Systematics of *Aeonium* (Crassulaceae)

景天科銀鱗草屬的系統分類

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ABSTRACT

LIU, HO-YIH. Systematics of *Aeonium* (Crassulaceae). NMNS Special Publication, number 3, 1989.---*Aeonium* Webb & Berth. is a large, polymorphic, and ecologically diverse genus growing in Macaronesia (Canary islands, Madeira archipelago, southern Morocco), eastern Africa, and Yemen. Based on an extensive field examination of native populations and a thorough morphological analysis of greenhouse material and herbarium specimens, the taxonomy and nomenclature of the genus at sectional and specific levels have been resolved. Thirty-seven taxa (thirty-one species and six varieties) were recognized and divided into seven sections. Thirty-six of the thirty-seven taxa have been examined chromosomally from forty-seven populations, and numbers of six taxa are reported here for the first time. Numerical phenetics were used to help evaluate patterns of morphological variation among taxa. Results from phenetic studies by using both cluster analyses and ordination have provided a better understanding of sectional, specific, and varietal groupings. Cladistic analyses were then used to develop hypotheses about evolutionary relationships among the taxa. Both phenetic and cladistic studies confirm the proposed infrageneric classification. The hypothetical relationships among taxa are combined with data from geology, climatology, and ecology to elucidate monophyletic adaptive radiation within the genus. The genus possibly originated in northern Africa during the Tertiary and reached Macaronesian islands from Moroccan coast at a time when the ancestral populations were widespread. The formation of Sahara desert during the Pleistocene may have caused its present disjunctional distribution. In response to many habitats available in Macaronesia, a wide range of different characteristics evolved in *Aeonium* including variation in growth from, plant size, branching patterns, stem and leaf succulence, wax distribution, pubescence, cold resistance, and photosynthetic pathways.

摘　　要

劉和義，銀麟草屬（景天科）的系統分類，國立自然科學博物館學術專刊第 3 號，民國七十八年，····銀麟草屬爲景天科中形態及生育環境變化甚大的一屬，其生長地爲西非、東非及葉門，依據廣泛的野外族群調查、標本館標本研究和溫室材料觀察，整屬被分類成七個節、卅一種及六變種，三十六個分類群的染色體被檢驗，其中六個分類群的染色體爲第一次報告。數學分類則用以評估形態變化的類型及演化關係，此結果支持所提的屬下分類系統。各種間的演化關係及地質、氣候、生態資料則加以結合以導出屬內適應輻射的情形。此屬很可起源於第三紀時的北非，並散佈至西非外的島嶼。更新世時撒哈拉沙漠的形成很可能是此屬現今隔離分佈的主因。而島嶼上多樣化的環境，爲整屬在生長型、尺寸、分枝情形、肉質、臘質分佈、毛茸、抗冷性、及光合作用途徑分化的主要誘因。

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HO-YIH LIU*

INTRODUCTION

Aeonium Webb & Berth. (Crassulaceae; Sempervivoideae) is a large, polymorphic, and ecologically diverse genus of 31 species and six varieties growing in Macaronesia (Canary islands, Cape Verde islands, Madeira, and southern Morocco), eastern Africa, and Yemen. The genus has its center of diversity, both in number of species and in morphological variation, in the Canary islands. Different growth forms are found within the genus in the archipelago, ranging from subacaulescent to shrubby, monocarpic to non-monocarpic, and including biennials and perennials. In addition, the Canarian species of Aeonium occupy a wide range of habitats, from subalpine cloud forests to coastal deserts.

The relationship between growth form and habitat in *Aeonium* on the Canary Islands was extensively studied by Lems (1960). He suggested that growth forms within the genus were the result of adaptive radiation, and because of this spectacular variation, even commented that the genus was comparable in many ways to Darwin's finches (Lems 1960). This study attracted much attention, and chemical (Eglinton *et al*. 1962), phytosociological (Voggenreiter 1974), and physiological (Lösch & Kappen 1981, 1983; Tenhunen *et al*. 1982; Lösch 1984) investigations have been done in the last two decades in an attempt to examine this evolutionarily dramatic system in more detail.

Besides previous interest in adaptive radiation within *Aeonium*, the attractive appearance of the genus has drawn attention from horticulturists. In fact, the last monograph on *Aeonium*, contained within *An Account of the Sempervivum Group* (Praeger 1932), was the result of a request from the Royal Horticultural Society of London for the needs of its members. Since the treatment was prepared for gardeners, the taxonomic delimitation of the genus, its sections and contained species, is inadequate. Also, it provides almost no insight into evolutionary relationships among the texa.

The main objectives of the present study, therefore, are to provide a modern revision and phylogenetic reconstruction of *Aeonium*. Based on three months of extensive field examinations of native populations and a thorough morphological analysis of greenhouse material and herbarium specimens, the taxonomy and nomenclature of the genus at the sectional and specific levels have been resolved. In addition to a modern taxonomic treatment, morphological, anatomical, cytological, and geographical considerations are evaluated for phylogenetic importance. The phylogeny and available ecological data are used to provide a better understanding of evolutionary modes and adaptive radiation in *Aeonium*.

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TAXONOMIC HISTORY

Species of *Aeonium* were apparently known to people in ancient civilizations for their medical usage. The *Codex Juliana*, prepared shortly after 500 A. D. (Gunther 1934), is a copy of Dioscorides' *Materia Medica* and contains a drawing of a species of *Aeonium*, "Aeizoon to mega" which means "large live for ever". This plate was probably based on *Aeonium arboreum* (L.) Webb & Berth., which has been widely cultivated and naturalized in the Mediterranean region for a long time (Praeger 1925, 1929).

Plants in the genus *Aeonium* were described as *Sempervivum* by Linnaeus (1753). De Candolle (1828) treated all *Aeonium* species known at that time in *Sempervivum* section *Chronobium*. Webb and Berthelot (1835–1850) divided section *Chronobium* into three groups and raised them to genera, one of which was *Aeonium* with twenty species. Christ (1888) transferred all species of *Aeonium* back into *Sempervivum* and placed them in two sections. One section was further divided into three informal groups with no diagnostic feature provided.

Berger (1930) classified all of the Crassulaceae, and used the woody habit as the sole criterion to distinguish *Aeonium* from related genera of the Sempervivoideae. Three subshrubby *Aichryson* taxa (*A. bethencourtianum*, *A.* x *domesticum*, and *A. tortuosum*), despite their typical *Aichryson* flowers, were transferred into *Aeonium*. Within *Aeonium*, species were distributed into eight sections corresponding basically to Christ's (1888) sections and informal groups.

Praeger (1932) treated the whole subfamily Sempervivoideae. He adopted Webb and Berthelot's (1835–1850) generic delimitation and removed the three *Aichryson* taxa mentioned above. Praeger recognized five sections, 32 species, one varieties, and 25 hybrids within the genus *Aeonium*. His sectional views basically followed Christ (1888) and Berger (1930).

In the present revision of *Aeonium*, the delimitation of taxa has been accomplished by an intuitive evolutionary approach (Michener 1970) based on all available evidence and aided by phenetic and cladistic analyses. Thirty-seven taxa (31 species and six varieties) are divided into seven sections and four series. A morphological species concept is used in this treatment. The varietal category is adopted for infraspecific categories here because of its historical usage in the genus. A list of sections, series, species, and varieties is given below with acronyms (used in the phenetic and cladistic studies) in brackets. The order of taxa presumably reflects their evolutionary affinities based on phylogenetic analyses and intuitive assessments of relationships.

Synopsis of Classification of *Aeonium*

I. Section *Petrothamnium* (Webb *ex* Christ) H.-Y. Liu
    1a. *A. lindleyi* Webb & Berth. var. *lindleyi* [LIN]
    1b. *A. lindleyi* Webb & Berth. var. *viscatum* (Webb *ex* Bolle) H.-Y. Liu [VIS]
    2. *A. goochiae* Webb & Berth. [GOO]
    3. *A. sedifolium* (Webb *ex* Bolle) Pit. & Proust [SED]
    4. *A. saundersii* Bolle [SAU]

II. Section *Chrysocome* Webb *ex* Christ
  i. Series *Simsii* H.-Y. Liu
    5. *A. simsii* (Sweet) Stearn [SIM]
  ii. Series *Chrysocome* H.-Y. Liu
    6. *A. spathulatum* (Hornem.) Praeger [SPA]
    7. *A. smithii* (Sims) Webb & Berth. [SMI]

III. Section *Patinaria* (Lowe) A. Berger
  i. Series *Praegeri* H.-Y. Liu

8. *A. cuneatum* Webb & Berth. [CUN]
ii. Series *Patinaria* H.–Y. Liu
9. *A. glandulosum* (Aiton) Webb & Berth. [GLA]
10a. *A. canariense* (L.) Webb & Berth. var. *canariense* [Can]
10b. *A. canariense* (L.) Webb & Berth. var. *palmense* (Webb *ex* Christ) H.–Y. Liu [PAL]
10c. *A. canariense* (L.) Webb & Berth. var. *subplanum* (Praeger) H.–Y. Liu [SUB]
10d. *A. canariense* (L.) Webb & Berth. var. *virgineum* (Webb *ex* Christ) H.–Y. Liu [VIR]
11. *A. tabuliforme* (Haw.) Webb & Berth. [TAB]

IV. Section *Aeonium*
12. *A. korneliuslemsii* H.–Y. Liu [KOR]
12. *A. balsamiferum* Webb & Berth. [BAL]
14a. *A. arboreum* (L.) Webb & Berth. var. *arboreum* [ARB]
14b. *A. arboreum* (L.) Webb & Berth. var. *holochrysum* H.–Y. Liu [HOL]
14c. *A. arboreum* (L.) Webb & Berth. var. *rubrolineatum* (Svent.) H.–Y. Liu [RUB]
15. *A. undulatum* Webb & Berth. [UND]

V. Section *Megalonium* A. Berger
16. *A. nobile* (Praeger) Praeger [NOB]

VI. Section *Pittonium* A. Berger
17. *A. glutinosum* (Aiton) Webb & Berth. [GLU]
18. *A. gorgoneum* J. A. Schmidt [GOR]
19. *A. leucoblepharum* Webb *ex* A. Richard [LEU]
20. *A. stuessyi* H.–Y. Liu [STU]

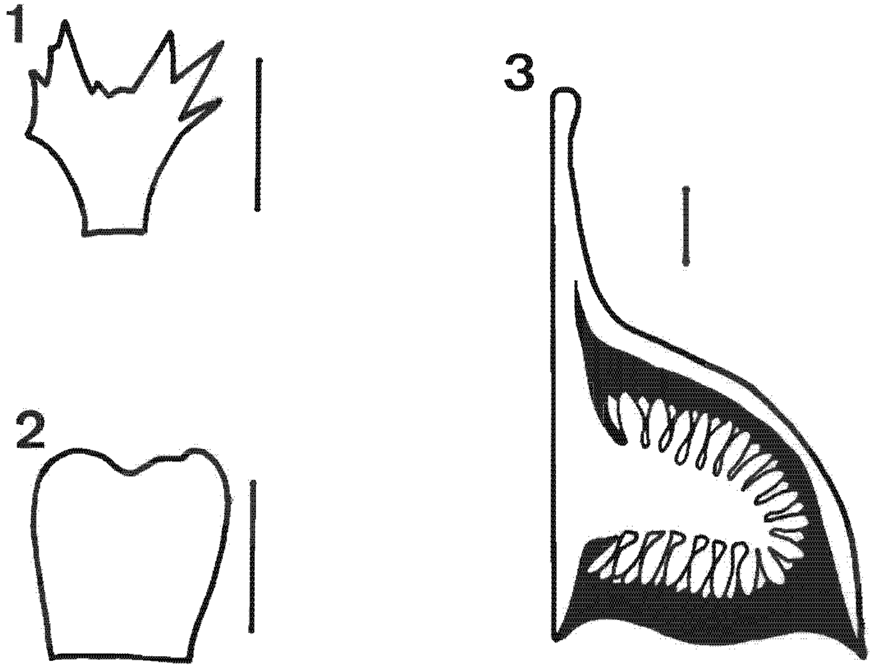
VII. Section Leuconium A. Berger
21. *A. lancerottense* (Praeger) Praeger [LAN]
22. *A. haworthii* Webb & Berth. [HAW]
23. *A. urbicum* (Chr. Smith *ex* Hornem.) Webb & Berth. [URB]
24. *A. gomerense* (Praeger) Praeger [GOM]
25. *A. ciliatum* Webb & Berth. [CIL]
26. *A. percarneum* (R. P. Murray) Pit. & Proust [PER]
27. *A. decorum* Webb *ex* Bolle [DEC]
28. *A. davidbramwellii* H.–Y. Liu [DAV]
29. *A. valverdense* (Praeger) Praeger [VAL]
30. *A. hierrense* (R. P. Murray) Pit. & Proust [HIE]
31. *A. castello–paivae* Bolle [CAS]

SYSTEMATIC POSITION AND GENERIC RELATIONSHIPS

Crassulaceae are a family of succulents comprising about 1500 species, 35 genera, and six subfamilies (Berger 1930). The genus *Aeonium* is in the subfamily Sempervivoideae, which is closely related to Sedoideae (Fröderström 1930; Hideux 1979).

There are six genera within the subfamily Sempervivoideae: *Aeonium*, *Aichryson*, *Greenovia*, *Jovibara*, *Monanthes*, and *Sempervivum* (Berger 1930; Praeger 1932; Rowley 1978). As in other subfamilies, the evolutionary relationships among genera of Sempervivoideae are possibly reticulate as well as linear (Baldwin 1939; Spongberg 1978). Also, except for *Monanthes*, the genera of Sempervivoideae are sufficiently morphologically similar to each other to complicate generic delimitation.

Species of *Aichryson* are held together taxonomically by digitate nectariferous glands (Fig. 1), which are borne externally on each carpel near the base. In addition, most *Aichryson* species are annuals, biennials, or triennials, with herbaceous stems, and are found predominantly in



Figs. 1-3. Diagnostic morphological feature of *Aeonium*, *Aichryson*, and *Greenovia*. 1, nectariferous gland of *Aichryson punctatum (Liu 2533*, OS) and 2, of *Aeonium arboreum* var. *arboreum (Liu 3027*, OS). 3, placentation of *Greenovia diplocycla* (*Liu 3292*, OS). Scale = 0.5 mm.

shady moist places. There *Aichryson* taxa, *A. bethencourtianum*, *A. tortuosum*, and *A.* x *domesticum*, are perennials with soft-wooded stems, and the two former species are growing on rocks of dry mountain cliffs. Berger (1930) transferred these taxa to *Aeonium* based on their perennial and woody characteristics. His treatment, however, was not accepted by subsequent monographic and floristic workers (e.g., Praeger 1932, Bramwell & Bramwell 1974, Lems & Holzapfel 1974, Hansen & Sunding 1984). In addition, these three taxa have chromosome numbers of $n = 15$ (Uhl 1961), which is different from $n = 18$ and 36 found in *Aeonium*. Kunkel (1977) erected a new genus *Macrobia* to accommodate these three taxa. Such a step seems unnecessary because they can easily be retained in *Aichryson* based on digitate nectariferous glands and the same basic chromosome number of $X = 15$.

Greenovia is similar to *Aeonium* section *Patinaria* superficially in subacaulescent habit, similar rosette morphology, and the same chromosome number of $n = 18$. However, the submarginal placentation with an intruded placenta (Fig. 3) clearly separates *Greenovia* from other genera of the Sempervivoideae. In addition, petal number is normally more than 18, whereas in *Aeonium* section *Patinaria* there are usually 8-12 petals. Further, species of *Greenovia do not have nectariferous glands, which are found in all taxa of Aeonium* section *Patinaria*. Physiologically these two taxa are also different as the species of *Greenovia* have C_3 type photosynthesis whereas species of Aeonium section Patinaria are intermediate between strong CAM and C_3 type photosynthesis (Tenhunen et al. 1982).

Sempervivum is a very diverse genus, and it is similar to *Aeonium* in many respects. However, *Sempervivum* contain herbaceous plants, and these are able to resist frosts and may tolerate experimental freezing to −25°C (Kellser 1935). *Aeonium* is woody and with limited cold resistance from −4° to −10°C (Praeger 1932; Lösch and Kappen 1981). *Jovibara* was formerly included in *Sempervivum* (Praeger 1932), and the differences between *Aeonium* and *Sempervivum* also apply to *Aeonium* and *Jovibara*. In addition, the petals in *Jovibara* are fimbriate, whereas those in *Aeonium* are more or less entire.

Monanthes differs from all other genera of Sempervivoideae by its petaloid nectariferous glands. In addition, leaves in this genus,are often papillose. Leaves of *Monanthes laxiflora* do not display the papillose feature, but they are opposite and silvery–mottled. On the contrary, leaves of *Aeonium* are alternate, never papillose, and never silvery–mottled in coloration.

COMPARATIVE MORPHOLOGY AND ANATOMY

To understand the systematic relationships within *Aeonium*, a discussion of morphological characters is essential. This is especially so in this genus because several features are not common in other dicot families. In addition, for clarification of errors in the horticultural literature, many general features, although not taxonomically diagnostic, are also described here.

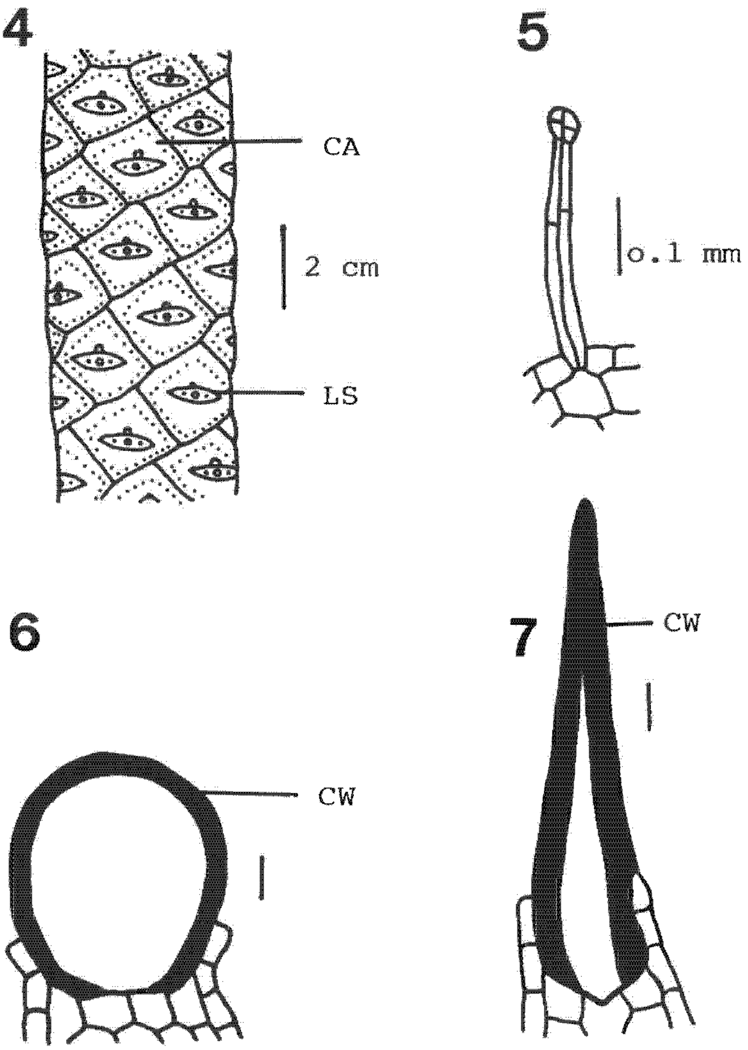
Habit, Stems, and Branching

All species of *Aeonium* are basically long–lived soft–wooded subshrubs or suffrutescent perennials. However, the biennial condition is common in *A. glandulosum* and occasionally found in *A. tabuliforme*. Under greenhouse conditions, all *Aeonium* species grow continuously, but in the wild they show periodicity. No growth rings have been found in any species either under greenhouse or wild conditions. The flush of vegetative growth in the wild is probably initiated by the beginning of the wet season.

Field observations reveal that species can be more or less divided into subacaulescent or subshrubby types although some intermediate individuals do exist. In addition to stem length, branching pattern, surface patterns, and woodiness are important characters for determining relationships among species and sections. Specific examples of these conditions are given below.

Subacaulescent stems generally are characteristic of section *Patinaria* and *Aeonium simsii* (section *Chrysocome*). In these taxa, the stems are generally very short, slow–growing, and hidden by withered leaves. Lateral rosettes are absent or very rare in *Aeonium canariense* var. *subplanum*, *A. glandulosum*, and *A. tabuliforme*. The architectural construction of these three taxa fits "Holttum's model" (Hallé *et al.* 1978). The lateral rosettes are distant from the parental rosette in *Aeonium cuneatum*, whereas other plants with lateral rosettes are growing in tufts. The form of the plants with lateral rosettes fits "Tomlinson's model" (Hallé *et al.* 1978).

The branching pattern in subshrubby species of *Aeonium* is taxonomically important. *Aeonium hierrense*, *A. nobile*, and *A. urbicum* are normally monocaulous and belong to "Holttum's model" architecturally. Among branched species, *Aeonium undulatum* is the only basitonically branched species with branches formed at the subterranean base of the plant, whereas in other species branches are formed distal on the axis. Architecturally, the from of *Aeonium undulatum* fits "Tomlinson's



Figs. 4-7. Vegetative feature of *Aeonium*. 4, stem reticulation in *Aeonium* section *Leuconium* (*A. urbicum; Liu 2541*, OS); CA, cicatrice; LS, leaf scar. 5, multicellular trichome in *Aeonium lindleyi* var. *lindleyi* (*Liu 2610*, OS). 6, unicellular trichome in *Aeonium ciliatum* (*Liu 3152*, OS) and 7, in *Aeonium glandulosum* (Liu 3325, OS). 5-7 same scale.

model" whereas that of other subshrubby species fits "Stone's model" (Hallé *et al*. 1978). The number of lateral branches and the length of the vegetative shoot in each species can vary, but these features have definite ranges and can be used taxonomically within certain limits.

The young wood portion immediately below the immature green stems in subshrubby species is systematically important. It shows a characteristic color for certain species (e.g., silver in *Aeonium lancerottense*), different degrees of woodiness for different sections, and a special surface pattern for section *Leuconium*. The surface pattern on the immature green parts below the terminal rosettes has very limited systematic value. On old stems, the activity of phellogen obscures all characteristic features.

The reticulation on the stem surface (Fig. 4) of section *Leuconium* is of special interest. A similar pattern may be occasionally found on the green stems of section *Pittonium*, and this indicates the close relationship between these two sections. In some species (*Aeonium ciliatum, A. decorum, A. gomerense*, and *A. haworthii*) the reticulations are raised above the surrounding surface whereas in other species they are flush with it. Anatomical study done here reveals that the reticulation is created by cortical cells. The number of cortical cells under the reticulate lines is greater than elsewhere in the stem. As a result, the epidermis and/or periderm are pushed out slightly to form the reticulate lines. In the species with raised reticulations the size of epidermal and subepidermal cells of the reticulate lines are larger. Leaf scars are enclosed by cicatrices, which developmentally are an impression made by the bottom of the unattached fleshy portion of the leaf bases. In most species cicatrices are near to the reticiulate lines, but in *Aeonium decorum* they are distant from them.

The degree of woodiness of the axis was used by Lems (1960) to construct evolutionary sequences among species of *Aeonium*. This is generally different on younger parts in different sections, but more or less the same in old stems. Subacaulescent plants (*A. cuneatum* and section *Patinaria*) have stems scarcely lignified (oligoxylic). *Aeonium hierrense, A. urbicum* (both in section *Leuconium*), *A. leucoblepharum, A. stuessyi* (both in section *Pittonium*), *A. nobile* (monotypic section *Megalonium*), *A. smithii* (section *Chrysocome*), and section *Aeonium* normally have stems with small xylem rings (hemixylic). Stems of *A. spathulatum* and section *Petrothamnium* approach a relatively large xylem ratio (holoxylic) in the younger wood. The lignification of the stem of other species in sections *Leuconium* and *Pittonium* is somewhere between holoxylic and hemixylic. My study of all taxa in the genus reveals that in spite of different woody ratios in the axis in different sections, the taller plants generally have longer vessel–elements and fibers than do the smaller ones. However, the dimensions of vessel–elements and fibers are variable.

Leaves

The leaves in *Aeonium* are succulent and without differentiation into blade and petiole, although those of *Aeonium goochiae* approach such differentiation. My anatomical study of all taxa in the genus has revealed similar internal leaf structures. The leaf is centric and without typical palisade. Stomata are anisocytic and on both surfaces. Mesophyll cells in a well–watered plant are usually irregular, but more or less regular towards the leaf apex and base. Hydathodes are visible in certain species (e.g., *Aeonium arboreum*) and have been reported in all species from Tenerife (Caballero and Jimenez 1978). Subepidermal idioblasts with tannin are found in *Aeonium saundersii, A. sedifolium*, and sections *Aeonium* and *Chrysocome*, although regular subepidermal cells with tannin are also found in many other taxa. Veins are poorly differentiated. At the base of the leaf, one primary vein exists with several secondary veins. All veins gradually branch and diminish into smaller veins, and finally end at submarginal fine vein loops. Among many leaf characters, coloration, phyllotaxy, shape, size, viscidness, thickness, and vestiture are of taxonomic importance primarily at the specific and infraspecific levels.

