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3

T. Halvorsen & L. Borgen

The perennial Macaronesian species of Bubonium (Compositae – Inuleae).

1986



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Six perennial Macaronesian species are recognized in *Bubonium* J. Hill emend. Briq.: the Cape Verdian *B. daltonii* (Webb) T. Halvorsen, with two subspecies, ssp. *daltonii* and ssp. *vogelii* (Webb) T. Halvorsen, and *B. smithii* (Webb) T. Halvorsen; and the Canarian *B. intermedium* (DC.) T. Halvorsen & Wikl., *B. graveolens* (Forssk.) Maire, with two subspecies, ssp. *odorum* (Schousb.) Wikl. and ssp. *stenophyllum* (Link) T. Halvorsen, *B. schultzii* (Bolle) Sventenius and *B. sericeum* (L.f.) T. Halvorsen & Wikl. Four Mediterranean annuals are superficially treated for Macaronesia: *B. aquaticum* (L.) Hill, *Asteriscus maritimus* (L.) Less., *A. hierochunticus* (Michon) Wikl. , and *A. spinosus* (L.) Sch. Bip. A key to the Macaronesian *Bubonium* species is provided. The chromosome number n=7 is reported for all the *Bubonium* species in Macaronesia;in *B. graveolens* ssp. *odorum*, *B. daltonii* ssp. *vogelii*, and *B. smithii* for the first time. The chromosome number n=6 is confirmed for *Asteriscus maritimus*. The self fertile annuals are not cross compatible with the other species. Among the predominantly self incompatible perennials internal barriers to gene exchange are weak. Only *B. schultzii* seems genetically isolated. Between the other perennials the crossability is complete and hybrid fertility high between species from the same archipelago, but reduced between species from different archipelagos. The present occurrence of the Canarian species *B. sericeum* and *B. intermedium* and the Cape Verdean *B. daltonii* and *B. smithii* seems relict. These frutescent endemics probably belong to an old element in the Macaronesian flora.

Keywords: Bubonium, Macaronesia, Taxonomy, Chromosome numbers, Cross compatibility, Variability.

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INTRODUCTION

Asteriscus Mill. s. lat. of the Compositae-Inuleae is distributed in the Macaronesian, Mediterranean, and Saharo-Sindian flora regions. It is placed in the *Inula* group of genera in the subtribe Inulinae (Merxmüller et al. 1977). The delimitation of subtribes in the Inuleae has been considered relatively simple (op. cit.), but deviating views have always been found in the generic delimitation.

The *Inula* group is characterized by mainly ligulate female florets, styles with rounded to obtuse arms and sweeping hairs in the upper parts (Merxmüller et al. 1977). Most of the genera in this group have a Mediterranean distribution centre and the basic chromosome numbers x=9 or x=10 (op. cit.). Exceptions are a few genera like *Asteriscus* s. str., *Bubonium* J. Hill emend. Briq. and *Pallenis* Cass., which have lower basic chromosome numbers (x=7,6,5) and are related to predominantly African genera (op. cit.).

The species previously recognized in *Asteriscus* s. lat. are listed below. According to their distribution, the species can be placed in six groups. Those perennials occurring solely in the Macaronesian flora region: the Canary Islands, the Cape Verde Islands and the Moroccan enclave (cf. Sunding 1979) (group 1), are revised. *Asteriscus odorus*, which has a Canarian-Moroccan distribution (group 2) is treated for the Canary Islands only. These species are marked +. In addition the Mediterranean annuals reaching the Macaronesian archipelagos are superficially studied and marked (+).

1) Macaronesian species
   + *A. daltonii* (Webb) Walp. (Cape Verde Islands)
   + *A. intermedius* (DC.) Pitard & Proust (Canary Islands)
   + *A. sericeus* (L.f.) DC. (Canary Islands)
   + *A. schultzii* (Bolle) Pitard & Proust (Canary Islands)
   + *A. smithii* (Webb) Walp. (Cape Verde Islands)
   + *A. stenophyllus* (Link in Buch) O. Kuntze (Canary Islands)
   + *A. vogelii* (Webb) Walp. (Cape Verde Islands)
2) Canarian-Moroccan species
   + *A. odorus* (Schousb.) DC.
3) Mediterranean-Macaronesian species
   (+) *A. aquaticus* (L.) Less.
   (+) *A. maritimus* (L.) Less.
   (+) *A. spinosus* (L.) Sch. Bip. (*Pallenis spinosa* (L.) Cass.)
4) Canarian-Saharo-Sindian species
   (+) *A. hierochunticus* (Michon) Wikl. (*A. pygmaeus* Coss. & Kral.)
5) Moroccan species
   A. imbricatus (Cav.) DC.
   A. pinifolius Maire & Wilczec
6) Saharo-Sindian species
   A. graveolens (Forssk.) Less.
   A. schimperi Boiss.

The taxonomic importance of fruit anatomy in the group was shown by Briquet (in Briquet & Cavillier 1917). More recently, Merxmüller & Grau (1977) investigated and compared about 25 genera of the *Inula* group with special respect to the fruit wall anatomy. Their work suggested splitting *Asteriscus* s. lat. into two genera, *Asteriscus* s. str. and *Bubonium*.

Baagøe (1977, 1978) compared ligule microcharacters in the Inuleae-Inulinae and found *Asteriscus* s. str. (*A. maritimus* and *A. pygmaeus*) and *Pallenis spinosa* noteworthy because of their adaxial epidermis cells with crested outer walls. The rest of the *Inula* group has a more rugose cuticle.

The present investigation is restricted to a local flora. It has been difficult to establish the generic delimitation for the species in question, but our results concerning fruit wall anatomy, karyology and crossability support a splitting of *Asteriscus* s. lat. and a grouping of the x=7 species in the separate genus *Bubonium*.

Parallel with our investigation, Wiklund (1983, 1985, in press) has tried to circumscribe the genera in *Asteriscus* s. lat. by a reconstruction of the species phylogeny, using among others the principles of Henning (1966). Her results further support a splitting of *Asteriscus* s. lat. The generic delimitation adopted by us is in accordance with Wiklund's circumscriptions.

The Macaronesian endemic species, the Canarian-Moroccan *A. odorus* and the Mediterranean-Macaronesian *A. aquaticus*, are thus referred to *Bubonium*, whereas the Mediterranean-Macaronesian *A. maritimus* and *A. spinosus* are retained in *Asteriscus* s. str. together with the Canarian-Saharo-Sindian *A. hierochunticus*. Among the remaining species in *Asteriscus* s. lat., *A. pinifolius* has been removed to the monotypic genus *Ighermia* (Wiklund 1983) and the others, *A. imbricatus*, *A. graveolens*, and *A. schimperi*, will be included in *Bubonium* by Wiklund (in press). Wiklund (in press) has lumped *B. odorum* and *B. graveolens* and reduced *A. schimperi* to synonymy with *B. graveolens* ssp. *graveolens*. *B. odorum* thus constitutes a subspecies only, *B. graveolens* (Forssk.) Maire ssp. *odorum* (Schousb.) Wikl. We have, with the permission of Wiklund, incorporated her combinations in this paper.

HISTORICAL OUTLINE

Tournefort (1700) introduced the generic name *Asteriscus*. He used flattened ray-cypselas as an important generic character, but this character is found in *A. spinosus* only.

Linnaeus (1753) described and included many widely different species in the genus *Buphthalmum* L., among them three species of *Asteriscus* s. lat., i.e. *Buphthalmum aquaticum* L., *B. maritimum* L. and *B. spinosum* L. Linné filius (1781) gave the first description of a Canarian endemic species, *Buphthalmum sericeum* L.f., which was discovered by Francis Masson in Fuerteventura and introduced to Kew Gardens in 1779.

Miller (1754) took up many of Tournefort's generic names and validly published *Asteriscus*. His circumscription is in accordance with that of Tournefort (1700), who regarded *A. spinosus* as typical for the genus.

The generic name *Bubonium* was introduced by J. Hill (1761). His description states: "The scales of the cup are dissimiliar and the lower range is long and leafy". This delimitation is too weak against *Buphthalmum* L. Following Linneaus (1753), he also included species now considered to belong to the Central American genus *Borrichia* Adans.

Necker (1790a) used unitary designations for his "species naturales" (today: genera) and introduced the name *Odontospermum*, which is not to be treated as a generic name unless validly published by a subsequent author (ICBN paragraph 20, cf. Stafleu & Cowan 1981). *Buphthalmum spinosum* L. was cited as a new "species naturales": *Athalmum* Necker (1790a).

Moench (1794) reinstated *Asteriscus* (Tourn.) Mill. His generic concept was narrow, and he gave superfluous names to species transferred from other genera, e.g. *Asteriscus sessilis* Moench (= *Buphtahlmum maritimum* L.).

Based on collections from Mogador, Morocco, Schousboe (1801) described *Buphthalmum odorum* Schousb. This species was later discovered in Gran Canaria by Webb & Berthelot (1844), but was wrongly reported from Porto Santo in the Madeira archipelago.

Cassini (1824-1825) established two new generic names, *Pallenis* Cass. and *Nauplius* Cass. The first has been widely applied to the annual *Asteriscus spinosus* (L.) Sch. Bip. (= *Pallenis spinosa* (L.) Cass.) while *Nauplius* Cass. has been applied by Webb (1839-1843) only.

Link (in Buch 1825) gave an account of two new species from the Canary Islands, *Buphthalmum stenophyllum* and *B. sericeum* Link, the latter a homonym for *B. sericeum* L.f. (Linné filius 1781).

Buphthalmum aquaticum L. and *B. maritimum* L. were validly transferred to *Asteriscus* by Lessing (1832) as *A. aquaticus* (L.) Less. and *A. maritimus* (L.) Less.

De Candolle (1836) reinstated *Asteriscus* sensu Moench (1794) and *Pallenis* sensu Cassini (1825). He gave a rather comprehensive treatment of the Canarian and Moroccan species of *Asteriscus*. His species concept was wide. Within the single species *A. sericeus* (L.f.) DC. he recognized three varieties later considered to be distinct species, i.e. var. *latifolius* DC. (= *A. sericeus*), var. *intermedius* DC. (= *A. intermedius*) and var. *stenophyllus* (Link) DC. (= *A. stenophyllus*).

A comprehensive and detailed study of *Asteriscus* was done by Schultz Bipontinus (1844). He combined the efforts of Necker (1790a) and Tournefort (1700), circumscribing the genus *Asteriscus* by a single species, *A. spinosus*. The other species were placed in *Odontospermum* Neck., now validly published as a generic name. Eight species were cited, six of which were supposed to occur in the Canary Islands. De Candolle's (1836) varieties of *Asteriscus sericeus* (L.f.) DC. were all given the rank of species. Illustrations of these were published under the generic name *Nauplius* Cass. by Webb (1839-1843). Owing to the great influence of Webb & Berthelot (1836-1850) on the subsequent botanical work in the Canary Islands, the name

Odontospermum Neck. has been extensively applied to the Macaronesian species up to the last decade.

Based on collections by Chr. Smith 1816, Forbes 1822, J.D. Hooker 1839 and Vogel 1841 in the Cape Verde Islands, Webb (1849) gave the first descriptions of the Cape Verdean species. They were published under the generic name *Odontospermum* as *O. daltoni* Webb, *O. smithii* Webb, and *O. vogelii* Webb in W.J. Hooker's "Niger flora". The three Cape Verdean species were transferred to *Asteriscus* by Walpers (1852). Later Chevalier (1935) realized the variability within the critical species *Asteriscus daltonii* (Webb) Walp. and *A. vogelii* (Webb) Walp. He reduced the latter to a variety of the first: *Odontospermum daltonii* Webb var. *vogelii* (Webb) A. Chev.

The last species to be discovered in the Canary Islands, *Odontospermum schultzii* Bolle, was described by Bolle (1859) from Fuerteventura.

In their Canarian flora Pitard & Proust (1908) made two new combinations in *Asteriscus* of species previously ascribed to *Odontospermum*, *Asteriscus intermedius* (DC.) Pitard & Proust and *A. schultzii* (Bolle) Pitard & Proust.

Briquet (in Briquet & Cavillier 1917) made a generic distinction between *Asteriscus* and *Bubonium* based on cypsela anatomy, mainly the occurrence or absence of resin canals. He reinstated *Bubonium* Hill emend. Briquet to circumscribe species with resin canals in the cypselas. Species without resin canals were referred to *Asteriscus*. The monotypic genus *Pallenis* Cass. was maintained by Briquet. Despite Briquet's precise treatment of these genera his views have not been widely adopted, probably because characters concerning fruit anatomy have been difficult to observe and use in practical floras. Only Maire (1936), for the Moroccan species, and Sventenius (1969), for *Bubonium schultzii*, followed Briquet. Merxmüller et al. (1977) and Merxmüller & Grau (1977) treated *Bubonium* as a section of *Asteriscus*.

MATERIAL

Material from the following herbaria (Holmgren et al. 1981) has been studied: B, BM, C, COI, FI-W, FR, G, GB, GOET, H, K, L, LE, LISC, LISJC, LISU, LY, MA, MO, MPU, NY, O, P, US, WAG, and the private collections of Wolfram Lobin, Frankfurt, from the Cape Verde Islands.

A major part of the *Bubonium* collections from the Cape Verde Islands is kept in the Botanical Museum, University of Oslo (O), collected by Per Sunding in 1972 and 1976, Liv Borgen and Øyvind H. Rustan in 1980 and Christian Brochmann and Øyvind H. Rustan in 1981-1982. The following abbreviations for collectors names are used: LB-Liv Borgen, CB-Christian Brochmann, RE-Reidar Elven, TH-Tore Halvorsen, ØHR-Øyvind H. Rustan, PS-Per Sunding. Herbarium material lacking precise locality data has been omitted, except in the case of types. Type collections of most Canarian species have been difficult to obtain. The material examined is listed for the rare species only, i.e. *Bubonium schultzii* and *B. smithii*. A complete record

of examined collections is kept in the Botanical Museum, University of Oslo (O).

Field studies have been undertaken in the Canary Islands by Halvorsen in 1979 and Borgen in 1967-1978; in the Cape Verde Islands by Borgen in 1980.

All the perennial Macaronesian species were grown in the greenhouses of the Botanical Garden, University of Oslo. Material of *Bubonium* from the Cape Verde Islands was grown from seeds collected by PS in 1976 and LB and ØHR in 1980. Seeds from the Canaries were received through seed exchange with other botanical gardens or collected by Halvorsen in 1979. Vouchers are kept in the Botanical Museum, University of Oslo (O), where the slides are also preserved.

METHODS

The morphological descriptions attempt to cover the total variation range, but, as they are based on selected herbarium specimens, rare extremes of some characters may be uncovered. For some species, especially *Bubonium schultzii* and *B. smithii*, the material was scarce and may not cover the total variation range. For each character 3-5 measurements were made per collection and the mean value calculated. The measurements in cm are given with an accuracy of 1 mm and those in mm with an accuracy of 0.1 mm. Figure 1 indicates how length and width of the reproductive parts were measured.

Floral parts were dissected and studied in a stereomicroscope after being boiled in water. Small structures were studied microscopically and drawn after mounting in Hoyer's solution. Leaf surfaces were studied after soaking in 10% KOH. Lignification was studied in the leaf petioles; free-hand sections were made and put into a saturated aqueous solution of phloroglucinol for a few minutes and covered with concentrated HCl turning lignified tissue bright purple-red (after Radford et al. 1974). Median cross-sections of cypselas were cut at 20-30 µm either on a freezing-microtome and embedded in Hoyer's solution; or on an ultra-microtome, embedded in paraffin after soaking in sodium dodecylsulphate (sodium laurylsulphate) for fourteen days, and stained in safranin and fast green (after Dittrich 1969).

The morphological variation in 60 specimens belonging to 11 populations of the *Bubonium graveolens* ssp. *odorum*- ssp. *stenophyllum* complex in Gran Canaria were examined by numerical methods. The material for the numerical analyses comprised 10 specimens from two populations of *B. graveolens* ssp. *odorum*; 38 specimens from eight populations of *B. graveolens* ssp. *stenophyllum*; and 12 specimens from a mixed population (Appendix 3).

Seven characters were used in the numerical analyses (Table 1): six continuous and two multistate ones. The characters were measured on organs of comparable development.

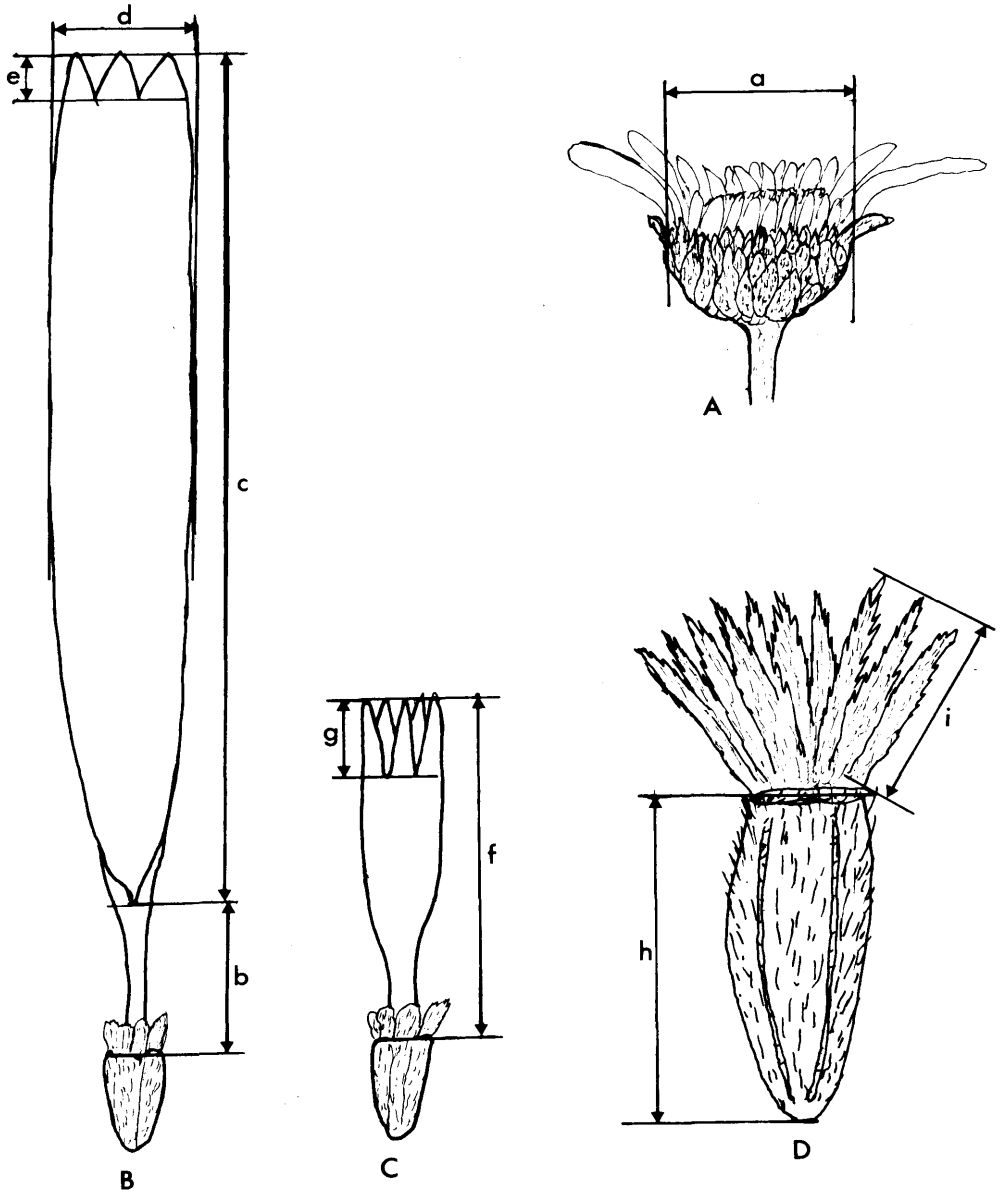


Fig. 1. Measurements of length and width. A: Capitula. B: Ray florets. C: Disc florets. D: Cypselas.

Table 1. Characters used in the numerical analysis of the *Bubonium graveolens* ssp. *odorum* - ssp. *stenophyllum* complex

Characters	Character states 0	0,5	1
1. Leaf width (mm)	continuous		
2. Leaf length: width ratio	continuous		
3. Leaf density (no. per 10 cm of stem apices)	continuous		
4. Involucre width mm	continuous		
5. Ligule length	continuous		
6. Habit	ascendent, lax	intermediate	erect, dense
7. Cypsela resin canals	undistinct	intermediate	distinct

The phenetic data analysis was performed on two data matrices, one on specimens and one on populations. Initially all characters were transformed to a uniform scale by ranging (Gower 1971). The similarity between all pairs of OTUs was then calculated by using Gower's general coefficient of similarity (Gower 1971). The similarity matrix produced was used as an input for an UPGMA cluster analysis (Sokal & Michener 1958) and a principal co-ordinate analysis (PCO) after Gower (1966). A distance diagram analysis (Wells 1980) was also performed with the ranged data as input.

The diagnostic key was produced by computer. Based on the distribution of character states among taxa, 13 characters were chosen as the diagnostically most valuable ones. These characters were recorded as binary with mutually exclusive states. The key constructing algorithm (Rustan 1983) produced a polythetic sequential key.

The data processing was carried out on a DEC-10 computer at the University of Oslo, using the programs BDP (Rustan 1982, 1984; filing data matrix, ranging, calculation of similarity), CLUSTAN (Wishart 1978, 1980; UPGMA), PRINCO (written by F. Albregtsen; PCO), PCOPLT (written by Ø.H. Rustan; plotting PCO results), and HYBRPL (written by F. Albregtsen; Wells distance diagram). The diagnostic key was constructed by KEYCON (Rustan 1983).

The drawings were made by Ø.H. Rustan and T. Halvorsen. Vegetative parts were drawn from dried material and floral parts from boiled material. Minute details of flower, cypsela, and indumentum morphology were illustrated by scanning photographs taken by E. Bråten at the Laboratory of Electron microscopy, University of Oslo.

The flowering periods were derived from the information on the herbarium labels, cultivation experiments and field observations.

Chromosome studies were made from root tip mitosis and PMC meiois. The root tips were either fixed in Navashin-Karpechenko, embedded in paraffin, microtomed cut at 8 µm and stained in crystal violet, or treated at 2-3^{0}C overnight, fixed in a 6:3:1 mixture of absolute alcohol: chloroform: acetic acid, stained in acetic orcein and squashed. Meiosis was studied in PMCs which were fixed in a 4:3:1 mixture of chloroform:alcohol:acetic acid, stained in acetic orcein and squashed. Some of the material was preserved in 70% alcohol for later staining.

The pollen stainability of parents and artificial hybrids was tested by 24 hours treatment in cotton blue-lactophenol. 100-200 pollen grains per capitulum were checked twice. Grains staining dark blue were considered viable.

The crossability between the parental species was determined by 1) seed set after crossing, shrinken and poorly developed cypselas being regarded as sterile, 2) germinability of the hybrid seeds, 3) viability of the hybrids, 4) meiotic observations, mostly at MI and AI, 5) pollen stainability in the hybrids, 6) backcrosses from F_1 to the parents.

To avoid other than intentional pollinations, the capitula of the desired parents were covered with small bags before anthesis. Self fertility of the parents was tested both by isolation experiments and by active pollination within the desired capitulum. Self fertilization never occurred without active pollination. Cross pollination was therefore done without emasculation and obtained by rubbing the stigmas of the female parent with anthers from the male parent. The flowers open centripetalously within a few days, and the pollination was therefore repeated for three to five successive days. The crossing attempts were reciprocal if enough material was available.

The capitula were kept in bags until the cypselas were ripe 1-2 months after pollination. Hybrid seeds were sown in March the following year. Germination usually occurred within two weeks. The hybrid seedlings were moved to individual pots about a month after sowing. A maximum of five F_1 plants were raised after each successfull combination.

DESCRIPTIVE TERMINOLOGY

The descriptive terminology follows, if not otherwise stated, Stearn (1973), Radford et al. (1974) and Swartz (1971). A few terms will be commented upon.

Outline and plane shapes. The terminology is adopted from the Systematics Association Committee for Descriptive Biological Terminology (1962).

Indumentum. The indumentum terms follow Payne (1978) and are defined as follows: Pubescent refers to any kind of hair-covering except glands and is the opposite of glabrous. Ciliate means fringed with conspicuous hairs on the margin. Hirsute means long, rather stiff trichomes. Scabrous is an indumentum which is rough and harsh to the touch, such as coarse papillae or trichome bases. Sericeous means covered with silky, usually appressed trichomes. Tomentose means densely wooly or pubescent with soft, matted, wool-like trichomes. Villose means long, soft, curly, but not matted hairs.

Cypselas. The term "achene" was defined by Necker (1790b) and redefined by De Candolle (1813) to describe the fruit derived from inferior ovaries. Here Mirbel's (1815) term cypsela is used in preferance to describe the bicarpellate coenocarpous inferior ovary of the Asteraceae (after Fahn 1967), since it is clearly not homologous with other monospermous fruits to which the former term was originally applied by Necker (1790b).

RESULTS

MORPHOLOGY AND ANATOMY

Habits and growth forms

The Macaronesian *Bubonium* species can be classified as chamaephytes or nanophanerophytes (Raunkiær 1934, 1936), except *B. aquaticum*, which is a therophyte. *Bubonium schultzii* was classified as a hemicryptophyte by Lems (1960b), but is here interpreted as a chamaephyte. The perennial *Bubonium species* form highly variable shrubs or shrublets. The branching pattern may vary within one species, as in *B. graveolens*, and even in one subspecies, as in *B. daltonii* ssp. *vogelii*. A lax, divergent branching is characteristic of *B. graveolens* ssp. *odorum*, *B. schultzii*, and *B. daltonii* ssp. *vogelii* growing in the arid coastal zones. *Bubonium daltonii* ssp. *vogelii* growing in the humid mountain zones forms more compact shrublets. Dense, compact branching occurs in *B. graveolens* ssp. *stenophyllum* and *B. sericeum*. These taxa grow in mountain slopes just below the cloud belt where the precipitation is higher than in the coastal regions. Large, regular, cushion-shaped shrubs are found in *B. sericeum* and *B. smithii*, which grow in the cloud belt. In these species, the branching pattern may approach the candelabra-form.

All species have solitary, terminal capitula. After flowering, vegetative growth is resumed by two alternate, lateral, and divergent branches beneath the capitulum (Fig. 2A). In some taxa suppression of one of the two lateral branches will result in lax and divergent branching, as in *B. graveolens* ssp. *odorum*, *B. schultzii*, and the coastal types of *B. daltonii* ssp. *vogelii*. In *B. sericeum* and *B. smithii* three to five lateral branches may radiate beneath the primordial central capitulum (Fig. 2B), resulting in more regular and candelabra-like branching.

In cultivation under greenhouse conditions all species revealed slight modifications in habit. Generally, the branches became more erect and the internodes longer. In addition, increased woodiness was observed in *B. graveolens* ssp. *odorum*, which may be due to the release from seasonality.

The cushion form found among chamaephytes like *B. odorum* ssp. *odorum* and *B. daltonii* ssp. *vogelii* have been interpreted as an ecological adaptation, giving the plant a favourable microclimate in arid and windy habitats (Quezel 1967), or as a result of drought damage (Sunding 1972). Sunding (1972) argues that the leaf shedding in the dry period of the year and the new formation of leaves when water supplies increase, promote the candelabra growth form characteristic of so many Macaronesian endemics.

However, such growth forms are also present in archipelagos like Juan Fernandez Islands, with no pronounced drought period (Skottsberg 1953). Therefore, the candelabra form might have other, probably historical, causes. This assumption is

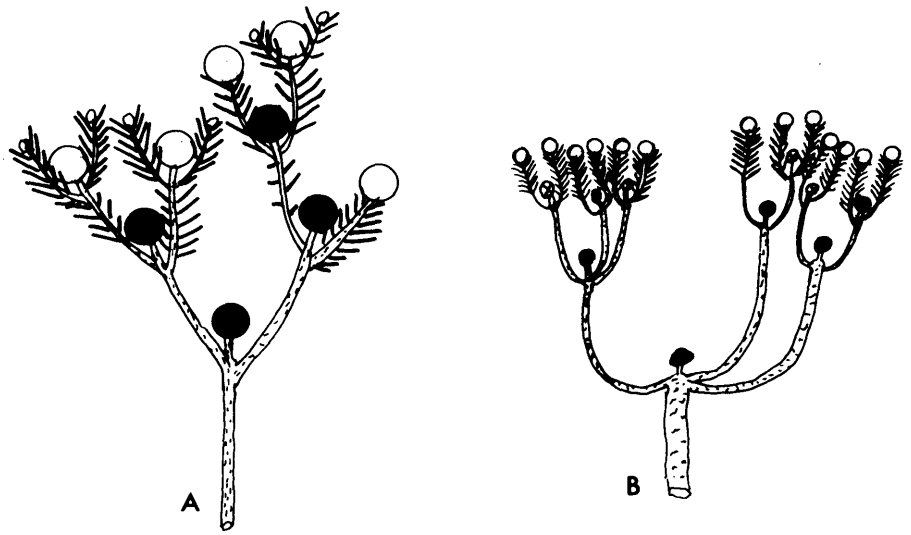


Fig. 2. Schematic drawings of growth forms in *Bubonium*. Withered capitula black. A: Common form. B: Form with three lateral branches developed beneath the primordial capitulum.

strengthened by the observation that cultivation and release of seasonality promotes woodiness in *B. graveolens* and candelabra form in *B. sericeum* (Meusel 1952).

Leaves

The leaves are alternate and the arrangement varies from distant (*B. graveolens* ssp. *odorum*) to densely crowded towards the apices (*B. graveolens* ssp. *stenophyllum*). In taxa with densely crowded leaves there is a high proportion of withered leaves in the lower part of the branches. These taxa are found in slightly more humid habitats than the distant leaved ones, as shown, for instance, by the ecological range of the two subspecies of *B. odorum* (p. 77). The Canarian *Bubonium* taxa show a reduction in leaf size from mountain xerophytic subhumid zone to arid south-facing lowland zone. A correlation between aridity and decreased mean leaf size is also found in other genera in the Canary Islands (cf. Børgesen 1924, Humphries 1979 a). Such small-leaved forms represent an adaptation to drought resistance.

