyrensis,* and *A. nigricans* as well as *A. mogadorensis, A. perezii* and *A. pinnatifida*;
3. the taxonomic relevance of the qualitative characters compared to the quantitative characters;
4. the recognition of highly variable species (*A. pinnatifida, A. ragusina, A. mogadorensis,* and *A. integrifolia*) for which *taxa* at a subspecies are proposed.

Phylogenetic analyses of nucleotide sequences of the internal transcribed spacers (ITS) and the external transcribed spacer (ETS) of nuclear ribosomal DNA (nrDNA), two chloroplast (cpDNA) markers (trnT-trnL and trnV-ndhC intergenic spacers), and one single-copy nuclear gene (sqs) was performed using Bayesian and maximum parsimony methods of inference. Results of this analysis (to some extent in concordance with the morphometric study) support:

1. the monophyletic origin of *Andryala,* as suggested by a previous molecular study;
2. three main lineages: two separate lineages corresponding to the relict species *A. agardhii* and *A. laevitomentosa* and another lineage including the Macaronesian and Mediterranean, the latter comprising mostly rather recent species as well as *A. maroccana,* a relatively old lineage, and *A. ragusina* which occurred (along with *A. maroccana*) in an early branching position in the phylogenetic analysis based on nuclear ribosomal markers (ITS + ETS);
3. the specific distinction of *A. mogadorensis,* traditionally recognised as a subspecies of *A. pinnatifida*.
4. the specific distinction of *taxa* with traditionally controversial taxonomic delimitation, namely *A. integrifolia, A. arenaria*, *A. dentata*, and *A. cossyrensis.*
5. the introgressive hybridisation of *A. ragusina* and *A. rothia* by *A. integrifolia.*
6. a single colonization event of the common ancestor of two endemic species (*A. glandulosa* and *A. crithmifolia*) from the Mediterranean region to Madeira and that of two other endemics (*A. perezii* and *A. pinnatifida*) to the Canary Islands.

Based on the results of the morphometric study and to a certain extent on the results of the phylogenetic analysis, several *Andryala* taxa are recognised: 17 species, 14 subspecies, and 3 hybrids. Among these, 5 species are Macaronesian endemics (*A. glandulosa*, *A. sparsiflora*, *A. crithmifolia* Aiton, *A. pinnatifida,* and *A. perezii*), 4 species are Northwest African endemics (*A. mogadorensis*, *A. maroccana*, *A. chevallieri,* and *A. nigricans*) and one species is endemic to Romania (*A. laevitomentosa*).

Concerning lectotypification, 10 taxa are noteworthy as the lectotypes designated herein will be published soon: *A. arenaria, A. chevallieri, A. cossyrensis, A. crithmifolia, A. dentata, A. glandulosa, A. maroccana, A. pinnatifida* subsp. *teydensis*, *A. ragusina* subsp. *spartioides,* and *A. rothia.*

New taxa and new status and/or combinations are proposed:

- *Andryala perezii* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. sp. nov. in Novon, 23(2). 2014;
- *Andryala crithmifolia* Aiton subsp. *coronopifolia* (Lowe) M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. stat. & comb. nov. in Silva Lusitana nº Especial: 143-157. 2014;
- *Andryala integrifolia* subsp. *corymbosa* (Lam.) M. Z. Ferreira, Alv. Fern. & M. Seq. stat. nov.
- *Andryala mogadorensis* subsp. *jahandiezii* (Maire) M. Z. Ferreira, Álv. Fern. & M. Seq. comb. nov. in Acta Bot. Malac. 39. 39: 283-293. 2014;
- *Andryala pinnatifida* subsp. *preauxiana* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq. comb. nov.;
- *Andryala pinnatifida* Aiton subsp. *cuneifolia* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq. stat. nov. in Novon 23(2). 2014;
- *Andryala pinnatifida* Aiton subsp. *webbiana* (Sch. Bip.) M. Z. Ferreira, Alv. Fern. & M. Seq. stat. nov.;
- *Andryala ragusina* L. subsp. *ramosissima* (Boiss. ex DC.) M. Z. Ferreira, Alv. Fern. & M. Seq. stat. nov.;
- *Andryala sparsiflora* (Lowe) M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. stat. & comb. nov.;
- *Andryala* x *dansereauoi* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. hyb. nov.

Based on morphological characters, a key to the *Andryala* species is proposed as well as keys to subspecies (*A. crithmifolia, A. mogadorensis, A. pinnatifida, A. ragusina,* and *A. integrifolia*) here recognised.

During the elaboration of this thesis many new questions emerged. Moreover, clearly some issues require further research in order to reach a better understanding of the genus. Hence, future research needs to focus on:

- karyology studies so as to determine the chromosome number all *Andryala* taxa.
- further phylogenetic studies based on alternative markers (low copy nuclear markers) to clearly resolve species relationships within *Andryala* and to further clarify colonisation events, namely in what concern the identification of the continental sister species of the Madeiran and Canarian *Andryala taxa.*
- additional phylogenetic analysis based on an adequate fossil-calibrated relaxed molecular clock in order to estimate the timing of the major divergence events in the genus.
- further research to investigate the source and receptor regions of *Andryala* as well dispersal routes, here hypothesized.
- additional experimental work (molecular and karyological studies) to confirm the hybrid nature of *Andryala* x *dansereauoi* and investigate the taxonomic placement of *Andryala* x *faurei* in *A. integrifolia*, here suggested.

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9 Appendices

9.1 Appendix 1: *Andryala integrifolia* L. (Asteraceae), a new alien species for the Island of Madeira (Portugal) – paper published in *Silva Lusitana*, 2011.

Silva Lusitana ***19****(1):111 - 125, 2011*
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Notas do Herbário Florestal do INRB (LISFA): Fasc. XXXII

ʃ1. *Novarum Flora Lusitana Commentarii*
In memoriam A.R. Pinto da Silva
(1912 – 1992)

A new combination in *Lotus glaucus* complex (Fabaceae, Loteae) from Porto Santo (Madeira Archipelago)

Lotus glaucus Aiton (Fabaceae, Loteae, section *Pedrosia*) from Madeira Island was the first described species of the *Lotus glaucus* complex (AITON, 1789). LOWE (1856) proposed a new genus, *Pedrosia* Lowe, to include the Macaronesian *Lotus* species with a distinct toothed style. In the same publication Lowe described a new species for Porto Santo Island, *Pedrosia florida* Lowe, that he distinguishes from *P. glauca* (Aiton) Lowe (*L. glaucus*), as follows:

"in its more silky, hoary foliage, lanceolate acute leaflets, larger, more numerous flowers, often four or five in a head, and larger, thicker, straighter, and even, instead of strangulato-torulose, pods".

Latter LOWE (1862, p.178), although recognizing *P. florida* as a distinct taxon, discusses its taxonomic status, clearly dismissing a species rank.

MASFERRER (1881) transferred *P. florida* to the genus *Lotus* as *L. floridus* and BRAND (1898) combined *L. floridus* as a variety of *L. glaucus*.

MENEZES (1914) considered *P. florida* within *Lotus glaucus* simply as a form. The subsequent Madeira flora authors do not recognize any taxonomical rank for *P. florida* (COSTA, 1946, 1948; PICKERING, 1962; HANSEN, 1969; HANSEN & SUNDING, 1985, 1993; VIEIRA, 1992; TURLAND, 1994; JARDIM & MENEZES DE SEQUEIRA, 2008).

Recently SANDRAL *et al.* (2006) studied the taxonomy of *Lotus* section *Pedrosia* and they also do not recognize taxonomically *P. floridus* (*L. floridus*), although they have studied some Porto Santo specimens they include *P. florida* as a synonymy of *Lotus glaucus* and also typified *Pedrosia florida* and *P. florida* var. *sulphurea* Lowe.

Traditionally *Lotus glaucus* was also recognized for all Canary Islands (e.g. HANSEN, 1985), but SANDRAL *et al.* (2006) refer to *L. glaucus* as an endemic species for the Madeira Archipelago. Distinguishing *L. glaucus* subsp. *glaucus* for Madeira, Porto Santo and Desertas and *L. glaucus* subsp. *salvagensis* (R.P.Murry) Sandral & D.D.Sokoloff. for Salvage Islands. Some specimens from Fuerteventura (Canary Islands) are considered by the same authors as uncertain, although others are include in different species.

The examination of collected material and herbarium specimens (MADJ, MADS, MADM, LISU and MA) and field observations in Porto Santo, Madeira and Desertas show that the Porto Santo plants of *Lotus glaucus* agree with the description given by Lowe for *Pedrosia florida* (Figure 1). Table 1 summarizes the diagnostic characters and compares them with *Lotus glaucus* subsp. *glaucus* (Figure 2). The morphological resemblance of *L. glaucus* with *L. floridus* and the restricted distribution of the later to the Porto Santo Island clearly suggest that a subspecific rank should be applied, accordingly a new status is proposed for *Lotus floridus*:

Lotus glaucus Aiton subsp. ***floridus*** (Lowe) R. Jardim & M. Seq., *comb. nov.*

≡ *Pedrosia florida* Lowe in Hooker's J. Bot. Kew Gard. Misc. 8: 294 (1856) (bas.)

≡ *Lotus floridus* (Lowe) Masf. in Anales Soc. Esp. Hist. Nat. 10:160. (1881)

≡ *Lotus glaucus* Aiton var. *floridus* (Lowe) Brand in Bot. Jahrb. Syst. 25: 200 (1898)

= *Pedrosia florida* Lowe var. *sulphurea* Lowe, Man. Fl. Madeira 1: 178 (1862)

Table 1 - Diagnostic characters of *Lotus glaucus* subsp. *glaucus versus L. glaucus* subsp. *floridus*

	Lotus glaucus* subsp. *glaucus	***Lotus glaucus* subsp. *floridus***
Indumentum	Greyish pubescent	Densely whitish pubescent or silky
Leaflets	Obovate, spatulate, obtuse	Elliptic-lanceolate or obovate-lanceolate, acute
Umbels	1-3(4) flowers	1-5(6) flowers
Calyx	5,0-7,35 mm	6,90-8,60 mm
Fruit	10-28 mm, usually with several constrictions	10-49 mm, usually cylindrical or with just a few constrictions

Figure 1 - *Lotus glaucus* subsp. *floridus* (A, flowers and leaves; B, habit)

Figure 2 - *Lotus glaucus* subsp. *glaucus* (Flowers, fruits, stems and leaves)

The original description of *Pedrosia florida* is here transcribed:

"*P. fruticulosa sericeo-albicans foliolosa, foliolis confertis parvulis lanceolatis v. obovato-lanceolatis acutis stipulisque conformibus omnino sessilibus, umbellis 2-5-floris, leguminibus rectis cylindricis glabris.*

Var. a; fl. laete aurantiacis.

Var. ß; fl. pallide sulphureo-stramineis.
HAB. In Portu Sancto".

Although some specimens with flower color corresponding to the description given by Lowe for *Pedrosia florida* Lowe var. *sulphurea* were studied, we agree with SANDRAL *et al.* (2006) in not recognizing them at any taxonomical rank.

Further studies should contribute to clarify the taxonomic relations between taxa included in the *Lotus glaucus* complex in Macaronesia.

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Andryala integrifolia L. (Asteraceae), a new alien species for the Island of Madeira (Portugal)

Introduction

Madeira is an archipelago from Macaronesia comprising Porto Santo Island (11-14 Ma) and Madeira and Desertas Islands which constitute a volcanic complex with 0-6 Ma. (GELDMACHER *et al.,* 2006). In Madeira Island, the more recent volcanic activity occurred 6,000-7,000 years ago (GELDMACHER *et al.*, 2000). This island is situated between 32°38′ and 32°52'N and 16°39' and 17°16'W, at approximately 600 km northwest of the Western African coast.

Andryala L. is represented in Macaronesia by at least 8 endemic taxa distributed in different archipelagos: 5 taxa in the Canary Islands (ACEBES-GINOVÉS *et al.*, 2010) and 3 in the archipelago of Madeira (JARDIM and MENEZES DE SEQUEIRA, 2008). The vascular flora of the archipelagos of Madeira and Selvagens comprises 1,204 taxa. Of these, 12.8% are endemic to the archipelagos of Madeira and Selvagens, and 6.1% are Macaronesian endemics (JARDIM and MENEZES DE SEQUEIRA, 2008).

Andryala integrifolia was described by LINNAEUS (1753) in his "Species Plantarum". SELL (1976) and TALAVERA (1987) assigned this species for SW Europe, the Mediterranean Region and Macaronesia. It can also be found in North Africa: Tunisia (POIRRET-ALAPETIT, 1981), Algeria (BATTANDIER and TRABUT, 1899) and Morocco (NÈGRE, 1962).

In what concerns Macaronesia, KUNKEL (1978) assigned *A. integrifolia* to the Canary Islands of El Hierro and Gran Canaria, and emphasized its Mediterranean origin. However, more recently ACEBES-GINOVÉS *et al.* (2010) referred *A. integrifolia* as a "probable native" species of these two islands. It also occurs in the Azores (SELL, 1976), namely in the islands of S. Jorge and Faial (FRANCO, 1984; HANSEN and SUNDING, 1993). SILVA *et al.* (2005) considered *A. integrifolia* as introduced in these Azorean islands. Recently SILVA *et al.* (2010) included St. Maria Island in the Azorean distribution, regarding *A. integrifolia* as naturalized.

Andryala integrifolia L. was recently found by us for the first time as a fully naturalized species in Madeira Island. Its morphological characters are clearly distinct from the endemics *Andryala glandulosa* Lam. and *Andryala crithmifolia* Aiton. A diagnostic key is provided and detailed images of the diagnostic characters are presented. The consequences of the introduction of *A. integrifolia* in Madeira Island are discussed.

Material and methods

Most of the observations were made upon herbarium specimens from the herbaria MA, LISU and TFC. Specimens collected during 2005-2010 in Madeira and in the Canary Islands were also revised. The macroscopic analysis was performed using a binocular microscope Zeiss model SV 11 APO. Micro characters were photographed using a Scanning Microscope (JEOL-TSM T330A). The distribution map is based on geographic coordinates of localities for the studied specimens and was plotted with the application QUIKMAP for Windows Version 1.02.

Results

During field work, plants with a contrasting morphology when compared with the *Andryala* Madeiran species (*Andryala glandulosa* Lam. and *Andryala crithmifolia* Aiton) were detected. Following various floras [Flora de Portugal (COUTINHO, 1939); Flora Europaea Vol. IV (SELL, 1976); Nova Flora de Portugal (FRANCO, 1984) and Flora Vascular de Andalucía Occidental (TALAVERA, 1987)] these plants correspond to *A. integrifolia*. The morphology of the vegetative and reproductive structures of this species differs from those recognized for the archipelago of Madeira (Figure 1). A key to Madeira archipelago *Andryala* L. is presented:

KEY TO MADEIRA ARCHIPELAGO ANDRYALA *L. SPECIES*

1. Lower leaves 1-2-pinnatissect with segments up to 3 mm in width; peduncles with short glandular hairs, ligules stellate-hairy at the apex of all the teeth. .... *A. crithmifolia*

   Lower leaves subentire to pinnatipartite; peduncles with long glandular hairs, ligules not stellate-hairy or rarely so at the apex of a few teeth 2

2. Stem with numerous long glandular hairs, all along the stem or at least on the superior part; involucral bracts involute, enfolding a floret; florets golden yellow, external ones rarely with a reddish stripe on the outer face. .... *A. glandulosa*

   Stem sometimes with few glandular hairs on the superior part; involucral bracts flat, not enfolding a floret; external florets pale yellow, frequently with a reddish stripe on the outer face. .... *A. integrifolia*

A. integrifolia has a very restrict distribution in Madeira (Figure 2). In 2009 it was found at Prazeres, Fajã da Ovelha and Paul da Serra, but more recently (2010) it was seen in abundance at Ponta do Pargo, the most far western locality of the island, co-existing with *Andryala glandulosa* Lam. subsp. *glandulosa* and *Andryala glandulosa* Lam. subsp. *cheiranthifolia* (L'Hér.) Greuter. *A. integrifolia* has been reported to grow on sandy, rocky or sterile terrains, uncultivated lands and stone walls (COUTINHO, 1939; FRANCO, 1984). In Madeira Island it grows on rocky road slopes (Figure 3) and uncultivated lands nearby roads, at altitudes between 539 m (road to Prazeres) and 1500 m (Paul da Serra) above sea level.

Studied material (*Andryala integrifolia* L.)