The morphology of leaf rosettes is taxonomically significant. In sections *Aeonium* and *Patinaria*, the center of the leaf rosette is flat during the dry season. This feature is especially conspicuous in *Aeonium canariense* var. *subplanum, A. glandulosum, A. tabuliforme*, and section *Aeonium*. In the wet season, the young leaves in these two sections tightly appress against the older ones; even the center of the leaf rosette may become more or less ascending. The center of the leaf rosette in other species of the genus is always ascending and not flat, and young leaves arise from the stem tip at a oblique angle to the older ones.

Phyllotaxy in *Aeonium* is alternate and the parastichic arrangement and orthostichic ratio can be determined from the helically arranged leaf scars on the stem. The two parameters vary between species and can be used taxonomically.

Coloration is very important for the delimitation of sections and certain species of *Aeonium*. Only in sections *Leuconium* and *Pittonium* are the leaf margins reddish. Brownish stripes, resulting from the abundance of chromoplasts in the epidermal cells on the surfaces and margin, are generally found in *Aeonium saundersii*, *A. sedifolium*, and sections *Aeonium* and *Pittonium*. If epicuticular wax is especially visible, such as in *Aeonium cuneatum* and sections *Leuconium* and *Pittonium* (except *A. glutinosum*), the leaves are glaucous. In *Aeonium sedifolium* and sections *Aeonium* and *Chrysocome* subepidermal idioblasts with dark green to reddish amorphous substances push epidermal cells above the general surface. As a result, dark green, bright green, reddish, or purplish stripes are seen on the surfaces. These were named "imbedded" or "immersed longitudinal glands" by Praeger (1932) and Lems and Holzapfel (1974). Histochemical tests using cupric acetate and methylene blue (Zimmerman 1901) have shown those amorphous substances to contain large quantities of tannin. For clarity, these color stripes are called "tannic stripes" in this treatment. In section *Chrysocome*, the leaves have many tannic stripes turning reddish or purplish with age on at the least the abaxial surface. The tannic stripes of *Aeonium sedifolium* appear as one broad pale-reddish band on the abaxial surface of the leaf and are usually masked by the brownish stripes. The tannic stripes are few in section *Aeonium* (only barely visible in *Aeonium balsamiferum*) and limited to the midrib portion of the leaf on the abaxial surface.

Although the size and shape of leaves are taxonomically useful, overall foliar dimensions of *Aeonium* are highly variable in response to changing environmental conditions. For example, in *Aeonium nobile* the leaves at the beginning of blooming time, depending upon the availability of water, may vary from 7 cm long, 4 cm wide, and 6 mm thick to 30 cm long, 20 cm wide, and 12 mm thick. Many other species show similar degrees of variation, but within limits, so that the dimensions can be used in some cases for determining relationships. Leaf shape is variable in most taxa, but in some (e.g., *Aeonium canariense* var. *subplanum*, *A. goochiae*, *A. nobile*) it is diagnostic.

Vestiture

Using Uphof's (1962) classification of trichome types as nomenclatural basis, two types of trichomes are found in *Aeonium*: multicellular (Fig. 5) and unicellular (Fig. 6–7). The particular kind of multicellular trichome is capitate and glandular. Unicellular trichomes are thick-walled and restricted to the leaf margin or submargin. Multicellular trichomes have a biseriate stalk and a spherical quadricellular head. The multicellular trichome head in some species is only slightly wider than the stalk itself, and Moreau (1984) reported such a trichome in *Aeonium virgineum* (= *Aeonium canariense* var. *virgineum*) as simple. Two layers and four cells in the biseriate stalk is the most common condition. Three to four layers are occasionally found in *Aeonium canariense* and *A. lindleyi* var. *lindleyi*. Stalks with only one layer are predominant in *Aeonium lindleyi* var. *viscatum* and *A. sedifolium*. The report of sessile trichomes in *Aeonium viscatum* (= *A. lindleyi* var. *viscatum*) by Moreau (1984) perhaps resulted from a misinterpretation of one layer stalk cells as ordinary epidermal cells.

Multicellular trichomes were reported to be related to the secretion of mucilage in *A. glutinosum* (Solereder 1908), and presumably responsible for the sticky nature of some *Aeonium* species (e.g., *A. canariense*, *A. goochiae*, *A. lindleyi*). Histochemical studies done here have revealed tannin in the multicellular trichome head of several species (e.g., *Aeonium* *canariense, A. lindleyi, A. sedifolium, A. smithii*). It is believed that tannin is secreted from the head of multicellular trichomes at certain times in all species of the genus. Unicellular trichomes may also be glandular, as tannin is generally found in the unicellular trichomes of *Aeonium valverdense.*

Developmental studies as part of this monograph have indicated that the initial cells of both unicellular and multicellular trichomes differ from other epidermal cells in the very early stages by having dense protoplasm and by protruding slightly beyond the general surface. The unicellular trichomes elongate and change from bead–shaped to conical–shaped during their development. Exceptions are the mature bead–shapes in *Aeonium glandulosum* and *A. spathulatum.* The orientation and curvature of mature unicellular trichomes are presumably affected by moisture (Uphof 1962) and have no taxonomic value. The initial cells of multicellular trichomes first undergo an anticlinal division, then two daughter cells later undergo periclinal divisions, cell elongation, and head enlargement. A similar developmental sequence has been shown in *Sempervivum arachnoideum* (Dintzl 1905), and possibly exists in all members of the Sempervivoideae. However, the phenomenon of twisted hairs in *Sempervivum arachnoideum* is only found in *Aeonium canariense*, and no trichome connation is seen in *Aeonium*.

The distribution and length of trichomes, especially multicellular trichomes, are generally significant taxonomically. Most species display a remarkable constancy in this regard. Berger (1930) and Praeger (1932) emphasized and used trichome characters in their delimitation of species and sections. Unicellular trichomes are macroscopic and found in most species except *Aeonium canariense, A. tabuliforme*, and section *Petrothamnium . Unicellular trichomes in Aeonium lancerottense* are weak and somewhat wrinkly. Multicellular trichomes are found in all species at least on very young leaves. The taxonomic value of multicellular trichomes on different plant parts are discussed below.

Trichome characters on the surface of young woody stems are used to distinguish certain species. *Aeonium castello–paivae*, and species in sections *Petrothamnium* and *Chrysocome* (except *A. smithii*) have microscopic multicellular trichomes. In *Aeonium smithii* (section *Chrysocome*) the multicellular trichomes are macroscopic (3–8 mm long), stiff, and perpendicular to the stem; Berger (1930) used this particular feature to establish a monotypic section *Trichonium.*

The glabrate or pubescent conditions on both leaf surfaces are reliable taxonomic characters. Glabrate leaves, however, usually have very thinly distributed and very tiny multicellular trichomes not observable even under the 40x dissecting microscope. They may be detected under observations with a compound incident–light microscope equiped with 10x or higher power objective lens. Pubescent leaves in some species (e.g., *Aeonium decorum, A. korneliuslemsii,* and *A. lindleyi* var. *viscatum*) may have extremely short multicellular trichomes (as short as 0.04 mm long) but can be seen under the dissecting microscope. In some glabrate–leaved species (e.g., *Aeonium arboreum,* and *A. ciliatum*), margins of some leaves (e.g., *Liu 2678* of the former taxon) occasionally have multicellular trichomes. The multicellular trichomes on mature leaves of *Aeonium tabuliforme* are of special interest, because they, like those unicellular trichomess in other *Aeonium* species, are only limited to the leaf margins. They develop much later than the other multicellular cells, which are difficult to observe and the leaf surface in this species is usually described as glabrate, and are almost macroscopically identical to unicellular trichomes.

The distribution of multicellular trichomes on reproductive parts is different among species and sections. The presence or absence of trichomes is the same on peduncles, pedicels, and sepals on the same plant. Trichomes do exist on petals and their distribution there (whether on one or both surfaces, or only on veins on the abaxial surface) is taxonomically important. The distribution of trichomes on carpels is similar to that on petals. Depending on the species, the whole ovary or just the exposed, adaxial side of the ovary may be covered by hairs, or the ovary may be glabrous.

Inflorescences

The inflorescences of almost all species of *Aeonium* are cymose and are born terminally on the erect shoots which arise individually from the center of the leaf rosettes. The inflorescence of *Aeonium simsii* is cymose but arises from the leaf axial at the base of the leaf rosette. The flowering sequence is basically determinate, with the terminal flower of each floweringg branch opening first. The flowering shoot persists until the seeds are shed, and in the branched subshrubby species it then disarticulates from the vegetative parts. Leaves of the rosettes beneath the terminal inflorescences shed all leaves during the development and blooming of the flower cluster. Lateral branches may develop at the base of the withered inflorescence when there is no seed set. In monocarpic *Aeonium urbicum*, an interesting phenomenon was observed on one plant (*Evans 373* in the OSU greenhouse) which several lateral leaf rosettes had formed at the base of the withering inflorescence when no seed had been produced, then one of those lateral leaf rosettes apparently had dropped to soil, rooted, and became an independent plant.

Understanding the structure of the inflorescence in *Aeonium* is necessary to be able to assess the relationships among species. In Troll's (1964) comprehensive survey, the inflorescences of three species of *Aeonium* (*A. arboreum, section Aeonium; A. tabuliforme,* section *Patinaria;* and *A. urbicum,* section *Leuconium*) were studied and documented to be homologous.

The simple, obconic, usually three-branched dichasium is common in *Aeonium saundersii* and *A. sedifolium*. For convenience in this discussion, this type of inflorescence is referred to as a pleiochasium, although this term can have a broader application. Its highly reduced form, the helicoid cyme, was observed on certain shoots in two species (e.g., *Aeonium saundersii, Murray s. n.*, 28 May 1894). More complex inflorescences, represented by the further branching of the pleiochasium and an increase in the number of branching pleiochasia, are found in *Aeonium goochiae* and *A. lindleyi* of section *Petrothamnium*.

An increase in the complexity of the inflorescence in sections other than in section *Petrothamnium* corresponds to an increase in the number of flowers per inflorescence. Not only are there more branches, but also more flowers per branch. This trend starts from little more than 100 flowers per inflorescence in section *Chrysocome,* through sections *Pittonium. Aeonium, Leuconium,* and *Patinaria,* to nearly 50,000 flowers per inflorescence in monotypic section *Megalonium*.

Besides variation in the degree of complexity, the shape of the inflorescence varies and has limited taxonomic value. Caution is needed, however, because a weak individual may not produce its characteristic inflorescence. Normally, a flat-topped inflorescence is typical in Aeonium glandulosum (section *Patinaria*) and *A. nobile* (monotypic section *Megalonium*), a dense, dome-shaped inflorescence is typical for most species within section *Leuconium,* a dense, pyramidal inflorescence occurs in sections *Aeonium* and *Pittonium,* and a loose, pyramidal inflorescence is in section *Patinaria.* The development of these more complex inflorescences in these sections approaches that of a racemose cluster, in which branching pleiochasia develop acropetally along the axis (Troll 1964).

Calyx

The flower of *Aeonium* is pedicellate and hypogynous. If viewed superficially from the outside, pedicel, receptacle, and calyx form a continuous structure, and the receptacle is easily mistaken as a part of the calyx. However, the point of insertion of sepals to the receptacle is easily seen if one looks carefully. The sepal length in Praeger's (1932) monograph presumably erroneously included the length of the receptacle. Sepals are united for a short distance just above their insertion, and the width of sepals, therefore, is measured between sinuses. Besides relative size, the color variegation and the number of sepals are taxonomically important. Sepals are generally green, with some species (e.g., *Aeonium nobile, A. lancerottense*) having pinkish or reddish pigmented–stripes. *Aeonium leucoblepharum, A. stuessyi* and section *Chrysocome* have tannic stripes on the sepals. The sepal number of any given species has a specific range and can be used taxonomically.

Corolla

Petals in all species of *Aeonium* are the same number as the sepals and opposite them. The petals are free and widespreading, although they may be semi-erect basally and turn outward above in some species (e.g., in *Aeonium saundersii* and *A. sedifolium*). Petal coloration is a very important taxonomic character. Yellow is found in sections *Petrothamnium* (except *A. goochiae*), *Chrysocome*, and *Aeonium*, white is restricted to section *Leuconium* and pale to very pale yellow is found in *Aeonium goochiae, A. nobile*, and sections *Patinaria* and *Pittonium*. Different variegations may occur within these basic colors. Pinkish stripes of varying width are in the median portion of petals in *Aeonium goochiae*, and most species in section *Leuconium* (except *Aeonium castello-paivae, A. ciliatum*, and *A. gomerense*). Reddish stripes on petals are found in *Aeonium arboreum* var. *rubrolineatum, A. nobile*, and in section *Pittonium*. The reddish stripes are so numerous in *Aeonium nobile* that the whole flower appears dark-red. Green stripes, usually pale, may appear on the median portion of the petal on the abaxial side in certain species (e.g., *Aeonium ciliatum* and *A. undulatum*). Tannic stripes are found in *Aeonium smithii* and *A. spathulatum*.

Androecium

Stamens are twice as many as the sepals, and adnate to the bases of petals. They are arranged in two whorls, with the inner interpetalous ones longer than the outer antipetalous ones. Except for relative size and vestiture, stamen characters are of minimal taxonomic value. Filaments are filiform and typically whitish, with occasional pinkish or reddish stripes if the same color is present on the petals. Species in section *Leuconium* and in a few other species (e.g., *Aeonium glutinosum* and *A. gorgoneum*) usually have their stamen filaments broadened toward the base. Anthers are basically yellow, or become pale yellow, whitish or brown in later stages. Pollen grains are basically isopolar and tricolporate, with exine striato-reticulate (Erdtman 1971; Perez de Paz 1977, 1980; Hideux 1979). In *Aeonium haworthii*, the exine is more or less psilate and smooth (Perez de Paz 1980).

Gyneocium, Fruits, and Seeds

The gynoecium of *Aeonium* is apocarpous with superior ovaries, which are the same number as the sepals. The color of the ovary is similar to that of the petals in any given species. The ovary gradually narrows into the style without any significant change. The ill-defined punctiform stigma develops after pollen is shed, and the fruit is a follicle.

Seed morphology in *Aeonium* is quite uniform. The surface pattern of seeds of the genus is very similar to that of *Sedum* section *Gormania* surveyed by Denton (1982). The seeds of *Aeonium* are ellipsoidal, 0.4–0.6 mm long, 0.02–0.04 mg, with longitudinal ridges resulting from the swollen ends of transversely oriented, rectangular cells.

Nectariferous Glands

At the base of each carpel, a scale-like, nectar-producing gland is generally found. It exudes nectar by its adaxial and/or apical stomata (Said 1982). The presence and color of nectariferous glands are useful for determining relationships. Four species (*Aeonium saundersii, A. sedifolium, A. smithii,* and *A. spathulatum*) are without any gland. Glands are white or greenish-white in sections *Leuconium* and *Patinaria,* and yellow in all other gland-bearing species. The shape and size of the nectariferous glands sometimes are useful for identification (e.g., varieties of *Aeonium canariense*). The glands in *Aeonium tabuliforme* are oblong, which is unique in the genus.

CYTOLOGY

Chromosome numbers of the taxa of *Aeonium* were obtained from mitotic and meiotic squashes using standard techniques (Sharma & Sharma 1980). Root tips were pretreated with 2% colchicine before fixation. Flower buds and root tips were fixed in Carnoy's fluid I or Carnoy's fluid II and were stained with aceto-carmine or acetic-orcein before squashing. Thirty-six of the 37 taxa of *Aeonium* have been examined chromosomally from 47 populations, and numbers of six taxa are reported here for the first time. All vouchers are on deposit at OS. The chromosome numbers of all taxa, including those previously reported, are listed in Table 1.

Most species of *Aeonium* have $n = 18$, which is clearly the basic number for the genus. *Aeonium arboreum* var. *arboreum* has diploid and tetraploid numbers, with the tetraploid number only being found in cultivated individuals. *Aeonium simsii* has diploid, triploid, and tetraploid numbers. Three other species (*Aeonium balsamiferum, A. haworthii,* and *A. korneliuslemsii*) are known only at the tetraploid level. An interesting correlation is that these taxa grow in relatively drier regions from other members of the genus.

Four previously reported numbers ($n = 30$; $2n = 30, 34, 50$) are other than a multiple of $n = 18$. These may have resulted from errors of observation and/or interpretation, misidentification of voucher material, or perhaps abnormal mitotic or meiotic divisions. It is also possible that these numbers may reflect naturally occurring infraspecific variation. Which of these may have occurred in a particular case is unknown, but infraspecific variation is not uncommon in Crassulaceae (Uhl and Moran 1972; Uhl 1976; Spongberg 1978).

Table 1. Chromosome numbers in *Aeonium*.

Taxa	***Chromosome Number*** **n**	**2n**	**Reference or Voucher**
A. arboreum var. *arboreum*	18		*Evans 227; Evans 256 Liu 3027*
	30		Skovstedt 1934
	36		Uhl 1961
		34	Sharma & Ghosh 1967
		c. 36	Uhl 1961
A. arboreum var. *holochrysum*	18		Uhl 1961; *Evans 282; Liu 3317*
		36	Uhl 1961; *Evans 300*
		50	Gagnieu et al. 1973
A. arboreum var. *rubrolineatum*	18		*Evans 194; Evans 197*
		36	Uhl 1961
A. balsamiferum		c. 72	Uhl 1961; *Evans 23*
A. canariense var. *canariense*	18		Uhl 1961; *Liu 3145*
		36	Gagnieu et al. 1973
A. canariense var. *palmense*	18		*Evans 210; Liu 3285*
		36	Uhl 1961
A. canariense var. *subplanum*	18		Uhl 1961; *Liu 3105*
A. canariense var. *virgineum*	18		*Liu 3034*
		36	Uhl 1961
A. ciliatum	18		Skovstedt 1934; *Liu 3152*
		36	Uhl 1961; Gagnieu et al. 1973
A. castello-paivae	18		Uhl 1961; *Liu 2635*
A. cuneatum	18		Uhl 1961
		36	Uhl 1961; Gagnieu et al. 1973; *Liu 2555*
A. davidbramwellii		36*	*Liu 3261*
A. decorum	18		Uhl 1961
		36	*Evans 441*
A. glandulosum	18*		*Liu 3325*
A. glutinosum	18		Uhl 1961; *Liu 2703*
		36	Uhl 1961; *Liu 2703*
A. gomerense	18		Uhl 1961
		36	*Liu 3124*
A. goochiae		36	Uhl 1961; *Liu 3262*

* first report.
** cultivated plant without collection number.

Table 1. Chromosome numbers in *Aeonium* (continued).

Taxa	Chromosome Number n	 2n	Reference or Voucher
A. gorgoneum		36*	cult.**
A. haworthii	36		Uhl 1961; *Liu 2573*
A. hierrense	18		*Liu 3269*
A. korneliuslemsii	36*		cult.**
A. lancerottense	18		Uhl 1961; *Liu 2636*
		36	Uhl 1961
A. leucoblepharum		36*	cult.**
A. lindleyi var. *lindleyi*	18		Uhl 1961
		36	Uhl 1961; Gagnieu et al. 1973; *Liu 2511*
A. lindleyi var. *viscatum*	18		Uhl 1961; *Liu 2610*
		36	Uhl 1961
A. nobile	18		Uhl 1961; *Liu 2648; Liu 3266*
		36	Uhl 1961
A. percarneum	18		Uhl 1961
		36	Uhl 1961; Michaelis 1964; *Liu 3025*
A. saundersii		36*	*Liu 2624*
A. sedifolium	18		Uhl 1961; *Evans 295*
		36	Gagnieu et al. 1973; *Liu 3165*
A. simsii	18		Uhl 1961; *Liu 2677*
	36		Uhl 1961
		c. 54	Uhl 1961
A. smithii	18		Uhl 1961
		36	*Liu 2669*
A. spathulatum	18		Uhl 1961
		30	Gagnieu et al. 1973
		36	*Liu 3024; Liu 3252*
A. tabuliforme	18		Skovstedt 1934; Uhl 1961
		36	Gagnieu et al. 1973; *Liu 2576*
A. undulatum	36		Skovstedt 1934; Uhl 1961; *Liu 3051*
		c. 72	Uhl 1961
A. urbicum	18		Uhl 1961; *Evans 373; Evans 384*
		36	Uhl 1961
A. valverdense		36	*Evans 214*
		36	Uhl 1961

* first report.

** cultivated plant without collection number.

HYBRIDIZATION

Hybridization is known to be a common phenomenon, both in nature and in the garden, among species of Sempervivoideae (Praeger 1932). It occurs between almost all sympatric taxa with overlapping flowering times. Currently, 38 putative natural hybrids among 30 taxa of *Aeonium* have been reported (Praeger 1929, 1932; Voggenreiter 1974; Santos 1983; Bañares 1986; and this study). In addition, four intergeneric hybrids between *Aeonium* and *Greenovia* are known (Praeger 1929, 1932; Voggenreiter 1974; Santos 1983). It must be kept in mind that most hybrids have been inferred from their possession of intermediate morphology without actual crossing studies to confirm the hypotheses. In this treatment all reported hybrids are listed under one of their putative parents and at the end of taxonomic treatment.

Hybrids, at least those seen in the course of the present study, seem vigorous. Pollen viability, inferred from an examination of more than 300 pollen grains per plant for stainability with aniline-blue-lactophenol (Maneval 1936), was found in the range of 80-90% in two flowering naturally occurring hybrids, *Aeonium sedifolium* x *urbicum (Liu 2568)* and *A. simsii* x *arboreum* var. *arboreum (Liu 3044)*. Meiosis is normal in both taxa (Uhl 1961; pers. obser.). Germinable seeds were obtained from the F 1 generation of the first hybrid combination (Uhl 1961). Self-crossing has been reported from *Aeonium ciliatum* x *arboreum* var. *holochrysum* and *A. castello-paivae* x *canariense var. subplanum (Praeger 1932) whereas all natural species are known to be out-crossing (Praeger 1932).*

In spite of the large number of crosses reported in Aeonium, hybrids are relatively rare in the field. Praeger (1929) only found a few individuals. Lems (1960) suggested that the absence of intermediate habitats, which is caused by the steep ecological gradients, is a possible explanation for the rarity of natural hybrids. In the Canary Islands, the change from a habitat to another is very sharp. It is believed that hybrid sterility may also be involved. In *Aeonium sedifolium* x *urbicum*, although the F 1 generation seemed to be normal, the F 2 generation showed meiotic irregularity and sterility (Uhl 1961). No seed has ever been found in the widely cultivated garden hybrid *Aeonium simsii* x *spathulatum* (Praeger 1932), and this condition may also occur in other hybrids as well.

Introgressive hybridization has been suggested to occur between several pairs of species (Praeger 1929, 1932), and all involve either *Aeonium hierrense* or *A. urbicum* (both perennial and monocarpic). As natural variation within the presumptive parental taxa was not dealt with meaningfully by Praeger (1932), the extent of introgressive hybridization, if any, is difficult to estimate at this time.

PHENETICS

The most important task in any revisionary study is to establish a classification that reflects the highest degree of evolutionary relationships among the taxa investigated. During the past thirty years, two new schools of taxonomy, phenetics and cladistics, have developed to provide explicit methods for determining relationships. Selected methods from these two schools were used to best intuitively generated relationships among taxa of *Aeonium* developed in the course of the present revision. Taxa in these studies are abbreviated using the first three letters of the specific and varietal epithets (see synopsis of classification on page 2).

Phenetics has proven useful in many plant groups for providing a better understanding of relationships within a particular group (for reviews, see Sneath & Sokal 1973, Clifford & Stephenson 1975, Duncan & Baum 1981, McNeil 1984). This approach seeks a summarized form of similarity or dissimilarity based on character-state distributions among taxa investigated (McNeil 1980, 1982). Although phenetics does not attempt to reflect evolution directly, its success in revealing patterns of relationships relates directly to evolution since character-state distributions are products of the evolutionary history of the taxa (McNeil 1982). The phenetic study of *Aeonium*, therefore was designed to (1) determine the phenetic affinity among taxa for better insights on constructing a maximally predictive classification; and to (2) seek clues to the evolutionary history of the taxa that might have been overlooked in the intuitive evolutionary and cladistic analyses.

The 37 taxa of *Aeonium* constitute the 37 Operational Taxonomic Units (OTUs) for the phenetic study. Thirty-nine characters (Table 2) were scored, and the basic data matrix is listed in Table 3. Some characters (e.g., stem color, leaf apex) were not used because they are discrete and constant in one part of the genus but continuous and variable in another. The data were analyzed using the numerical techniques included in the NT-SYS package (Rohlf *et al.* 1972). Data were standardized, and both correlation and distance matrices were computed. Missing and unknown character states were ignored in the computation. Single linkage, complete linkage, and unweighted pair group method using arithmetic means (UPGMA) were used to perform cluster analyses on each of the matrices. The cophenetic correlation coefficient was calculated to measure the distortion of the phenogram from the matrix. Besides cluster analyses, ordinations were performed by principal component analysis (PCA) and principal coordinates analysis (PCO).

The results of cluster analyses and PCO are summarized in Figs. 8 and 9. The clustering method which produced the phenogram with the highest cophenetic correlation coefficient (0.827) is UPGMA using the correlation matrix (Fig. 8). This is the only phenogram presented here for discussion. A perspective three-dimensional projection of the OTUs on the axes representing the first three factors derived from distance matrix through PCO is also shown (Fig. 9). Although results from PCA and PCO are very similar, PCO is preferred to PCA because the former is less affected by missing data (Rohlf 1972), which is the case in a few characters in *Aeonium*. These three factors encompass 52.68% of the total variation in the data set.

