MACARONESIAN SONCHUS SUBGENUS DENDROSONCHUS S.L. (COMPOSITAE - LACTUCEAE), INCLUDING A REAPPRAISAL OF THE SPECIES CONCEPT AND NEW COMBINATIONS.

ANGELA E. ALDRIDGE

Botany Departament Plant Science Laboratories Reading University

RESUMEN

Boulos, en su reciente revisión del género Sonchus L., dió las claves de las especies de los miembros macaronésicos de este género y de los géneros emparentados. La variación en ciertos caracteres morfológicos de amplio material de Dendrosonchus s.l. se muestra aquí como mucho más extensa de lo que Boulos anticipó.

Nuevos conceptos de especies y subespecies son descritos seguidos por una sinopsis de reconocida taxa y nuevas combinaciones incluyendo una nueva subespecie, S. ustulatus Lowe subesp. maderensis Aldridge. Se han suministrado nuevas claves para las especies y sub-especies.

SUMMARY

Boulos, in his recent revision of the genus Sonchus L., gave keys to the species of the Macaronesian members of this and related segregate genera. The variation in certain morphological characters of ample material of *Dendrosonchus* s.l. is shown here to be far more extensive than Boulos anticipated. New species and subspecies concepts are outlined followed by a synopsis of recognised taxa and new combinations including one new subspecies, S. usulatus Lowe subsp. maderensis Aldridge. New keys to the species and subspecies are provided.

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INTRODUCTION

In the spring of 1973 I visited the seven principal islands of the Canaries for a period of four months. During this time extensive collections and observations were made of the members of the subgenus *Dendrosonchus* Webb ex Schultz Bip. This subgenus constitutes the woody and pachycaulous group of the genus *Sonchus* L. (Compositae, tribe Lactuceae) and is endemic to the islands of the Canaries, Madeira and Cape Verdes with one species also occurring in Western Morocco. At this time, keys to the species had been published by Boulos (1968, 1972) and these were applied in the field. It soon became apparent that many taxa could not be identified with the aid of these keys.

In a previous paper (Aldridge, 1976) it has been established that the subgenus *Dendrosonchus* includes the genera *Babcockia* Boulos (Boulos, 1965) and *Taeckholmia* Boulos (Boulos, 1967a) and also that Boulos' key to these genera has no value. The plants collected by me and those stored in the herbaria of the Royal Botanic Gardens, Kew, the British Museum (Natural History), London and Reading University were then thoroughly examined and a new revision of the group was found to be necessary (Aldridge, 1975).

MORPHOLOGICAL VARIATION AND SPECIES DELIMITATION

The variation within and between the species recognised by Boulos is far greater than he appeared to have observed. In his keys, Boulos stressed the value of such characters as leaf-lobe width, number of florets and length of corolla, especially for the members of the subgenus which possess highly dissected leaves. As the greatest discrepancies between my data and those of Boulos arise within this group, they are discussed in some detail below.

Boulos (1976a) placed six species into the genus Taeckholmia, the value of which has previously been discussed (Aldridge, 1976). These species were T. pinnata (L. fil.) Boulos (= Sonchus leptocephalus Cass.), T. canariensis Boulos (= S. filifolius Svent.), T. capillaris (Svent.) Boulos (= S. capillaris Svent.), T. microcarpa Boulos, T. heterophylla Boulos, T. regis-jubae (Pitard) Boulos (= S. regis-jubae Pitard) and T. arborea (DC.) Boulos (= S. arboreus DC.). The Sonchus nomenclature will be used in this discussion. Boulos separated S. arboreus and S. regis-jubae from the other members of the group on the basis of the leaf-lobe width and the ratio of ligule to tube of the corolla. The leaf-lobe width is an extremely variable character as demonstrated in Figure 1. The ran-





ge of leaf-lobe width for each of a few selected samples from each of the above taxa, excluding T. *heterophylla*, is shown in this figure. The lines indicate single samples using ten leaves per plant and it is evident that this character does not distinguish the two groups.

Boulos used the length of the corolla and length of the pappus in separating the taxa S. leptocephalus and S. filifolius, considered in the present study to be synonymous. The variation in the length of the corolla is illustrated for the whole group in Figure 2. Even when only one corolla per plant in four to five plants per species are examined it is apparent from Figure 2 that S. leptocephalus and S. filifolius cannot be distinguished on this character. Taeckholmia heterophylla has not been included in these figures as I consider it to be a hybrid from Gomera. Boulos described this species as having variable leaves, but it possesses intermediate leaves and capitula between S. arboreus and S. leptocephalus. These species grow in close proximity to one another on Gomera.

