

A CRITICAL REAPPRAISAL OF THE MACARONESIAN SONCHUS SUBGENUS DENDROSONCHUS S.L. (COMPOSITAE - LACTUCEAE).

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RESUMEN

En su reciente revisión del género *Sonchus* L., Boulos reconoció tres géneros segregados, viz. *Babcockia*, *Taeckholmia* y *Embergeria*. Aquí se demuestra, por extensas investigaciones morfológicas, que el género *Babcockia* y *Taeckholmia* no pueden ser distinguidos de los miembros macaronésicos del género *Sonchus* L. sub-género *Dendrosionchus* Webb ex Schultz Bip., y también la consideración de *Embergeria* como género es posible que sea dudosa. La literatura taxonómica del subgénero *Dendrosionchus* s.l. es revisada y se da una explicación para el uso del nombre *Atalanthus* mejor que *Taeckholmia* a nivel de sección. Los conceptos del autor sobre las categorías del género, subgénero y sección dentro de este grupo de la Compositae. tribu Lactuceae están descritos.

SUMMARY

In his recent revision of the genus *Sonchus* L., Boulos recognised three segregate genera, viz *Babcockia*, *Taeckholmia* and *Embergeria*. It is shown here, by extensive morphological investigations, that the genera *Babcockia* and *Taeckholmia* cannot be distinguished from the Macaronesian members of the genus *Sonchus* L. subgenus *Dendrosionchus* Webb ex Schultz Bip., and also the status of the genus *Embergeria* is considered to be in doubt. The taxonomic literature on the subgenus *Dendrosionchus* s.l. is reviewed and an explanation is given for the use of the name *Atalanthus* rather than *Taeckholmia* at sectional level. The author's concepts of the categories genus, subgenus and section within this group of the Compositae, tribe Lactuceae are outlined.

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INTRODUCTION

The genus *Sonchus* L. (Compositae, tribe Lactuceae) has recently been revised by Boulos (1972, 1973, 1974a 1974b), Pons & Boulos (1972) and Roux & Boulos (1972), and the subgenera *Sonchus*, *Origosonchus* Boulos and *Dendrosonchus* Schultz Bip. ex Boulos were recognised. Boulos made no groupings within the subgenus *Dendrosonchus* in his first publication dealing with the genus (Boulos, 1960) but he recognised fourteen species which he later grouped into three separate genera. These were *Babcockia* Boulos, a monotypic genus (Boulos, 1965), *Taekholmia* Boulos, comprising seven species (Boulos, 1967a) and the remaining species were kept in the subgenus *Dendrosonchus* of *Sonchus*. During research into the anatomy and evolution of *Dendrosonchus* s.l. (Aldridge, 1975) it was found necessary to reappraise the taxonomy of this Macaronesian group.

HISTORICAL TAXONOMIC SURVEY

The woody pachycaulous species of *Sonchus* which are endemic to the islands of the Canaries, Cape Verdes and Madeira with one species also occurring in Western Morocco, were first considered to be distinct from all other species of this genus by Schultz Bipontinus (1949-50). He gave a detailed descriptive account of the group in the famous work *Phytographia Canariensis* of Webb & Berthelot (1936-50) in which he recognised six subgenera of Macaronesian *Sonchus* species based upon vegetative and floral differences. Two of these have since been included in the widespread genus *Launaea* Cass., one has been raised to generic level of *Lactucosonchus* (Schultz Bip.) Svent. which is a herbaceous, monotypic genus endemic to La Palma, and two subgenera which were composed of herbaceous species have since been placed into the subgenus *Sonchus* by Boulos (1973). Schultz Bipontinus recognised two groups in the remaining subgenus *Dendrosonchus* Webb ex

Schultz Bip. on the basis of the numbers of florets in the capitula and he called these *Macrocephali* Schultz Bip. and *Microcephali* Schultz Bip. respectively. As Schultz Bipontinus gave these groups the categories "Div. I" and "Div. II" respectively, Boulos (1972) did not consider the subgenus *Dendrosonchus* Schultz Bip. to be validly published. He explained that the subgenus *Dendrosonchus* Schultz Bip. "est invalide en raison de l'article 33, note 2 du Code (sous-genre subdivisé en divisions) est ici valide", and consequently published the name *Dendrosonchus* Schultz Bip. ex Boulos. According to article 33, note 2 of the International Code of Botanical Nomenclature (1972) it is the names given to taxa whose ranks are denoted by misplaced terms, in this case the divisions *Macrocephali* and *Microcephali* which are not validly published. Boulos has, therefore, misunderstood the application of this article. In the present work the subgenus *Dendrosonchus* Webb ex Schultz Bip., is, therefore, considered to be validly published. It is quite clear, however, that Schultz Bipontinus did not intend his two groups of *Dendrosonchus* to be divisions in the modern sense. *Macrocephali* contained the type species, *Sonchus congestus* Willd., for the subgenus and must, therefore, be called *Dendrosonchus*. Schultz Bipontinus recognised two species in *Microcephali* of which one, *S. leptcephalus* Cass., was previously placed in the genus *Prenanthes* by C. Linné (1781). Don (1829) later recognised a new genus, *Atalanthus* D. Don, which is now typified by this species but later *Atalanthus* was sunk back into *Sonchus* as a section by A. P. De Candolle (1838). This is discussed in more detail below. The use of this particular article is, therefore, irrelevant to the nomenclature of the group.

Throughout the history of the subgenus *Dendrosonchus* a distinction between two morphological groups has been recognised (except by Boulos, 1960). Don (1829) distinguished the genus *Atalanthus* from *Sonchus* on the basis of their life-forms, being shrubs as opposed to herbs. The other shrubby, Macaronesian elements were not, however, taken into account. A. P. De Candolle (1838) recognised the two groups on the number of florets and by the indumentum of the capitulum. Section *Eusonchus* DC. subsection *Fruticosi* DC. was stated to have capitula with a subtomentose indumentum as distinct from section *Atalanthus* (D. Don) DC. which lacks this character. Since the work of De Candolle the erroneous placement of *S. pinnatus* Aiton within the section *Dendrosonchus* has been maintained to the present day. This species does not possess tomentose capitula and, therefore, should be associated with the other members of section *Atalanthus*. Even though this character was disregarded by later authors the alleged close relationship of *S. pinna-*

tus to other members of section *Dendrosonchus* was not sundered. This point is illustrated by the work of Schultz Bipontinus (1849-50) who recognised nine species, including *S. pinnatus* with two Canarian varieties and four Madeiran forms, in the *Macrocephali* group and two species in *Microcephali*. The division was made on the number of florets alone.

Lowe (1868) used the characters herbaceous perennial and shrubby perennial to distinguish between *S. ustulatus* Lowe and the shrubby species of *S. pinnatus* and *S. fruticosus* L. fil. when describing these species from Madeira. This distinction, although not categorized by Lowe, was later emphasised by Boulos (1972) in recognising the section *Pinnati* Boulos of the subgenus *Dendrosonchus*. Within this section *S. pinnatus* was grouped with the varieties recognised by Schultz Bipontinus, which Boulos raised to species, with various other new species possessing highly dissected leaves, as well as *S. fruticosus*. This latter species resembles the others of the section *Pinnati* only in its tree-like habit.

The distinction between the two groups, *Dendrosonchus* and *Atalanthus* was again recognised by Pitard and Proust (1908) who followed De Candolle (1838) in placing the Macaronesian species of *Sonchus* into the two separate sections, *Eusonchus* and *Atalanthus*. Within *Eusonchus* the Canarian woody element was placed in a separate series called *Fruticosi* DC. consisting of twelve species. These included *S. pinnatus*, its varieties and one new species, *S. gando-geri*, which also had highly dissected leaves. Three species were included in section *Atalanthus*. Boulos (1967a) in separating the genus *Taeckholmia* accentuated the differences prevalent within its members from those of *Dendrosonchus*. The natural affinities of the *Atalanthus* group to *S. pinnatus* s.l. have, however, once more been overlooked. *Bobcockia* and *Taeckholmia* are simply the extreme forms of the very variable subgenus *Dendrosonchus* and, as discussed below, are extremely difficult to delimit.

In his revision of the subgenus *Dendrosonchus*, Boulos (1972) recognised three sections which were *Dendrosonchus*, with eleven species, *Brachylobi*, with one species and two varieties, and *Pinnati*, with seven species and two subspecies. The sections were described in detail but the distinguishing features were basically the growth-form which characterized section *Pinnati* Boulos, and the leaf shape and presence of rhizomes which characterized section *Brachylobi* Boulos. *Sonchus brachylobus* Webb ex Schultz Bip. var. *canariae* (Pitard) Boulos has leaves which are not lyrate, and

neither variety has been seen by me to have rhizomes. On the basis of these characters this section is not, therefore, acceptable. The section *Pinnati* was separated because of the tree-like habit of its species and, therefore, *S. fruticosus* was included.

The taxonomic treatments of the subgenus *Dendrosonchus* have all more or less followed the original workers in the separation of *S. leptcephalus* and similar taxa, in the retention of *S. pinnatus* and similar taxa within the body of the broad-leaved group and finally, in the grouping of *S. fruticosus* with the *pinnatus* group. Boulos' treatment differs only in the rank accorded to each group and in the recognition of the large headed *S. platylepis* Webb ex Schultz Bip. as distinct by placing it in a separate genus. On the basis of morphological features I have reorganised these well-established groups in order to reflect more natural affinities between the members. The section is chosen as the most suitable rank for subdividing the subgenus *Dendrosonchus* into *Dendrosonchus* and *Atalanthus* (D. Don) DC. These two sections accommodate the two most natural morphological groups of the woody, endemic and Macaronesian species of *Sonchus*.

Two other monotypic, Canarian genera which are closely related to *Sonchus* may be mentioned here. The first, *Lactucosonchus* (Schultz Bip.) Svent., was originally described by Schultz Bipontinus as a subgenus of *Sonchus* with one species, *S. webbii* Schultz Bip., endemic to La Palma. Sventenius (1968b) later gave it generic status. It is a herbaceous perennial with an extremely long, tuberous root, cypselas with a pappus of one type of seta and a leaf shape not known in any *Sonchus* species, even though the degree of dissection is very variable. Boulos (1974b) could not have examined this taxon in great detail as he reduced it to synonymy with *Taekholmia heterophylla* Boulos, a dubious species described as a tall, woody shrub and which had the typical *Sonchus* pappus (see below). The other allied genus is *Sventenia* Font Quer with one species, *S. bupleuroides* Font Quer, which is endemic to Gran Canaria. Font Quer (1948) first described and illustrated this monotypic genus, the species of which is a low, perennial shrub and distinguished from any member of *Sonchus* by its entire leaves, beaked cypselas and yellow-tipped glandular hairs covering the inflorescence stalk, peduncles and involucre bracts.

Various authors have made contributions to the taxonomy of woody, Macaronesian species of *Sonchus* (C. Linné, 1781; Aiton, 1789; Cavanilles, 1801; Willdenow, 1807; Dumont de Courset, 1811;

Link, 1825; De Candolle, 1838). These works were of considerable importance to the classification of the subgenus *Dendrosonchus* by Schultz Bipontinus (1849-50). During this time much confusion arose in the nomenclature of the species *S. acaulis* Dum.—Courset and *S. congestus* Willd. The type specimens for these names and their many synonyms were later established by Boulos (1967b) and I am in agreement with his conclusions. A few synonyms, however, which Boulos quoted are a little dubious as several of the descriptions by Schultz Bipontinus consisted of only a brief statement. An example is *S. polyodon* Webb ex Schultz Bip. which was described as a variety of *S. abbreviatus* Link by the words "caule elongate gracili". Boulos placed this into synonymy with *S. acaulis* Dum.—Courset and correctly made *S. abbreviatus* Link synonymous with *S. congestus* Willd. The above description does not indicate that the elongated stem is a flowering stem and, therefore, could not be considered to be synonymous with *S. acaulis* with any certainty. Other authors who have contributed to the taxonomy of *Dendrosonchus* are Webb (1849), Lowe (1831, 1851), Pitard and Proust (1908), Knoche (1923) and Sventenius (1960, 1968a, 1968b). Sventenius (1960) gave highly informative descriptions of four new species of *Dendrosonchus* in his *Additamentum ad Floram Canariensem*. Each description was accompanied by a type locality, a collection date and an illustration. Boulos (1967a, 1967b) rejected these names stating that they were not validly published under article 37 of the Code, and consequently described three of these taxa under new names. In the introduction of his work, however, Sventenius stated that the plates were drawn from the holotypes. These are conserved in the herbarium of the Centro Regional de Investigaciones Agrarias in Valle de Guerra, Tenerife to where they were removed from the Orotava Botanical Garden (TENE). Bramwell (1970) argued that the publication of new species in *Additamentum ad Floram Canariensem* complies with the International Code of Botanical Nomenclature and his conclusions have been fully accepted in the present work.

SYNOPSIS OF RECOGNISED TAXA

The following is a synopsis of recognised taxa which are used throughout the present work.

Sonchus L.

Subgenus *Dendrosonchus* Webb ex Schultz Bip.