The relationships revealed through UPGMA are very similar to those of the intuitive classification. Different sections are generally distinct in UPGMA with a few exceptions. Sections *Chrysocome* and *Petrothamnium* are mixed. However, *Aeonium simsii* is in its own series *Simsii* and the remaining taxa (*Aeonium smithii* and *A. spathulatum*) of section Chrysocome do have a high correlation coefficient with it. In section *Patinaria*, species of its two series are not well separated. *Aeonium glutinosum* shows some similarity with *A. nobile* which is placed in its own section. Correlations among varieties of the same species are generally higher than among species. Correlations among varieties of *Aeonium canariense* (VIR to PAL) are the highest of all in the analysis. Correlations among sections are low, mostly below 0.2, with section *Leuconium* representing the most distinct group in the UPGMA phenogram.

Similar features are seen in the results from PCO. However, there are several differences with UPGMA that need to be noted. *Aeonium nobile* is near to section

Patinaria and distant from *A. glutinosum*, in PCO. Two series (CUN vs. other taxa) of section *Patinaria* become separable in PCO, as do sections *Petrothamnium* and *Chrysocome*. In general, the results from PCO are closer to the intuitive classification, although some sections are not sharply differentiated. As ordination is considered to be a better reflection of maximally predictive properties of phenetic grouping (McNeil 1980), the intuitive classification is therefore supported as an adequate reflection of overall similarity as revealed by the phenetic study. Sections are generally separated well from each other. The lack of resolution in parts of the UPGMA phenogram is possibly due to parallel evolution in quantitative features within the genus, a not uncommon problem in groups that have undergone striking adaptive radiation (e.g., in *Melampodium*, Stuessy 1979).

Data of leaf cuticle alkanes in 23 taxa of *Aeonium*, taken from the study by Eglinton et al. (1962), have also been analyzed phenetically during the course of this study using the same techniques described above. Infraspecific variation is so broad that different populations of the same species are placed in different groups in the resultant phenograms (both cluster analyses and ordination). The populations of section *Leuconium*, however, do tend to group together, and this is additional evidence to support section *Leuconium* as a natural unit.

Table 2. Characters and character states of taxa of *Aeonium* used in the phenetic and cladistic analyses. All characters were used for the phenetic analyses; characters with an asterisk are those used in the cladistic analyses, in which case 0 = primitive and 1 (or 2) = derived. The character state tree for character 29 has 0 giving rise to 1 and 2 sequently; the character state trees for all other multistate characters has 0 giving rise to 1 in one direction and 2 independently in the other.

Plant. 1, height (cm). 2, number of lateral branches. 3*, branching type: acrotonic (0), basitonic (1).

Stem. 4*, vestiture: pubescent to puberulent (0), glabrate (1). 5*, surface reticulation: absent (0), present (1).

Leaves. 6, length (cm). 7, width (mm). 8, thickness (mm). 9*, surface vestiture: pubescent (0), glabrate (1). 10*, glaucescence: not glaucous (0), glaucous (1). 11*, viscidness: smooth, not sticky (0), sticky (1). 12*, tannic stripes: absent (0), limited to the central portion of the abaxial surface (1), abundant on the abaxial surface (2). 13*, brownish stripes: absent (0), present (1). 14*, leaf margin color: green or brown (0), red (1). 15*, unicellular trichomes: absent (0), present (1). 16*, center of the leaf rosette in dry season: suberect (0), flattened (1). 17, phyllotaxy: 2/5 (0), 3/8 (1), 5/13 (2), 8/21 (3)

Inflorescence. 18*, position: terminal (0), lateral (1). 19, height (cm). 20, diam. (cm).

Calyx. 21, number of sepals. 22, sepal length (mm). 23, sepal width (mm). 24*, vestiture: puberulent (0), glabrous (1). 25*, color: green (0), green with pinkish or reddish variegation (1). 26*, tannic stripes: absent (0), present (1).

Corolla. 27, petal length (mm). 28, petal width (mm). 29*, background color: yellow (0), pale yellow (1), whitish (2). 30*, color of variegation: greenish or no color variegation (0), pink (1), red (2). 31*, vestiture: glabrate (0), puberulent on the abaxial surface (1), puberulent on both surfaces (2). 32*, tannic stripes: absent (0), present (1).

Stamens. 33, length (mm). 34*, filament vestiture: glabrous (0), puberulent (1). 35*, filament shape: filiform (0), tapering (1).

Nectariferous glands. 36*, present (0), absent (1). 37, color: yellow (0), white or greenish white (1).

Carpels. 38, length (mm). 39*, vestiture: glabrous (0), puberulent (1).

Table 3. Basic data matrix of states of characters in taxa of *Aeonium*. Characters used for cladistic analyses are in bold faces (these were also used for phenetic analyses). NC = missing or unknown character states.

										Characters										
Taxa	**1**	**2**	***3***	***4***	***5***	**6**	**7**	**8**	***9***	***10***	***11***	***12***	***13***	***14***	***15***	***16***	**17**	***18***	**19**	**20**
ARB	200	9	**0**	**1**	**0**	10	25	2	**1**	**0**	**0**	**1**	**1**	**0**	**1**	**1**	3	**0**	18	10
BAL	150	8	**0**	**1**	**0**	5	25	2	**1**	**0**	**0**	**0**	**1**	**0**	**1**	**1**	3	**0**	20	8
CAN	3	2	**0**	**1**	**0**	25	60	6	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	1	**0**	38	9
CAS	60	60	**0**	**0**	**1**	3	14	3	**1**	**1**	**0**	**0**	**0**	**1**	**1**	**0**	2	**0**	13	8
CIL	90	6	**0**	**1**	**1**	8	35	6	**1**	**1**	**0**	**0**	**0**	**1**	**1**	**0**	3	**0**	28	8
CUN	3	2	**0**	**1**	**0**	18	65	7	**1**	**1**	**0**	**0**	**0**	**0**	**1**	**1**	2	**0**	39	9
DAV	100	8	**0**	**1**	**1**	8	30	4	**0**	**1**	**0**	**0**	**0**	**1**	**1**	**0**	2	**0**	28	7
DEC	60	50	**0**	**1**	**1**	4	13	3	**0**	**1**	**0**	**0**	**0**	**1**	**1**	**0**	2	**0**	19	7
GLA	3	0	**0**	**1**	**0**	10	50	4	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	3	**0**	18	11
GLU	100	5	**0**	**1**	**0**	10	33	3	**1**	**0**	**1**	**0**	**1**	**1**	**1**	**0**	2	**0**	28	9
GOM	200	5	**0**	**1**	**1**	10	33	5	**1**	**1**	**0**	**0**	**0**	**1**	**1**	**0**	3	**0**	28	8
GOO	40	30	**0**	**0**	**0**	4	20	1	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	2	**0**	4	8
GOR	200	7	**0**	**1**	**0**	8	23	4	**1**	**1**	**0**	**0**	**1**	**1**	**1**	**0**	2	**0**	7	9
HAW	60	40	**0**	**1**	**1**	4	22	3	**1**	**1**	**0**	**0**	**0**	**1**	**1**	**0**	2	**0**	11	8
HIE	120	0	**0**	**1**	**1**	15	55	6	**1**	**1**	**0**	**0**	**0**	**1**	**1**	**0**	3	**0**	33	8
HOL	200	10	**0**	**1**	**0**	10	25	2	**1**	**0**	**0**	**1**	**1**	**0**	**1**	**1**	3	**0**	18	10
KOR	150	9	**0**	**1**	**0**	7	25	2	**0**	**0**	**0**	**1**	**0**	**0**	**1**	**1**	3	**0**	13	8
LAN	60	10	**0**	**1**	**1**	7	28	4	**1**	**1**	**0**	**0**	**0**	**1**	**1**	**0**	3	**0**	19	8
LEU	150	4	**0**	**1**	**0**	9	25	3	**1**	**1**	**0**	**0**	**1**	**1**	**1**	**0**	2	**0**	12	9
LIN	50	50	**0**	**0**	**0**	3	12	6	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	2	**0**	5	9
NOB	60	0	**0**	**1**	**0**	19	120	9	**1**	**0**	**1**	**0**	**1**	**0**	**1**	**0**	2	**0**	30	8
PAL	3	3	**0**	**1**	**0**	25	60	6	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	1	**0**	50	9
PER	150	8	**0**	**1**	**1**	7	30	4	**1**	**1**	**0**	**0**	**0**	**1**	**1**	**0**	3	**0**	20	9
RUB	180	8	**0**	**1**	**0**	10	25	2	**1**	**0**	**0**	**1**	**1**	**0**	**1**	**1**	3	**0**	11	10
SAU	25	30	**0**	**0**	**0**	2	10	2	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	1	**0**	5	14
SED	40	100	**0**	**0**	**0**	1	7	4	**0**	**0**	**0**	**1**	**1**	**0**	**0**	**0**	0	**0**	5	10
SIM	3	8	**0**	**1**	**0**	4	13	2	**0**	**0**	**0**	**2**	**0**	**0**	**1**	**0**	2	**1**	4	8
SMI	50	8	**0**	**0**	**0**	5	22	1	**0**	**0**	**0**	**2**	**0**	**0**	**1**	**0**	2	**0**	9	10
SPA	50	80	**0**	**0**	**0**	2	6	1	**0**	**0**	**0**	**2**	**0**	**0**	**1**	**0**	2	**0**	6	9
STU	100	4	**0**	**1**	**0**	9	30	4	**0**	**1**	**1**	**0**	**1**	**1**	**1**	**0**	2	**0**	12	9
SUB	3	0	**0**	**1**	**0**	20	50	5	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	1	**0**	24	11
TAB	3	0	**0**	**1**	**0**	12	30	4	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	3	**0**	23	8
UND	220	1	**1**	**1**	**0**	12	35	2	**1**	**0**	**0**	**1**	**1**	**0**	**1**	**1**	3	**0**	31	11
URB	150	0	**0**	**1**	**1**	13	38	6	**1**	**1**	**0**	**0**	**0**	**1**	**1**	**0**	3	**0**	45	9
VAL	100	3	**0**	**1**	**1**	9	50	6	**0**	**1**	**0**	**0**	**0**	**1**	**1**	**0**	2	**0**	20	8
VIR	3	2	**0**	**1**	**0**	20	50	5	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	1	**0**	30	8
VIS	40	50	**0**	**0**	**0**	4	10	3	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	2	**0**	5	8

Table 3. Basic data matrix of states of characters in taxa of *Aeonium.* Characters used for cladistic analyses are in bold faces (these were also used for phenetic analyses). NC = missing or unknown character states(continued).

	Characters																		
Taxa	**21**	**22**	**23**	***24***	***25***	***26***	**27**	**28**	***29***	***30***	***31***	***32***	**33**	***34***	***35***	***36***	**37**	**38**	***39***
ARB	10	2.8	1.3	**0**	**0**	**0**	6.0	1.8	**0**	**0**	**0**	**0**	6	**0**	**0**	**0**	0	5	**0**
BAL	8	1.9	1.3	**1**	**0**	**0**	7.0	1.4	**0**	**0**	**0**	**0**	7	**0**	**0**	**0**	0	6	**0**
CAN	9	4.5	1.8	**0**	**0**	**0**	8.0	1.8	**1**	**0**	**1**	**0**	7	**0**	**0**	**0**	1	6	**1**
CAS	8	3.0	1.6	**0**	**0**	**0**	9.0	1.3	**2**	**0**	**2**	**0**	7	**1**	**1**	**0**	1	6	**2**
CIL	8	2.8	1.3	**0**	**0**	**0**	8.5	1.6	**2**	**0**	**1**	**0**	7	**0**	**1**	**0**	1	7	**0**
CUN	9	3.5	1.4	**0**	**0**	**0**	7.0	1.5	**0**	**0**	**0**	**0**	6	**0**	**0**	**0**	1	7	**1**
DAV	7	2.0	1.5	**0**	**0**	**0**	7.8	2.0	**2**	**0**	**1**	**0**	7	**1**	**1**	**0**	1	6	**2**
DEC	7	3.5	1.3	**0**	**1**	**0**	7.5	2.3	**2**	**1**	**1**	**0**	7	**1**	**1**	**0**	1	6	**2**
GLA	11	6.5	2.8	**0**	**0**	**0**	9.0	3.5	**1**	**0**	**0**	**0**	7	**0**	**0**	**0**	0	6	**0**
GLU	9	2.0	1.8	**0**	**1**	**0**	6.0	2.5	**1**	**2**	**0**	**0**	5	**0**	**1**	**0**	0	3	**0**
GOM	8	3.5	1.3	**1**	**0**	**0**	9.0	1.8	**2**	**0**	**0**	**0**	8	**0**	**1**	**0**	NC	7	**0**
GOO	8	3.2	0.9	**0**	**0**	**0**	6.0	1.5	**1**	**1**	**1**	**0**	7	**0**	**0**	**0**	0	5	**2**
GOR	9	2.5	0.9	**1**	**1**	**0**	5.5	1.3	**1**	**2**	**0**	**0**	6	**0**	**1**	**0**	NC	5	**0**
HAW	8	3.5	1.8	**1**	**1**	**0**	8.0	1.5	**2**	**1**	**0**	**0**	8	**0**	**1**	**0**	1	7	**0**
HIE	8	2.8	1.3	**0**	**0**	**0**	8.0	1.8	**2**	**1**	**1**	**0**	8	**1**	**1**	**0**	1	7	**1**
HOL	10	2.8	1.3	**1**	**0**	**0**	6.0	1.8	**0**	**0**	**0**	**0**	6	**0**	**0**	**0**	0	5	**0**
KOR	8	1.6	1.3	**0**	**0**	**0**	5.3	2.0	**0**	**0**	**0**	**0**	4	**0**	**0**	**0**	0	5	**0**
LAN	8	2.3	1.4	**0**	**1**	**0**	7.5	1.3	**2**	**1**	**0**	**0**	7	**0**	**1**	**0**	1	7	**0**
LEU	9	2.6	1.6	**0**	**1**	**1**	7.0	2.1	**1**	**2**	**0**	**0**	7	**0**	**0**	**0**	NC	6	**0**
LIN	9	3.2	1.7	**0**	**0**	**0**	6.0	1.7	**0**	**0**	**1**	**0**	7	**0**	**0**	**0**	0	5	**2**
NOB	8	2.5	1.3	**0**	**1**	**0**	4.0	1.3	**1**	**2**	**0**	**0**	5	**0**	**1**	**0**	0	5	**0**
PAL	9	5.0	2.5	**0**	**0**	**0**	8.5	2.5	**1**	**0**	**1**	**0**	6	**0**	**0**	**0**	1	6	**1**
PER	9	2.5	1.2	**0**	**0**	**0**	7.5	1.5	**2**	**1**	**1**	**0**	7	**1**	**0**	**0**	1	6	**1**
RUB	10	2.8	1.3	**1**	**1**	**0**	6.0	1.8	**0**	**2**	**0**	**0**	6	**0**	**0**	**0**	0	5	**0**
SAU	14	4.0	1.1	**0**	**0**	**0**	7.5	2.2	**0**	**0**	**1**	**0**	6	**0**	**1**	**1**	NC	6	**2**
SED	10	2.8	1.8	**0**	**1**	**0**	6.0	2.2	**0**	**0**	**0**	**0**	5	**1**	**0**	**1**	NC	5	**2**
SIM	8	2.3	1.2	**0**	**0**	**1**	5.5	1.5	**0**	**0**	**0**	**0**	6	**0**	**0**	**0**	0	3	**0**
SMI	10	3.5	1.5	**0**	**0**	**1**	8.0	2.3	**0**	**0**	**2**	**1**	5	**0**	**0**	**1**	NC	5	**2**
SPA	9	1.7	0.8	**0**	**0**	**1**	5.7	1.8	**0**	**0**	**0**	**1**	5	**0**	**0**	**1**	NC	4	**1**
STU	9	2.5	1.8	**0**	**1**	**1**	7.5	2.0	**1**	**2**	**0**	**0**	8	**0**	**0**	**0**	0	6	**0**
SUB	11	4.5	1.8	**0**	**0**	**0**	8.5	2.3	**1**	**0**	**1**	**0**	8	**0**	**0**	**0**	1	6	**1**
TAB	8	3.5	1.8	**0**	**0**	**0**	6.5	1.8	**1**	**0**	**1**	**0**	6	**0**	**0**	**0**	1	6	**1**
UND	11	1.7	0.9	**1**	**0**	**0**	6.0	2.5	**0**	**0**	**0**	**0**	7	**0**	**0**	**0**	0	5	**0**
URB	9	2.5	1.3	**1**	**0**	**0**	8.5	2.4	**2**	**1**	**0**	**0**	9	**0**	**1**	**0**	1	9	**0**
VAL	8	4.3	1.3	**0**	**0**	**0**	11.0	2.3	**2**	**1**	**2**	**0**	10	**1**	**1**	**0**	1	9	**2**
VIR	8	4.0	2.0	**0**	**0**	**0**	8.0	2.0	**1**	**0**	**1**	**0**	6	**0**	**0**	**0**	1	6	**1**
VIS	8	3.2	1.2	**0**	**0**	**0**	6.0	1.3	**0**	**0**	**1**	**0**	5	**0**	**1**	**0**	0	4	**2**

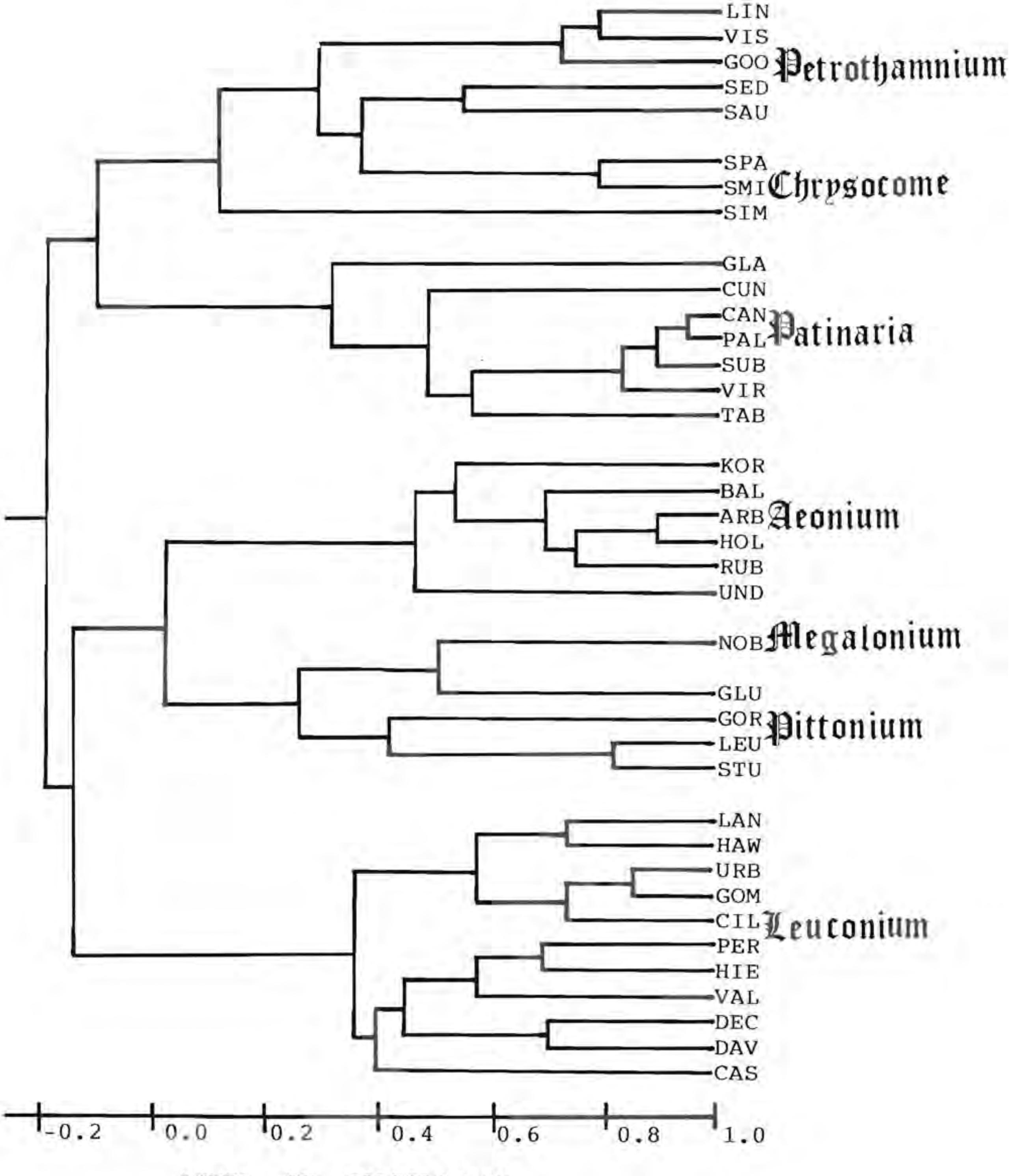


Fig. 8. Phenogram of taxa of *Aeonium* using UPGMA cluster analysis.

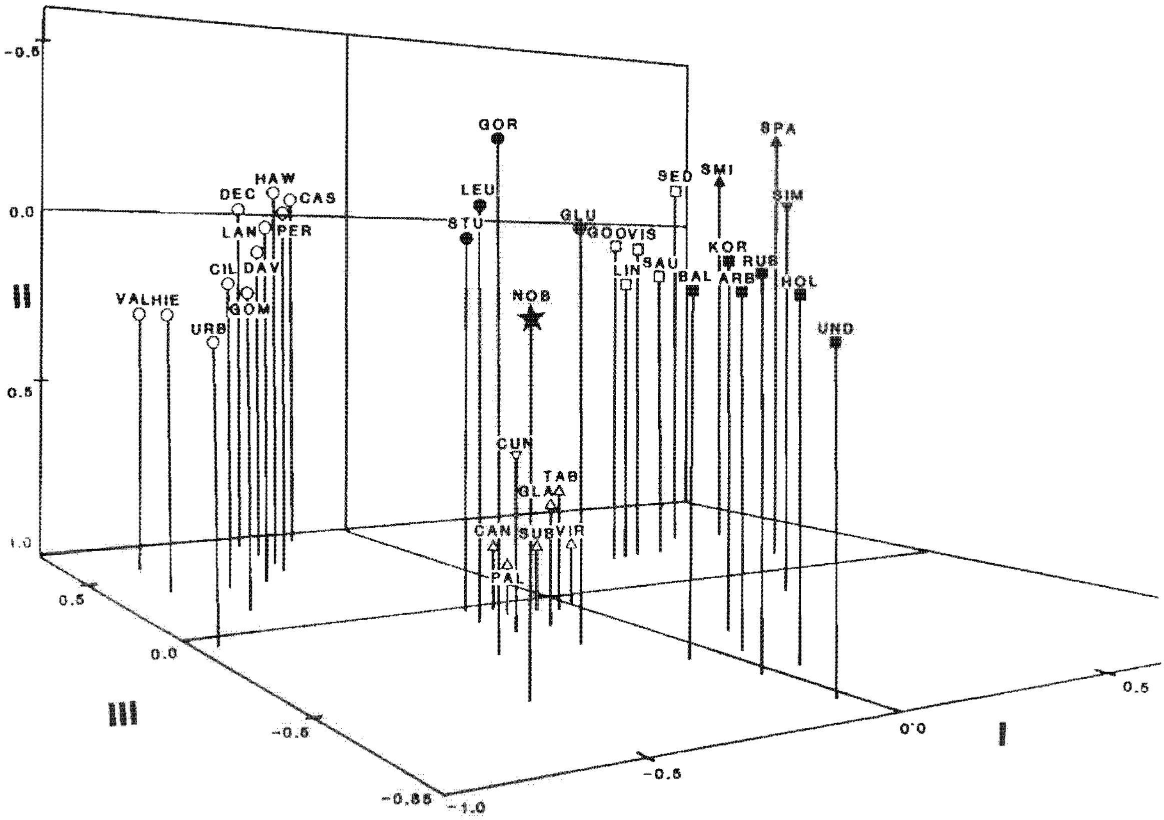


Fig. 9. Principal coordinates analysis of taxa of *Aeonium* showing three-dimensional projection of OTUs on axes representing the first three factors. Symbols for sections: *Aeonium*, solid squares; *Chrysocome*, solid triangles (series *Chrysocome*, upright ones; series *Simsii*, inverted one); *Leuconium*, circles; *Megalonium*, star; *Patinaria*, open triangles (series *Patinaria*, upright ones; series *Praegeri*, inverted one); *Petrothamnium*, open squares; *Pittonium*, dots.

PHYLOGENETIC RECONSTRUCTION

A number of cladistic methods have been developed in the past two decades (Duncan and Stuessy 1985) all of which have clearly stated assumptions and procedures for "phylogenetic" reconstruction. Cladistic analyses of *Aeonium* were undertaken to (1) provide insights into genealogical relationships among taxa, and to (2) provide another independent test for the intuitively generated classification.