The Macaronesian species have more or less entire leaves (Fig. 3). *Bubonium schultzii* occasionally has remotely toothed leaves (Fig. 3G) in the Canary Islands, whereas Moroccan specimens have more deeply toothed leaves (Davis 1980). The Moroccan sister-species, *B. imbricatum*, has double-serrate leaf

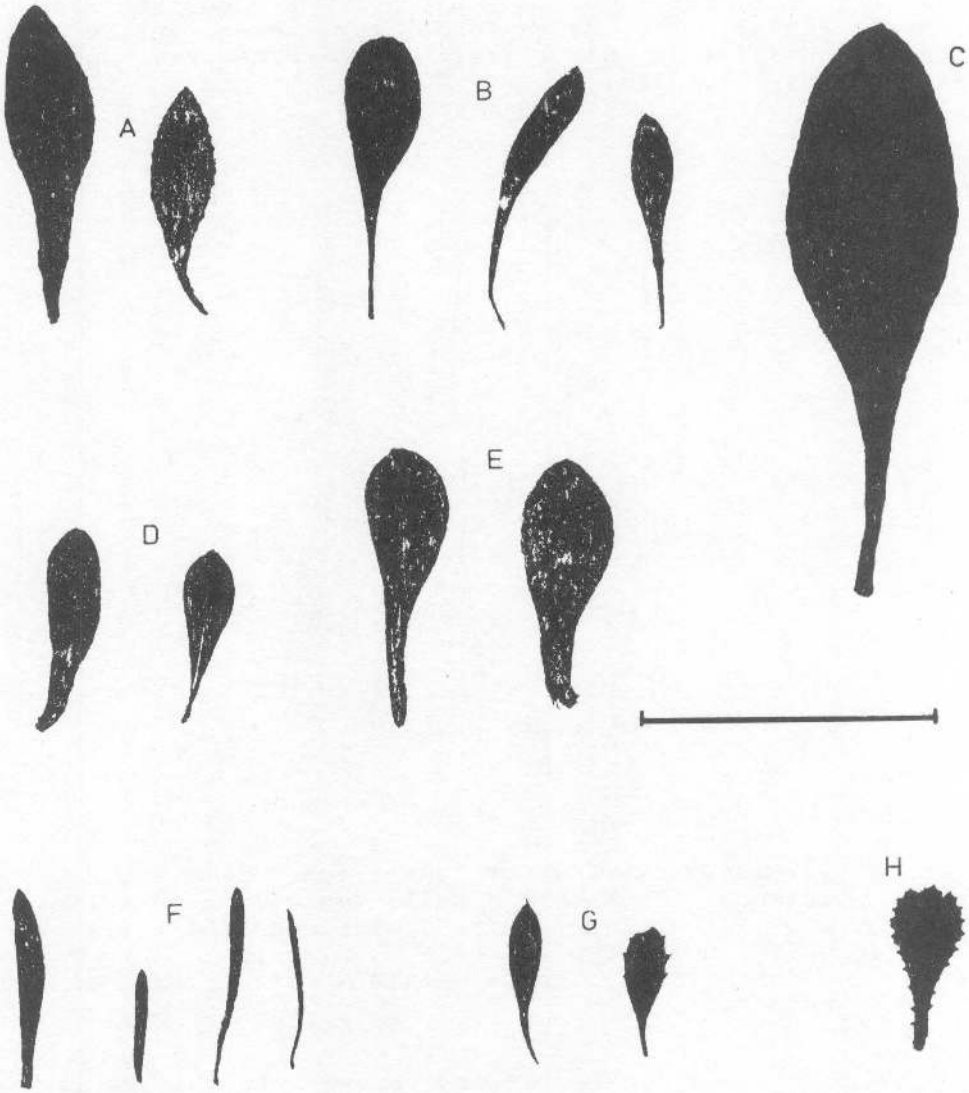


Fig. 3. Mature leaves of *Bubonium*. Scale 5 cm. A: *B. daltonii* ssp. *daltonii*. B: *B. daltonii* ssp. *vogelii*. C: *B. smithii*. D: *B. intermedium*. E: *B. sericeum*. F: *B. graveolens* ssp. *odorum*. G: *B. schultzii*. H: *B. imbricatum*.

margins (Fig. 3H). In *B. sericeum* young leaves have a denticulate margin towards the leaf apex, while mature leaves are entire or only minutely denticulate (Fig. 3E). The leaves of *B. graveolens* are occasionally very remotely toothed. This toothing occurs in both subspecies and is not a diagnostic

character for ssp. *odorum* only, as argued by Bramwell & Bramwell (1974). The Cape Verde taxa have entire leaves, except *B. daltonii* ssp. *daltonii* which may have denticulate leaf margins (Fig. 3A).

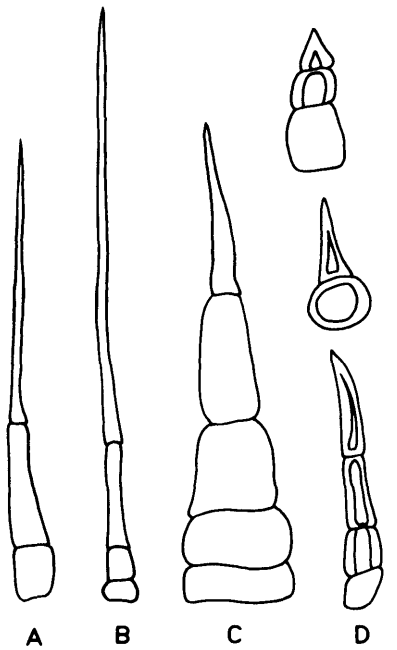


Fig. 4. Schematic drawings of leaf trichomes in *Bubonium*. A-B: Trichomes with oblong cells typical of *B. smithii* (A) and *B. sericeum* (B). C: Trichomes with transversely oblong cells typical of *B. daltonii*. D: Trichomes with short, thick-walled cells typical of *B. schultzii*.

The leaf shape varies from obovate to oblanceolate or linear with obovate to oblanceolate as the most common and probably ancestral condition (Fig. 3). The leaf bases are usually attenuate, but in some taxa weakly amplexicaule, e.g. *B. aquaticum* and *B. graveolens* ssp. *odorum*. The width of the leaf bases varies from 0.8 mm in *B. odorum* ssp. *stenophyllum* to 5.0 mm in *B. smithii*.

Leaf succulence occurs in the Moroccan desert species *B. imbricatum*, but is absent in all the Macaronesian species. However, the species of the driest lowland areas, e.g. *B. graveolens* ssp. *odorum*, *B. daltonii* ssp. *vogelii* and *B. schultzii*, have fleshier and thicker leaves than those growing in more humid habitats at higher altitudes. In particular some specimens of *B. daltonii* ssp. *vogelii* from Santo Antão, the Cape Verde Islands, have somewhat succulent leaves.

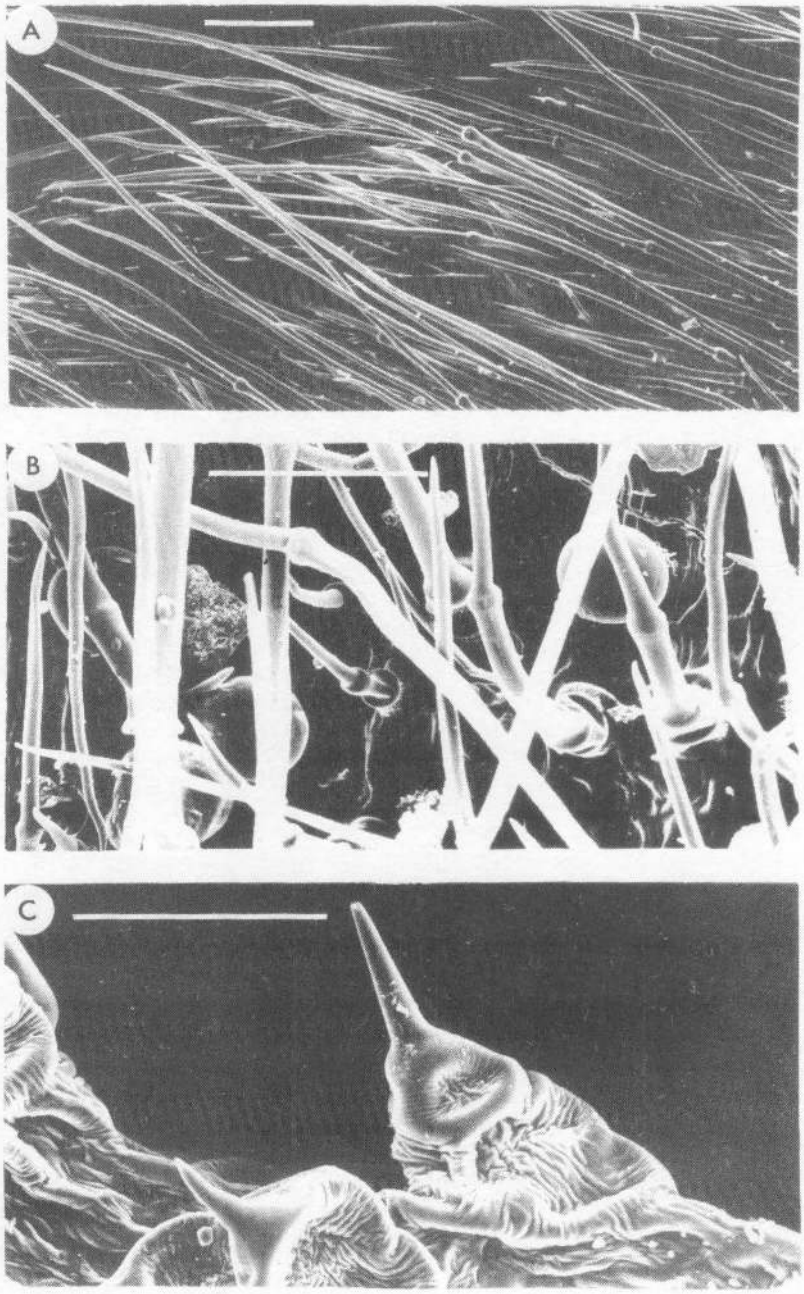


Fig. 5. SEM photographs of leaf indumentum in *Bubonium*. Scale: 20 µm. A: *B. sericeum*, TH 105 (O), sericeous indumentum. B: *B. aquaticum*, Kunkel 14867 (G), villose indumentum with glands. C: *B. schultzii*, TH 53 (O), scabrous indumentum.

The leaves are pinnately netted, most clearly on the ventral leaf surface. The veins are more conspicuous on the leaves of the Cape Verdean species than the Canarian ones. In all species the midrib is accompanied by three fibre bundles of sclerenchymatous (lignified) tissue. There are often smaller fibres running along the margins of the leaves. The strongest leaf lignification is found in *B. schultzii*. The relatively high proportion of lignified tissue in the narrow leaves of *B. graveolens* indicates leaf size reduction in this species with retention of lignification.

The leaf trichomes are simple, uniseriate, and multicellular up to four or five cells (Fig. 4 A-D). The apical cells are often somewhat osteolate, while the basal cells in most taxa are oblong or transversely oblong (Fig. 4 A-C). *Bubonium schultzii* has smaller, stiffer trichomes with a thick cell wall and a slightly serrulate basal cell (Fig. 4 D).

The indumentum is in most species densely sericeous consisting of very soft, appressed trichomes (Fig. 5A). The annuals and the species with a coastal distribution may have the indumentum reduced to a lax covering of soft hairs, i.e. villose (Fig. 5B). Scabrous leaves are found in *B. schultzii* only (Fig. 5C). The leaves are never quite glabrous as in the Moroccan species *B. imbricatum*.

All species except *B. schultzii* have glandular leaves, the glands being essentially of the same kind in all of them: multicellular, indistinctly differentiated into foot and head and situated level with the epidermis. The highest density of glands is found in *B. imbricatum* and *B. graveolens*. The latter has a strong, characteristic smell. The most sericeous species have the glands concentrated along the midrib near the base or apex of the leaf. Some of the taxa, like *B. graveolens* ssp. *stenophyllum* are characteristic of plant communities influenzed by grazing (Sunding 1972). *Buboniums* are always left by the animals and seem favoured by the grazing activity. The leaf glands seem to produce a secretion distasteful to grazing animals.

Involucre

In the endemic Macaronesian *Bubonium* taxa the involucre protects the buds in the capitula and does not aid dispersal, in contrast to the coriaceous and hygrochastic bracts found in *Asteriscus* s.str. A transitional condition is found in the annual *B. aquaticum*, which has outer bracts with a coriaceous base and leaf like upper parts.

The involucral bracts are arranged in many rows, most often four or five. The outermost bracts are usually leaflike, varying in length from 5 to 20 mm, with three parallel veins in their lower parts. The innermost bracts approach the receptacular scales in shape, but they are more flattened and not boatshaped and carinate like the receptacular scales.

The bracts of the Cape Verdean species are generally thicker and more coalesced with the receptacle than the bracts of the Canarian species. As emphasized by Webb (1849) and Schmidt (1852), the bracts of the Cape Verdean species are coalesced with each other at the base. Anomalous, succulent

bracts were found in a single population of *B. daltonii* ssp. *vogelii* in Fogo, the Cape Verde Islands.

The outermost bracts have an indumentum similar to the leaf indumentum. The margins of the innermost bracts are occasionally fringed with unicellular, rigid and sharp-pointed trichomes. These rigid trichomes are frequently found in *Asteriscus* s.str., but are scarce in the Canarian species of *Bubonium* and totally absent in the Cape Verdean species.

The occurrence of leaf glands and involucral glands is correlated; species with highly glandular leaves usually have highly glandular bracts. Among the Cape Verdean taxa, *B. daltonii* ssp. *daltonii* is outstanding in having densely glandular bracts. The function of glands and hairs (the latter is common in the annuals) might be to obstruct the access to the delicate immature cypselas at the bottom of the capitulum, as suggested for *Relhania* L'Hér. by Bremer (1976).

Receptacle

The Canarian species have a flattened to convex receptacle (Fig. 6B), while the Cape Verdean species have a more conical receptacle (Fig. 6 A). The solid form is lenticular or narrow transversely rhomboid, respectively. The conical shape raises the central disc florets in the capitulum. *Bubonium schultzii* has a discoid receptacle with depressed margins (Fig. 6 C). A shallow cup-shaped receptacle characterizes *Asteriscus* s.str. (Fig. 6 D).

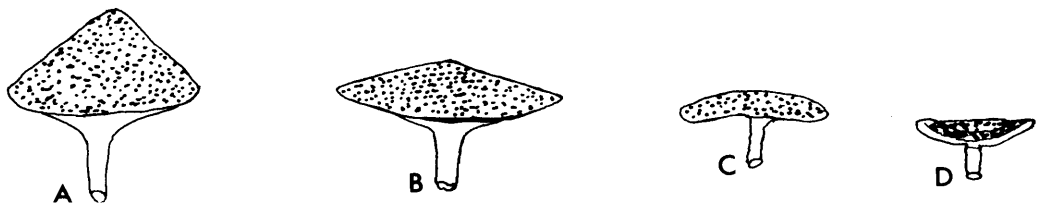


Fig. 6. Types of receptacles in *Bubonium* and *Asteriscus* s. str. A: *B. smithii*. B: *B. sericeum*. C: *B. schultzii*. D: *A. hierochunticus*.

All species of *Asteriscus* s. lat. are paleate, i.e. the receptacle is furnished with bracts, paleae, supporting each disc floret. In *Bubonium* the paleae are variable. Most species have thick and apically pubescent paleae which resemble the innermost involucral bracts and are narrowly boat-shaped (cymbiform) with a thin carina dorsally. This shape protects and gives a dense packing to the disc cypselas in the capitulum.

In *Asteriscus* s.str. the paleae are reduced to thin and hyaline scales which are shallow cymbiform or flattened with a broader base than those in *Bubonium*. A dorsal resin canal, but no carina, is present in *Asteriscus* s.str.

In *Bubonium*, the paleae are glandular, most distinctly in *B. graveolens* ssp. *odorum* and *B. daltonii* ssp. *daltonii*. The paleae have trichomes similar to those of the involucral bracts and the leaves, but in addition the margins of the paleae are often fringed with stiff, unicellular trichomes.

The perennial *Bubonium* species have persistent paleae, the Cape Verdean species more so than the Canarian ones. *Bubonium smithii* has paleae with a pointed foot penetrating 0.5-1.0 mm into the receptacle. The persistent paleae result in dispersal of the cypselas the year after ripening of the capitulum. This slow dispersal of the diaspores delays the reproduction.

Florets

The capitulum in *Bubonium*, as in most other composites (Burtt 1977), is functionally protogynous. The styles of the female ray florets are receptive before the anthers of the hermaphroditic disc florets open, thus promoting cross pollination. In the Cape Verdean taxa the central disc florets are elevated owing to the conical shape of the receptacle and further increase the opportunity of cross pollination, which probably is done by insects.

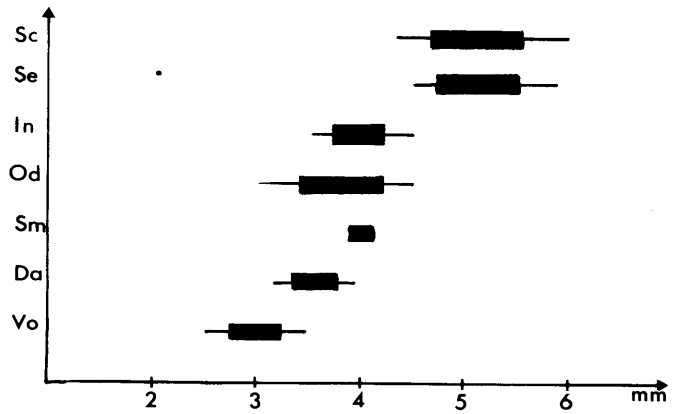


Fig. 7. Variation in length of the disc florets in *Bubonium*. The horisontal line indicates the range and the dark bar the standard deviation. Sc: *B. schultzii*, Se: *B. sericeum*, In: *B. intermedium*, Od: *B. graveolens* ssp. *odorum*, Sm: *B. smithii*, Da: *B. daltonii* ssp. *daltonii*, Vo: *B. daltonii* ssp. *vogelii*.

There is little variation in floral characters in *Bubonium*. All species have perfect disc florets and female, fertile ray florets. Rudiments of anthers in the ray florets are occasionally found in the Canarian species *B. intermedium* and *B. sericeum*. An anomalous specimen of *B. graveolens* ssp. *stenophyllum* (TH 135, O) had ray florets only.

The disc florets are always yellow, and the corolla is divided into a lower tube and an upper five-lobed limb. In some species the distinctness of tube and limb is not clear, or variable, as in *B. graveolens* and *B. daltonii*. This variation is continuous and, in contradiction to Webb (1849), found to be of no diagnostic value. The corolla tube is generally terete, but occasionally weakly laterally compressed. The possession of two narrow lateral wings on the corolla tube is characteristic for *A. spinosus* only.

The variation in the length of the disc florets is shown in Fig. 7. The Canarian *B. schultzii* and *B. sericeum* have the longest disc florets; the Cape Verdean *B. daltonii* the shortest. Overlap in length occurs between the Cape Verdean species and the Canarian *B. graveolens* and *B. intermedium*; and between *B. schultzii* and *B. sericeum*.

The disc florets of the *Bubonium* spp. in the Cape Verde Islands are characterized by a dry and sclerous base. This sclerous tissue consists of six to seven layers of dead cells.

The morphological variation in the lobes of the corolla limbs (Fig. 8) is the taxonomically most important floral character. Nearly all species have corolla lobes dorsally dotted with functional glands. The Cape Verdean species have the most glandular corolla lobes (Fig. 8 A,B), while the Canarian *B. sericeum* has very few glands (Fig. 8 C). *Asteriscus* spp. and *B. schultzii* lack glands (Fig. 8 D). Species with highly glandular corolla lobes generally have more rough and membranous lobe margins than species without glands.

The ray florets are yellow, as in most species in the Inuleae (Small 1918, Cronquist 1955, Harborne 1977b), except in *B. schultzii*. White or whitish ray florets as in *B. schultzii*, are rare in the Inuleae and probably a derived character (Small 1918).

The variation in length of laminas of ray florets is shown in Fig. 9. The largest laminas are found in the Canarian *B. schultzii* and *B. sericeum*; the shortest in the Cape Verdean *B. daltonii*. The other species have intermediate lengths. Overlap occurs between *B. schultzii* and *B. sericeum*; between *B. intermedium*, *B. graveolens*, and *B. smithii*; and between *B. intermedium*, *B. graveolens*, and *B. daltonii*.

The lamina of the ray florets of *B. schultzii* has often a red-purple stripe on the abaxial side. This feature is common to a number of widely different Composites, for instance *Relhania* L'Hér. of the Inuleae (Bremer 1976) and *Anacyclus* L. of the Anthemideae (Humphries 1979b). The stripe is only visible from above during the bud stage. Bremer (1976) suggests that it might be a signal block for pollinators.

Most species in *Bubonium*, except *B. schultzii*, have glands scattered on the abaxial side of the ray floret laminas (Fig. 8 E). The annuals *Asteriscus pygmaeus* and *B. aquaticum* have a rather dense covering of multicellular trichomes on the laminas. The perennial *Bubonium* spp. have some scattered trichomes on the ray florets.

The veins of the ray florets fork in the lower part of the ligule, then run as six nearly parallel strands towards the lobes, where the adjacent veins unite in the apex of each lobe. *Bubonium schultzii* and the annuals have somewhat stronger veins in the lobes than the other species.

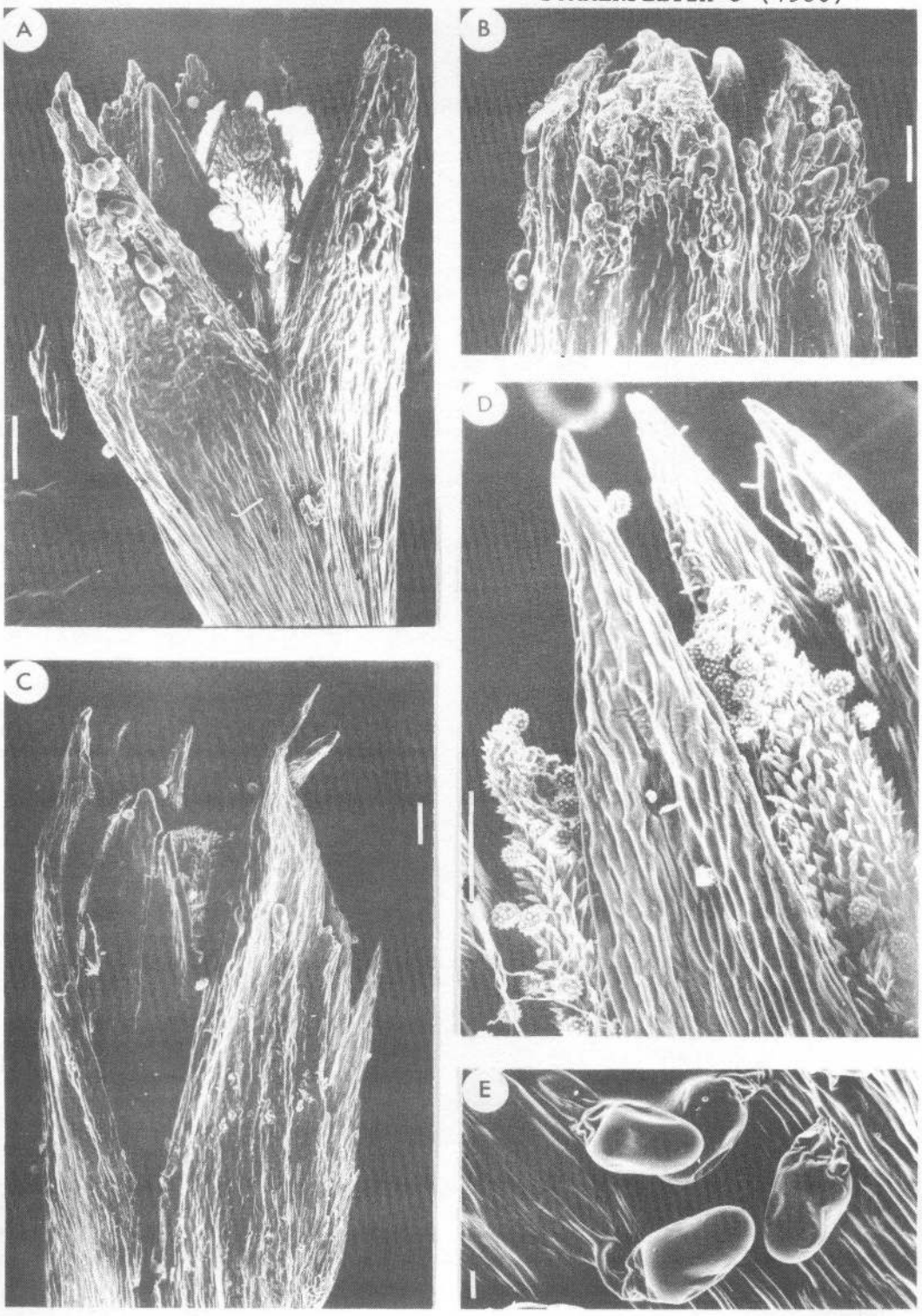


Fig. 8. SEM photographs of corolla lobes (8A-D) and glands (8E). Scale: 20 µm. A: *B. daltonii* ssp. *daltonii*, ØHR 801 (O). B: *B. smithii*, PS 3776 (O). C: *B. sericeum*, TH 105 (O). D: *B. schultzii*, TH 53 (O). E: *B. daltonii* ssp. *daltonii*, ØHR 801 (O).

The style branches are slightly longer in the ray florets than in the disc florets. The styles have rounded to obtuse arms with sweeping hairs in the upper part.

The anthers are in all species rather uniform with branching tails and a trullate to narrowly trullate connective. The Canarian species have somewhat longer style branches and anthers than the Cape Verdean species.

Cypsela morphology

The different cypsela types in *Bubonium* are illustrated in Fig. 10 A-D. The cypselas in *Bubonium* are slightly heteromorphic. The solid form of the ray cypselas (Fig. 10 C) is obpyramidal, and they are always triquetrous in median transverse section. The disc cypselas are more or less terete, widely ovate to widely trullate in median transverse section, with four to six resin canals seen as indistinct ribs (Fig. 10 A,B,D). In *Asteriscus* s. lat. capitulum heteromorphism is pronounced in the annual *A. spinosus* only, which has flattened ray cypselas and terete disc cypselas. Such a capitulum diversification is rare in the Asteraceae (Burtt 1977).

The pappus is small in all *Bubonium* species and consists of free or connate scales of elongated cells in one or two layers. The scales are not true scales, but tufted hairs derived from the surfaces of the cypselas. The Canarian species have a thin, scarious and colourless pappus (Fig. 10 A,B), while the Cape Verdean species have a reduced and much thicker and light brown pappus with cells in two layers (Fig. 10 C,D). True bristles are never found, but the free scales of most Canarian species are somewhat prolonged at the centre. The Cape Verdean species and *B. schultzii* have more or less connate scales protruding from the apical corners of the cypselas.

The variation in length of the disc cypselas is shown in Fig. 11; of the pappus scales in Fig. 12. A considerable overlap occurs in disc cypsela length. *Bubonium graveolens* and *B. daltonii* ssp. *vogelii* have the shortest disc cypselas; *B. sericeum* the longest. The pappus scales are very reduced in *B. smithii*, being less than 0.3 mm long. In *B. sericeum* the pappus is best developed and more than 1.5 mm long. The other species have intermediate pappus lengths. Variability in this character in *B. daltonii* ssp. *vogelii* and *B. intermedium* results in some overlapping.

Only soft hairs are present on the surfaces of the cypselas, most pronounced along the resin canals and towards the pappus (Fig. 10). The annuals *Asteriscus hierochunticus* and *Bubonium aquaticum* have the densest hair covering. The Canarian species have more or less hirsute cypselas, while the Cape Verdean species have a reduced ciliate or ciliolate cypsela

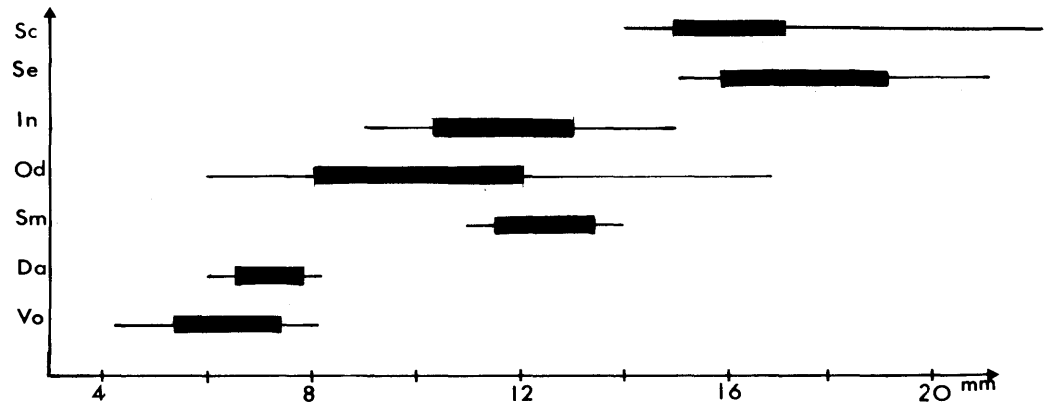


Fig. 9. Variation in lamina length. Sc: *B. schultzii*, Se: *B. sericeum*, In: *B. intermedium*, Od: *B. graveolens* ssp. odorum, Sm: *B. smithii*, Da: *B. daltonii* ssp. *daltonii*, Vo: *B. daltonii* ssp. *vogelii*.

indumentum.

The cypsela hairs are of the twin-type ("Zwillingshaare") (Fig. 12 A-D) described by Hess (1938). They consist of a basal cell and two parallel elongated cells. Owing to further division of the cells, four or five-cellular hairs may occur.

The cypsela twin-hairs in *Asteriscus* s.lat. are of two different types. The Mediterranean and Canarian species in *Asteriscus* s.lat., except *Bubonium imbricatum* and *B. schultzii*, have hairs with very elongated, 0.2-0.8 mm long, parallel cells that are apically bifurcate (Fig. 12 A-B). The other hair type (Fig. 12 C-D), found in *B. schultzii*, the Cape Verdean group and in the *B. imbricatum* group, have shorter, 0.1-0.2 mm long, parallel cells that are apically rounded. Within a single cypsela, however, there may be considerable variation in length of the hairs. The longest hairs are always found towards the pappus.

The peripheral ray cypselas are retained and pressed against the inner surface of the involucre when the inner disc cypselas are blown away. Thus the ray cypselas seem extremely adapted to near dispersal. The cypsela hairs and pappus scales affect the dispersal ability most (Hess 1938), but neither ray nor disc cypselas of the Macaronesian perennials are provided with such hairs and scales that they can be spread over long distances. In particular the very short cypsela hairs and pappus scales (Fig. 13) in the Cape Verdean species indicate a poor dispersability. More widespread *Bubonium* taxa, like *B. aquaticum* , have invariably longer pappus scales.

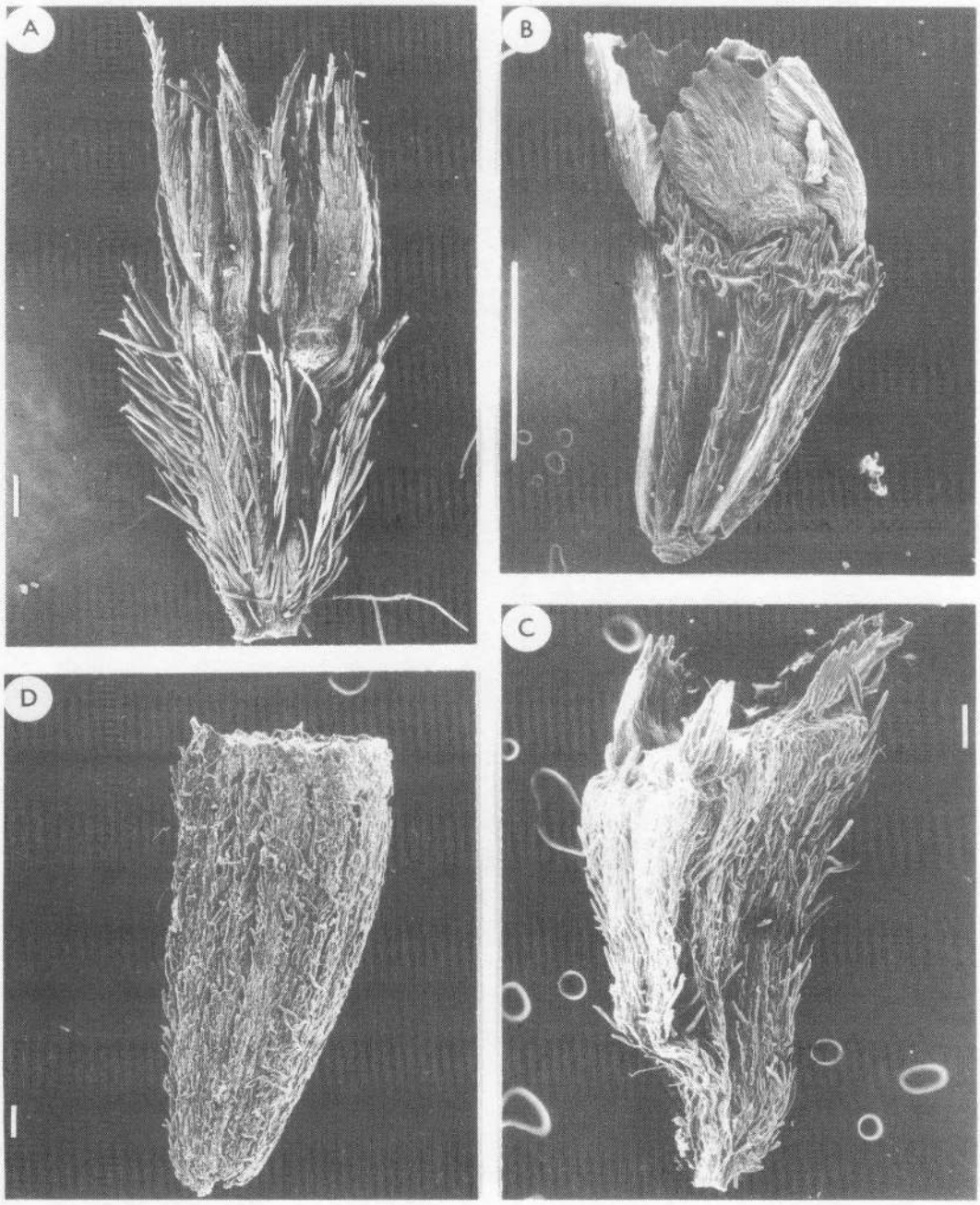


Fig. 10. SEM photographs of cypsela types in *Bubonium*. Scale: 20 µm. A: *B. odorum* ssp. *odorum*, TH 7 (O), disc cypsela. B: *B. schultzii*, TH 53 (O), disc cypsela. C: *B. daltonii* ssp. *vogelii*, LB 3492 (O), ray cypsela. D: *B. smithii*, PS 3776 (O), disc cypsela.