PORTUGAL. Madeira: Paul da Serra, talude rochoso junto à Estrada, 24.VII.2009, M. Sequeira, A. Pupo Correia, A. Figueiredo, Z. Ferreira (MA 801896); Madeira: Estrada para os Prazeres, Alt. 590, 29.VII.2009, Z. Ferreira, M. Benedito & M. Sequeira (MA 801898); Madeira: Estrada para os Prazeres, no talude da via rápida, 29.VII.2009, Z. Ferreira, M. Benedito & M. Sequeira (MA 801897); Beira Baixa: Barca d'Alva, taludes do caminho de ferro, VI.1915, R. Palhinha e F. Mendes (LISU 40310); Beira Litoral: Lousã, Quinta da Alfocheira, R.F. Palhinha (LISU 40284); Estremadura: Setúbal, Arrábida, Casais da Serra, erva anual, com cerca de 50 cm, folhas onduladas, 06.VI.1979, João Paulo Lopes (LISU 139690); Ribatejo: Pancas, a sudoeste do Espanadal, linha de água que termina no Mosqueteiro, sebe ao longo da linha de água, na periferia, erva anual com ca. de 80 cm, capítulos amarelos, 22.VII.1982, M. Correia & J. Cardoso (LISU 150967); Trás-os-Montes: Nantes, Serra da Brunheira, VI.1910, Dr. R. Palhinha, H. Navel e F. Mendes (LISU 40337)

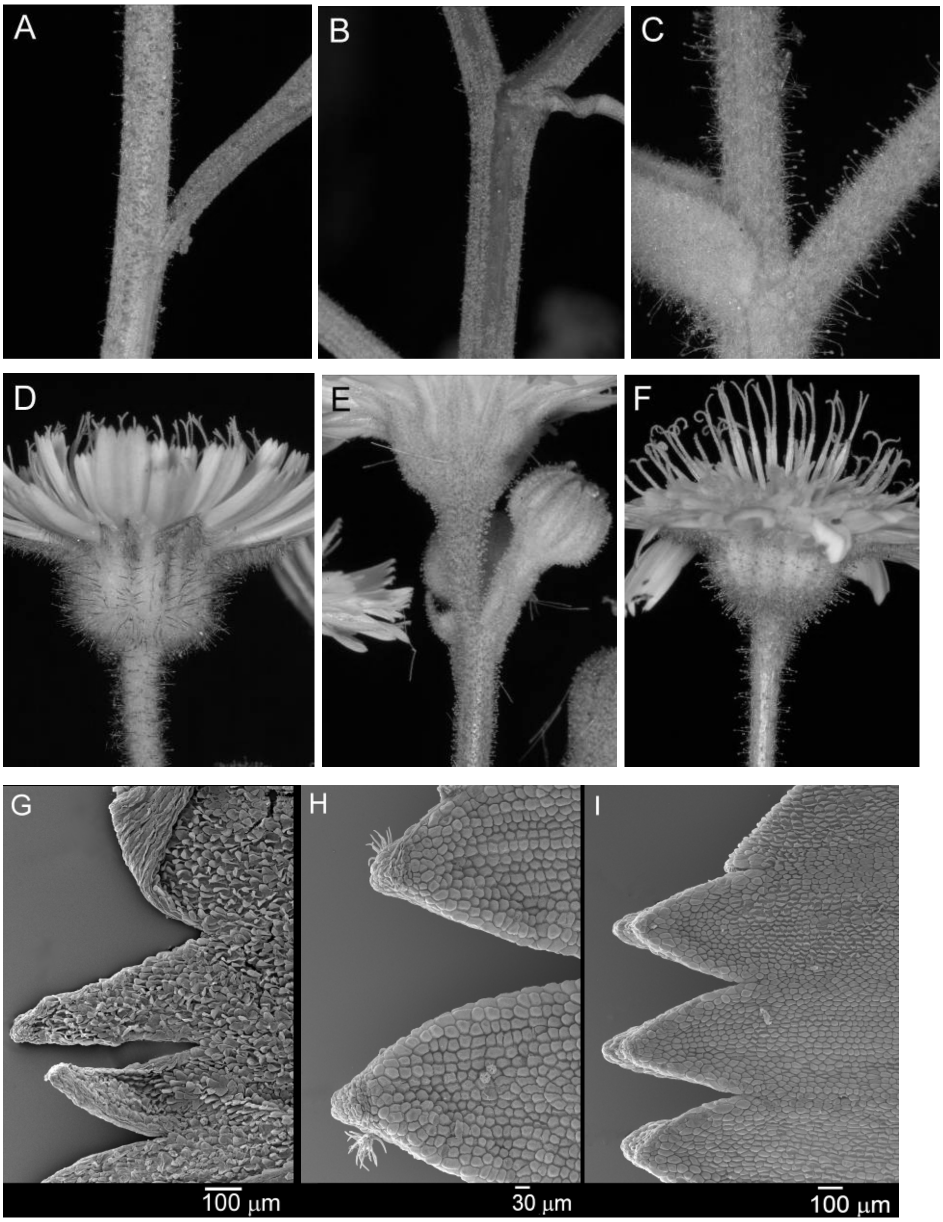

Figure 1 - Stem: A - *A. integrifolia*; B - *A. crithmifolia*; C - *A. glandulosa*
Peduncle: D - *A. integrifolia*; E - *A. crithmifolia*; F - *A. glandulosa*
Teeth of the ligules: G - *A. integrifolia*; H - *A. crithmifolia*; I. - *A. glandulosa*

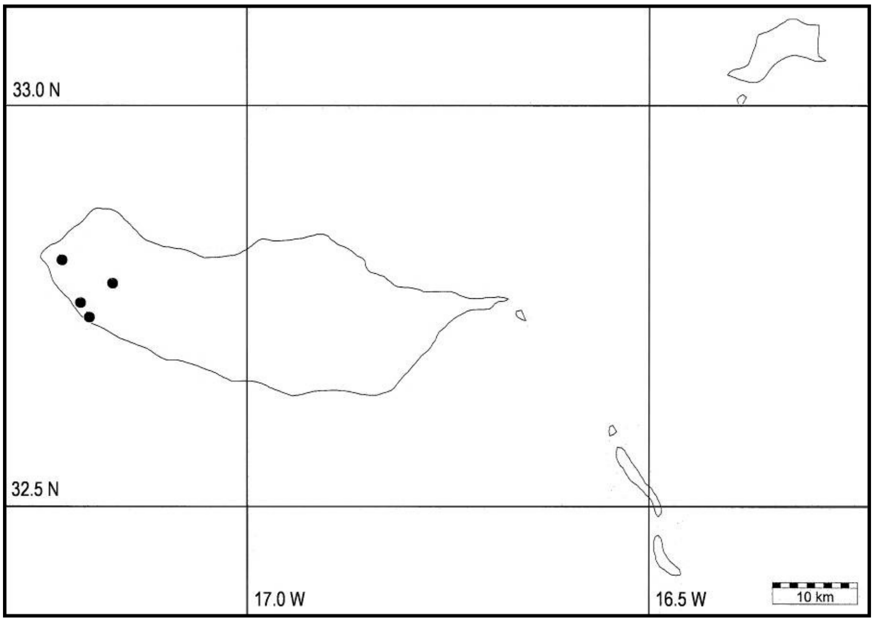

Figure 2 - Distribution area of *Andryala integrifolia* in Madeira

Figure 3 - *A. integrifolia* (to the left), *A. glandulosa* (to the right)

SPAIN. Canary Islands: San Andrés, El Pinar (El Hierro), borde carretera, 28.III.2004, Miguel António Padrón Mederos (TFC 45089); Canárias: Vega de S. Mateo, Matazano (Gran Canária), en eriales de cultivos abandonados y zonas de pastoreo de las medianías altas, 23.V.1999, A. Marrero (MA 632723); Burgos: cercanías de Huidobro, paramera caliza, 22.VII.1984, Galán Cela & A. Martín (MA 639931); Cantabria: Valderredible, Ruijas, cuneta, 780 m, 29.VI.2000, M. Pardo de Santayana (MA 726270); Madrid: Sierra de Guadarrama, Collado Mediano, 26.VI.1995, M.A. Carrasco & S. Pajarón (MA582315).

Discussion

AITON (1789) assigned *A. integrifolia* to South Europe and considered two *Andryala* species for Madeira, both endemic: *A. crithmifolia* Aiton and *Andryala cheiranthifolia* L'Hér. (presently included in *A. glandulosa*). Likewise, no references to the presence of *A. integrifolia* in the Madeira archipelago are found on the basic floras by LOWE (1868), MENEZES (1914), PRESS & SHORT (1994) and VIEIRA (2002), neither do JARDIM and MENEZES DE SEQUEIRA (2008) make any allusion. Thus, *A. integrifolia* can be considered a new alien species in Madeira.

According to DAISIE [Delivering Alien Invasive Species Inventories for Europe (*http://www.europe-aliens.org/*)], *A. integrifolia* is considered an alien species in Austria (not established) and the Azores (established). Alien plants are those whose presence in a given area is due to human involvement, or which have arrived there without people's intervention from an area in which they are alien (PYŠEK *et al.*, 2004). These can become naturalized if they sustain self-replacing populations for at least 10 years without direct intervention by people (or in spite of human intervention) by recruitment from seed or ramets capable of independent growth. Naturalized plant species acquire an invasive status when producing reproductive offspring, often in very large numbers, at considerable distances from the parent plants, thus exhibiting potential to spread over a large area (PYŠEK *et al.*, op cit.).

Invasive species can alter the evolutionary pathway of native species by niche displacement, competitive exclusion, hybridization, introgression, and ultimately extinction (MOONEY and CLELAND, 2001). Invasive plants can displace native species through propagation abilities, soil chemistry alteration, allelopathic effects, competition for nutrients, water, etc (GLEADOW and ASHTON, 1981; D'ANTONIO and MAHALL, 1991; BAARS and KELLY, 1996; CLEVERLY *et al.*, 1997; FOGARTY and FACELLI, 1999; CORDEIRO and SILVA, 2003; VAN DEN BOSCH *et al.*, 2004; ASNER and VITOUSEK, 2005; BOLAND, 2006; REASER, 2007; NIU, 2007; SILVA *et al.*, 2008; GALLO *et al.*, 2008; BOWMAN, 2008; CONSER and CONNOR, 2009).

Natural hybridization can increase genetic diversity at both the population and species level, and new species can be derived through this process (GALLEZ *et al.*, 1982; RIESEBERG, 1991a; ARNOLD, 1993; WANG *et al.*, 1994; MENEZES DE SEQUEIRA and CASTROVIEJO, 2007; SHERMAN and BURKE, 2009). However, hybridization due to the introduction of non-native species can threaten the genetic integrity and persistence of native species (KRAHULCOVÁ *et al.*, 1996; GALLAGHER *et al.*, 1997; ANTTILA *et al.*, 1998; HUXEL, 1999; VILÀ *et al.*, 2000; ABBOTT *et al.*, 2003).

There is increasing evidence that invasive alien species have become the most significant driver of population declines and species extinction in island ecosystems (VITOUSEK *et al.*, 1987; SMITH and TUNISON, 1992; REASER, 2007). The fairly recent, deliberate introduction of alien plants in Macaronesia has unfortunately meant considerable changes to the landscape during the 20th century and in some cases also meant a threat to the very survival of native types of vegetation (SJÖGREN, 2000). In the Canary Archipelago, the total of alien vascular plants species is about 701, of which 82 are invasive (ACEBES GINOVÉS *et al.*, 2010). While in the Azores no less than 60% of the vascular plant taxa is non-indigenous (SILVA and SMITH, 2004), in the archipelagos of Madeira and Selvagens about 33.3% of the vascular flora is introduced (JARDIM and MENEZES DE SEQUEIRA, 2008).

The introduction of new plant species in Madeira seems to continue at a strong rhythm, and, apart from *A. integrifolia*, *Solidago chilensis* Meyen (GONÇALVES SILVA *et al.*, 2008) and *Viburnum tinus* L. (SILVA *et al.*, 2009) were recently detected. The introduction of *A. integrifolia* will certainly not have the same impact as some phanerophytes (e.g. *Acacia mearnsii* De Wild) have in the Madeiran landscape and ecosystems. Although the ecological impacts are expected to be negligible, the possible hybridization with endemics (*A. crithmifolia* and *A. glandulosa*) could lead to a biodiversity loss. The fact that there are several records of hybridization within *Andryala*, with *A. integrifolia* as one of the parental species, contributes to raise concerns in this matter. For instance, KUNKEL (1978) described the hybrid *x Andryala christii* Kunkel (= *A. integrifolia* L. x *A. pinnatifida* Aiton) for Gran Canaria. MAIRE (1926) described an algerian hybrid, *x Andryala faurei* Maire (= *Andryala arenaria* Boiss. et Reut. x *A. integrifolia* L.), considering it closer to *A. integrifolia*, which indicates that breeding probably resulted from pollination by this parental species. Later MAIRE (1937) described a new hybrid for Algeria: *x Andryala dichroa* Maire (= *A. integrifolia* L. x *A. laxiflora* Salzm.), which is closer to *A. laxiflora*, although the male parent is again *A. integrifolia*. Besides, *A. glandulosa* and *A. integrifolia* are both diploids with 2n=18 (DALGAARD, 1985; IZUZQUIZA, 1988), and therefore hybridization is quite possible. Hybridization is even more feasible at Ponta do Pargo, where *A. integrifolia* co-exists with both subspecies of *A. glandulosa*.

Hybridization and subsequent introgression between abundant exotic taxa and rare native congeners can promote extinction of the latter (RHYMER and SIMBERLOFF, 1996; LEVIN *et al.*, 1996; WOLF, 2001). Small insular populations are particularly vulnerable to extinction by hybridization (RIESEBERG, 1991b; LEVIN *et al.*, 1996; MOONEY and CLELAND, 2001). In Madeira the populations of *A. crithmifolia* occur only in a few sites and are numerically small. Hence, the probability of extinction of this critically endangered endemism may be increased by hybridization with *A. integrifolia*, encase this congener becomes a widespread species invading areas where populations of *A. crithmifolia* occur.

All the well-documented examples of invasive alien plants around the world, and especially on islands, clearly show that most of them constitute a serious conservation issue. Alien species may stay at a fairly low population size for years and then explode at some later date. This so-called lag effect may simply be the result of the normal increase in size and distribution of a population (MOONEY and CLELAND, 2001; e.g. *Lantana camara* L. in Galapagos Archipelago, TYE, 2001). *A. integrifolia* is fully naturalized in Madeira, and may become a conservation problem in a near future. It is currently growing in western localities of Madeira Island, but it may be going through a time-lag effect and the possibility of it becoming invasive must not be discarded. The fact that *A. integrifolia* was recently found on another Azorean island shows that its spreading ability should not be underestimated.

In order to implement efficient control methods, it is essential to understand how alien plants affect native vegetation. Relatively to *A. integrifolia* in Madeira, the impacts may seem insignificant when compared to other alien plants, but the strong possibility that two endemic *Andryala* species can be threatened by the presence of *A. integrifolia*, justifies the need of constant monitoring, since naturalized species can reach an invasive status replacing even endemisms. An early eradication at the sites where it co-habits with *A. glandulosa* could help prevent hybridization and inherent consequences.

Globalization facilitates the spread of invasive alien species as international commerce develops new trade routes, markets, and products (MEYERSON and MOONEY, 2007). By trade, transport, travel and tourism, invasive alien species are introduced through various pathways, which can be intentional or unintentional (BURGIEL *et al.*, 2006). Some major pathways of introduction for alien plants are forestry, seed contaminant, feral crop, horticulture, hitchhikers, and ornamental (HULME *et al.,* 2008). The introduction of *A. integrifolia* L. in Madeira was most likely unintentional as a by-product of trade either as seed contaminants or accidental hitchhikers attached to vehicles or machinery. The increasing global rate of road construction is leading to a parallel increase of areas of degraded soil conditions and steep slopes that need revegetation. Hydro seeding with commercial seeds of fast-growing grasses and legumes is a common practice in revegetation of motorway slopes (MATESANZ *et al.*, 2006). In Madeira *A. integrifolia* grows on roadsides, and since road construction and road use are disturbed habitats related to weed proliferation (FORCELLA and HARVEY, 1983), another plausible explanation for the introduction of *A. integrifolia* is the hydro seeding of the roadsides with seed mixtures including alien species. Hydro seeding is a good method of revegetation as long as local species are used instead of the available commercial species (TORMO *et al.*, 2007). To impede further introductions of *A. integrifolia* in Madeira, an especial attention should be given to seed and plant trade, bearing in mind that the success of restoration by hydro seeding dwells in the selection of native species from the local flora that are more able to overcome the specific limitations of the disturbed area to be restored (BOCHET *et al.*, 2009).

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9.2 Appendix 2: *Andryala perezii* (Asteraceae), a New Species from the Canary Islands – paper published in *Novon*, 2014

Andryala perezii (Asteraceae), a New Species from the Canary Islands

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Abstract. *Andryala perezii* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. (Asteraceae), a new species from the Canary Islands, is described and illustrated. Although formerly included in *A. glandulosa* Lam., the new species differs remarkably from Madeiran populations by its woolly stellate pubescence, scattered glandular pubescence restricted to the peduncles and involucral bracts, peduncles flattened and enlarged at the base of the capitula, and smaller cypselae. *Andryala perezii* has a habit similar to that of the Canarian *A. pinnatifida* Aiton but may be identified by its densely stellate pubescence on the stems; grayish white or glaucous, congested leaves with dense stellate pubescence on both surfaces and undulate-crispate margins; longer peduncles; and smaller cypselae with a ring of short teeth at the apex equivalent to the height of the prolongation of the ribs. Comments on the chromosome numbers, geographic distribution, habitat, and conservation status are also presented. The name *A. pinnatifida* Aiton f. *cuneifolia* Sch. Bip. is lectotypified and is transferred in rank as *A. pinnatifida* subsp. *cuneifolia* (Sch. Bip.) M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq.; lectotypes are designated for its synonyms, *A. pinnatifida* f. *buchiana* Sch. Bip. and *A. pinnatifida* var. *latifolia* Bornm. The name *A. pinnatifida* is also lectotypified. A key for Macaronesian *Andryala* L. taxa is provided.

Key words: Andryala, Asteraceae, IUCN Red List, Madeira, Spain.

Based on present taxonomic concepts, the genus *Andryala* L. comprises 13 species that are distributed across the Mediterranean Basin, being also present in Macaronesia and Romania (Greuter, 2006+). In Macaronesia, *Andryala* is represented by *A. integrifolia* L. and *A. laxiflora* DC. and at least eight endemic taxa distributed in the Canary and Madeira archipelagos (Jardim & Menezes de Sequeira, 2008; Acebes Ginovés et al., 2010). The Madeira Archipelago hosts *A. integrifolia* (recently introduced), *A. crithmifolia* Aiton (a rare endemic), and *A. glandulosa* Lam. (Press, 1994; Ferreira et al., 2011), the latter including *A. glandulosa* subsp. *glandulosa* and *A. glandulosa* subsp. *cheiranthifolia* (L'Hér.) Greuter. For the Canary Islands, Acebes Ginovés et al. (2010) recognized *A. integrifolia* (as probably native), *A. laxiflora* (as introduced), and two endemic species: *A. webbii* (Sch. Bip. ex Christ) A. Santos and *A. pinnatifida* Aiton, the latter including four subspecies: *A. pinnatifida* subsp. *pinnatifida*, *A. pinnatifida* subsp. *preauxiana* (Sch. Bip.) G. Kunkel, *A. pinnatifida* subsp. *buchiana* (Sch. Bip.) Reyes-Bet. & A. Santos, and *A. pinnatifida* subsp. *teydensis* (Sch. Bip.) Rivas-Mart., Wildpret, del Arco, O. Rodr., Pérez de Pérez, Garciá Gallo, Acebes, T. E. Díaz & Fern.-Gonz.