The first step for cladogram construction is to select characters of evolutionary important and to determine polarity of the character states. Several criteria for resolving polarities of character states have been reviewed by many authors (e.g., Crisci & Stuessy 1980; Stevens 1980; Bishop 1982; Stuessy & Crisci 1984). Among all criteria reviewed, out-group analysis is viewed as the least fallable and has been used in the detemnination of evolutionary directionality of character states in *Aeonium*, although it is acknowledged that out-group analysis is also flawed (Colless 1985). *Aichryson* was chosen as the outgroup for the following considerations: (1) among genera of Sempervivoideae, it is closely related to *Aeonium* morphologically; and (2) it has been considered to be closely related to *Sedum* (Uhl 1961) of the subfamily Sedoideae, which may have given rise to the Sempervivoideae (Froderstrom 1930; Hideux 1979). The characters, the polarity of character states, and the basic data matrix for cladistic study are listed in Tables 2-3. Multistate characters were changed into a series of two-state characters (Kluge & Farris 1969) before computation.

A number of computer programs are available for cladogram construction (e.g., Underwood 1982; Swofford 1983; Felsenstein 1984). For *Aeonium* two programs, Mixed Method Parsimony (MIX) and character compatibility (CLIQUE) in PHYLIP (Felsenstein 1984) were used. The results of both cladistic analyses are very similar, and only one is presented (Fig. 10) for discussion. Seventy-four character states have changed in the cladogram based on parsimony. Each section is found to be monophyletic except section *Pittonium* which also contain the monotypic section *Megalonium*.

Sections *Petrothamnium* and *Chrysocome* were mixed in the UPGMA phenogram, but they are clearly apart in the cladogram. This suggests that many phenetic characters in these two sections might have resulted from parallel evolution. The strong tie between *Aeonium nobile* and *A. glutinosum* (also shown in the phenetic study) indicates that the two taxa were probably derived from the same immediate ancestor.

The results of the cladistic study in which most of the sections are well-differentiated also suggest that the divergence of the sections might have occurred early in the history of the genus. The cladogram also shows a high level of parallelisms and reversals within the genus. Section *Leuconium* has the largest number of taxa and also shows the highest number of parallelisms and reversals. Close examination of the geographical distribution of different species within the same section reveals that they generally occupy different islands or areas. Different taxa on different islands with the same wide-spread immediate ancestor might have evolved the same morphological features in parallel.

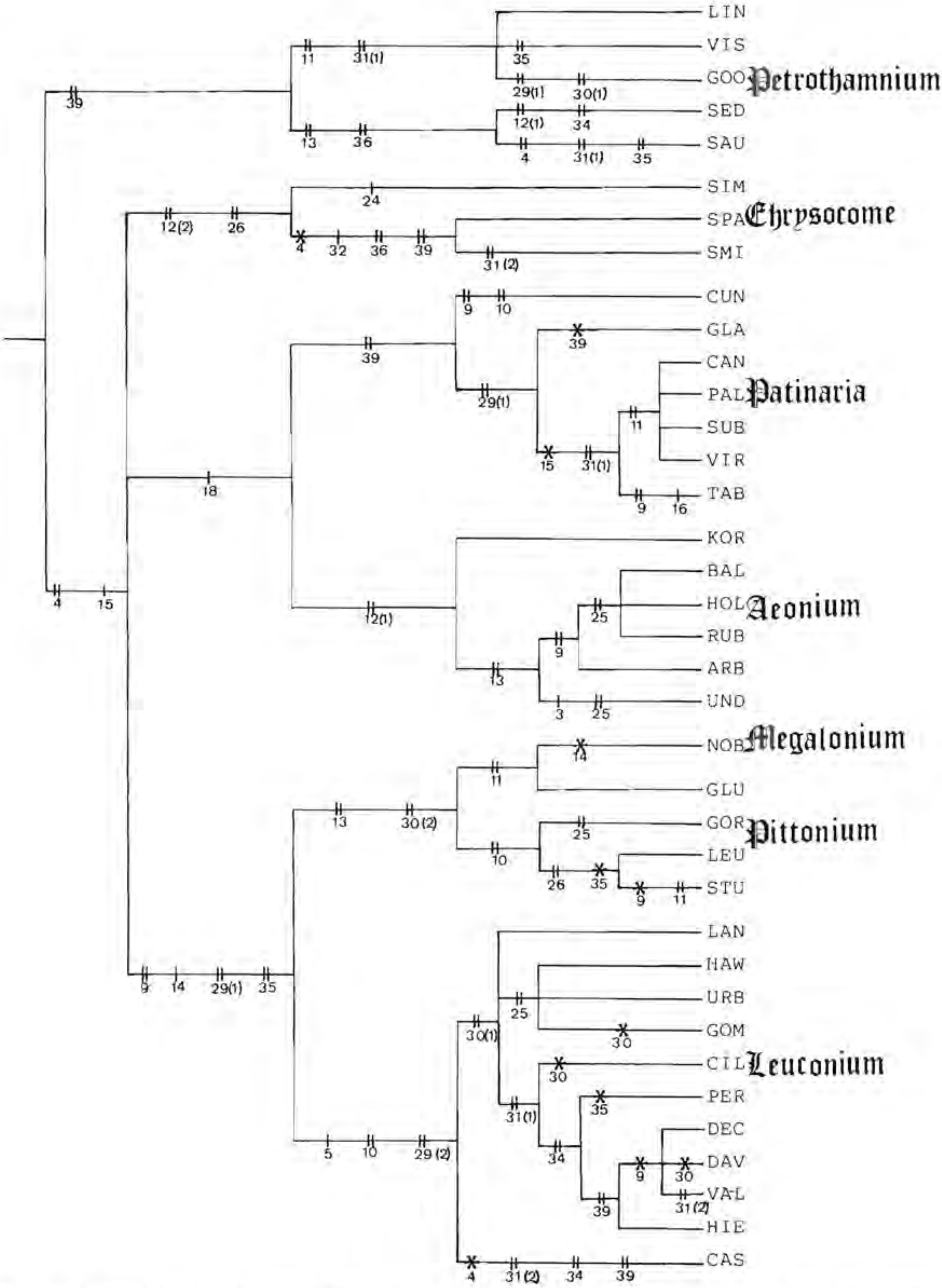


Fig. 10. Cladogram of taxa of *Aeonium* based on parsimony. Derived character states are indicated by numbers and single bars. Double bars indicate parallelisms. Asterisks indicate reversals.

Fig. 11. Geographical distribution of genera of the subfamily Sempervivoideae.

PHYTOGEOGRAPHY

The revised taxonomic treatment and the phylogenetic reconstruction presented here allow for the phytogeography of *Aeonium* to be examined in detail. This is especially pertinent because the genus is largely confined to the Canary islands, some of which (Gomera, Gran Canaria, Hierro, La Palma, and Tenerife) are volcanic islands and others of which (Fuerteventura and Lanzarote) are of continental origin. Further, the species of *Aeonium* have a disjunctional distribution (Fig. 11) with most species endemic to Macaronesia (Canary islands, Cape Verde islands, Madeira, and southern Morocco) but with two widespread taxa (*A. leucoblepharum* and *A. stuessyi*) in eastern Africa and Yemen. This also requires explanation.

Since *Aeonium* is mainly a Macaronesian genus, its origin may be identical, or at least very similar, to the origin of other elements of the Macaronesian flora. The origin of this flora has been reviewed by many authors (e.g., Engler 1879; Ciferri

1962; Bramwell 1976, 1985; Sunding 1979). Based on phytogeographical and paleobotanical evidence, all of the authors indicate that a great number of Macaronesian endemic elements, despite their current affinity to other regions, must be considered as relicts of an once wide-spread humid subtropical flora in Mediterranean regions that persisted until the late Tertiary (Pliocene and Miocene). Current distribution of Sempervivoideae (Fig. 11) suggests that the ancestor of the subfamily might be a member of that wide-spread flora.

Two theories about the disjunctional distribution of *Aeonium* suggest different places and times for the origin of the genus. Lems (1960) suggested that the genus arrived in the Macaronesian islands from the Moroccan coast at a time when the ancestral populations were widespread in northern Africa. The formation of Sahara desert during the Pleistocene brought about extinction of the central part of the range and separated Macaronesian populations from eastern Africa and Yemen's. As Crassulaceae may have originated in the Eocene (MacGinitie 1969), the time of the origin of *Aeonium* would be between the Eocene and Pleistocene. An alternative explanation is offered by Carlquist (1974). He suggested that the mainland African species were possibly the result of long-distance dispersal from the Macaronesian islands eastward to the mainland, and therefore are not relicts. This theory may also imply that the origin of *Aeonium* from its immediate ancestor occurred in Macaronesia rather than in northern Africa, although it does not wholly exclude the possibility that the immediate ancestor had immigrated from northern Africa to Macaronesian islands before extincted in the mainland Africa. An examination of likely pathways of dispersal and migration may help indicate which theory is more plausible. Seeds of crassulaceous plants are dust-like and suitable for wind-dispersal (van der Pijl 1982). Judging from the major wind directions in Macaronesian region (Fig. 12), the principal direction of dispersal would be westward and/or southward (Fernandopullé 1976). It is unlikely that the eastern Africa and Yemen populations of *Aeonium*, therefore, would have been derived by long-distance dispersal. On the basis of all evidence, *Aeonium* was probably of Tertiary origin somewhere in northern Africa.

The detailed phytogeographical relationships of sections and species within *Aeonium* are more difficult to demonstrate. The cladistic analyses indicate that each section is more or less equally divergent. Hence, the evolutionary sequence of differentiation of all sections and their phytogeography cannot be reliably estimated. In other words, there is no evidence, direct or indirect, to suggest whether Macaronian islands or northern Africa, where a wide range of topography was available in the past as in today, is the place where Canarian sections originated. However, some aspects of phytogeography of several sections can be speculated upon with information from ecology, geography, geology, and morphology. Generally, the taxa in the western islands of the Canary islands tend to have more derived chacter states than the taxa of the same section in the eastern islands, and could have evolved from the latter taxa.

The monotypic section *Megalonium (Aeonium nobile)* is distinguished by its massive leaves and inflorescences, and its phyletic relationship with other species was previously unknown (Praeger 1932; Lems & Holzapfel 1974). Both phenetic and cladistic analyses show a close tie between *Aeonium nobile* and *A. glutinosum*. The former is native to La Palma and the latter is native to Madeira archipelago. Madeira is geologically older than La Palma (Schmincke 1976; Abranche & Storetve 1984) and the wind blows southward from Madeira to La Palma, and therefore the likely direction of migration was from Madeira to La Palma (Fig. 12). Hence, it is probable that *Aeonium nobile* evolved

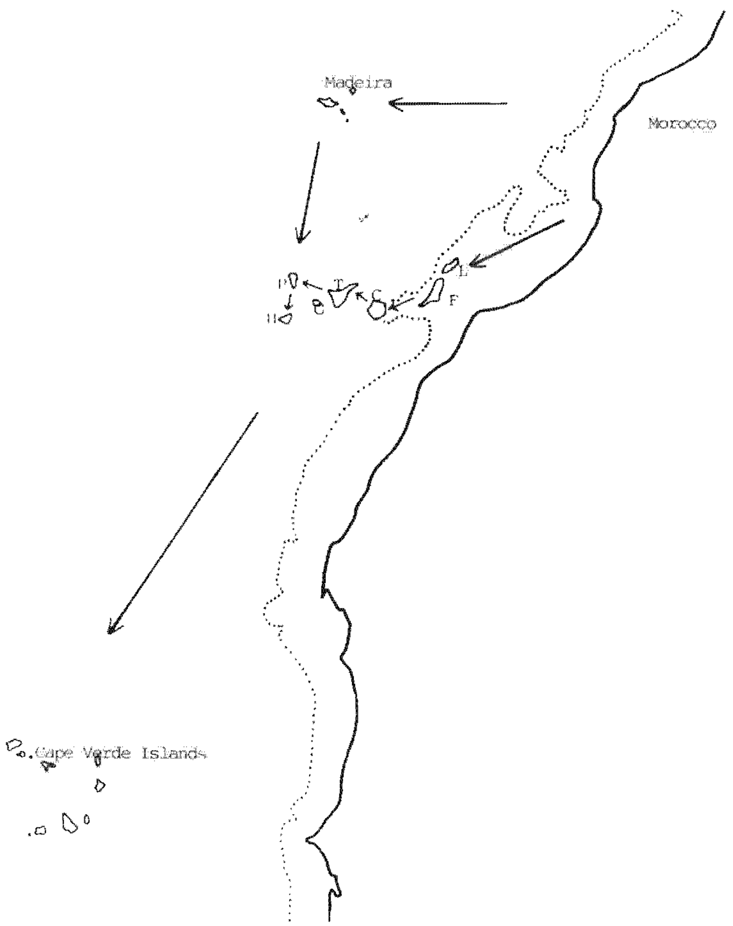


Fig. 12 Major wind directions near the Canary Islands. The continental crusts are indicated by the dotted line. C, Gran Canaria; F, Fuerteventura; G, Gomera; H, Hierro; L, Lanzarote; P, La Palma; T, Tenerife.

from *A. glutinosum*—like plants with a corresponding increase in succulence in response to drier environments of La Palma.

Information about phytogeography within each section sometimes may be obtained from paleogeography. For example, *Aeonium cuneatum* (section *Patinaria*) is found disjunctionally on the eastern and western ends of Tenerife (Figs. 13 & 19). These contain Miocene outcrops and the central part of Tenerife is covered by more recent Pliocene basalt and volcanic lava from the Quaternary (Schmincke 1976). Thus, current populations of *Aeonium cuneatum* are probably relics of a broader ancestral population once distributed throughout the island. The absence of this species in the central part of Tenerife today probably have resulted from drastically changed habitats or by competition from other better-adapted species in the region. As a relic of the population which may have existed as early as the Miocene, it is possible that *Aeonium cuneatum* resembles the immediate ancestor of the section.

The distribution of varieties of *A. canariense* (Fig. 19) in section *Patinaria* also probably can be used to evaluate some paleogeological hypotheses. The evolution of these varieties could have been a vicarious event as it has been suggested that all islands of the Canary archipelago were once connected (Hausen 1958), although most geological data do not support this view (Schmincke 1976). An alternative explanation for the distribution of these varieties might be dispersal from one island to the other followed by morphological differentiation. Within the distributional range of these varieties, Hierro is geographically closer to Gomera than to La Palma. If vicariance did take place, one would expect that the population on Hierro would be more similar to the population on Gomera than to that on La Palma. On the other hand, if dispersal played a major role in the evolution of these varieties, then the population on Hierro would be expected to be closer to the population on La Palma since the likely dispersal route was from La Palma to Hierro. The populations in La Palma and Hierro belong to variety *palmense*, whereas the population in Gomera belong to variety *subplanum*. The strong relationship between populations on La Palma and Hierro supports the latter hypothesis.

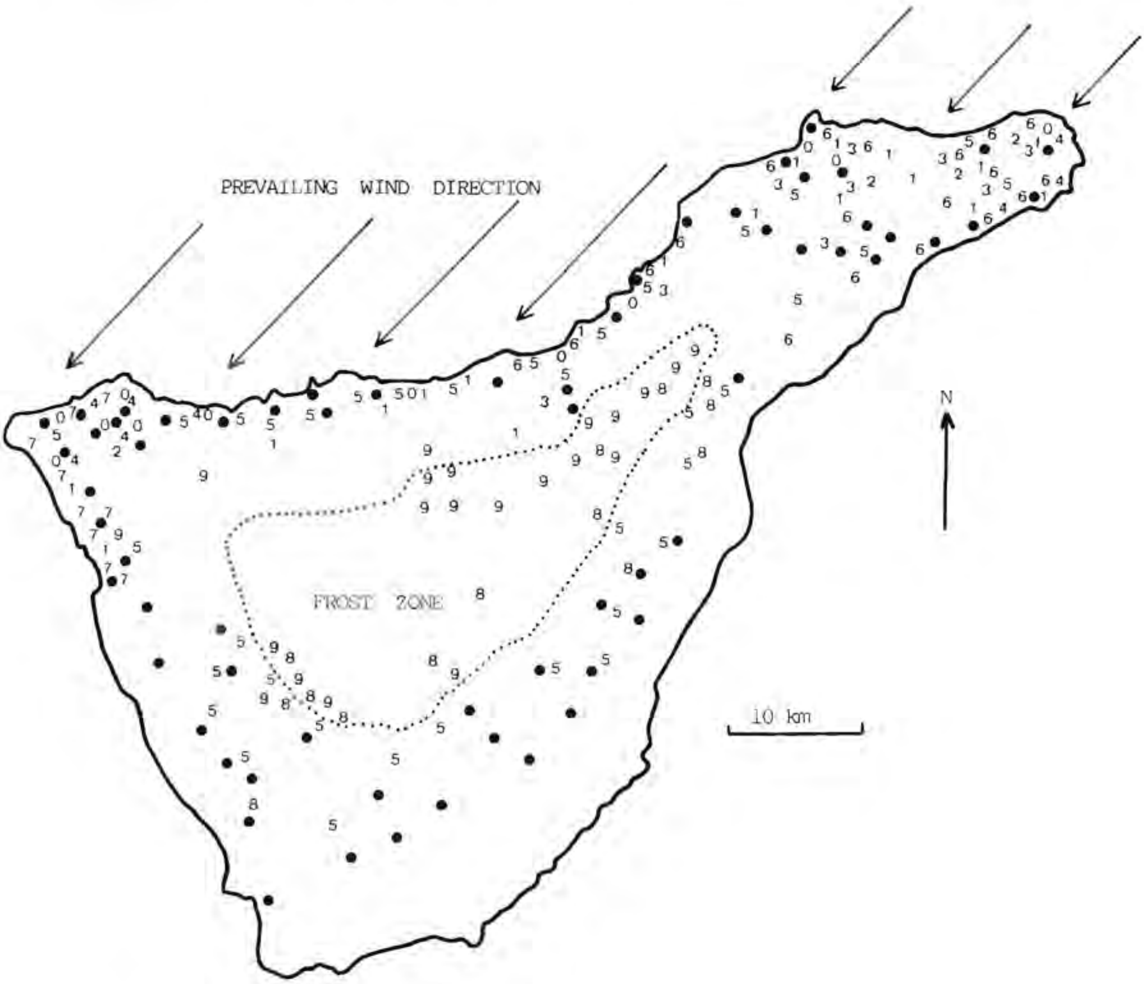


Fig. 13. Topography of Tenerife with indication of direction of trade winds (arrows) and areas of frost. Distributions of species of *Aeonium* on the island are also indicated: 1, *A. canariense* var *canariense*; 2, *A. cuneatum*; 3, *A. ciliatum*; 4, *A. haworthii*; 5, *A. arboreum* var. *holochrysum;* 6, *A. lindleyi* var. *lindleyi*; 7, *A. sedifolium*; 8, *A. smithii*; 9, *A. spathulatum*; 0, *A. tabuliforme*; dots, *A. urbicum*.

ADAPTIVE RADIATION

Adaptive radiation connotes the divergence of a monophyletic group of organisms into a variety of habitats (Carlquist 1974). Although all groups of organisms have undergone adaptive radiation to some extent, the term is best restricted to an insular group with exceptional differences. Insular groups thus can serve as models against which other groups can be compared. Differences in morphological and physiological features can be used to infer their adaptive nature by correlation with available habitats.

The diversity of growth forms in *Aeonium* and their evolutionary significance have been regarded as a spectacular example of adaptive radiation (Lems 1960). New data accumulated in the past two decades, however, suggests a re-examination of these ideas. The revised taxonomic treatment, including results from phenetic analyses, offers a refined view of limits of taxa and patterns of geographical distribution. The cladistic studies provide a hypothetical phylogeny in which evolutionary relationships within a particular lineage can be examined closely. In addition, the recent exhaustive study of Voggenreiter (1974) provides detailed ecological information for many of the taxa of the genus. Further, physiological data (Lösch & Kappen 1981, 1983; Tenhunen et al. 1982; Lösch 1984) can be compared with those from ecological differentiation. All these assembled data, therefore, provide an opportunity to examine adaptive radiation in *Aeonium* from a new perspective.

Apparent differences of morphological and physiological features among species of *Aeonium* can be used to imply different "ecological strategies". Increasing the degree of succulence would allow a plant to be more drought resistant. Increasing wax thickness would decrease water loss from the plant surfaces. Increasing hair density would decrease water loss by increasing reflection and transpiration resistance (Uphof 1962; Johnson 1975); it also would likely increase water absorption (Solereder 1908; Johnson 1975) when the surrounding air is humid. Different types of photosynthesis (known in different taxa of *Aeonium*; Tenhunen *et al.* 1982; Lösch 1984) can also be used as indicators of different arid-tolerant abilities. If each morphological or physiological feature mentioned above is arbitrarily scaled, it is possible to indicate the relative arid tolerance of taxa of *Aeonium*. The known different cold-and salt-resistant abilities (Lösch and Kappen 1981) of species of *Aeonium* can also be combined with the above data to indicate further the habitat tolerance of the taxa. The overall plants size of in *Aeonium* can affect their use of substrate. Small plants can grow on more steep rock with less soil. On the other hand, large plants can only grow in flatter areas with layered soil, because they have deeper roots and need stronger support. A similar situation prevails with stem length and the number of branches. Short stems with no or few lateral branches enable plants to grow on steeper rock crevices whereas plants with large stems and many branches require flatter areas with deeper soil. In view of these features, therefore, one can infer the hypothetical minimum degrees of slope and rock erosion suitable for each taxon of *Aeonium* to grow and survive. Combining the hypothetical responses to aridity, cold (or salt), and substrate, it is found that almost all taxa have different "ecological strategies" (Fig. 14).

For simplicity and because more complete data are available, only taxa of *Aeonium* on Tenerife are examined in detail here. Tenerife was selected as an example to illustrate the correlation between different habitats and "ecological strategies" because (1) it contains the largest number, eleven, of taxa of the genus; (2) ecological differences among taxa on Tenerife can be inferred more easily from the detailed data provided by Voggenreiter (1974); and (3) it has the most diverse climatic conditions among all the Canary islands because of its position and topography.

The habitats of the Canary islands are differentiated primarily by climatic zonation (Fernandopullé 1976) and by the age and degree of erosion of the substrate (Lems 1960), and this is also true for Tenerife. The island can be divided into the Anaga region (eastern end), Teno region (western end), and the central part (Fig. 13). The former two regions consist of many deep valleys and abrupt, vertical cliffs. The mountains of the central part arise sharply with the highest peak at 3707 m. Areas with layered soils are restricted in the south and north (around Puerto La Cruz). The north side of the island and the Anaga region are subject to humid north-east trade winds. The central portion of the island, because of high elevation, contains a frost zone (Fig. 13). Humidity and precipitation are generally higher on the northern side, although rainfall increases with elevation. This is an area of forest with high humidity. For a given area of Tenerife, therefore, it is possible to know more or less the dryness and coolness of the habitat. From the detailed phytosociological survey made by Voggenreiter (1974) and my personal observations, it is found that the distribution of different taxa in their habitats basically correlates well with their characteristic features (Fig. 14). Comments on these correlations for each taxon will be discussed below.

Aeonium smithii and *A. spathulatum* (section *Chrysocome*) are the only species growing in upper mountain and subalpine frost regions (Figs. 13 & 15). The species are allopatric (Voggenreiter 1974), although both are usually associated with pine forests. *Aeonium spathulatum* is a cold-resistant species able to tolerate temperature of −10°C (Lösch and Kappen 1981), whereas *A. smithii* is more sensitive to cold (Praeger 1932). In nature, *Aeonium smithii* is mostly found growing half-smothered in pine needles on rock ledges. These probably function as insulation, so that the temperature around *A. smithii* is not as cold as the surrounding area. *Aeonium spathulatum* is a C_3 plant whereas *A. smithii* has its photosynthetic ability intermediate between C_3 and strong CAM (Tenhunen et al. 1982). This difference in photosynthesis, in addition to the very succlent stems of *A. smithii*, indicate *A. smithii* is better suited than *A. spathulatum* for a drier climatic zone which is dominant on the south side of the island. This is seen to be the case in which *A. smithii* is primarily on the south side and *A. spathulatum* mainly on the north side (Fig. 13). Leaves of both species are very thin and highly sensitive to drying, and this may be why both species are absent from the drier, lower elevations.

Section *Leuconium* has strong CAM photosynthetic pathway (Tenhunen et al. 1982) and glaucous leaves, and therefore species of this section are well adapted to most arid areas at lower elevations. Three taxa (*A. ciliatum, A. haworthii*, and *A. urbicum*) are found in Tenerife (Figs. 13, 15 & 27). All three taxa need deep soill for optimal growth. However, *Aeonium urbicum* is a monocaulous species, whereas the other two taxa are branched subshrubs. Thus, *Aeonium urbicum* is able to grow in smaller soil-packets in rock area. Among the latter two species, *Aeonium haworthii* has greater tolerance of arid conditions because of its markedly glaucous leaves. *Aeonium urbicum* is wide-spread on the open, very dry areas of the island, whereas the other two taxa are limited to both ends of the island in less arid environments but still associated with other species in the xerophytic scrub. In the Teno region *Aeonium ciliatum* is limited to the north side near the coastline whereas in the Anaga region *A. haworthii* is restricted to the extreme southern part. *Aeonium ciliatum* is found in relatively humid areas in the Anaga and Teno regions, whereas the more arid tolerant *A. haworthii* is found in drier areas. The disjunctional distributions of both species are probably due to historical events.

Aeonium arboreum var. *holochrysum* (section *Aeonium*) is the tallest branched species of the genus. It cannot tolerate much dryness. Hence, it is primarily found in the damp valleys and abundantly associated with other shrubs. During the dry season, plants of this variety shed their large leaves, stop growing and retain a very small disc-shaped leaf rosette.