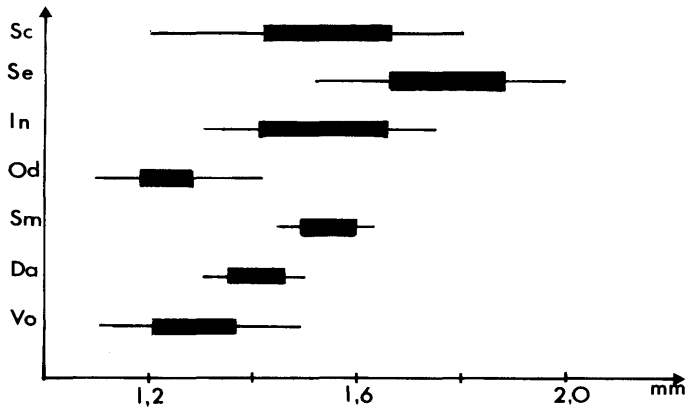


Fig. 11. Variation of disc cypsela length in *Bubonium*. Sc: *B. schultzii*. Se: *B. sericeum*. In: *B. intermedium*. Od: *B. graveolens* ssp. *odorum*. Sm: *B. smithii*. Da: *B. daltonii* ssp. *daltonii*. Vo: *B. daltonii* ssp. *vogelii*.

Cypsela anatomy

The anatomical characters of the fruit wall in *Asteriscus* s.lat. are summarized in Table 2. Schematic drawings of median transverse sections of cypselas in *Asteriscus* s. lat. are presented in Fig. 14. In *Asteriscus* s.lat. it is easy to separate the testa from the fruit wall and the pericarp may be interpreted as two-layered, with epicarp and mesocarp. The pericarp and integument are often tightly attached, but not coalesced, and the integument is clearly separated from the fruit wall.

All species within *Asteriscus* s.lat. have fruits with a thick-walled epicarp. It is best developed in the Cape Verdean species (Fig. 14 A). Each cell of the epicarp contains one large, prismatic calsium oxalate crystal (Fig. 12 B,D). Such crystals are found in many of the genera in the *Inula* group which centres on the Mediterranean area (Merxmüller & Grau 1977). The crystals are larger in *Asteriscus* s.str. than in *Bubonium*.

The mesocarp consists of parenchyma, sclerenchyma and/or resin canals and varies as to the distribution and occurrence of resin canals and sclerenchyma (Fig. 14). The parenchyma is rather undifferentiated, consisting of shrunken cells with thin walls. The sclerenchyma may form a multilayered continuous ring inside the epicarp in the Cape Verdean species (Fig. 14 A). In the Canarian species the sclerenchymatic tissue is reduced to free or aggregated cells (Fig. 14 B-D). These species have large resin canals with secretion cells. In the Cape Verdean species the resin canals are weakly developed and surrounded by a dense ring of sclerenchyma. *Bubonium schultzii* and *B.*

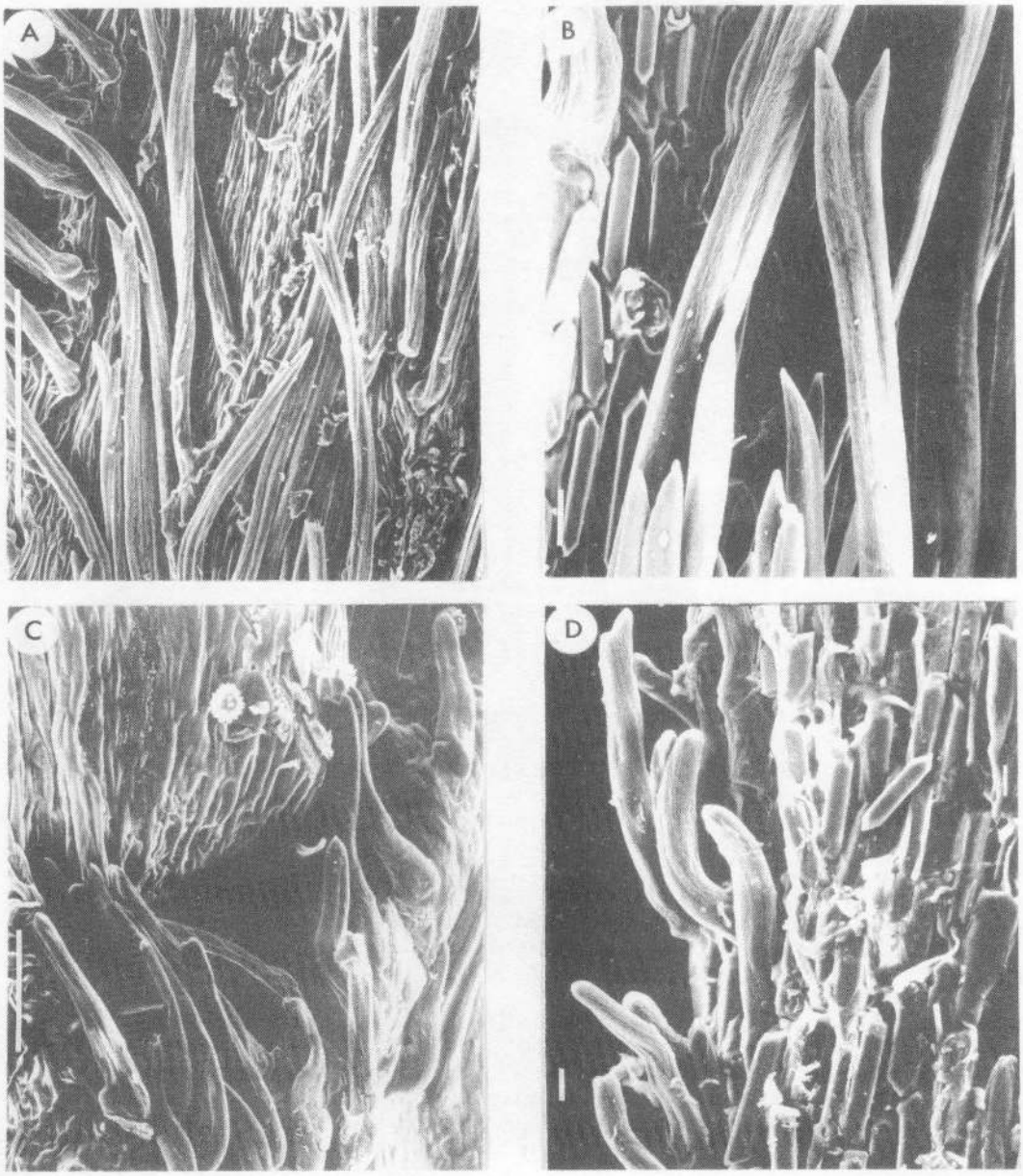


Fig. 12. SEM photographs of cypsela hair types in *Bubonium*. Scale: 20 µm. A: *B. graveolens* ssp. *odorum*, TH 7 (O), bifurcate cypsela hairs. B: *B. aquaticum*, Kunkel 14867 (O), bifurcate cypsela hairs. Note the prismatic calcium oxalate crystals. C: *B. schultzii*, TH 53 (O), rounded cypsela hairs. D: *B. smithii*, PS 3776 (O), rounded cypsela hairs. Note the prismatic calcium oxalate crystals.

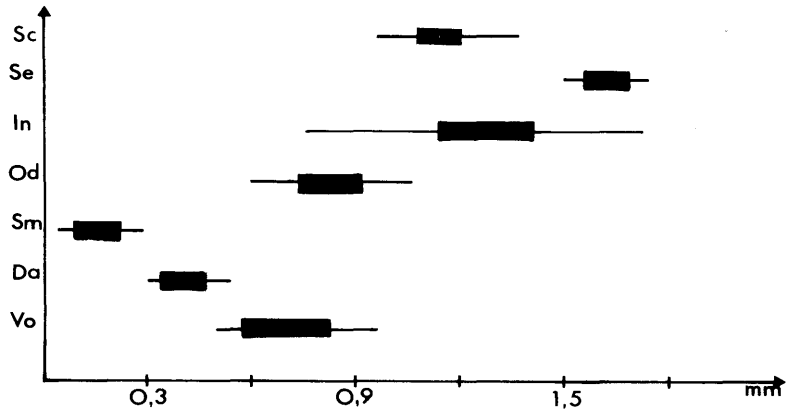


Fig. 13. Variation in pappus scale length in *Bubonium*. Sc: *B. schultzii*. Se: *B. sericeum*. In: *B. intermedium*. Od: *B. graveolens* ssp. *odorum*. Sm: *B. smithii*. Da: *B. daltonii* ssp. *daltonii*. Vo: *B. daltonii* ssp. *vogelii*.

imbricatum have the sclerenchyma densely aggregated in one corner of the disc cypselas (Fig. 14). In *Asteriscus* s.str., resin canals are completely lacking and sclerenchymatic cells nearly absent (Fig. 14 E-F). The mesocarp is generally thinner in the annuals than in the perennials. Merxmüller & Grau (1977) interpreted ribbed cypselas with resin canals as ancestral in the *Inula* group.

The thick cypsela walls in most *Bubonium* spp. may be adaptations to long dormancy and delayed germination of the seeds. Such adaptations are useful in areas like the Cape Verde Islands with long periods of drought.

Although the cypselas in *Bubonium* are slightly heteromorphic, the fruit wall anatomy is fairly uniform in ray and disc cypselas, but the number of resin canals is somewhat higher in the disc cypselas (4-6) than in the ray cypselas (0-3). The difference is most pronounced in *B. schultzii*, with aggregates of sclerenchyma in one corner of the disc cypselas and scattered sclerenchymatic cells in the ray cypselas.

Table 2. Fruit wall anatomical character states within *Asteriscus* s.lat.

Species	No. of investigated specimens	Epicarp: Cuticle	Epicarp: Crystal size <40 µm	Epicarp: Crystal size >40 µm	Mesocarp: Without resin canals	Mesocarp: With resin canals	Mesocarp: Canal size 1-3	Mesocarp: Canal size 3-6	Mesocarp: Canal size <0.05 mm	Mesocarp: Canal size 0.05-0.1 mm	Mesocarp: Canal size >0.1 mm	Sclenrenchyma: Absent	Sclenrenchyma: Present	Sclenrenchyma: Scattered cells only	Sclenrenchyma: Aggregated in one corner	Sclenrenchyma: 1-2 layers continuous layers	Parenchyma: Absent	Parenchyma: Present
Bubonium daltonii	10	+	+			+	+		+				+			+	(+)	
B. smithii	5	+	+		+	+	+		+				+			+	(+)	
B. intermedium	3		+			+	+	+		+			+			+		+
B. graveolens	10		+			+	+	+		+			+			+		+
B. sericeum	3		+			+	+	+			+		+			+		+
B. aquaticum	3			+		+	+	+			+		+	+		+		+
B. schultzii	6			+		+	+	+			+		+		+	+		+
Asteriscus maritimus	5			+	+							(+)		+				(+)
A. hierochunticus	5			+	+							+						(+)
A. spinosus	3			+	+							+						(+)

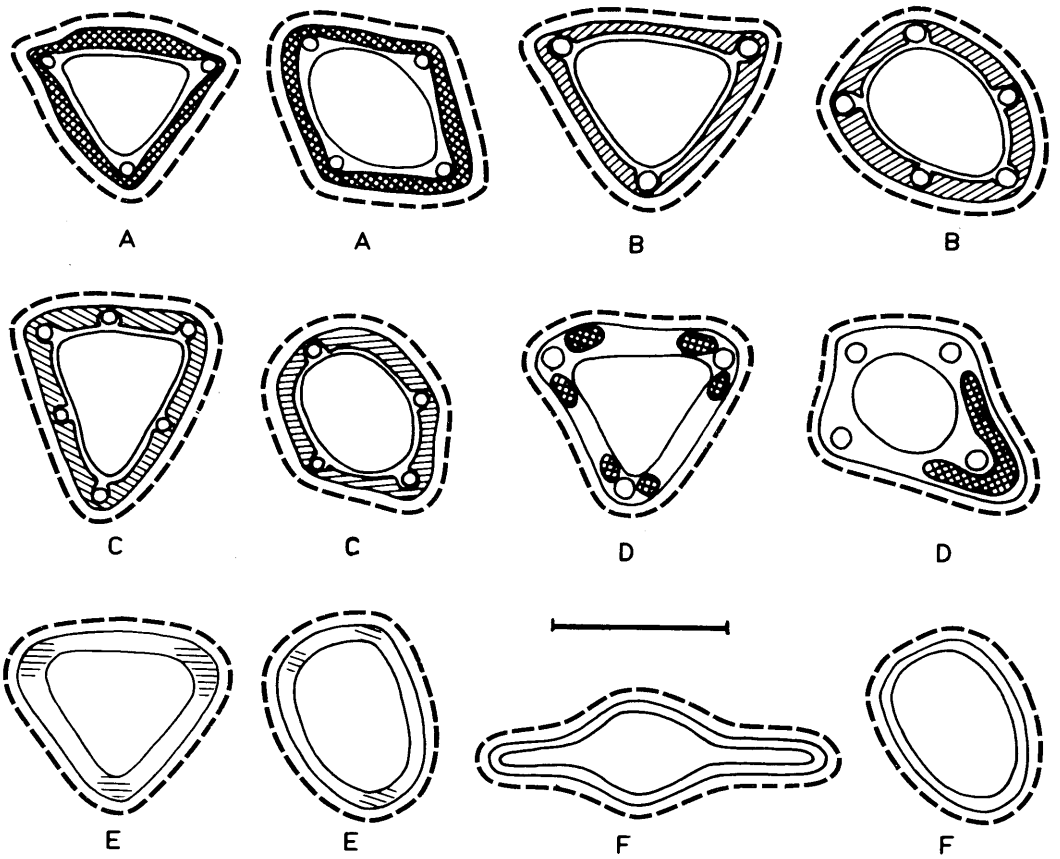


Fig. 14. Schematic drawings of median cross sections of cypselas in *Asteriscus s.*lat. Scale: 1 mm. Rings: resin canals. Hatchings: mesocarpic sclerenchyma as scattered cells. Crosshatchings: mesocarpic sclerenchyma. Left hand column: ray cypselas. Right hand column: disc cypselas. A: *Bubonium daltonii*. B: *B. sericeum*. C: *B. intermedium*. D: *B. schultzii*. E: *Asteriscus hierochunticus*. F: *A. spinosus*.

VARIATION IN *BUBONIUM GRAVEOLENS* IN GRAN CANARIA

Two species and one variety have previously been recognized within the ssp. *odorum* - ssp. *stenophyllum* complex in Gran Canaria. The ssp. *stenophyllum* has been separated from ssp. *odorum* on the basis of its somewhat larger capitula, longer ray florets and more narrow and crowded leaves. The most narrow leafed form of ssp. *stenophyllum* has been recognized as a variety, var. *filifolium*. The characters used to separate these taxa seemed to us to exhibit an almost continuous variation in Gran Canaria, and the morphology of this complex was therefore examined by numerical analysis to reveal the variation along as many dimensions as possible simultaneously (Sneath & Sokal 1973, Dunn & Everitt 1982). The locations of the populations analysed are shown in Fig. 15, and the characters used were listed in Table 1, p. 12. The results are displayed in a distance diagram in Fig. 16; a phenogram from a cluster analysis in Fig. 17; scatter diagrams of all specimens on the first three axes of PCO in Fig. 18, and scatter diagrams of 10 populations and the 12 specimens from the population "Perchel" on the first three axes of PCO in Fig. 19.

Distance diagram

In the construction of the distance diagram (Fig. 16) the most typical specimens of ssp. *odorum* (population "La Isleta") and ssp. *stenophyllum* var. *filifolium* (population "Bco. Lajilla in Tasartico"), were chosen as the two extremes, corresponding to the parents of Wells (1980). These extremes fell into two separate clusters (Fig. 16). The rest of the specimens showed a continuum of forms between these two extremes. The evidence from the distance diagram is consistent with the proposed lumping of the two species.

Cluster analysis

Four clusters were formed at level 0.235, three at level 0.297 and two at level 0.425 (Fig. 17). Specimens nos. 13-18 from population "La Isleta" and nos. 19-22 from population "Patalavaca" clustered in one group together with two specimens, nos. 1 and 11, from population "Perchel" and one specimen, no. 44, from population "La Fajanita". The populations "La Isleta" and "Patalavaca" represent typical ssp. *odorum* and the specimens from the two populations were quite intermixed in one, fairly distinct cluster.

Population "Perchel" is very heterogeneous and the specimens from this population, nos. 1-12, were scattered on three different clusters. This population probably represents a hybrid swarm between narrow leafed ssp. *stenophyllum* (i.e. var. *filifolium*) and ssp. *odorum*.

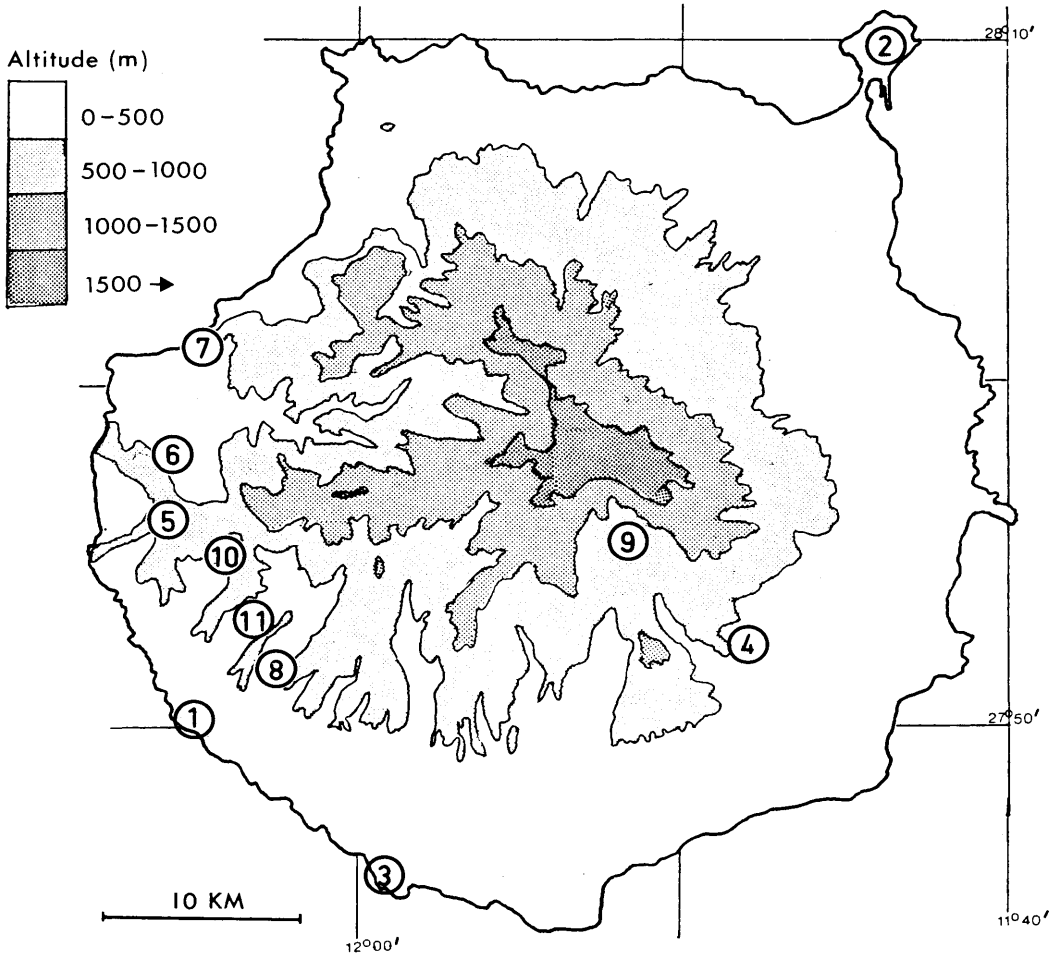


Fig. 15. The location of the 11 investigated populations of *Bubonium graveolens* in Gran Canaria (for details see Appendix 3).

The eight populations representing ssp. *stenophyllum* were united in one cluster at level 0.297, but displayed three distinct subgroups at levels between 0.213 and 0.255. Population "Perchel" was evenly distributed in two of these clusters. The other populations also tended to spread on different clusters, but there was a slight tendency for specimens belonging to populations of ssp. *stenophyllum* s. str. and ssp. *stenophyllum* var. *filifolium*, respectively to group together in separate clusters.

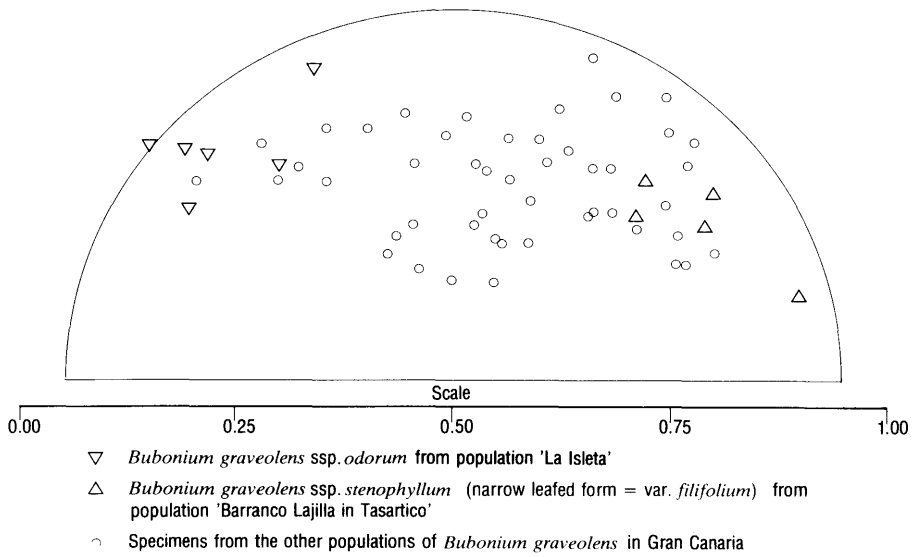


Fig. 16. Wells' distance diagram of 60 individuals of *Bubonium graveolens* in Gran Canaria.

From the cluster analysis (Fig. 17) it is apparent that no good separation occurs within ssp. *stenophyllum*. The ssp. *odorum* and the ssp. *stenophyllum* are distinct taxa, but the differences are not so great that the maintenance of two separate species is justified. A grouping in two subspecies seems more appropriate.

Principal co-ordinate analysis

In the principal coordinate analysis (PCO) with specimens as OTUs, the first three axes account for 52% of the total variance: 29% on axis 1, 14% on axis 2 and 8.6% on axis 3. Fig. 18 depicts axes I and II (43%) and axes I and III (37.6%). The high percentage value of axes 1 and 2 implies that the significant amount of the extracted variance is expressed in the two dimensions.

Axes I and II and axes I and III revealed no isolated cluster of points, but specimens nos. 13-18 from population "La Isleta" and nos. 19-22 from population "Patalavaca" clustered together. Although this cluster also included specimens nos. 1 and 11 from population "Perchel" it corresponds fairly well to ssp. *odorum*. Specimens nos. 48-51 from population "Temisas" also clustered together and represent ssp. *stenophyllum* s.str. More loosely so did specimens nos. 32-36 from population "Lajilla, Tasartico", which represents ssp. *stenophyllum* var. *filifolium* and specimens nos. 37-40 from population "San

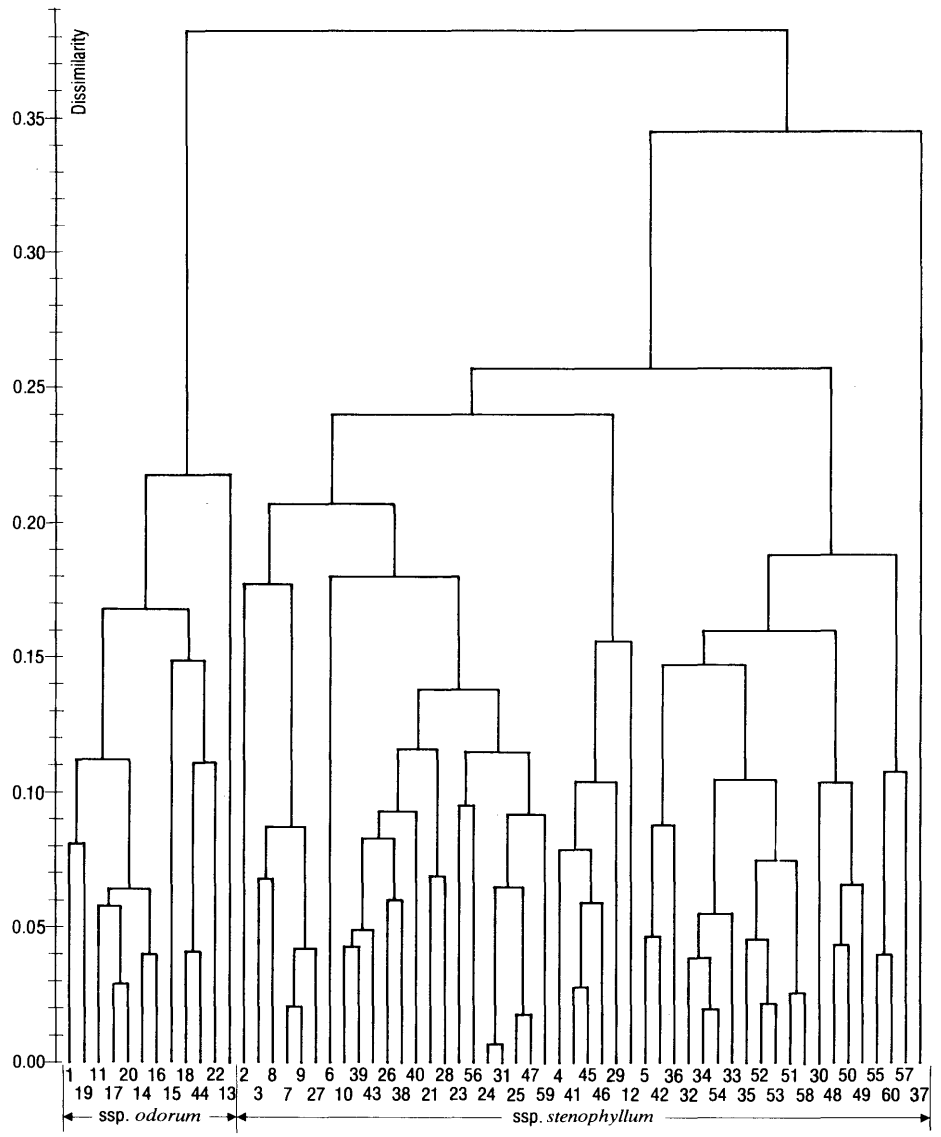


Fig. 17. Phenetic cluster dendrogram (phenogram) from unweighted pair group method using arithmetic average linkage cluster analysis of 60 specimens (OTU's) of *Bubonium graveolens* from Gran Canaria.

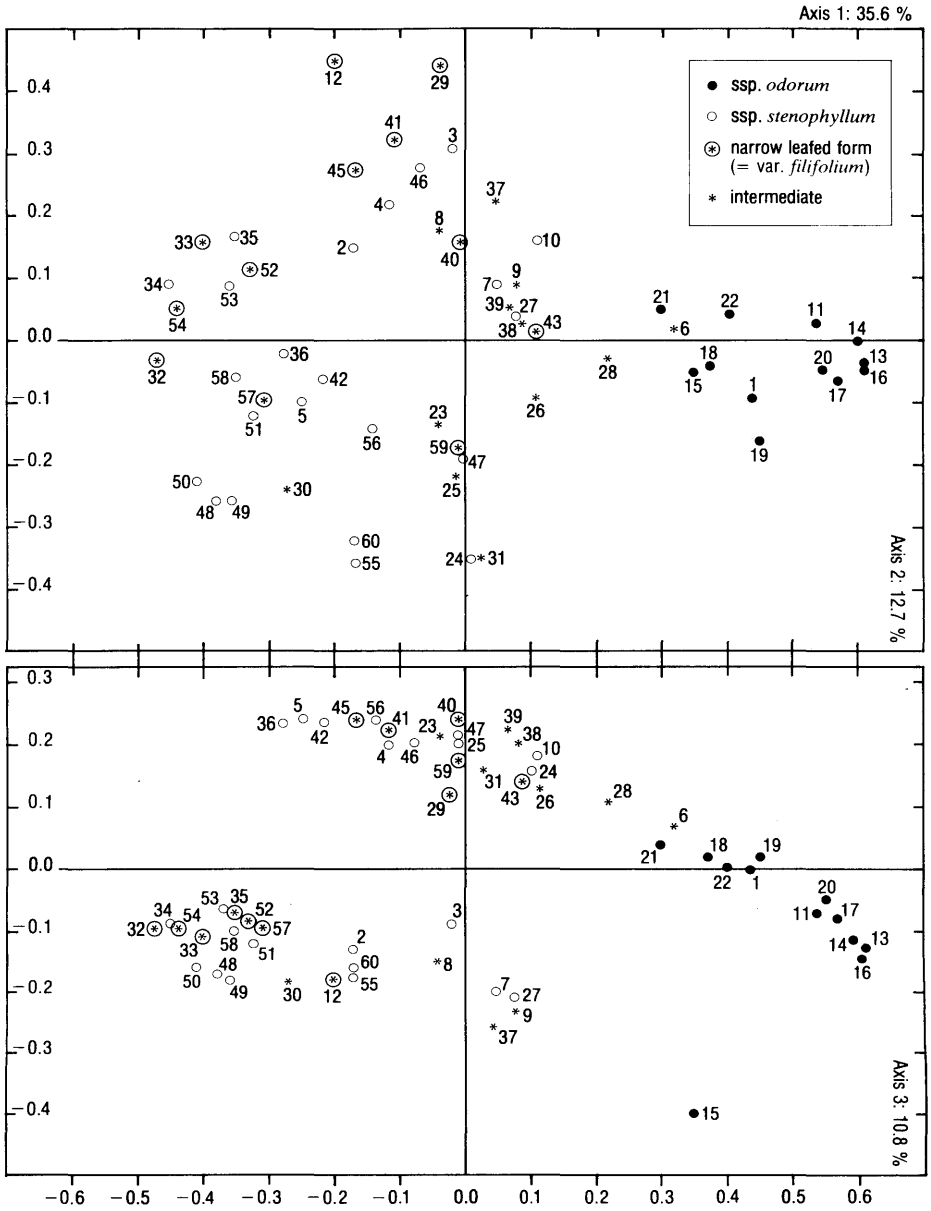


Fig. 18. Principal co-ordinate analysis, 60 specimens, axes I and II and axes I and III.