The *Andryala* populations on the eastern Canary Islands (Lanzarote and Fuerteventura) were originally included by Schultz Bipontinus (1849), together with populations from Tenerife, as the form *A. pinnatifida* f. *buchiana* Sch. Bip. of the polymorphic *A. pinnatifida* from the Canary Islands. Later Lid and Lid (1967) and Kunkel (1977, 1978, 1980) placed these populations in the Madeiran *A. glandulosa* (including *A. cheiranthifolia* L'Hér.), as did Hansen and Sunding (1993) and Acebes Ginovés et al.

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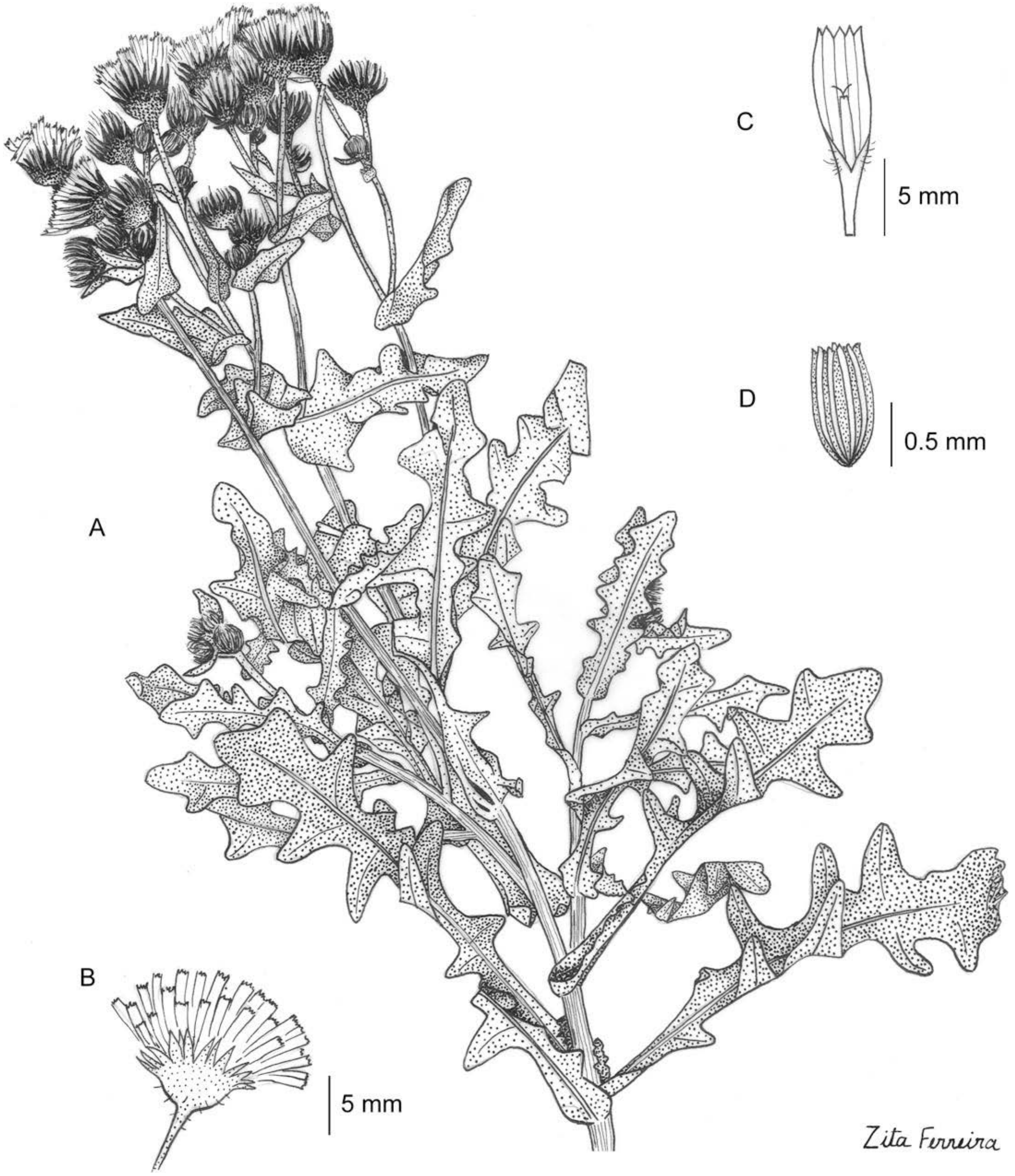

Figure 1. *Andryala perezii* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. —A. Fertile habit. —B. Capitulum. —C. Floret. —D. Cypsela; note the characteristic apical ring of small teeth. Drawn from the paratype *J. A. Reyes-Betancort* (TFC-37826).

(2004). More recently, A. Santos Guerra and J. A. Reyes-Betancort (in Greuter & von Raab-Straube, 2009) excluded these populations from *A. glandulosa* and included them again in *A. pinnatifida* as *A. pinnatifida* subsp. *buchiana*.

The examination of herbarium specimens demonstrated the presence of a distinct taxon exclusively from Lanzarote and Fuerteventura, and accordingly a new species is described herein.

1. **Andryala perezii** M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq., sp. nov. TYPE: Spain. Lanzarote: Haría, altos del Bco de Chafarís, 23 Feb. 1994, *J. A. Reyes-Betancort, W. W. de la Torre & P. L. Pérez de Paz s.n.* (holotype, TFC-39728). Figures 1, 2.

Andryala pinnatifida Aiton f. *buchiana* Sch. Bip. Hist. Nat. Iles Canaries (Phytogr.). 2: 415. 1849. p.p. quoad.

Andryala pinnatifida Aiton subsp. *buchiana* (Sch. Bip.) Reyes-Bet. & A. Santos in *Willdenowia* 39: 328. 2010. p.p. quoad.

Nova plantarum species quae ab *Andryala pinnatifida* Aiton caulibus indumentum densius ostendentibus, foliis congestioribus marginibus undulatis utrinque aequaliter tomentosis trichomatibus stellatis, pedunculis longioribus et cypselarum annuli apicalis dentibus costarum extensiones subaequentibus; ab *A. glandulosa* Lam. caulibus foliisque stellato-tomentosis sed trichomatibus glandulosis carentibus; ab ambabus pedunculis complanatis ad capitulorum basem ampliatis differt.

Plants from basal rosettes; stems 10–25 cm, woody at the base, branched from the base or from the middle upward, branches erect to patent (sometimes slightly ascending), with a dense tomentum of whitish stellate trichomes (Fig. 3A). Leaves congested at base of stem; leaf blades grayish white or glaucous, tomentose with dense stellate trichomes (Fig. 3B) on both surfaces, lower leaves 93–95 × 25–40 mm, narrowed at the base into a winged petiole 21–24 mm, oblong to lanceolate, lamina deeply lobed to pinnatisect, margin crispate-undulate, the apex acute; cauline leaves 31–66(–92) × 12–29 mm, cordate at the base, semiamplexicaul or amplexicaul, oblong, lamina pinnatifid or deeply lobed, margin crispate-undulate, the apex obtuse; upper leaves 8.3(–13)–21.7 × 2.3–8.6 mm, amplexicaul, ovate-oblong to ovate-lanceolate, entire, cordate at the base, the apex acute to acuminate. Inflorescences in corymbs of 3 to 8 heads; capitula 15–22 mm diam.; peduncles 26–43 mm, flattened and enlarged at the base of the capitulum, with dense stellate trichomes and few glandular trichomes (Fig. 3C); involucre 10–12 × 11–18 mm, ± hemispherical with involucral bracts in 2 or 3 rows; outer involucral bracts 7–7.5 × 1.2–1.6 mm, apex acuminate to subulate, involute enclosing a floret, the external surface with dense white or yellowish stellate trichomes and also abundant glandular trichomes 1.2–1.9 mm, especially along the middle nerve, the trichomes usually yellow or dark at the base; inner involucral bracts 6.5–8 × 1.5–2.3 mm, with narrow scariose margins; the receptacle convex, puberulous to tomentose, with long silky trichomes 3.3–4.2 mm (3 to 4 times longer than the cypselae). Florets ligulate, golden-yellow, tube 4–6.5 mm and ligule 7.4–10 × 1.9–3.1 mm, anther tube ca. 3 mm and style arms 1–2 mm. Cypselae 0.9–1.1 × 0.4–0.5 mm (Fig. 3D), oblong, dark brown with brownish red ribs; the apex with an inner ring of short teeth, as long as the outer (i.e., the prolongation of the ribs); pappus of white bristles 4.8–5.2 mm.

Distribution, habitat, and IUCN Red List category. *Andryala perezii* is found in Lanzarote and Fuerteventura, where it is common on rocky slopes, growing also on roadsides and volcanic substrates, at elevations from 90 to 580 m. Kunkel (1977) considered the Canarian *A. glandulosa* (i.e., *A. perezii*, as treated here) locally common in both islands, despite grazing by rabbits and goats, and did not regard it as a threatened taxon. *Andryala perezii* was evaluated under the name *A. glandulosa* for the Canary Islands and was not included in the *Red Data Book of the Canarian Flora* (Beltrán Tejera et al., 1999), nor was it mentioned in "Memoria de Evaluación de Especies Amenazadas de Canarias 2009" (Servicio de Biodiversidad del Gobierno de Canarias, 2009). Although *A. perezii* has a restricted distribution in the Canary Archipelago, it is locally common in parts of its range and therefore should be listed as Least Concern (LC) according to IUCN Red List categories and criteria (IUCN, 2001).

Etymology. *Andryala perezii* is named in honor of the botanist Pedro Luís Pérez de Paz (1949–), University of La Laguna (Tenerife), who has greatly contributed to the knowledge of the Canary Islands flora and is a co-collector of the type specimen.

Karyology. Borgen (1970: 150) and Van Loon (1974: 155) counted 18 chromosomes in root tips of plants collected in Lanzarote, originally identified as *Andryala cheiranthifolia*. A careful observation of the herbarium voucher of the plant on which Borgen (1970) performed the chromosome counts made it clear that this specimen corresponds to the newly described species. These chromosome numbers correspond to all other counts known in the genus *Andryala* (e.g., Humphries et al., 1978; Moore, 1982; Goldblatt, 1988; Goldblatt & Johnson, 1990; Castroviejo & Valdés Bermejo, 1991; Pastor Díaz, 1992).

Taxonomic remarks. In the original description of *Andryala glandulosa*, Lamarck (1783) referred to its 3-foot stem height and the glandular pubescence observed on the branches, leaves, peduncles, and involucral bracts, as well as the sessile, lanceolate, and entire leaves. This morphology corresponds undoubtedly to the Madeiran populations of *A. glandulosa*, and the name was therefore misapplied to plants from the Canary Islands by several authors (e.g., Lid & Lid, 1967; Kunkel, 1980; Bramwell & Bramwell, 2001). Lamarck (1783: 154) was uncertain about the origin of this species ("Elle provient, je crois, de graines du voyage de Cook"). However, the likelihood of a Madeiran origin for material of *A. glandulosa* is quite high. James Cook, in his first voyage around the world, reached Madeira in September 1768. On board were the naturalists Sir

Figure 2. Holotype of *Andryala perezii* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq., collected by *J. A. Reyes-Betancort, W. W. de la Torre & P. L. Pérez de Paz* (TFC-39728).

Joseph Banks and D. C. Solander, who investigated the natural history of Madeira during the few days spent on the island (Silva & Menezes, 1998), but their plant list was never published. The uncertainty on the seed origin for Lamarck's *A. glandulosa* suggests another possibility: that the seeds correspond to later collections by Francis Masson (1741–1805). Between 1776 and 1779 Masson undertook

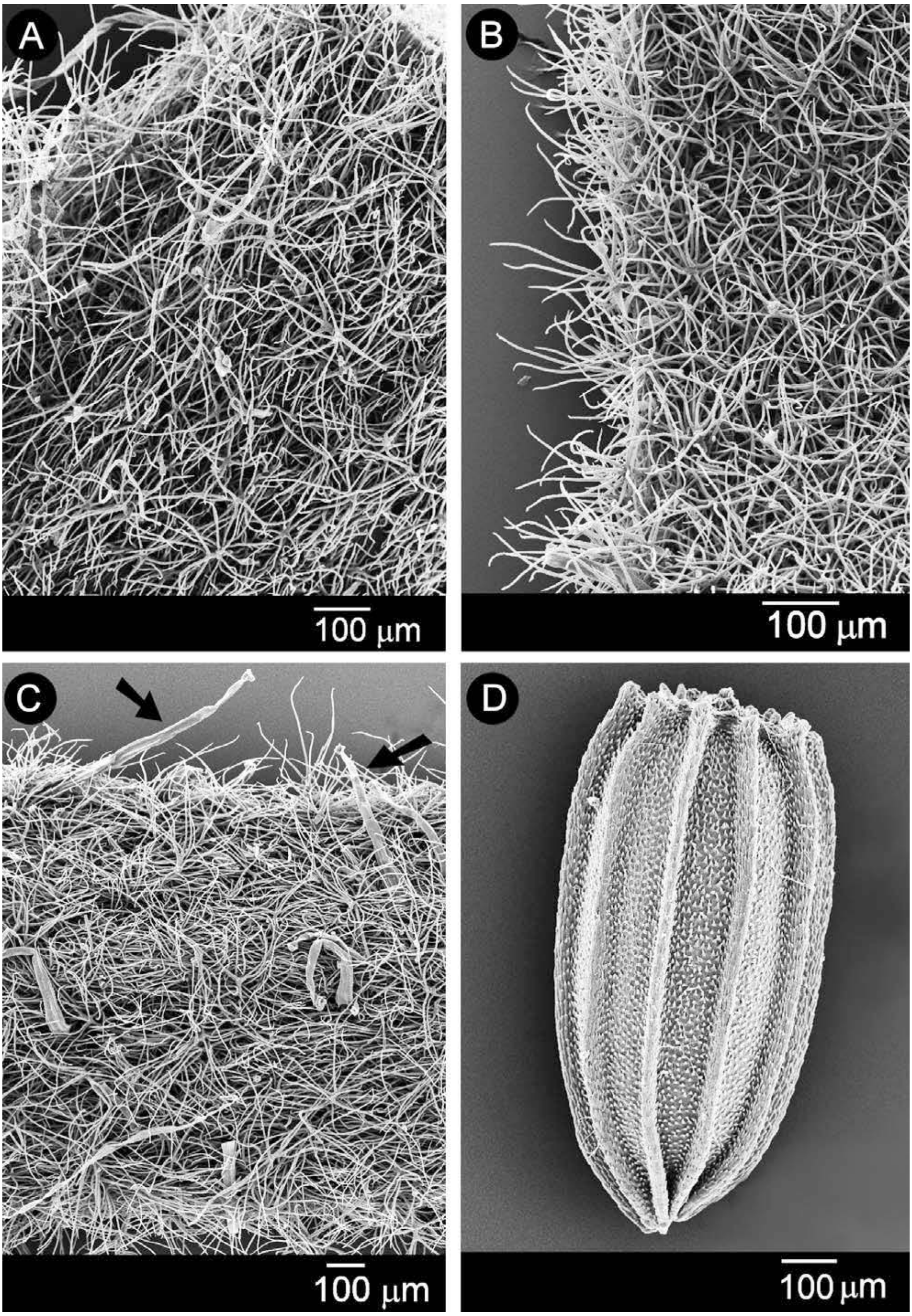

Figure 3. *Andryala perezii* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. —A. Stem indumentum, tomentose with stellate trichomes. —B. Leaf indumentum, showing the abaxial blade surface as tomentose stellate. —C. Peduncle indumentum, densely stellate, with scattered glandular trichomes. —D. Longitudinal view of cypsela, showing the distinctive apical ring of teeth equivalent in height to the cypsela rib prolongations.

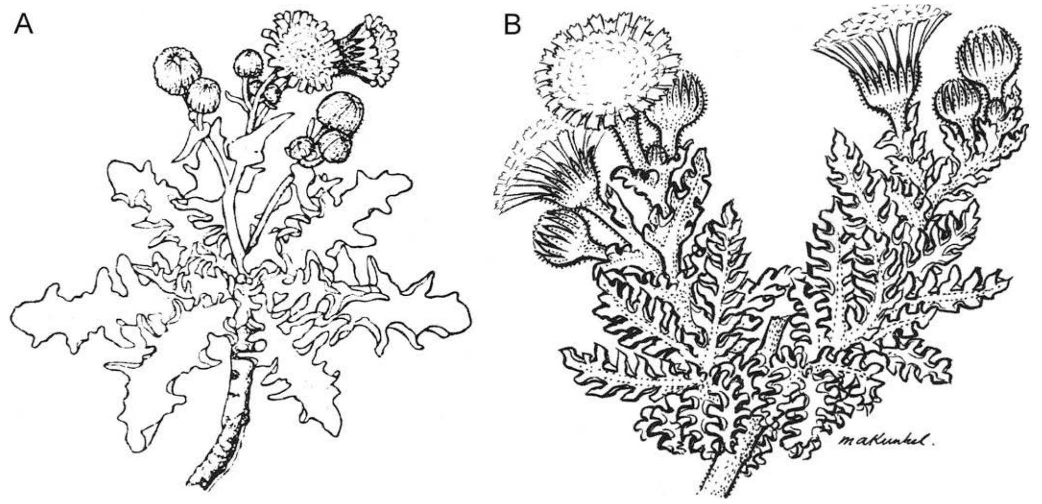

Figure 4. —A. Illustration of *Andryala cheiranthifolia* L'Hér. from the Canary Islands by Dagny Tande Lid, *Contributions to the Flora of the Canary Islands*, 1967. © Dagny Tande Lid/BONO 2013. —B. Illustration of *A. glandulosa* Lam. from Kunkel (1978). Reprinted with permission from Organismo Autónomo Parques Nacionales.

extensive plant collecting in Macaronesia, and Madeira was the main hub for his collecting activities (Francisco-Ortega et al., 2008). These plants were the basis for the description of many new species, including several by L'Héritier, but not *A. cheiranthifolia* (Francisco-Ortega et al., 2008).