Taxa of section *Patinaria* are subacaulescent plants with very thick leaves. However, they are absent from the south side of Tenerife probably due to the extreme aridity. Three taxa of section *Patinaria (A. canariense* var. *canariense, A. cuneatum*, and *A. tabuliforme*) are found on Tenerife (Fig. 13). *Aeonium cuneatum* is primarily found in the laurel forest, whereas the other two taxa are primarily growing from laurel forest down to the coast. In the laurel forest where open spots are scattered, the stoloniferous form of *Aeonium cuneatum* would be more able to reach open spots than the other two taxa. *Aeonium cuneatum* has not been found outside of the laurel forest. Away from the laurel forest, the habitats become drier. Leaves of *Aeonium cuneatum* are glaucous and those of the other two taxa are covered with long hairs. Both waxes and long hairs prevent the loss of water. However, the wax in *Aeonium cuneatum* is easily washed away by rain, whereas the hairs of the other two taxa can probably absorb water from the air carried by the moist northeast trade winds. In addition, *A. cuneatum* has C_3 photosynthesis, whereas the other two taxa are intermediate between C_3 and strong CAM (Tenhunen *et al.* 1982). Both conditions indicate that *A. cuneatum* may not be well adapted to drier environments at low elevations, which help explain its absence outside of the laurel forest. *Aeonium tabuliforme* has a very flattish rosette and shallow root system, and is found primarily in rock crevices. Because of the imbricate leaves, long hairs on leaf margins and young leaves of *A. tabuliforme* cover all the exposed parts of the plant to prevent water loss. In flatter areas with more soil, *A. canariense* var. *canariense* occurs with a clumped habit, very thick leaves, and a deep and wide-spreading root system. This set of features would be better to accumulate nutrients and to tolerate aridity, and the distribution of this taxon in the south side of the Anaga region reflects these conditions.

Aeonium lindleyi (section *Petrothamnium*) is limited to the northeastern side of Tenerife (Fig. 13) where cliffs and rugged topography are common. Its small size enables this taxon to grow among small rocks and crevices where other species are not able to support themselves. A similar situation is found in *A. sedifolium* in the same section, which is restricted to the western end of the island. Both species can tolerate high salinity and are found near the sea (Fig. 15).

From the evidence just presented, clearly species of *Aeonium* have adapted to many different environments on Tenerife. From field observations, this is also the case with the rest of the species in the genus. Different taxa have different morphological and physiological features which correlate with different ecological habitats in the archipelago.

To address the adaptive radiation in the genus *Aeonium* further, it is necessary to examine the relationships of the different taxa as shown on the cladogram (Fig. 10) and indicate the changes that have occurred in the evolution of the genus (Fig. 16). Growth forms are arranged in accordance with the hypothetical phylogeny to indicate a number of possible sequences. The hypothetical degrees of slopes and rock erosion suitable for each growth form are also indicated. The growth forms A to C are probably most similar to those of the immediate ancestors. Usually, growth form evolves towards larger size. Also, there is a general trend toward the monocaulous condition (F, K, M). In addition, the taxa at the end of each evolutionary line have more arid tolerant feature.

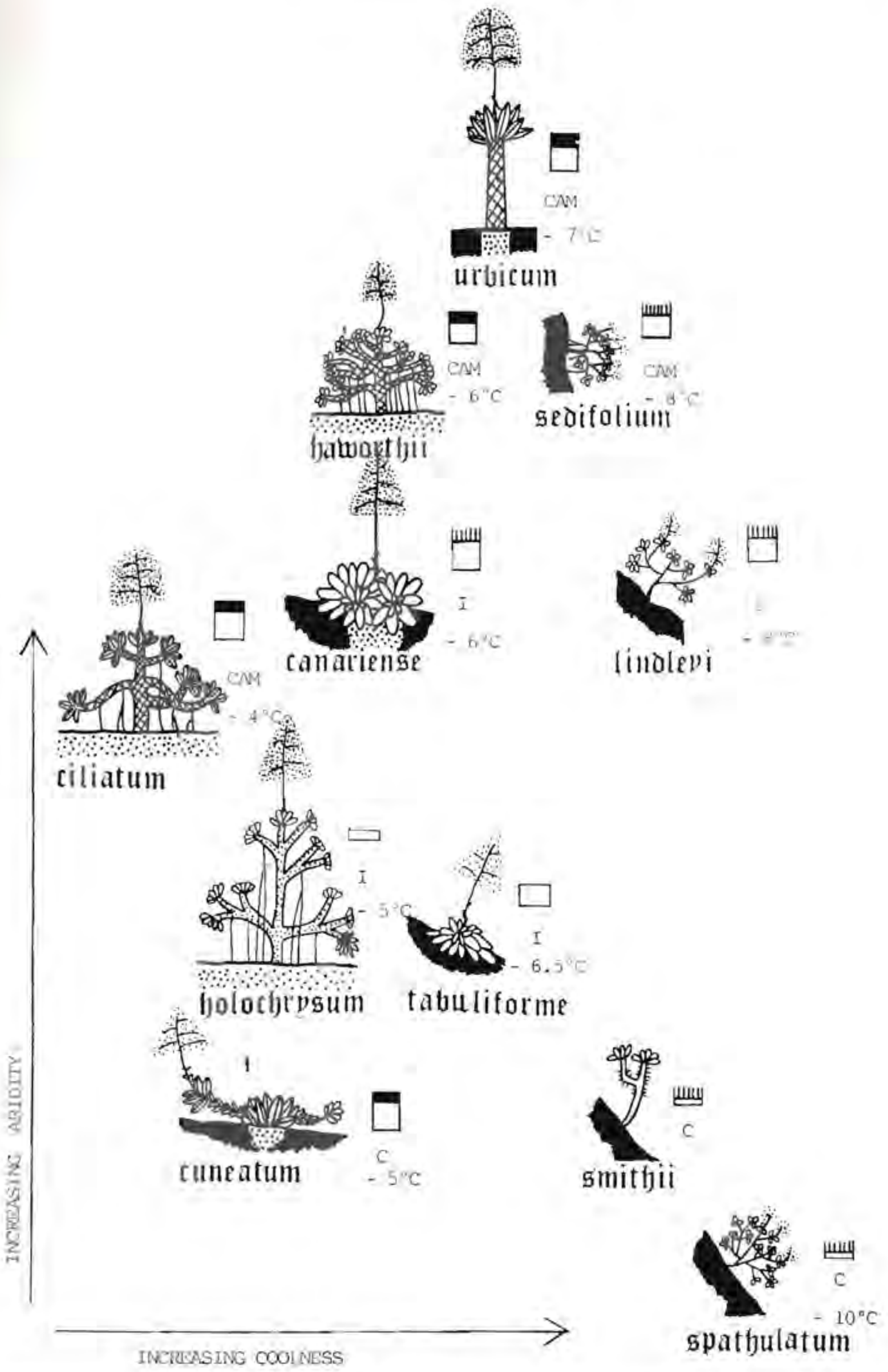


Fig. 14. Different "ecological strategies" of taxa of Aeonium on Tenerife. Taxa are positioned to indicate their relative tolerance to aridity and coolness. Photosynthetic pathways and cold-resistance of each taxon after Tenhunen *et al.* (1982) and Losch & Kappen (1981). CAM, strong CAM photosynthesis; I, intermediate between C_3 and strong CAM; C, C_3 photosynthesis. Degrees of succulence of leaves and stems are indicated by the height of rectangles. Distributions of waxes (dark area) and pubescence (lines) are shown on the upper side of rectangles. The slope of substrate suitable for growing is also indicated. Unmodified rock is indicated by solid areas and soil packets by dotted areas.

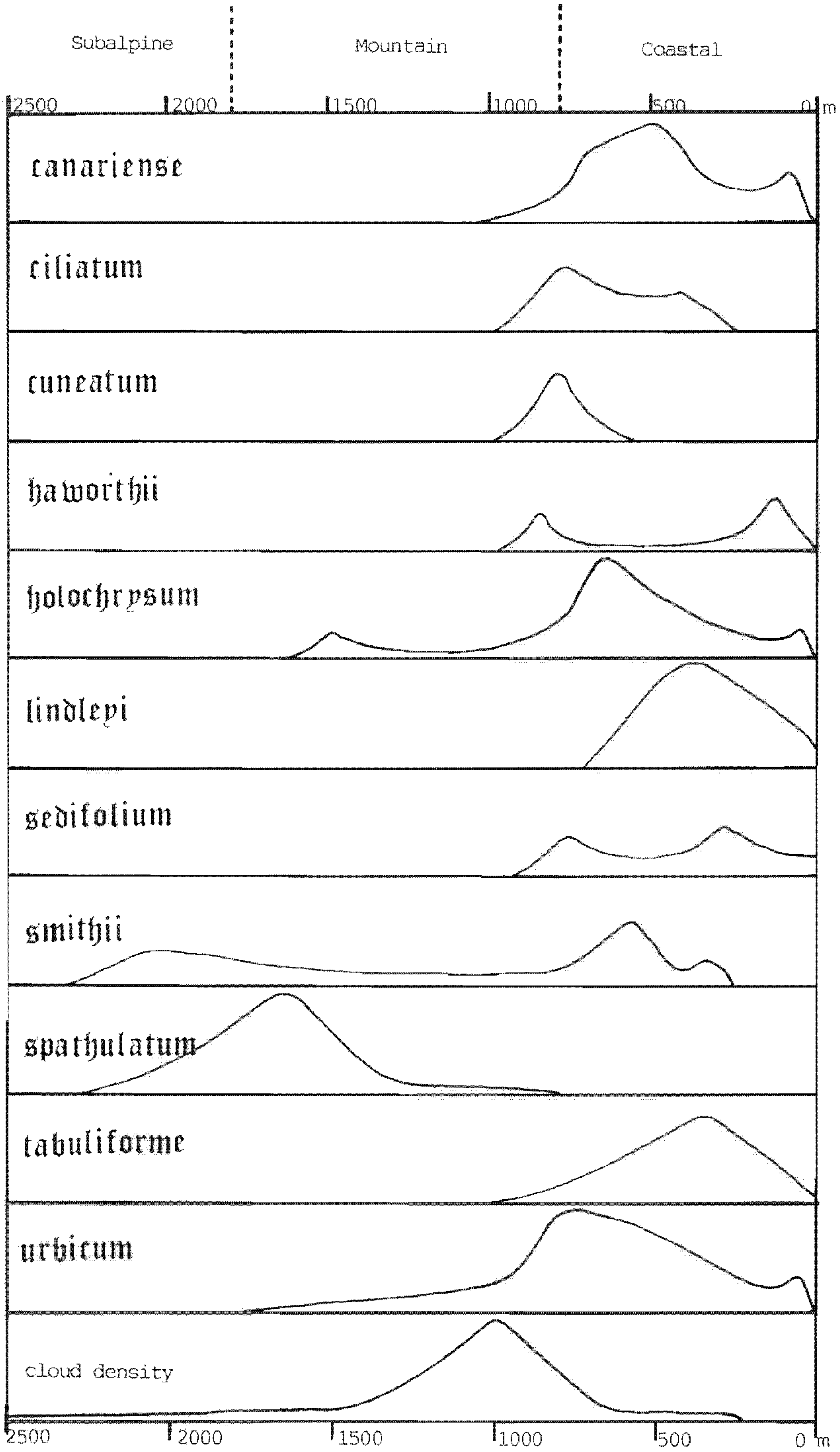


Fig. 15. Altitudinal distribution of species *Aeonium* on Tenerife, Canary Islands (modified from Voggenreiter 1974).

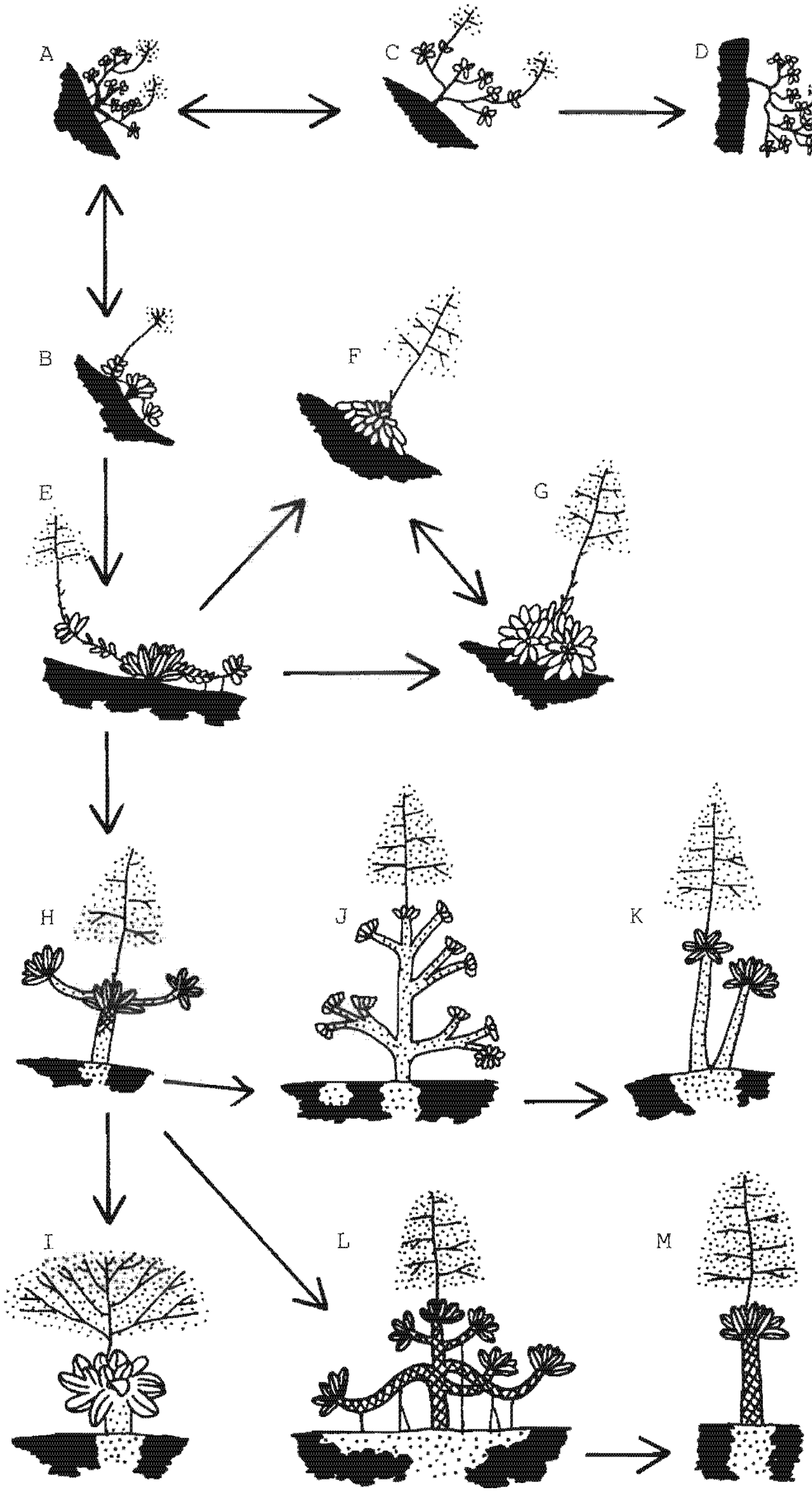


Fig. 16. The growth forms of *Aeonium* arranged in possible evolutionary sequences. A, *A. smithii* and *A. spathulatum*; B, *A. simsii*; C; *A. goochiae* and *A. lindleyi*; D, *A. saundersii* and *A. sedifolium*; E, *A. cuneatum*; F, *A. glandulosum* and *A. tabuliforme*; G, *A. canariense*; H, sect. *Pittonium*; I, *A. nobile*; J, *A. arboreum*, *A. balsamiferum*, and *A. korneliuslemsii*; K, *A. undulatum*; L, sect. *Leuconium* except taxa of M; M, *A. hierrense* and *A. urbicum*.

TAXONOMY

Aeonium Webb & Berth., Hist. Nat. Iles Canar. 3(2.1): 184. 1840. *Sempervivum* L. subgenus *Aeonium* (Webb & Berth.) J. D. Hook in Benth. & J. D. Hook., Gen. pl. 1: 660. 1865. *Sempervivum* L. sect. *Aeonium* (Webb & Berth.) Webb *ex* Christ, Bot. Jahrb. Syst. 9:117. 1888. LECTOTYPE (here designated): *Aeonium arboreum* (L.) Webb & Berth.

Succulent, evergreen, monocarpic to polycarpic herbs to subshrubs, terrestrial or occasionally epiphytic. Roots fibrous, with root-tips red, and often with aerial roots as prop roots, Stems erect to scandent, usually woody, at least at base, unbranched or branched; branches terete, acrotonic (basitonic in *Aeonium undulatum*), with subacaulescent plants stoloniferous or clumping, with leaves only toward apex, and usually with distinct, oblique leaf scars; axillary buds naked; bark fissured or shaggy with persistent, withered leaves; cortex fleshy, often green; xylem a continuous cylinder; pith continuous. Leaves in dense concave or flattish rosettes, exstipulate, alternate, simple, sessile to subsessile, fleshy and succulent, 1-12 mm thick, convex below, flattened or convex above, although sometimes with central, adaxial grooves, usually obovate spathulate, glabrous, glaucous, sparsely puberulent, or glandular-pubescent, with margin entire, or occasionally weakly denticulate, mostly ciliate; leaves of vegetative and flowerig shoots often dissimilar. Inflorescence a terminal, bracteate, pleiochasium. Flowers perfect, actinomorphic, hypogynous, protandrous, glabrous, sparsely puberulent, or glandular-pubescent (vestiture on different floral parts varies); calyx valvate, green, sometimes variegated with pink or red, fleshy, much shorter than corolla, campanulate, with segments 6-16 parted, triangular to lanceolate; petals the same number as calyx-segments, valvate or convolute, free or connate near the base, whitish to yellow, sometimes variegated with pink or red, oblong to lanceolate, sometimes contracted towards the bases, flattened or sometimes keeled, usually longer than the stamens; stamens twice as many as petals, adnate to petal base, the inner, interpetalous ones longer than the outer, antipetalous ones, with filaments filiform, or sometimes broadened towards the base, white to yellow, with anthers basifixed, tetrasporangiate, dithecial, dehiscing longitudinally, whitish, light to golden yellow, or brown, and thecae parallel; pollen grains binuclear, isopolar, tricolporate, exine striato-reticulate to psilate; nectariferous glands the same number as carpels, rarely absent, adnate to ovary bases, nectariferous, scale-like, white to yellow, with apical and adaxial stomata, or sometimes with adaxial stomata only; carpels the same number as calyx-segments, or occasionally fewer, free or slightly connate basally, with styles erect or divergent, with stigma apical, small, poorly differentiated with ovaries 1-loculate, superior, with placenta submarginal, with ovules numerous, anatropous, crassinucellar, bitegmic. Fruit a follicle, dehiscing adaxially; seeds numerous, small, elongate-ovate or oblique-pyriform, longitudinally striate or ridged, yellowish-brown or brown; embryos straight, ovate. Chromosome numbers, $n = 18, 36$.

In the description of individual species, the term "paralectotype" is used to cover the group of types which remains when a lectotype and isolectotype have been selected from the syntypes (Hansen & Seberg 1984). The citation of microfiches follows Hepper (1968).

Several key characteristics of some taxa (e.g., stem surface reticulation in *A. haworthii*), are not easily observed. These taxa, therefore, appear more than once in the following key. Geographical distributions are also listed, because in most cases the locality can be very helpful in distinguishing close relatives.

Key to species and varieties of *Aeonium*

1. Stem surfaces reticulate; leaf margin reddish; corolla whitish, with or without green and/or pink streaks, rarely orange-pink.

2. Stem surface reticulations rising above the general stem surface.

3. Corolla entirely white or greenish white; stems laxly branching with few (usually less than 10) branches.

4. Calyx and anthers pubescent; stem surface reticulations with distinct tubercles; Tenerife.

25. *A. ciliatum.*

4. Calyx and anthers glabrous; stems surface reticulations with indistinct horizontal ribs and cracks; Gomera.

24. *A. gomerense.*

3. Corolla pinkish or orange-pinkish; stems densely branching with many (usually more than 30) branches.

5. Stem surface reticulations distant from leaf cicatrices and/or leaf bases, with distinct horizontal ribs and cracks; leaves shinny; Gomera.

27. *A. decorum.*

5. Stem surface reticulation adjacent to leaf cicatrices and/or leaf bases (see Fig. 4), with very indistinct tubercles; leaves stongly glaucous or deep green; Tenerife.

22. *A. haworthii.*

2.Stem surface reticulations flush with the general stem surface.

6.Leaves distinctly puberulent on both surfaces.

7. Leaves obovate, more than 4 cm wide, usually brownish, with submarginal unicellular trichomes usually yellow; Hierro.

29. *A. valverdense.*

7. Leaves spathulate, 4 cm wide or less, usually purplish or deep green, with marginal unicellular trichomes whitish; La Palma.

28. *A. davidbramwellii.*

6.Leaves glabrate.

8. Corolla entirely white or greenish white; Gomera.

9. Calyx and corolla pubescent; stems densely branching with many (usually more than 30) branches, puberulent with multicellular trichomes whitish.

31. *A. castello-paivae.*

9. Calyx and corolla glabrous; stems laxly branching with few (usually less than 10) branches, glabrous.

24. *A. gomerense.*

8. Corolla pinkish or orange-pinkish.

10. Leaves weakly denticulate, with wrinkly unicellular trichomes; stems shinny-slivery; Lanzarote.

21. *A. lancerottense.*

10. Leaves entire, with (or rarely without) straight or curved unicellular trichomes; stems dull-grayish.

11. Corolla orange-pinkish; stems densely branching with many (usually more than 30) branches; Tenerife.

22. *A. haworthii.*

11. Corolla pinkish; stems unbranched or with less than 10 branches.

12. Stems branched; leaves purplish, pink or green with purple or brown tinge; Gran Canaria.
26. *A. percarneum.*

12. Stems monocaulous; leaves green or rarely with a few brownish lines.

13. Calyx and corolla pubescent; leaves 5-9 cm wide, often with apex arcuate, Hierro, La Palma.
30. *A. hierrense.*

13. Calyx and corolla glabrous; leaves 3-6 cm wide, often with apex applanate; Gomera, Tenerife.
23. *A. urbicum.*

1. Stem surfaces smooth and without reticulation; leaf margin brownish, green, or yellowish-green; corolla yellow, pale yellow, reddish (pinkish in *A. goochiae*).

14. Plants subacaulescent; stems usually hidden by the marcescent leaves.

15. Leaves glabrate on both surfaces.

16. Leaf rosette planar; leaves closely imbricate; Tenerife.
11. *A. tabuliforme.*

16. Leaf rosette cup-shaped; leaves loosely arranged.

17. Inflorescence lateral; leaves with many distinct dark-green to reddish tannic stripes on both sides; Gran Canaria.
5. *A. simsii.*

17. Inflorescence terminal; leaves without any dark green or reddish stripes.

18. Leaves strongly glaucous, smooth, with dense marginal unicellular trichomes; corolla entirely yellow; Tenerife.
8. *A. cuneatum.*

18. Leaves not glaucous, usually sticky, with or without scattered unicellular trichomes; corolla pale yellow with reddish variegation.