I. Section *Dendrosonchus*

1. *Sonchus brachylobus* Webb ex Schultz Bip.
2. *S. congestus* Willd.
3. *S. fruticosus* L. fil.
4. *S. pinnatifidus* Cav.
5. *S. platylepis* Webb ex Schultz Bip.
6. *S. fauces-orci* Knoche
7. *S. radicans* Aiton
 - 7A. subspecies *radicans*
 - 7B. subspecies *gummifer* (Link) Aldridge
 - 7C. subspecies *tectifolius* (Svent.) Aldridge
8. *S. gonzalezpadroni* Svent.
9. *S. ustulatus* Lowe
 - 9A. subspecies *ustulatus*
 - 9B. subspecies *maderensis* Aldridge
10. *S. ortunoi* Svent.
11. *S. hierrensis* (Pitard) Boulos
12. *S. daltonii* Webb
13. *S. bornmuelleri* Pitard
14. *S. acaulis* Dum.—Courset
- II. section *Atalanthus* (D. Don) DC.
 15. *S. arboreus* DC.
 16. *S. leptcephalus* Cass.
 - 16A. subspecies *leptocephalus*
 - 16B. subspecies *capillaris* (Svent.) Aldridge
 17. *S. pinnatus* Aiton
 - 17A. subspecies *pinnatus*
 - 17B. subspecies *canariensis* (Schultz Bip.) Aldridge
 - 17C. subspecies *palmensis* (Webb ex Schultz Bip.) Aldridge

MORPHOLOGY

In recognising the genera *Taeckholmia* and *Babcockia*, Boulos (1965, 1967a) relied on several characters which were stated to distinguish them from *Sonchus*. These characters are thoroughly examined here to show that these genera were inadequately based and consequently are not accepted. The species of the two genera have been included in *Sonchus* L. subgenus *Dendrosonchus* Webb ex Schultz Bip. throughout these investigations. The branching patterns, seedling, leaf and capitula morphology of several species of *Dendrosonchus* have recently been described in detail by Ebel (1971). The following results extend this information to all the members of *Dendrosonchus* s. l. to describe the morphological characteristics which typify the subgenus.

HABIT

The life-forms of *Dendrosonchus* species are either suffruticose chamaephytes or nanophanerophytes (Raunkier, 1934). Both types have their shoot apices partially protected by the withered remains of the leaves during the unfavourable or dry season. The growth-forms are rosette shrubs (Warming, 1909). As they are plants which grow on rocks or soil poor in water, they could be termed chylrophytes (Warming, 1923). Figures 1 and 2 illustrate the growth-forms of some species of the subgenus. The roots are large and tuberous with many lateral tubers completely covered by matted fibrous roots. Reports of some of the species being rhizomatous are erroneous (cf. Boulos, 1974a). Buds, however, develop on the roots allowing propagation of the plants by root stocks. This root-bud development commonly occurs in *Sonchus leptocephalus* subspecies *leptocephalus* (Fig. 1B) and *capillaris*, giving these plants a shrubby habit. This branching from the root can occur in all the species of *Dendrosonchus* and does so especially when the main stem is damaged.

The degree of woodiness varies within the subgenus. All the members of section *Atalanthus* have a tall, shrubby or tree-like, much-branched habit. *Sonchus pinnatus* subspecies *palmensis* (Fig. 1C), *pinnatus* and *canariensis* and *S. arboreus* (Fig. 1A) are all low, tree-like shrubs. The tallest shrubs are found in section *Dendrosonchus*. *Sonchus hierrensis*, *S. congestus* (Fig. 2C) and *S. fruticosus* may all attain heights of up to five metres. In all species of the subgenus, inflorescences are terminal and branching occurs behind these flowering stems after they die down. Also in section *Dendrosonchus* many species are caudex (or short, woody-stemmed) perennials with caudices up to 100 cm high. *Sonchus acaulis* (Fig. 2E), *S. radicans* subspecies *radicans* (Fig. 2B), *tectifolius* and *gummifer*, *S. gonzalezpadroni*, *S. ustulatus* subspecies *ustulatus* and *maderensis*, *S. fauces-orci*, *S. daltonii* and *S. bornmuelleri* are all caudex perennials with a very short stem or caudex and a tall inflorescence stem. *Sonchus platylepis* (Fig. 2D) has an intermediate type of habit in that it is a low shrub. *Sonchus brachylobus* (Fig. 2A) has an unusual growth habit as the woody stems arise mainly from the root and many grow horizontally above the ground. The internodes of all species are congested and the leaves are in a terminal rosette.

The members of *Taekholmia* were distinguished by Boulos (1967a) by possessing a frutescent habit with solid, often stick-like branches. This is obviously not a distinguishing feature as the frutescent habit is found in all members of *Dendrosonchus* s. l. and the stick-like branches can be seen in *S. brachylobus* and *S. pinnatif-*

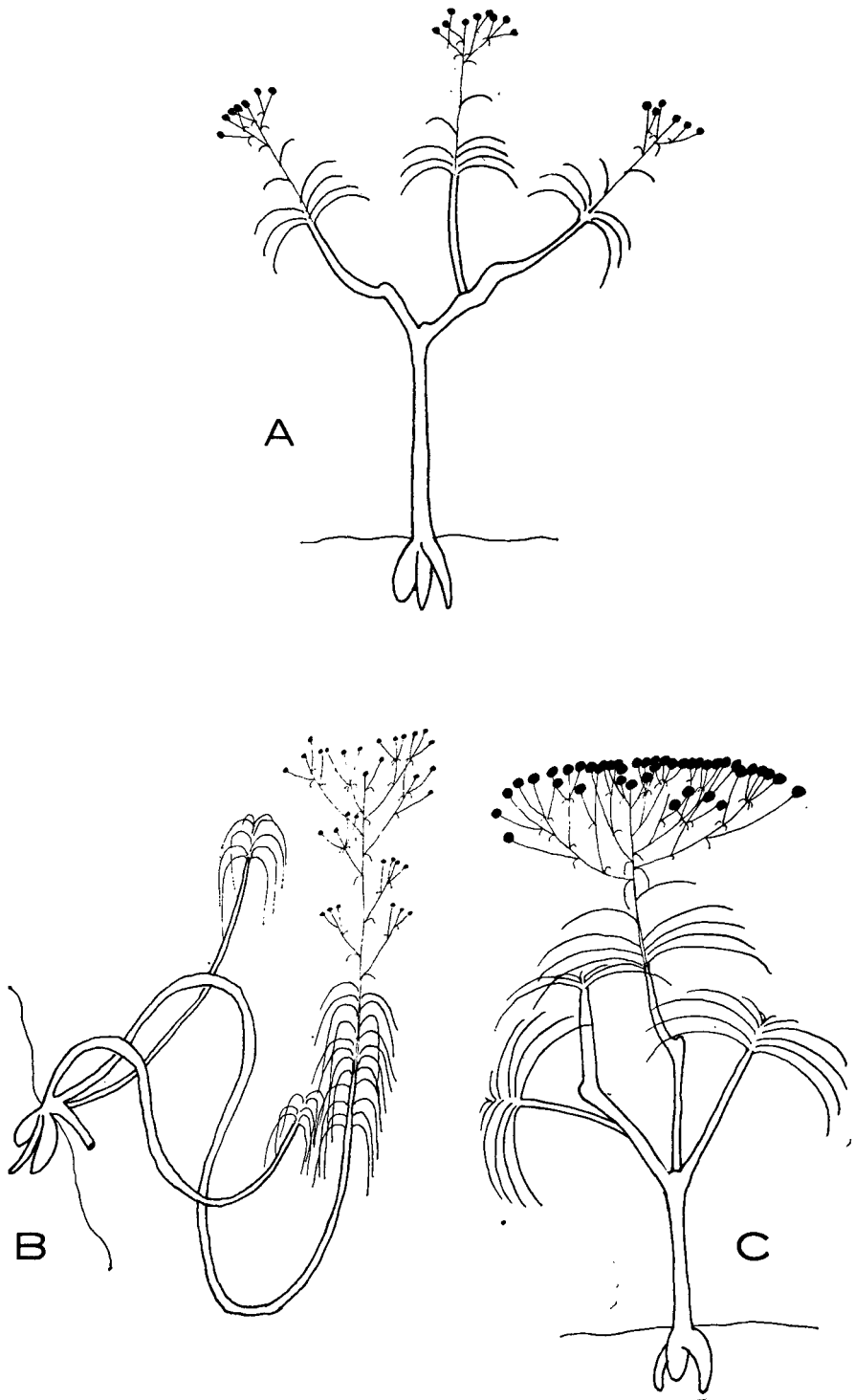


Figure 1 Growth forms of *Sonchus* subgenus *Dendrosonchus* section *Atalanthus* (not to scale). A. *Sonchus arboreus*, B. *S. leptocephalus*, C. *S. pinnatus* subsp. *palmensis*.

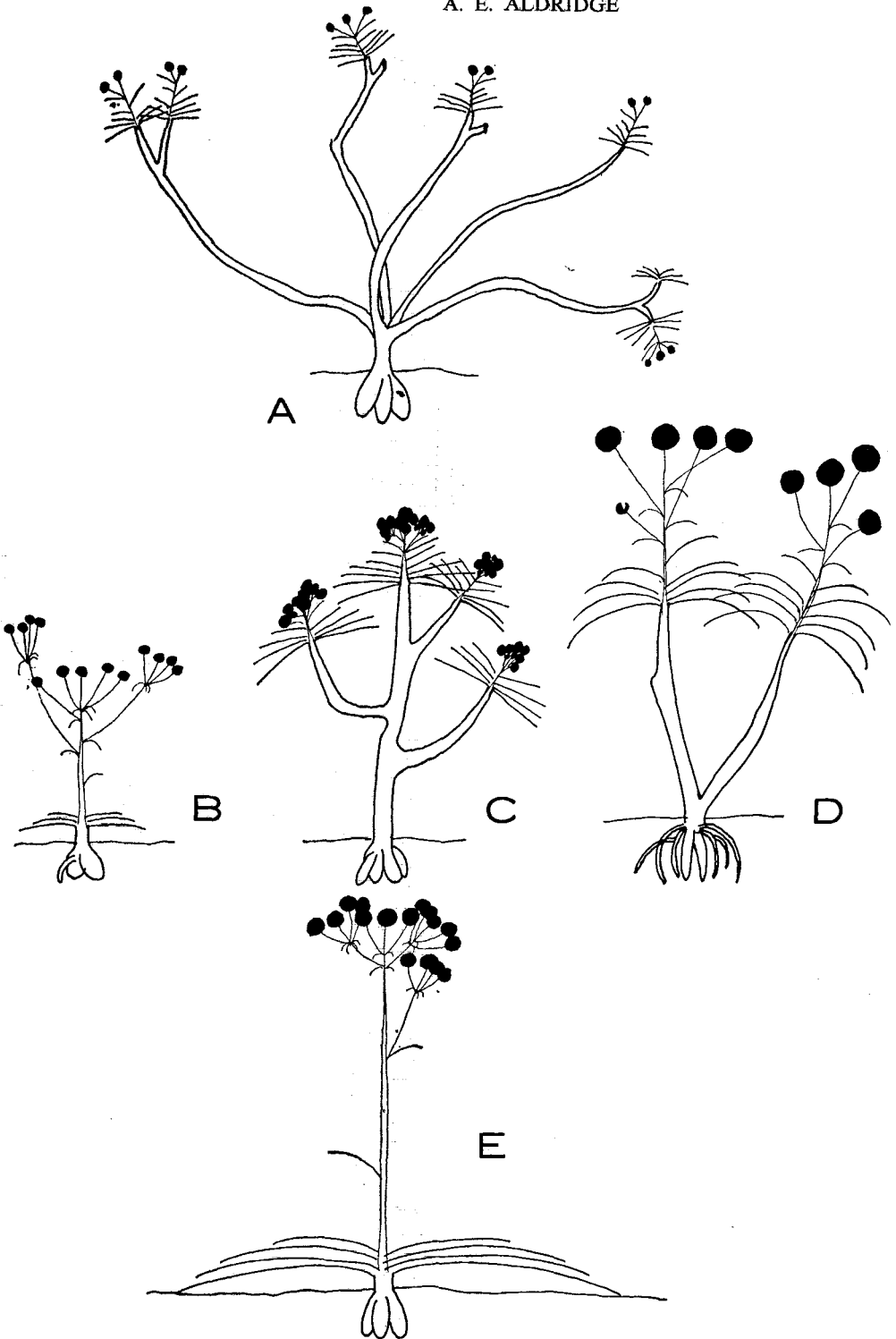


Figure 2 Growth forms of *Sonchus* subgenus *Dendrosonchus* section *Dendrosonchus* (not to scale). A. *Sonchus brachylobus*, B. *S. radicans*, C. *S. congestus*, D. *S. platylepis*, E. *S. acaulis*.

pus as well as *S. pinnatus* and its three subspecies which were not included in *Taeckholmia* although the latter species most closely resembles the members of this segregate genus.

LEAVES

The leaves are arranged spirally around the stem and the young leaves are crowded at the stem apices in terminal rosettes. In section *Atalanthus* (Fig. 3) the leaves are differentiated into lamina and petiole. The lamina is pinnatisect with the leaf-lobes filiform, linear or linear- to oblong-lanceolate. The numbers, widths and lengths of leaf-lobes are all very variable for each species and in some cases where the plants have been damaged, more than one type of leaf can be found on one plant. The morphological differences of the leaves for each species are maintained in cultivation and are generally useful taxonomically. Hybrid plants can easily be recognised by their possession of intermediate or very variable leaves (e. g. *Taeckholmia heterophylla* Boulos (Boulos, 1967a), a probable hybrid between *S. arboreus* and *S. leptcephalus* on Gomera). The leaf margins within this section are entire or sparsely denticulate. The denticles or spinules in both sections are the sites of hydathodes where the veins end blindly at the margins of the leaves.

In the section *Dendrosonchus* the leaves are also pinnatifid to pinnatisect. Figures 4, 5 and 6 show the leaf morphology of most of the members of this section. *Sonchus brachylobus* var. *canariae* is shown at the top of Figure 4 to illustrate that the leaf morphology is very similar to *S. pinnatifidus* (Fig. 4C) and *S. congestus* (Fig. 4E). Most of the species within this section have leaves with a sheathing base and the petioles are obscured by this. *Sonchus pinnatifidus* (Fig. 4C) and *S. fauces-orci* (Fig. 5A) are petiolate.

The leaf-lobes are narrowly- to broadly-triangular, ovate or broadly-ovate. In *S. fauces-orci* (Fig. 5A), the subspecies of *S. radicans* (Fig. 5B, C and D), *S. gonzalezpadroni* and *S. ustulatus* subsp. *maderensis*, the lobes are angular with the proximal angle more pronounced. In some cases these extended angles of the leaf-lobes overlap the immediate proximal lobes and the midrib (e.g. *S. radicans* subsp. *tectifolius*, Fig. 5D). The margins of the leaves are sparsely denticulate, denticulate, doubly spinulose or doubly serrulate and are useful taxonomically. *Sonchus congestus* (Fig. 4E) can easily be distinguished from any other taxon within the subgenus by its doubly serrulate leaf margins. The largest leaves of the subgenus are found in *S. acaulis* (Fig. 6C) in which they may attain the length of 80 cm.