Other examples of a wider range in variation seen by me than observed by Boulos for the preparation of his keys, can be illustrated by an examination of his subgenus Dendrosonchus. Boulos (1974a) included in the subgenus Dendrosonchus several species with narrow leaf-lobes. These were S. palmensis (Schultz Bip.) Boulos, S. pinnatus Aiton, S. canariensis (Schultz Bip.) Boulos, S. canariensis subsp. orotavensis Boulos and S. gandogeri Pitard. Within this group S. canariensis subsp. orotavensis, from Tenerife, and S. gandogeri, from Hierro, are probably hybrids between members of the S. pinnatus group and those of either narrower or broader leaf-lobed species. Sonchus gandogeri is probably the result of hybridization between S. pinnatus subsp. canariensis and S. hierrensis and it may now prove to be a well-established species following more detailed field investigations. Sonchus pitardii and S. lidii which were also described by Boulos (1976b), also possess intermediate characteristics between members of the S. gandogeri population and S. hierrensis. These hybrid-like taxa all originate from localities in which they were very rare and surrounded by other, more widely distributed species. An investigation into the origination of all these rare samples by crossing experiments would take many years as in many species it takes two to three years to attain maturity. It seems, however, premature to recognise every variant at the species level as this type of treatment results in a large and unwieldy number of indistinct taxa. It is essential that the potential variability within plant groups, which is exhibited by the occasional rarity, is taken into consideration before a revision of that group is attempted.

Boulos used the number of florets as the sole, key character in the separation of \dot{S} . *palmensis* from the other narrow, leaf-lobed species which are listed above. The number of florets is generally quite constant for a species but an overlap between the species is





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quite usual. Figure 3 illustrates the variation in number of florets for this narrow, leaf-lobed group. This variation was found by counting the number of florets in one capitulum per plant and in one to five plants per species. If the species S. gandogeri and S. canariensis subsp. orotavensis are not taken into consideration for the reasons given above, then the number of florets would be useful as a character for separating S. palmensis from S. pinnatus and S. canariensis. The size of the involucre, however, is a more





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FIGURE 4. Variation in Leaf-lobe width. Each line represents one plant (from 10 leaves/plant).

useful character for keying out S. pinnatus subsp. palmensis from the other two subspecies, as they are recognised here, especially for field observations.

In the same keys, Boulos again used the leaf-lobe width for separating S. canariensis from its subspecies orotavensis. The range in leaf-lobe width is shown in Figure 4 for all the members of this narrow leaf-lobed group. When only ten leaves per plant and

one to five plants per species are examined the ranges can be seen to overlap in all cases. In many other respects the keys produced by Boulos are highly impracticable, and were usually unreliable in the field.

From these observations it is clear that the classification of the woody members of the genus *Sonchus* which was provided by Boulos requires revision. The subgenus *Dendrosonchus* comprises species which have evolved rapidly by adaptive radiation in response to the high selective pressures resulting from biotic and environmental factors. As the adaptive features produced by these selection pressures have possibly occurred only since the Tertiary period, the resultant taxa still show close relationships with one another, especially in features of the leaf, capitulum and cypsela. The evolution of the subgenus will be dealt with in more detail in a later paper.

THE USE OF TAXONOMIC CATEGORIES

The concepts of the genus, subgenus and section have been dealt with in a previous paper (Aldridge, 1976) and the concepts of the species and subspecies are discussed here.

THE SPECIES

Boulos (1972, 1973, 1974a 1974b) employed a narrow species concept in his recent revision of the genus *Sonchus* s.l. This type of treatment is generally applicable to little-worked areas where material is limited. A wider species concept would cause confusion at this pioneer phase (Davis & Heywood, 1965). I have examined abundant material which was in part collected from the Canary Islands, Madeira and Morocco during the course of study, and in part stored in the herbaria of Reading University, the Royal Botanic Gardens, Kew and the British Museum (Natural History), London. Although much of this material was available to Boulos, and although he made his own collections from the Canary Islands and Madeira, the resulting treatment of the species appears not to take into consideration the continuity of variation within the group. Many of the "species" recognised by Boulos cannot be determined unless their origin is known.