The illustration of *Andryala glandulosa* in Poiret's *Tableau Encyclopedique* (1823: pl. 567) does not correspond to the protologue published in 1783 by Lamarck. The specimen illustrated better resembles, by its lanceolate and deeply divided lower leaves, *A. cheiranthifolia* [≡ *A. glandulosa* subsp. *cheiranthifolia*]. When L'Héritier described *A. cheiranthifolia* in 1784, he explicitly assigned it to Madeira, although he was referring to a plant grown in what he noted was the "Hortus regius Parisiensis" (L'Héritier, 1784). Lid and Lid (1967) later accepted *A. cheiranthifolia* for the Canary flora, and the illustration presented by these authors corresponds taxonomically to the newly described *A. perezii* (Fig. 4A). Kunkel (1978) described the Canarian *A. glandulosa* as an herb, 10–25 cm tall, woody at the base, with smooth, whitish, and velvety, pinnapartite or pinnatisect leaves, as well as yellow and rather large capitula. This description was accompanied by an illustration (Fig. 4B), and both fit the new species perfectly.

Schultz Bipontinus (1849: 416) described *Andryala pinnatifida* f. *buchiana* and comprehensively discussed its morphology and distribution, assigning it to the Canary Islands of Tenerife ("in campis villa Orotava usque ad summitatem Cumbre Lagunæ") and Lanzarote ("in summo monte Chache et ad oppidulum Haría"). In respect to the plants from Lanzarote, Schultz Bipontinus (1849: 416) expressed some doubt about their taxonomic position: "*Andr. pinnatifida* var. *major*? an *Andr. cheiranthifoliæ var.*?" For this island (specifically at "la Mancha Blanca") the author described a unique specimen that matches *A. perezii* given its description ("caule abbreviato, palmari, robusto, foliis profundius pinnatifidis, valde undulatis, lobis triangularibus, obtusis, subintegris, capitulos majoribus, corymbosis, floribus aureis, involucro, pilis glanduliferis, flavo-virentibus, præcipue basi hispidissimo"). However, included in *A. pinnatifida* f. *buchiana*, this author also considered a specimen from Tenerife ("ad rupes atlas, de las Mercedes") that, by its description ("folia subcuneata, paulo angustiora, sinuato-dentata, dentius non tam obtusis, supra glabrescentia, capitula corymboso-racemosa, minora, involucra cum pedunculis hispida, flores pallide aurei"), corresponds, together with *A. pinnatifida* f. *cuneifolia* Sch. Bip., to the much later described *A. pinnatifida* var. *latifolia* Bornm., assigned by Bornmüller (1904) to Tenerife and El Hierro and usually not accepted by authors of the Canarian flora (e.g., Acebes Ginovés et al., 2010). This taxon was later combined by Kunkel (1980) as *A. pinnatifida* subsp. *latifolia* (Bornm.) G. Kunkel. Not surprisingly, Schultz Bipontinus (1849) stressed that *A. pinnatifida* f. *cuneifolia*, from El Hierro, is close to *A. pinnatifida* f. *buchiana*, particularly to the specimen from Tenerife. It is obvious that the

Table 1. Diagnostic characters of *Andryala perezii* compared with *A. glandulosa* and *A. pinnatifida*.

Characters	*A. perezii*	*A. glandulosa*	*A. pinnatifida*
Stems	10–25 cm; woolly stellate, without glandular trichomes	21–112 cm; stellate tomentose, with glandular trichomes at least in the upper part	14–81 cm; stellate pubescent or tomentose with glandular trichomes or not
Leaf blades	not pale to dark green, but grayish white or glaucous; all densely stellate tomentose on both surfaces, without glandular trichomes; margins undulate-crispate	pale to dark green, not glaucous; uppermost leaves stellate and glandular pubescent; cauline and basal leaves sometimes glandular pubescent; margins not undulate-crispate	grayish white, pale, or dark green, not glaucous; stellate pubescent more so abaxially; uppermost leaves sometimes glandular pubescent; margins not undulate-crispate
Peduncles	26–43 mm; flattened and enlarged at bases of capitula; densely stellate tomentose, with a few glandular trichomes	19.2–80 mm; cylindrical and not enlarged at bases of capitula; stellate and densely glandular pubescent	7.6–26 mm; ± cylindrical and not enlarged at bases of capitula; stellate pubescent, with ± abundant glandular trichomes or without
Involucres	outer involucral bracts enclosing the florets	outer involucral bracts enclosing the florets	outer involucral bracts rarely enclosing the florets
Cypselae	0.9–1.1 × 0.4–0.5 mm; reddish brown ribs; apex with an inner ring of short teeth, as long as the outer (i.e., the prolongation of the ribs)	1.1–1.7 × 0.4–0.6 mm; usually whitish ribs; apex with an inner ring of short teeth ± equal to or slightly exceeding the outer (i.e., the prolongation of the ribs)	0.9–1.6 × 0.4–0.5 mm; reddish brown ribs; apex with an inner ring of teeth much shorter than the outer (i.e., the prolongation of the ribs, very pronounced)

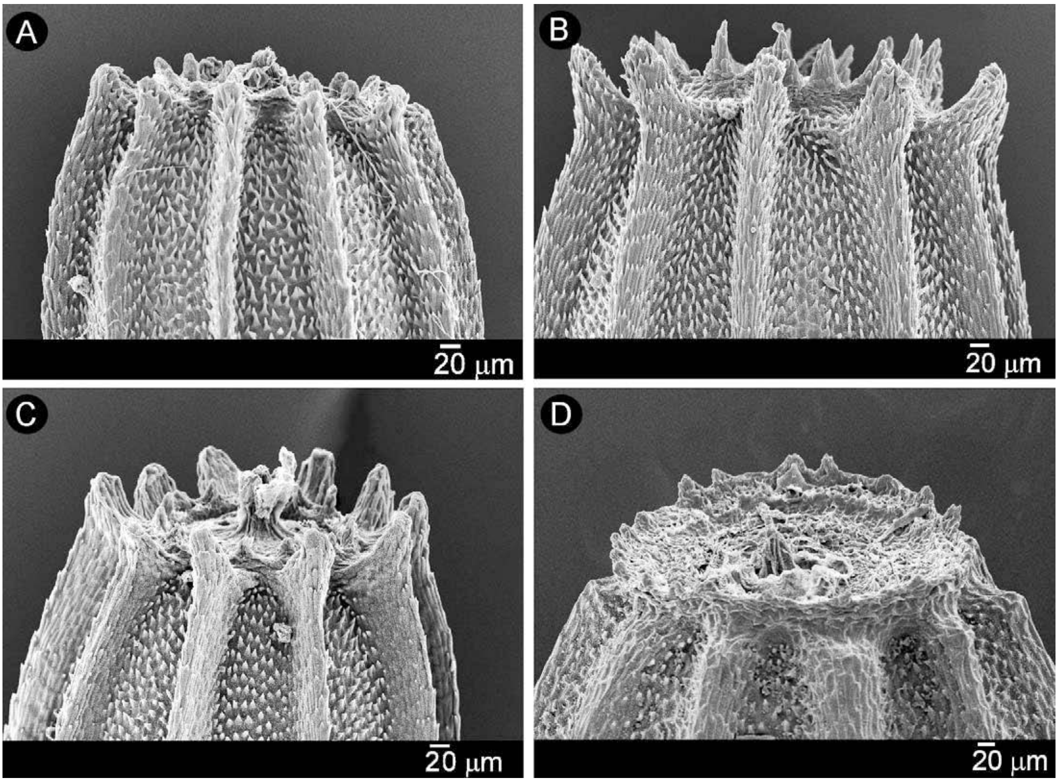

Figure 5. Apex of cypselae. —A. *Andryala perezii* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq., taken from J. A. Reyes-Betancort (TFC-37826). —B. *Andryala glandulosa* Lam., from *Z. Ferreira, M. Sequeira & A. Pupo Correia MA-801899.* —C. *Andryala pinnatifida* Aiton subsp. *preauxiana* (Sch. Bip.) G. Kunkel from the Canary Islands, taken from *C. Suárez & G. Rodríguez* (TFC-31801). —D. *Andryala pinnatifida* Aiton subsp. *mogadorensis* (Hook. f.) Greuter from North Africa, taken from *Z. Ferreira & I. Á. Fernández* (MA-870318).

specimens from Lanzarote and Tenerife referred by Schultz Bipontinus belong to two different taxa. The specimens corresponding to the Schultz Bipontinus publication were located at the Paris (P) and Florence (FI) herbaria. They are FI-W109935, FI-W109928, and P-02462105, and their observation supports the recognition of two distinct taxonomic entities. The specimens FI-W109928 and FI-W109935, both from Lanzarote, were identified originally as "*Andryala cheiranthifolia* var.?" and only the first includes a note by Schultz Bipontinus: "*A. pinnatifida* f. *buchiana* C. H. Schultz. Bip." In 2005, Santos-Guerra annotated on the herbarium sheet FI-W109935 "*Andryala pinnatifida* Ait. f. *buchiana* typus." Apparently he ignored the existence of P-02462105, the specimen from Tenerife that was clearly identified as *A. pinnatifida* f. *buchiana* by Schultz Bipontinus himself. Furthermore, all information on the herbarium label is in conformity with the one in the protologue, including the collector number, which means that P-02462105, having no other name associated with it, is to be considered the lectotype of *A. pinnatifida* f. *buchiana*. Thus, herbarium material (FI-W109928 and FI-W109935), as well as earlier literature, support specimens from Lanzarote as taxonomically concordant with *A. perezii*, here excluded from *A. pinnatifida* f. *buchiana*. Later the plants from Lanzarote, corresponding to the application of the name *A. glandulosa* to the east Canarian plants, were recognized as *A. pinnatifida* subsp. *buchiana* (Greuter & von Raab-Straube, 2009), but no lectotype was designated. Moreover, Santos-Guerra and Reyes-Betancort, when publishing *A. pinnatifida* subsp. *buchiana* as a transfer in rank from form to subspecies, did not mention that the taxon originally included elements from both Tenerife and Lanzarote. Given the confusion attached to the name *A. pinnatifida* f. *buchiana* and to the respective protologue (indeed, three descriptions in total), and taking into account the morphological differences between the specimens from Tenerife and Lanzarote, we have chosen to recognize the eastern Canary plants (from Lanzarote and Fuerteventura) as a new species with a new type, *A. perezii* M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq.

The description of the Tenerife plants by Schultz Bipontinus and the specimen (P-02462105) better match *Andryala pinnatifida* f. *cuneifolia*. The later described *A. pinnatifida* var. *latifolia* clearly corresponds to the previously described taxon, hereby recognized at the rank of subspecies.

2. Andryala pinnatifida Aiton, Hort. Kew. [W. Aiton] 3:129. 1789. TYPE: Spain. Canary Islands, Tenerife, 1778, *Fr. Masson* (lectotype, designated here, BM000753022).

2a. Andryala pinnatifida Aiton subsp. **cuneifolia** (Sch. Bip.) M. Z. Ferreira, R. Jardim, Alv. Fern. & M. Seq. stat. nov. Basionym: *Andryala pinnatifida* Aiton f. *cuneifolia* Sch. Bip., Hist. Nat. Iles Canaries (Phytogr.). 2: 417. 1849. TYPE: Spain. El Hierro, Monte Savinosa, 18 June 1845, *Bourgeau n°. 9* (lectotype, designated here, P02462115).

Andryala pinnatifida Aiton f. *buchiana* Sch. Bip. Hist. Nat. Iles Canaries (Phytogr.). 2: 415. 1849. TYPE: Spain, Canary Islands, Tenerife: contre les rochers élevésde las Mercedes, 9 June 1846, *Bourgeau, n° 7* (lectotype, designated here, P02462105).

Andryala pinnatifida Aiton subsp. *latifolia* (Bornm.) G. Kunkel in Vieraea 8: 344. 1980, syn. nov. Basionym: *Andryala pinnatifida* Aiton var. *latifolia* Bornm., Bot. Jahrb. Syst. 33: 489. 1904. TYPE: Spain. Canary Islands, Tenerife: Cumbre de Anaga, 27 June 1901, *Bornmüller, n°. 863* (lectotype, designated here, P02462137; isolectotype, JE00013921).

Further, the publication of a new species name is strongly supported by the fact that *Andryala perezii* differs remarkably from the Madeiran *A. glandulosa* (e.g., indumentum, leaf margins, peduncle shape, and cypsela size), as well as from the Canarian *A. pinnatifida* taxa (e.g., indumentum, leaf margins, involucre shape, and cypsela apex). Table 1 summarizes the diagnostic characters of *A. perezii* versus *A. glandulosa* and the Canarian *A. pinnatifida*. The new species is also notably distinct from the North African *A. pinnatifida* taxa, namely with regard to leaf margin, involucre indumentum, involucre bract margin, and apex of cypsela, the latter being an important diagnostic feature within the genus *Andryala*. In all North African *A. pinnatifida* subspecies, the cypsela apex is quite distinct compared to that in *A. perezii*, *A. glandulosa*, and *A. pinnatifida* from the Canary Islands. *Andryala pinnatifida* subsp. *mogadorensis* (Hook. f.) Greuter is presented as an example: the ribs at the apex of the cypsela are not extended, and the inner ring of teeth is larger in diameter (Fig. 5).

KEY TO THE MACARONESIAN SPECIES OF *ANDRYALA*

1a. Cauline leaves crowded, deeply pinnatisect; all flowers with ligule teeth stellate pubescent .... *A. crithmifolia*
1b. Cauline leaves entire to pinnatisect (if pinnatisect, never crowded); ligule teeth not stellate pubescent, seldom a few flowers scarcely so. .... 2.

2a. Leaves usually more stellate pubescent abaxially, cypsela apical ring with teeth much shorter than the prolongation of the ribs .... *A. pinnatifida*
2b. Leaves equally stellate pubescent on both faces, cypsela apical ring with teeth ± equaling or exceeding the prolongation of the ribs.. 3.
3a. Involucral bracts subulate, receptacular trichomes not longer than the cypsela, cypsela apical ring with teeth largely exceeding the prolongation of the ribs .... *A. laxiflora*
3b. Involucral bracts acute to acuminate or seldom subulate, receptacular trichomes longer than the cypsela, cypsela apical ring with teeth ± equaling or slightly exceeding the prolongation of the ribs... 4.
4a. Therophyte to hemicryptophyte plants; involucral bracts flat, not enfolding a floret... *A. integrifolia*
4b. Chamaephyte or seldom hemicritophyte plants; external involucral bracts involute, enfolding a floret. .... 5.
5a. Stems stellate tomentose and glandular pubescent at least in the upper part, uppermost leaves glandular pubescent and sometimes stellate tomentose; peduncles cylindrical and not enlarged at the base of the capitula, densely glandular pubescent .... *A. glandulosa*
5b. Stems densely stellate tomentose but not glandular pubescent, all leaves stellate tomentose but not glandular pubescent; peduncles somewhat flattened and enlarged at the base of the capitula, with a few glandular trichomes .... *A. perezii*

Key to the Macaronesian *Andryala pinnatifida* Subspecies

1a. Plants without glandular trichomes; stems up to 90 cm; cauline leaves pinnatisect (with linear segments) to linear pinnatifid-dentate; capitula arranged in racemes .... *A. pinnatifida* subsp. *teydensis*
1b. Plants usually with glandular trichomes; stems up to 75 cm; cauline leaves pinnatipartite to dentate with broader, never linear segments; capitula arranged in racemes or corymbs .... 2.
2a. Stems stellate tomentose to densely stellate tomentose below; leaves lanceolate to ellipitic-lanceolate; inflorescence usually corymbose-racemose, sometimes racemose; peduncles without glandular trichomes or with glandular trichomes 0.3–1.5 mm long .... 3.
2b. Stems usually stellate puberulous to finely stellate tomentose below; leaves obovate, obovate-cuneate to subcuneate, or elliptic; inflorescence corymbose; peduncles always with glandular trichomes 1–2.8 mm long .... 4.
3a. Lower leaves narrow (2–3 cm wide), lanceolate, pinnatifid with entire lobes; peduncles 0.5–2 cm long .... *A. pinnatifida* subsp. *pinnatifida*
3b. Lower leaves broad (3–6 cm wide), lanceolate or elliptic-lanceolate, pinnatifid to pinnatipartite with divided lobes; peduncles 0.8–3 cm long .... *A. pinnatifida* subsp. *preauxiana*
4a. Stems sometimes purplish; leaves not crowded, obovate or elliptic, dentate, abaxial surface stellate tomentose .... *A. pinnatifida* Aiton subsp. *webbii* (Sch. Bip. ex Christ) G. Kunkel
4b. Stems never purplish; leaves crowded, obovate-cuneate to subcuneate, sinuate to sinuate-dentate, abaxial surface stellate lanate .... *A. pinnatifida* subsp. *cuneifolia*

Paratypes. SPAIN [CANARY ISLANDS]. **Fuerteventura:** Pico del Fraile, 24 July 1979, *A. Banãres* (TFC-21147). **Lanzarote:** Risco de Famara, 25 Mar. 1975, *J. R. Acebes & P. L. Pérez de Paz* (TFMC-1770); Risco de las Nieves, 19 Jan. 1983, *M. del Arco Aguilar, P. L. Pérez de Paz & W. Wildpret de la Torre* (TFC-28870); Teguise, casas de Famara, 4 Apr. 2006, *C. Aedo, L. Medina & A. Quintanar*, CA12532 (MA-750660); Haría, riscos de Famara, penas de Chache, 3 Apr. 2006, *C. Aedo, L. Medina & A. Quintanar*, CA12417 (MA-751304); San Bartolomé, Monte Medina, 7 Apr. 2006, *C. Aedo, L. Medina & A. Quintanar*, AQ1846 (MA-750866); Montanã Blanca, 31 Mar. 1994, *J. A. Reyes-Betancort* (TFC-37826).