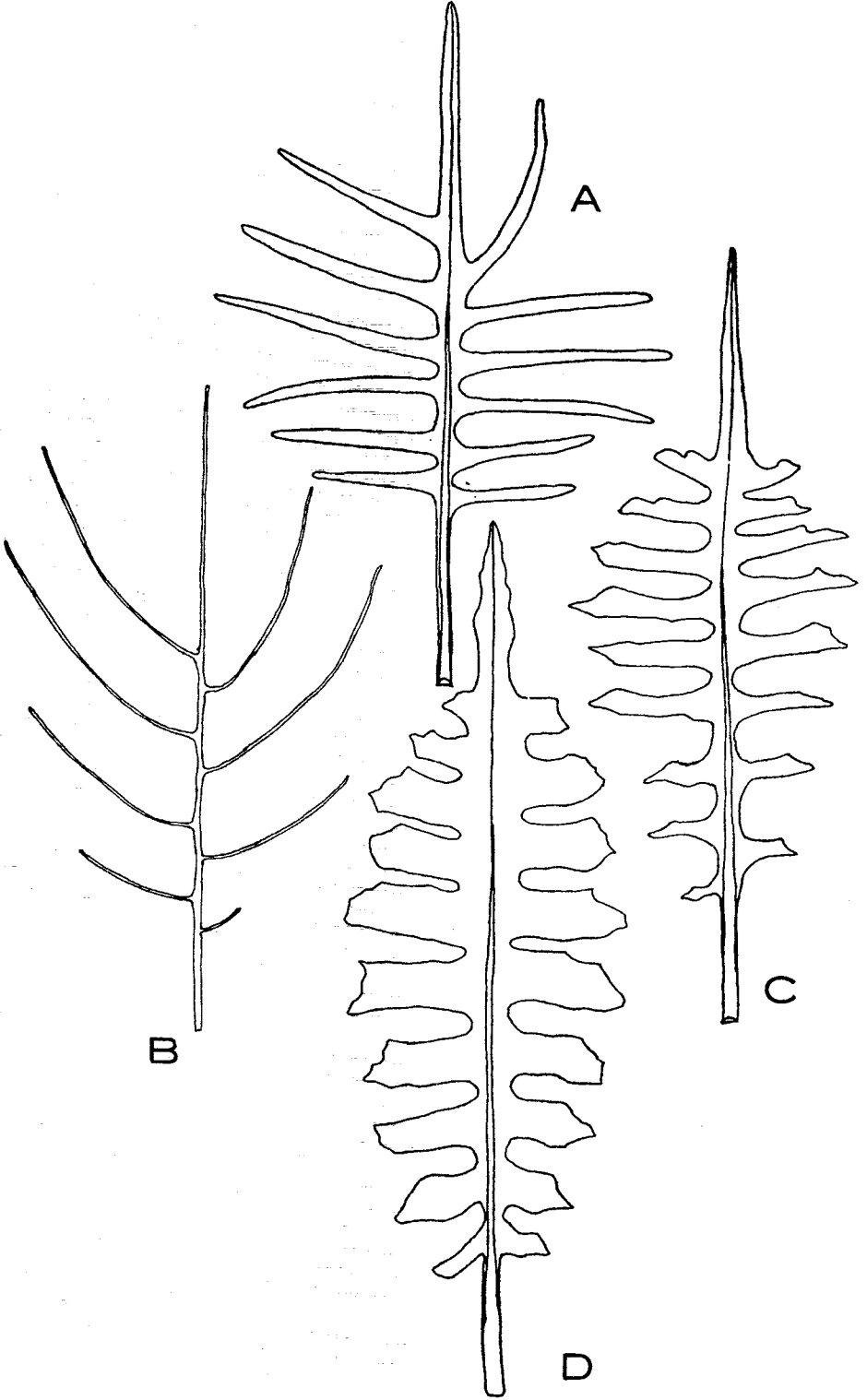


Figure 3 Leaf shapes - section *Atalanthus* (not to scale). A. *Sonchus arboreus*, B. *S. leptocephalus* subsp. *capillaris*, C. *S. pinnatus* subsp. *canariensis*, D. *S. pinnatus* subsp. *palmensis*.

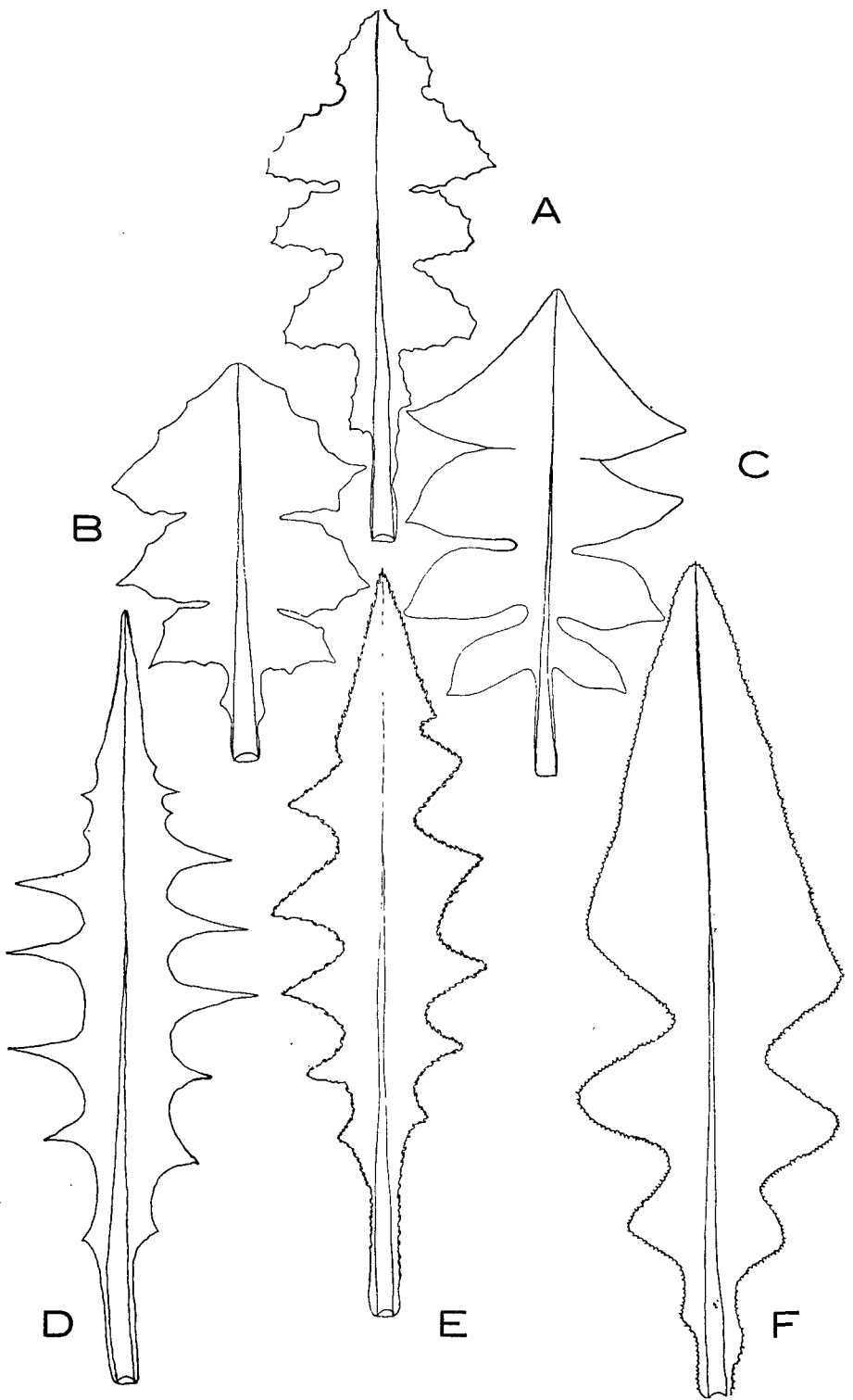


Figure 4 Leaf shapes- section *Dendrosonchus* (not to scale). A. *Sonchus brachylobus* var. *canariae*, B. *S. brachylobus*, C. *S. pinnatifidus*, D. *S. platylepis*, E. *S. congestus*, F. *S. fruticosus*.

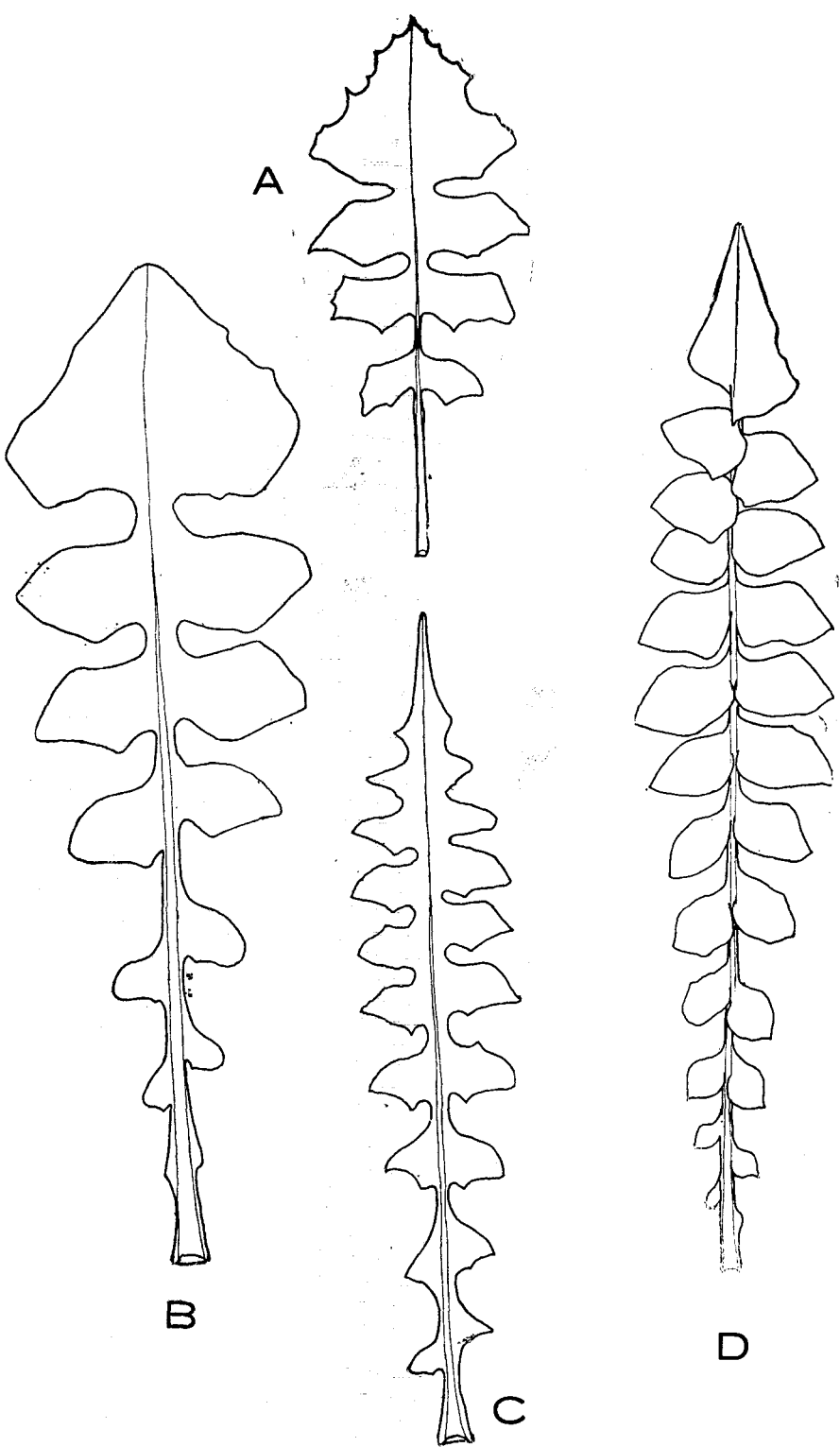


Figure 5 Leaf shapes - section *Dendrosonchus* (not to scale). A. *Sonchus fauces-orci*, B. *S. radicans* subsp. *radicans*, C. *S. radicans* subsp. *gummifer*, D. *S. radicans* subsp. *tectifolius*.