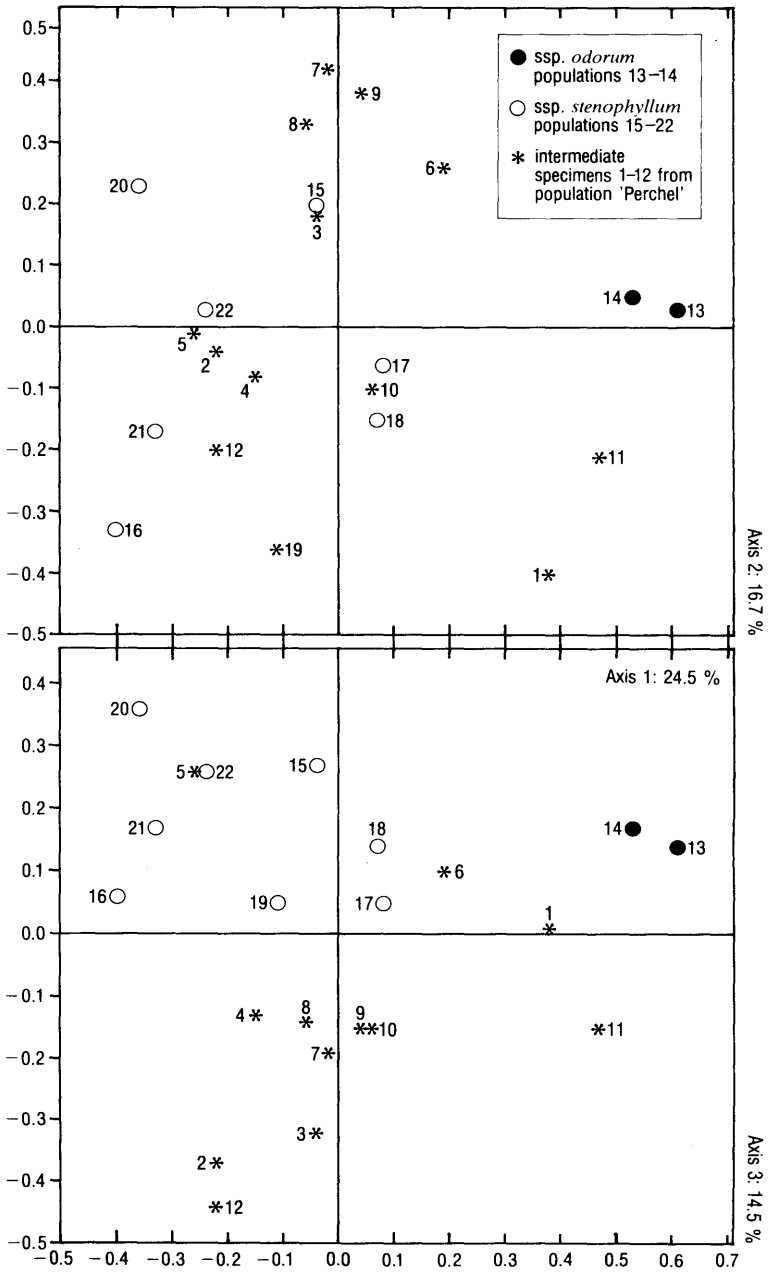


Fig. 19. Principal co-ordinate analysis, 10 populations and 12 specimens, axes I and II and axes I and III.

Nicolas", which represent, more or less, ssp. *stenophyllum* s.str. The figure shows, however, that a continuum exists between all three taxa and especially between the varieties of ssp. *stenophyllum*. There seems to be a complete phenetic bridging between the different taxa analysed.

In Fig. 19, 10 of the populations are used as OTUs instead of single specimens. Nos. 13-22 in the figure thus represent population plots, while the specimens from the heterogeneous population "Perchel" is kept as single OTUs, nos. 1-12, in the figure. The first three axes now account for 56% of the total variance, 24.5, 16.7 and 14.5% respectively. Fig. 19 displays axes 1 and 2 and axes 1 and 3.

In both cases the ssp. *odorum*, populations nos. 13-14 ("La Isleta" and "Patalavaca"), occupy a fairly isolated position. Along axes 1 and 2 the "Perchel" specimens, nos. 1-12, are evenly distributed through the plot, whereas they are more concentrated along axes 1 and 3.

The principal co-ordinate analysis reveals no distinct morphological differences between the specimens belonging to ssp. *stenophyllum* s.lat., but a fairly clear separation of this taxon from ssp. *odorum*. Hybridization seems to occur in the "Perchel" population and a subspecific rank for the two taxa, ssp. *odorum* and ssp. *stenophyllum*, seems justified.

VARIATION IN *BUBONIUM* IN THE CAPE VERDE ISLANDS

Bubonium occurs in all the western Cape Verde Islands except Santa Luzia, for owing to their high altitudes and the prevailing northeasterly wind systems they have favourable local climates. *Bubonium* is totally absent from the low and arid, eastern islands, i.e. Sal, Boa Vista and Maio. The extreme values with respect to annual precipitation in the ecological range of the genus are illustrated by the climate diagrams in Fig. 20 (from Klug 1974). The local climate is influenced not only by precipitation, but also by fog, local exposure and wind (Barbosa 1968, Klug 1974).

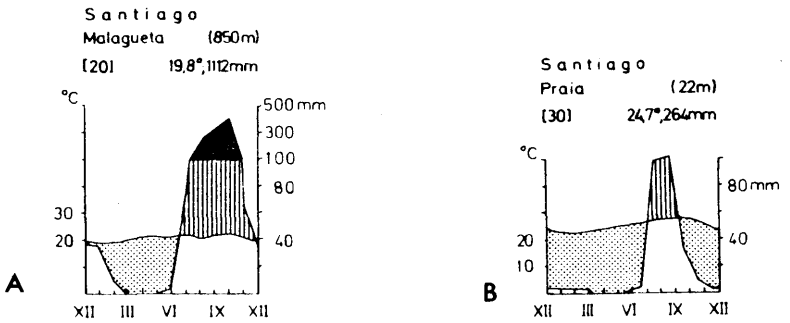


Fig. 20. Climate diagrams from Klug (1974) illustrating the two extreme climatic conditions for *Bubonium* in Santiago. A. Humid mountain zone. B. Arid coastal zone.

The results of a comparison between seven Cape Verdean *Bubonium* populations with respect to the variation in four quantitative characters are presented in Figs. 22-25, with key to the symbols in Fig. 21. Two additional qualitative characters are shown in Figs. 22-23.

The most humid habitats, in the mountains of Santiago, are occupied by populations of *Bubonium daltonii* ssp. *daltonii* (Figs. 22-25, ST1). Here yearly precipitation may reach values above 1100 mm (Fig 20 A). Other important ecological factors in this area are fog and low night temperatures, which result in dewfall and decreased annual mean temperature.

Bubonium daltonii ssp. *vogelii* grows copiously under more arid conditions than ssp. *daltonii* and occurs in all the western islands. Owing to ecogeographical isolation of its many populations, habit and leaf shape are more variable in ssp. *vogelii* than in ssp. *daltonii*. Extreme aridity is found for the coastal populations in Fogo and partly in Santo Antão (Figs. 22-25; F, SA1). In the high central part of Santo Antão (Figs. 22-25, SA2) low night temperatures may give some dewfall, but the influence of fog is small. A corresponding water situation is found for the population SN1 (Figs. 22-25) in São Nicolau,

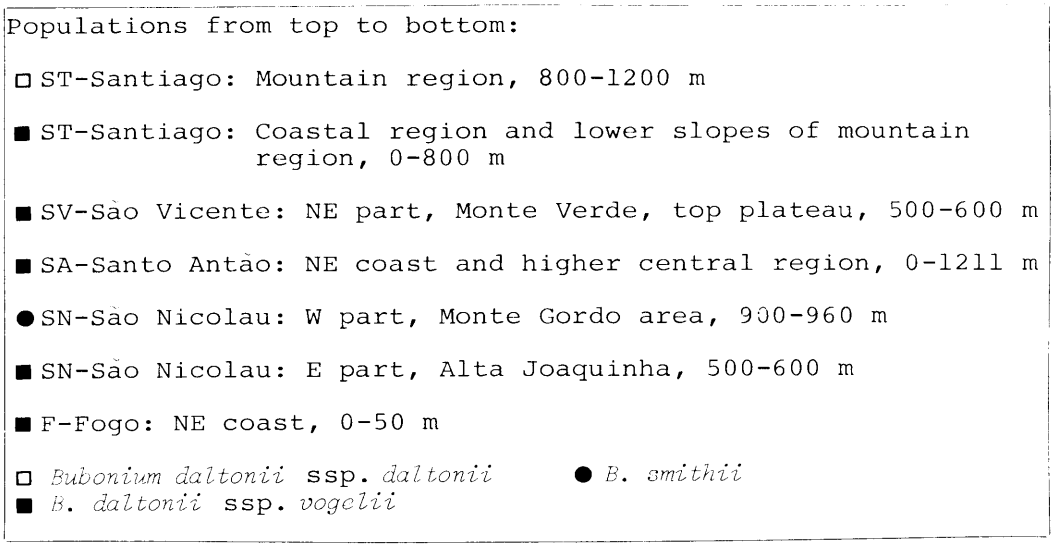


Fig. 21. Key to the symbols in Figs. 22-25.

where yearly precipitation sometimes exceeds 300 mm (Nunes 1962) and fog condensation may have an important local effect. The influence of fog is probably still larger in the northerly exposed Monte Verde, São Vicente (Figs. 22-25, SV).

Bubonium smithii is restricted to a small area in the western part of São Nicolau (SN1, Figs. 22-25) where yearly precipitation exceeds 500 mm (Nunes 1962). Additional fog influence probably increases the humidity further.

Figure 22 shows that the highest length/width ratio of the leaves, i.e. narrow leaves, is found in the populations F, ST2 and SA of coastal or high altitudinal zones of great aridity. Under more humid conditions the leaves are broader, as in ST1, SV, SN1, and SN2. Only specimens of the population ST1 have the denticulate leaf margins characteristic of *B. daltonii* ssp. *daltonii*.

Bubonium smithii is characterized by larger capitula (Fig. 23) and longer ray florets (Fig. 24) than *B. daltonii*. The capitula are also slightly larger in *B. daltonii* ssp. *daltonii* than in ssp. *vogelii* (Fig. 23).

The population SN2 (Figs. 22-25) shows similarities to *B. daltonii* ssp. *vogelii* in some qualitative characters (Figs. 22-23), but to *B. smithii* in some quantitative ones (Figs. 22 and 25). The populations SN1 and SN2 in São Nicolau are geographically isolated and restricted to small areas. They are both characterized by very short pappus scales (Fig. 25). The Alta Joaquinha population (SN2) may have undergone convergent evolution with the Monte Gordo population (SN1) of *B. smithii* in ecological vicariant habitats in São Nicolau. Owing to the similarities in habit and reproductive parts between the Alta Joaquinha specimens and *B. daltoni* ssp.

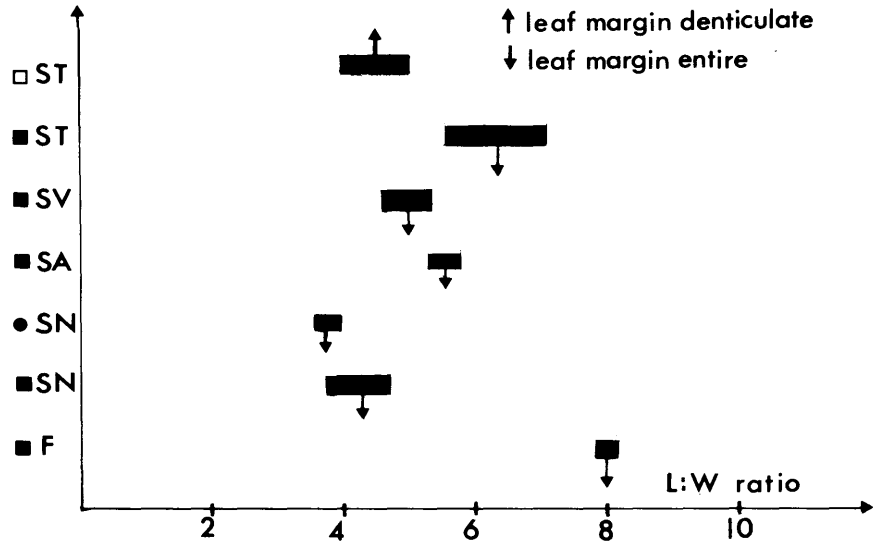


Fig. 22. Length: width ratio of leaves in seven *Bubonium* populations in the Cape Verde Islands.

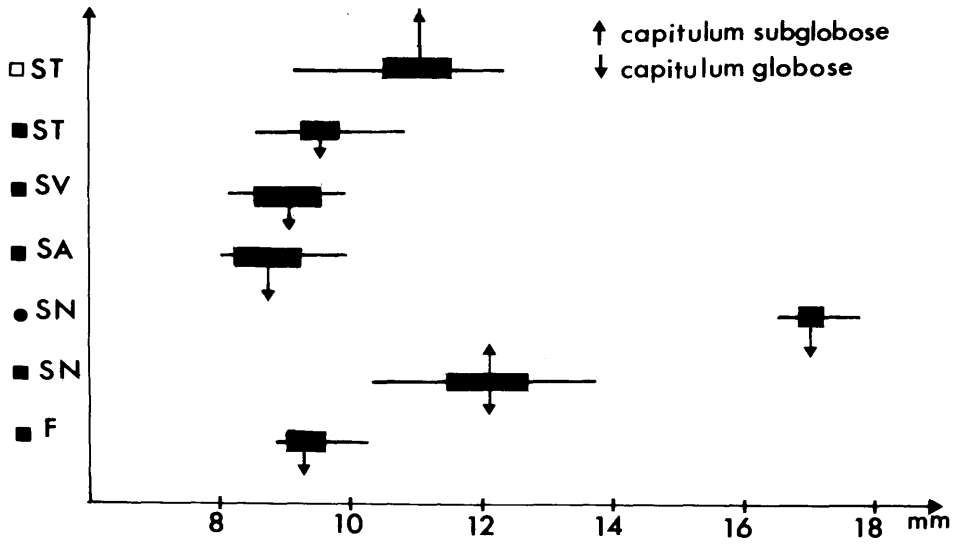


Fig. 23. Width of involucre in seven *Bubonium* populations in the Cape Verde Islands.

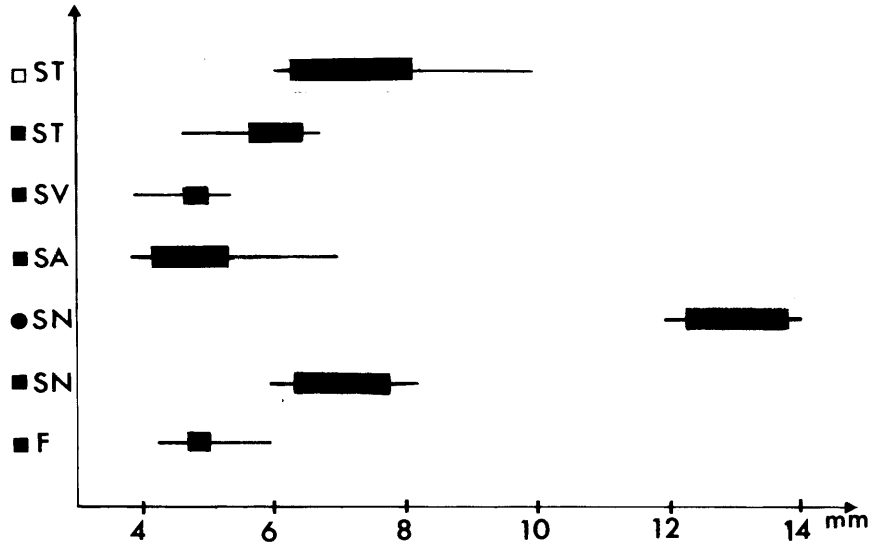


Fig. 24. Length of ray floret lamina in seven *Bubonium* populations in the Cape Verde Islands.

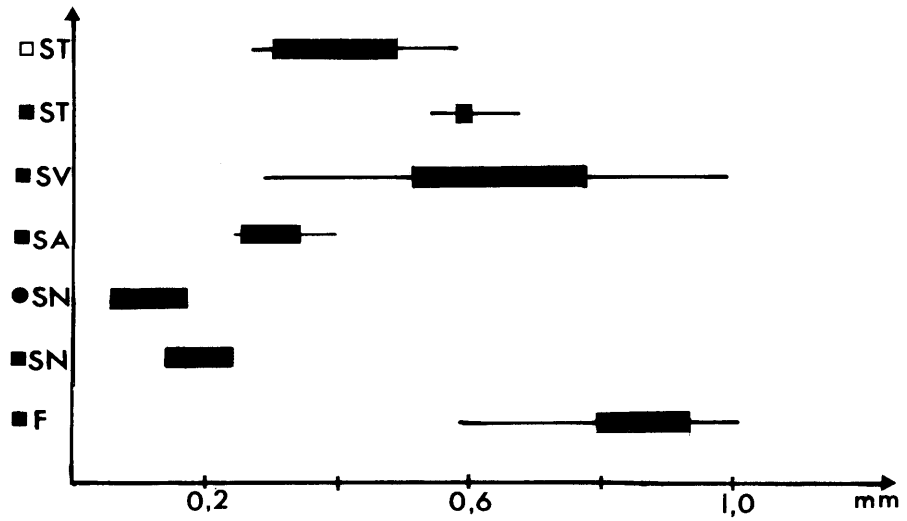


Fig. 25. Length of pappus scales in seven *Bubonium* populations in the Cape Verde Islands.

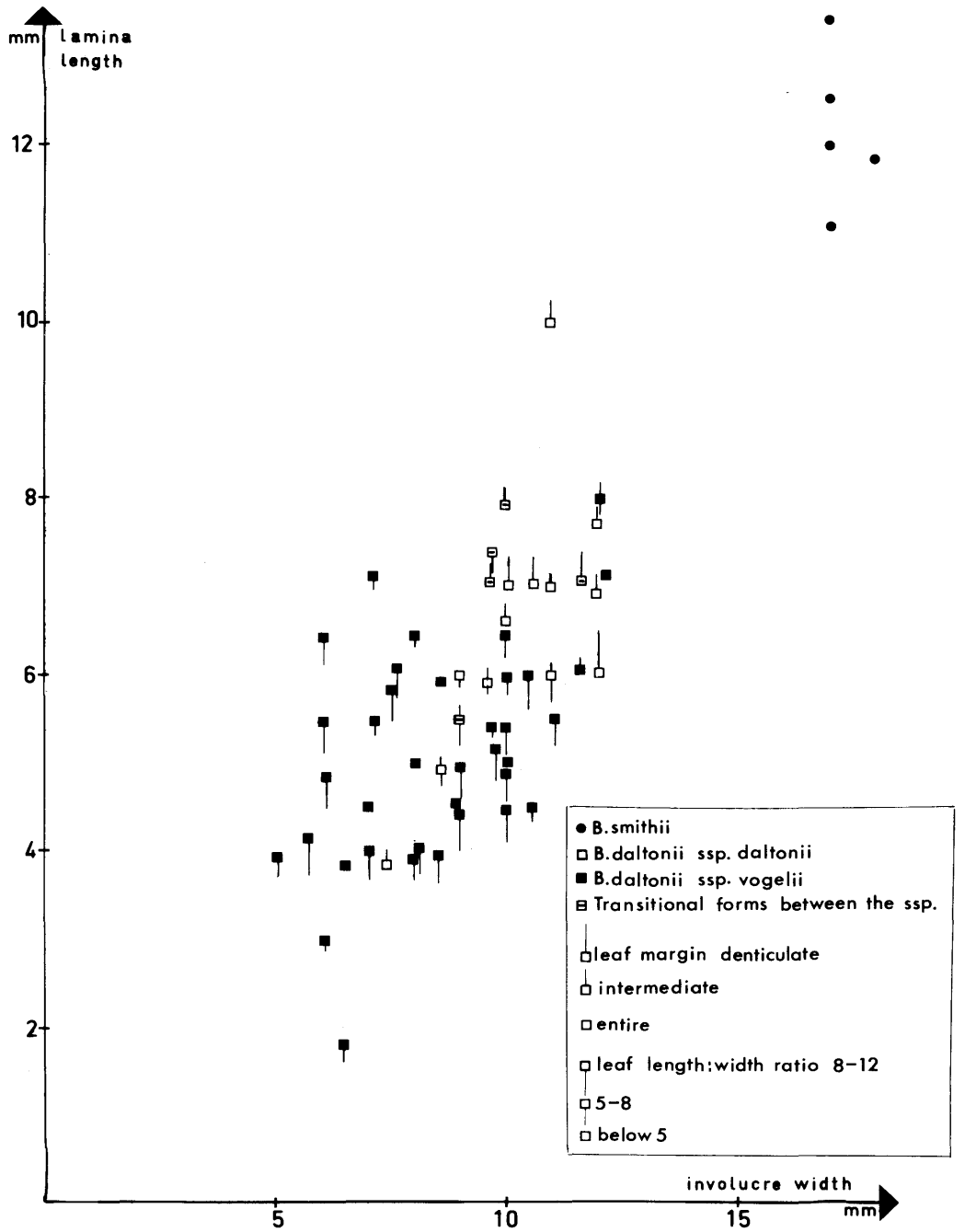


Fig. 26. Pictorialized scatter diagram illustrating differences between the three taxa in the Cape Verde Islands. Each plot represents one specimen.

vogelii (Figs. 23-24) we have chosen to include the Alta Joaquinha population in this taxon (see pp. 82-85).

The pictorialized scatter diagram (Fig. 26) illustrates the character differences between the Cape Verdean taxa of *Bubonium*. Qualitative characters in paleae and leaves separate the two subspecies of *B. daltonii*, whereas quantitative characters such as width of involucre and length of ray floret laminas show complete intergradation (Fig. 24). On the semi-arid mountain slopes, at about 600-800 m altitude in Santiago, the two subspecies meet and here transitional forms occur (see Fig. 24). *Bubonium smithii* is distinct from *B. daltonii* in qualitative characters concerning disc florets and cypselas (see also Figs. 7 and 11) and in quantitative ones, such as capitula size and ray floret length (Fig. 24). *B. daltonii* and *B. smithii* are given specific rank based on the morphological differences, whereas *daltonii* and *vogelii* are treated as subspecies under *B. daltonii*.

PHENETIC RELATIONSHIP BETWEEN MACARONESIAN SPECIES OF *ASTERISCUS* S. LAT.

Table 3 presents character differences between 10 species of *Asteriscus* s. lat. A plus sign (+) marks the characters present for each taxon. Somewhat intermediate character states are marked "i". On the basis of these characters a dendrogram of phenetic similarity was constructed by the SMC-UPGMA method (Fig. 27).

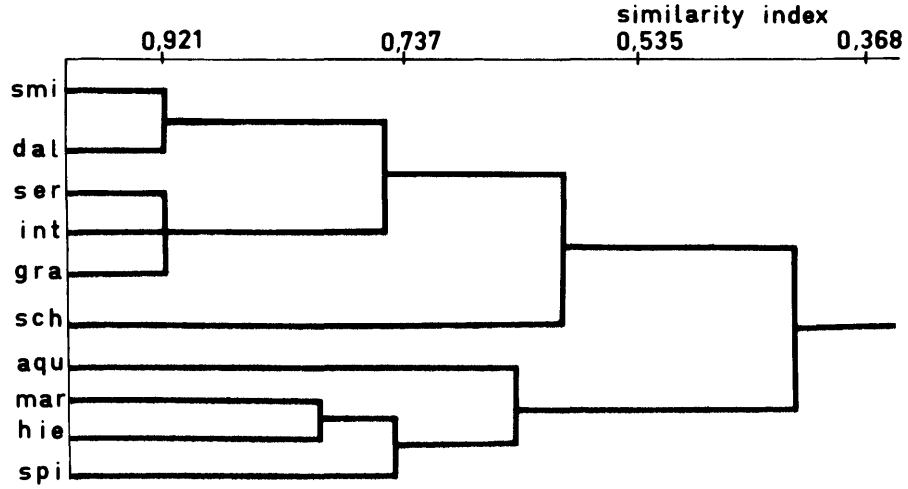


Fig. 27. Dendrogram of phenetic similarity between 10 species of *Asteriscus* s. lat. Abbreviations: smi - *Bubonium smithii*, dal - *B. daltonii*, ser - *B. sericeum*, int - *B. intermedium*, gra - *B. graveolens*, sch - *B. schultzii*, aqu - *B. aquaticum*, mar - *Asteriscus maritimus*, hie - *A. hierochunticus*, spi - *A. spinosus*.

Bubonium aquaticum cluster together with *Asteriscus* s. str. owing to similar habit and growth forms (Fig. 27). Differences between *Asteriscus* s. str. and *Bubonium* are found in (1) paleae flattened in *Asteriscus* s. str., cymbiform in *Bubonium*; (2) paleae with resin canals in *Asteriscus* s. str., without in *Bubonium*; (3) cypselas without resin canals in *Asteriscus* s. str., with in *Bubonium*; and (4) chromosome number 2n=10-12 in *Asteriscus* s. str., 2n=14 in *Bubonium*.

Within *Bubonium* the perennial species, except *B. schultzii*, remain close together owing to their high overall similarity. Both the Canarian and Cape Verdean perennials have a woody habit, sericeous leaves, leaf like bracts, glands, cypsela sclerencyma, boat shaped paleae, and chromosome number 2n=14. The Canarian and Cape Verdean species form, however, separate clusters, owing to such differences as persistent or deciduous

Table 3. Character differences between 10 species of *Asteriscus* s. lat. A = *Asteriscus* s. str. B = *Bubonium*. + = character state present. - = character state absent. i = character state intermediate.

Characters	B. smithii	B. daltonii	B. sericeum	B. intermedium	B. graveolens	B. schultzii	B. aquaticum	A. maritimus	A. hierochunticus	A. spinosus
Perennial	+	+	+	+	i	+	-	i	-	-
Annual	-	-	-	-	i	-	+	i	+	+
Secondary thickening	+	+	+	+	i	i	-	i	i	-
Leaf rosettes	-	-	-	-	-	-	+	i	+	+
Leaves homomorphic	+	+	i	+	i	i	+	+	i	-
Leaves broad	+	i	+	+	-	+	+	+	i	+
Leaves sericeous/tomentose	+	+	+	+	i	-	i	i	i	i
Leaves scabrous/glabrous	-	-	-	-	i	+	i	i	i	i
Leaves fleshy	-	-	-	-	-	+	-	i	-	-
Leaf margins entire	+	i	i	+	i	i	+	+	+	+
Leaf margins dentate	-	+	i	-	i	i	-	-	-	-
Central capitulum	+	+	+	+	+	+	-	-	-	-
Capitula globose/capitate	+	+	i	i	i	-	-	-	-	-
Capitula flattened/cupshaped	-	-	i	i	i	+	+	+	+	+
Involucral bracts leaf like	+	+	+	+	+	+	i	-	-	-
Palaea pubescent	+	i	+	+	+	-	i	-	-	-
Palaea glabrous	-	i	-	-	-	+	i	+	+	+
Palaea persistent	+	i	-	-	-	+	+	+	i	i
Palaea cymbiform	+	+	+	+	+	+	+	-	-	-
Palaea flattened	-	-	-	-	-	-	-	+	+	+
Palaea resin canals	-	-	-	-	-	-	i	+	+	+
Ligules yellow	+	+	+	+	+	-	+	+	i	-
Ligules whitish	-	-	-	-	-	+	-	-	i	+
Ray florets in one row	+	+	i	+	+	+	+	+	i	-
Ray florets in two or more rows	-	-	i	-	-	-	-	-	i	+
Disc floret lobes glandular	+	+	+	+	+	-	i	+	+	+
Ray cypselas triquetrous	+	+	+	+	+	+	+	+	+	-
Ray cypselas flattened	-	-	-	-	-	-	-	-	-	+
Cypsela resin canals	-	i	i	+	+	+	+	-	-	-
Cypsela schlerenchyma	+	+	i	i	i	i	i	-	-	-
Cypsela hairs long, bifurcate	-	-	+	+	+	-	+	+	+	+
Cypsela hairs short, rounded	+	+	-	-	-	+	-	-	-	-
Pappus scales long, bristle like	-	-	+	+	+	-	+	+	+	+
Pappus scales short, connate	+	+	-	-	-	+	-	-	-	-
Chromosome number 2n=14	+	+	+	+	+	+	+	-	-	-
Chromosome number 2n=10,12	-	-	-	-	-	-	-	+	+	+

paleae, homomorphic or heteromorphic leaves, cypsela hair types, pappus scales, and cypsela resin canals.

Bubonium schultzii seems more remotely related to the other perennials. This species is the only one with scabrous leaves, flattened capitula, whitish ray florets, and non-glandular leaves. It resembles the Cape Verdean species in the lack of cypsela sclerenchyma and the type of cypsela hairs (short, rounded), but the Canarian ones in the occurrence of cypsela resin canals.

KARYOLOGY

Previously published chromosome numbers in *Asteriscus* s. lat. are listed in Table 4. Borgen's (1975) count of 2n=18 in *B. daltonii* from Santo Antão, Cape Verde Islands was based on misidentified material and is omitted. The deviating count of n=8 in *B. sericeum* (Powell et al. 1974) was on cultivated material and is uncertain.

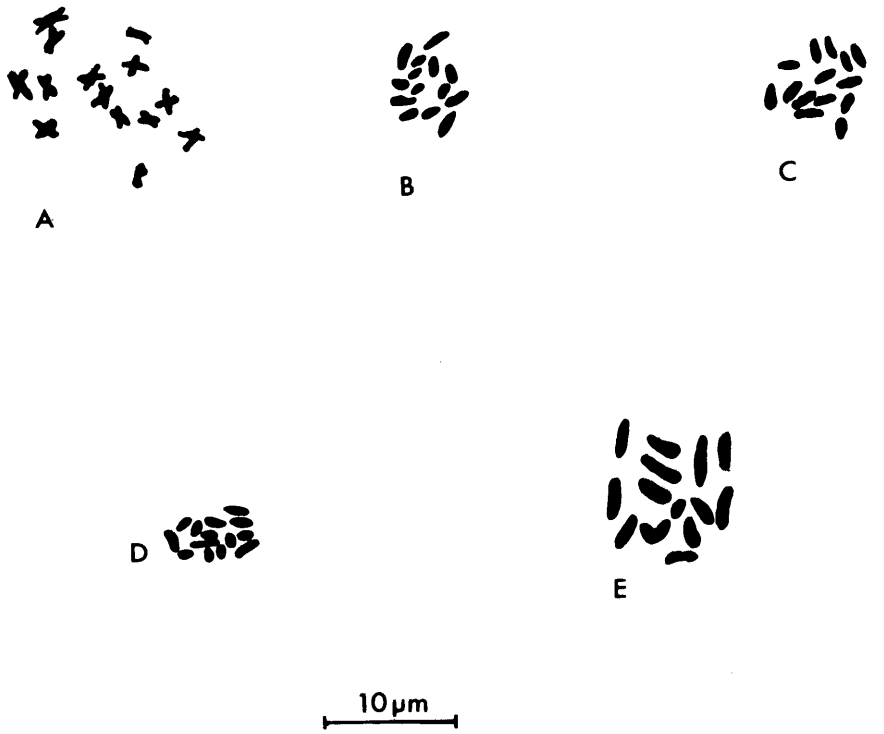


Fig. 28. Root tip mitosis. A. *Bubonium daltonii* ssp. *daltonii*, cult. No. 78-254, 2n=14. B. *B. daltonii* ssp. *vogelii*, cult. No. 78-256, 2n=14. C. *B. smithii*, cult. No. 77-312, 2n=14. E. *B. sericeum*, cult. No. 78-307, 2n=14.

The chromosome numbers determined in the present investigation are listed in Appendix 1. *Bubonium odorum* ssp. *odorum*, *B. daltonii* ssp. *vogelii* and *B. smithii* were studied karyologically for the first time. All the present counts on Macaronesian *Bubonium* species confirm n=7 as the basic number for the genus. Both mitosis (Fig. 28) and meiosis (Fig. 29) were regular in all species. Endomitotic pylysomaty was

Table 4. Chromosome numbers in *Asteriscus* s.lat. previously published. Can.: Canary Islands. CVI: Cape Verde Islands.