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9.3 Appendix 3: Notes on North African *Andryala* L. (Asteraceae): a new combination and typifications – paper published in *Acta Botánica Malacitana*, 2014.

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CONTRIBUCIONES A LA FLORA VASCULAR DE MARRUECOS

(21-22)

21. NOTES ON NORTH AFRICAN *ANDRYALA* L. (ASTERACEAE): A NEW COMBINATION AND TYPIFICATIONS

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Notas sobre Andryala L. (Asteraceae) en el Norte de África: una nueva combinación y tipificaciones

Key words. *Andryala*, Cichorieae, Compositae, Morocco, nomenclature, taxonomy, typification.

Palabras clave. *Andryala*, Cichorieae, Compositae, Marruecos, nomenclatura, taxonomía, tipificación.

According to present knowledge and taxonomic concept, the genus *Andryala* comprises about 16 species distributed in the Mediterranean Basin and Macaronesia (one endemic species occurs in the Eastern Carpathians), which main centres of diversity are located in NW Africa, Iberian Peninsula, and in the Canary Islands. This genus includes both morphologically homogeneous species distributed in small geographical areas [glacial relicts; *A. agardhii* DC. and *A. laevitomentosa* (Nyár. ex Sennikov) P.D. Sell ex Greuter] and highly variable species (or species complexes if the more splitting approach is adopted) widely distributed. The most remarkable representatives of the latter group are *A. integrifolia* (Western and Central part of Mediterranean Basin, introduced to Macaronesia) and NW Africa in hitherto accepted classification). Infraspecific classification of *A. pinnatifida* has been a matter of debate for a long time and several taxonomic concepts were proposed, the latest by Greuter (2003) and Arechavaleta *et al.* (2010). Greuter (2003) recognized four subspecies of *A. pinnatifida* in NW Africa, namely, *A. pinnatifida* subsp. *ducellieri* (Batt.) Greuter, *A. pinnatifida* subsp. *jahandiezii* (Maire) Greuter, *A. pinnatifida* subsp. *maroccana*

(Maire) Greuter and *A. pinnatifida* subsp. *mogadorensis* (Hook.f.) Greuter. Noteworthy is an additional NW African putative *A. pinnatifida*. Originally described as *A. antonii* Maire (Maire, 1927), this taxon was later combined as *A. canariensis* subsp. *antonii* (Maire) Maire in Jahandiez & Maire (1934) and, more recently, as *A. pinnatifida* subsp. *antonii* (Maire) Dobignard (Greuter & von Raab-Straube, 2007). Nonetheless, given the morphological differences (e.g. stems slender; leaves narrow ± dentate or slightly lobed, lower cauline leaves narrow lanceolate, attenuate at the base into a short petiole, upper ones linear and entire, cypsela with excurrent ribs at the apex and a inner ring of short teeth), it is herein excluded from *A. pinnatifida*. Being morphologically similar to *A. integrifolia* L., it should instead be included in this species. In the Canary Islands *Andryala pinnatifida* is a big complex, including about five subspecies which are more or less traditionally recognized (Kunkel, 1980; Arechavaleta *et al.*, 2010; Ferreira *et al*, 2014).

The lack of agreement among various authors prompted us to re-examine the variation in *A. pinnatifida* s. lat. in detail, especially focused on Canarian and African plants. Consequently, here we propose a new taxonomic concept for *A. pinnatifida*, restricting it to the Canary Islands. Additionally, lectotypes for all synonyms of *Andryala mogadorensis* Coss. ex Hook.f. are designated.

1. *Andryala mogadorensis* Coss. ex Hook.f. in Bot. Mag. 99: t. 6010. 1873 [January]

≡ *Andryala canariensis* Lowe subsp. *mogadorensis* (Coss. ex Hook.f.) Maire *in* Bull. Soc. Hist. Nat. Afrique N. 19: 59. 1928

≡ *Andryala pinnatifida* Aiton subsp. *mogadorensis* (Coss. ex Hook.f.) Greuter *in* Willdenowia 33(2): 232. 2003

Ind. loc.: "…on a little rocky islet in the bay of Mogadore, on the Western Marocco Coast, in lat. 31 10/2 N, and has hitherto been found nowhere else. It was discovered by Balansa in 1868, and gathered by Messrs. Maw, Ball, and myself there in May, 1871. Mr. Maw was so fortunate as to transit a living plant to this garden at Benthal Hall, Broseley, which flowered in the following April, and is here figured."

Typus: Morocco, "*Isle de Mogador*", B. Balansa, 25-04-1867 [**lectotype, designated here,** K000251901!; syntypes: P02462215! (specimen on the right), P02462221!, BM000949980!]

1a. *Andryala mogadorensis* Coss. ex Hook.f. subsp. *mogadorensis*

= *Andryala mogadorensis* Coss. et Bal. ex Cosson *in* Bull. Soc. Bot. France. 20: 252. 1873 [November]

Ind. loc.: "In maritimis insulae Mogador detexit cl. Balansa. 25 April. 1867 florifera et fructifera lecta."

Typus: *Andryala mogadorensis* sp. nov. (Coss.). Ile de Mogador. 25 avril. B. Balansa, pl. du Maroc, 1867 [**lectotype, designated here,** P02462219! ex herb. Cosson; isolectotypes: P02462218! ex herb. Cosson, P02462215! (specimen on the left) ex herb. Cosson]

= *Andryala ducellieri* Batt. *in* Bull. Soc. Hist. Nat. Afrique N. 9: 120. 1918. basion.

Andryala canariensis Lowe subsp. *ducellieri* (Batt.) Maire *in* Jahandiez & Maire, Cat. Pl. Maroc. 3: 840. 1934

Andryala pinnatifida Aiton subsp. *ducellieri* (Batt.) Greuter *in* Willdenowia 33(2): 232. 2003

Ind. loc.: "… sur les falaises de Safi par M. Ducellier" [Battandier, 1918]

Typus: [Morocco], Falaises de Safi, Ducellier [**lectotype, designated here,** MPU020221 (specimen on the left); isolectotype MPU020221 (specimen on the right); syntype MPU020220]

= *Andryala canariensis* Lowe subsp. *maroccana* Maire *in* Bull. Soc. Hist. Nat. Afrique N. 19: 58. 1928.

Andryala pinnatifida Aiton subsp.

maroccana Maire *in* Mém. Soc. Sci. Nat. Maroc. 8 (1): 239. 1924, nom. nud.

Andryala pinnatifida Aiton subsp. *maroccana* (Maire) Greuter *in* Willdenowia 33: 232. 2003

Ind. loc.: "Hab. in arenosis litoris nec non in collibus aridis Imperii Maroccani austro-occidentalis, ubi a martio usque ad aestatem floret: in arenis prope Mogador copiosissime crescit." [Maire, 1928]

Typus: [Morocco], Dunes de Mogador, Jahandiez E., nº 368, 6-4-1920 (**lectotype, designated here,** MPU001913; syntypes MPU001906, MPU001907, MPU001909, MPU001910, MPU001911, MPU001912)

= *Andryala mogadorensis* Coss. et Bal. ex Cosson. f. *sinuatifolia* H. Lindb., Itin. Mediterr. (Act. Soc. Sc. Fenn. n. s. B, i. No. 2) 152. 1932

Andryala canariensis Lowe subsp. *mogadorensis* Coss. et Bal. ex Cosson f. *sinuatifolia* (H. Lindb.) Maire in Jahandiez & Maire, Cat. Pl. Maroc. 3: 840. 1934

Ind. loc.: "Mogador loco sterili in Insula Magna"

Typus: Morocco, occ., prope opp. Mogador, in sterilibus in Insula Magna, Harald Lindberg 2012, 11 May 1926 (H-1451919), designated by Väre in Phytotaxa 47: 15. 2012.

Andryala mogadorensis Coss. ex Hook.f. was validly published by Joseph Dalton Hooker in January of 1873. In the protologue several types were mentioned, including specimens from Balansa (1867). This material was found at the K, P and GOET herbaria and corresponds to specimens gathered in 25 April 1867 and labeled by Balansa himself as "*Andryala Mogadorensis sp. nov. (Coss.)*". Apparently, the name is of Cosson's authority, but in fact it was Hooker who first described the species. Hooker was one of the Directors of the Royal Botanic Gardens, Kew, hence it is more likely that the original description was based on Balansa's specimen at K herbarium than the ones deposited in P herbarium. Thus, the specimen from K herbarium was selected as the lectotype. Hooker (1873) restricted *A. mogadorensis* to the rocky islet in the bay of Mogador (city on the western coast of Morocco which is currently known as Essaouira). Therefore, all the type specimens selected were collected on this Moroccan island. The specimen P02462215, collected by Ball in April 1871, might be a syntype, although the collection date (27 April 1871) does not exactly match with the one in the protologue (May, 1871). Months later, in November of 1873 Ernest Cosson published several new species for Morocco, including "*Andryala mogadorensis* Coss. et Bal.". It appears that Cosson (1873) described this species based on specimens of *A. mogadorensis* also from Balansa, according to the indication given in the protologue "Bal. pl. Mar. (1867)" and the authority of the name. The description was based on specimens deposited in the Paris herbarium ex Cosson and labeled "B. Balansa, Pl. du Maroc, 1867" [P02462219, P02462218 and P02462215]. The specimen P02462219 was chosen as lectotype since it is the one that best fits the original description. However, *A. mogadorensis* Coss. et Bal. is an illegitimate name, because it is a later homonym. Maire (1928) considered *A. mogadorensis* at a subspecies level, designating it as *Andryala canariensis* subsp. *mogadorensis* (Coss. ex Hook. f.) Maire. Thus, Maire (1928) adopted the name *Andryala canariensis* suggested by Lowe (1872: 564) for the Canarian *Andryala pinnatifida* Aiton. More recently, Greuter (2003) presented a new combination, *Andryala pinnatifida* subsp. *mogadorensis* (Coss. ex Hook. f.) Greuter, in order to restore the earliest validly published name, but no typification was proposed.

Battandier (1918) described *Andryala ducellieri* Batt. as a Moroccan botanical novelty, underlining that this *Andryala* was collected at the cliffs of Safi by M. Ducellier. Indeed three specimens collected by Ducellier in Safi were located at MPU herbarium, all of them including a printed version of the protologue. Although all bear original labels with the name *Andryala mogadorensis,* these specimens were later identified as *Andryala ducellieri* Batt. On the label of the herbarium sheet MPU020221 we can read "*Andryala Ducellieri species nova, Safi*" and since there are two specimens on the same sheet, the one on the left which is the best conserved, is here designated as lectotype. The labels on the specimens MPU020221 and MPU020220 by P. A. Schäfer, indicate the first as the holotype and the second as an isotype, but since no type designation was included in the protologue, a lectotype must be designated. In the protologue, Battandier (1918) noted the resemblance of the new species to *A. mogadorensis* ("*Par ses ligules et ses achaines, il se rapproche de l´A. Mogadorensis Cosson.*") and emphasized the morphological characters which differentiate it from *A. mogadorensis* ("*Il s'en distingue par sa couleur blanchâtre, par ses feuilles moins larges et non arrondies, obtuses au sommet, par ses inflorescences longuement hispides ainsi que les pédicelles et les capitules hérissés de poils blancs ou un peu jaunâtres, jamais noirs.*"). Actually, these morphological differences are observable on the lectotype here designated. Several years before, Ball (1878) referred to *A. mogadorensis* plants growing along the coastline from the city Safi southwards, and distinguished them from the ones found on the Island of Mogador by their narrower, oblong and subsinuate leaves. A specimen collected by Ball in 1871 on the coastline near Safi is kept at Kew herbarium (K000251902). It was originally identified as *Andryala mogadorensis* Coss. var. *intermedia*, name that was never published, and indeed it corresponds to *A. ducellieri* Batt., herein included in *A. mogadorensis* Coss. ex Hook.f. In the publication by Jahandiez & Maire (1934), Maire transferred *A. ducellieri* to a subspecies rank under the name *A. canariensis* subsp. *ducellieri* (Batt.) Maire, and later Greuter (2003) made a new combination: *A. pinnatifida* subsp. *ducellieri* (Batt.) Greuter, but no typifications were suggested. *Andryala pinnatifida* subsp. *ducellieri* is herein synonymized to *A. mogadorensis* subsp. *mogadorensis* since both are perennials exhibiting robust stems, covered with a dense whitish-lanate stellate indumentum, with long glandular hairs, especially in the upper part and inflorescence; crowded leaves, the lower ones petiolate, cauline semi-amplexicaul to amplexicaule, cordate or auriculate at the base, rounded or acute-obtuse at the apex; leafy inflorescences; densely glandular-hairy involucres, and receptacle bearing long setose hairs.

Braun-Blanquet & Maire (1924) cited *A. pinnatifida* subsp. *maroccana* Maire for the first time, confining it to "*Dunes de Mogador dans le Retametum*", but no description was provided, which makes it an invalid name. Maire (1928) validly published the new taxon under the name *A. canariensis* subsp. *maroccana* Maire, stressing that it is found abundantly on dunes near Mogador. In the protologue Maire indicated where the type specimens were deposited: "Typus in Herb. Univers. Algerensis". Since all specimens from this herbarium were transferred to the P and MPU herbaria and Maire (op.cit.) did not mention a specific specimen as holotype, a lectotype was designated among the original material located in MPU. All the type specimens mentioned above belonged initially to the herbarium of the University of Algiers and most are labelled "*Andryala pinnatifida* Ait. ssp. *maroccana* Maire" and accompanied by a printed copy of the protologue. Furthermore, all were collected from the dunes of Mogador (Essaouira), except for the specimen MPU001907 which is from the dunes near Diabet (town to the south of Essaouira). Maire (1928) distinguished *A. canariensis* subsp. *maroccana* Maire from *A. canariensis* subsp. *mogadorensis* based on leaf characters ("*foliis plus minusve pinnatifidis apice acutiusculis*") and further stated that *A.*

canariensis subsp. *maroccana* corresponds to a plant incorrectly cited by Ball (1878) as *A. ragusina* L. var. *lyrata* (Pourr.) DC. Indeed, Ball (1878) identified a specimen collected in the vicinity of Mogador based on leaf characters ("*Folia in spec. nostris pinnatifida lobis oblongis obtusis.*") as *A. ragusina* var. *lyrata.* Since this plant was not yet in anthesis, Ball (1878) revealed some uncertainty about its true identity and stressed that it could eventually correspond to the very polymorphic Macaronesian species, *A. pinnatifida* Aiton. Ball (op. cit.) highlighted that the specimen in question was deposited at Kew herbarium, but unfortunately it was not found. However, there is no current evidence of the presence of *A. ragusina* near Mogador and the specimen could indeed correspond to *A. mogadorensis* subsp. *maroccana* taking into account the geographic distribution. Later, Greuter (2003) combined *A. canariensis* subsp. *maroccana* as *A. pinnatifida* subsp. *maroccana* (Maire) Greuter, here synonymized to *A. mogadorensis* subsp. *mogadorensis* since it resembles this taxon in all morphological features, except for the leaf margin (the lower and cauline leaves are more or less pinnatifid, instead of entire or sinuate-dentate).

1b. *Andryala mogadorensis* Coss. ex Hook.f. subsp. *jahandiezii* (Maire) M.Z.Ferreira, Álv.Fern. & M.Seq., comb. nov.

≡ *Andryala jahandiezii* Maire *in* Mem. Soc. Sc. Nat. Maroc, 15: 46. 1927. basion.

≡ *Andryala canariensis* Lowe subsp. *jahandiezii* (Maire) Maire *in* Jahandiez & Maire, Cat. Pl. Maroc, 3: 840. 1934

≡ *Andryala pinnatifida* Aiton subsp. *jahandiezii* (Maire) Greuter *in* Willdenowia 33: 232. 2003

Ind. loc.: "In planitiebus arenosis inter flumina Sous et Massa (Maire, 1922)."

Typus: [Morocco], Sous, plaines sabloneuses entre l'Oued Sous et l'Oued Massa, Maire, 02-04-1922 (**lectotype, designated here,** P00710614!; isolectotypes RAB078016; MPU001815; syntypes MPU001816, MPU001817, P04277958!)

= *Andryala jahandiezii* Maire var. *microcarpa* Maire *in* Mem. Soc. Sc. Nat. Maroc, 15: 47. 1927

Ind. loc.: "In arenosis maritimis ad meridiem urbis Agadir-n-Ighir (Jahandiez, 1923; Maire, 1926)."

Typus: [Morocco], Agadir-n-Ighir, dunes, Jahandiez, nº 203, 28-04-1923 (**lectotype, designated here,** MPU001818; isolectotypes P02462208!, P04308378!).