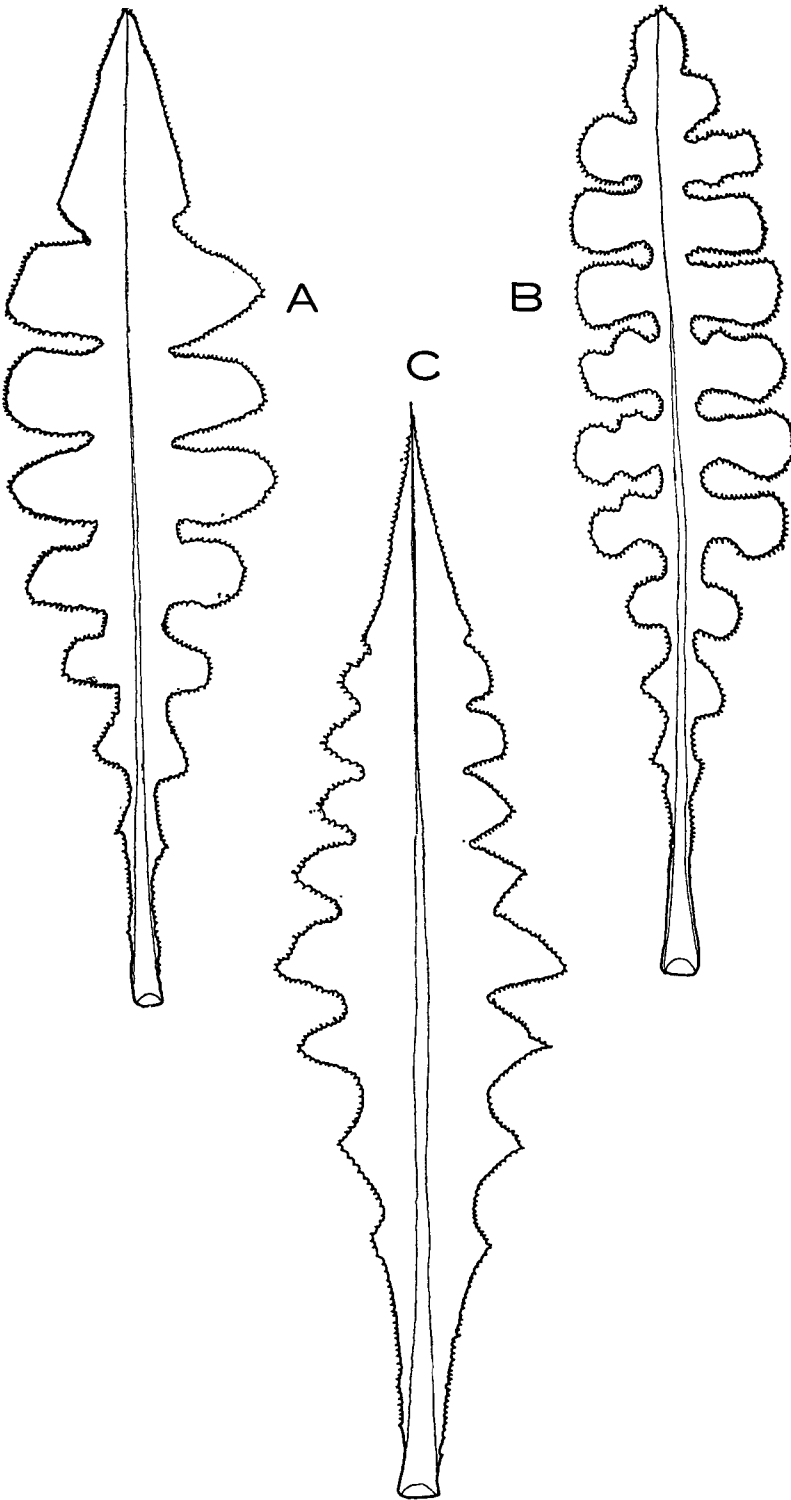


Figure 6 Leaf shapes - section *Dendrosionchus* (not to scale). A. *Sonchus hierrensis*, B. *S. bornmuelleri*, C. *S. acaulis*.

The leaves of section *Atalanthus* are glabrous. Many species of section *Dendrosonchus* have leaves which are pruinose, being covered with a waxy secretion of the epidermis which is easily rubbed off (e.g. *S. radicans* and *S. platylepis*). This pruina is found over the rest of the plant in these species and especially on the involucre bracts and the peduncles. In some other species of section *Dendrosonchus* the leaves are floccose-tomentose or sparsely tomentose (e.g. *S. acaulis* and *S. hierrensis*) and a few species have glabrous leaves (e.g. *S. bornmuelleri* and *S. pinnatifidus*). In all species of the subgenus the leaves of the young bud are protected by a heavy covering of white floccose-tomentose hairs.

A relationship between the degree of dissection of the leaves and rainfall, as was the case for the genus *Argyranthemum* Webb ex Schultz Bip. in the Canary Islands (Humphries, 1976), is not easily seen in this subgenus. The finely dissected leaves of *S. leptocephalus* subsp. *capillaris* are associated with extremely xerophytic conditions such as are found on the south coasts of Tenerife and Gran Canaria. Other species of both sections which possess broader leaf-lobes are also found in xerophytic conditions (e.g. *S. fauces-orci*, *S. pinnatifidus* and *S. platylepis*). A pruinose covering of the leaves is generally associated with coastal conditions (e.g. *S. radicans* and *S. ustulatus*) but it is also found in *S. platylepis* which can be found in xerophytic high altitudes above the cloud zone. This latter species which has broad leaves also occurs in the cloud zone and broad-leaved species are found in mesic habitats (e.g. *S. acaulis*, *S. hierrensis* and *S. fruticosus*). *Sonchus pinnatus* subsp. *palmensis*, however, has dissected leaves and is also found in these conditions.

Boulos (1967a) partially characterized *Taackholmia* by the possession of leaves which are not auriculate, are in more or less dense groups at the summits of the vegetative branches or at the bases of the flowering shoots and are deeply dissected into narrow lobes. All species of subgenus *Dendrosonchus* have this arrangement of leaves. *Sonchus pinnatus* subspecies *pinnatus*, *palmensis* and *canariensis* were not included in *Taackholmia* even though they have deeply dissected leaves with narrow lobes.

INFLORESCENCES

The inflorescences are corymbose, determinate, monochasial cymes (e.g. *S. arboreus* and *S. platylepis*) or determinate, dichasial, umbel-like cymes (e.g. *S. radicans* and *S. acaulis*). In all species the inflorescences are terminal on the main stem or branches.

The numbers of capitula per inflorescence ranges from about 8 in *S. platylepis* to approximately 350 in *S. leptocephalus*. The branching patterns of the inflorescences of five species of *Dendrosonchus* s.l. have been described by Ebel (1971).

As the inflorescence develops, the main axis of the stem or caudex elongates and the leaves become separated by longer internodes. These cauline inflorescence leaves are smaller, generally auriculate and often possess fewer lobes than the caudical leaves. Higher up the inflorescence these cauline leaves give way to smaller bracts of the peduncles. The numbers, sizes and shapes of all these leaves and bracts are sometimes useful taxonomically (e.g. the peduncle bracts of *S. fauces-orci* and the inflorescence bracts of *S. ustulatus*).

The majority of capitula have peduncles but when very young they often appear to be sessile. The peduncles range in length from 1 mm (e.g. in all species of section *Atalanthus*) to 100 mm (e.g. *S. radicans*, *S. ustulatus* and *S. platylepis*). They sometimes have an identical indumentum to that of the involucre bracts but in most species are glabrous. The majority of species have a low number (0—4) of bracts on the peduncles, but up to 21 can be present in *S. fauces-orci*.

In distinguishing the genus *Babcockia*, Boulos stated that the diagnostic characters include the extraordinary length of the peduncles (up to 18 cm) and the presence of a large number of bracts on the peduncles (up to 15). The range of peduncle length of *S. platylepis*, which was the only species placed in the genus *Babcockia*, ranges from 30 to 90 mm, which overlaps with the ranges for all other members of the section *Dendrosonchus*. Boulos's measurement of 18 cm for *S. platylepis* is indeed "extraordinary". As mentioned above the highest number of peduncle bracts is in *S. fauces-orci*, whereas only 2 to 4 bracts are present in *S. platylepis*. The high number of 15 given by Boulos was not encountered in this study but it does not exceed that found regularly in *S. fauces-orci*. The shape of the peduncle bracts for *Babcockia platylepis* was stated by Boulos to be long and acuminate but I do not consider this character to be any more important than the distinct leaf shape possessed by *S. platylepis*.

CAPITULA

The smallest capitula are found in *S. leptocephalus* (6-9 mm x 1.5-4 mm at anthesis) and the largest in *S. platylepis* (20-30 mm x 18-30 mm). The former species was assigned to the genus *Taeck-*

holmia and the latter to *Babcockia* by Boulos (1967a, 1965 respectively) who used the sizes of the capitula and the component numbers of involucre bracts and florets as criteria to distinguish them from *Sonchus*. All sizes of capitula between these two limits are found in subgenus *Dendrosonchus*. Boulos gave the capitula sizes of the genus *Taeckholmia* to be 3-7 mm x 2-3 mm with 10-12 mm x 3-4 mm in one species. Those species which Boulos placed into this new genus have been examined here and quite different measurements were obtained. The ranges are 6-10 mm x 1.5-5 mm in *S. arboreus*, *S. leptcephalus* and its two subspecies (all members of Boulos's new genus), 7-15 mm x 3-12 mm in *S. pinnatus* and its three subspecies (all considered by Boulos to be the closest, morphologically to *Taeckholmia*) and 9-30 mm x 4-30 mm in all the members of section *Dendrosonchus*. As the measurements given by Boulos show a much smaller length of the capitulum, I assume that they were taken from young capitula and not from heads at anthesis, which is the most commonly accepted method in floristic works of today. This measurement is easily repeatable, whereas the young capitulum measurement certainly is not. In his descriptions of the species of subgenus *Dendrosonchus*, Boulos (1974a) often gave measurements of the capitula before and after anthesis. Unfortunately the measurement before anthesis in many cases seems to be of the young bud, and those after anthesis definitely included the ligules which project above the involucre. Both measurements are not easily repeatable and are, therefore, unreliable.

The heads are compressed-globose in bud, becoming subconical at anthesis and after flowering the bases of the outer involucre bracts in many species become swollen, giving the heads a conical appearance (e.g. *S. hierrensis*, *S. acaulis* and *S. radicans*). This swelling of the bracts closes the involucre during maturation of the cypselas. When the cypselas have reached maturity the involucre dries and withers, releasing the ripened fruits. In the species of section *Atalanthus* the swelling of the outer bracts is not so pronounced and yet the same mechanism for protection of the maturing fruits is still prevalent.

The larger capitula are generally found in mesic conditions and the smaller in xerophytic habitats. *Sonchus platylepis* appears to be the exception to this rule with its extra large heads and by growing in the high altitudes of Gran Canaria which are generally above the cloud zone. It is, however, also found in the cloud zone as well as these sub-alpine conditions. The coastal species have capitula of an intermediate size (e.g. *S. radicans* and *S. ustulatus*) The shape of the capitulum is very characteristic for each species and Figure 7 illustrates a few of these.

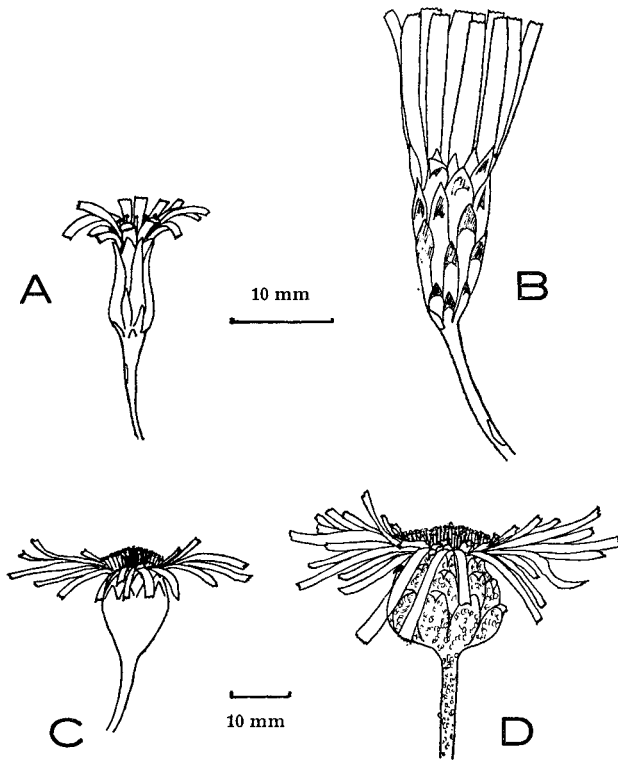


Figure 7 Capitula types of some members of subgenus *Dendrosonchus*. A. *Sonchus arbores*, B. *S. fauces-orci*, C. *S. radicans* subsp. *radicans*, D. *S. acaulis*.

INVOLUCRAL BRACTS

The involucre bracts are imbricate and spirally arranged into three to six, rarely seven, series with the outer bracts shorter than the inner. In section *Atalanthus* the bracts are arranged into three or four series. The numbers of bracts for this section range from 13 in *S. leptcephalus* to 48 in *S. pinnatus*. The involucre bracts are usually glabrous but occasionally small appendages on the midrib were seen in some samples of *S. pinnatus* subsp. *palmenis* and *S. leptcephalus* subsp. *capillaris*. These, apparently functionless, appendages are distinct from the elaborate, glandular hairs on the involucre bracts and peduncles of several species in the subgenus *Sonchus* and of the closely related, monotypic genus, *Sventenia*. In section *Dendrosonchus* the involucre bracts are arranged in from four to six series, rarely seven as in *S. platylepis*. The numbers of bracts for this section range from 20 in *S. brachylobus* to about 75 in *S. radicans* and *S. acaulis*. The involucre bracts of the

coastal species, those which have pruinose leaves, are usually pruinose. The appendages mentioned above were also seen in some samples of *S. brachylobus* and *S. ustulatus* subsp. *maderensis*. Involucral bracts which are floccose-tomentose, at least at the base, are present in *S. hierrensis*, *S. acaulis*, *S. bornmuelleri*, *S. congestus* and *S. ortunoi*. The inner bracts of *S. fauces-orci* are very distinctive in having a yellow colouration making them difficult to distinguish from the florets.

The involucral bracts of subgenus *Dendrosonchus* are generally of three to four types. The outer bracts are smallest and are triangular or ovate. The margins are entire to shortly ciliate, sometimes revolute (e.g. *S. hierrensis*) and very slightly scarious. These outer bracts merge gradually into the peduncle bracts below and the inner involucral bracts above. The intermediate bracts are less thickened and ovate, broadly-ovate or spatulate. The inner bracts are scarious and usually linear-lanceolate. Ebel (1971) illustrated these types for two species of section *Atalanthus* and three of section *Dendrosonchus*.

Boulos (1965) used the number of involucral bracts to distinguish *Babcockia* from *Sonchus*. His estimate of " \pm " 98 bracts for *S. platylepis*, which he placed into the new genus, was not observed for this or any other species within the subgenus *Dendrosonchus* during the present study. *Sonchus platylepis* usually has from 44 to 68 involucral bracts and a higher number is frequently present in *S. acaulis* and *S. radicans* as noted above. Many of the large-headed species of section *Dendrosonchus* have involucral bracts of four or more types and, therefore, this character does not distinguish *Babcockia* from *Sonchus* as was suggested by Boulos. To distinguish the genus *Taekholmia*, Boulos (1967a) used the low number of involucral bracts as one of the diagnostic characters. This character is unreliable as equally low numbers of bracts are present in *S. pinnatus* subspecies *pinnatus* and *palmensis* of section *Atalanthus* and in *S. brachylobus* and *S. fauces-orci* of section *Dendrosonchus*.