Taxon	n	2n	Locality	Author
A. maritimus	6	12	Spain: Cadiz	Bjørkquist et al. 1969
	6		Spain: Almeria	Ubera 1980
		12	Portugal: Alcarraque	Queiros 1973
		12	Unreported	Wiklund 1985
A. hierochunticus	6		Morocco	Reese 1957
		10	Morocco	Humphries et al. 1978
		12	Algeria	Wiklund 1985
A. spinosus	5		Morocco	Tongiori 1935, 1942, Reese 1957
		10	Portugal	Fernandes & Queiros 1971
B. aquaticum		14	Spain: Balearic Islands	Dahlgren et al. 1971
		14	Can: Gran Canaria	Borgen 1970
B. daltonii ssp. daltonii		14	CVI: San Tiago	Borgen 1975
B. intermedium		14	Can: Lanzarote	Borgen 1974, Van Loon 1974
B. graveolens ssp. stenophyllum		14	Can: Gran Canaria	Borgen 1970, Bramwell et al. 1972
B. schultzii		14	Can: Fuerteventura	Borgen 1974
B. sericeum	8		Cult.	Powell et al. 1974
		14	Cult.	Larsen 1958, 1960, Borgen 1969

observed in a single specimen of *B. graveolens* ssp. *odorum*. The count of n=6 in *Asteriscus maritimus* confirms the earlier results for this species.

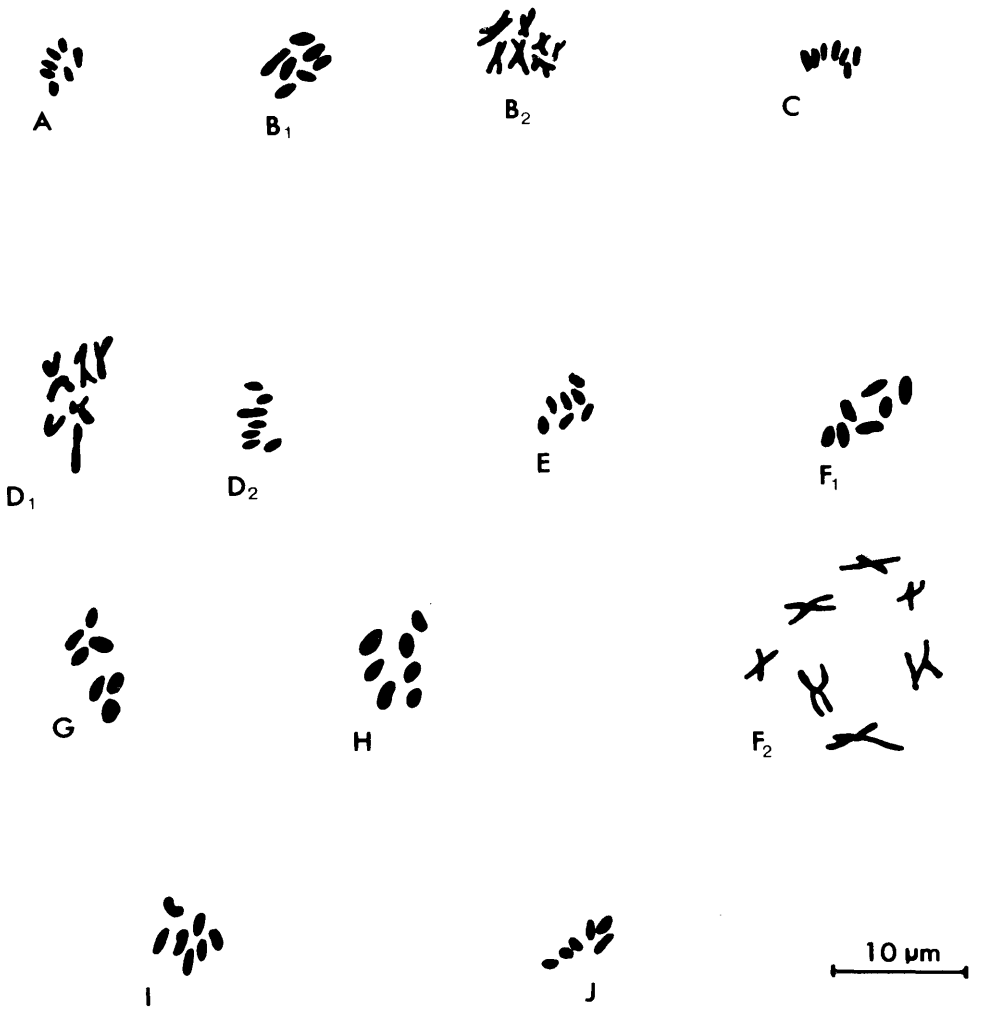


Fig. 29. PMC meiosis. A. *Bubonium daltonii* ssp. *daltonii*, cult. No. 78-254, n=7. B. *B. daltonii* ssp. *vogelii*, cult. No. 78-256, n=7. C. *B. smithii*, cult. No. 78-255, n=7. D. *B. intermedium*. D_1, cult. No. 78-155, n=7. D_2, cult. No. 77-324, n=7. E. *B. sericeum*, TH 96, n=7. F_1-$_2$. *B. graveolens* ssp. *odorum*, cult. No. 76-1342, n=7. G. *B. graveolens* ssp. *stenophyllum*, TH 44, n=7. H. *B. schultzii*, cult. No. 79-304, n=7. I. B. *aquaticum*, cult. No. 79-293, n=7. J. *Asteriscus maritimus*, cult. No. 78-148, n=6.

CROSSING EXPERIMENTS

Fertility of parental species

High pollen stainability values for the parental species were found in most specimens (Table 5). Only two of the 31 investigated plants had values below 80%. The lowest values recorded were 65% for the one available specimen of *B. schultzii* and slightly below 80% for one of the nine specimens of *B. daltonii* ssp. *vogelii*.

Table 5. Pollen fertility in parental species of *Asteriscus s. lat.*, by the number of plants with pollen stainability values <80%, 80-90%, and >90% in experimental populations. "n" indicates the number of plants investigated and "N" the number of populations studied.

Taxon	Mean	<80	80-90	>90	n	N
B. intermedium	90		4	3	7	4
B. sericeum	90		2	2	4	2
B. graveolens ssp. odorum	96			2	2	2
B. graveolens ssp. stenophyllum	93		1	1	2	1
B. schultzii	65	1			1	1
B. smithii	95			1	1	1
B. daltonii ssp. daltonii	89		1	1	2	1
B. daltonii ssp. vogelii	86	1	5	3	9	6
B. aquaticum	90			1	1	1
A. maritimus	90		1	1	2	2

Selfing experiments (Table 6) showed that the perennial *Bubonium* species tested are nearly, but not completely, self incompatible. Isolated capitula never developed seeds if not actively pollinated. The Cape Verdean species did not develop seeds even by active self pollination and seem to be completely self sterile. The Canarian species *B. intermedium* and *B. sericeum* each developed seeds in one of six attempts of active self pollination, but the 10 plants raised from the selfed seeds were, with one exception, sterile. These Canarian species are therefore regarded as predominantly self sterile. The Canarian-Moroccan *B. gravolens* ssp. *odorum* seems slightly more self fertile, with seed set in two of the four selfing attempts and pollen stainability values of 60 and 95% respectively in the two specimens of selfed offspring obtained.

The annuals *B. aquaticum* and *Asteriscus maritimus* are probably completely self fertile. Selfed seeds of *B. aquaticum* developed highly fertile plants with pollen stainability values between 80 and 100%.

Table 6. Seed development by artificial self-pollinations in experimental populations of *Asteriscus* s. lat. ATT) Number of attempted self-pollinations, SUCC) Number of self-pollinations resulting in seeds, SEED) Number of sedlings obtained, FERT) Fertility of self-pollinated specimens.

Culture No.	ATT	SUCC	SEED	FERT
B. intermedium				
76-1303	3	0	0	0
76-709	1	0	0	0
77-324	1	1	5	0-98%
78-155	1	0	0	0
B. sericeum				
76-1315	4	1	20	0
78-307	2	0	0	0
B. graveolens ssp. odorum				
76-1342	1	1	2	60-95%
79-298	1	0	0	0
B. graveolens ssp. stenophyllum				
79-300	2	1	not sown	
B. daltonii ssp. daltonii				
78-254	3	0	0	0
B. daltonii ssp. vogelii				
78-256	1	0	0	0
78-257	4	0	0	0
B. aquaticum				
79-252	1	1	2	80-95%
A. maritimus				
78-147	2	1	not sown	

Cross compatibililty

A survey of 54 crosses in 10 taxa of *Asteriscus* s.lat. is given in Appendix 2.

None of the 15 attempts to cross different species of *Bubonium* with *Asteriscus maritimus* resulted in fertile seeds. The capitula were also somewhat deformed. Thus there seem to be strong internal barriers against gene exchange between *Asteriscus* s.str., represented by *A. maritimus*, and *Bubonium*,

as would be expected from the differences in chromosome numbers between the two genera.

All crosses within *Bubonium* resulted in normal capitula, but only 20 crosses of the 39 attempts gave fertile seeds. The development of fertile seeds seems, however, to be somewhat arbitrary. For instance, only one of four attempts to cross different populations of a *B. sericeum* female with *B. intermedium* male resulted in fertile seeds. Nevertheless, these two species seem to be reciprocally cross compatible, with good germinability of the fertile seeds obtained and high fertililty of the hybrid offspring. The number of crossing attempts between the different species are therefore clearly too few to give fully reliable results and the conclusions must be drawn with the scarcity of material in mind. In particular, it is reasonable to look upon the unsuccessful crossing attempts with some caution.

Not all apparently well developed, seemingly fertile, seeds germinated well (Appendix 2). A maximum of 25 seeds were sown for each combination, and the number of seedlings obtained varied from zero to about 20. The germinabililty of the seeds was 10% for the successful cross *B. gravolens* ssp. *odorum* x *B. intermedium*; 35% for *B. intermedium* x *B. gravolens* ssp. *odorum*, and *B. intermedium* x *B. gravolens* ssp. *stenophyllum*; and 100% for *B. sericeum* x *B. intermedium*, *B. intermedium* x *B. sericeum*, and *B. sericeum* x *B. gravolens* ssp. *odorum*; with a mean value of 67% for these Canarian combinations. The germinability of the seeds from the successful crosses between Canarian and Cape Verdean taxa was 5% for *B. daltonii* x *B. intermedium*; 48% for *B. sericeum* x *B. daltonii* ssp. *daltonii*; 96% for *B. daltonii* ssp. *vogelii* x *B. gravolens* ssp. *odorum*; and 100% for *B. sericeum* x *B. smithii*; with a mean value of 45% for these Canarian - Cape Verdean combinations. A single intraspecific cross within *B. daltonii* had 95% germinability.

The pollen fertility in the hybrids showed a variation range of ± 10% in the two independent checks of the stainability in cotton blue lactophenol. A good, but not consistent, correlation between germinability of the hybrid seeds and pollen fertililty in the F_1 families was observed. In the crosses with the lowest germinability, i.e. 5% for *B. daltonii* ssp. *daltonii* female crossed with *B. sericeum* and *B. intermedium* males, no fertile pollen was developed at all. In the cross *B. gravolens* ssp. *odorum* x *B. intermedium* with 10% germinability, the pollen fertility was 50%. The combinations with 100% germinability varied, however, as to pollen fertility. Seed germinability therefore seems to give an indication of the cross compatibility between the parental species, but experimental difficulties probably have some additional and undeterminable effect on it.

A more consistent correlation was found between the frequency of flowering hybrids in each F_1 family and the average percentage fertile pollen in the flowering hybrids. In fact the values were identical in most cases. It follows that the germinability, flower formation, and pollen fertility are all influenced by the cross compatibility between the parental species and can be used as a measure for their ability to exchange genes.

In most of the successful combinations the hybrids developed normally and occasionally showed a pronounced hybrid vigour. The hybrids were generally intermediate between the parental species.

Meiosis was normal in all flowering F_1 families, except three of the six F_1 families obtained from crosses between Canarian and Cape Verdean species. Only 5% of the offspring from the crosses *B. sericeum* x *B. smithii*, *B. daltonii* ssp. *daltonii* x *B. sericeum*, and *B. daltonii* ssp. *daltonii* x *B. intermedium* ever flowered and the meiosis was defective in all three cases. In the two crosses with *B. daltonii* ssp. *daltonii* as the female parent the flowering broke down at the bud stage. These combinations were therefore sterile.

Only 7 of the 17 attempts to cross Canarian with Cape Verdean species developed seeds at all. The only successful combinations between Canarian and Cape Verdean species were: *B. sericeum* x *B. daltonii* ssp. *daltonii*, with 72% pollen fertility; *B. intermedium* x *B. daltonii* ssp. *vogelii*, with 62% pollen fertililty; and *B. daltonii* ssp. *vogelii* x *B. graveolens* ssp. *odorum*, with 90% pollen fertility.

Most cross combinations between the Canarian species were successful in one direction or the other, with pollen fertility values between 50 and 90%, which is a slightly reduced pollen fertility compared to the parental species. Only two combinations gave no seeds: the reciprocal attempts to cross *B. graveolens* with the annual *B. aquaticum*, and *B. schultzii* with *B. intermedium*.

In conclusion it seems to be more difficult to cross the Canarian with the Cape Verdean species than to cross the Canarian species among themselves. Only the annual *B. aquaticum* and the perennial *B. schultzii* seem to be internally isolated from the other Canarian species.

DISCUSSION

ISOLATION BARRIERS AND FERTILITY RELATIONSHIPS

The crossing polygon in Fig. 30 summarizes the cross compatibility between ten taxa of *Asteriscus* s. lat., based on seed set after crossing and fertility of the hybrids. Since the material was rather scarce, the figure must be read with caution.

The annuals, *Bubonium aquaticum* and *Asteriscus maritimus*, probably are autogamous and isolated from each other and all the other species by initial barriers to crossability. This correlation between sterility barriers and annual life form is in accordance with the results obtained in many other groups of plants (Grant 1981).

Differences in chromosome numbers between *Asteriscus maritimus* (n=6) and *Bubonium* (n=7) represent another barrier to gene exchange. The chromosome number divergence between *Asteriscus* s.str. (n=5,6) and *Bubonium* (n=7) has apparantly occasioned strong internal barriers to gene exchange between the two genera.

In addition *Bubonium aquaticum*, which shares the chromosome number n=7 with the perennial *Bubonium* species, seems to be isolated from them by chromosomal or genic barriers. Such internal barriers between annuals and perennials are present in many other genera (see Grant 1981), and are also found in the Macaronesian species of *Scrophularia* (Dalgaard 1979) and *Lobularia* (Borgen 1984). These barriers may be due to chromosomal repatterning, which seems to be prevalent among autogamous annuals owing to inbreeding, which induces chromosome breakage and rearrangements (Lewis & Raven 1958, Lewis 1962). *Bubonium aquaticum* is probably an example of this mode of speciation.

The perennial *Bubonium* species are mainly out-crossing: the Canarian ones predominantly self incompatible and the Cape Verdean ones completely so. Most successful crosses between these perennials gave vigourous and fertile F_1 hybrids, with regular meiosis and pollen fertility values above 50%.

The breakdown of the meiosis in the three F_1 families from crosses between Cape Verdean and Canarian species indicates a partial hybrid sterility between the species from the two archipelagos. Such a drop in hybrid fertility with increasing distance between the parental populations is also found in other groups, for instance in the species *Streptanthus glandulosus* (Kruckeberg 1957) and between the Canarian and Madeiran species of *Scrophularia* (Dalgaard 1979).

Besides the geographical isolation between the species from the two archipelagos, there is a seasonal isolation. The Canarian species of *Bubonium* start to flower two months after the Cape Verdean ones in nature. Under green house conditions the flowering of the Cape Verde species are delayed by one or two months compared with the Canarian ones.

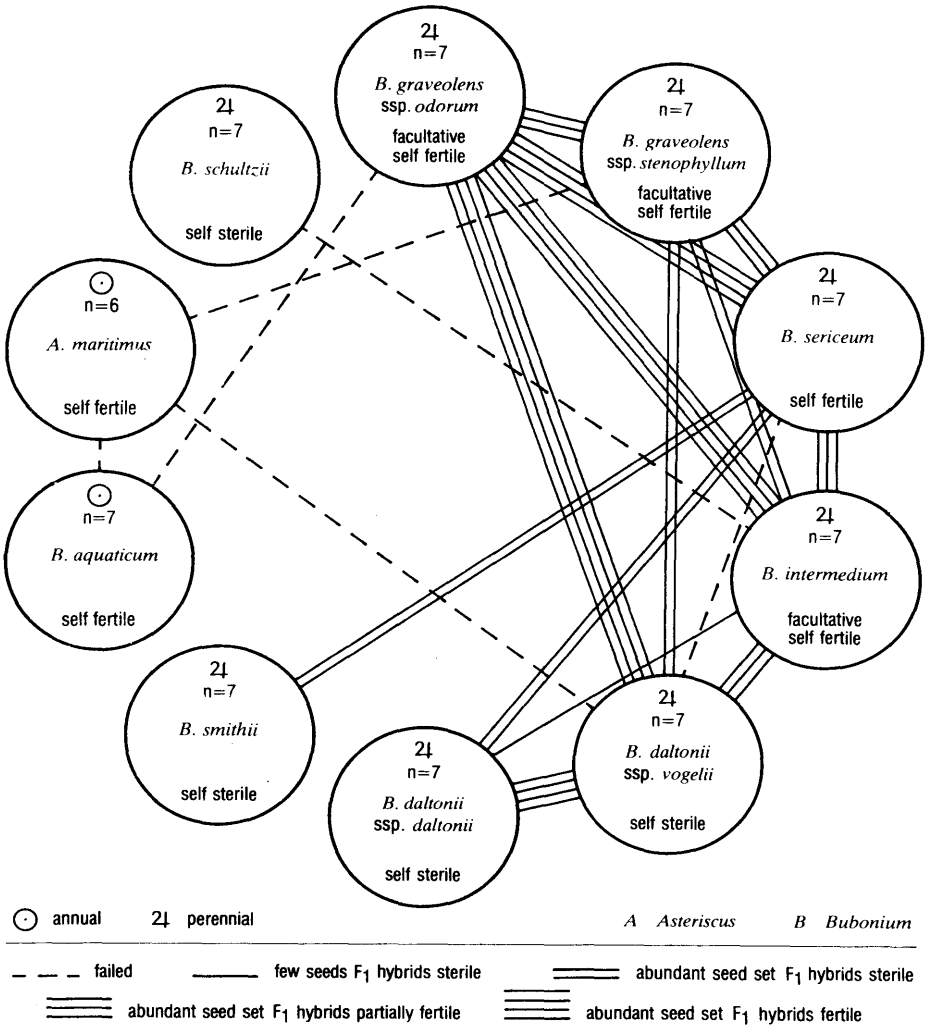


Fig. 30. Cross compatibility between ten taxa of *Asteriscus* s. lat.

Experimental crosses among the Cape Verdean species are few, but the two subspecies of *B. daltonii* were found to be completely cross compatible. Hybrids between them have also been observed in one locality in Santiago where they grow sympatrically. Otherwise the three taxa in the Cape Verde Islands are allopatric, and geographical isolation maintains species and subspecies integrity. Different ecologial preferences further strengthen the external barriers to gene exchange.

Among the perennial Canarian species, internal barriers to gene exchange are absent or weak, except between *B. schultzii* and the others. *Bubonium schultzii* is sympatric with *B. intermedium* in Lanzarote. Natural hybrids between the two species have never been observed. The experimental evidence for internal barriers is scarce, but one reciprocal crossing attempt gave no seeds. The somewhat decreased pollen fertility observed in *B. schultzii* may indicate minor structural chromosome rearrangements.

The other Canarian species are allopatric, but the two subspecies of *B. graveolens* meet in Gran Canaria and form a hybrid swarm in one locality. Again, mostly geographical and ecological barriers maintain species and subspecies integrity within the archipelago and the fertility relationship between most of the Canarian perennials corresponds to the *Ceanothus* pattern described by Grant (Grant 1981).

To apply the biosystematic categories to the Macaronesian *Buboniums* is difficult, partly because of the scarcity of the experimental data and partly because the results do not entirely fit the definitions of each category (Grant 1981). Most of the perennial *Bubonium* species seem to be ecospecies. They are able to exchange genes freely, without serious loss of fertility or vigour in the offspring (cf. Clausen et al. 1945). The Canarian populations, except those of *B. schultzii* and *B. aquaticum*, constitute an assemblage of such ecospecies. The Cape Verdean populations seem to constitute another assemblage of ecospecies and since the incompatibility barriers between the populations from the two archipelagos are fairly strong, the Canarian and Cape Verdean populations should be interpreted as different coenospecies. *Bubonium schultzii* and *B. aquaticum* seem isolated from each other and from all the other *Bubonium* species in Macaronesia by strong internal incompatibility barriers and are separate coenospecies.

In nature internal barriers are only one aspect of the isolation between species. External isolation is strong among all the Macaronesian *Bubonium* species. *Bubonium* therefore is another example of a Macaronesian group with weakly developed internal and well developed external isolation, like *Argyranthemum* (Humphries 1976, 1979a), the Macaronesian species in the *Scorodonia* group of *Scrophularia* (Dalgaard 1979), *Sinapidendron* (Rustan 1980), and the Macaronesian species of *Diplotaxis* (Rustan 1980) and *Lobularia* (Borgen 1984).

ORIGIN AND EVOLUTION

A general discussion on the origin of the Macaronesian flora is given by Bramwell (1972b, 1976), Humphries (1979a), and Sunding (1970, 1979), who all emphasize the land bridge theory and a Tertiary origin for some of the Macaronesian flora elements.

The eastern Canary Islands, Lanzarote and Fuerteventura, are partly continental (Raven & Axelrod 1974, Schminke 1976). Evidence for land bridges to the Cape Verde Islands is more scanty. Deposition of rock material in Maio during the opening of the South Atlantic (Rothe 1968) might point to a continental nature of the eastern Cape Verde Islands, and Sunding (1979)

postulates dispersal over short ocean distances or land bridges to explain the small Macaronesian element (11%) in the Cape Verdean flora.

Land bridges to the eastern islands of each archipelago may thus have served as migration routes for plants. The theory implies that both archipelagos could have been colonized by woody plants from the forest flora of the Tethyan-Tertiary region (Wulff 1944, Takhtajan 1969, Bramwell 1972, 1976, and Sunding 1979). Fossil evidence supports this theory (Saporta 1862-1874, Depape 1922).

The predominance of woody life forms in the Canaries has been considered by several authors to be a characteristic of relict plants (Meusel 1952, Lems 1960a, Bramwell 1972, 1976, and Sunding 1970, 1979). Meusel (1952) derived many modern Mediterranean growth forms, including species in *Asteriscus* s. lat., from basic forms similar to those now found only in the Canaries, like *Bubonium sericeum*.

Others, mainly Carlquist (1961, 1965, 1966, 1970a,b, 1971, 1974), argue that the endemic, frutescent species in oceanic islands like Hawaii and the Canaries are the result of an increase in woodiness in response to the uniformity of insular climates. This theory has gained little support and has been rejected by Aldridge (1977, 1978, 1979) on the basis of her studies of wood anatomy in the Canarian species of *Sonchus*, subgenus *Dendrosonchus*.

The ancestral *Bubonium* in Macaronesia may therefore have been woody, resembling the Canarian *B. sericeum* and *B. intermedium* and the Cape Verdean *B. smithii* and *B. daltonii* ssp. *daltonii*, and date back to the Tertiary. During the progressively cooler and drier climate in Pliocene times, *Bubonium* could have survived in the Canary Islands by a vertical migration in the Jandia area in Fuerteventura (*B. sericeum*), the Famara massif in Lanzarote (*B. intermedium*); and in the Cape Verde Islands likewise in the Monte Gordo area in São Nicolau (*B. smithii*), and the mountain massifs in Santiago (*B. daltonii* ssp. *daltonii*), resulting in a very local distribution of these taxa today.

The Canarian *Bubonium* species inhabit the eastern Canarian islands Lanzarote, Fuerteventura, and Gran Canaria only. They show affinity to northwest African species, and their origin might be sought in the present day flora of the northwest African region. However, the woody endemics *B. sericeum* and *B. intermedium* have a relict distribution and could be remnants of the Tethyan-Tertiary flora (cf. Wulff 1944, Meusel 1952, Bramwell 1972a, 1976).

The Canarian *B. graveolens* with two sspp., *odorum* and *stenophyllum*, is less woody and more variable, occurs under more xeric conditions, and has a wider distribution than *B. sericeum* and *B. intermedium*. The ssp. *odorum* also occurs in Morocco (cf. Wiklund in press) and is closely allied to the Moroccan *B. graveolens* ssp. *graveolens*. *Bubonium graveolens* ssp. *odorum* therefore probably has a more recent origin in the islands.

Bubonium schultzii is another Canarian xeric species with slight lignification only. It has a restricted distribution in Lanzarote - Fuerteventura and in the Macaronesian enclave in Morocco. Morphologically this species has a rather isolated

position among the Macaronesian perennial taxa and is the only one with scabrous leaves, flattened capitula, whitish ray florets, and non-glandular leaves. It has cypsela resin canals in common with the Canarian endemics and short, connate pappus scales in common with the Cape Verdean endemics. It also seems genetically isolated from the other species. It is, however, morphologically close to the Moroccan *B. imbricatum*. Whether it belongs to an ancient Macaronesian element or not is uncertain.

All three Cape Verdean *Bubonium* taxa have poorly developed dispersal agencies (i.e. very short cypsela hairs and pappus scales). They all inhabit the western Cape Verde Islands only. Even if dispersability is secondarily reduced (Carlquist 1974), long distance dispersal by birds, wind or waves from the African mainland directly to the western Cape Verde Islands seems unlikely. Dispersal between the two archipelagos is even more unlikely, the distance being 1400 km and the wind systems highly unfavourable (Fernandopullé 1976). Migration may have proceeded from the African mainland to the oceanic western islands via the presumably more continental eastern islands very long ago, resulting in the present relict distribution. In particular the very local taxa *B. daltonii* ssp. *daltonii* and *B. smithii* seem to be relict.

Bubonium daltonii ssp. *vogelii* has a much wider distribution than the other Cape Verdean taxa and occurs in all the western islands. The ssp. *vogelii* is also more variable and grows under more xeric conditions. Xeric forms like ssp. *vogelii* may have been favoured by the progressively drier climate and thus been able to survive and/or spread over larger areas. It has certain plesiomorphic features, such as the retention of strong leaf lignification despite a small leaf area. This may indicate that *B. daltonii* ssp. *vogelii* is still close to the presumed woody, ancestral stock. Its origin may therefore date back to the origin of the Macaronesian element in the Cape Verdean flora, presumably in the Tertiary (cf. Sunding 1979).

Apart from one probably erronous count of n=8, the basic chromosome number in *Bubonium* is invariably x=7 and all species in Macaronesia are diploids. According to the system of classification of endemics based on ploidy level (Favarger & Contandriopoulos 1961), the endemic Macaronesian *Bubonium* species are schizoendemics.

As in many other schizoendemic groups in Macaronesia, evolution in *Bubonium* has taken place by a gradual divergence by means of adaptive radiation and/or vicariant evolution. Such evolutionary patterns have been amply demonstrated for *Aeonium* (Lems 1960a), *Echium* (Lems & Holzapfel 1968, Bramwell 1972a, 1975), *Argyranthemum* (Humphries 1976, 1979a), and *Sonchus*, subgenus *Dendrosonchus* (Bramwell 1972b, 1976). However, *Bubonium* does not exhibit the same evolutionary potential as these genera, which have adaptively radiated into a wide range of habitats and comprise a high number of species. The low number of species in *Bubonium* in Macaronesia indicates a narrower ecological preference of the genus as a whole and a lack of adaptability to widely different habitats.

Within Macaronesia, *Bubonium* has diverged into a rather limited range of ecological habitats and geographical isolation has apparently been an important factor in the evolution. The present day pattern of morphologically distinct populations which occupy small and essentially similar habitats indicates a process of gradual migration of the ancestors with repeated isolation. Most taxa today probably represent isolated parts of a once more or less conjoined ancestral population (Croizat et al. 1974, Platnik & Nelson 1978, Rosen 1978). The pattern may reflect either an interaction of genetic drift and weak selection (Bramwell 1972b) or slight edaphic and microclimatological adaptations (Humphries 1979a), like the patterns found in, for instance, *Centaurea*, sect. *Cheirolophus* and the *Sonchus radicatus* complex.

In the evolution of the infraspecific taxa in *B. graveolens* and *B. daltonii* adaptive radiation in combination with slight ecogeographical isolation may have been the major force. Adaptations from mesic frutescent species to less frutescent or herbaceous species of xeric conditions have been outlined for many Macaronesian groups, for instance *Argyranthemum* (Humphries 1976, 1979a) and *Plantago*, subgenus *Psyllium* (Bramwell 1976). The xeric *B. daltonii* ssp. *vogelii* may thus be interpreted as being derived from the more mesic and more frutescent *B. daltonii* ssp. *daltonii*. However, xeric or semi-xeric adaptations may be reversible, as suggested by Stebbins (1974, 1977). Adaptive trends from drier to moister habitats probably exist in *B. graveolens* in Gran Canaria. The populations of *B. graveolens* exhibit clinal patterns in some morphological characters: habit, woodiness, and foliage, and the narrow leaved ssp. *stenophyllum* of semi-xeric habitats in Gran Canaria may be derived from the more broad leaved ssp. *odorum* of the most xeric habitats.

However, adaptive radiation has been far less important than vicariant evolution. Examples of vicariant taxa in *Bubonium* with respect to, for instance, leaf morphology are: *B. sericeum* (Canary Islands) and *B. smithii* (Cape Verde Islands), and *B. intermedium* (Canary Islands) and *B. daltonii* ssp. *vogelii* (Cape Verde Islands). This resemblence in leaf morphology between the Canarian and Cape Verdean species confused some of the first botanists visiting the Cape Verde Islands, such as Christen Smith (Sunding 1980). Vicariant pairs are reported in other genera in Macaronesia, for instance *Parolinia* (Bramwell 1970), *Sonchus* (Bramwell 1972b), *Crambe*, sect. *Dendrocrambe* (Bramwell 1972) and *Argyranthemum* (Humphries 1976, 1979a), but these examples are restricted to the Canary Islands.

Crossing experiments and chromosome studies, although scarce, have revealed a fairly close relationship between the Canarian and the Cape Verdean *Bubonium* species. The endemic Canarian and Cape Verdean species also show high overall similarity. Both groups have retained many features which can be interpreted as plesiomorphous: woody habit, sericeous leaves,leaf-like bracts, glands, cypsela sclerenchyma, boat-shaped paleae, and chromosome number 2n=14. An origin from a common mainland stock of *Bubonium* may explain this relatedness.

Chance dispersal from the African mainland may have occurred, both in ancient times and more recently. However, the lack of good dispersal agencies and the present distribution of *Bubonium* in the western Cape Verde Islands and the isolated occurrence of *B. sericeum* and *B. intermedium* in the Canary Islands cannot, in our opinion, be explained solely by chance dispersal. There must be historical causes also.

We postulate, as the most plausible hypothesis, that the progenitors of the woody *Bubonium* species with a relict distribution today have most likely also been woody and that the origin of these species must be sought in the Tethyan-Tertiary flora. We do not deny the possible more recent origin of some of the species in Macaronesia, i.e. *B. aquaticum* and *B. graveolens*. However, in our opinion the frutescent *Bubonium* species mainly belong to an old element in the Macaronesian flora, an element common to the Canary Islands and the Cape Verde Islands.

SPECIES AND SUBSPECIES CONCEPT

In the present revision we have accepted a predominantly morphologically defined species concept, otherwise most perennial Macaronesian *Bubonium* species would have been lumped into one large, very variable and unpractical species. We have therefore chosen to refer two populations to separate species if sharp discontinuities exist in several morphological characters.

We use the category 'subspecies' for a series of populations which have certain morphological characteristics in common, are allopatric and/or inhabit different ecological habitats in comparison with the rest of the species. Morphologically intermediate individuals between the subspecies and the rest of the species may occur, but only in populations geographically located between the subspecies and the remainder of the species.