In 1927 Maire described a species from the province of Sous in Morocco, *Andryala jahandiezii* Maire. The protologue includes information on the location of the type specimens: "*Typi in Herb. Univers. Algeriensis et in Herb. Inst. Imper. Scient. Rabatensis*". The specimens from the University of Algiers were incorporated in the P and MPU herbaria, where indeed some type specimens of *A. jahandiezii* Maire were found. The author recognized two varieties based upon the size of the cypselae: *A. jahandiezii* var. *typica* Maire, occurring on sandy shores between the rivers Sous and Massa, and *A. jahandiezii* var. *microcarpa* Maire, found on sandy maritime shores near the city of Agadir-n-Ighir. According to the protologue, specimens representing the typical variety were collected by Maire in 1922. Three herbarium sheets from different herbaria (MPU, P and RAB) with the same collection date and collector (Maire, 2-4-1922) were found. The specimen MPU001815 was labelled by Muriel Durand and Caroline Loupe as the holotype, but Maire (op. cit.) made no reference to a particular specimen in the protologue and there are two type specimens (MPU001814 and MPU001815) labelled as "*Andryala jahandiezii* n.sp.". Thus, the best conserved specimen (P00710614) is herein designated as the lectotype and the specimens MPU001815 and RAB078016 are considered as isolectotypes. In the protologue, Maire (1927) made reference to specimens of *A. jahandiezii* var. *microcarpa* collected by Jahandiez in 1923. Actually, the specimen MPU001818 is labeled "*Andryala jahandiezii* var. *microcarpa* n.sp." and was collected by Jahandiez on 24 April 1923, and therefore it was chosen as the lectotype. There are additional specimens (P02462208 and P04308378) collected by Jahandiez on the same day and locality, labeled "*Andryala mogadorensis* Cosson", for which reason these are herein considered as isolectotypes. In the protologue, Maire referred to specimens of *A. jahandiezii* var. *microcarpa* Maire collected by himself in 1926. These were located in the herbaria MPU and P (MPU001816, MPU001817 and P04277958) under the name *Andryala jahandiezii* Maire, but since they were collected in a different locality from the one mentioned in the protologue ("*In arenosis ad ostium fluminis Sous*", where the typical variety is found), they could be considered as syntypes of *A. jahandiezii* Maire. In the original description, Maire (1927) considered *A. jahandiezii* Maire morphologically close to *A. pinnatifida* subsp. *maroccana* (Maire) Greuter, differing in the habit, leaf margin and indumentum ("*habitu magis virgato, foliis integris nec lobatis, pilis glanduliferis parcissimis*"). Jahandiez & Maire (1934) transferred *A. jahandiezii* Maire to a subspecies rank under the name *A. canariensis* subsp. *jahandiezii* (Maire) Maire and later, Greuter (2003) presented a new combination: *A. pinnatifida* subsp. *jahandiezii* (Maire) Greuter. Indeed, this taxon is worthy of distinction at a subspecies level considering its morphological differences compared to *A. mogadorensis* subsp. *mogadorensis.* Besides, it is found in the Region of Souss-Massa-Drâa while the typical subspecies can be found northwards along the western coast of Morocco.

The Moroccan taxa herein included in *A. mogadorensis* Coss. ex Hook.f. were formerly recognized as North African subspecies of *A. pinnatifida* Aiton. However, these are

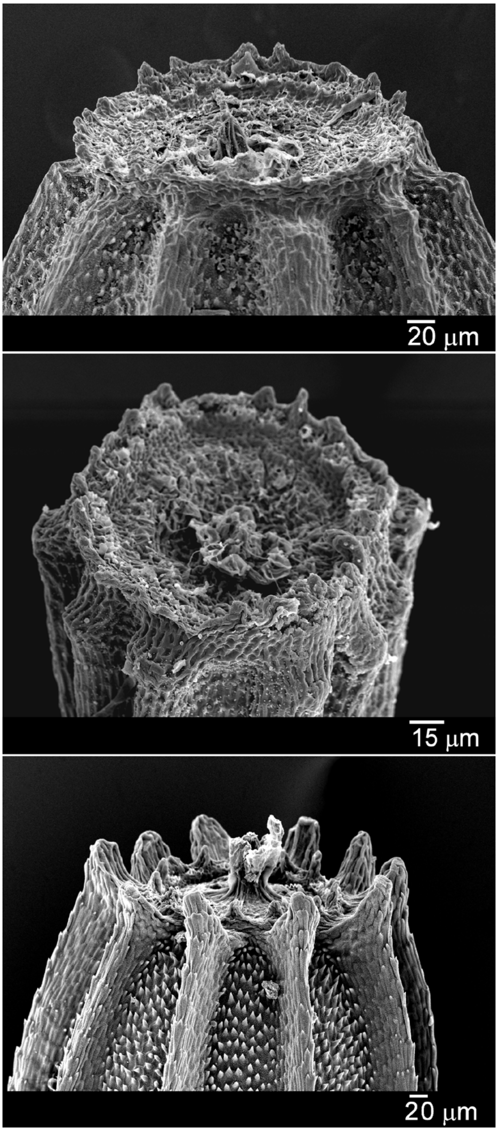

Figure 1. Apex of cypsela: A - *A. mogadorensis* subsp. *mogadorensis* (MA870318); B - *A. mogadorensis* subsp. *jahandiezii* (Maire) M.Z. Ferreira, Álv. Fern. & M. Seq. (P04308378, left specimen), © Muséum National d'Histoire Naturelle (MNHN) - Paris Herbarium (P); C - *A. pinnatifida* Aiton (TFC31801). *Ápice de la cipsela: A - A. mogadorensis subsp. mogadorensis (MA870318); B - A. mogadorensis subsp. jahandiezii (Maire) M.Z. Ferreira, Álv. Fern. & M.Seq. (P04308378, espécimen de la izquierda), © Muséum National d'Histoire Naturelle (MNHN) - Paris Herbarium (P); C - A. pinnatifida Aiton (TFC31801).*

morphologically distinct compared to *A. pinnatifida* Aiton from the Canary Islands (involucre indumentum, leave shape, cypselae apex). The cypsela morphology is very important in Asteraceae classification, mainly at the generic and specific level (Bremer, 1994). In effect, *A. mogadorensis* Coss. ex Hook.f. exhibits cypsela ribs scarcely excurrent at the apex, not exceeding the inner ring of teeth, while in the Canarian *A. pinnatifida* Aiton the cypsela ribs are very prominent at the apex, largely exceeding the inner ring of teeth (Fig. 1). Confusion arose when Ball (1878) cited *A. ragusina* var. *lyrata* (Pourr.) DC. for western Morocco, not discarding, however, a possible correspondence of this taxon to *A. pinnatifida* Aiton. This view was adopted by later authors and the error persisted until now since no effective morphological comparison with *A. pinnatifida* Aiton from the Canary Islands was ever made. For instance, in Jahandiez & Maire (1934), Maire included *A. mogadorensis* Coss. ex Hook.f., *A. pinnatifida* subsp. *maroccana* Maire (nom. nudum., as stated by the author), *A. jahandiezii* Maire and *A. ducellieri* Batt. in *A. canariensis* as subspecies, but did not justify this taxonomic placement based on morphological features. A similar situation occurred with the *Andryala* taxa from Madeira. Aiton (1789) erroneously considered a variety of *A. pinnatifida* Aiton for Madeira. Lowe (1872), a naturalist who extensively studied the Madeiran flora, stressed that so much confusion is attached to the name *A. pinnatifida* that the adoption of a new name for the Canarian taxa (*Andryala canariensis*) would be warrantable.

In view of the foregoing, *A. pinnatifida* Aiton should be restricted to the Canary Islands and the North African taxa addressed in this paper [except for *A. pinnatifida* subsp. *antonii* (Maire) Dobignard] should be included in *A. mogadorensis* Coss. ex Hook.f.

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22. NUEVO NOMBRE EN *RHODANTHEMUM* (COMPOSITAE, ANTHEMIDEAE).

Francisco GÓMIZ GARCÍA

Recibido el 26 de mayo de 2014, acetado para su publicación el 30 de junio de 2014

New name in Rhodanthemum (Compositae, Anthemideae).

Palabras clave. *Rhodanthemum redieri* subsp. *soriae, Leucanthemum redieri* var. *cuneatum*, Flora, Taxonomía, Marruecos, Norte de África

Key words. *Rhodanthemum redieri* subsp. *soriae, Leucanthemum redieri* var. *cuneatum*, Flora, Taxonomy, Morocco, North Africa.

Rhodanthemum (Vogt) Wilcox, Bremer & Humphries*,* es un género perteneciente a la tribu *Anthemideae*, subtribu *Leucantheminae*, (*Compositae*), cuyo área de distribución se extiende por el norte de África (Argelia y Marruecos) y el sudoeste de Europa (España) (Bremer & Humphries, 1993) (Oberprieler, Himmelreich & Vogt, 2007).

En Marruecos está representado por una docena de especies endémicas, más otras dos de distribución argelino-marroquí y una más hispano-marroquí (Ibn Tattou & Fennane,

9.4 Appendix 4: Lectotypification of ten *taxa* in *Andryala* L. (Asteraceae) – paper published in *Taxon*, 2015.

Lectotypification of ten taxa in *Andryala* (Asteraceae)

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Abstract In this paper ten names in *Andryala* are lectotypified. All are either accepted species or subspecies names in a forthcoming taxonomic revision of the genus.

Keywords *Andryala*; Compositae; Macaronesia; Mediterranean region; nomenclature; typification

■ INTRODUCTION

The genus *Andryala* L. (Asteraceae: Cichorieae) comprises about 17 species distributed in the Mediterranean region (with centers of diversity in the Iberian Peninsula and North Africa), Macaronesia, and Romania, where it is represented by a single relict endemic. Although validly published in 1754, it is a poorly known genus. Indeed there are some taxonomic studies circumscribing species from particular regions (e.g., Murbeck, 1905; Jahandiez & Maire, 1934; Coutinho, 1939; Sell, 1976; Talavera, 1987; Blanca, 2009, 2011), but no comprehensive revision of *Andryala* is yet available. Since earlier protologues do not provide descriptions to characterize the different taxa adequately, the study of original material is critical in determining the correct application of names. There are a few papers specifically dealing with typification of names in *Andryala* or at least containing some lectotypifications (Burdet & al., 1983; Jarvis & al., 1993: 18; Jarvis & Turland, 1998; Aghababyan & al., 2008; Ferreira & al., 2014a, b). However, during analysis of herbarium material and a careful study of the literature it was apparent that some names had never been typified.

■ MATERIALS AND METHODS

Protologues of all typified names were examined and original material was located. Important information and digital specimen images, provided by staff from several herbaria (BC, BM, FI, G, HBG, JE, M, MA, MPU, NAP, P, PAL, W, WAG) upon request, were analysed. Specimens from BM and P were observed in person. Some type specimens were located in online databases (e.g., JSTOR Global Plants, http://plants.jstor.org/) and virtual herbaria. In order to enhance nomenclatural stability, and based on our comprehensive taxonomic research, we here propose lectotypes for all currently used names applying to taxa that we accept at specific or subspecific level, except those previously lectotypified (i.e., *A. integrifolia* L., *A. ragusina* L., *A. agardhii* DC., *A. laevitomentosa* (Nyár. ex Sennikov) Greuter, *A. mogadorensis* Coss. ex Hook.f., *A. mogadorensis* subsp. *jahandiezii* (Maire) M.Z.Ferreira & al., *A. perezii* M.Z.Ferreira & al., *A. pinnatifida* Aiton, *A. pinnatifida* subsp. *cuneifolia* (Sch.Bip.) M.Z.Ferreira & al.) and the names for which our current information or the available original material is insufficient. The entries are arranged alphabetically.

■ TYPIFICATIONS

Andryala arenaria (DC.) Boiss. & Reut., Pugill. Pl. Afr. Bor. Hispan.: 71. 1852 ≡ *A. tenuifolia* var. *arenaria* DC., Prodr. 7: 245. 1838 ≡ *A. parviflora* var. *arenaria* (DC.) Boiss., Voy. Bot. Espagne: 394. 1841 ≡ *A. integrifolia* var. *arenaria* (DC.) Ball. in J. Linn. Soc., Bot. 8(93): 541. 1878 ≡ *A. dentata* subsp. *arenaria* (DC.) Nyman, Consp. Fl. Eur.: 438. 1879 – **Lectotype (designated here):** [Spain]. In arenis maritimis Gibraltario, 1838, *Edm. Boissier s.n.* (G-DC barcode G00319814 [digital image!]).

The specimen here designated as lectotype was most surely the basis of the original description of *A. tenuifolia* var. *arenaria* by Candolle (1838) as the collector and collection locality coincide with those in the protologue. According to Stafleu & Cowan (1976) the herbarium and types of Boissier are kept at G herbarium. This botanist was one of Candolle's pupils at the school of systematic botany in Geneva who greatly contributed to the *Prodromus* (Sigrist & Bungener, 2008) in which *A. tenuifolia* var. *arenaria* was described. Boissier made his first botanical trip to southern Spain in 1837 and some of the Asteraceae material collected by him constituted the basis of certain descriptions in this work (González Bueno, 2010). Boissier spent the last days of 1837 and the first months of 1838, studying his Spanish collections (González Bueno, 2010). The specimen here designated as lectotype was originally identified as "*Andryala arenaria*" (accompanied by the information:

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"*affinis Andr. tenuifolia DC.*"). In what seems to be a later label, handwritten by Candolle, a new determination was added: "*Andryala tenuifolia* γ *arenaria* DC."

Andryala chevallieri Barratte ex L.Chevall. in Mém. Herb. Boissier 1900 (Mém. 7): 10. 1900 – **Lectotype (designated here):** [Algeria]. Ain-Sefra, in agger. arenae mobilis, 29 May 1899, *L. Chevallier 341* (P barcode P03290615!; isolectotypes: HBG, JE, MA, P!, W, WAG [except P: digital images!]).

Among several candidates, the specimen here designated as lectotype is the best-developed one, clearly showing the habit of the plant. Several specimens from HBG, JE, MA, P, W, and WAG are isolectotypes given that Chevallier, the validating author, did not mention a particular specimen as holotype or the herbarium in which it was deposited.

Andryala cossyrensis Guss., Fl. Sicul. Syn. 2(1): 407. 1844 ≡ *A. sinuata* var. *cossyrensis* (Guss.) Arcang., Comp. Fl. Ital.: 447. 1882 ≡ *A. rothia* subsp. *cossyrensis* (Guss.) Maire in Emberger & Maire [Jahandiez], Cat. Pl. Maroc 4: 1167. 1941 – **Lectotype (designated here):** [Italy]. Isola Pantellaria, 1831, *M. Gussone s.n.* (G-DC barcode G00493395 [digital image!]).

Candolle (1838) described *Andryala tenuifolia* β *lyrata* Guss. ex DC. stating that Gussone saw the specimen but did not validly publish the name ["*A. tenuifolia* β *lyrata* (Guss.! in litt.")]. Later Gussone (1843) validly published *A. cossyrensis*, citing *A. tenuifolia* β *lyrata* Guss. ex DC. as a synonym. Given that Gussone merely transferred *A. tenuifolia* β *lyrata* to species rank, the lectotype should be chosen from herbarium material that was used as basis for the original description. Indeed, in the Candolle collection held at G there is a specimen under *Andryala tenuifolia* β *lyrata* DC., handwritten by Candolle, which fits the original description very well. Besides, the collector and collection locality match those in the protologue. Therefore, this specimen is here designated as lectotype.

Andryala crithmifolia Aiton, Hort. Kew. 3: 129. 1789 – **Lectotype (designated here):** [Portugal]. Madeira, 1776, *Fr. Masson s.n.* (BM barcode BM000829762!).

Aiton (1789) described several new species cultivated at the Royal Botanic Gardens, Kew, among them *A. crithmifolia*. According to the protologue, this species was introduced to the Royal Botanic Gardens in 1778. Aiton also mentioned Francis Masson as the collector for this species. Indeed, Masson was the first official plant collector of the Royal Botanic Gardens, Kew, who undertook extensive plant collecting on the Macaronesian archipelagos of Madeira, the Azores and the Canaries, between 1776 and 1779 (Francisco-Ortega & al., 2008). Furthermore, the specimens collected by Masson in Macaronesia, together with material grown from the introduced seeds, formed the basis for the description of many new species, mostly in the three volumes of the first edition of *Hortus kewensis* (Francisco-Ortega & al., 2008). Considering that the core of the herbarium specimens collected by Masson in Macaronesia is currently deposited at BM (Francisco-Ortega & al., 2008), the specimen BM000829762 is here designated as lectotype.

Andryala dentata Sm. in Sibthorp & Smith, Fl. Graec. Prodr. 2: 140. 1813 ≡ *A. sinuata* subsp. *dentata* (Sm.) Arcang., Comp. Fl. Ital.: 447. 1882 ≡ *A. rothii* subsp. *dentata* (Sm.) Pignatti in Giorn. Bot. Ital. 111: 57. 1977 – **Lectotype (designated here):** [Greece, Milos], *sine coll.* (OXF No. Sib-1944, specimen on the left [digital image!]; isolectotype: OXF No. Sib-1944, specimen on the right [digital image!]).

The illustration from *Flora graeca* (Sibthorp & Smith, 1837: pl. 811) referred to in the protologue could have been considered as the holotype if no type specimens were located. However, two specimens under the name "*Andryala dentata* nov. sp." (handwritten by Smith) can be found in the Sibthorpian Herbarium, deposited at the Fielding-Druce herbarium (hb. Sibthorp, OXF). Although the collector is not given, the herbarium sheet has a printed label indicating that they are from Sibthorp's collection. The collector could have been Sibthorp himself as he collected plants on two trips to the Mediterranean. Sibthorp died soon after the second trip and James Smith was appointed to continue Sibthorp's work (based on manuscripts, drawings and specimens from Sibthorp) and it was also this botanist who published *Flora graeca* and *Florae Graecae prodromus* (Stafleu & Cowan, 1985). *Andryala dentata* was validly published in the latter work. Therefore, it seems possible that the specimens from Sibthorp's collection correspond to original material. The specimen on the left represents *A. dentata* fairly well and is here designated as lectotype.

Andryala glandulosa Lam., Encycl. 1: 154. 1783 – **Lectotype (designated here):** [Portugal, Madeira] *Andryala glandulosa* H. R. P. Delamarck Diction., *sine coll.* (P barcode P03772030!).

Lamarck (1783) described *A. glandulosa* based on material cultivated at Jardin du Roi in Paris. There is only one specimen in Lamarck's herbarium under *Andryala glandulosa*, but it does not fit the original description very well and no date is included. Nonetheless, we found a specimen in P, originally from the collection of Poiret—who was one of Lamarck's collaborators—that matches the original description perfectly. This material includes the name *Andryala glandulosa* handwritten by Lamarck, and the letters: "H. R. P." (Hortus Regius Parisiensis), which means a plant cultivated at Jardin du Roi, just as mentioned in the protologue. This specimen is therefore here selected as lectotype.

Andryala maroccana (Caball.) Maire in Bull. Soc. Hist. Nat. Afrique N. 13(6): 218. 1922 ≡ *Paua maroccana* Caball. in Bol. Soc. Esp. Hist. Nat. 16: 541. 1916 – **Lectotype (designated here):** [Morocco]. "Hab. - In arenosis maritimis - Calablanca", 6 Jun 1915, *Caballero s.n.* (BC barcode BC-36157 [digital image!]; isolectotype: BC [digital image!]).