FLORETS

The florets are typical for the tribe, being all ligulate with five corolla teeth and five anthers which are laterally connate around a stigma with two terminal and papillate branches. All species of the genus have yellow florets which range from yellow (e.g. *S. arboreus* and *S. leptcephalus*) to a deep orange-yellow (e.g. *S. radicans* and *S. acaulis*). The ligules are linear-lanceolate

with five equal or unequal, acute or rounded teeth. The junction between the ligule and the tube is covered with white unicellular hairs. These hairs extend down the tube becoming more sparse nearer the inferior ovary. The ligule is glabrous and is provided with six vascular strands which supply the marginal positions of each segment of the five lobed corolla. The ratio of the length of the ligule to the length of the tube is more or less constant for a species and ranges from 1 to 2. The tube is usually shorter than the ligule but rarely, as in *S. bornmuelleri*, the tube is constantly longer.

The numbers of florets per capitulum in section *Atalanthus* range from 5 in *S. leptcephalus* to about 170 in *S. pinnatus*. This count of five florets in one sample of *S. leptcephalus* from Gran Canaria is low for this species (usually 9-29) and is unusual for the genus. The numbers of florets per capitulum in section *Dendrosonchus* range from 52 in *S. brachylobus* to about 660, which is high for the tribe, in *S. platylepis*. The number of florets is more or less constant for each taxon and the dimensions of the florets are useful taxonomically.

Boulos (1965) used the high number of florets to distinguish *Babcockia* from *Sonchus*. He gave a figure of "plus de 500" but the specimens counted in the present study revealed a range in floret number of from 300 to 600 in *S. platylepis*. Although this is the highest number of florets encountered in this subgenus, other species have numbers which come within this range (e.g. *S. acaulis* with 240-450 florets and *S. radicans* with 140-540 florets). Similarly, Boulos (1976a) used the low number of florets to distinguish the genus *Taekholmia* from *Sonchus*. He gave a range of 12-29 florets for this new genus but for those species involved this range is extended to (5) 9-29 in the present work. Within section *Atalanthus* a low number of florets is typical, apart from *S. pinnatus* subsp. *canariensis*. In *S. pinnatus* subspecies *pinnatus* and *palmensis* as few as 25 florets have frequently been counted. This character is, therefore, equally unreliable for the distinction of the genus *Taekholmia*.

The anther tube is usually 3-4 mm long with narrowly-triangular tails. The stilar branches are 1-3 mm long with small rounded papillae on their inner surfaces and long pointed papillae on the outer surfaces. Dehiscence is typically introrse and the pollen is pushed from the staminal tube by the elongating style.

RECEPTACLE

The receptacle of all the species of this subgenus is flat and reticulately pitted. Each small pit corresponds to the position at which a cypselia was attached and has little or no surrounding wall.

CYPSELAS AND PAPPUS

The cypsela and pappus morphologies provide the clearest distinguishing features of the genus *Sonchus*. The cypselas are compressed, beakless, attenuated towards both ends and slightly curved. The pappus is composed of two dissimilar types of seta, some being fine, flexuous hairs which are fasciculate at their bases and others being much longer, coarser, straight bristles which are separate. Both types of seta are scabrid by the extension of tips of the component cells directed away from the main body and towards the apex of the seta. The bristles are thicker than the hairs as they are composed of many more cells. The difference in length between the two types of seta is not so distinct in section *Atalanthus* as it is in section *Dendrosonchus*. In general the bristles are more caducous than the hairs, but in *S. leptocephalus* both types of seta are more or less equally deciduous. In *S. arboreus* and *S. leptocephalus* subspecies *leptocephalus* and *capillaris* there are setae of intermediate lengths and thicknesses between the hairs and the bristles. Another distinguishing feature of the pappus is that the hairs usually have hooked tips, whereas the bristles are acute. The hooked tips are formed by the doubled back apices of the individual cells which terminate the hairs (illustrated by a pappus hair of *S. radicans* in Plate 2a). The typical bristle tip is composed of cells which are pointed at their apices (illustrated by a pappus bristle of *S. leptocephalus* in Plate 2b).

Other distinguishing features of the cypsela and pappus are present but are a little more variable than those mentioned above. The surfaces of the cypselas have ribs running from the apex to the base. In the majority of species of *Sonchus* the number of prominent ribs is usually one to two on each side of the compressed cypselas, together with the two laterals. Between these ribs are smaller and less conspicuous ones which vary in number. Anatomical examination of the cypselas of each taxon of *Dendrosonchus* has proved to be useful taxonomically and this will be discussed in more detail in a later paper concerning the anatomy and evolution of the subgenus. Boulos (1960) noted that the number of prominent ribs on each face of the cypsela was generally three. If this was the case then an average of six major ribs per cypsela would be expected. The commonest number per cypsela, however, is four. The number given by Boulos probably included the two lateral ribs and these were probably counted twice if both faces of the cypsela were examined separately. Boulos also mentioned that the presence or absence of tubercles on the prominent ribs is a character of taxonomic importance for the separation of closely allied species. These tu-

bercles, here termed papillae, are found not only on the prominent ribs in the species which possess them but all over the cypsela surface (e.g. *S. pinnatifidus*, Plate 1b). Generally, the cypselas are devoid of papillae (e.g. *S. brachylobus*, Plate 1a). The presence or absence of papillae may be a useful taxonomic character at the level of species. All the species of the subgenus have homocarpous fruits and all these fruits are fertile.

Much attention has been given by Boulos (1965, 1967a, 1972, 1974b) to the features of the cypsela from the standpoint of separation of the two genera *Babcockia* and *Taeckholmia* from the subgenus *Dendrosonchus*. It is necessary to discuss these opinions in detail because these two genera are not accepted here. Boulos (1965) recognised *Babcockia* with one species, *B. platylepis* (Webb) Boulos, as distinct from *Dendrosonchus* on the basis of several features of which the following apply to the cypsela and pappus:

- “1. Les akènes \pm cylindriques et dépourvus de côtes.
2. L'apex des deux types de soies de l'aigrette est \pm identique”.

In his generic description of *Babcockia*, Boulos stated that the cypselas are 5.5 mm x 1 mm, have four grooves and are dimorphic, the outer being brown and rugose and the inner being cream-yellow and smooth. The pappus was described as having bristles 9-12 mm long with well developed lateral spines and apical cells reflexed towards the base and having hairs 4 mm long with few lateral spines and reflexed tips.

The anatomy of the cypselas of *S. platylepis* with respect to their ribbing and outline in transverse view does not distinguish it from other members of the subgenus *Dendrosonchus*. The cypselas of *S. platylepis* are the longest found within the subgenus and range from 5-7 mm. This is the *only* character which shows no overlap with other members of the subgenus which have cypselas of 1-4 mm in length. The width of the fruits between the lateral ribs of this species is 0.8-1.8 mm and the width between the two faces is 0.5-0.9 mm, thus indicating that they are definitely compressed. No evidence for the presence of dimorphic fruits, as suggested by Boulos, can be seen in the mature cypselas. I suggest that the two types of cypsela described by him are simply mature and immature fruits. The maturation of the cypselas in the capitulum of any species of this subgenus proceeds from the outside to the inside and in a developing head the fruits on the inside are yellow and smooth as they have not yet achieved maturity.

Boulos's observation that the tips of the two types of pappus setae in *S. platylepis* both have reflexed cells was, to some extent, confirmed during the present study. This feature is, however, also

present in many other species of the subgenus. Hooked bristles are present occasionally in *S. arboreus*, *S. leptocephalus* subsp. *capillaris* and *S. brachylobus* as well as in *S. platylepis*. On average the number of hooked cells on the hairs is about 8 but the tips of these hairs are just as variable in possessing hooks as the bristles. Some hairs which do not have the typical reflexed cells are occasionally present in *S. arboreus*, *S. leptocephalus* subspecies *leptocephalus* and *capillaris*, *S. ustulatus* subspecies *ustulatus* and *maderensis* and *S. fruticosus* as well as in *S. platylepis*. The tips of the hairs which lack reflexed cells appear to be reductions from the typical hooked apex. The bristles with hooked tips appear to have obtained reflexed cells as a secondary feature. Boulos (1960) suggested that the flexuous hair is derived from the coarse bristle and the presence of intermediate types of seta, seen during the present study in some of the species, seems to support this view. Boulos (1974b) gave another list of features to distinguish the genus *Babcockia* from *Sonchus* but in this list the characteristics of the pappus were omitted.

Boulos (1967a) described another genus, *Taeckholmia*, which comprised seven species, originally of the subgenus *Dendrosonchus*. The cypsela was used to provide one of the most important characteristics of this new genus. The following features of the cypsela were used:

“The small size of achenes (1.7-2.5 mm long and about 0.6 mm broad) which are attenuated towards both ends and are of variable shape within the same capitulum. The achenes are provided at their upper end with a protuberance surrounded by a white disc.”

In his generic description of *Taeckholmia*, Boulos stated that the cypselas are rugose, possess about four ribs on each side and are heteromorphic. The cypselas were described as either narrowly oblanceolate, more or less narrowly elliptic or more or less narrowly rectangular and also that they are either erect or curved. Comparing the cypsela sizes of the members of *Taeckholmia* with those of subgenus *Dendrosonchus* reveals that this particular character is definitely of no taxonomic value at the generic level. *Sonchus arboreus*, *S. leptocephalus* subspecies *leptocephalus* and *capillaris* (which constitute all the species of *Taeckholmia*) have a range of cypsela sizes from 1 to 3 mm long by 0.4 to 1.1 mm broad, which is a much wider range than that given by Boulos (1967a). The range of cypsela sizes for all the subspecies of *S. pinnatus* is 1.5 to 3 mm long by 0.7 to 1.6 mm broad. The ranges of the two groups can hardly be separated. As mentioned previously, the typical *Sonchus* cypsela is attenuated towards both apices and, therefore, this character does

not distinguish the genus *Taeckholmia* either. The third feature mentioned by Boulos in his diagnosis concerning the variability in the shape of the cypsels within the same capitulum is not seriously considered. This variability may be observed throughout the genus *Sonchus* and is probably due merely to small, genetic or developmental differences as are expressed in any plant or part of a plant. The cypsels of section *Atalanthus* are equally as homomorphic as those within section *Dendrosonchus*. The statement by Boulos that the cypsels of *Taeckholmia* species possess four ribs on each face is inaccurate. This condition does not exist in any of the species of subgenus *Dendrosonchus* s.l. Plate 3 shows the range in cypsel morphology for the two sections, *Atalanthus* (3a and b) and *Dendrosonchus* (3c and d) respectively. That Boulos should have used the feature of the cypsels possessing a protuberance surrounded by a white disc at the upper end to distinguish the genus *Taeckholmia*, as the sole character in a key, seems totally unjustified. This central protuberance is nothing more than the remains of the floret after it has broken away from the cypsel during maturation. This feature is illustrated by Plate 4. A slight protuberance was seen in *S. arboreus*, *S. platylepis* (Plate 4d) and *S. pinnatifidus* (Plate 4c) but not in any of the other members of either section. When the fruits are not fertilized the remnant of the floret at the tip of the cypsel is more likely to be found as it does not appear to detach itself as readily from the undeveloped cypsel.

Boulos (1972) gave a key to the genera which he recognised, thus stressing certain features discussed above which have been shown to have no taxonomic value at this level. His key to the genera was as follows:

- | | |
|---|---------------------|
| “1. Akène non comprimé (+ cylindrique) | <i>Babcockia</i> |
| 1. Akène comprimé | |
| 2. Akène pourvu au sommet d'un disque blanc à protubérance centrale | <i>Taeckholmia</i> |
| 2. Akene sanes disque blanc an sommet | |
| 3. Akène 0.5-1.75 mm de large | <i>Sonchus</i> |
| 3. Akène 2-3 mm de large | <i>Embergeria</i> ” |

I have little knowledge of the two Australasian species of *Embergeria* but at least two species of section *Dendrosonchus* have cypselas up to 2 mm in width. This part of the key is, therefore, also questionable.

POLLEN

The basic structure of the pollen grains in the subgenus *Dendrosonchus* s.l. is the same as that shown in the work by Pons and Boulos (1972) for *Sonchus* s.l. In distinguishing *Babcockia* from *Sonchus*, Boulos (1965) placed great emphasis on pollen morphology. Similarly, Boulos (1967a) used this as another feature to distinguish the genus *Taeckholmia* from *Sonchus*. In both cases no details were given but information was later provided by Pons and Boulos (1972).

The first detailed palynological study of the genus *Sonchus* was by Saad (1961). He acetolysed, chlorinated and embedded the pollen grains in glycerine jelly which, according to Pons and Boulos, causes a swelling of 20-30% in the overall sizes as compared to acetolysed and chlorinated grains mounted in pure glycerine, the technique used by the latter authors. In these two works the measurements of the pollen grains were obtained from light microscopy. In the present work the pollen grains of all species of *Dendrosonchus* s.l. were examined untreated, from fresh and herbarium material, under a scanning electron microscope. The measurements obtained from this method showed constant differences from those of Pons and Boulos of from 20 to 30%. The effect of the vacuum in the scanning electron microscope may have been to cause slight shrinkage, but as little damage to the grains was seen it is probable that the effect of acetolysis, chlorination and mounting in pure glycerine is greater on the disturbance of the grains. When some pollen grains were mounted in pure glycerine the measurements obtained with the light microscope were found to be equivalent to those given by Pons and Boulos. As the differences in dimensions were constant the relative sizes obtained from the two techniques are considered to be comparable.