According to Davis & Heywood (1965), splitting is often the result of having a limited flora to deal with or of a lack of appreciation of variability, which may be because the plants have not been studied in the field or because the biological nature of the group is not understood. In the works by Boulos there is no mention of any cultivation of the plants in question and it appears that a very limited time was spent in the field. The argument that small groups are more natural and easier to use does not apply to this situation as it has been shown here that the small groups recognised by Boulos are difficult to distinguish when sufficient material is examined. The systematic investigations made and discussed in this and the previous paper (Aldridge, 1976) have revealed that more natural and easily identifiable groups result from a broader species concept than that held by Boulos. The species are recognised by unique combinations of several morphological characters. These are essentially phenetic species and it is intended that any observer should have little hesitation in recognising them as they are delimited here.

Du Rietz (1930) defined the species on the basis of recognising discontinuity in natural variation. This concept forms the basis of the systematic investigations discussed in this and the previous paper. An essential part of the formulation of taxonomic decisions involving the subgenus *Dendrosonchus* was found to result from extensive field observations. These studies of the variation of the plants in their natural environments may not have been sufficient or comprehensive enough for exact interpretations of the discontinuities between the species, but it is obvious that a broader species concept, than that previously shown by Boulos, is required to account for this variation observed in natural populations.

Due to geographical barriers the species are in effect isolated breeding units in nature, although they cross freely when brought together. Where geographical barriers have been removed by man in the course of road building and land development, hybridization often occurs. Where the natural geographical barriers are not so pronounced there is a more continuous variation between two taxa. In these cases the rank of subspecies has been used (see below). In several instances a species occurs on more than one island and the members are effectively isolated. These components of a species may be termed vicariads as they are obviously geographically, as well as reproductively, isolated. Several very similar species occurring on different islands but in similar habitats may also be considered as vicariads. The possible origin of these taxa will be treated in a later paper.

THE SUBSPECIES

The rank of subspecies is well defined in the literature (Davis & Heywood, 1965; Du Rietz, 1930; Rothmaler, 1944, 1943, 1955). It generally relates to a considerable portion of a species which is more or less distinct by a combination of morphological characters, but is

essentially isolated geographically. They may be entirely isolated geographically or they may overlap in part. In the former case the subspecies have become more distinct than in the latter. Where subsspecies of the same species overlap, hybridization may occur.

SYNOPSIS OF RECOGNISED TAXA AND NEW COMBINATIONS IN THE SUBGENUS DENDROSONCHUS

Subgenus Dendrosonchus Webb ex Schultz Bip. in Webb & Berth., Phyt. Canar., 3(2): 425 (1849-50).

Syn. Dendrosonchus Schultz Bip. ex Boulos in Bot. Not., 125: 297 (1972).

- section Dendrosonchus T.
 - Sonchus subgenus Dendrosonchus section Brachylobi Boulos in Bot. Not., 125: Syn. 299 (1972).
 - Sonchus subgenus Dendrosonchus section Pinnati Boulos, loc. cit., pro parte.
 - Sonchus brachylobus Webb ex Schultz Bip. in Webb & Berth., Phyt. Canar. 3(2): 438 1. (1849-50).
 - S. neglectus Pitard in Pitard & Proust, Iles Canaries Fl. Archipel. : 261 (1908). Svn. S. canariae Pitard in Pitard & Proust, loc. cit.
 - S. branchylobus var. canariae (Pitard) Boulos in Nytt. Mag. Bot., 14: 13 (1967).

ULPGC. Biblioteca Unive

- 2. Sonchus congestus Willd. in Ges. Naturf. Freunde Berlin Mag., 1: 136 (1807).
 - S. fructicosus Jacq., Collect. Bot., 1: 83 (1786) non L. fil. (1781). Svn.

 - S. jracquinii DC., Cat. Pl. Horti Monsp., : 147 (1813). S. macranthus Poiret, Encycl. Suppl., 3: 289 (1813). S. broussonetii Desf., Tabl. Ecole Bot., : 101 (1815). S. abbreviatus Link in Buch, Phys. Beschr. Canar., : 149 (1825). S. jacquinii Sprengel, Syst. Veg., 3: 647 (1826) pro parte.
 - S. abbreviatus var. gibbosus Svent., Plantae Macaronesienses novae vel minus cognitae, 1: 55 (1968).
- 3.
- Sonchus fruticosus L. fil., Suppl. Pl., : 346 (1781). Syn. S. laevigatus Willd., Enum. Pl. Horti Berol. Suppl., : 54 (1814).