On both the lectotype and isolectotype the collector, collection date, and locality match the ones in the protologue. The herbarium material filed as BC-36157 is here selected as lectotype because it is a complete specimen.

Andryala pinnatifida subsp. ***teydensis*** (Sch.Bip.) Rivas Mart. & al. in Itin. Geobot. 7: 350. 1993 ≡ *A. pinnatifida* f. *teydensis* Sch.Bip. in Webb & Berthelot, Hist. Nat. Iles Canaries 3(2,2): 416. 1849 – **Lectotype (designated here):** [Spain. Canary Islands], Teneriffa – las Cañadas del Teyde, 9 Sep 1845, *E. Bourgeau 3* (P barcode P02462114!; isolectotype: FI-W [digital image!]; syntypes: FI-W [digital image!], P!).

The specimen P02462114 is here selected as lectotype because the collector and number, date and locality correspond exactly to the information in the protologue. The label of herbarium sheet FI-W 109939 referring to the middle specimen shows exactly the same information, but is without collector (although mostly likely the collector was again E. Bourgeau). Moreover, even though this specimen is better preserved, it is partially covered by the specimen on the right and, therefore it is here considered as an isolectotype rather than lectotype. In the protologue another collection locality was mentioned: "Teneriffa, prope pagum *Chasna* in rupibus aridis ad austrum montis alti (*el Pico de Teyde*) ad alt. 4800 ped. circiter super Oceanum." Thus the specimen P02462171, exhibiting precisely this information on the label, can be considered as a syntype. As the specimen FI-W 109939 (on the right) was also collected by Bourgeau at Chasna, but made one year after the lectotype, it is here accepted as a syntype.

Andryala ragusina subsp. ***spartioides*** Pomel ex Batt. in Battandier & Trabut, Fl. Algérie [1]: 566. 1889 ≡ *A. spartioides* (Pomel ex Batt.) Barratte in Cosson & Barratte, Ill. Fl. Atlant. 2: 74, t. 145. 1893 – **Lectotype (designated here):** [Algeria]. El Outaïa, *Battandier s.n.* (MPU barcode MPU019886 [digital image!]; syntypes: MPU [digital image!], P!).

Battandier (1889: 566) described *A. ragusina* subsp. *spartioides* based on specimens under the herbarium names *A. spartioides* Pomel (from the Pomel herbarium, as mentioned in the protologue) and *A. ragusina* var. *virgata* Cosson (presumably from the Cosson herbarium). The specimen MPU019886, here designated as lectotype, is originally from Battandier's herbarium (included in the Maire collection now at MPU) and is labelled as *Andryala spartioides* in Pomel's hand. Moreover, it was collected in a locality mentioned in the protologue and matches the original description quite well. Although a few other specimens under the name *A. spartioides* Pomel were found (MPU019884 and MPU019885—fragments of the same plant—and MPU019883—a duplicate), they are not suitable for lectotypification given their poor preservation state. However, they are here considered as syntypes. Similarly, all specimens under the herbarium name *A. ragusina* var. *virgata* from the Cosson herbarium, now deposited at MPU and P, are here considered as syntypes.

Andryala rothia Pers., Syn. Pl. 2: 378. 1807 ≡ *Voigtia tomentosa* Roth in Bot. Mag. (Römer & Usteri) 4(10): 17. 1790, syn. subst. ≡ *Rothia andryaloides* Gaertn., Fruct. Sem. Pl. 2: 371. 1791, nom. illeg. – **Lectotype (designated here):** *A.W. Roth s.n.* (M barcode M-0031113 [digital image!]).

Roth (1790) described the genus *Voigtia* Roth, comprising a single species: *Voigtia tomentosa*. Later, Gaertner (1791) combined *Voigtia tomentosa* into *Rothia* Schreb. under the name *Rothia andryaloides*, which is illegitimate, because the epithet *tomentosa* should have instead been used according to Art. 6.10 of the *ICN* (McNeill & al., 2012). Much later Persoon (1807) included *Voigtia tomentosa* in the genus *Andryala*, but under the name *A. rothia* given that *A. tomentosa* Scop. (Scopoli, 1787) already existed.

There is one specimen at M accompanied by the original description of *V. tomentosa* handwritten on the sheet by Roth; this sheet also includes the name *R. andryaloides* lately added by him. There is another specimen at B-W under the same name handwritten by Roth as well, but no reference to the name *V. tomentosa* is included. In this case, the first specimen is here selected as lectotype.

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9.5 Appendix 5: On the recognition of a new subspecies of *Andryala crithmifolia* Aiton (Asteraceae) from Madeira Island (Portugal) – paper published in *Silva Lusitana*, 2014

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On the recognition of a new subspecies of *Andryala crithmifolia* Aiton (Asteraceae) from Madeira Island (Portugal)

***Maria Zita Ferreira, **Inés Álvarez Fernández, *Roberto Jardim and *Miguel Menezes de Sequeira**

Abstract. Based on morphological characters a new combination for *Andryala crithmifolia* Aiton, endemic from Madeira Island (Portugal), is proposed: *Andryala crithmifolia* subsp. *coronopifolia* (Lowe) M.Z.Ferreira, R.Jardim, Álv. Fern. & M.Seq. This taxon is presently known from one isolated population on the sea cliff of Cabo Girão. A detailed description is included as well as an illustration and SEM images. Comments on taxonomy, habitat, distribution and conservation status are presented. Diagnostic characters and nomenclatural aspects are discussed and a diagnostic key for all Madeiran *Andryala* L. taxa is also included.

Key words: *Andryala glandulosa* Lam., taxonomy, endemism, threatened species

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Uma nova subespécie de *Andryala crithmifolia* (Asteraceae) para a ilha da Madeira (Portugal)

Sumário. Com base em caracteres morfológicos é proposta uma nova combinação e status para *Andryala crithmifolia* Aiton, endémica da Ilha da Madeira (Portugal): *Andryala crithmifolia* subsp. *coronopifolia* (Lowe) M.Z.Ferreira, R.Jardim, Álv. Fern. & M.Seq. Presentemente é apenas conhecida uma população isolada na falésia do Cabo Girão. Incluem-se uma descrição detalhada, uma ilustração e imagens MEV. São apresentados comentários sobre a taxonomia, habitat, distribuição e estado de conservação. São discutidos caracteres diagnóstico e aspectos nomenclaturais e inclui-se uma chave dicotómica para identificação de todos os taxa de *Andryala* L. da Madeira.

Palavras-chave: *Andryala glandulosa* Lam., taxonomia, endemismo, espécie ameaçada

Une nouvelle sous-espèce de *Andryala crithmifolia* (Asteraceae) pour l'Île de Madère (Portugal)

Résumé. Fondée sur caractères morphologiques une nouvelle combinaison et statut pour *Andryala crithmifolia* Aiton endémique de Madère (Portugal) est proposée: *Andryala crithmifolia* subsp. *coronopifolia* (Lowe) M.Z.Ferreira, R.Jardim, Álv. Fern. & M.Seq. Ce taxon a une répartition très restreinte, survenant dans une population isolée sur les falaises du Cabo Girão. Cela comprend une description détaillée, une illustration et images MEB. Commentaires sur la taxonomie, l'habitat, la distribution et l'état de conservation sont présentés. Les caractères diagnostiques et les aspects de nomenclature sont discutés et une clé dichotomique pour identifier tous les taxa de *Andryala* L. de Madère et inclus.

Mots clés: *Andryala glandulosa* Lam, taxonomie, endémisme, espèces menacées

Introduction

The Madeira archipelago includes two groups of islands: Porto Santo (11-14 Ma), and Madeira and Desertas (up to 6 Ma), the latter sharing a common geological origin (GELDMACHER *et al*. 2006). Madeira Island is situated at ca. 600 km northwest of the Western African coast, has 737 km^2 and a maximum altitude of 1,861 masl and harbours the highest cape in Europe (the second in the world) known as Cabo Girão (580 masl).

Andryala L. is represented in Macaronesia by eight endemic taxa distributed in different archipelagos: five taxa in the Canary Islands (ACEBES-GINOVÉS *et al*., 2010) and three in the archipelago of Madeira (JARDIM and MENEZES DE SEQUEIRA, 2008).

MENEZES (1914), HANSEN and SUNDING (1993), PRESS (1994) and JARDIM and MENEZES DE SEQUEIRA (2008) recognised two *Andryala* species for Madeira: *A. crithmifolia* Aiton and *A. glandulosa* Lam. (including two subspecies), the first being an exclusive endemic for Madeira and the second a Macaronesian endemic shared with the Canary Islands (HANSEN and SUNDING,1993; PRESS, 1994). The Canarian *A. glandulosa* populations were recognised as a new species, *A. perezii* M.Z.Ferreira, R.Jardim, Álv. Fern. & M.Seq. (FERREIRA *et al*., 2014). The recognition of *A. integrifolia* L. as naturalised (FERREIRA *et al*., 2011) increased the number of *Andryala* taxa in Madeira to four.

Andryala crithmifolia was described by AITON (1789). LOWE (1872) recognised this species for Madeira, along with *A. cheiranthifolia* L'Hér. comprising two varieties: *A. cheiranthifolia* L´Hér. var. α *congesta* Lowe and *A. cheiranthifolia* L´Hér. var. β *sparsiflora* Lowe. For the latter taxon LOWE (*op. cit*.) described three sub varieties: *A. cheiranthifolia* var. β *sparsiflora* subvar. *integrifolia, A. cheiranthifolia* var. β *sparsiflora* subvar. *runcinata* and *A. cheiranthifolia* var. β *sparsiflora* subvar. *coronopifolia.* In the same publication Lowe regarded the third sub variety as "*an extreme maritime form of A. cheiranthifolia var.* β *sparsiflora subvar. runcinata, with more divided tomentose canescent leaves, but not presenting the other peculiar characters of the true A. crithmifolia Aiton*". DE CANDOLLE (1838) recognised a variety based on a plant sent by Lowe in 1832, naming it *A. varia* Lowe ex DC. var. *crithmifolia.* In spite of stating *A. crithmifolia* Aiton as a synonym, DE CANDOLLE (*op.cit*.) questioned if it could instead correspond to the *A. pinnatifida* Aiton from Madeira (that is, *A. pinnatifida* var. α). LOWE (1872) highlighted that DE CANDOLLE correctly placed *A. varia* var. *crithmifolia* under *A. varia* Lowe ex DC., since it corresponds to *A. cheiranthifolia* var. β *sparsiflora* subvar. *coronopifolia* and not to the true *A. crithmifolia* Aiton. Nonetheless, PRESS (1994) included *A. cheiranthifolia* var. β *sparsiflora* subvar. *coronopifolia* in *A. crithmifolia*, stressing that "herbarium specimens show no discernible differences between the two taxa". PRESS (*op. cit.*) regarded *A. crithmifolia* Aiton as a rare maritime endemic found only at a few sites along the south coast of Madeira, from Funchal west to Madalena do Mar. More recently, it was confined to only one locality: Pináculo (JARDIM *et al.*, 2006). LOWE (1872) referred a broader distribution area for this species, from Pináculo to Garajau (east of Funchal).

Material and methods

This study was based upon the revision of herbarium specimens from LISI, LISU, MA, MADM and MADJ and specimens collected during field work (2005-2010).

Macroscopic analysis and photography were performed using a binocular microscope Zeiss model SV 11 APO. Micro characters were photographed with a Scanning Microscope (JEOL-TSM T330A). SEM images were obtained from various structures/organs collected during field work and preserved in ethanol 70%. The samples were prepared for scanning electron microscopy by dehydration in increasing acetone concentrations (30%, 50%, 70%, 80%, 90%, 95% and 100%) followed by critical point drying and gold-coating.

Results

Andryala crithmifolia Aiton. subsp. *coronopifolia* is morphologically similar to the typical subspecies (e.g. leaf margin, peduncle indumentum, flower indumentum) (Table 1). However, the differences between both *A. crithmifolia* populations (e.g. peduncle length, capitulum diameter, ligule size) support the proposal of a distinct subspecies currently occurring in Cabo Girão (Figure 1). These two subspecies occur in two isolated populations about 13 km apart. There are records of other subspecies occurring in areas not so far from each other. For instance, both subspecies of *A. glandulosa* can be found in close western localities of Madeira.

Andryala crithmifolia exhibits a very distinct morphology when compared to *A. glandulosa*, although *Andryala crithmifolia* subsp. *coronopifolia* slightly resembles some specimens of *A. glandulosa* subsp. *cheiranthifolia* by the more divided leaves. This would explain why LOWE (1872) firstly confounded *A. cheiranthifolia* var. *sparsiflora* subvar. *coronopifolia* with the typical subspecies of *A. crithmifolia*, as he himself admitted. Curiously, LOWE (*op. cit.)* did not make any reference to any *Andryala* growing on the sea cliff of Cabo Girão. However, the observation of micro characters on type material of *A. cheiranthifolia* var. *sparsiflora* subvar. *coronopifolia*, hosted at the BM herbarium, showed that this specimen is morphologically similar to the *A. crithmifolia* from Pináculo, namely in what concerns the presence of stellate hairs on the apex of the teeth of the ligule Thus, in accordance with PRESS (1994), we defend the inclusion of Lowe´s *A. cheiranthifolia* var. *sparsiflora* subvar. *coronopifolia* in *A. crithmifolia* and propose a new combination and status.

Andryala crithmifolia Aiton subsp. ***coronopifolia* (Lowe)** M.Z.Ferreira, R.Jardim, Álv. Fern. & M.Seq., **comb. et status nov.** ≡ *A. cheiranthifolia* L'Hér. var. *sparsiflora* subv. *coronopifolia* Lowe, Man. Fl. Madeira. 564 (1872)

Description. Biennial herb, STEMS up to 134 cm, woody at the base, branched from the base or above the middle, branches erect-patent or slightly ascendant (Figure 2A), pubescent to tomentose below with stellate hairs and tomentose above with stellate and glandular hairs. LEAVES glaucous, crowded towards the base (Figure 3), sparse above, tomentose on both surfaces, with stellate hairs, frequently mixed with glandular hairs on the uppermost leaves; lower leaves 94-210 x 18-65(-83) mm, with petiole 17-36(-57) mm enlarged at the base, obovate-lanceolate, apex acute to acuminate and margin pinnatisect; cauline leaves 47-135 x 13-40(-54) mm, attenuate in petiole 8-38 mm, lanceolate to obovate-lanceolate, apex acute to acuminate and margin pinnatisect; the uppermost 15-30 x 2-3 mm, semiamplexicaule, linear-lanceolate, base more or less rounded, apex acuminate and margin frequently entire. SINFLORESCENCES arranged in corymbs of 5-10 (-12) capitula. CAPITULA (11-)14-26 mm in diameter (Figure 2B), peduncles 18-31 mm with numerous short glandular hairs 0.5-0.9 mm combined with some stellate hairs; involucre 9-12 x 12-19 mm, usually campanulate with 3 rows of bracts; external involucre bracts 7.7-9.5 x 1.0-1.5 mm, apex acuminate, involving a flower, with dense yellow stellate and short glandular hairs 0.7-1.1 mm; internal involucre bracts 6.0-7.5 x 1.0-1.2 mm with a large scariose margin, receptacle flat or slightly convex, villous with setose hairs 4.3-5.5(-7.0) mm (3-5 times longer than the cypselae). FLOWERS golden-yellow, tube 2.8-3.2 mm , ligules 5.8-8.0 x 1.6-2.4 mm (Figure 2C), stellate hairs on the apex of the teeth of the ligule (Figure 4). CYPSELAE dark-brown, 1.4-1.9 x 0.4-0.6 mm (Figure 2D), usually obconical, with reddish-brown ribs, apex with a ring of short teeth, not exceeding the very short extension of the ribs; pappus fulvous white 4.7-5.5 mm.

Figure 1 *- Cabo Girão - occurrence area of A. crithmifolia subsp. coronopifolia (Lowe) M.Z.Ferreira, R.Jardim, Álv. Fern. & M.Seq. (steep sea cliffs).*

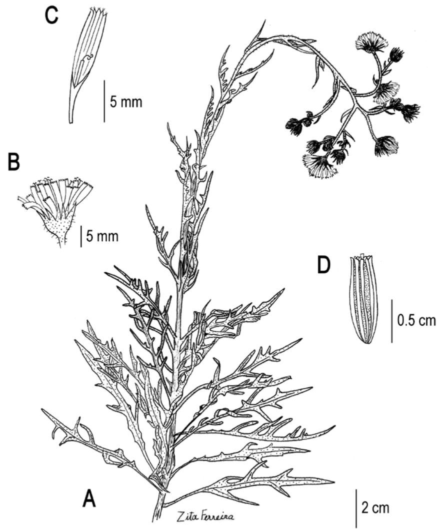

Figure 2 *- A. crithmifolia subsp. coronopifolia (Lowe) M.Z.Ferreira, R.Jardim, Álv. Fern. & M.Seq. (A. Stem: upper part, B. Capitulum, C. Flower, D. Cypsela).*

Figure 3 *- Andryala crithmifolia subsp. coronopifolia (Lowe) M.Z.Ferreira, R.Jardim, Álv. Fern. & M.Seq. (habit).*

Type specimen. Portugal, Madeira: sea cliffs, P^{ta}. do Sol, 20-VII-1850, Lowe 680 (lectotype, designated here, BM000072526)

Habitat. *Andryala crithmifolia* subsp. *coronopifolia* can be found on xerophytic clearings and on rocky and steep sea cliffs of the low micro-forest of Madeiran Olive [*Olea maderensis* (Lowe) Rivas Mart. & del Arco] (Figure 1). (CAPELO *et al.*, 2005).

Distribution. *Andryala crithmifolia* occurs only in the south coast of Madeira. *Andryala crithmifolia* subsp. *coronopifolia* is known from one population at Cabo Girão (west of Funchal), whereas the typical subspecies can be found to the east of Funchal at Pináculo. Based on the material studied, the new subspecies possibly had a wider distribution in the past, having also occurred to the west of Cabo Girão (Figure 5).