19. Stems branched; leaves obovate-spathulate; corolla with reddish marginal lines only; Madeira.
17. *A. glutinosum.*

19. Stems monocaulous; leaves obovate to semicircular; corolla with numerous reddish stripes; La Palma.
16. *A. nobile.*

15. Leaves distinctly pubescent on both surfaces.

20. Leaves puberulous; Madeira.
9. *A. glandulosum.*

20. Leaves velvety.

21. Corolla whitish; nectariferous glands depressed obovate; leaf rosette cup-shaped; leaves not sticky, with 5-15 hairs per 0.1 mm^2, with hairs comnonly 0.7-1 mm long; Tenerife.
10a. *A. canariense* var. *canariense.*

21. Corolla pale to light greenish-yellow.

22. Nectariferous glands usually mushroom-shaped; leaf rosette cup-shaped; leaves sticky, with 30-60 hairs per 0.1 mm^2, with hairs mostly 0.3-0.6 mm long; Hierro, La Palma.
10b. *A. canariense var. palmense.*

22. Nectariferous glands widely obovate; leaves smooth and not sticky.

23. Leaf rosettes planar; leaves with 5-15 hairs per 0.1 mm^2, with hairs commonly 0.3-1 mm long; Gomera.
10c. *A. canariense* var. *subplanum.*

23. Leaf rosettes cup-shaped; leaves with 10-20 hairs per mm^2, with hairs mostly 0.6-0.9 mm long; Gran Canaria.
10d. *A. canariense* var. *virgineum.*

- 14. Plants with distinct, visible stems below the leaf rosettes.
  - 24. Leaf rosette center flattened, with young leaves tightly appressed to the older ones.
    - 25. Calyx pubescent.
      - 26. Leaves obovate-spathulate, puberulent; Morocco. 12. *A. korneliuslemsii*.
      - 26. Leaves more or less lanceolate, glabrous; Gran Canaria.
    - 25. Calyx glabrous. 14a. *A. arboreum* var. *arboreum*.
      - 27. Leaves grayish; plants with strong balsamiferous odor; Fuerteventura, Lanzarote. 13. *A. balsamiferum*.
      - 27. Leaves green, with or without brownish stripes, plants without any odor or with a very weak balsamiferous odor.
        - 28. Corolla yellow to pale yellow with reddish variegation; inflorescence usually hemispherical; Gomera. 14c. *A. arboreom* var. *rubrolineatum*.
        - 28. Corolla entirely yellow; inflorescence usually ovoid-conical.
          - 29. Stems clumped with branches basitonic; Gran Canaria. 15. *A. undulatum*.
          - 29. Stems with spreading, acrotonic branches; Gomera, Hierro, La Palma, Tenerife. 14b. *A. arboreum* var. *holochrysum*.
  - 24. Leaf rosette center ascending, not flattened, with young leaves arising suberectly, at an angle to the older ones.
    - 30. Leaves with many distinct abaxial longitudinal, dark green, reddish, or purplish tannic stripes scattered on the abaxial surface.
      - 31. Stems thick and succulent, hirsute below the leaf rosettes; leaves more than 3 cm long, undulate; Tenerife. 7. *A. smithii*.
      - 31. Stems twiggy, minutely puberulent below the leaf rosettes; leaves less than 3 cm long, more or less planar; Gran Canaria, Gomera, Hierro, La Palma, Tenerife. 6. *A. spathulatum*.
    - 30. Leaves without distinct longitudinal tannic stripes scattered on the abaxial surface.
      - 32. Leaf margin with distinct unicellular trichomes.
        - 33. Stems unbranched; leaves obovate to semicircular; corolla with numerous dark reddish stripes; La Palma. 16. *A. nobile*.
        - 33. Stems branched; leaves obovate-spathulate to spathulate; corolla yellow and often with few reddish lines.
          - 34. Leaves strongly glaucous; Cape Verde Islands. 18. *A. gorgoneum*.
          - 34. Leaves green, occasionally slightly glaucous.
            - 35. Leaves sticky with mucilage at the center of the leaf rosette; inflorescence lax; stems dark brown to chocolate; Madeira. 17. *A. glutinosum*.
            - 35. Leaves without mucilage at the center of the leaf rosette; inflorescence dense, stems gray to grayish brown.
              - 36. Leaves puberulent.
                - 37. Leaves ovate-spathulate, c. 2 mm thick; Morocco. 12. *A. korneliuslemsii*.
                - 37. Leaves spathulate, more than 3 mm thick; eastern Africa.

20. *A. stuessyi.*

36. Leaves glabrate.
    38. Leaves 1-3 mm thick; plants with strong balsamiferous odor; Fuerteventura, Lanzarote.
        13. *A. balsamiferum.*
    38. Leaves more than 3 mm thick; plants without any odor; eastern Africa, Yemen.
        19. *A. leucoblepharum.*

32. Leaf margin with multicellular trichomes or entire.
    39. Leaves with hairs visible to the naked eyes.
        40. Leaves elliptic to circular; corolla pinkish; La Palma.
            2. *A. goochiae.*
        40. Leaves obovate to oblanceolate-spathulate; corolla yellow.
            41. Leaves more than 4 mm thick, entirely green; nectariferous glands present; Tenerife.
                1a. *A. lindleyi* var. *lindleyi.*
            41. Leaves less than 2 mm thick, with reddish spots on the abaxial surface; nectariferous glands absent; Gomera.
                4. *A. saundersii.*
    39. Leaves with hairs so small that they appear glabrous to the naked eye.
        42. Leaves 6 cm long or more.
            43. Stems branched; leaves obovate-spathulate; corolla with reddish marginal lines only; Madeira.
                17. *A. glutinosum.*
            43. Stems monocaulous; leaves obovate to semicircular; corolla with numerous reddish stripes; La Palma.
                16. *A. nobile.*
        42. Leaves less than 6 cm long.
            44. Leaves green with brownish to pale reddish color variegation; nectariferous glands absent; La Palma, Tenerife.
                3. *A. sedifolium.*
            44. Leaves entirely green without any color variegation; nectariferous glands present; Gomera.
                1b. *A. lindleyi* var. *viscatum.*

I. *Aeonium* sect. *Petrothamnium* (Webb *ex* Christ) H.-Y. Liu, *comb. nov.* *Greenovia* Webb & Berth. sect. *Petrothamnium* Webb *ex* Christ, Bot. Jahrb. Syst. 9:115. 1888. TYPE: *Aeonium sedifolium* (Webb *ex* Bolle) Pit. & Proust.

Aeonium sect. *Goochia* (Christ) Praeger, Acc. Sempervivum 191. 1932. *Sempervivum* L. sect. *Goochia* Christ, Bot. Jahrb. Syst. 9:117. 1888. TYPE: *Aeonium lindleyi* Webb & Berth.

Aeonium sect. *Anodontonium* A. Berger in Engl., Nat. Pflanzenfam. ed. 2, 18a:426. 1930. LECTOTYPE (here designated): *Aeonium lindleyi* Webb & Berth.

Small twiggy subshrubs, usually 15-30 cm tall. Stems fructicose with acrotonic, ascending branches, with lateral branches overtopping the parental branches; bark smooth or slightly fissured. Leaves 1-5 cm long, glandular-pubescent, without conical or bead-shaped cartilaginous trichomes; young leaves arising suberectly, not tightly against the older ones. Inflorescence a helicoid cyme or cymose panicle. Flowers with sepals glandular-pubescent; petals yellow (pinkish in *A. goochiae*); stamens yellow.

The section derives its name from the rock-growing shrubby habit of its members, although this feature is also found in other species of the genus.

1. *Aeonium lindleyi* Webb & Berth., Hist. Nat. Iles Canaries 3(2.1):189. 1840. *Sempervivum lindleyi* (Webb & Berth.) Webb *ex* Christ, Bot. Jahrb. Syst. 9:117. 1888. *Sempervivum tortuosum* Aiton var. *lindleyi* (Webb & Berth.) Kuntz, Revis. gen. pl. 1:232. 1891. TYPE: Spain, Canary Islands, Tenerife, collector and date unknown (holotype: FI!; photograph:OS!)

Perennial terrestrial subshrubs, with balsam odor. Stems up to 50 cm tall, 3-15 mm diam.; young branches puberulent, green to brown, viscid; bark grayish to whitish, slightly fissured. Leaf rosettes 4-9 cm diam.; phyllotaxy 5/13. Leaves obovate, obovate-oblanceolate to obovate-spathulate, 2-4.5 cm long, 0.6-1.6 cm wide, depressed obovate in cross-section, 3-7 mm thick, yellow-green to dark green, viscid, pubescent to puberulent, at base attenuate, at apex obtuse to acute. Inflorescence cymose panicle, 2-7 cm long, 3-9 cm diam., 15-85-flowered; peduncles 1-9 cm long; bracts similar to foliage leaves; pedicels 1-10 mm long, puberulent. Sepals 7-9, 3-3.5 mm long, 1-2 mm wide, at apex acute to acuminate; petals narowly elliptic to lanceolate, 5-7 mm long, 1.5-2 mm wide, yellow, puberulent on abaxial surface, at apex acuminate; stamens with filaments glabrous, with anthers yellow; nectariferous glands yellowish, at apex obtuse to crenulate; carpels with ovaries 2-3 mm long, c. 1 mm diam., puberulent, with styles 2-3 mm long. Chromosome number, $n = 18$.

The leaf shape and viscidity of *A. lindleyi* resemble that of *A. goochiae* and can be distinguished from that species by the former's fleshy leves and bright yellow flowers. Also, under normal conditions the leaves of *A. lindleyi* are thicker and narrower than in *A. goochiae* (usually more than 3 mm thick and narrower than 1.2 cm, whereas in *A. goochiae* they are about 1 mm thick and wider than 1.5 cm).

1a. *Aeonium lindleyi* Webb & Berth. var. *lindleyi*

Stems up to 50 cm tall, occasionally with marcescent leaves; leaf scars narrowly transversely elliptic, c. 1.5 mm wide and 0.2 mm tall. Leaves depressed-obovate in cross-section, 5-7 mm thick, with dense, fine multicellular trichomes 0.1-0.2 mm long. Sepals 8-9, ovate, 3-3.5 mm long, 1.4-2 mm wide; petals narrowly elliptic to lanceolate, 5-7 mm long, 1.5-2 mm wide; stamens with interpetalous ones 7-8 mm long, with antipetalous ones 6.5-7.5 mm long; nectariferous glands widely obovate, c. 1 mm long and 1 mm wide; carpels with ovaries 2.5-3 mm long, with styles 2-3 mm long.

Phenology. Flowering from June to September.

Distribution. (Fig. 17). Common on hot rocks or sunny cliffs; 0-1000 m; in NE sector of Tenerife, Canary Islands, most commonly around 200-500 m. Other distributional map of this variety has been provided by Voggenreiter (1974). Reports about its presence in La Palma (Burchard 1929) need to be confirmed (no specimen examined by the author came from La Palma).

Representative specimens. Spain. Canary Islands. Tenerife. Tacoronte, 7 May 1933, *Asplund s.n.* (S); Laguna, Barranco Santo, 14 Jul 1855, *Bourgeau s.n.* (C, E, G, JE); La Paz, *Burchard 130* (LY, O); W of Lgueste, 12 Aug 1976, *Elven s.n.* (O); 2 km N of San Andres, *Evans 334* (OS); Punta Hidalgo, *Evans 349* (OS); barranco above Punta Hidalgo, *Hansen 1092* (C); Taganana, Roque Animas, *Lems 2236* (MICH); Punta Hidalgo, Barranco Rio, *Lems 2813* (MICH), *Lems 5671* (MICH); between Bajamar and Punta Hidalgo, *Liu 2511* (OS); Taganana, *Liu 3154* (OS), 17 Jul

1858, *Lowe s.n.* (BM, GH, K, LE, MO); Santa Cruz, 10 Mar 1855, *Perraudiere s.n.* (G, GH, K); Orotava, Mar 1925, *Praeger s.n.* (K); Puerto Cruz, *Sventenius 222* (BH, S).

Named after John Lindley (1799-1865), British botanist, professor of botany at University College, London (1829-1860).

Aeonium lindleyi var. *lindleyi* can be distinguished from var. *viscatum* by its extremely fleshy (usually more than 5 mm thick) and distinctly pubescent leaves. Leaves of *A. lindleyi* var. *viscatum* are less than 4 mm thick and have extremely short hairs (less than 0.04 mm long).

A fascinated plant was reported from Taganana (Praeger 1932).

This variety hybridizes with *A. tabuliforme* (Burchard 1929, Praeger 1929). Bramwell and Rowley's (Jacobsen & Rowley 1973) name *A.* x *anagensis* for this hybrid is not validly published since no nomenclatural type was indicated (ICBN articles H.10.1. and 37).

1b. Aeonium lindleyi Webb & Berth. var. *viscatum* (Bolle) H.-Y. Liu, *comb. nov. Aeonium viscatum* Bolle, Bonplandia 7:241. 1859. *Sempervivum viscatum* (Bolle) Christ, Bot. Jahrb. Syst. 9:117. 1888. *Sempervivum tortuosum* Aiton var. *viscatum* (Bolle) Kuntze, Rev. gen. pl. 1:232. 1891. Type: Spain, Canary Islands, Gomera, Barranco San Sebastina, Hermigna, 9 Apr 1845, *E. Bourgeau 736* (lectotype, here designated: FI!; isolectotype: G[2]!).

Stems up to 40 cm tall; leaf scars transversely depressed obtrullate, c. 1.1 mm wide and 0.3 mm tall. Leaves depressed obovate in cross-section, 3-4 mm thick, with extremely short muticellular trichomes 0.04 mm long or less. Sepals 7-9, narrowly triangular, 3-3.5 mm long, 1-1.5 mm wide, at apex acuminate; petals lanceolate, 5-7 mm long, 1-1.5 mm wide; stamens with interpetalous ones 4-5.5 mm long, with antipetalous ones 3.5-4.5 mm long, with filaments slightly tapering; nectariferous glands obdeltate, c. 0.8 mm long 0.7 mm wide; carpels with ovaries 2-2.5 mm long, with styles 2-2.5 mm long.

Phenology. Flowering February to July.

Distribution. (Fig. 17). On dry rocks, 100-900 m in SE and NE sectors of Gomera.

Representative specimens. Spain. Canary Islands. Gomera. San Sebastian, *Cuatrecasas 293* (MAF); Chejelipes, *Evans 207* (OS); Barranco Agua, *Elven 13288* (O); Monte Agua, Hilva, 13 Aug 1931, *Frey and Ssara s. n.* (H); Barranco Alamos, 30 Aug 1957, *Gillie s.n.* (BH); between Vallehermoso and Agulo, 2 Feb 1896, *Kuegler s.n.* (JE); Cumbre Carbonera, *Kunkel 18547* (G); Barranco La Villa, *Lems 6210* (MICH), *Lems 7216* (MICH); hills E of Vallehermoso, *Lems 7341* (MICH); Valle Arriba, near Hermigua, *Liu 2610* (OS).

Named for the strong viscidness of its leaves.

Leaves of *Aennium lindleyi var. viscatum* are usually shinny because of very sticky substances on the surface. A fasciated plant was reported near Agulo (Praeger 1932).

This variety hybridizes with *A. canariense* var. *subplanum* and *A. castello-paivae (Praeger 1929). The names A.* x *bravoanum* Bramwell & Rowley and *A.* x *vegamorai* Bramwell & Rowley (Jacobsen & Rowley 1973) for these two hybrids were not validly published since no type was indicated.

2. *Aeonium goochiae* Webb & Berth., Hist. Nat. Iles Canaries 3(2.1):190. 1840. *Sempervivum goochiae* Webb &

Berth., Hist. Nat. Iles Canaries 3(2.1):t.32. 1836; *nom. nud.* *Sempervivum goochiae* (Webb & Berth.) Webb *ex* Christ, Bot. Jahrb. Syst. 9:117. 1888. *Sempervivum tortuosum* Aiton var. *goochiae* (Webb & Berth.) Kuntz, Revis. gen. pl. 1:232. 1891. TYPE: Spain, Canary Islands, La Palma, collector and date unknown. (lectotype, here designated: FI!; isolectotype: FI[2]!K!).

Perennial terrestrial subshrubs. Stems up to 40 cm tall, 2-10 mm diam., often with marcescent leaves; young branches pubescent, green, slightly viscid; leaf scars transversely depressed obtrullate, c. 1.5 mm wide and 0.4 mm tall, far apart; bark pale brown, slightly fissured. Leaf rosettes 3-12 cm diam.; phyllotaxy 5/13. Leaves with lower portions petiole-like; lower portions 0.5-1.5 cm long, c. 0.25 cm wide and 1 mm thick, pale green to colorless, pubescent; upper portions elliptic to circle, 1.5-5 cm long, 1.5-2.5 cm wide, rhombic to shallowly obtriangular in cross-section, c. 1 mm thick, pale green to yellow-green, occasionally with reddish tinge, viscid, pubescent with multicellular trichomes 0.1 mm long or less, at base attenuate, at apex rounded, retuse to acute, at margin involute. Inflorescence a cymose panicle, 2-5 cm long, 3-11 cm diam., 10-45-flowered, subsessile or with a peduncle to 1 cm long; bracts oblanceolate-spathulate, 1-2.5 cm long, 0.2-0.9 cm wide; pedicels 1-15 mm long, puberulent. Sepals 7-8, narrowly triangular, 3-3.5 mm long, 0.7-1 mm wide, at apex acute; petals oblanceolate, 5-7 mm long, 1-2 mm wide, very pale yellow (nearly whitish), with central portions pink, at apex acute, sparsely puberulent on abaxial surface; stamens with interpetalous ones 6-7 mm long, with antipetalous ones 5.5-6.5 mm long, with filaments glabrous, with anthers yellow; nectariferous glands obovate, c. 0.8 mm long, 0.6 mm wide, yellowish, at apex rounded to retuse; carpels with ovaries 2-3 mm long, c. 0.8 mm diam., puberulent, with styles 2.5-3 mm long. Chromosome number, $n = 18$.

Phenology. Flowering from February to June.

Distribution. (Fig. 17). Common on rocks, walls, cliffs, and sometimes soil banks, in open fields but usually under shadow of trees or rocks, fairly moist habitats; 100-700 m; in NE, N, and NW sectors of La Palma, Canary islands. Other distributional maps can be seen in Voggenreiter's (1974) and Santos's (1983) publications.

Representative specimens. Spain. Canary Islands. La Palma: Barranco Jieque, *Borgen 2589* (O); Santa Cruz, Barranco Carmen, *Bornmuller 2339* (G, GH, JE, LE, MO, WRSL); Los Tilos, Barranco San Andres and Sauces, *Lems 2907* (MICH); Barranco La Galga, *Lems 7784* (MICH); La Galga, *Liu 2653* (OS), *Liu 2654* (OS); between Garafia and Cueva de Agua, *Liu 3262* (OS); Barranco La Galga, on road to Los Sauces, 25 May 1858, *Lowe s.n.* (BM).

Named after P. B. Webb's mother, whose maiden name was Gooch.

Aeonium goochiae is a very distinctive species in the section *Petrothamnium* without close ties to any other taxon. It can be distinguished from all other species by its pinkish-appearing flowers and by its very thin, elliptic to circular leaves. However, its viscidness, nectariferous glands and leaf morphology connect it somewhat distantly to *Aeonium lindleyi*.

Aeonium goochiae was suspected to connect *Aeonium* and *Aichryson* because its leaf thickness and shape are somewhat similar to those of most *Aichryson* taxa (Lems 1960). However, its distinctly woody habit and flower coloration indicate an advanced position relative to most other species of *Aeonium*, whereas *Aichryson* is considered to be more primitive than *Aeonium*. The leaf thickness and shape of *A. goochiae* might be the result of parallel or reversed evolution.

Three herbarium sheets are in the Webb herbarium. Two are without labels, although one has attached the draft of the figure of this taxon published four years earlier. The third one with a label has the species name and collecting locality, and this is herein designated as the lectotype. There are two specimens mounted on one sheet at Kew with labels bearing Webb's handwriting 'Aeonium goochiae Nob.', but one of these is definitely not the type because its label indicates the specimen was made in 1851. The other specimen, however, may be regarded as a possible isolectotype.

This species is reported to hybridize with *A. palmense* (= *A. canariense* var. *palmense*) (Praeger 1929) and with *A. sedifolium* (Santos 1983; Bañares 1986), but I have not locate any specimens. The name *A.* x *santossianum* Bramwell & Rowley for the former hybrid (Jacobsen & Rowley 1973) was not validly published because no nomenclatural type was indicated.

3\. *Aeonium sedifolium* (Webb *ex* Bolle) Pit. & Proust, Iles canaries 193. 1908. *Aichryson sedifolium* Webb *ex* Bolle, Bonplandia 7:242. 1859. *Greenovia sedifolium* (Webb *ex* Bolle) Webb *ex* Christ, Bot. Jahrb. Syst. 9:115. 1888. *Sempervivum sedifolium* (Webb *ex* Bolle) Christ, Bot. Jahrb. Syst. 9:161. 1888. TYPE: Spain, Canary Islands, Tenerife, Masca, 5 Jul 1846, *Bourgeau 741* (lectotype, here designated: FI!; isolectotype: BM! G! K!).

Sempervivum masferreri Hillebrand, Anales Soc. Esp. de Hist. Nat. 10:137. 1881. TYPE: Spain, Canary Islands, Tenerife, cultivated in Botanic Garden at Orotava, introduced from Buenavista [probably destroyed in Berlin during World War II; Praeger (1928b) saw one possible type specimen in Berlin, but it has not been located during the course of this study].

Perennial terrestrial subshrubs. Stems up to 40 cm tall, 1-5 mm diam.; young branches sparsely puberulent, dark brown, lustrous, viscid; leaf scars transversely rhombic, c. 1 mm wide and 0.5 mm tall; bark gray or grayish-brown and fissured. Leaf rosettes 1.4-3 cm diam., imbricate and globose during the dry season; phyllotaxy 2/5. Leaves sessile, ovate to obovate, 0.7-1.5 cm long, 0.4-1.0 cm wide, transversly elliptic to depressed obovate in cross-section, 3-5 mm thick, green to yellowish-green, lustrous, puberulent with multicellular trichomes 0.08 mm long or less, abaxially with continuous pale reddish tannic stripes on the midrib, and variegated with many brownish lines near the apex, adaxially usually with reddish midrib near the apex, viscid, at base cuneate, at apex rounded. Inflorescence 2-7 cm long, 2-5 cm diam., 6-15-flowered; peduncles 2-8 cm long; bracts with similar shape and slightly smaller size of foliage leaves; pedicels 5-16 mm long, puberulent. Sepals 9-11, elliptic, 2.5-3 mm long, 1.5-2 mn wide, puberulent, at apex obtuse to mucronulate, and often variegated with reddish lines; petals obovate-oblanceolate, 5-7 mm long, 2-2.5 mm wide, yellow, at apex acute to obtuse, often reflexed and toothed, glabrous; stamens with interpetalous ones 4.5-5.5 mm long, with antipetalous ones 4-5 mm long, with filaments sparsely puberulent; nectariferous glands absent; carpels with ovaries 1.5-2 mm long, c. 1 mm diam., puberulent, with styles 2.5-3 mm long. Chromosome number, $n = 18$.

Phenology. Flowering from March to July.

Distribution. (Fig. 17). Common on dry rocks and cliffs; 0-1000 m; in the west end (Teno region) of Tenerife and NW sector of La Palma, Canary Islands. Other distributional maps of this species on La Palma and Tenerife have been provided by

Voggenreiter (1973, 1974). Based on geographical position, topographical features, and wind direction, Voggenreiter (1974) suggested that this species should also be in certain parts of Fuerteventura, Gomera, Gran Canaria, and Hierro. A search for this taxon in these areas of Canary Islands has not been successful.

Representative specimens. Spain. Canary Islands. La Palma: SE of El Time, *Borgen 902* (O); El Time, *Evans 295* (OS), *Lems 7778* (MICH); near Candelaria, 13 Jun 1892, *Murray s.n.* (K); Tazacorte, Mar 1905, *Pitard s.n.* (G, LY, MO). Tenerife: Teno, *Burchard 118* (S), *Burchard 239* (E, F, G, O); between Buenavista and Punta de Teno, *Charpin, Lear, & Arco 18667* (G); near Tamaimo, *Evans 385* (OS); W slope from Tamaimo to Chio, *Lems 5917* (MICH); Masca, *Lems 7382* (MICH), *Liu 2558* (OS), *Liu 3165* (OS), 4 Jun 1907, *Murray s.n.* (BM), *Sunding 4082* (O), *Sventenius 223* (BH, S).

Named for the resemblance of its leaves to some species of *Sedum*.

Aeonium sedifolium can be easily identified by its dense, dwarf habit and very small shinny sticky leaves marked with crimson lines at the apex. The vegetative branches of *Aeonium sedifolium* form a compact mass, and the plants are typically scattered on very dry cliffs. When in flower, many inflorescences develop simultaneously which provide a conspicuous bright yellow cover.

Aeonium sedifolium is closely related to *A. saundersii* as indicated by their reduced, lax inflorescences with large flowers, absence of nectariferous glands, and sticky, reddish leaves. Both species fold their young leaves into an imbricately globose structure during the dry season. *Aeonium sedifolium* can be distinguished from *A. saundersii* by the former's smaller (usually less than 1 cm long) and thicker (usually more than 3 mm thick) leaves with abaxial pale-reddish tannic stripes. In addition, hairs on the leaves are visible to the naked eye in *A. saundersii*, but microscopic in *A. sedifolium*.

The multicellular trichomes of *Aeonium sedifolium* are very short. Praeger (1932) called them "beads", not hairs, and used this to relate *A. sedifolium* with *A. spathulatum*. However, the bead-shaped trichomes of *A. spathulatum* are unicellular trichomes on the leaf margin, whereas in *A. sedifolium* they are multicellular and cover the entire leaf surface.

Aeonium sedifolium is known to hybridize with *A. canariense* var. *palmensis*, *A. davidbramwellii*, *A. goochiae*, *A. haworthii*, and *A. urbicum*. The hybrid between *A. goochiae* and *A. sedifolium* was first reported as a garden hybrid by Santos (1983; also see Bañares 1986). *Aeonium* × *burchardii* (Praeger) Praeger (Pro sp.) was first published as a species of *Sempervivum* (1925), then transferred to *Aeonium* (Praeger 1929). It was Uhl (1961) who first suggested the hybrid natural of this taxon between *A. sedifolium* and *A. urbicum*, later confirmed by artificial hybridization (Uhl, pers. comm.). The natural distribution of this hybrid is limited to valleys in the Masca area, Tenerife. It is not uncommon there, although no flowering individual was encountered in the field during the present study. Two morphological forms of *A.* x *burchardii* have been found. The corolla color of these two forms is basically similar to that of the maternal species (Bramwell, pers. comm.). Vegetatively, this hybrid can be easily identified by its brownish branches and dark green obovate-spathulate leaves marked with crimson lines near the apex. *Aeonium* x *mascaense* Bramwell (pro sp.) was published recently as a rare species (Bramwell 1984). Having examined several cultivated materials and the type specimen, I regard this taxon as a hybrid between *A. haworthii* and *A. sedifolium* because of its intermediate morphology. Other hybrids (*A.* x *cilifolium Bañares* = *A. davidbramwellii* x *sedifolium;* and *A.* x *nogalesii* = *A. canariense* var. *palmense* x *sedifolium*) were reported by Bañares (1986).