A consequence of these principles of taxonomic delimitation is that specific status is given to markedly distinct and discontinuous populations with respect to morphology, although many of them seem to be completely interfertile and constitute ecospecies in the biosystematic hierarchy. Similarly, our subspecies are equivalent to ecotypes in the biosystematic hierarchy; they are distinguished as to morphological characteristics and are also ecologically differentiated, but completely interfertile, and, although they are predominantly allopatric, intermediates occur in nature.

TAXONOMY AND PHYTOGEOGRAPHY

KEY TO SPECIES AND SUBSPECIES

1. Indumentum scabrous
   Rayflorets white ..... 2. B. schultzii
1. Indumentum sericeous-tomentose
   Rayflorets yellow 2

2. (1) Cypselas unribbed
   Pappus < 0,8 mm long 3
2. Cypselas ribbed
   Pappus > 0,8 mm long 5

3. (2) Leaves crowded towards apices of stems
   Involucre > 15 mm wide ..... 7. B. smithii
3. Leaves distant towards apices of stems
   Involucre < 15 mm wide 4

4. (3) Leaf margins denticulate
   Palea apically glabrous ..... 8. B. daltonii ssp. daltonii
4. Leaf margins entire
   Palea apically pubescent ..... 9. B. daltonii ssp. vogelii

5. (2) Ray florets > 15 mm long ..... 4. B. sericeum
5. Ray florets < 15 mm long 6

6. (5) Annual herbs ..... 1. B. aquaticum
6. Perennial shrubs or shrublets 7

7. (6) Leaves crowded towards apices of stems 6. B. graveolens ssp. stenophyllum
7. Leaves distant towards apices of stems 8

8. (7) Leaves linear-narrowly oblong ..... 5. B. graveolens ssp. odorum
8. Leaves oblanceolate-obovate ..... 3. B. intermedium

DESCRIPTION AND DISTRIBUTION

Bubonium schultzii (Bolle) Sventenius Fig. 31

Index Seminum Hortus Acclimat. Plantarum Arautapae 1969: 52, 1969. - Basionym: *Odontospermum schultzii* Bolle, Bonplandia 7:295, 1859. Type: Bolle, Fuerteventura, La Oliva, avril -52 (-57?)(P-type selected by Anette Wiklund, Wiklund in press). *Asteriscus schultzii* (Bolle) Pit. & Proust, Les Iles Canaries.

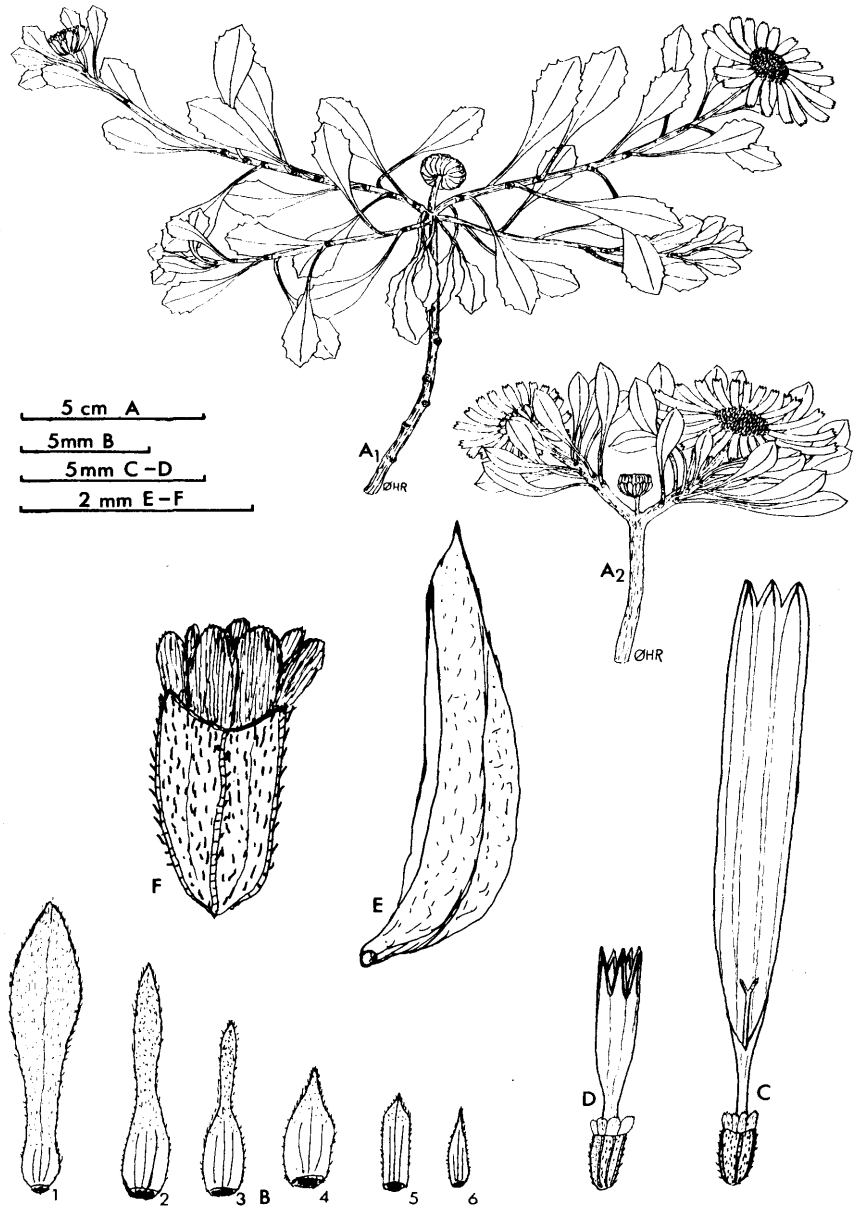


Fig. 31. *Bubonium schultzii*. A. Habitus. A_1, plant from Lanzarote, Playa de Famara. A_2, plant from Fuerteventura, La Oliva. B. Involucral bracts. C. Ray floret. D. Disc floret. E. Palea. F. Disc cypsela.

Flore de l'archipel: 224, 1908.

Odontospermum lanzarotenze Hutchinson, Kew Bull.: 231, 1916, *nom. superfl.* Type selected here: R.T. Lowe, Lanzarote, road Haria to Arrecife (K-lectotype! BM-isolectotype!).

Nomenclatural note: Bolle's original collection in B has not been traced and is probably destroyed. One specimen of this species collected by Bolle was found by Anette Wiklund at P (Wiklund in press).

Illustration: Kunkel 1982: Fig. 16.

A moderately branched, slender suffrutex or shrublet, up to 0.3 m high, up to 0.3 m wide. Stems slender-erect, scabrous towards apices, the rest glabrous, brownish.

Leaves alternate, distant, flat, sometimes slightly succulent fleshy, widely oblanceolate, 25-70 mm long, 9-32 mm wide, scabrous-scabridulous, margins entire to sinuate with rounded remote teeth or serrate towards mucronate apex, base attenuate and villose.

Capitula solitary, pedunculoid, terminal. Involucre cyathoid-subglobose, 13-15 mm wide. Involucral bracts in 4-6 rows, scabrous without glands, the outermost oblanceolate with an ovate limb, up to 12 mm long, up to 2 mm wide, the innermost narrowly triangular. Receptacle flattened with depressed margins, 6-7 mm wide, paleate. Paleae shallow cymbiform, acuminate, about 5 mm long, scabrous without glands, persistent.

Ray florets 24-40, whitish-pale yellow, abaxial side of lamina occasionally with a red purple stripe. Tube cylindrical -triquetrous, up to 2 mm long, glabrous without glands. Lamina 13-25 mm long, up to 3 mm wide, glabrous, lobes distinctly veined, about 1 mm long. Ray cypselas triquetrous, ribs 3, longitudinally obpyramidal, 1.2-1.5 mm long, the rest as in the disc cypselas.

Disc florets perfect. Corolla 4.5-6.0 mm long, tube terete, distinctly divided in tube and upper wider limb, lobes 1.0-1.5 mm long, narrowly triangular with entire margins, distinctly veined without glands. Style branches about 1.0 mm long. Anthers about 2.5 mm long, tails about 1/4 of the length of the anther. Disc cypselas terete or slightly obtrullate in median cross-section, ciliate, 1.2-1.8 mm long, ribs distinct and up to 6. Pappus of tufted hairs resembling connate, obovate scales, about 1.0 mm long.

Variation. This species is highly variable with respect to leaf morphology and ray floret colour. Generally, the specimens from Fuerteventura have narrower leaves and more yellowish ray florets than those from Lanzarote. Leaf shape is, however, variable within single populations (e.g. in the Playa de Famara population in Lanzarote). The material from the two islands is therefore not treated as different taxa.

Flowering period. March-June (Bolle 1859).

Chromosome number. 2n=14.

Related species: 1) *Bubonium imbricatum* (Cav.) Pau, a Moroccan desert species occasionally confused with *B. schultzii*, but distinguished by strongly yellow ray florets, succulent and glabrous leaves with double serrate margins and glands. Reports of this species from the Canary Islands are probably due to confusion with *B. schultzii*. A sheet labelled:

Buphthalmum chrysanthemoides, Broussonet, Canaries (P), in Broussonet's own handwriting (Burdet 1972), is a specimen of *B. imbricatum* and probably mislabelled out of Broussonet's Mogador material. 2) *Asteriscus maritimus* (L.) Less. The citation in Berthelot (1835-1842) of this Mediterranean species in Lanzarote, might be a superficial confusion with *B. schultzii*, which was until then undescribed. The short description of Canarian material of *A. maritimus* by Schultz Bipontinus (in Webb & Berthelot 1844), may support this theory. No preserved material exists to verify confusion between *Asteriscus maritimus* and *Bubonium schultzii*.

Distribution: Fig. 34. *Bubonium schultzii* grows on coastal rocks at Playa de Famara, Lanzarote, and in dry sandy or rocky flats in the northern part of Fuerteventura. The species has recently been discovered in S.W. Morocco (Davis 1980) (Identifications by A. Wiklund).

Collections: About 15 collections were examined; Fuerteventura: Burchard 383, IV 1913, La Oliva, (K, O); R.T. Lowe, road la Oliva to Rio de Las Palmas, (BM); PS, 2 km S of Corralejo, (O-seed coll.); TH 53-57, 61-66, Lanzarote: coastal rocks at Playa de Famara, (O); R.T. Lowe, road Haria to Arrecife, (BM, K).

Bubonium intermedium (DC.) T. Halvorsen & Wikl., comb. nov.
Fig. 32.

Basionym: *Asteriscus sericeus* (L.f.) DC. var. *intermedius* DC., Prodr. syst. nat. regni veg. 5: 486, 1836. Type: Chr. Smith, Lancerotte in arid. camp., 1816 (G-DC-holotype, seen by Anette Wiklund). - *Buphthalmum sericeum* Link in Buch. Phys. Beschr. Can. Ins.: 150, 1825 (homonym). - *Nauplius intermedius* (DC.) Webb in Webb et Berth., Hist. Nat. Iles Can. III. Bot. 2. Phytogr. Can.: Fig. 86A, 1843. - *Odontospermum intermedium* (DC.) Schultz Bip. in Webb et Berth., Hist. Nat. Iles Can. III. Bot. 2. Phytogr. Can.: 236-237, 1844. - *Asteriscus intermedius* (DC.) Pit. & Proust. Les Iles Canaries. Flore de l'archipel: 224, 1908.

Nomenclatural note: *Buphthalmum sericeum* Link is probably a later homonym of *Buphthalmum sericeum* L.f., but it has been impossible to trace any of Link's material which could elucidate his application of this name.

Illustrations: Webb 1843: Fig. 86 A. Lid 1968: Fig. 25 A. Bramwell & Bramwell 1974: Fig. 91. Kunkel 1978a: Fig. 6.

Common name: Tojio.

A moderately branched shrub, up to 0.5 m high, irregularly dichotomous, occasionally with candelabra branching. Stems ascending-erect, tomentose, becoming sericeous and finally more or less glabrous in older stem parts, marked with leaf scars, greyish-brownish.

Leaves alternate, distant or occasionally crowded towards apices of stems, flat, obovate-oblanceolate, 15-42 mm long, 6-14 mm wide, densely sericeous, margins entire, petioles up to 3.5 mm wide with indistinct lateral wings.

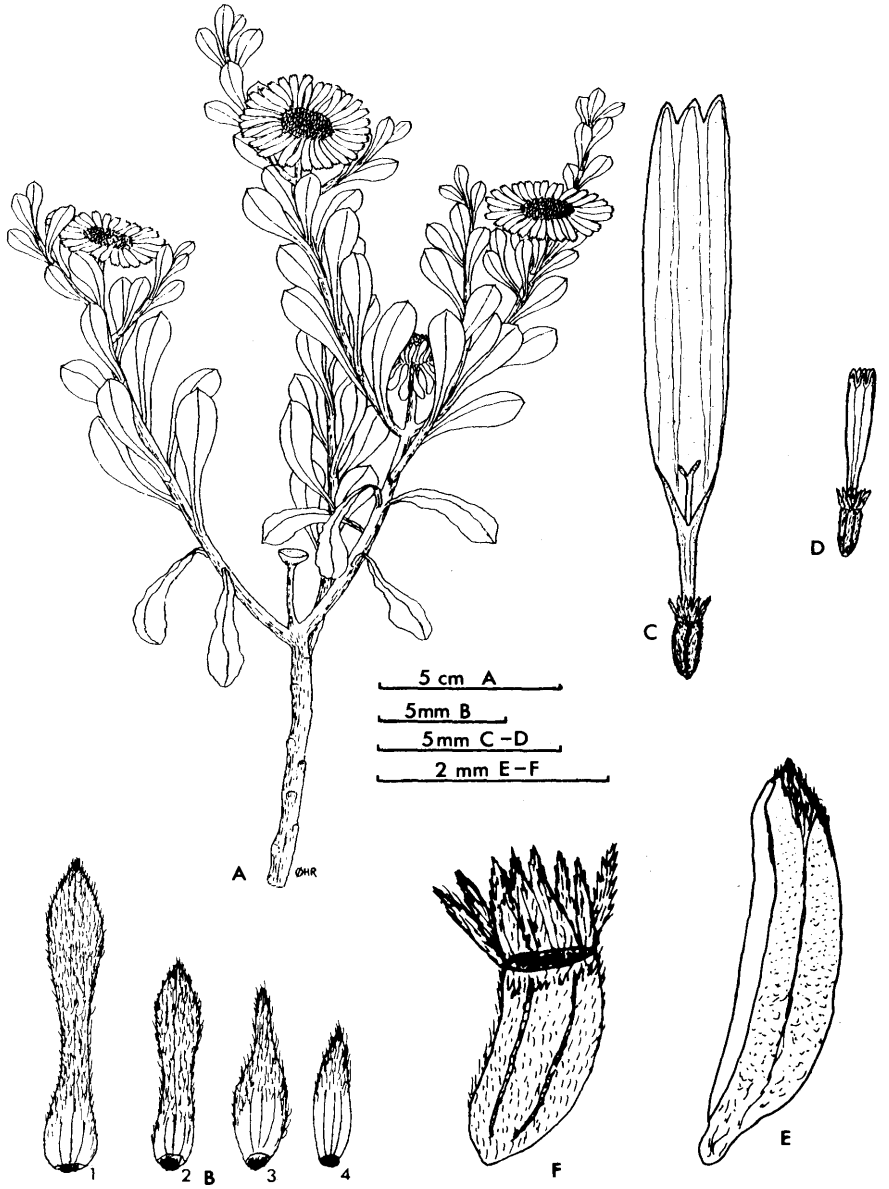


Fig. 32. *Bubonium intermedium.* A. Habitus. B. Involucral bracts. C. Ray floret. D. Disc floret. E. Palea. F. Disc cypsela.

Capitula solitary, shortly pedunculoid, terminal. Involucre flattened-subglobose, 12-18 mm wide. Involucral bracts 60-80, narrowly oblong-lanceolate, the outermost sericeous with a lanceolate-ovate apical limb, up to 15 mm long, up to 5 mm wide, the innermost apically pubescent. Receptacle flattened to narrowly transversely rhomboid, up to 8 mm wide, paleate. Paleae cymbiform, dorsally carinate, 4.0-4.5 mm long, pubescent and weakly glandular towards the acute apex, deciduous to persistent.

Ray florets 35-50. Tube cylindrical-triquetrous, up to 3 mm long, weakly gladular, anther rudiments occasionally present. Lamina narrowly oblong with scattered glands, 9-15 mm long, about 2.5 mm wide, lobes 0.75-2.5 mm long. Style branches narrowly oblong, 1.0-1.5 mm long. Ray cypselas triquetrous, ribs 3, longitudinally obpyramidal, the rest as in the disc cypselas.

Disc florets perfect. Corolla 3.5-4.5 mm long, tube terete, tube and limb indistinct, lobes 0.7-1.2 mm long, triangular with small incisions along the margins, dorsally glandular. Style branches as in the ray florets, but somewhat shorter. Anthers up to 2 mm long, tails about 1/3 of the length of the anther. Disc cypselas terete, 1.3-1.75 mm long, hirsute, ribs 3-6. Pappus of tufted hairs resembling free scales, 0.75-1.25 mm long.

Flowering period: February-April.

Chromosome number: 2n=14.

Related species: 1) *Bubonium sericeum*, see this. 2) *B. daltonii* ssp. *vogelii* (the Cape Verde Islands), is habitually closely related, but cypsela characters separate the two taxa.

Distribution: Fig. 34. *Bubonium intermedium* grows on dry slopes in Lanzarote from sea level to higher mountain peaks, most frequently in the Famara massif in the northern part of the island. Accounts from Fuerteventura by Link (in Buch 1825) and Burchard (1929) are probably confusions with *B. sericeum*.

Collections: About 90 collections were examined, mainly from the Famara massif in Lanzarote.

Bubonium sericeum (L.f.) T. Halvorsen & Wikl. comb. nov.
Fig. 33

Basionym: *Buphthalmum sericeum* L.f., Supplementum plantarum: 379, 1781. Type selected here: Francis Masson, Fuerte Ventura (Insula Canaria), 1778 (BM-lectotype!) - *Nauplius sericeus* (L.f.) Cass., Dict. sci. nat. 33-37: 274, 1825. - *Odontospermum sericeum* (L.f.) Schultz Bip. in Webb et Berth., Hist. nat. Iles Can. III Bot. 2. Phytogr. Can.: 234-235, 1844.

Asteriscus sericeus (L.f.) var. *latifolius* DC., Prodr. syst. nat. regni veg. 5: 486, 1836.

Nomenclatural note: The endorsement on the reverse side of the herbarium sheet with the type specimen is written by Solander (Marshall 1978). The sheet has two specimens. The upper one is a collection of *Bubonium graveolens* ssp. *odorum* from Tenerife by Broussonet.

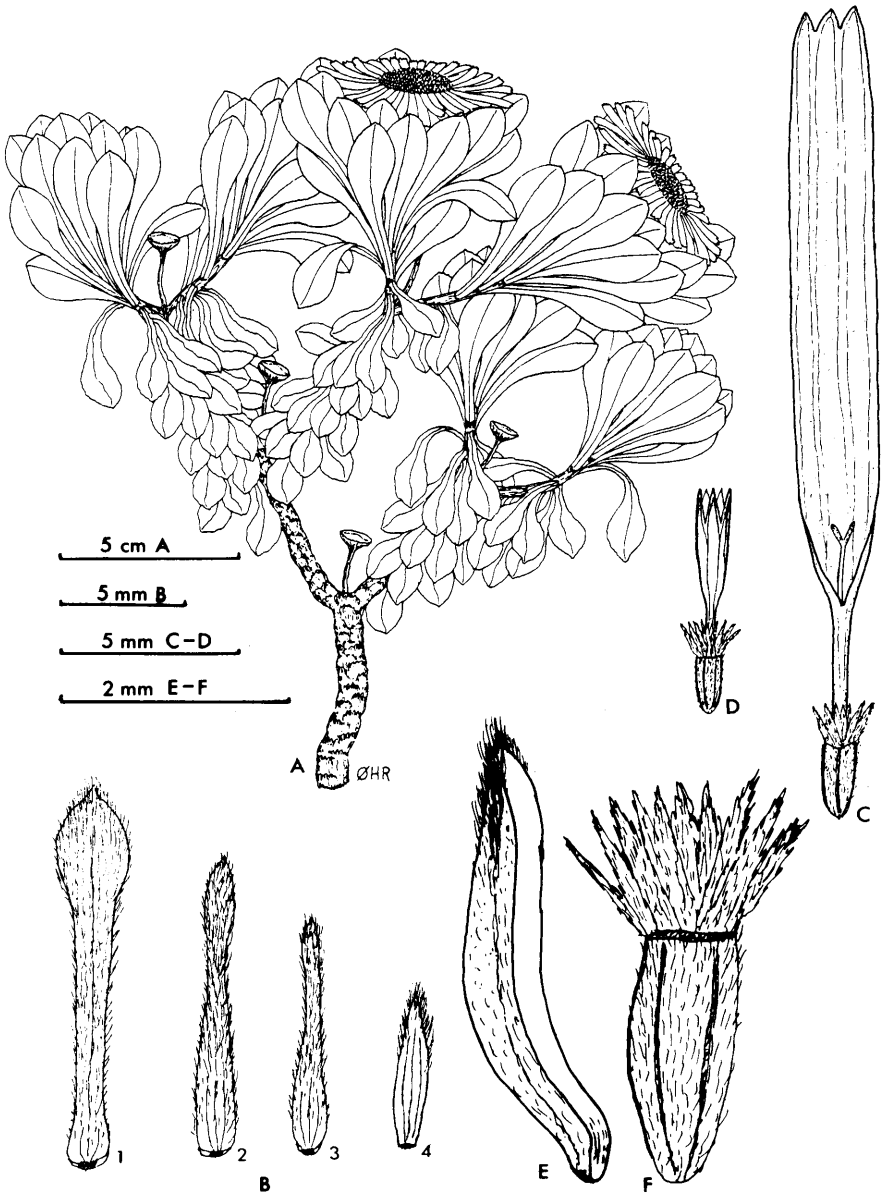


Fig. 33. *Bubonium sericeum*. A. Habitus. B. Involucral bracts. C. Ray floret. D. Disc floret. E. Palea. F. Disc cypsela.

Illustrations: Sims 1816: Fig. 1836, Webb 1841: Fig. 87, Bramwell & Bramwell 1974: Fig. 274.

Common names: Jorado or Jorjada, after Bolle also Joriada or Tojia (Kunkel 1977).

A moderately branched shrub, candelabra branching in sheltered localities, but often more regularly dichotomous, up to 0.7 m high, up to 2 m wide. Stems ascending-erect, tomentose-villose, marked with leaf scars, greyish-blackish.

Leaves alternate, very densely crowded towards apices of stems. Young leaves dentate towards apex, mature leaves entire to remotely toothed, flat, erect, sharply obovate-oblanceolate, 35-71 mm long, 11-22 mm wide, densely sericeous on both sides, petioles flattened with lateral 1-3 mm wide wings.

Capitula solitary, shortly pedunculoid, terminal. Involucre flattened-subglobose, 18-24 mm wide. Involucral bracts 80-100, linear-lanceolate, the outermost with an ovate apical limb, up to 20 mm long, up to 6 mm wide, sericeous, the innermost with ciliate margins towards apices only. Receptacle flattened to narrowly transversely rhomboid, up to 10 mm wide, paleate. Paleae cymbiform, dorsally rounded or slightly carinate, pubescent and weakly glandular towards the acute apex, 4.5-5.5 mm long, deciduous.

Ray florets about 60. Tube cylindrical-triquetrous, 3-4 mm long, weakly glandular, anther rudiments occasionally present. Lamina narrowly oblong with scattered glands, 15-23 mm long, up to 2.5 mm wide, lobes 0.6-1.0 mm long. Style branches narrowly oblong, 1-2 mm long. Ray cypselas triquetrous, ribs 3, longitudinally obpyramidal, the rest as in the disc cypselas.

Disc florets perfect. Corolla 4.2-5.8 mm long, tube terete, tube and upper wider limb distinctive, lobes 1.0-1.5 mm long, narrowly triangular with entire margins, dorsally weakly glandular. Style branches about 1.0 mm long. Anthers about 2.5 mm long, tails about 1/4 of the length of the anther. Disc cypselas terete, 1.5-2.0 mm long, hirsute, ribs 3-6. Pappus of tufted hairs resembling free scales, 1.5-1.8 mm long.

Flowering period: February-April.

Chromosome number: 2n=14.

Related species: 1) *Bubonium intermedium*, but *B. sericeum* is distinguished by a generally more crowded leaf arrangement, wider involucre, longer ray florets and more linear involucral bracts. 2) *Bubonium smithii*, (the Cape Verde Islands), has a superficial resemblance with *B. sericeum*. Quantitative characters in involucre, ray florets and leaves and qualitative characters in e.g. cypselas and disc florets distinguish the two species.

Distribution: Fig. 34. *Bubonium sericeum* is confined to semi-arid mountain slopes above 500 m altitude in Fuerteventura. Reports of this species from Lanzarote, e.g. Knoche (1923) and Lindinger (1926), probably result from confusion with *B. intermedium*. The only collection seen that supports an occurrence of *B. sericeum* in Lanzarote is one of Pitard from Haria in 1905 (P). Since the species is commonly cultivated in the Canary Islands, this could be a cultivation escape, or it might be a mislabelled specimen.

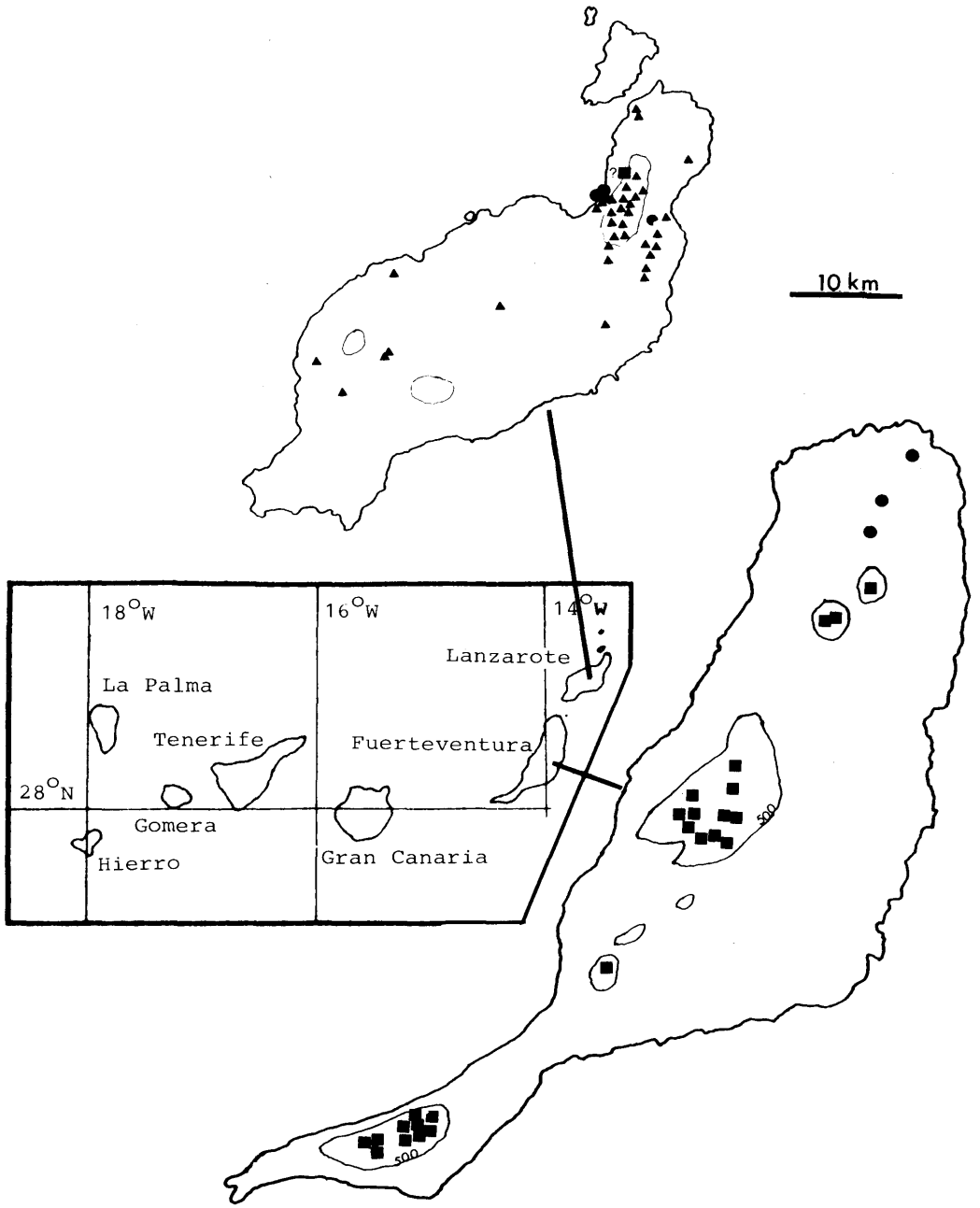


Fig. 34. Distribution of ● *Bubonium schultzii*, ▲ *B. intermedium*, and ■ *B. sericeum* in the Canary Islands. The question mark indicates a dubious collection of *B. sericeum* from Lanzarote.

Collections: About 50 collections were examined, mainly from Jandia massif (S-region) and the Betancuria area (central region) of Fuerteventura.

Bubonium graveolens (Forssk.) Maire ssp. *odorum* (Schousb.) Wikl. comb. et stat. nov. Fig. 35.

Basionym: *Buphthalmum odorum* Schousb., Iagttagelser over vextriget i Marokko. 1: 199, 1801. Type: Schousboe, Mogador in Morocco (C-lectotype selected by A. Wiklund, P-isolectotype). - *Asteriscus odorus* (Schousb.) DC., Prodr. syst. nat. regni veg. 5: 486, 1836. - *Odontospermum odorum* (Schousb.) Schultz Bip. in Webb et Berth., Hist. Nat. Iles Can. III. Bot. 2. Phytogr. Can.: 238, 1844. - *Bubonium odorum* (Schousb.) Maire, Bull. Soc. Hist. Nat. Afr. N. 27(6): 233, 1936.

Odontospermum odorum (Schousb.) Sch. Bip. var. *angustifolium* Ball, J. Linn. Soc. Bot. 16: 502-503, 1878, nom. rejic. - Type: Bourgeau 1384, Gran Canaria, Isleta, in arenosis maritimis; 8.5.1855 (P-lectotype selected by Anette Wiklund (Wiklund in press), G, K, MA, MPU, UPS, W (isolectotypes).

Asteriscus stenophyllus (Link) Kuntze var. *villososericeus* Kuntze, Rev. Gen. Plant. 1: 319, 1891. - Type: O. Kuntze, Tenerife, Güimar 10.1.1888 (NY - holotype!)

Nomenclatural note: Except for the original description of *B. odorum* by Schousboe (1801), all names are applied to Canarian material only. The Moroccan material is treated by Maire (1936) and Wiklund (in press.). All microspecies described by Gandoger (1887) are ignored. His binomials denoting these taxa are not validly published and can be disregarded (ICBN paragraph 24). Kuntze's type for v. *villosocericeus* is of dubious origin. He has another collection of ssp. *odorum* from the same date made in La Isleta, Gran Canaria.

Suffrutex, 0.2-0.5 m high, 0.2-0.5 m wide. Branching moderate, dichotomous, lax and slender with depressions of one of the axes. Stem creeping or ascending-erect, young parts usually purplish, tomentose-villose, densely glandular, becoming greyish-brownish and nearly glabrous with a few glands only.

Leaves alternate, spreading-erect, distant towards apices of stems with less than two leaves per cm of stem, flat, narrowly oblong, length/width ratio below 11, the lower occasionally very remotely toothed, 18-60 mm long, 1.5-6.0 mm wide, base attenuate-clasping. Young leaves moderately sericeous, mature leaves usually becoming more glabrous, densely glandular.

Capitula solitary, somewhat pedunculoid, terminal. Involucre globose, 6-10 mm wide. Involucral bracts narrowly oblong-lanceolate, the innermost more often narrowly obtrullate and weakly pubescent, the outermost up to 12 mm long and sericeous. Receptacle transversely rhomboid, 4-6 mm wide, paleate. Paleae cymbiform, distinctly carinate, 3.5-4.2 mm long, densely glandular towards the acute and pubescent apex, deciduous to persistent.