Conservation status. *Andryala crithmifolia* subsp. *coronopifolia* is Critically Endangered (B2ac(iv); C2b) according to the IUCN Red List Categories and criteria (IUCN, 2012). It is threatened by invasive plants, exotic forest, agricultural activity and human construction. The typical subspecies is also a CR taxon (JARDIM *et al.*, 2006) and is protected under the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention) and the Habitats Directive (Annex II). Furthermore, it occurs in a protected area included in the Natura 2000 Network. Conversely, *Andryala crithmifolia* subsp. *coronopifolia* does not occur in a legally protected area nor is it included in any conservation project.

Both *A. crithmifolia* populations are quite small. This fact enhances the risk of extinction, since small populations are more likely to become extinct due to the loss of genetic diversity through genetic drift and inbreeding depression (ELLSTRAND and ELAM, 1993; FRANKHAM, 1996). The concern of extinction is even greater considering that island populations are much more prone to this process than mainland populations due to small population size, restricted genetic diversity, narrow ranges prior to human colonization, and because human actions destroy an already-limited critical habitat (VITOUSEK, 1988). Besides, island endemic species have higher extinction rates than non-endemic species (FRANKHAM, 1997; 1998). Furthermore, probability of extinction may be increased by hybridization with native and introduced congeners (FERREIRA *et al.,* 2011).

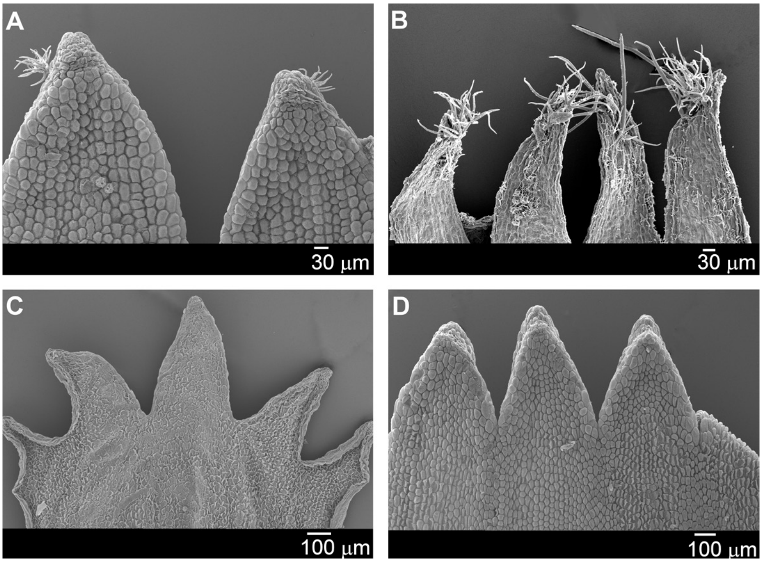

Figure 4 *- Apex of ligule. A- A. crithmifolia subsp. crithmifolia; B- A. crithmifolia subsp. coronopifolia; C- A. glandulosa subsp. glandulosa; D- A. glandulosa subsp. cheiranthifolia.*

Nomenclature. Accepted taxa and synonyms of Madeira *Andryala* taxa.

***Andryala crithmifolia* Aiton**, Hort. Kew. 3: 129 (1789)

A. crithmifolia* subsp. *crithmifolia
***A. crithmifolia* subsp. *coronopifolia* (Lowe) M.Z.Ferreira, R.Jardim, Álv. Fern. & M.Seq. stat. & comb. nov.**
≡ *A. cheiranthifolia* L'Hér. var. *sparsiflora* subv. *coronopifolia* Lowe, Man. Fl. Madeira. 564 (1872)
A. cheiranthifolia L'Hér. subsp. v*aria* var. *coronopifolia* (Lowe) Bornm., *in* Bot. Jahrb. Syst. 33: 489 (1904)
A.varia Lowe ex DC. subsp. *sparsiflora* Lowe f. *coronopifolia* (Lowe) Menezes, Fl. Madeira. 101 (1914)
A. glandulosa Lam. subsp. *varia* var. *varia* f. *coronopifolia* (Lowe) R. Fern. *in* Anuario Soc. Brot. 15: 26 (1959)
= *A. varia* Lowe ex DC. var. *crithmifolia* DC., Prodr. (DC.) 7: 246 (1838)

***Andryala glandulosa* Lam.** Encyc. 1: 154 (1783)

Andryala glandulosa* Lam. subsp. *glandulosa
= *A. tomentosa* Scop., Delic. Fl. Faun. Insubr. 2: 12 (1787), non *Andryala tomentosa* Chaix, Hist. Pl. Dauphiné (Villars) 1: 366 (1786)
= *A. candidissima* Desf., Cat. Pl. Horti Paris. ed. 3: 399 (1829)
A. varia Lowe ex DC. var. *candidissima* (Desf.) DC., Prodr. (DC.) 7: 245 (1838)
= *A. varia* Lowe ex DC. var. *angustifolia* DC., Prodr. (DC.) 7: 245 (1838)
= *A. robusta* Lowe *in* Trans. Cambridge Philos. Soc. 4: 540 (1838)
A. cheiranthifolia L'Hér. subsp. *robusta* (Lowe) Bornm., *in* Bot. Jahrb. Syst. 33: 489 (1904)
= *A. cheiranthifolia* L'Hér. var. *congesta* Lowe, Man. Fl. Madeira. 561 (1872)
A. varia subsp. *congesta* (Lowe) Menezes, Fl. Madeira. 101 (1914)

***Andryala glandulosa* Lam. subsp. *cheiranthifolia* (L'Her.) Greuter**, Willdenowia, 33: 232 (2003)
≡ *A. cheiranthifolia* L'Hér., Stirp. Nov. 1 (2): 35. (1784)
A. varia Lowe ex DC. var. *cheiranthifolia* (L'Hér.) DC., Prodr. (DC.) 7: 246 (1838)
= *A. cheiranthifolia* L'Hér. var. *sparsiflora* Lowe, Man. Fl. Madeira. 563 (1872)
A. varia Lowe ex DC. subsp. *sparsiflora* (Lowe) Menezes, Fl. Madeira. 101 (1914)

A. cheiranthifolia L'Hér. subsp. v*aria* sensu Bornm., *in* Bot. Jahrb. Syst. 33: 489 (1904)

A. glandulosa Lam. subsp. *varia* sensu R. Fern., *in* Anuário Soc. Brot., 25: 28 (1959)

= *A. varia* Lowe ex DC. var. *subglabrata* DC., Prodr. (DC.) 7: 246 (1838)

= *A. varia* Lowe ex DC. var. *aprica* DC., Prodr. (DC.) 7: 246 (1838)

= *A. cheiranthifolia* L'Hér. var. *sparsiflora* subv. *integrifolia* Lowe, Man. Fl. Madeira. 563 (1872)

A. cheiranthifolia L'Hér. subsp. v*aria* var. *integrifolia* (Lowe) Bornm., *in* Bot. Jahrb. Syst. 33: 489 (1904)

A. varia Lowe ex DC. subsp. *sparsiflora* f. *integrifolia* (Lowe) Menezes, Fl. Madeira. 101 (1914)

A. glandulosa Lam. subsp. *varia* var. *varia* f. *varia* sensu R. Fern., *in* Anuario Soc. Brot. 15: 26 (1959)

= *A. cheiranthifolia* L'Hér. var. *sparsiflora* subv. *runcinata* Lowe, Man. Fl. Madeira. 564 (1872)

A. cheiranthifolia L'Hér. subsp. v*aria* var. *runcinata* (Lowe) Bornm., *in* Bot. Jahrb. Syst. 33: 489 (1904)

A. varia Lowe ex DC. subsp. *sparsiflora* f. *runcinata* (Lowe) Menezes, Fl. Madeira. 101 (1914)

A. glandulosa Lam. subsp. *varia* var. *varia* f. *runcinata* (Lowe) R. Fern. *in* Anuario Soc. Brot. 15: 26 (1959)

Key to the *Andryala* L. taxa of the Archipelago of Madeira

1a. Stem with some glandular hairs on the upper part; involucral bracts flat, not enfolding a flower; flowers pale yellow, frequently with a reddish stripe on the outer face. .... *A. integrifolia*

1b. Stem glandular hairy at least on the upper part; involucral bracts involute, enfolding a flower; flowers golden yellow, seldom with a reddish stripe on the outer face. 2

2a. Lower leaves entire to pinnatipartite with lobes more than 3 mm width; peduncles frequently with long glandular hairs 0.9-4.0 mm; ligules not stellate-hairy at the apex of the teeth or rarely so. 3

2b. Lower leaves 1-2-pinnatisect with segments up to 3 mm width; peduncles with short glandular hairs 0.4-0.9 mm; ligules stellate-hairy at the apex of the teeth. 4

3a. Plant up to 112 cm; stems all glandular hairy; leaves entire to sinuate, lower ones sometimes pinnatifid; uppermost, cauline leaves, and sometimes lower leaves, glandular hairy, peduncles usually stout. .... *A. glandulosa* subsp. *glandulosa*

3b. Plant up to 72 cm; stems glandular hairy on the upper part, not or sparsely so below, leaves subentire to pinnatipartite, uppermost leaves glandular hairy; peduncles slender. .... *A. glandulosa* subsp. *cheiranthifolia*

4a. Leaf segments less than 2 mm width; peduncle 10-18 mm; external involucral bracts with glandular hairs 0.3-0.5 mm; ligules 4.8-5.3 x 1.9-2.9 mm. .... *A. crithmifolia* subsp. *crithmifolia*

4b. Leaf segments 2-3 mm width; peduncle 18-31 mm, external involucral bracts with glandular hairs 0.7-1 mm; ligules 5.8-8.0 x 1.6-2.4 mm. .... *A. crithmifolia* subsp. *coronopifolia*

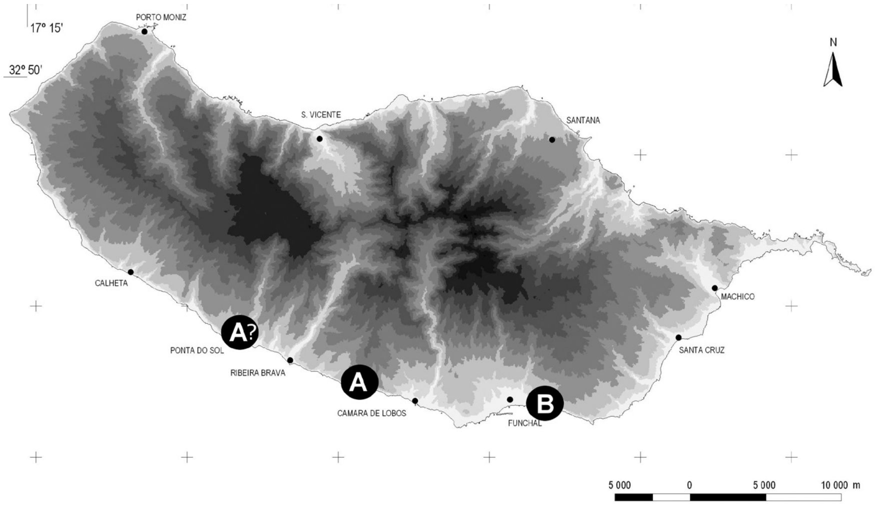

Figure 5 *- Distribution map of Andryala crithmifolia Aiton:*
A – A. crithmifolia subsp. coronopifolia (Cabo Girão), A? population not found (Ponta do Sol);
B – A. crithmifolia subsp. crithmifolia (Pináculo).

Conclusions

Morphological differences and distribution pattern support the recognition of the taxon *A. crithmifolia* Aiton. subsp. *coronopifolia* (Lowe) M.Z.Ferreira, R.Jardim, Álv. Fern. & M.Seq., acknowledged as highly threatened and therefore to be included in future conservation programs. Conservation strategies must aim to increase population size and priority must be given to *in situ* conservation strategies, namely by including the known populations in a protected area.

Studied material

A. crithmifolia subsp. *crithmifolia*
PORTUGAL. Madeira, F. Masson, 1776, BM000829762. Funchal, São Gonçalo: 25-V-1865, J.M. Moniz BM000072525a. Funchal: Sea cliffs to the eastward in as line with the 1st. chapel at the top of the cliff on the Caniço road, 07-VI-1837, C. Lemann, BM000072525b. Funchal, São Gonçalo: Miradouro do Pináculo, ca. 210 m.s.m., 20-V-1954, J. Malato Beliz, 543, MA, 239099. Bei der Aussichtsterrasse an der Strasse São Gonçalo - Caniço, 280 m, 07-VII-1971, C. Simon, s/ nº, MADM. Pináculo - São Gonçalo, 10-III-1988, Nóbrega, s/nº, MADJ, 05534. Pináculo - São Gonçalo, 06-VI-1988, Nóbrega, s/nº, MADJ, 06913. Pináculo, São Gonçalo, junto com *Opuntia tuna, Echium nervosum, Carlina salicifolia, Olea europaea,* 30-VI-2006, Z. Ferreira, nº 139, UMad. Rochas marítimas do Pico de S. Gonçalo, Menezes, s/nº, LISU, 43557. São Gonçalo, s/nº, MADJ, 00792. Pináculo, 30-VI-2006, 32º 44′ N, 16º 55′ W, Z. Ferreira, ZF139, UMad. Pináculo - S. Gonçalo, muito raro e só na falésia, abaixo do miradouro, 12-VIII-2009, 32º 38′ N, 16º 53′ W, Z. Ferreira, ZF260,UMad. Pináculo - S. Gonçalo, muito raro e só na falésia, abaixo do miradouro, 12-VIII-2009, 32º 38′ N, 16º 53′ W, Z. Ferreira, ZF261,UMad. Pináculo - S. Gonçalo, muito raro e só na falésia, abaixo do miradouro, 12-VIII-2009, 32º 38′ N, 16º 53′ W, Z. Ferreira, ZF262, UMad.

A. crithmifolia subsp. *coronopifolia*
PORTUGAL. Madeira: Sea cliffs, Pta. do Sol, 20-VII-1850, Lowe 680 (lectotype, designated here, BM000072526). Rochas do Cabo Girão, no chamado Poio do Capitão, descendo até cerca de 250 metros acima do nível do mar, espécie muito rara, 02-VI-1982, Nóbrega, s/nº, MADJ, 02943. Cabo Girão (base), 21-VII-1998, F. Fernandes, s/nº, MADJ, 08953. Rochas do Cabo Girão, abaixo do Chão da Vigia,

15-V-1988, Nóbrega, s/nº, MADJ, 06914. Cabo Girão, 32º 40′ N, 17º 00′, 30-VI-2006, Z. Ferreira, UMad. Cabo Girão, base da falésia, 32º 39.212 N 16º 59.601 W, 09-VIII-2009, Z. Ferreira, I. Ferreira, ZF258, MA 853265. Cabo Girão (base), 09-VIII-2009, 32º 39′ N, 16º 59′ W, Z. Ferreira, I. Ferreira, ZF259,UMad.

***Table 1** - Diagnostic characters of A. crithmifolia Aiton subsp. coronopifolia versus A. crithmifolia subsp. crithmifolia, A. glandulosa subsp. glandulosa and A. glandulosa subsp. cheiranthifolia.*

Diagnostic characters	*A. crithmifolia* subsp. *crithmifolia*	*A. crithmifolia* subsp. *coronopifolia*	*A. glandulosa* subsp. *glandulosa*	*A. glandulosa* subsp. *cheiranthifolia*
Stem	Up to 152 cm.	Up to 134 cm.	Up to 112 cm.	Up to 72 cm.
Leaves	Glaucous, crowded towards the base, lower and cauline 1-2-pinnatisect, (filiform segments less than 2 mm width); cauline petiolate, uppermost almost linear.	Glaucous, crowded towards the base, lower and cauline 1-2-pinnatisect (segments 2-3 mm width), cauline petiolate, uppermost almost linear.	Usually pale-green, sometimes crowded towards the base, lower entire or sometimes sinuate-pinnatifid, cauline usually entire, semiclasping or clasping the stem, uppermost ovate-oblong.	Glaucous to dark-green, sometimes crowded towards the base, lower and cauline sub entire to pinnatipartite (lobes more than 3 mm width), cauline semiclasping the stem, uppermost ovate-lanceolate.
Peduncle	10-18 mm, yellow glandular hairs 0.4-0.7 mm.	18-31 mm, yellow glandular hairs 0.5-0.9 mm.	19-79(-86) mm, yellow glandular hair 0.9-4.0 mm.	20-77 mm, yellow or dark brown glandular hairs 0.9-1.8 (2.6) mm.
Sinflorescence	5-12 capitula arranged in corymbs.	5-10 (-12) capitula arranged in corymbs.	2-11 capitula arranged in corymbs or less frequently corymbs somewhat paniculate.	5-12 capitula arranged in corymbs or less frequently corymbs somewhat paniculate.
Capitula	10-21 mm	14-26 mm	16-37 mm	16-30 mm
Involucre	6-8 x 9-12 (-14) mm, ± hemispherical at anthesis.	9-12 x 12-19 mm, ± hemispherical at anthesis.	11-20 x 14-31 mm, hemispherical at anthesis.	9-13 x 12-18(-22) mm, usually campanulate at anthesis.
External involucral bracts	Glandular hairs 0.3-0.5 mm	Glandular hairs 0.7-1.1 mm	Dense glandular hairs 0.7-3.0 mm	Glandular hairs 1.0-1.6 (-2.5) mm
Flowers	Tube 2.0-3.3 mm, ligule 4.8-5.3 x 1.9-2.9 mm, stellate hairs on the apex of the teeth of the ligules.	Tube 2.8-3.2 mm, ligule 5.8-8.0 x 1.6-2.4 mm, stellate hairs on the apex of the teeth of the ligules.	Tube 3.0-6.3 mm, ligule (6.5) 8.0-13.2 x 2.0-4.2 mm, no stellate hairs on the apex of the teeth of the ligules.	Tube 2.8-3.5 mm, ligule 8.0-11.9 x 2.3-2.6 mm, no stellate hairs on the apex of the teeth of the ligules or rarely so.

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