Saad (1961) found four types of pollen grain in the genus *Sonchus*. Each type was based upon the differences in the polar thickenings. Type 3 was stated to be the most common in subgenus *Dendrosonchus* although types 2 and 4 were also recorded. Type 3 is that in which the polar thickenings are small, triangular areas surrounded by three large polar lacunae which are between the parapolar lacunae (cf. Plate 6A and B). Type 2 has moderately developed polar thickenings with smaller polar lacunae and type 4 has a much reduced polar thickening (cf. Plate 6C and 7D). Each type was illustrated by Saad. He concluded that the direction of evolution of the pollen grain types has been from type 1 to type 4. Eleven species of subgenus *Dendrosonchus* s.l. were examined by Saad and the largest pollen grains were found in *S. abbreviatus* Link (= *S. congestus*) and *S. bornmuelleri*.

Pons and Boulos (1972) gave a detailed table of the measurements and features of the pollen grains for the genus *Sonchus* and its allied genera. Comparative measurements were made in the present study for the subgenus *Dendrosonchus* s.l. The genus *Babcockia* was stated by Pons and Boulos to possess pollen grains which could be distinguished from those of *Sonchus*. The characters used were the large size (38.9-42 μm), the thickness of the ridges (6-6.5 μm), the type 2-3 polar thickening and a large number of polar spines (18-22). In the present study the measurements, as explained above, were generally 20-30% smaller than those of Pons and Boulos. The measurements obtained from pollen grains of *S. platylepis*, however, showed a difference of up to 40%. The reason for this is not at all clear since, as explained above, the majority of other measurements were relatively comparable. The range of pollen sizes in the section *Dendrosonchus* is from 21.6 μm in *S. ustulatus* to 29.7 μm in *S. congestus* and *S. ortunoi*, with *S. platylepis* having a range in pollen diameter of 23.3 to 24.6 μm . Pons and Boulos also recorded a large size for the pollen grains of *S. hierrensis* (39-42 μm) which are, therefore, not separable, even in their own studies, from *S. platylepis*. The range in the thickness of the ridges in section *Dendrosonchus* is from 1.8 μm in *S. pinnatifidus* to 4.3 μm in *S. platylepis*. The range for *S. platylepis* is 2.8 to 4.3 μm which is a 50% difference between the measurements found here and those of Pons and Boulos as given above. *Sonchus hierrensis* has a range of 2.5 to 3.6 μm in its ridge thickness and, therefore, overlaps with that of *S. platylepis*. Pons and Boulos also showed *S. hierrensis* to have high ridges (3.9 μm). The type 2-3 polar thickening is present in *S. radicans* subsp. *gummifer* and *S. congestus* as well as in *S. platylepis* of section *Dendrosonchus* (cf. Plate 7C). Pons and Boulos found this type 2-3 range within *S. congestus* and *S. ustulatus* and it is, therefore, not a feature confined to *S. platylepis*. The range in the number of polar spines for section *Dendrosonchus* is from 4 in *S. ustulatus* to 22 in *S. brachylobus*. The highest number of polar spines was found by Pons and Boulos to be 25 in *S. hierrensis*. *Sonchus platylepis* (Plate 7C) was found here to possess 12-16 polar spines, a much lower number than was recorded by Pons and Boulos.

The genus *Taeckholmia* was distinguished by Boulos (1967a) from *Sonchus* with the aid of pollen characters. Pons and Boulos stated that the grains of the species within this genus are heteromorphic and have variable dimensions, polar thickenings and numbers of polar spines. They gave the diameter of the pollen (26-36.5 μm) as a distinguishing feature as well as the type 2-4 range in polar thickening. For comparisons of data only those species of sec-

tion *Atalanthus* which Boulos placed in *Taeckholmia* will be considered. A range in total diameter of these species is from 20.6 μm in *S. leptcephalus* subsp. *capillaris* to 24.6 μm in *S. arboreus* and *S. leptcephalus* subsp. *leptcephalus*. The range in total diameter of the other members of section *Atalanthus* is 22.6 μm in *S. pinnatus* subsp. *pinnatus* to 26.4 μm in *S. pinnatus* subsp. *canariensis*. As given above, the total range of diameter for the section *Dendrosonchus* is 21.6-29.7 μm and, therefore, there is almost a complete overlap with the dimensions of the genus *Taeckholmia*. The type 2-4 range in polar thickening, recorded by Pons and Boulos, was not seen in section *Atalanthus*. The usual type is the 3 or 4 which is also typical for the subgenus (Plate 6). Pons and Boulos recorded the type 1 polar thickening for *S. canariensis* (= *S. pinnatus* subsp. *canariensis*) and for *S. hierrensis*. Both of these taxa were found here to have the type 3 polar thickening.

Tetracolporate pollen has previously only been recorded for the subgenus *Sonchus* (Saad, 1961). In the present study three samples with tetracolporate pollen grains have been seen. A sample of *S. arboreus* from La Palma and one of its progeny grown in the greenhouse at Reading possessed a mixture of tricolporate and tetracolporate pollen (Plate 5A). The tetracolporate pollen was also seen in herbarium specimens (*Bramwell* 1180, *Kunkel* 1285, both held in RNG). These specimens were collected from Gran Canaria, were different morphologically and were considered by their respective collectors to be new species. They are, however, probably variants of *S. leptcephalus* subsp. *leptcephalus* as they have broader leaf-lobes, larger capitula and various other combinations of features not seen in any other collection of this subgenus. The presence of tetracolporate pollen may, therefore, be indicative of genetic abnormalities. The sample of *S. arboreus* from La Palma was taken from a very localized population of one or two individuals and may have retained this abnormality of the pollen without any adverse affects. Plates 5B and C show the equatorial and polar views respectively, of *S. pinnatus* subsp. *canariensis* to illustrate the typical structure of *Dendrosonchus* pollen.

Plate 6 shows polar views of three species from the section *Atalanthus*. A polar view of a pollen grain of *S. arboreus* with the type 3 polar thickening and 17 polar spines is shown in 6A. A pollen grain of *S. pinnatus* subsp. *pinnatus* with the type 3 polar thickening and 18 polar spines is shown in 6B. Plate 6C shows a pollen grain of *S. leptcephalus* subsp. *leptcephalus* with the type 4 polar thickening and 3 polar spines. Plate 7 shows the polar views of four species of section *Dendrosonchus*. Plate 7A is a pollen grain of *S. fauces-orci* with the type 3 polar thickening and 20 polar spi-

nes. Pollen of *S. congestus* with the type 3 polar thickening and 17 polar spines is shown in 7B. This species has the largest pollen grains encountered in this study. Plate 7C shows pollen of *S. platylepis* which possesses very high ridges, the type 2-3 polar thickening and 13 polar spines, and 7D is a pollen grain of *S. ustulatus* subsp. *maderensis* which has the smallest diameter and the lowest number of polar spines found within this section. It has the type 4 polar thickening and 4 polar spines.

With reference to the opinion of Saad (1961) that the evolution of the pollen has been from type 1 to type 4, it can be seen that within the two separate sections of *Dendrosonchus* the trend from type 3 to type 4 is apparent. This is in agreement with the lines of evolution which will be proposed on anatomical evidence in later papers. As so many differences, however, prevail in the qualitative as well as quantitative data between those recorded by Pons and Boulos and those given here, it is probable that the pollen surface features are so variable in this group as to be almost useless taxonomically. Thorough population studies in the field would be of immense value in clearing up this point.

DISCUSSION AND CONCLUSIONS

Throughout this study the two genera *Babcockia* and *Taeckholmia* have been critically reviewed in relation to the individual characteristics by which they have been recognised by Boulos. It is quite apparent that neither genus is of any taxonomic value and some doubt has also been mentioned concerning the validity of the genus *Embergeria*. The genus *Taeckholmia* might have been more acceptable if all the other members of section *Atalanthus* had been included. If this genus were accepted its correct name would have to be *Atalanthus* as it has priority over *Taeckholmia*.

A conflict has arisen in the literature concerning *Launaea* and *Sonchus* as to the use of the name *Atalanthus* for a genus. It was originally described by Don (1829) with *Prenanthes pinnata* L. and *P. spinosa* Vahl as its only members. *Prenanthes pinnata* L. is synonymous with *Sonchus leptcephalus* Cass., and Jeffrey (1966) has shown that *Prenanthes spinosa* Vahl is now known as *Launaea spinosa* (Forssk.) Schultz Bip. and Don's description was in no way based upon this distinct species. He suggested that Don's description was based upon *Lactuca spinosa* Lam which is a synonym of *Launaea arborescens* (Batt.) Murb. From the latin description it is obvious that the name *Atalanthus* applies to *Sonchus leptcephalus* and not to *Launaea arborescens* because Don described the pappus

as being composed of two types of seta, one longer and thicker than the other, and also the cypselas as being compressed. These being typical *Sonchus* features and not seen in *Launaea* it is difficult to understand how the conflict arose. All the features described by Don are applicable to *S. leptcephalus* whereas only a few of them are present in *Launaea arborescens*. Pomel (1874), Kirpichnikov (1964) and Boulos (1967a) all considered *Atalanthus* to be lectotypified by *Launaea arborescens* (Batt.) Murb. Only Jeffrey (1966) has previously recognised that *Atalanthus* should be lectotypified by *Prenanthes pinnata* L. and I am in full agreement with his decision. I have no intention, however, of retaining or even reorganising the boundaries of either of the genera recognised by Boulos for the reason that both possess all the typical defining characteristic of the genus *Sonchus* L. and in particular those of subgenus *Dendrosonchus* Webb ex Schultz Bip.

THE USE OF TAXONOMIC CATEGORIES

THE GENUS

There are a number of distinct characters which, when used together, consistently identify the genus *Sonchus* L. Briefly, these are the compressed and curved cypselas without beaks, the two types of seta in the pappus, the flattened and naked receptacle and the yellow ligules. Boulos split the group into four genera on the basis of leaf-lobe widths, numbers of florets, lengths of corollas, sizes of capitula and cypselas, all of which are characters shown to be highly variable. The pollen and cypselas characters chosen by Boulos to distinguish the genera *Babcockia* (Boulos, 1965) and *Taeckholmia* (Boulos, 1967a) have equally been shown to be of no taxonomic significance at this level. The members of these two genera are treated here as belonging to the genus *Sonchus* as they all possess the combination of characters which define the group.

THE SUBGENUS

The subgenus *Dendrosonchus* Webb ex Schultz Bip. can clearly be distinguished from all others of the genus on the basis of the woody habit of its members. A few members of the subgenera *Sonchus* and *Origosonchus* Boulos also have a slightly woody caudex but the habit of these plants is generally much more reduced than any found in the woody, Macaronesian element. The leaves of the subgenus *Dendrosonchus* are crowded at the apices of the woody caudices or

branches and the general construction of the plants is pachycaulous. Pachycauls have a wide pith, a broad apex, few branches and rosettes of leaves at the ends of these branches. None of the species of the subgenus *Sonchus* or *Origosonchus* have this pachycaul construction. The pith of these plants has a constant diameter from base to apex. The leaves of the members of *Dendrosonchus* are generally petiolate or sheathing and sessile. Only the cauline leaves, of which there are a few confined to the inflorescence-stem, are auriculate. The members of the other two subgenera have auriculate leaves which are mostly cauline.

THE SECTION

It is apparent that within the subgenus *Dendrosonchus* two distinct morphological groups exist. The differences between these have been recognised by various authors in the earlier literature, as discussed above. The exact delimitation of these groups has differed from treatment to treatment, leading to confusion as to the affinities of one species to another. Essentially, the differences between the two groups are in the capitula and leaf morphologies. The section *Atalanthus* (D. Don) DC. can be recognised by the shrubby or low, tree-like habit and the petiolate, pinnatisect leaves with linear or filiform leaf-lobes. All members are glabrous and have capitula which are the smallest for the genus. The section *Dendrosonchus* also has members with a shrubby or low, tree-like habit as well as a caudex (or short, woody-stemmed perennial habit. The leaves may also be dissected but the leaf-lobes are either triangular or ovate and they are sheathing and sessile or rarely petiolate. Some members of this section have involucre bracts and leaves with a white, floccose-tomentose indumentum and the capitula are the largest for the genus.

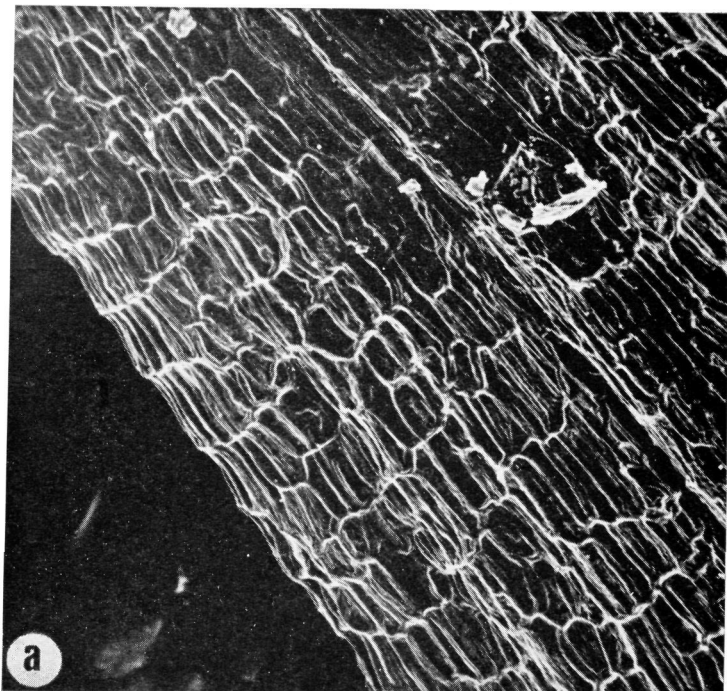
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REFERENCES