 - S. lyratus Willd., op. cit., : 53 (1814). S. squarrosus DC., Cat. Pl. Horti Monsp., : 147 (1813).
 - S. laevigatus var. lyratus DC., Prodr., 7(1): 188 (1838).
 - Sonchus pinnatifidus Cav. in Anal. Cienc. Nat., 4: 78 (1801).
 - Syn.
- S. acidus Schousboe ex Willd., Sp. Pl., 3(3): 1511 (1803). S. runcinatus Vent. ex Schultz Bip. in Webb & Berth., Phyt. Canar. 3(2): 434 (1849-50).
- 5. Sonchus platylepis Webb ex Schultz Bip. in Webb & Berth., Phyt. Canar., 3(2): 433 (1849-50).
 - Syn. Babcockia platylepis (Webb ex Schultz Bip.) Boulos in Bull. Jard. Bot. État Brux., 35: 64 (1965).
- Sonchus fauces-orci Knoche, Vagandi Mos. Reiseskizzen Botanikers. I. Kanar. Ins., : 6. 244 (1923).
- 7. Sonchus radicatus Aiton, Hort. Kew, 3: 116 (1789).
- 7A. subspecies radicatus

4.

- subspecies gummifer (Ling) Aldridge, comb. et stat. nov. 7B.
 - Syn. Sonchus gummifer Link in Buch, Beschr. Canar. Ins., : 146 (1825).
- subspecies tectifolius (Svent.) Aldridge, comb. et stat. nov. 7C. Syn. Sonchus tectifolius Svent., Plantae Macaronesienses novae vel minus cognitae, 1: 14 (1968).
- Sonchus gonzalezpadroni Svent., Addit. Fl. Canar., 1: 79 (1960). 8.
 - Syn. S. gomerensis Boulos in Nytt Mag. Bot., 14: 11 (1967).
- Sonchus ustulatus Lowe in Trans. Camb. Philos. Soc., 4: 22 (1831). 9.
- Syn. S. dentatus Sol. ex Lowe in op. cit. : 23 (1831), non S. dentatus Ledeb., (1829). 9A. subspecies ustulatus
 - Syn. Sonchus ustulatus var. a angustifolia Lowe in Trans. Camb. Philos. Soc., 4: 22 (1831).

- 9B. subspecies maderensis Aldridge, subsp. nov.
 - Typus: 'Madeira, S .ustulatus var. 8 Lowe (DC.), Mason 249' (BM-BH!).
 - Syn. Sonchus ustulatus var. β latifolia Lowe in Trans. Camb. Philos. Soc., 4: 22 (1831). S. ustulatus var. 8 latifolia Lowe, Man. Fl. Mad., : 548 (1868).
 - S. ustulatus var. β imbricata Lowe, loc. cit. S. naturatus var β imbricata Lowe loc. cit. Folia pinnatipartita vel pinnatisecta; lobi terminales 8-30 mm longi, lanceolati vel ovati; lobi laterales 10-15, 6-40 x 6-28 mm, ovati vel lati ovati, imbricati vel distantes, angulares cum angulus proximalis prolatus, integri, in angulis apiculati; pagina supera pruinosa. Corolla 12-14 mm longa; ligula 7-9 mm longa; tubus 4.5-5.0 mm longus.

Distribution: North and North-East Madeira, Desertas, Porto Santo.