4. *Aeonium saundersii Bolle, Bonplandia 7:241. 1859. Sempervivum saundersii* (Bolle) Christ, Bot. Jahrb. Syst. 9:161. 1888. TYPE: Spain, Canary Islands, Gomera, Barranco de La Villa, collector and date unknown (type specimen not located).

Perennial terrestrial subshrubs, with balsam odor. Stems up to 25 cm tall, 1-4 mm diam.; young branches dark brown, lustrous, glabrate, slightly viscid; leaf scars narrowly transversly elliptic, c. 1.5 mm wide and 0.4 mm tall, somewhat elevated, bark brown to gray, more or less smooth. Leaf rosettes 2.5-6 cm diam., imbricated and globose during the drought season; phyllotaxy 3/8. Leaves elliptic to obovate, 1.2-3.5 cm long, 0.7-1.3 cm wide, narrowly transversely elliptic-obtriangular with adaxial side concave in cross section, 1.5-2.5 mm thick, green to yellow-green, pubescent with multicellular trichomes 0.2-0.6 mm long, abaxially variegated with few reddish spots, at base cuneate to attenuate, at apex retuse to rounded. Inflorescence 3-8 cm long, 2-15 cm diam., 5-70-flowered; peduncles 3-8 cm long; bracts few, minute to similar to foliage leaf; pedicels 3-12 mm long, puberulent. Sepals 12-16, lanceolate, 3.5-4.5 mm long, 1-1.3 mm wide, puberulent, at apex acute; petals oblanceolate, 6-9 mm long, 1.5-2.5 mm wide, yellow, at apex acuminate, with adaxial surface glabrous, with abaxial surface and margin sparsely puberulent; stamens with interpetalous ones 5-6 mm long, with antipetalous ones 4.5-5.5 mm long, with filaments glabrous, tapering; nectariferous gland absent; carpels with ovaries 2.5-4 mm long, c. 1 mm diam., puberulent, with styles 2-3.5 mm long. Chromosome number, $n = 18$.

Phenology. Flowering from April to June.

Distribution. (Fig. 17). Common on vertical rocks both in sun and shade; 150-800 m; in Barranco de La Villa and La Laja of Gomera.

Representative specimens. Canary Islands. Gomera: Barranco La Laja, *Burchard 311* (JE, O), 5 Dec 1976, *Elven s.n.* (O); Barranco La Laja, from Chejelipes to Roques Ojila, *Lems 2277* (L, MICH); La Laja, *Liu 2624* (OS), *Liu 2676* (OS); Barranco de La Villa, *Liu 3104* (OS).

Named after William Wilson Saunders (1809-1879), British botanist, horticulturist, entomologist, and the treasurer of the Linnean Society of London (1861-1873).

Aeonium saundersii is a distinct species and well distinguished by its small rosettes of elliptic to obovate, hairy, concave leaves. Under dry conditions, young leaves close tightly in globular buds. Leaves under cultivation normally grow larger than in the wild because of increasing availability of water. This species grows on vertical rocks and forms dangling masses. The inflorescence has a long stalk and is very conspicuous even from a distance. This species is closely related to *A. sedifolium*.

Bolle's original herbarium is at B, and his Canary Islands collection duplicates are at FI, K, MO, P, S, and W (Stafleu and Cowan 1976). Because no type material of *Aeonium saundersii* was found in any of the above herbaria, it is assumed that either the specimen was destroyed in Berlin during World War II or that the original description was based only on living material.

This species hybridizes with *A. canariense* var. *subplanum* (Praeger 1929). The name *A* x *sanctisebastianii* Bramwell & Rowley (Jacobsen & Rowley 1973) was not validly published since no nomenclatural type was indicated.

II. *Aeonium* sect. *Chrysocome* Webb *ex* Christ, Bot. Jahrb. Syst. 9:109, 1888. LECTOTYPE (here designated): *Aeonium spathulatum* (Hornem.) Praeger.

Aeonium sect. *Auonium* A. Berger in Engl., Nat. Pflanzenfam. ed. 2, 18a:427. 1930. LECTOTYPE (here designated): *Aeonium spathulatum* (Hornem.) Praeger.

Aeonium sect. *Trichonium* A. Berger in Engl., Nat. Pflanzenfam. ed. 2, 18a:428. 1930. TYPE: *Aeonium smithii* (Sims) Webb & Berth.

Small perennial subshrubs. Leaves glandular-pubescent, at margin ciliate with conical or bead-shaped unicellular trichomes, at abaxial surface with conspicuous, green to brown, longitudinal tannic stripes; young leaves arising suberectly, not tightly against the older ones. Inflorescence a cymose panicle, with bracts decreasing in size. Sepals with longitudinal tannic stripes; petals and stamens yellow.

Named for the yellow flowers, although this feature is also found in many species of other sections.

i. *Aeonium* sect. *Chrysocome* series *Simsii* H.-Y. Liu, *ser. nov.* TYPUS: *Aeonium simsii* (Sweet) Stearn.

A series *Chrysocome* rosulis subsessilibus, inflorescentiis lateralibus differt.

Perrennial terrestrial plants. Stems subsessile, rosetted, and stoloniferous. Leaves with tannic stripes on both surfaces. Inflorescence lateral. Petals without tannic stripes; nectariferous glands present.

5. *Aeonium simsii* (Sweet) Stearn, Gard. Chron. ser. 3, 130:169. 1951. *Sempervivum ciliatum* Sims, Bot. Mag. 45:*t.1978*. 1818; *non* Gilib. 1782; *non* Willd. 1809. *Sempervivum simsii* Sweet, Hort. suburb. lond. 230. 1818. *Sempervivum caespitosum* Chr. Smith *ex* Otto in Nees, Horae phys. berol. 38. 1820; *nom. illeg.* *Aeonium caespitosum* (Chr. Smith *ex* Otto) Webb & Berth., Hist. Nat. Iles Canaries 3(2.1):191. 1840. *Sempervivum ciliare* Haw., Saxifrag. enum. 2:64.1821; *nom. superfl.* TYPE: introduced from Canary Islands in 1815 by Chr. Smith, cultivated at Apothecaries botanical garden, Chelsea, England (the plate in the protologue is selected as the lectotype)

Sempervivum barbatum Chr. Smith *ex* Hornem., Suppl. hort. bot. hafn. 61. 1819. TYPE: Spain, Canary Island, 1816, *Chr. Smith s.n.*, detailed locality and date unknown (holotype: C!).

Sempervivum ligulare Haw., Saxifrag. enum. 2:64. 1821. *pro syn.* under *S. ciliare*.

Perennial terrestrial herbs. Stems caespitose, rarely with visible stems up to 15 cm tall, erect, with marcescent leaves; leafy stolon c. 0.2 cm diam., brown, decumbent, glabrous, lustrous; leaf scars indistinct. Leaf rosettes 4-12 cm diam.; phyllotaxy 5/13. Leaves lanceolate, 2-6 cm long, 0.6-2 cm wide, very shallowly obtriangular in cross-section, c. 2 mm thick, puberulent with multicellular trichomes 0.1 mm long or less, at base cuneate, at apex acuminate, at margin ciliate with conical unicellular trichomes 1-2.5 mm long and with multicellular trichomes 0.1 mm long or less. Inflorescence from basal axils of rosettes, 2-5 cm tall, 2-8 cm diam.; peduncles 5-30 cm long; pedicels 1-9 mm long, glabrous. Sepals 7-9, elliptic, 2-2.5mm long, 1-1.3 mm wide, glabrous, at apex acute to acuminate; petals oblanceolate, 5-6 mm long, 1.2-1.8 mm wide, at apex acute, yellow, glabrous; stamens with interpetalous ones 5.5-6 mm long, with antipetalous ones 5-5.5 mm long, with filaments glabrous, with anthers yellow; nectariferous glands widely oblong, c. 0.4 mm tall and 0.3 mm wide; carpels with ovaries 1.5-2 mm long, c. 1.2 mm diam., glabrous, with styles 1-2 mm long. Chromosome number, $n = 18$.

Phenology. Flowering from March to August.

Distribution. (Fig. 18). Very common on rocks and cliffs, occasionally on walls and roofs; 500-1900 m; in the central sector of Gran Canaria.

Representative specimens. Spain. Canary Islands. Gran Canaria. Barranco Tejeda, *Aldridge 1533* (BM, MO, RNG); San Mateo, *Bornmuller 649* (G, L); Paso de La Plata, Apr 1846, *Bourgeau s.n.* (BH, BM, E, G, GH, WRSL), 30 Apr 1855, *Bourgeau s.n.* (C, G, GH, JE, LY); Tirajana, *Burchard 338* (E, F, G, S); near Moya, *Evans 35* (OS); Cruz de Tejeda, *Evans 268* (OS); 1 km S of Tejeda, *Evans 270* (OS); Los Tilos de Moya, 16 Apr 1973, *Hansen s.n.* (C); San Bartholome, Apr 1965, *Hulten s.n.* (S); Roque Sancillo, *Kunkel 9026* (G); Las Lagunetas, *Kunkel 11036* (G); Tenteniguada, *Liu 2677* (OS); between Valleseco and Tejeda, *Liu 3026* (OS).

Named after John Sims (1749-1831), British physician and botanist, editor of *Annals of Botany* (1804-1806) and *The Botanical Magazine* (1800-1826).

Aeonium simsii can be easily identified by its close tufted habit, long ciliated leaf margins, lorate leaves with tannic stripes on both surfaces, and lateral inflorescences. The systematic position of this species is as a distant relative of *A. smithii* and *A. spathulatum* from which it can be separated by the characteristics mentioned above.

The general appearance of *A. simsii* is very similar to *Sempervivum*, especially to *S. arachnoideum* superficially, but its woody habit clearly place it in *Aeonium*. The lateral inflorescences in *A. simsii* are of special interest in the subfamily Sempervivoideae, being found otherwise only in *Monanthes*. Species of *Monanthes* with lateral inflorescences also possess a habit similar to *A. simsii* but are herbaceous and with typical *Monanthes* petaloid nectariferous glands. It is believed that these similar characters in *A. simsii* are due to parallel evolution.

The plants of this species were collected by Christen Smith and brought back to London. Sims published it as *Sempervivum ciliatum*, a name which had been used previously by Gilibert and Willdenow. Sweet later in the same year coined a new epithet "simsii" to resolve the homonym problem. Hornemann in 1819 published another name for this species based on the specimen sent by Chr. Smith. Otto published a new epithet *caespitosum* in 1820 and cited both Sims' and Hornemann's names in synonyms. Therefore, the name *S. caespitosum* is an illegitimate name. The name Webb and Berthelot (1840) used was based on the Otto's name and is illegimitate too. Stearn made the correct combination in 1951.

This species hybridizes with *A. canariense, A. arboreum* var. *arboreum, A. percarneum, A. spathulatum* (see under this taxon), and *A. undulatum* (Praeger 1929, 1932). The hybrid between this species and *A. canariense* is a garden hybrid long in cultivation as *S. x velutinosum* N.E. Br. (Praeger 1932), but which variety of *A. canariense* was the parent is unknow. The hybrid between *A. simsii* and *A. percarneum* was named *A. x lidii* (Sunding and Kunkel 1972), the hybrid between *A. simsii* and *A.* undulatum was named *A.* x *praegeri* (Kunkel 1969); and the hybrid between *A. simsii* and *A. arboreum* was named *sventenii* by Kunkel (1972).

ii. *Aeonium* sect. *Chrysocome* series *Chrysocome* H.-Y. Liu, *ser. nov.* TYPUS: *Aeonium spathulatum* (Hornem.) Praeger.

A series *Simsii* habitibus fructicosus, inflorescentiis terminalibus differt.

Perennial terrestrial twiggy subshrubs. Stems with acrotonic, ascending branches. Leaves with tannic stripes at abaxial surface only. Inflorescence terminal. Petals with tannic stripes; nectariferous glands absent.

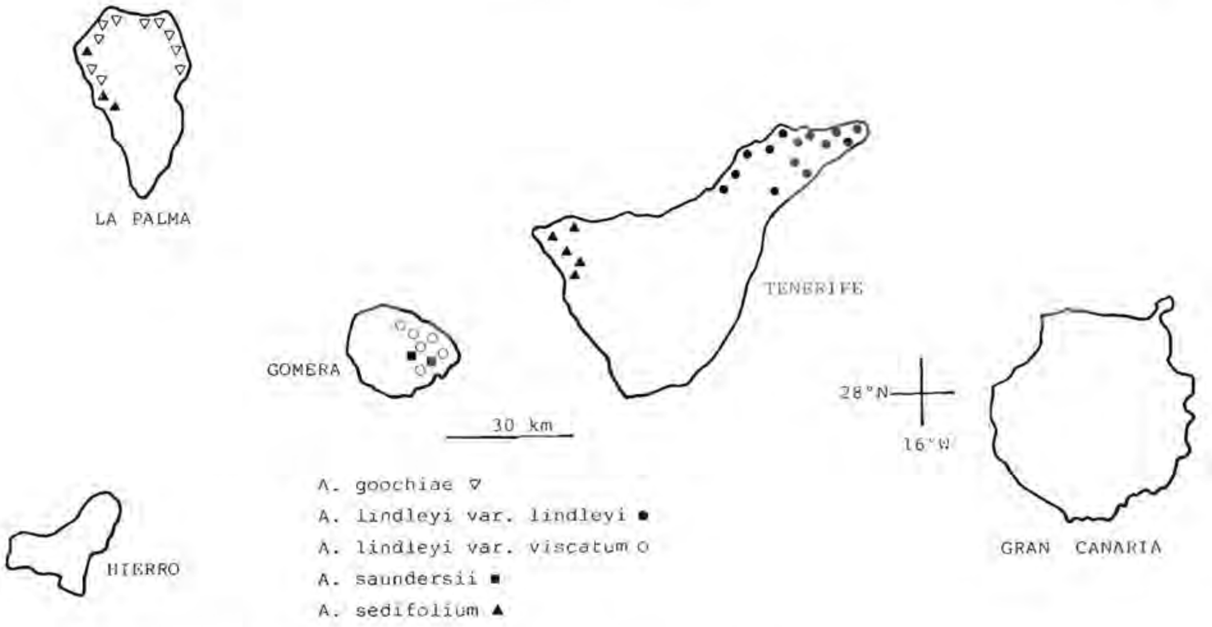


Fig. 17. Distribution of *Aeonium* section *Petrothamnium*.

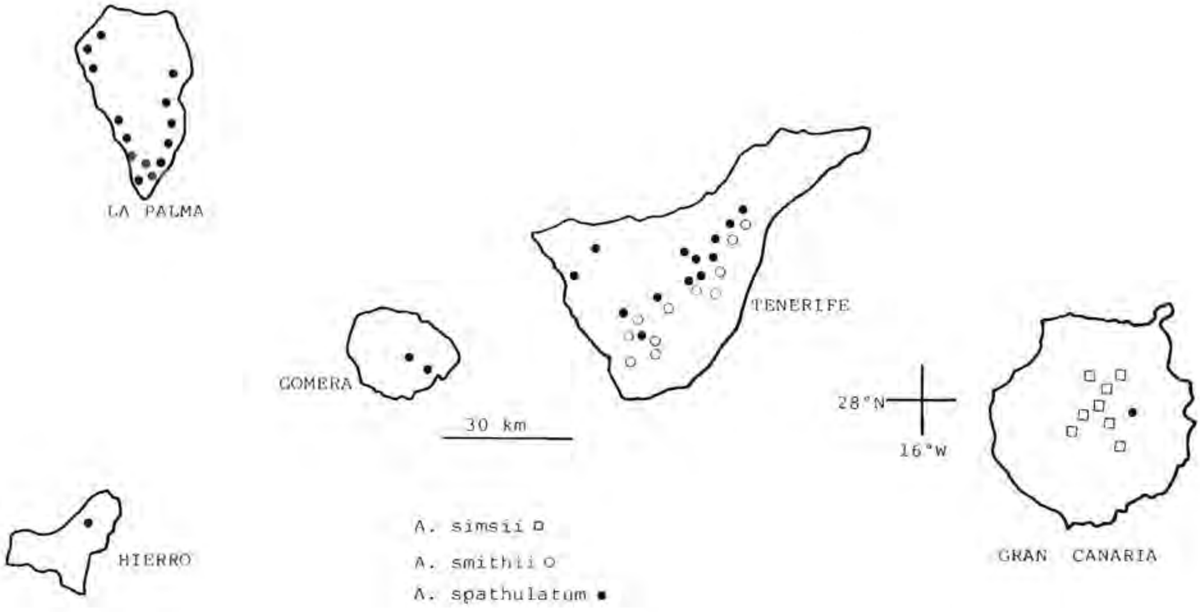


Fig. 18. Distribution of *Aeonium* section *Chrysocome*.

6. *Aeonium spathulatum* (Hornem.) Praeger, Proc. Roy. Irish Acad. 38B:482. 1929. *Sempervivum spathulatum* Hornem., Suppl. hort. bot. hafn. 60. 1819. *Sempervivum barbatum* Chr. Smith *ex* Otto in Nees, Horae phys. berol. 37. 1820; *nom. illeg. non* Hornem. 1819. TYPE: Spain, Canary Islands, 1816, *Chr. Smith s.n.* (lectotype, here designated: C!). Two type specimens with the name only were found at C, one of which with ample material has been selected as the lectotype.

Sempervivum lineolare Haw., Suppl. pl. succ. 69. 1819. TYPE: garden plants, introduced from Madeira [?] in 1815 (type not located).

Sempervivum villosum Lindley, Edward's Bot. Reg. 19:t.1553. 1832. TYPE: introduced by Webb from the Canary Islands and cultivated in his own garden at Milford, England (the plate from the protologue is taken as the lectotype).

Aeonium cruentum Webb & Berth., Hist. Nat. Iles Canaries 3(2.1):186. 1840. *Sempervivum cruentum* (Webb & Berth.) Webb *ex* Christ, Bot. Jahrb. Syst. 9:117. 1888. *Aeonium spathulatum* var. *cruentum* (Webb & Berth.) Praeger, Proc. Roy. Irish Acad. 38B:482. 1929. *Sempervivum strepsicladum* var. *cruentum* (Webb & Berth.) Burchard, Biblioth. Bot. 98:140. 1929. TYPE: Spain, Canary Islands, La Palma, collector and date unknown (lectotype, here designated: FI!; isolectotype: FI!). Three specimens with this name are in the Webb herbarium, and all are without collector and date. The specimen labeled "*Aeonium cruentum* Nob." has been selected as the lectotype.

Aeonium strepsicladum Webb & Berth., Hist. Nat. Iles Canaries 3(2.1):187. 1840. *Sempervivum strepsicladum* (Webb & Berth.) Webb *ex* Christ, Bot. Jahrb. Syst. 9:117. 1888. TYPE: Spain, Canary Islands, Tenerife, Chasna, collector and date unknown (holotype: FI!).

Aichryson pulchellum C.A. Mey. in Fisch., C. A. Mey., and Ave-Lall., Index sem. hort. petrop. 9: 55. 1842. *Sempervivum pulchellum* (C. A. Mey.) Walpers, Repert. Bot. Syst. 2:95. 1843. TYPE: cultivated in Botanic Gardens in St. Petersburg (type not located; Meyer's herbarium is in LE, and no type has been located; it is assumed that the description was based on living material only).

Aeonium bentejui Webb *ex* Christ, Bot. Jahrb. Syst. 9:109. 1888. *Sempervivum bentejui* (Webb *ex* Christ) Christ, Bot. Jahrb. Syst. 9:160. 1888. TYPE: Spain, Canary Islands, Gran Canaria, Tenteniguada, date unknown, *E. Bourgeau s.n.* (no specimen with this name was located during the author's visit to the Webb herbarium).

Perennial terrestrial subshrubs. Stems up to 60 cm tall, 1-3 cm diam., suberect or ascending, fruticose with acrocaulous branches; branches ascending or decumbent, green to grayish brown, puberulent; bark slightly fissured; leaf scars narrowly transversely elliptic, c. 1 mm wide, 0.3 mm tall, elevated. Leaf rosettes 1-5 cm diam.; phyllotaxy 5/13. Leaves obovate spathulate, 0.5-2.5 cm long, 0.3-0.9 cm wide, narrowly transversely elliptic-oblong with upper side flattened in cross-section, c. 1 mm thick, puberulent with multicellular trichomes 0.06 mm long or less, at base cuneate to attenuate, at apex obtuse, at margin ciliate with bead-shaped unicellular trichomes c. 1 mm long and with multicellular trichomes 0.06 mm long or less. Inflorescence 3-10 cm long, 3-15 cm diam.; peduncles 5-20 cm long; pedicels 1-10 mm long, puberulent. Sepals 8-10, elliptic, 1.5-2 mm long, 0.7-0.9 mm wide, puberulent, at apex acute; petals lanceolate to oblanceolate, 4.5-6 mm long, 1.5-2 mm wide, yellow, at apex obtuse, glabrous, with tannic stripes; stamens with interpetaloms ones 4.5-5.5 mm long, with antipetalous ones 4-5 mm long, with filaments glabrous, with anthers yellow; nectariferous glands absent; carpels with ovaries 2-2.5 mm long, c. 1 mm diam., puberulent adaxially, with styles 1.5-2 mm long. Chromosome number, $n = 18$.

Phenology. Flowering from March to June.

Distribution. (Fig. 18). Common on rocks, walls, stoneheaps, and roofs; 250-2500 m; on Gran Canaria, Tenerife, Gomera, La Palma, Hierro. Usually at the edge of pine forests. Other distributional maps of this species on La Palma and Tenerife have been provided by Voggenreiter (1973, 1974).

Representative specimens. Spain. Canary Islands. Gomera. Roque Zarzita, *Kunkel 18263* (G); Roque Agando, *Kunkel 18318* (G), *Lems 7327* (MICH); above Aguamansa, *Mulford 154* (RNG); Las Aguillas, El Portillo, *Sventenius 224* (S). Gran Canaria. Tenteniguada, Apr 1846, *Bourgeau 440* (BH, G, GH, WRSL), *Lems 6211* (MICH), *Lems 7952* (MICH), *Liu 3024* (OS), *Sunding 2257* (O); between Santa Lucia and Tenteniguada, *Kunkel 14173* (G). Hierro. between San Andres and Tinor, *Aldridge 13S6* (BM, MO, RNG); between Valverde and Tinor, *Borgen 935* (O); Pinar de Julan, *Lems 6013* (MICH); between San Andres and Isora, at road intersection, *Liu 3309* (OS); Pinar, Apr 1905, *Pitard s.n. (G, LY, MO); 2 km N of Isora, Sunding 4001* (O). La Palma. near Los Aremales, S of Las Caletas, *Aldriage 1429* (BM, MO, RNG); near Tacande de Abajo, *Borgen 1676* (O); San Nicolas, *Borgen and Elven 2056* (O); Cumbre, *Bornmuller 2341* (JE, MO); El Gorralejo, *Bramwell 1839* (RNG); Tijarafe, Barranco Candelaria, *Bramwell 1921* (RNG); Los Llanos, 12 Mar 1961, *Hummel s.n.* (S); Refugio Forestal de Los Roques, Cumbre above El Paso, *Lems 2975* (MICH); El Charco, *Lems 5799* (MICH); vicinity of Valcan San Antonio, Fuencaliente, *Lems 7696* (MICH); between Puntagorda and Tijarafe, *Leonard 7068* (C); near La Galga, *Liu 2667* (OS); between Fuentaliente and Mazo, *Liu 3253* (OS); Cumbre summit, 12 Jun 1858, *Lowe s.n.* (GH); Monte Santo, Sunding 3102 (O); Tacande de Abajo, *Sunding 3146* (O); Cumbre Nueva, *Van Steenis 21540* (L). Tenerife. Guimar, Barranco del Rio, 25 Apr 1933, *Asplund s.n.* (G, S); Aguamansa, *Bramwell 1496* (C, E, MO, RNG); Las Canadas, La Fortaleza, 19 May 1846, *Bourgeau 732* (BM, E, G, GH); Ladera Guimar, 6 Jun 1855, *Bourgeau 1293* (BM, C, E, C, JE, LE, LY, MA, S); Chasna, *Burchard 127* (GH, LY, O); Cumbre de Ayosa, *Charpin and Wildpret 18752* (G); Las Canadas, Roques del Cedro, *Elven s.n.* (O); above Vilaflor, 12 Jul 1957, *Gillie s.n.* (BH); Valle de Orotava, *Kunkel 15723* (G); Las Canadas, Portillo de la Villa, Roque de La Rosa, *Lems 2592* (MICH, RNG); near Los Organos, above Aguamansa, *Long 5623* (E, RNG); Vilaflor, 16 Jun 1899, *Murray s.n.* (BM, E); Orotava, 3 Jun 1855, *Perraudiere s.n.* (C, G, GH, S, WRSL); Pico de Teyde, 15 Mar 1949, *Stormer s.n.* (O); Portillo, *Sventenius 224* (BH).

Named for the spathulate shape of its leaves.

Aeonium spathulatum is well distinguished by its slender branches, small obovate-spathulate leaves (usually less than 2 cm long) marked with tannic stripes abaxially, and with two kinds of trichomes at the margin of the leaves. This species is related to *A. smithii*, the only other species in the same series. The later species has a very succulent stems with hirsute hairs, larger and undulate leaves, and puberulent corolla and carpels. In the dry season the young leaves of *A. spathulatum* are in tiny globose buds. Similar features are seen in *A. saundersii* and *A. sedifolium*.