- AITON, W. 1789. *Hortus Kewensis; or, a catalogue of the plants cultivated in the Royal Botanic Gardens at Kew*. Ed. 1, 3: 116. London.
- ALDRIDGE, A. E., 1975. *Taxonomic and anatomical studies in Sonchus L. subgenus Dendrosonchus Webb ex Schultz Bip. and related genera*. Unpubl. PhD Thesis, University of Reading.
- BOULOS, L., 1960. Cytotaxonomic studies in the genus *Sonchus* 2. The genus *Sonchus* a general systematic treatment. *Bot. Not.*, 113(4): 400-20.
- BOULOS, L., 1965. *Babcockia*, un nouveau genre de Composées des îles Canaries. *Bull. Jard. bot. État*, 35: 63-6.
- BOULOS, L., 1967a. *Taekholmia*, a new genus of Compositae from Canary Islands. *Bot. Not.*, 120: 95-108.
- BOULOS, L., 1967b. Nomenclatural changes and new taxa in *Sonchus* from the Canary Islands. *Nytt Mag. Bot.*, 14: 7-18.
- BOULOS, L., 1972. Révision systématique du genre *Sonchus* L. s.l. I. Introduction et classification. *Bot. Not.*, 125: 287-305.
- BOULOS, L., 1973. Révision systématique du genre *Sonchus* L. s.l. IV. Sous-genre 1. *Sonchus*. *Bot. Not.*, 126: 155-96.
- BOULOS, L., 1974a. Révision systématique du genre *Sonchus* L. s.l. V. Sous-genre 2. *Dendrosonchus*. *Bot. Not.* 127: 7-37.
- BOULOS, L., 1974b. Révision systématique du genre *Sonchus* L. s.l. VI. Sous-genre 3. *Origosonchus*. Genres *Embergeria*, *Babcockia* et *Taekholmia*. Species exclusae et dubiae. *Index. Bot. Not.*, 127: 402-51.
- BRAMWELL, D., 1970. On some recent nomenclatural changes in the Canary Islands Flora. *Cuad. Bot. (Gran Canaria)*, 9: 17-19.
- CAVANILLES, A. J., 1801. De las plantas que el ciudadano Augusto Broussonet colectó en las costas septentrionales de la Africa y en las Canarias. *Anales C. Nat.*, 4: 78-9.
- DE CANDOLLE, A. P., 1838. *Prodromus Systematis naturalis Regni vegetabilis*, 7(1): 184-9. Paris.
- DON, D., 1829. An attempt at a new classification of the Cichoraceae with some observations on the geographical distribution of this family. *Edinburgh New Philos. J.*, 6: 305-12.
- DUMONT DE COURSET, G. L. M., 1811. *Le Botaniste Cultivateur*. Ed. 2, 4: 9. Paris.
- EBEL, F., 1971. Zur Morphologie einiger Kanarischen *Sonchus* - Arten. *Wiss. Z. Martin-Luther-Univ. Halle-Wittenberg*, 20(2): 39-71.
- FONT QUER, P., 1948. *Plantae novae. Collect. Bot. (Barcelona)*, 2: 201-3.
- HUMPHRIES, C. J., 1976. A revision of the Macaronesian genus *Argyranthemum* Webb ex Schultz Bip. (Compositae - Anthemideae). *Bull. Br. Mus. nat. Hist. (Bot.)*, 5(4): 147-240.
- INTERNATIONAL CODE OF BOTANICAL NOMENCLATURE, 1972. Adopted by the eleventh International Botanical Congress. Seattle, 1969. Utrecht.
- JEFFREY, C., 1966. Notes in Compositae I. The Cichoreae in East Tropical Africa. *Kew Bull.*, 18: 475.
- KIRPICHNIKOV, M. E., 1964. In E. G. BOBROV & N. N. TSVELYOV eds. *Flora URSS*, 29: 241-2.
- KNOCHE, H., 1923. *Vagandi Mos. Reiseskizzen eines Botanikers I. Die Kanarische Inseln*, : 244. Strasbourg and Paris.
- LINK, H. F., 1825. *Sonchus gummifer*. In L. VON BUCH *Physikalische Beschreibung der Canarischen Inseln*, : 146. Berlin.
- LINNÉ, C. VON, FIL., 1781. *Supplementum Plantarum Systematis Vegetabilium Editionis XIII, Generum Plantarum Editionis VI et Specierum Plantarum Editionis II*, : 346-7. Brunsvigae.
- LOWE, R. T., 1831. *Primitiae Faunae et Florae Maderae et Portus Sancti; sive Species quaedam novae vel hactenus minus rite cognitae Animalium et Plantarum in his Insulis degentium breviter descriptae* (reprinted from *Trans. Cambridge Philos. Soc.*, 4, 1831), : 22-3. Cambridge.
- LOWE, R. T., 1851. *Primitiae et Novitiae Faunae et Florae Maderae et Portus Sancti - Two memoirs on the ferns, flowering plants and land shells of Madeira and Porto Santo ... with an Appendix* (reprinted from *Trans. Cambridge Philos. Soc.*, 6, 1838), : 22-3. London.
- LOWE, R. T., 1868. *A Manual Flora of Madeira and the Adjacent Islands of Porto Santo and the Desertas I. Dichlamydeae*. J. van Vörst, London.
- PITARD, C. J. & PROUST, L., 1908. *Les Iles Canaries. Flore de L'Archipel*. Paris.
- POMEL, A., 1874. *Nouveaux Matériaux pour La Flore Atlantique*, : 6-7. Paris and Alger.
- PONS, A. & BOULOS, L., 1972. Révision systématique du genre *Sonchus* L. s.l. III. Étude palynologique. *Bot. Not.*, 125: 310-19.

- RAUNKIAER, C., 1934. *The Life Forms of Plants and Statistical Plant Geography*. Clarendon Press. Oxford.
- ROUX, J. & BOULOS, L., 1972. Révision systématique du genre *Sonchus* L. s.l. II. Étude caryologique. *Bot. Not.*, 125: 306-9.
- SAAD, S. I., 1961. Pollen morphology in the genus *Sonchus*. *Pollen & Spores*, 3(2): 247-60.
- SCHULTZ BIPONTINUS, C. H., 1849-50. In P. B. WEBB & S. BERTHELOT, 1836-50, *Phytographia Canariensis*, Vol. 3(2) of *Histoire Naturelle des Iles Canaries*. Paris.
- SVENTENIUS, E. R. S., 1960. *Additamentum ad Floram Canariensem I*. Inst. Nac. Invest. Agronom. Minist. Agricult. Madrid.
- SVENTENIUS, E. R. S., 1968a. In J. BERMEJO, J. L. BRETON, A. G. GONZALEZ & A. VILLAR DEL FRESNO, Terpenoides de los *Sonchus* VII. Lactonas sesquiterpénicas de *Sonchus hierrensis* (Pit.) Svent., stat. nov. var. *benehoavensis* Svent. var. nova. *An. R. Soc. esp. Fis. Quim.*, 64: 893.
- SVENTENIUS, E. R. S., 1968b. *Plantae macaronesienses novae vel minus cognitae*, 1: 1-18.
- WARMING, E., 1909. *Oecology of Plants. An Introduction to the Study of Plant Communities*. Oxford.
- WARMING, E., 1923. Ökologiens Grundformer. Udkast til en systematik Ordning. *Kongel. Dansk. Vidensk. Selsk. Naturvidensk. Math. Aft. V*, 8.
- WEBB, P. B., 1849. *Spicilegia Gorgonea* or a catalogue of all the plants as yet discovered in the Cape de Verd Islands. In W. J. HOOKER & J. D. HOOKER eds. *Niger Flora*, : 144-5. London.
- WEBB, P. B. & BERTHELOT, S., 1836-50. *Phytographia Canariensis*. Vol. 3 (2) of *Histoire Naturelle des Iles Canaries*. Paris.
- WILLDENOW, C. L., 1807. *Sonchus congestus*. In *Ges. Naturf. Freunde Berlin Mag.*, 1: 136.



100 μm

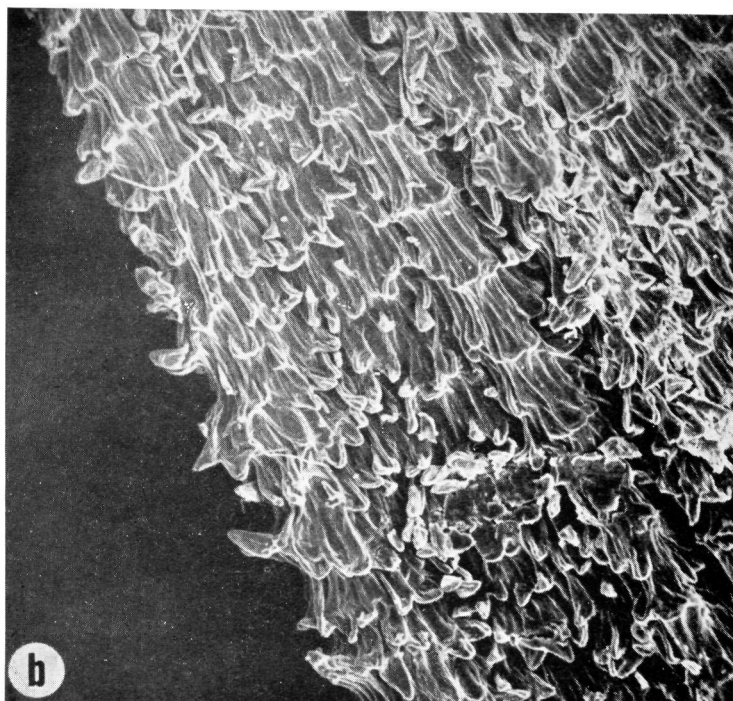
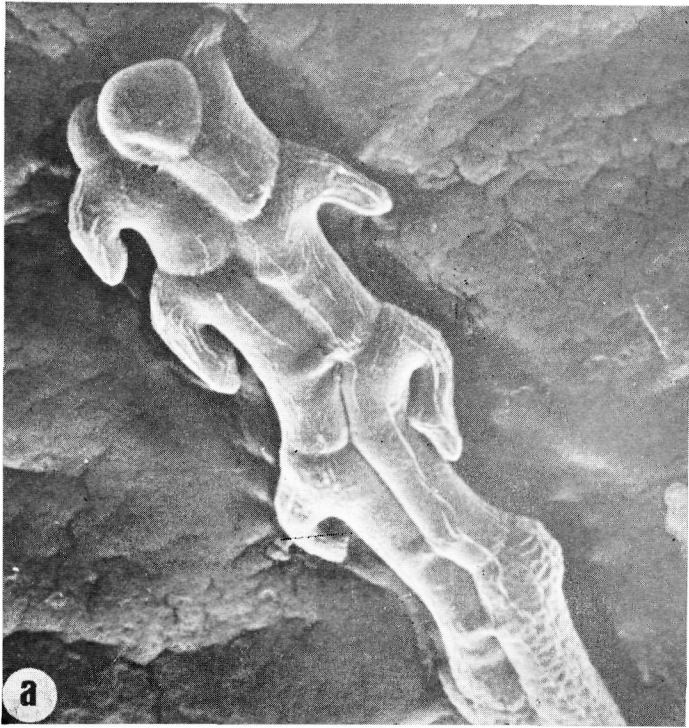
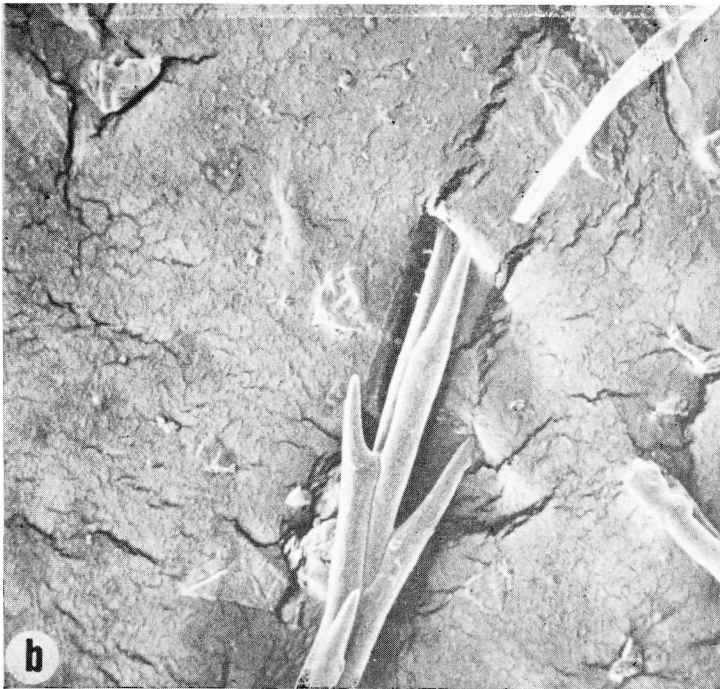


Plate 1 Cypsel surfaces. a. *Sonchus brachylobus*. b. *S. pinnatifidus*.

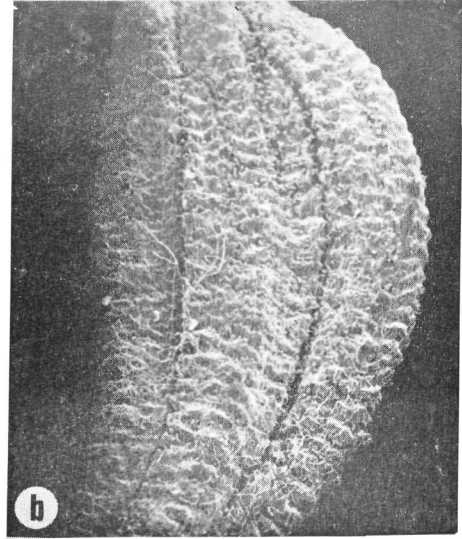
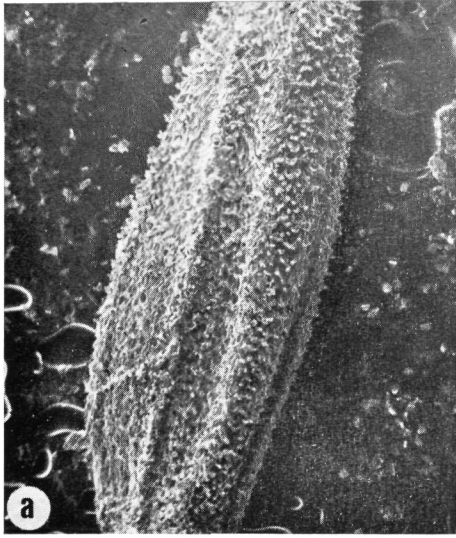


10 μm



20 μm

Plate 2 Pappus setae. a. Typical hair tip. b. Typical bristle tip.