- 10. Sonchus ortunoi Svent., Addit. Fl. Canar., : 81 (1960).
- 11. Sonchus hierrensis (Pitard) Boulos in Nytt Mag. Bot., 14: 11 (1967).
 - S. jacquini var. hierrensis Pitard in Pitard & Proust, Iles Canar. Fl. Archipel., : Syn. 258 (1908).
 - S. congestus var. palmensis Schultz Bip. in Webb & Berth., Phyt. Canar., 3(2): 432 (1849-50).
 - S. hierrensis var. benehoavensis Svent. in Anales Real Soc. Esp. Fis. y Quim., 64: 893 (1968).
- Sonchus daltonii Webb in Hooker, Niger Fl., : 144 (1849). 12.
- Sonchus bornmuelleri Pitard in Pitard & Proust, Iles Canar. Fl. Archipel., : 259 (1908). 13.
- Sonchus acaulis Dum.-Courset, Bot. Cult., (ed. 2) 4: 12 (1811).
 Syn. S. jacquinii Sprengel, Syst. Veg., 3: 647 (1826) pro parte.
 S. chuquitensis Meyen ex Walp. in Nov. Act. Nat. Cur., 19(1): 294 (1843). 14.
- п.
- section Atalanthus (D. Don) DC., Prodr., 7: 189 (1838). Syn. Atalanthus D. Don in Edinb. New Philos. Jour., 6: 311 (1829). Taeckholmia Boulos in Bot. Not., 120: 97 (1967). Sonchus subgenus Dendrosonchus section Pinnati Boulos in Bot. Not., 125: 299 (1972) pro parte.
- 15. Sonchus arboreus DC., Prodr., 7: 189 (1838).
 - Syn. Prenanthes arborea Brouss., Elenchus Plant. Horti Bot. Monsp., : 47 (1805) nom. nud.
 - Sonchus regis-jubae Pitard in Pitard & Proust, Iles Canar. Fl. Archipel., : 262 (1908).
 - Taeckholmia regis-jubae (Pitard) Boulos in Bot. Not., 120: 104 (1967).
 - Taeckholmia arborea (DC.) Boulos, op. cit., : 106 (1967).
- 16. Sonchus leptocephalus Cass. in Dict. Sci. Nat., 43: 281 (1826).
 - Syn. Prenanthes pinnata L. fil., Suppl., : 347 (1781) non Sonchus pinnatus Aiton (1789). Chondrilla pinnata (L. fil.) Lam., Encycl. Meth. Bot., 2: 79 (1786). Taeckholmia pinnata (L. fil.) Boulos in Bot. Not., 120: 99 (1967).
- 16A. subspecies leptocephalus
- Syn. Sonchus filifolius Svent., Addit. Fl. Canar., 1: 83 (1960). Taeckholmia canariensis Boulos in Bot. Not., 120: 100 (1967). Taeckholmia filifolia (Svent.) Kunkel in Cuad. Bot. Can., 22: 28 (1974).
- 16B. subspecies capillaris (Svent.) Aldridge, comb. et stat. nov. Svn. Sonchus capillaris Svent., Addit. Fl. Canar., 1: 85 (1960). Taeckholmia capillaris (Svent.) Boulos in Bot. Not., 120: 100 (1967). Taeckholmia microcarpa Boulos, op. cit., : 102 (1967).
- 17. Sonchus pinnatus Aiton, Hort. Kew, 3: 116 (1789).

 - Syn. S. hyoseridifolius Hornem, Hort. Hafn., 2: 752 (1815). S. pinnatus var. β latiloba Lowe, Man. Fl. Mad., 1: 551 (1868).
 - S. pinnatus var. ∞ angustiloba Lowe, loc. cit.
- 17A. subspecies pinnatus
- 17B. subspecies canariensis (Schultz Bip.) Aldridge, comb. et stat. nov. Syn.
 - Sonchus pinnatus var. canariensis Schultz Bip. in Webb & Berth., Phyt. Canar., 3(2): 411 (1849-50).

Sonchus canariensis (Schultz Bip.) Boulos in Nytt Mag. Bot., 14: 14 (1967).

17C. subspecies palmensis (Schultz Bip.) Aldridge, comb. et stat. nov. Syn. Sonchus pinnatus var. palmensis Schultz Bip. in Webb & Berth., Phyt. Canar., 3(2): 441 (1849-50).

Sonchus palmensis (Schultz Bip.) Boulos in Nytt Mag. Bot., 14: 13 (1967).