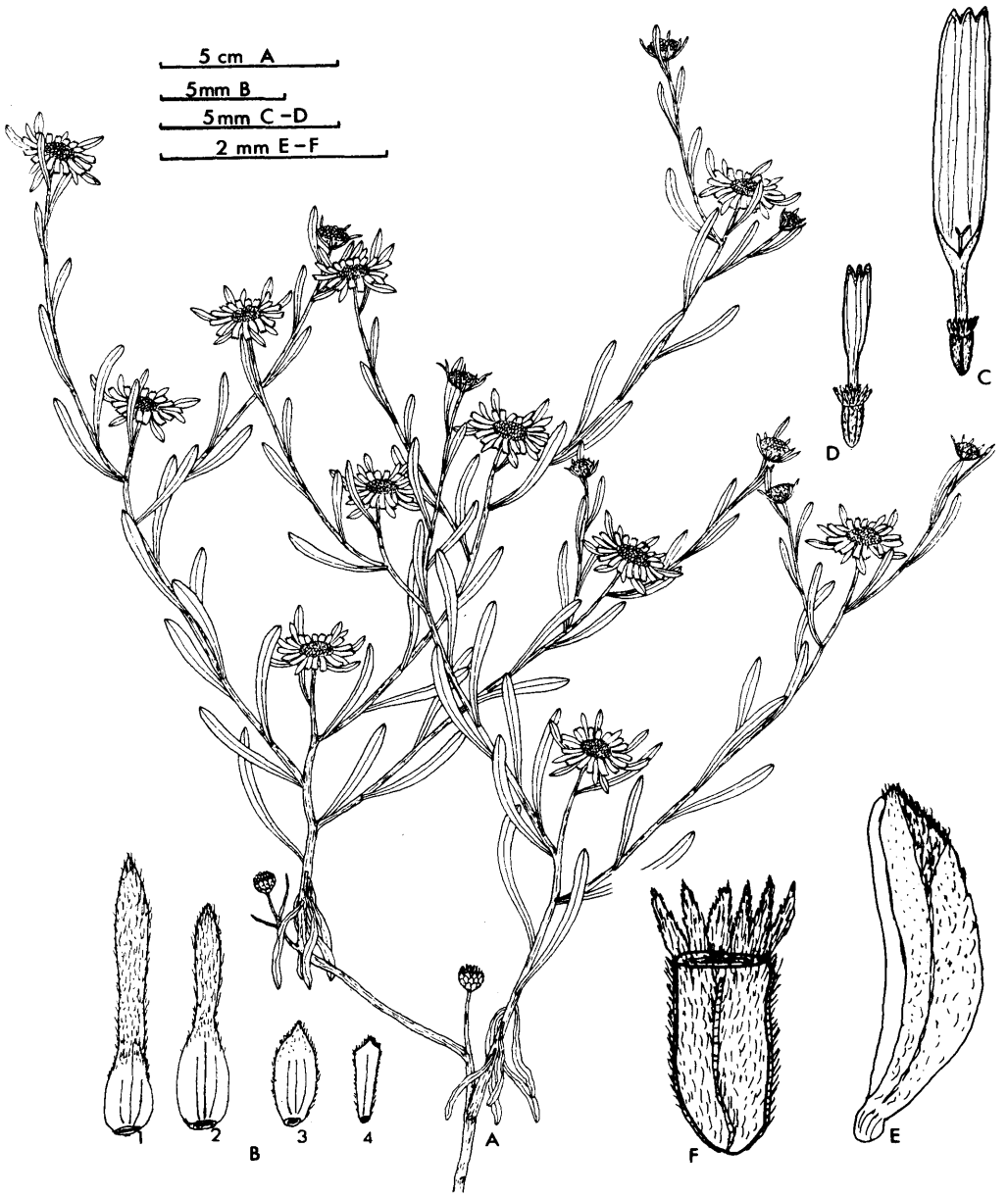


Fig. 35. *Bubonium graveolens* ssp. *odorum*. A. Habitus. B. Involucral bracts. C. Ray floret. D. Disc floret. E. Palea. F. Disc cypsela.

Ray florets 25-35. Tube cylindrical-triquetrous, up to 1.5 mm long, densely glandular. Lamina narrowly oblong with glands more scattered than on the tube, 4-8 mm long, 1.5-2.5 mm wide, lobes 0.4-0.6 mm long. Style branches oblanceolate-ovate, 0.75-1.5 mm long. Ray cypselas triquetrous, longitudinally obpyramidal, 1.0-1.4 mm long, ribs 3-6 rather indistinct, the rest as in the disc cypselas.

Disc florets perfect. Corolla 3.0-4.5 mm long, tube terete, occasionally very slightly laterally compressed, distinctly divided in tube and upper wider limb, lobes 0.5-0.8 mm long, triangular-ovate with small incisions along a hyalin margin, dorsally gland-dotted. Style branches as in the ray florets, but somewhat shorter. Anthers up to 2 mm long, tails about 1/5 of the length of the anther. Disc cypselas terete, 1.0-1.4 mm long, hirsute, ribs 3-6 rather indistinct. Pappus of tufted hairs, resembling free scales, 0.7-1.2 mm long.

Variation: For Gran Canaria, see pp. 33-39. The variation in Morocco is treated by Maire (1936) and Wiklund (in press).

Flowering period: In Gran Canaria in February-April, with a weak seasonal isolation towards ssp. *stenophyllum*, which starts a week or two later.

Chromosome number: 2n=14.

Related species: *Bubonium graveolens* ssp. *graveolens* is a Moroccan taxon closely related to *B. graveolens* ssp. *odorum*. The former is characterized by pinnatifid leaves.

Distribution: Fig. 37. In Gran Canaria, *Bubonium graveolens* ssp. *odorum* is confined to the arid coastal zone from 20 m up to 150 m altituded; i.e. La Isleta and along the north coast; Patalavaca 1 km NW of Arguineguin in the southern sector; and Barranco de Perchel in the SW sector. It is also recorded from Morocco (Maire 1936, Wiklund in press).

Collections: About 70 collections were examined.

Bubonium graveolens ssp. *stenophyllum* (Link) T. Halvorsen, comb. et stat. nov. Fig. 36.

Basionym:*Buphthalmum stenophyllum* Link in Buch, Phys. Beschr. Can. Ins.: 150, 1828. Type selected here: Kunkel 12467 (Exsicc. no. 45), Gran Canaria, Bco. de Tirajana, 650 m. (BM-neotype! C, H, GOET, MO, WAG-isoneotypes!). - *Asteriscus sericeus* (L.f.) DC. var. *stenophyllus* (Link) DC, Prodr. syst. nat. regni veg. 5: 486, 1836. - *Nauplius stenophyllus* (Link) Webb in Webb et Berth., Hist. Nat. Iles Can. III. Bot. 2. Phytogr. Can.: Fig. 86B, 1839. - *Odontospermum stenophyllum* (Link) Schultz Bip. in Webb et Berth., Hist. Nat. Iles Can. III. Bot. 2. Phytogr. Can.: 237, 1844. - *Asteriscus stenophyllus* (Link) O. Kuntze, Rev. Gen. Plant. 1: 319, 1891.

Odontospermum stenophyllum (Link) Sch. Bip. var. *filifolium* Kunkel, Cuad. Bot. Canar. 9: 11, 1970. Type: Kunkel 10642, Gran Canaria, Bco. Lajilla en Tasartico, (C- holotype!, G-isotype!).

Asteriscus stenophyllus (Link) O. Kuntze var. *filifolius* (Kunk.) Hansen & Sunding, Flora of Macaronesia. Checklist of vascular plants. 2 ed.: 92, 1979.

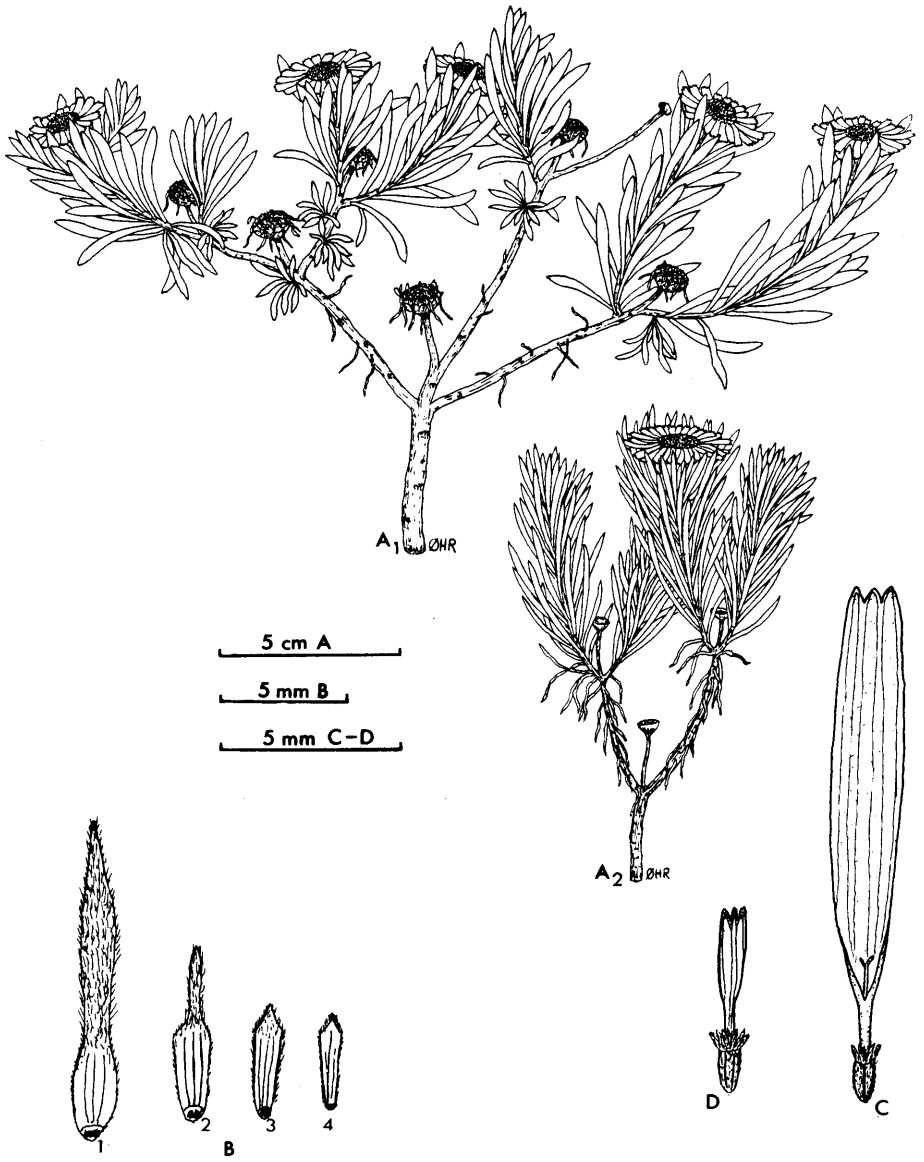


Fig. 36. *Bubonium graveolens* ssp. *stenophyllum*. A. Habitus. A_1, main form. A_2, form with narrow leaves, i.e. var. filifolium. B. Involucral bracts. C. Ray floret. D. Disc floret. E. Palea. F. Disc cypsela (see Fig. 41).

Odontospermum stenophyllum (Link) Sch. Bip. f. *tenui-ascendens* Kunkel, Vieraea 8: 350, 1978. Type: Kunkel 14683, Gran Canaria, Bco. de Temisas, 300 m, (G-holotype!).

Nomenclatural note: It has been impossible to trace any material or original collections of Link's *Buphthalmum stenophyllum*. The type specimen of *Odontospermum stenophyllum* (Link) Sch. Bip., designated by Schultz Bipontinus (1844): "Gran Canaria, Los Andenes de Goyedra" (FI-W), is found to be untypical for ssp. *stenophyllum* and to represent an intermediate between the two subspecies in Gran Canaria. A collection by Kunkel (12467) from the main distribution area of ssp. *stenophyllum* has been selected as a neotype.

Illustrations: Webb 1839: Fig. 86B, Lid 1968: Fig. 26C, Bramwell & Bramwell 1974: Fig. 275.

Common name: Botonera.

Schrublet 0.2-0.7 m high, 0.2-1.0 m wide. Branching dense, dichotomous. Stem ascending-erect, young parts usually purplish or occasionally greyish, tomentose-villose, densely glandular, becoming greyish-brownish and nearly glabrous with a few glands only.

Leaves alternate, spreading-erect, densely crowded towards apices of stems with more than two leaves per cm of stem-, flat-canaliculate, linear, length/width ratio above 11, the lower occasionally very remotely toothed, 18-60 mm long, 1.5-6.0 mm wide, base attenuate. Leaves always sericeous-tomentose, ± grandular.

Capitula solitary, sessile to shortly pedunculoid, terminal. Involucre globose, 8-13 mm wide. Involucral bracts linear-lanceolate, acuminate, the innermost more often narrowly obtrullate and weakly pubescent, the outermost ut to 15 mm long and sericeous. Receptacle transversely rhomboid, 5-8 mm wide, paleate. Paleae cymbiform, distinctly carinate, 3.8-4-5 mm long, moderately glandular towards the acute and pubescent apex, deciduous to persistent.

Ray florets 35-45. Tube cylindrical-triquetrous, up to 2 m long, densely glandular. Lamina narrowly oblong with glands more scattered than on the tube, 7-12 mm long, 1.5-2.5 mm wide, lobes 0.6-2.0 mm long. Style branches oblanceolate-ovate, 0.75-1 m long. Ray cypselas triquetrous, longitudinally obpyramidal, 1.0-1.4 mm long, ribs 3-6 distinct, the rest as in the disc cypselas.

Disc florets perfect. Corolla 3.5-4.5 mm long, tube terete, occasionally very slightly laterally compressed, distinctly divided in tube and upper wider limb, lobes 0.5-0.8 mm long, triangular to ovate with small incisions along a hyaline margin, dorsally gland-dotted. Style branches as in the ray florets, but somewhat shorter. Anthers up to 2 mm long, tails about 1/5 of the length of the anther. Disc cypselas terete, 1.0-1.4 mm long, hirsute, ribs 3-6 , ± distinct. Pappus of tufted hairs, resembling free scales, 0.7-1.2 mm long.

Distribution: Fig. 37. In Gran Canaria, *Bubonium graveolens* ssp. *stenophyllum* grows copiously in the semi-arid mountain slopes up to 700 m altitude in the SE sector. In the SW sector the subspecies may reach down to 50 m altitude in semiarid and arid barrancos. Collections. About 100 collections from Gran Canaria were examined.

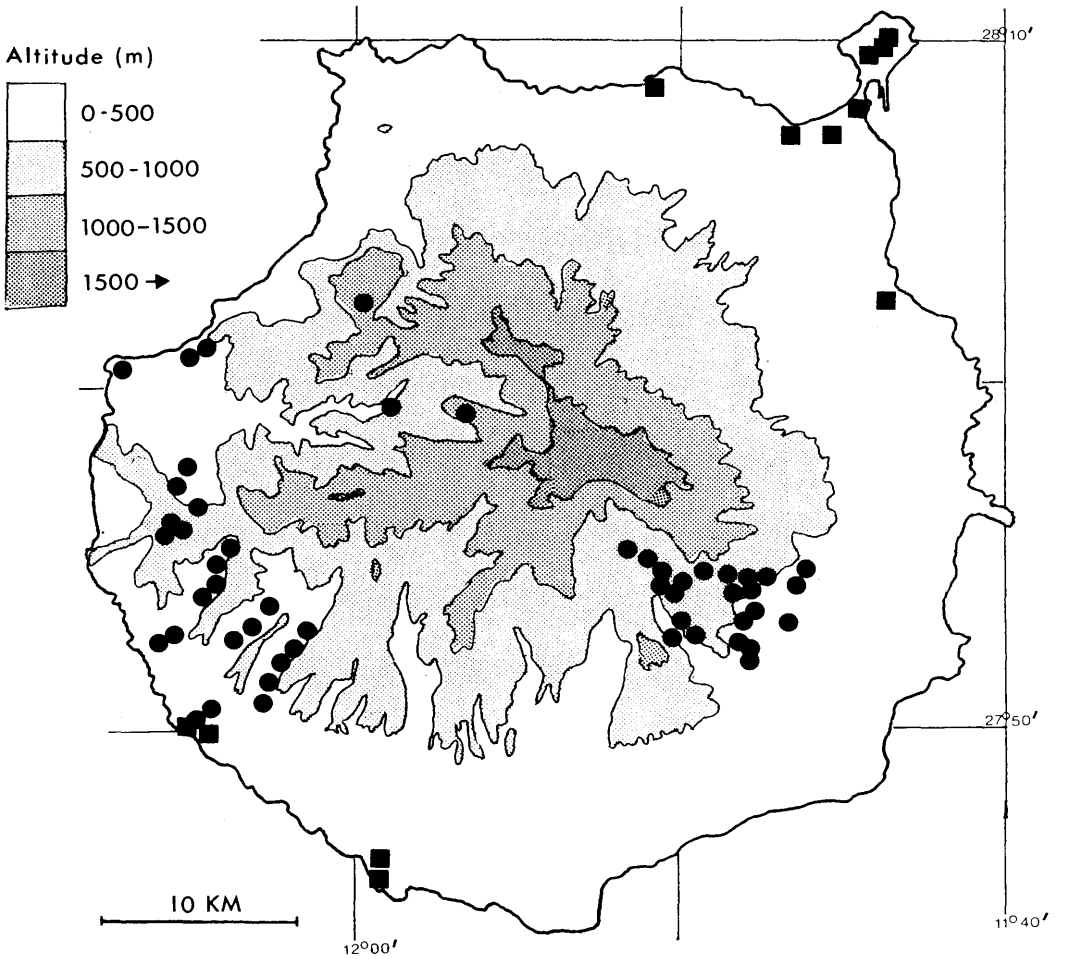


Fig. 37. Distribution of ■ *Bubonium graveolens* ssp. *odorum* and ● ssp. *stenophyllum* in the Canary Islands, Gran Canaria.

Bubonium smithii (Webb) T. Halvorsen, comb. nov. Fig. 38.

Basionym: *Odontospermum smithii* Webb in Hook., Niger Flora: 139, 1849. Type selected here: Forbes 6, 30. March 1822, [Cape Verde Islands], "Monte Grande, St. Nicolas", (São Nicolau), (GE-herb. Boissier, lectotype!). - *Asteriscus smithii* (Webb) Walp., Ann. bot. syst. 2: 844, 1852.

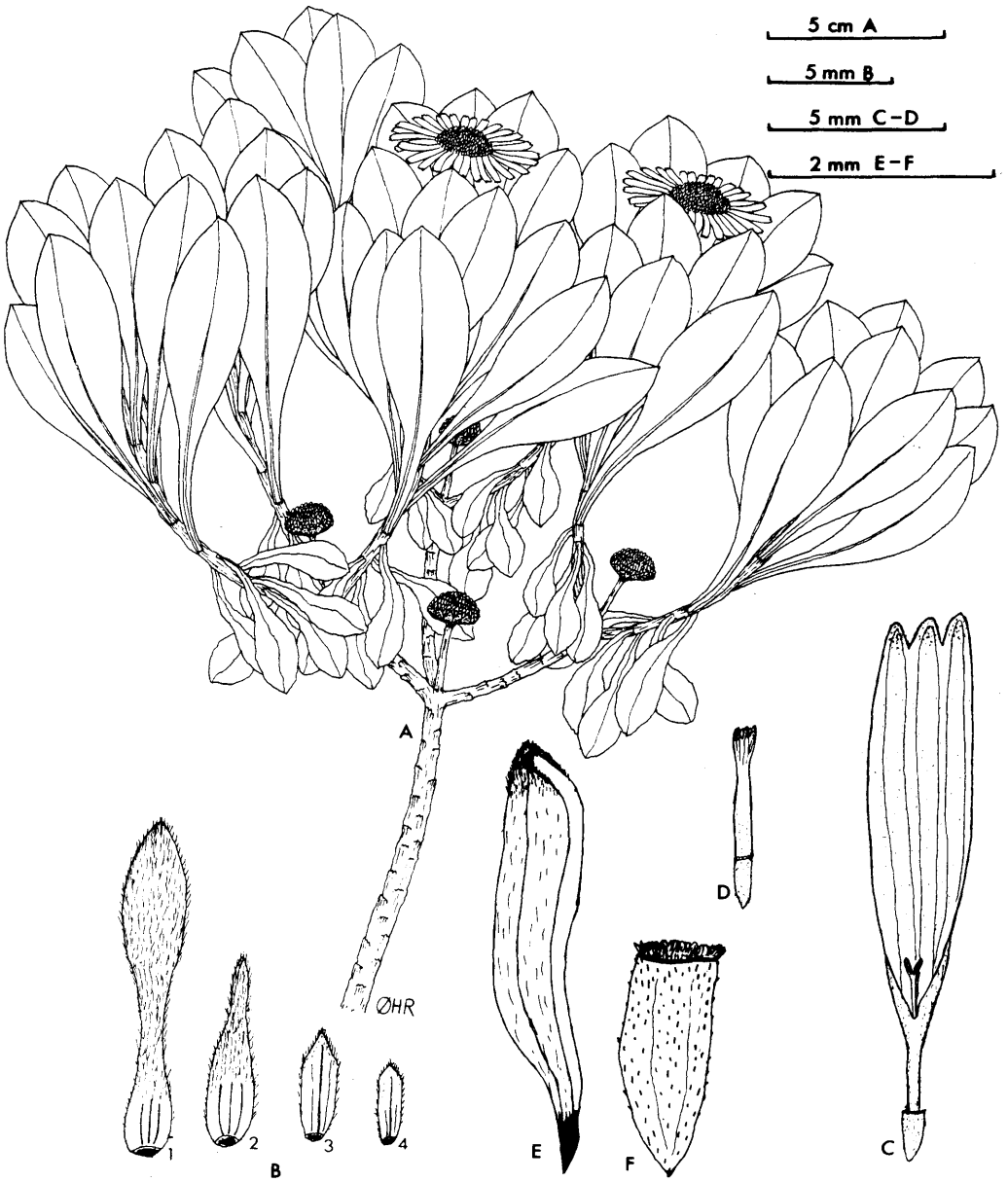


Fig. 38. *Bubonium smithii*. A. Habitus. B. Involucral bracts. C. Ray floret. D. Disc floret. E. Palea. F. Disc cypsela.

Illustration: Sunding 1982: Pl. 1.
Common name: Macela.

A sparsely to moderately branched shrub, up to 0.7 m high, up to 1.5 m wide, regularly cushion-shaped. Stems thick, slender-erect, villose, leafy, becoming glabrous and marked with leaf scars, greyish-brownish.

Leaves alternate, + crowded towards apices of stems, spreading-erect, flat, soft, lower side very disinctly pinnately nerved, oblanceolate-obovate, 40-110 mm long, 12-40 mm wide, sericeous, margins entire, apices rounded, petioles up to 5 mm wide and attenuate.

Capitula solitary, pedunculoid, terminal. Involucre globose, 16-19 mm wide. Involucral bracts basally coalesced with the receptacle ± glandular, the outermost oblanceolate-narrowly oblong, up to 16 mm long, the innermost narrowly obtrullate, about 4 mm long with pubescent margins. Receptacle transversely rhomboid, up to 9 mm wide, paleate. Paleae cymbiform, 3.5-4.0 mm long, dorsally rounded or slightly carinate, nearly glabrous, apex rounded-acute, the base with a pointed foot penetrating about 1.0 mm down in the receptacle, highly persistent.

Ray florets 45-60. Tube cylindrical-triquetrous, up to 3.0 mm long, glandular. Lamina ovate-narrowly elliptic, 11-14 mm long, 3-3.5 mm wide, lobes about 1.0 mm long, densely glandular. Style branches narrowly elliptic to narrowly oblong, about 1.0 mm long. Ray cypselas triquetrous, longitudinally obpyramidal, 1.4-1.6 mm long, unribbed, base acute, the rest as in the disc cypselas.

Disc florets perfect. Corolla 3.5-4.0 mm long, tube terete and sclerous basally, tube and limb not distinctly separate, lobes up to 1.0 mm long, ovate, margins ± hyaline and rough, dorsally densely glandular. Style branches up to 0.8 mm long. Anthers about 2.0 mm long, tails about 1/5 of the length of the anthers.

Disc cypselas terete to widely obtrullate in transverse cross-section, 1.3-1.6 mm long, ciliolate, base somewhat acute. Pappus of tufted brown hairs from the apical corners of the cypselas, resembling connate scales, 0.05-0.2 mm long.

Flowering period. November-February.

Chromosome number. 2n=14.

Related species. *Bubonium smithii* has a superficial resemblance with *B. sericeum* (see above). *Bubonium smithii* is separated from the other Cape Verdean *Bubonium* taxa by shorter pappus, larger leaves, wider involucre and longer ray florets.

Distribution: Fig. 41. *Bubonium smithii* is restricted to a small area of a few square km in São Nicolau, the Cape Verde Islands; SE of Monte Gordo and towards the neighbouring mountain in the east. The species is dominant in grassy slopes together with *Euphorbia tuckeyana* Steud., 900-1000 m altitude. The locality in Santo Antao; Tarrafal, (Cardoso 10, (LISU)), is uncertain and has not been rediscovered.

Collections: 1) São Nicolau, Monte Gordo area: Forbes 6, (GE), R.T. Lowe (BM), Cardoso 7, 71, (COI, LISU), Lobin 229, (Private herbarium), ØHR 882, LB 3464 and PS 3776, (O). 2) Santo Antao, Tarrafal: Cardoso 10, (LISU).

Bubonium daltonii (Webb) T. Halvorsen comb. nov. ssp. *daltonii*
Fig. 39.

Basionym: *Odontospermum daltoni* Webb in Hook., Niger Flora: 140, 1849. Type selected here: J.D. Hooker 204, November 1839, [Cape Verde Islands], "In collibus alt. 1000 ad 2000 ped. que vallem S. Dominici obvallant in ins. S. Jacobi", (Santiago), (FI-W, lectotype!). - *Asteriscus daltoni* (Webb) Walp., Ann. bot. syst. 2: 844, 1852.

Nomenclatural note: Webb in Hooker (1849) included collections from Santo Antão in his circumscription of *Odontospermum daltoni* Webb. These collections are referred to ssp. *vogelii*. The spelling of the epithet *daltoni* is corrected to *daltonii* (ICBN paragraph 73).

Common names: Macela or Marcela.

Moderately branched shrubs, 0.2-0.5 m high, 0.2-0.6 m wide. Stem ascending-erect, tomentose-villose, leafy, becoming more glabrous, greyish-blackish, marked with leaf scars.

Leaves alternate, spreading-erect, flat, distinctly pinnately nerved on lower side, oblanceolate, 35-70 mm long, 6-15 mm wide; length/width ratio below 8, sericeous, apices acute, margins entire-denticulate, petioles attenuate, up to 3 mm wide.

Capitula solitary, sessile-pedunculoid, terminal. Involucre subglobose, 9-13 mm wide. Involucral bracts basally coalesced with the receptacle, acute, densely glandular, the outermost bracts narrowly oblong-oblanceolate-trullate, up to 10 mm long, the innermost bracts generally narrowly obtrullate, up to 4 mm long with ciliolate margins. Receptacle transversely rhomboid, up to 7 mm wide, paleate. Paleae always glabrous, densely glandular, up to 4 mm long, cymbiform, distinctly carinate, persistent.

Ray florets 40-50. Tube cylindrical-triquetrous, 2.0-2.5 mm long, glandular. Lamina oblong-ovate, glandular, 6-10 mm long, 1.5-2.0 mm wide, lobes 0.5-1.5 mm long. Style branches narrowly elliptic-narrowly oblong, about 0.8 mm long. Ray cypselas triquetrous, longitudinally obpyramidal., 1.0-1.4 mm long, the rest as in the disc cypselas.

Disc florets perfect. Corolla 3.0-4.0 mm long, tube terete and ± distinct from the upper limb, lobes up to 0.8 mm long, ovate with clear incisions along the hyaline margins, dorsally glandular. Styles branches as in the ray florets, but somewhat shorter. Anthers 1.5-2.0 mm long, tails about 1/4 of the length of the anther. Disc cypselas terete, widely trullate in transverse cross-section, 1.1-1.5 mm long, ciliolate-ciliate, base rounded. Pappus of tufted brown hairs from the upper apical corners of the cypselas, resembling connate scales, 0.3-0.6 mm long.

Variation: See pp. 40-45.

Flowering period: November-February.

Chromosome number: 2n=14.

Related species: 1) *Bubonium smithii*, see above. 2) *B. intermedium*, see above.

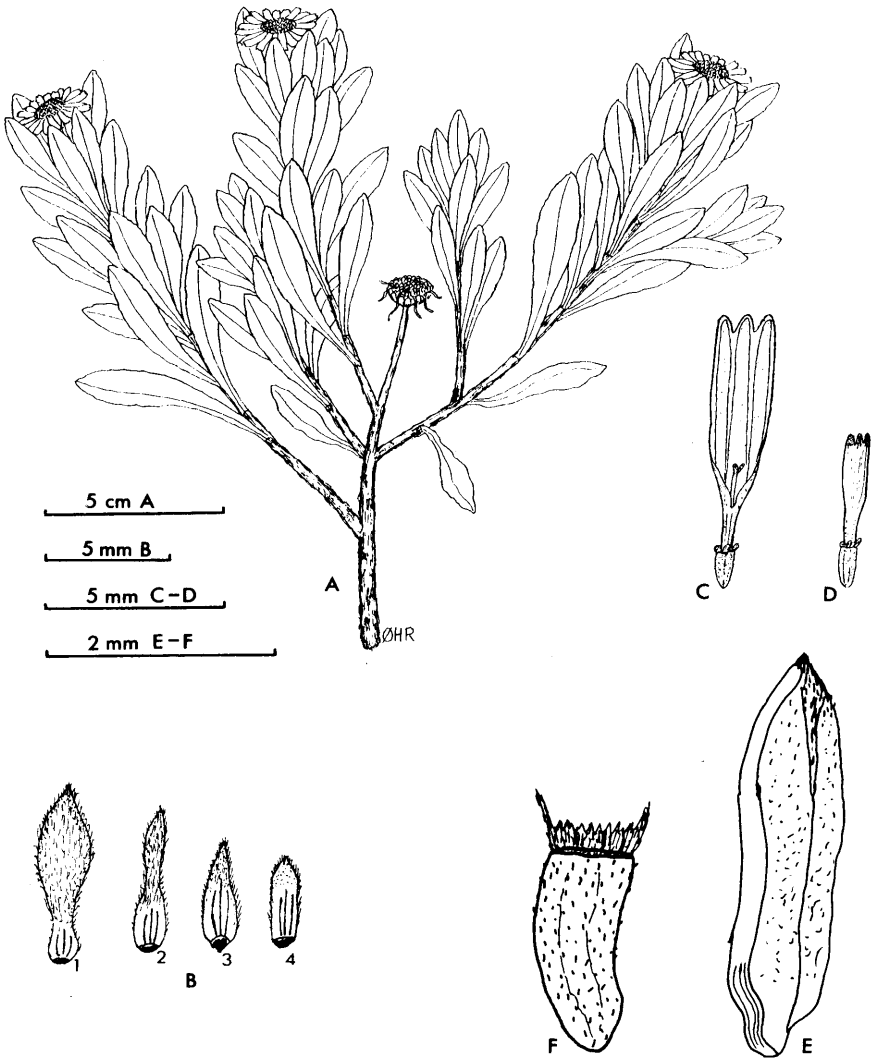


Fig. 39. *Bubonium daltonii* ssp. *daltonii*. A. Habitus. B. Involucral bracts. C. Ray floret. D. Disc floret. E. Palea. F. Disc cypsela.

Distribution: Fig. 41. *Bubonium daltonii* ssp. *daltonii* is confined to subhumid higher mountain zones of San Tiago, i.e. the slopes of Serra da Malagueta and Serra do Pico da Antonia, 600-1000 m altitude.

Collections: About 25 collections from the above mentioned areas of San Tiago were examined.

Bubonium daltonii (Webb) T. Halvorsen ssp. *vogelii* (Webb) T. Halvorsen, comb. et stat. nov. Fig. 40.