0,5 mm

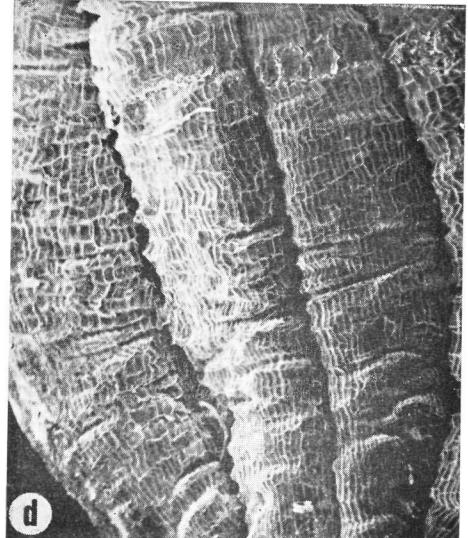
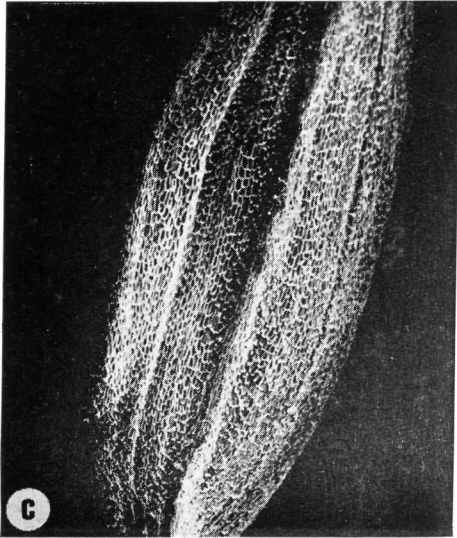
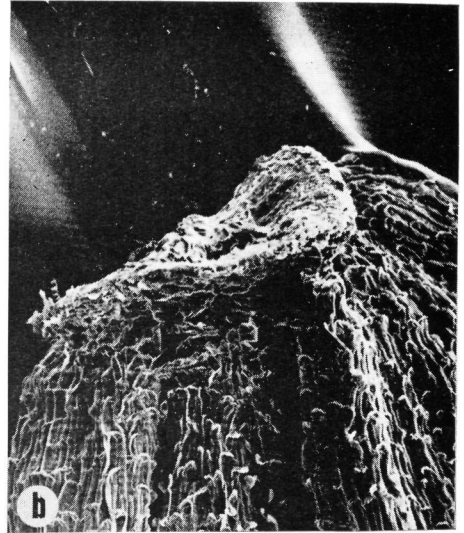
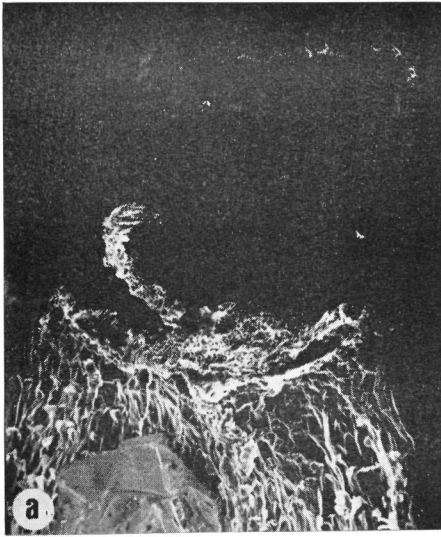


Plate 3 Cypselas. a. *Sonchus arboreus*. b. *S. pinnatus* subsp. *canariensis*. c. *S. brachylobus*. d. *S. acaulis*.



0.1 mm

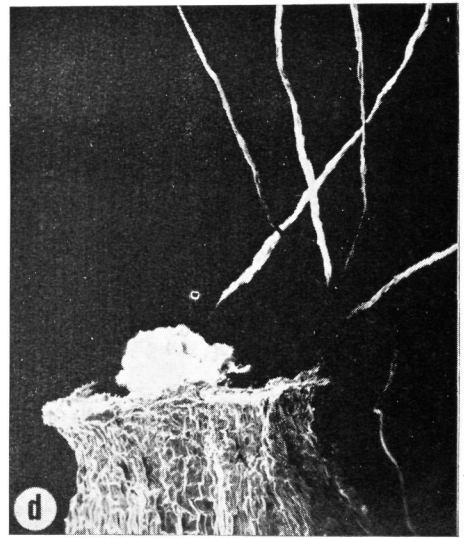
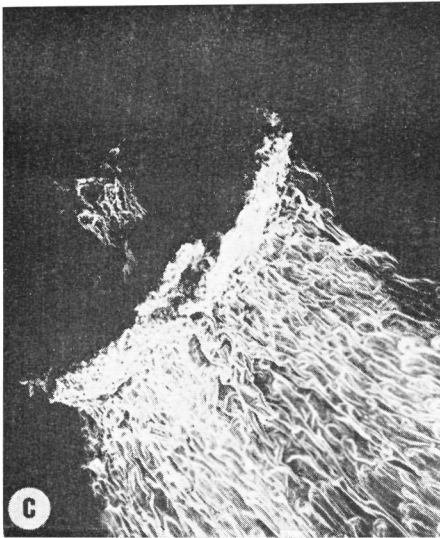
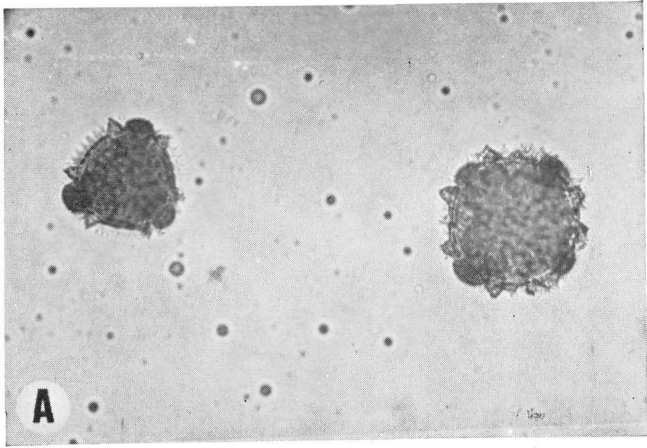
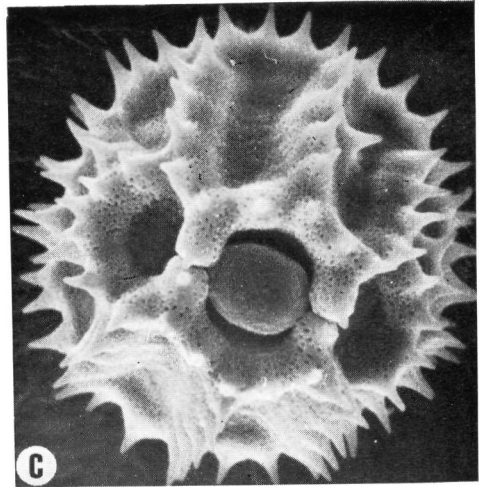
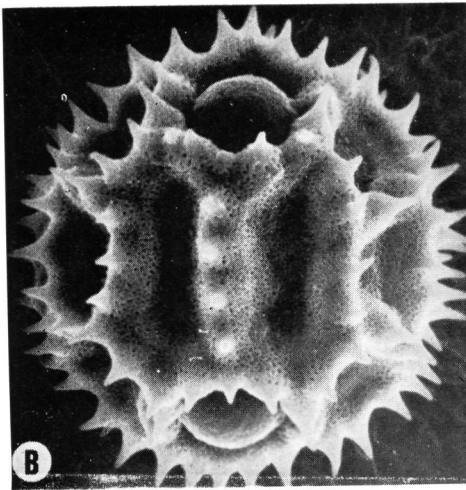


Plate 4 Cypsel apexes. a. *Sonchus leptocephalus* subsp. *capillaris*. b. *S. radicans* subsp. *radicans*. c. *S. pinnatifidus*. d. *S. platylepis*.

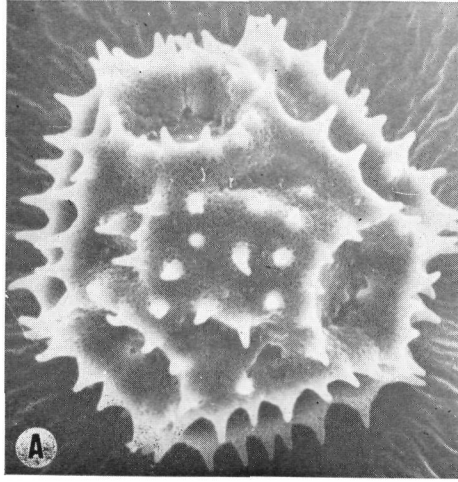


30 μm



6 μm

Plate 5 Pollen form and wall sculpturing. A. Tetracolporate and tricolporate pollen in *Sonchus arboreus*. B. Typical equatorial view. C. Typical poral view.



6 μm

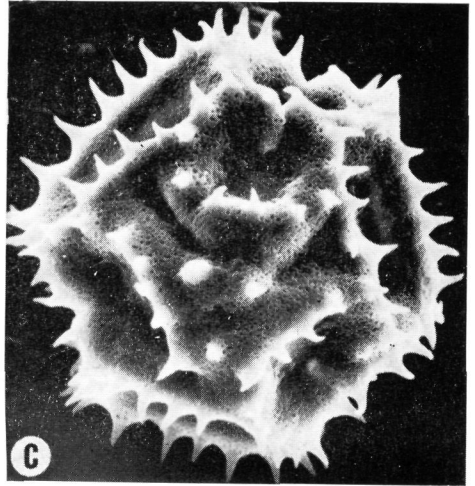
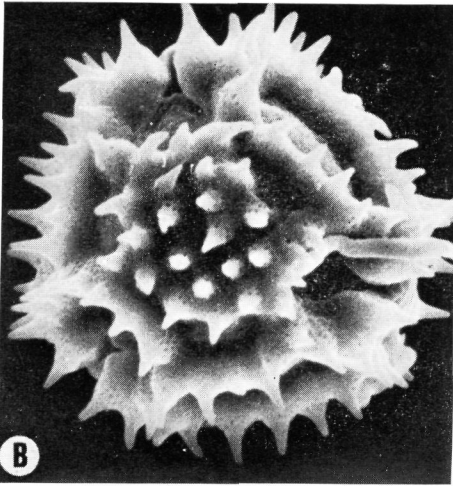
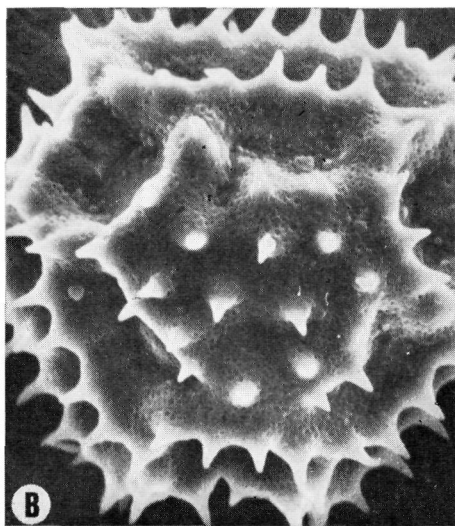
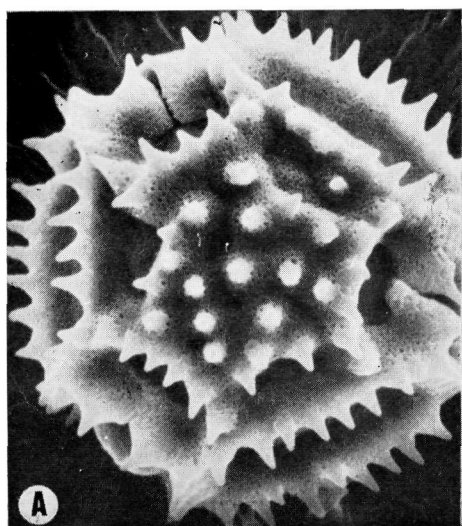


Plate 6 Pollen (polar view) - section *Atalanthus*. A. *Sonchus arboreus*. B. *S. pinnatus* subsp. *pinnatus*. C. *S. leptcephalus* subsp. *leptocephalus*.



6 μm

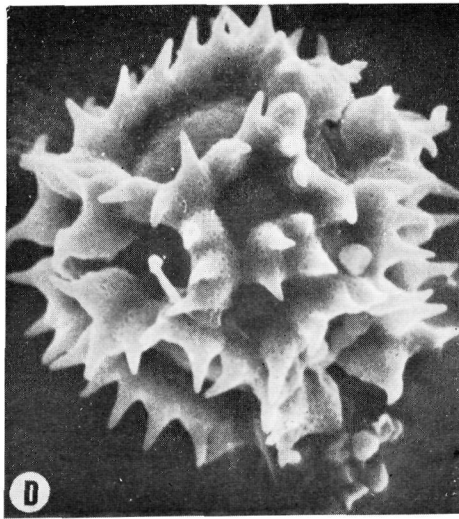
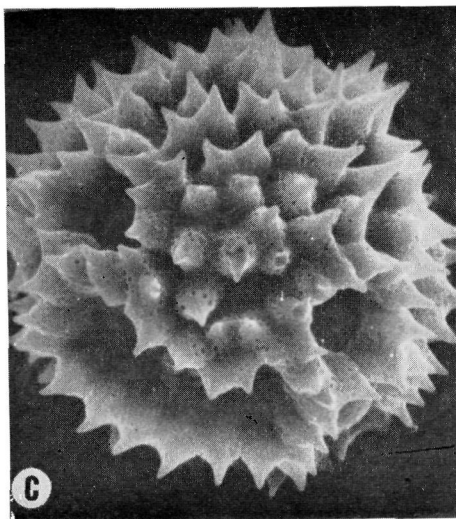


Plate 7 Pollen (polar view) - section *Dendrosonchus*. A. *Sonchus fauces-orci*. B. *S. congestus*. C. *S. platylepis*. D. *S. ustulatus* subsp. *maderensis*.