KEY TO THE SPECIES

1 Involucres floccose-tomentose, at least at the base
2 Leaf-margins doubly serrulate
2 Leaf-margins doubly spinulose, denticulate or sparsely denticulate
3 Involucres densely floccose-tomentose throughout
4 Capitula 10 - 11 x 9 - 10 mm
4 Capitula 17 - 23 x 14 - 18 mm 14. acaulis
3 Involucres floccose-tomentose only at the base
5 Stem tall and branched, 30 - 150 cm high 11. hierrensis
5 Stem a short caudex, 1 - 10 cm high
6 Capitula 10 - 13 x 10 - 13 mm 8. gonzalezpadroni
6 Capitula 18 - 20 x 14 - 15 mm 10. ortunoi
1 Involucres glabrous
7 Leaves petiolate
8 Leaf-lobes narrowly-triangular to triangular or angular-ovate
9 Leaf-lobes angular-ovate, with the proximal angle more pronounced; penduncle
bracts 10 - 21
9 Leaf-lobes narrowly-triangular to triangular; peduncle bracts 2 - 8 4. <i>pinnatifidus</i>
8 Leaf-lobes filiform or linear- to oblong-lanceolate
10 Leaf-lobes lanceolate to oblong-lanceolate, mostly more than 5 mm wide; ca-
pitula 10 - 15 x 3.5 - 12 mm 17. pinnatus
10 Leaf-lobes filiform, linear or linear-lanceolate, mostly less than 5 mm wide;
capitula 5 - 10 x 1.5 - 5 mm. \sim
11 Corolla 6.5 - 10 mm long; pendant shrubs 16. leptocephalus
11 Corolla 12 - 14 mm long; erect tree-like shrubs 15. arboreus
7 Leaves sessile with sheathing bases
12 Leaves pruinose
13 Leaf-lobes narrowly- to broadly-triangular; capitula 22 - 30 x 18 - 30 mm
13 Leaf-lobes ovate to broadly-ovate, angular with the proximal angle more pro-
nounced; capitula 9 - 14 x 8 - 13 mm
14 Lower inflorescence-bracts lobed, auriculate, not scarious 7. radicatus
14 Lower inflorescence-bracts mostly entire, not auriculate, scarious 9. ustulatus
12 Leaves glabrous
15 Stem a short caudex, 1 - 12 cm, scarcely branched
16 Inflorescence lax; capitula 8 - 13 mm long
16 Inflorescence dense; capitula 15 - 1/ mm long 12. aaltonii
15 Stem long, 15 - 400 cm, much oranched
17 Capitula 11 - 14 x 5 - 7 mm 1. brachylobus
1/ Capitula 10 - 22 X 10 - 20 mm

KEYS TO THE SUBSPECIES

Sonchus radicatus Aiton

1	Capitula arising in clusters of three or more, at least at the termination of the primary in-
	Suprime anothing in chaoters of antice of the other at the termination of the primery in
	florescence-stem; plant erect on cliff ledges (North coast, Tenerite; North-east, Gomera)
	TA andiantus
	TA. raaicaius
1	Conitule arising singly rarely in pairs from along the length of the inflorescence-stem.
τ.	Capitula ansing singly, fally in parts, from along the length of the inforestence-stenn,
	plant pendant on vertical cliffs
	print pondant on volter in the
	2 Leaf-lobes with proximal angles not overlapping the midrib (South coast, Tenerite)
	7B <i>aummifar</i>
	in gunninger
	2 Leaf-lobes with proximal angles overlapping the midrib (East Tenerife) 7C tectifolius
	2 Elear-todes with prominar angles eventapping the matrie (East venetice) venetice)
Sc	onchus ustulatus Lowe
4	Test taken linear large slate compating almost signatified (South apost Madaira
L	Lear-robes mear-ranceorate, sometimes annost primatric (South Coast, Madena
	9A ustulatus
1	Leaf-lobes ovate to broadly-ovate, sometimes angular (North coast, Madeira; Porto
-	
	Santo; Desertas)

Sonchus leptocephalus Cass. 1 Leaf-lobes linear, plane (Gomera; North Tenerife; North Gran Canaria)

16A. leptocephalus

1 Leaf-lobes filiform, terete (South Tenerife; South Gran Canaria) 16B. capillaris

- Sonchus pinnatus Aiton 1 All leaves with depth of lamina to midrib between lobes 0 - 1.5 mm (Madeira) 17A. pinnatus
- Most leaves with depth of lamina to midrib between lobes more than 1.5 mm 1
 - 2 Capitula 10 12 mm in diameter (Gran Canaria; Tenerife) 17B. canariensis 2
 - Capitula 3.5 6 mm in diameter (La Palma) 17C. palmensis

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