Basionym: *Odontospermum vogelii* Webb in Hook.,Niger Flora: 140, 1849. Type selected here: Th. Vogel 46 and 80, June 1841, [Cape Verde Islands], "Spitze der Mont Verde, ins. Sao Vicente", (K- herb. Hook., lectotype!, FI-W, isolectotype!). - *Asteriscus vogelii* (Webb) Walp., Ann. bot. syst. 2: 844, 1852. - *Odontospermum daltoni* Webb var. *vogelii* (Webb) A. Chev., Les iles du Cap Vert. Flore de l'Archipel: 147, 1935.

Odontospermum vogelii Webb var. *darwinii* Webb in Hook., Niger Flora: 140, 1849. Type: Darwin, [Cape Verde Islands], "Sp. florida", (FI-W, holotype!). - *Asteriscus vogelii* (Webb) Walp. var. *darwinii* (Webb) Walp., Ann. bot. syst. 2: 844, 1852.

Odontospermum arboresens Gandoger, Bull. Soc. Bot. France 65: 24-69 *nom. superfl.* Type: Thiebaut, February 1879, [Cape Verde Islands], Sao Vicente, (LY-holotype!).

Illustrations: Wawra 1866: Fig. 80.

Highly branched shrubs, shrublets or suffrutices, 0.2-0.5 m high, 0.2-0.6 m wide. Stem ascending - erect - spreading, tomentose-villose, leafy, becoming more glabrous, greyish-blackish, marked with leaf scars.

Leaves alternate, spreading-erect, flat, ± indistinctly nerved on the lower side, oblanceolate-linear, 25-70 mm long, 3-15 mm wide; length/width ratio above 8, sericeous or occasionally tomentose, apices rounded-acute, margins entire, petioles attenuate, up to 3 mm wide.

Capitula solitary, sessile-pedunculoid, terminal. Involucre globose, 5-13 mm wide. Involucral bracts basally coalesced with the receptacle, apices rounded-acute, glandular, the outermost bracts narrowly oblong-oblanceolate-trullate, up to 10 mm long, the innermost bracts generally narrowly obtrullate, up to 4 mm long with pubescent-ciliolate margins. Receptacle transversely rhomboid, up to 6 mm wide, paleate. Paleae pubescent and glandular, 3.6-3.8 mm long, cymbiform, distinctly carinate, persistent.

Ray florets 35-45. Tube cylindrical-triquetrous, 1.5-2.5 mm long, glandular. Lamina oblong-ovate, glandular, 2-8 mm long, 1.5-2.0 mm wide, lobes 0.5-1.5 mm long. Style branches narrowly elliptic to narrowly oblong, up to 0.8 mm long. Ray cypselas triquetrous, longitudinally obpyramidal, 1.0-1.4 mm long, the rest as in the disc cypselas.

Disc florets perfect. Corolla 2.5-3.5 mm long, tube terete and ± distinct from the upper limb, lobes up to 0.8 mm long, ovate with clear incisions along the hyaline margins, dorsally glandular. Style branches as in the ray florets, but somewhat shorter. Anthers 1.5-2.0 mm long, tails about 1/4 of the length of the anther. Disc cypselas terete, widely trullate in transverse cross-section, 1.1-1.5 mm long, ciliolate-ciliate,

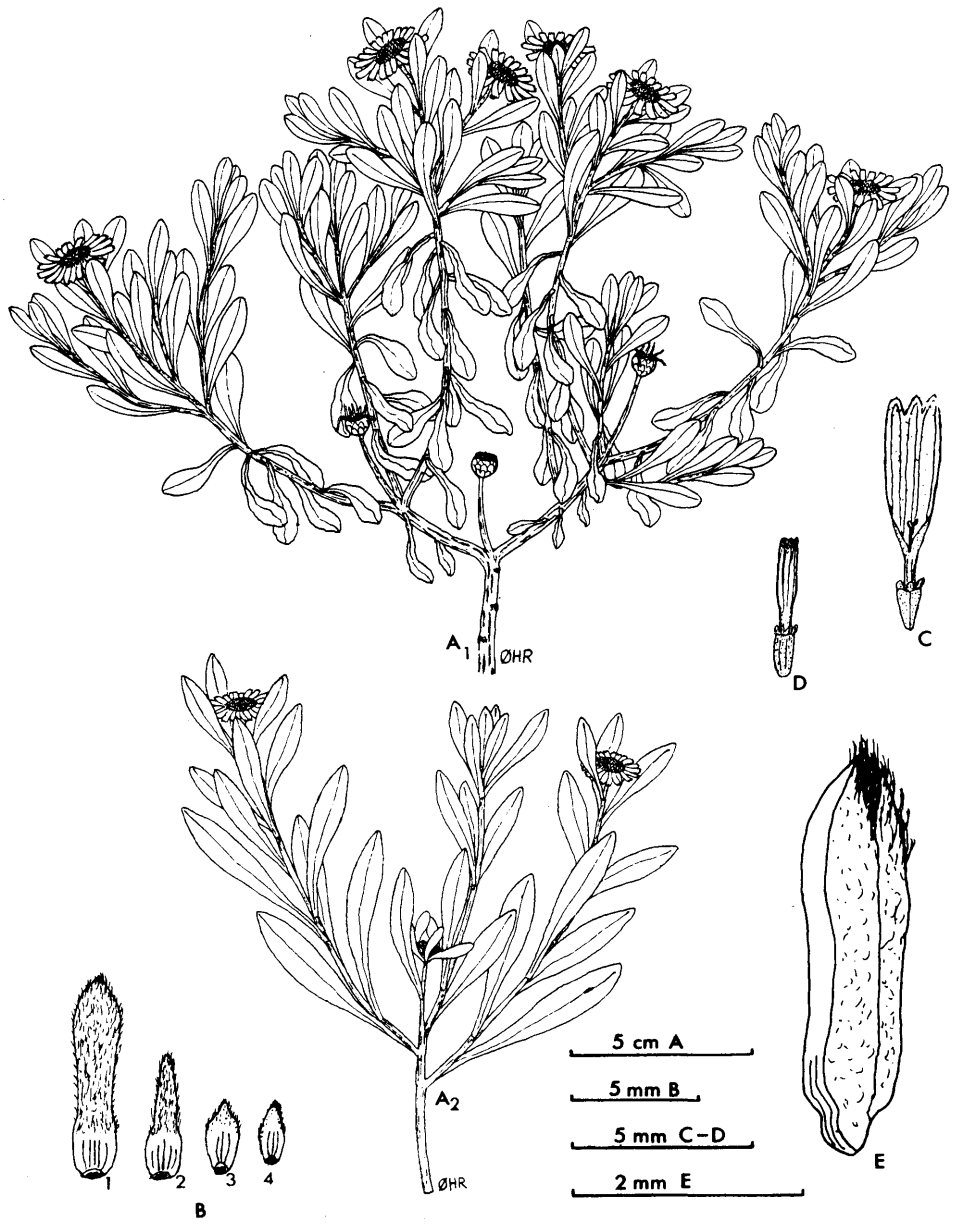


Fig. 40. *Bubonium daltonii* sp. *vogelii*. A. Habitus. A_1, main form from mountain areas. A_2, coastal form. B. Involucral bracts. C. Ray floret. D. Disc floret. E. Palea. F. Disc cypsela (see Fig. 39).

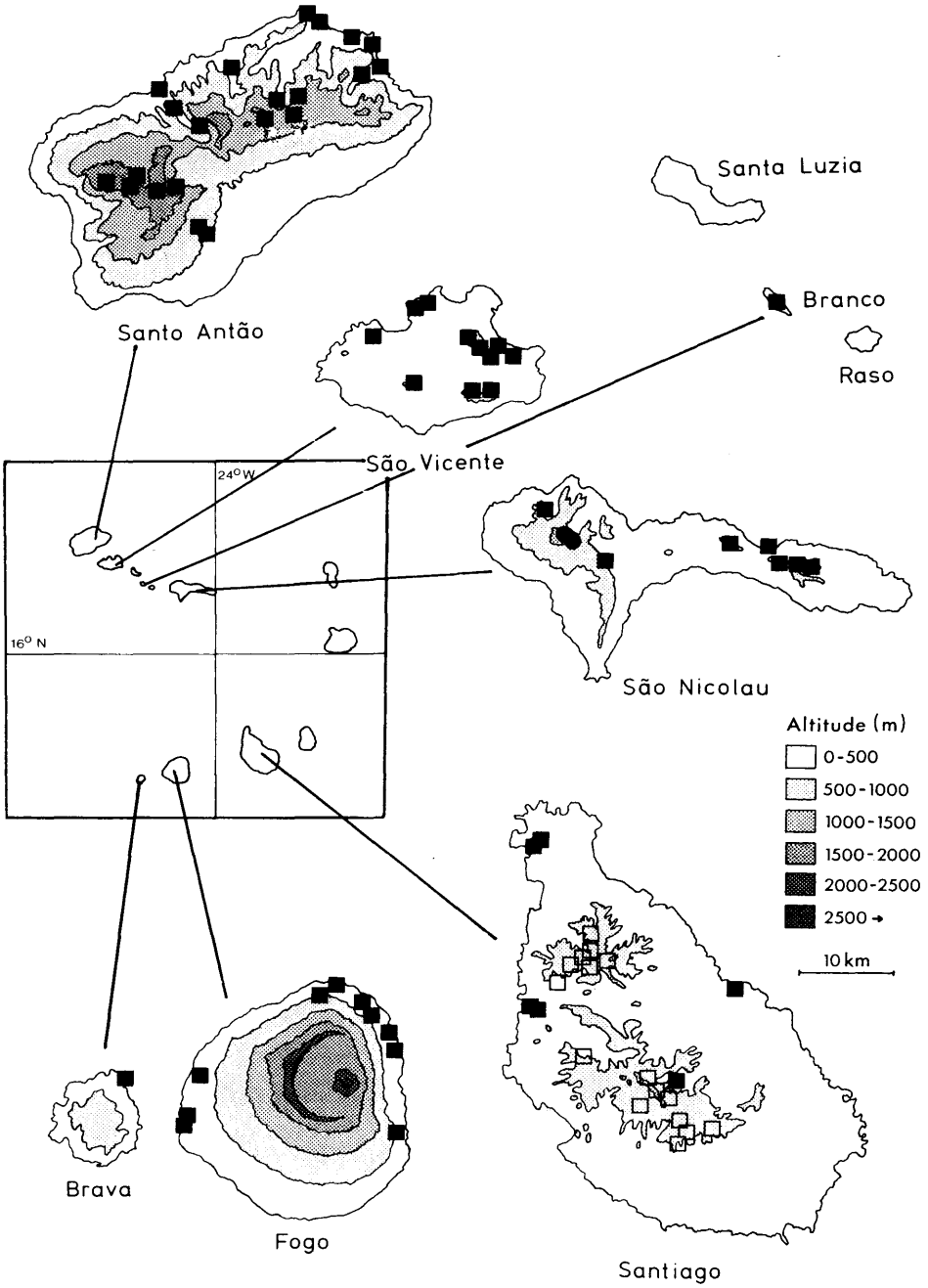


Fig. 41. Distribution of ● *Bubonium smithii*, □ *B. daltonii* ssp. *daltonii*, and ■ *B. daltonii* ssp. *vogelii* in the Cape Verde Islands.

base rounded. Pappus of tufted brown hairs from the upper apical corners of the cypselas, resembling connate scales, 0.1-1.0 mm long.

Distribution: Fig. 41. *Bubonium daltonii* ssp. *vogelii* grows in arid or semi-arid parts of all the western Cape Verde Islands; i.e. Santo Antão, São Vicente, São Nicolau, San Tiago, Fogo and Brava, from sea-level to about 1300 m altitude.

Collections: About 70 collections from all above mentioned islands were examined.

REMARKS ON THE ANNUALS *ASTERISCUS HIEROCHUNTICUS* AND *BUBONIUM AQUATICUM* IN MACARONESIA

The annuals in *Asteriscus* s.lat. fall outside the scope of this treatment, but some remarks on the character differences of the two species and their distribution are given below.

Bubonium aquaticum has a coastal distribution in some of the Canary Islands, i.e. mainly Tenerife and Gran Canaria, and in Porto Santo and Deserta Grande, the Madeira archipelago. Citations in literature of this species from Fuerteventura (Bolle 1892), and from Lanzarote (Pitard & Proust 1908), are probably due to confusions with *Asteriscus hierochunticus*.

The Saharo-Sindian species *Asteriscus hierochunticus* is within Macaronesia confined to the Canary Island. We have seen herbarium specimens from Fuerteventura only and the following collections have been examined: Pitard 187, Puerto de Lajas, about 5 km N of Puerto del Rosario (G, L, LY, P, MO), - Brooke 306, Gran Tarajal, sea level (BM), - Burchard 345 (K, O), - Kunkel 18910, Betancuria, Llano Sta. Catalina (G).

Superficially the two species have much in common. Young plants of *Bubonium aquaticum* especially are superficially similar to *Asteriscus hierochunticus*. The main differences are outlined below.

Bubonium aquaticum (L.) Hill. Caulescent annual, 10-40 cm high, erect, basally without lateral branches. Upper leaves clasping stem, the lower attenuate. Length/width ratio of leaves below 6. Involucral bracts basally coriaceous, but never hygrochastic. Paleae shallow cymbiform without dorsal resin canal. Cypselas with sclerenchyma and well-developed ribs (resin canals). Disc florets with gland-dotted corolla lobes. Pappus 1.2-1.5 mm long.

Asteriscus hierochunticus (Michon) Wikl. Acaulin annual, up to 10 cm high, basally with lateral branches. All leaves attenuate, length/width ratio of leaves above 6. Involucral bracts thick and coriaceous, hygrochastic. Paleae flattened with a distinct dorsal resin canal. Cypselas lacking sclerenchyma and ribs (resin canals). Corolla lobes of disc florets without glands. Pappus 0.7-1.2 mm long.

EXCLUDED TAXA

Bubonium arborescens (L.) Hill 1769: 13 =
Borrichia arborescens (L.) De Candolle 1836: 489
Bubonium frutescens (L.) Hill 1761: 74 =
Borrichia frutescens (L.) De Candolle 1836: 489
Bubonium maritimum (L.) Hill 1761: 74 =
Asteriscus maritimus (L.) Lessing 1832: 210
Bubonium spinosum (L.) Hill 1761: 74 =
Asteriscus spinosus (L.) Schultz Bipontinus 1844: 230

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APPENDIX 1 A. POPULATIONS KEPT IN CULTIVATION.
Populations, for which the chromosome numbers have been determined, are marked with *(n) and **(2n).

Bubonium daltonii ssp. *daltonii* (2n=14)

78-254-S** CVI, San Tiago: Serra da Malagueta, W of the summit, 850 m. PS, 17.11.1976.
80-222-S CVI, San Tiago: Serra da Malagueta, near Malagueta, cliffs 1020 m, ØHR 796, 15.1.1980.
80-230-S** CVI, San Tiago: Serra da Malagueta, 920-1020 m. LB 3337, 15.1.1980.

Bubonium daltonii ssp. *vogelii* (2n=14)

78-256-S** CVI, Santo Antão: Monte Jado d'Arado, 1300 m. PS, 8.11.19761.
78-257-S** CVI, São Vicente: Monte Verde, 500 m. PS, 4.11. 1976.
80-224-S* CVI, São Nicolau: Alto Joaquinha, S-side, gravel, 590-618 m. ØHR 900, 27.1.1980.
80-225-S** CVI, São Vicente: Monte Verde, summit plateau, 680 m. ØHR 906, 29.1.1980.
80-226-S CVI, São Vicente: Monte Verde, summit plateau, 680 m. ØHR 907, 29.1.1980.
80-229-S* CVI, Fogo: Ponta de Vale de Cavaleiros, gravel, 50 m. ØHR 938, 3.2.1980.
80-231-S CVI, San Tiago: NW part, above Ribeira da Barca, 150-230 m. LB 3350, 15.1.1980.

Bubonium smithii (2n=14)

78-255-S** CVI, São Nicolau: Between Cachaco and Monte Gordo, 900 m. PS, 21.11.1976.
80-223-S * CVI, São Nicolau: SE of Monte Gordo, near Pico Caldeirinha, ØHR 882, 25.1.1980.

Bubonium aquaticum (2n=14)

79-252-S Madeira, Deserta Grande: Docca Beach, 5 m. ØHR, 2.7.1978.
79-293-S* Can, Gran Canaria: Valle de Agaete, 1 km SSE of Agaete, 160 m. TH 158, 6.4.1979.

Bubonium intermedium (2n=14)

76-709-S* Can, Lanzarote: Famara, (seeds from Bot. Garden, Liège 75/76 cat.no. 2091).
76-1303-S Can, Lanzarote: Haria, dry lava slopes, RE, 12.4. 1975.

APPENDIX 1 A. (continued)

77-312-S* Can, Lanzarote: Between Penas de Chache and Haria, (seeds from Bot. Garden, Tafira Alta, ex spont. Coll: Sventenius & Bramwell).
77-324-S* Can. Lanzarote: Jameos de Agua, (seeds from Bot. Garden, Liège 76/77: 1880).
78-155-S** Can, Lanzarote: Jameos de Agua, (seeds from Bot. Garden, Liège 77/78: 1910).
79-294-S Can, Lanzarote: Famara massif, between El Gallo and El Valle, 420 m. TH 72, 23.3.1979.

Bubonium graveolens ssp. *odorum* (2n=14)

76-1342-S* Can, Gran Canaria: La Isleta, (seeds from Bot. Garden, Orotava).
79-298-S* Can, Gran Canaria: Patalavaca, Barranco de la Verga. TH 82, 24.3.1979.

Bubonium graveolens ssp. *stenophyllum* (2n=14)

79-300-S* Can, Gran Canaria: Barranco Lajilla in Tasartico, SE slopes, 400 m. TH 44, 18.3.1979.
79-301-S Can, Gran Canaria: Barranco Perchel, between Puerto de MOgan and Barranco de Veneguera, 125 m. TH 86, 25.3.1979.

Bubonium sericeum (2n=14)

76-1315-S* Can, Fuerteventura: Seeds from Bot. Garden, Kew 74/75: 195/04, ex spont. Coll: Melville & Bramwell.
78-307-S** Can, Fuerteventura: Jandia, Kunkel 1972, (seeds from Kew 77/78: 195/04, cult. Tafira Alta, Gran Canaria).

Bubonium schultzii (2n=14)

79-302-S* Can, Lanzarote: Playa de Famara, W of Montana de Ganada, 10 m. TH 61, 22.3.1979.
79-304-S* Can, Lanzarote: Playa de Famara, W of Montana de Ganada, 10 m. TH 65, 22.3.1979.

Asteriscus maritimus (2n=12)

78-147-S* Spain: Regno Murcico, Cabo de Palos, (seeds from Bot. Garden, Barcelona).
78-148.S* Spain: Valentia, Illa Plana (Paix vinalopo), (seeds from Bot. Garden, Barcelona).

APPENDIX 1 B. MEIOTIC CHROMOSOME NUMBERS FROM FIELD FIXATIONS IN THE CANARY ISLANDS 1979.

Bubonium graveolens ssp. *odorum* (n=7)

Gran Canaria: Patalavaca, Barranco de la Verga, TH 2, 5.3. 1979.
Gran Canaria: La Isleta, Montana del Vigia, 120 m. TH 138, 5.4.1979.

Bubonium graveolens ssp. *stenophyllum*(n=7)

Gran Canaria: 1 km S of Santa Lucia, 660 m. TH 7, 8.3.1979.
Gran Canaria: Barranco Lajilla in Tasartico, 400 m. TH 44, 18.3.1979.
Gran Canaria: Barranco de Angostura, 250 m. TH 129, 1.4.1979.

Bubonium schultzii (n=7)

Lanzarote: Playa de Famara, W of Montana de Ganada, 10 m. TH 54, 22.3.1979.

Bubonium sericeum (n=7)

Fuerteventura: 1.5 km N of Betancuria, 570 m. TH 96, 2.3.1979.
Fuerteventura: Jandia, South of Pico de la Zarza, 580 m. TH 113, 29.3.1979.

APPENDIX 2. CROSSES.

Code to the column headings: NO) Crossing number, SEED) Seed set; (-) no seeds obtained, (+) ray cypselas fertile, (++) both ray and disc cypselas fertile, GERM) % germinability of hybrid seeds, FLOW) frequency of flowering hybrids in each F_1 family, MEI) Meiotic observations: (+) regular meiosis, POLL) average percentage good pollen in flowering hybrids of each F_1 family, BACK) back crossed to one (+) or both (++) parents with good result, ?) no observations.

Crosses within Macaronesian *Bubonium*.

NO	FEMALE	MALE	SEED	GERM	FLOW	MEI	POLL	BACK
B. schultzii X B. intermedium								
54	79-304	76-709-2	-	-	-	-	-	-
B. sericeum X B. intermedium								
1	76-1315-1	76-1303	-	-	-	-	-	-
7	78-307-2	77-312	-	-	-	-	-	-
22	76-1315-3	78-155	++	100	60	+	80	++
B. sericeum X B. graveolens ssp. odorum								
23	76-1315-3	76-1342	++	100	65	+	65	++
B. sericeum X B. graveolens ssp. stenophyllum								
45	78-307-1	79-300	++	?	?	?	?	?
B. sericeum X B. daltonii ssp. daltonii								
39	76-1315-3	78-254	++	48	72	+	72	-
B. sericeum X B. daltonii ssp. vogelii								
13	76-1315-3	78-256	-	-	-	-	-	-
38	76-1315-3	78-257	-	-	-	-	-	-
B. sericeum X B. smithii								
40	76-1315-3	78-255	++	100	5	defect	-	-
B. intermedium X B. schultzii								
53	76-709-2	79-304	-	-	-	-	-	-
B. intermedium X B. sericeum								
25	76-1303-1	76-1315	++	100	90	+	90	-
B. intermedium X B. graveolens ssp. odorum								
27	77-312-2	76-1342	++	35	84	+	84	++
49	77-312-2	76-1342	+	?	?	?	?	?
B. intermedium X B. graveolens ssp. stenophyllum								
44	78-155-1	79-300	+	?	?	?	?	?
48	79-294-1	79-300	++	?	?	?	?	?
B. intermedium X B. daltonii ssp. vogelii								
26	76-1303-1	78-256	+	35	62	+	62	+

APPENDIX 2. (continued)

NO	FEMALE	MALE	SEED	GERM	FLOW	MEI	POLL	BACK
B. graveolens ssp. odorum X ssp. stenophyllum								
43	79-298-1	79-300	++	?	?	?	?	?
46	79-298-1	79-300	+	?	?	?	?	?
B. graveolens ssp. odorum X B. sericeum								
24	76-1342-1	76-1315	-	-	-	-	-	-
B. graveolens ssp. odorum X B. intermedium								
10	76-1342-1	77-312	+	10	50	+	50	-
B. graveolens ssp. odorum X B. aquaticum								
12	76-1342-2	97-252	-	-	-	-	-	-
B. graveolens ssp. stenophyllum X B. graveolens ssp. odorum								
42	79-300-1	76-1342	-	-	-	-	-	-
B. graveolens ssp. stenophyllum X B. intermedium								
47	79-300-2	78-155	+	-	-	-	-	-
B. aquaticum X B. graveolens sp. odorum								
9	79-252-1	76-1342	-	-	-	-	-	-
B. daltonii ssp. daltonii X B. sericeum								
15	78-254-1	78-307	+	5	5	defect	-	-
B. daltonii ssp. daltonii X B. intermedium								
16	78-254-1	78-155	+	5	5	defect	-	-
B. daltonii ssp. vogelii X sp. daltonii								
41	78-256-2	78-254	-	-	-	-	-	-
B. daltonii ssp. vogelii X B. sericeum								
20	78-256-1	78-307	-	-	-	-	-	-
21	78-256-1	78-1315	-	-	-	-	-	-
B. daltonii ssp. vogelii X B. intermedium								
5	78-256-2	77-324	-	-	-	-	-	-
8	78-256-2	78-155	-	-	-	-	-	-
B. daltonii ssp. vogelii X B. odorum ssp. odorum								
11	78-257-2	76-1342	-	-	-	-	-	-
33	78-256-2	76-1342	-	-	-	-	-	
37	78-257-2	76-1342	++	93	90	+	90	++
B. daltonii ssp. vogelii X B. odorum ssp. stenophyllum								
52	80-225-3	79-300	++	?	?	?	?	?
B. smithii X B. sericeum								
17	78-255-5	78-307	-	-	-	-	-	-

APPENDIX 2. (continued)
Crosses between *Bubonium* and *Asteriscus*.

NO	FEMALE	MALE	SEED	GERM	FLOW	MEI	POLL	BACK
B. sericeum X A. maritimus								
4	76-1315-2	78-148	-	-	-	-	-	-
B. intermedium X A. maritimus								
28	78-155-5	78-147	-	-	-	-	-	-
29	78-155-4	78-147	-	-	-	-	-	-
34	76-1303-1	78-148	-	-	-	-	-	-
B. graveolens ssp. odorum X A. maritimus								
30	76-1342-2	78-148	-	-	-	-	-	-
35	76-1342-2	78-147	-	-	-	-	-	-
B. graveolens ssp. stenophyllum X A. maritimus								
50	79-300	78-148	-	-	-	-	-	-
B. aquaticum X A. maritimus								
6	79-252	78-147	-	-	-	-	-	-
B. daltonii ssp. vogelii X A. maritimus								
18	78-256-2	78-148	-	-	-	-	-	-
32	78-257-1	78-147	-	-	-	-	-	-
A. maritimus X B. intermedium								
2	78-147-4	76-1303	-	-	-	-	-	-
A. maritimus X B. graveolens ssp. odorum								
31	78-148-1	76-1342	-	-	-	-	-	-
A. maritimus X B. graveolens ssp. stenophyllum								
51	78-147-3	79-300	-	-	-	-	-	-
A. maritimus X B. aquaticum								
36	79-147-2	79-292	-	-	-	-	-	-
A. maritimus X B. daltonii ssp. vogelii								
18	78-148-1	78-256	-	-	-	-	-	-

APPENDIX 3. OPERATIONAL TAXONOMIC UNITS (OTUs) AND CHARACTER STATES USED IN NUMERICAL ANALYSIS OF THE *BUBONIUM GRAVEOLENS* SSP. *ODORUM* - *B. GRAVEOLENS* SSP. *STENOPHYLLUM* COMPLEX IN GRAN CANARIA.

OTU no.	Leaf width mm	Leaf length/ width	Leaf density	Involucre width mm	Ligule length mm	Branching	Cypsela resin canals	Population no.	Locality	Specimen
1	2.0	17.5	8	10.0	8.0	0	0	1	Barranco de Perchel	TH 29
2	2.8	17.8	60	11.0	8.0	0.5	1		between Puerto de	TH 28
3	3.0	13.3	50	8.5	8.0	0.5	1		Mogan and Barranco	TH 27
4	3.0	16.6	35	8.5	10.0	1	0.5		de Veneguera, 20-190	TH 84
5	3.2	12.5	30	11.0	11.0	1	0.5		m alt.	TH 88
6	3.5	10.0	20	8.5	8.5	0.5	0			TH 89
7	4.0	12.5	22	8.5	8.5	0.5	1			TH 90
8	3.5	11.4	36	8.5	9.0	0.5	1			TH 91
9	3.5	12.3	20	8.5	8.0	0.5	1			TH 94
10	2.5	16.0	30	8.5	9.0	0.5	0.5			TH 93
11	2.5	16.4	15	8.5	6.5	0	0			TH 95
12	2.0	20.0	55	8.0	8.5	1	1			TH 30
13	2.0	10.0	10	8.0	7.0	0	0	2	La Isleta, Montaña	TH 138
14	2.0	9.5	10	8.0	6.0	0	0		del Vigia, 120-130 m	TH 139
15	2.0	10.0	9	8.0	6.0	0	1		alt.	TH 141
16	6.0	7.5	8	8.0	6.0	0	0			TH 142
17	3.0	8.3	10	9.0	6.0	0	0			LB 2776
18	2.6	8.1	10	8.5	9.0	0	0.5			LB 2780
19	5.0	9.0	10	9.5	9.0	0	0	3	Patalavaca, Barranco	TH 10
20	2.5	8.0	9	9.0	7.0	0	0		de La Verga, 10-89 m	TH 74
21	2.4	9.2	10	8.0	7.5	0.5	0.5		alt.	TH 75
22	2.1	10.5	20	9.0	6.0	0	0.5			TH 79
23	2.6	8.1	30	10.0	12.0	0.5	0.5	4	Barranco de la Ango-	TH 19
24	4.2	10.7	10	11.0	11.0	0.5	0.5		stura, 4 km S of	TH 20
25	4.0	11.0	20	11.0	10.0	0.5	0.5		Temisas, 240-290 m	TH 125
26	3.5	10.0	20	10.5	8.0	0.5	0.5		alt.	TH 127
27	3.2	8.4	17	9.0	8.0	0.5	1			TH 128
28	3.8	10.5	12	9.0	8.5	0.5	0.5			TH 129
29	1.4	17.8	50	8.0	7.5	1.0	0.5			TH 130
30	5.0	10.0	10	10.5	12.0	1.0	1			TH 133
31	5.0	10.0	10	11.0	11.0	0.5	0.5			TH 135

APPENDIX 3. (continued)

OTU no.	Leaf width mm	Leaf length/ width	Leaf density	Involucre width mm	Ligule length mm	Branching	Cypsela resin canals	Population no.	Locality	Specimen
32	2.5	14.0	40	12.0	11.0	1	1	5	Barranco Lajilla in	TH 12
33	2.0	22.5	45	12.0	9.0	1	1		Tasartico, 330-550 m	TH 13
34	1.5	16.7	45	12.0	10.0	1	1		alt.	TH 16
35	1.7	14.7	40	10.0	10.0	1	1			TH 44
36	3.2	14.0	35	12.0	10.0	1	0.5			TH 45
37	2.4	8.3	25	8.0	8.0	0.5	1	6	About 3 km S of San	TH 148
38	2.1	15.2	25	10.0	8.5	0.5	0.5		Nicolas, along the	TH 149
39	3.2	11.2	30	9.5	9.0	0.5	0.5		road to Mogan, 370 m	TH 150
40	2.0	15.0	45	10.0	9.0	0.5	0.5		alt.	TH 151
41	2.0	16.5	45	9.5	8.5	1	0.5	7	La Fajanita, 4 km N of	TH 152
42	1.8	16.6	25	10.5	11.0	1	0.5		San Nicolas along the	TH 153
43	2.5	10.0	25	9.0	9.5	0.5	0.5		road to Agaete, 350 m	TH 154
44	2.7	8.5	15	8.0	8.5	0	0.5		alt.	TH 14
45	2.1	18.0	46	9.5	9.5	1	0.5	8	Barranco de Mogan,	TH 17
46	2.0	18.0	34	9.0	8.5	1	0.5		220 m alt.	TH 46
47	2.2	13.1	20	11.0	10.0	0.5	0.5			TH 47
48	3.6	8.9	20	12.5	12.0	1	1	9	Barranco de Temisas,	TH 7
49	3.8	12.6	15	12.0	11.5	1	1		about 1 km SSE of	TH 8
50	4.0	10.0	25	13.0	12.5	1	1		Santa Lucia, 620-660	TH 9
51	3.7	10.5	23	10.5	11.0	1	1		m alt.	TH 34
52	2.3	16.5	32	10.5	9.5	1	1	10	Barranco de Tasarte,	TH 40
53	2.5	16.0	35	10.5	10.0	1	1		100-650 m alt.	TH 41
54	2.1	16.1	40	12.0	10.0	1	1			TH 42
55	3.5	10.0	12	12.0	11.0	0.5	1			TH 43
56	2.4	11.6	38	11.5	11.0	0.5	0.5			TH 38
57	2.1	15.2	42	12.0	11.5	0.5	1			TH 39
58	2.4	15.8	25	10.5	11.0	1	1	11	Barranco de Veneguera,	TH 31
59	3.0	10.6	22	12.0	9.0	0.5	0.5		170-220 m alt.	TH 32
60	2.8	15.0	12	11.5	11.5	0.5	1			TH 33

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