The plants of this species in Hierro, La Palma, and the upper montane regions of Tenerife were referred as var. *cruentum* (Praeger 1932). The plants in these areas are with more upright and copper red branches, although similar features can be seen in populations in Gran Canaria and montane region of Tenerife. Praeger (1932) pointed out that these two populations can not be distinguished from each other if no locality information is given. For the interest of gardeners, typical forms of these two populations might be called different cultivarieties.

Haworth's species *A. lineolare* is definitely the same species of *A. spathulatum* based on its description. It is said to be native in Madeira, but no specimen has ever been found on that island. Haworth did not always make herbarium specimen of new species he grew (Stafleu & Cowan 1979). Haworth's herbarium was bought by Fielding who used it for study and threw away most of the specimens (Clokie 1964; Stearn 1965) with the remainder being deposited at Oxford. A few of Haworth's specimens have also been found at Kew (Stearn 1965). The author has visited both herbaria and no authentic specimen was found. Therefore, it is assumed that the original description was either based on living material only or the specimen was destroyed by Fielding.

This species hybridizes with *A. smithii* on Tenerife (Praeger 1929), with *A. arboreum* var. *holochrysum* (= *A.* x *holospathulatum* Bañares; Bañares 1986) on Tenerife, with *A. arboreum* var. *rubrolineatum* (= *A.* x *sanchezii* Bañares; Bañares 1986) on Gomera, and with *a. davidbramwellii* and *Greenovia diplocycla* on La Palma (Santos 1983). *Aeonium smithii* x *spathulatum* were found above Vilaflor and above Guimar, with the plants above Vialaflor half-way between its two parents, and with the plants above Guimar approaching *A. spathulatum* (Praeger 1932). The name *A.* x *rowleyi* Bramwell (Jacobsen and Rowley 1973) for *A. smithii* x *spathulatum* was not validly published since no type was indicated. The garden hybrid between this species and *A. simsii* is widely cultivated. The correct name for this widely cultivated hybrid is *A.* x *hybridum* (Haw.) Rowley. Its nomenclatural discussion was presented by Rowley (1969). *Aeonium* x *floribundum* A. Berger (1930) is a synonym of this hybrid. This species also hybridizes with *Greenoria dodrentalis* in Tenerife (Praeger 1929).

7. *Aeonium smithii* (Sims) Webb & Berth., Hist. Nat. Iles Canaries 3(2.1):187. 1840. *Sempervivum smithii* Sims, Bot. Mag. 45:t.1980. 1818. *Sempervivum foliosum* Chr. Smith *ex* Otto in Nees, Horae phys. berol. 38. 1820; *nom. superfl.* TYPE: introduced from Tenerife, Canary Islands in 1815 by Chr. Smith, cultivated at Apothecaries botanical garden, Chelsea, England (the plate from the protologue is selected as the lectotype).

Sempervivum hispicaule Haw., Suppl. pl. succ. 68. 1819.; *pro syn.* under *S. smithii*.

Perennial terrestrial herbs. Stems up to 60 cm tall, 0.7-3 cm diam., erect, hirsute with multicelluar trichomes 3-8 mm long, unbranched or fruticose with acrocaulous branches; branches ascending, green to yellowish brown, hirsute; bark smooth; leaf scars depressed obovate, 3-5 mm wide, c. 1 mm long. Leaf rosettes 6-15 cm diam.; phyllotaxy 5/13. Leaves obtrullate, 3-7 cm long, 1.3-3 cm wide, narrowly transversely elliptic in cross-section, c. 1.2 mm thick, lustrous adaxially, puberulent with multicellular trichomes 0.1-0.5 mm long, at base cuneate, at apex acuminate, at margin ciliate with conical unicellular trichomes c. 0.3 mm long and with multicellular trichomes 0.1-0.5 mm long, often undulate and occasionally reddish. Inflorescence 4-15 cm long, 4-9 cm diam.; peduncles 4-40 cm long; pedicels 1-9 mm long, puberulent. Sepals 8-12, elliptic, 3-4 mm long, 1.2-1.8 mm wide, puberulent, at apex acumimate; petals lanceolate, 7-9 mm long, 2-2.5 mm wide, yellow, with longitudinal tannic stripes, puberulent, at apex acute; stamens with interpetalous ones 5-5.5 mm long, with antipetalous ones 4.5-5 mm long, with filaments glabrous, with anthers yellow; nectariferous glands absent; carpels with ovaries 2.5-3.5 mm long, c. 1 mm diam., puberulents, with styles 2-2.5 mm long. Chromosome number, $n = 18$.

Phenology. Flowering from March to October.

Distribution. (Fig. 18). On rocks and cliffs, most commonly in forest zone; 150-2150 m; on Tenerife, Canary Islands. Other distributional map was provided by Voggenreiter (1974).

Representative specimens. Spain. Canary Islands. Tenerife. Barranco Tgueste, Jun 1846, *Bourgeau 442* (G, GH, LE, LY, WRSL); Canadas del Teyde, Jul 1855, *Bourgeau s.n.* (C, E, G, JE); Chasna, *Burchard 128* (LY, O); Roque del Cedro, 12 Jan 1976, *Elven s.n.* (O); Las Tablas, near Tgueste, 12 Oct 1969, *Kers and Wanntorp s.n.* (S); Montana Diego Hernandez, Canadas del Teide, *Lems 5564* (MICH); Barranco Chacorche, 15 Apr 1954, *Lid s.n.* (O); above Viaflor, *Liu 2669* (OS); above Arguayo, 23 Apr 1861, *Lowe s.n.* (BM, GH); Teide, *Mulford 177* (RNG); Tilo de las Canadas, between Portillo and Guajara, 12 Jun 1899, *Murray s.n.* (BM); Tgueste de Candelaria, 10 May 1902, *Murray s.n.* (BM); Arico, 1 Mar 1855, *Perraudiere s.n.* (WRSL); Los Llanosos, *Sunding 4376* (O).

Named after Christen Smith (1785-1816), Norwegian botanist and physician, professor of botany at the University of Christiania (Oslo).

Aeonium smithii can be easily identified by its hispid branches, undulate leaves with both unicellular and multicellular trichomes, distinct tannic stripes on leaves and flowers, and without nectariferous glands. A plant with 10 obtuse sepals, green and oblanceolate-spathulate petals (both structures similar to leaves), and nectariferous glands was reported by Praeger (1932). The presence of nectariferous glands seems to be an indication that this missing character is a result of evolutionary reduction.

Sims in 1818 indicated that the description of *Sempervivum smithii* was based on living material, and the plant from which the drawing was based was blooming at that time. Sims' herbarium is at Kew and no specimen is found there. The figure in *Botanical Magazine*, therefore, is chosen as the lectotype (ICBN Article 9.3). The lectotypification of *A. simsii* has been done in this same wy.

See under *A. spathulatum* for a discussion of the hybridization with *A. smithii*.

III. Aeonium sect. *Patinaria* (R. Lowe) A. Berger in Engl., Nat. Pflanzenfam. ed. 2, 18a: 428. 1930. *Sempervivum* L. *Patinaria* R. Lowe, Man. fl. Madeira 332. 1864; *stat. tax. non indic.* TYPE: *Aeonium glandulosum* (Aiton) Webb & Berth.

Aeonium sect. *Canariensia* (Christ) Praeger, Acc. Sempervivum. 129. 1932. *Sempervivum* L. sect. *Aeonium* (Webb & Berth.) J. D. Hook. *Canariensia* Christ, Bot. Jahrb. Syst. 9:118. 1888; *stat. tax. non indic.* TYPE: *Aeonium canariense* (L.) Webb & Berth.

Biennial to perennial, terrestrial or epiphytic herbs. Stems usually very short, under 5 cm, concealed under marcescent leaves, brown, shaggy, soft, woody only at the base. Leaves usually more than 10 cm long; young leaves arising tightly against the older ones. Inflorescence a terminal panicle, pyramidal, usually more than 30 cm long, lax, puberulent, with bracts decreasing in size. Sepals puberulent, entirely green; petals yellow, pale yellow to pale yellowish-green, or nearly white.

Named from the bowl-shaped rosettes which are common in most species of this section.

i. *Aeonium* sect. *Patinaria* series *Praegeri* H.-Y. Liu, *ser. nov.* *TYPE: Aeonium cuneatum* Webb & Berth.

A series *Patinaria* rosulis stoloniferis, foliis glabris et glaucis differt.

Perennial herbs. Stems leafy stoloniferous. Leaves glaucous, glabrous, at margin with conical unicellular trichomes. Petals bright yellow, minutely denticulate.

Named after R. Lloyd Praeger (1865–1953), Irish botanist who published a comprehensive monograph on *Aeonium* in 1932.

8. *Aeonium cuneatum* Webb & Berth., Hist. Nat. Iles Canaries 3(2.1):197. 1841. *Sempervivum cuneatum* (Webb & Berth.) Webb & Berth. *ex* Christ, Bot. Jahrb. Syst. 9:161. 1888. TYPE: Spain, Canary Islands, detailed locality, collector and date unknown; cultivated in Webb's own garden at Milford, England (type specimen has not been located in the Webb herbarium).

Perennial terrestrial or epiphytic herbs. Stems very short, often stoloniferous, 0.5–3 cm diam., brown, erect; stolones to 25 cm long, decumbent, glabrous, leafy. Leaf rosettes 15–50 cm diam.; phyllotaxy 5/13. Leaves obovate to obovate-oblanceolate, 10–25 cm long, 5–8 cm wide, narrowly transversely rhombic in cross-section, 5–9 mm thick, glabrate, at base cuneate, at apex mucronate, at margin ciliate with conical unicellular trichomes c. 0.4 mm long, and sometimes with portions of margin undulate. Inflorescence 18–60 cm long, 12–30 cm diam.; peduncles 15–50 cm long; pedicels 1–6 mm long, puberulent. Sepals 8–9, triangular, 3–4 mm long, 1.2–1.6 mm wide, puberulent, at apex acute; petals oblanceolate, 6.5–7.5 mm long, 1.3–1.6 mm wide, yellow, glabrous, at apex acuminate, at margin minutely denticulate; stamens with interpetalous ones 5.5–6 mm long, with antipetalous ones 5–5.5 mm long, with filaments glabrous, with anthers yellow; nectariferous glands widely obovate, c. 0.7 mm long, 0.6 mm wide, greenish, at apex rounded and slightly emarginate; carpels with ovaries 3–3.5 mm long, c. 1.8 mm diam., sparsely puberulent adaxially, with styles 3.5–4 mm long. Chromosome number, $n = 18$.

Phenology. Flowering from April to June.

Distribution. (Fig. 19). Common on rocks, soil banks, and among bushes, occasionally on trees, in fairly moist habitats; 500–950 m; in the laurel forest regions of the eastern and western ends of Tenerife, Canary Islands.

Representative specimens. Spain. Canary Islands. Tenerife. Montes de Anaga, Cruz de Taganana, 16 May 1933, *Asplund s.n.* (G); Cumbre de Anaga, Cruz de Taganana, *Bornmuller 657* (JE, WRSL); Cruz de Taganana, 29 May 1901, *Bornmuller 2356* (G, LE, WRSL); Taganana, 13 Jun 1846, *Bourgeau 740* (K), 9 Jun 1855, *Bourgeau s.n.* (K, JE); Taganana, *Lems 2212* (MICH), *Lems 2243* (MICH); Anaga Hills, near Cruz de Taganana, 17 Jun 1890, *Murray s.n.* (BM), 11 Jun 1899, *Murray s.n.* (K).

Named for its cuneate-shaped leaves.

Aeonium cuneatum resembles *A. canariense* morphologically, and can be distinguished from the latter by the decumbent, leafy stolons, the glabrous and glaucous leaves with teethed margins, and the bright yellow, minutely denticulate petals. Its leaf morphology approaches to that of species in section *Leuconium*, but differs by its shape (lorate instead of oblanceolate), margin color (green instead of reddish), and straight unicellular trichomes (not curved).

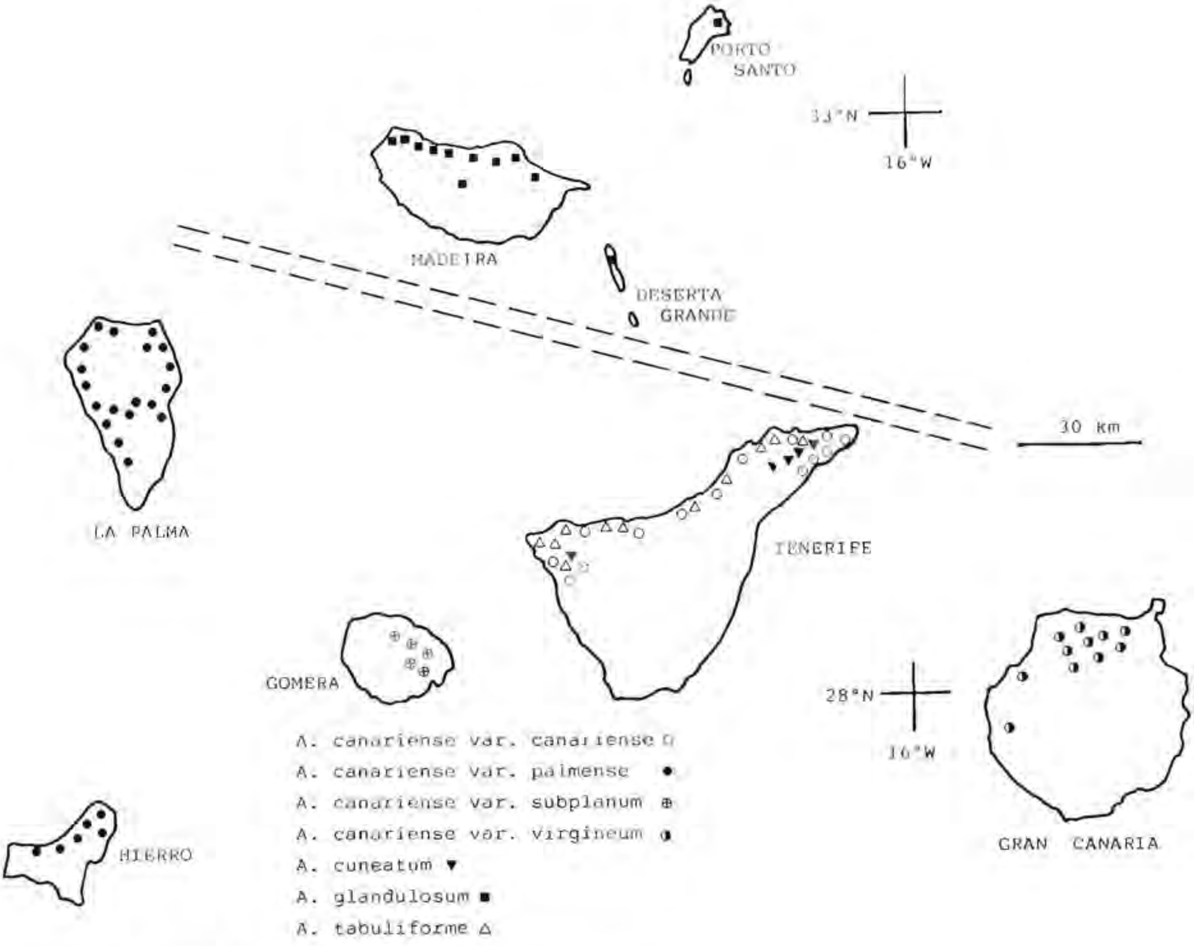


Fig. 19. Distribution of *Aeonium* section *Patinaria*.

This species hybridizes with *A. canariense* (see under *A. canariense* var. *canariense*), and was suggested to possibly cross with *A. urbicum* (Praeger 1929).

ii. *Aeonium* section *Patinaria* series *Patinaria* H.-Y. Liu, *ser. nov.* TYPUS: *Aeonium canariense* (L.) Webb & Berth.

A series *Praegeri* rosulis non stoloniferis, foliis puberuliis et chlorinis differt.

Biennial to perennial herbs. Stems unbranched or caespitose. Leaves green, pubescent or at least with multicellular trichomes at margin when mature. Petals pale yellow to pale yellowish-green, or nearly white, entire.

9. *Aeonium glandulosum* (Aiton) Webb & Berth., Hist. Nat. Iles Canaries 3(2.1):185. 1840. *Sempervivum glandulosum* Aiton, Hort. kew. 2: 148. 1789. TYPE: introduced from Madeira Island by F. Masson in 1777, cultivated in the Botanical Garden at Kew (type specimen not

located). Aiton's herbarium is known to be at BM, but no type material has been located at BM or K.

Aeonium meyerheimii Bolle, Bonplandia 7:239. 1859. *Sempervivum meyerheimii* (Bolle) Murray, J. Bot. 37:203. 1899. TYPE: cultivated in Botanical Garden in Berlin, introduced from Madeira by N. Krohn in 1856 (type specimen not located; the description may have been based on living material only). Bolle's herbarium is at B, but no type specimen has been found there.

Sempervivum patina Lowe, Man. fl. Madeira 1:332. 1864; *pro syn.* under *A. glandulosum*.

Biennial to perennial terrestrial herbs with strong balsam odor. Stems very short, unbranched or occasionally stoloniferous (Porto Santo populations commonly stoloniferous), 0.5–1.5 cm diam., erect; branches decumbent. Leaf rosettes (6–)8–30(–45) cm diam., phyllotaxy 8/21. Leaves obovate to oblanceolate, (3–)8–12(–22) cm long, (1–)4–6(–8) cm wide, transversely elliptic in upper one third, and narrowly oblong-linear in lower half or two-thirds, narrowly transversely rhombic in cross-section, 3–5 mm thick, puberulent with multicellular trichomes 0.1 mm long, at base cuneate, at apex mucronulate, at margin ciliate with bead-shaped unicellular trichomes c. 0.6 mm long and multicellular trichomes 0.1 mm long or less. Inflorescence (6–)10–25 cm long, (9–)15–40 cm diam., much wider than tall; peduncles 2–10 cm long; pedicels 3–18 mm long. Sepals 8–13, triangular, 4–9 mm long, 1.5–4 mn wide, at apex acuminate; petals lanceolate, 7–11 mm long, 3–4 mm wide, straw-yellow, glabrous, contracted at the base, at apex acute; stamens with interpetalous ones 6–7 mm long, with antipetalous ones 5–6 mm long, with filaments glabrous, with anthers yellow to brown; nectariferous glands oblong, c. 0.8 mm long, 0.7 mm wide, at apex rounded or slightly emarginate; carpels with ovaries 2.5–3 mm long, c. 2 mm diam., glabrous; with styles 3–4 mm long. Chromosome number, $n = 18$.

Phenology. Flowering from April to July.

Distribution. (Fig. 19). Common on rocks, ravine, sea-cliffs, and walls; 0–1500 m; in Madeira archipelago, especially common on sea cliffs along the north coast of Madeira.

Representative specimens. Portugal. Madeira archipelago. Deserta Granda. from Doca to Cabeco da Doca, *Rustan 571* (O). Madeira. Porto da Cruz, 31 May 1874, *Ayner s.n.* (S); between Porto Moniz and Seixal, *Beliz & Santo 1520* (MADJ); Ribeira de Santa Luzia, *Bornmuller 652* (JE); Gran Curral, 29 May 1929, *Cyren s.n.* (S); Ribeira Brava, May 1888, *Favrat 122* (G); Faja da Nogueira, *Hamshire 165* (BM); Sao Vicente, *Hansen 637* (C, MADJ); Ribeira de Janela, 30 May 1969, *Hansen s.n.* (C); Funchal, *Koster 101* (L); Between Sao Vicente and Seixal, *Lems 7536* (MICH); Currel, 25 July 1847, *Lowe s.n.* (K); Serra D'Agua, 2 Jul 1957, *Malmberg s.n.* (H); Ribeira de Sao Jorge, Jul–Aug 1867, *Mandon s.n.* (BM, C, E, G, K, JE, LE, S); Porto de Sao Jorge, 18 Jun 1895, *Murray s.n.* (BM); between Funchal and San Antonio, *Pickering 44* (BM); above Funchal, Mar 1926, *Praeger s.n.* (K), Jan 1928, *Praeger s.n.* (K); Faja do Cerejo, *Rustan 156* (O); Ponta do Sol, Santos 227 (MADJ); Ribeira do Inferno, *Short and Hampshire 7 (BM)*; Santa Cruz, 17 Jun 1896, *Trelease s.n.* (MO). Porto Santo. Pico Branco, without date, *Costa s.n.* (MADS); Ribeira do Pedregal, *Hansen 378* (C); Moledo, *Santos 122* (MADJ).

Named for its large, bead-like "glandular" unicellular trichomes.

The habit of *Aeonium glandulosum* resembles that of *Aeonium canariense* var. *subplanum* and *A. tabuliforme*, but it can be well distinguished by the leaves with two kinds of cilia.

Specimens from the mountain areas (Pico Branco and Moledo) of Porto Santo are of special interest. They are caespitose, not unbranched as in other *Aeonium glandulosum* populations, and tend to be smaller in size. Costa (*in sched.*) recongnized these as a new species, *Aeonium portosantanum*, and so did Pickering (1962). However, specimens from Desert Island is somewhat intermediate in size between these populations and populations elsewhere; and populations on the north coast of Porto Santo are not caespitose and similar in size to populations growing on Madeira.

The hybrid between *Aeonium glandulosum* and *A. glutinosum* (Praeger 1929), is often found to grow next to *A. glandulosum* and with similar habit, but its leaves are slightly sticky, more rigid and with brownish stripes. The name *A.* x *lowei* Bramwell & Rowley (Jacobsen & Rowley 1973) was not validly published because no type was indicated.

10. *Aeonium canariense* (L.) Webb & Berth., Hist. Nat. Iles Canaries 3(2.1):196. 1841. *Sempervivum canariense* L., Sp. Pl. 464. 1753. *Sempervivum latifolium* Salisb., Prodr. Strip. Chap. Allerton 308. 1796; *nom. superfl. Sempervivum canariense* L. subsp. *typicum* Burchard, Biblioth. Bot. 98:127. 1929. TYPE: J. Commelijn, Horti med. amstelod. 2:189. 1687. *t.95.* Wijnands (1983) lectotypified this species by the Commelijn's plate which Linnaeus cited (1753) although the figure number was misprinted.

Aeonium giganteum Webb *ex* Christ, Bot. Jahrb. Syst. 9:111. 1888; *pro syn.* under *A. canariense.*

Perennial terrestrial herbs. Stems usually caespitose, or very short and unbranched, rarely with visible stems up to 35 cm tall, 0.5–3 cm diam., erect. Leaf rosettes 10–40(–80) cm diam.; phyllotaxy 3/8. Leaves obovate to oblanceolate, 6–20(–45) cm long, 3–8(–15) cm wide, narrowly transversely rhombic to very narrowly obtriangular with midrib portion convex on both sides in cross-section, 3–8(–10) mm thick, flattened to undulate, green, velvety, at base cuneate, at apex rounded to mucronate, sometimes with portion of margin undulate. Inflorescence 15–60 cm long, 12–30 cm diam.; peduncles 12–30 cm long; pedicels 0.5–5 mm long, pubescent. Sepals 6–12, lanceolate to ovate, 3–6 cm long, 1.5–3 cm wide, at apex acute to acuminate and sometimes squarrose; petals narrowly elliptic to lanceolate, 7–10 mm long, 1.5–2.5 mm wide, at apex acute, with abaxial surface sparsely puberulent on veins; stamens with interpetalous ones 6–9 mm long, with antipetalous ones 5–8 mm long, with filaments glabrous, with anthers yellow; carpels with ovaries 2–4 mm long, 1.5–2.5 mm diam., puberulent adaxially, with styles 2.5–3.5 mm long. Chromosome number, $n = 18$.

Named for the Canary Islands, where most *Aeonium* species are endemic.

Aeonium canariense (L.) Webb & Berth. comprises the following vicarious varieties: var. *canariense* on Tenerife, var. *palmense* on Hierro and La Palma, var. *subplanum* on Gomera, and var. *virgineum* on Gran Canaria. Besides geographical distribution, these varieties can be distinguished from each other by the characters listed in the key.

Aeonium canariense is closely related to *A. cuneatum* and *A. tabuliforme*. Both taxa have subacaulescent rosettes similar to this species superficially. *Aeonium cuneatum* differs from *A. canariense* by its glabrous and glaucous leaves, long and leafy lateral rosettes, and bright yellow corollas. *Aeonium tabuliforme* has a young rosette stage very similar to *A. canariense* except with much thinner leaves, and it also differs by its more lax inflorescence and glabrate mature leaves.

10a. *Aeonium canariense* var. *canariense*

Rosettes cup-shaped. Leaves with glandular hairs mostly 0.7-1 mm long and up to 1.4 mm long. Inflorescence 30-45 cm long, 20-30 cm diam. Sepals 8-10, 3.5-5.5 mm long, 1.5-2 mm wide; petals narrowly elliptic, 7-9 mm long, 1.5-2 mm wide, very pale yellow green (nearly white); stamens with interpetalous ones 6-7.5 mm long, with antipetalous ones 5-6.5 mm long, with filaments whitish; nectariferous glands depressed ovate, c. 0.4 mm tall, 0.6-0.8 mm wide, greenish, at apex rounded.

Phenology. Flowering from April to August.

Distribution. (Fig. 19). Common on rocks, soil banks, and cliffs, in fairly dry habitats; 0-1000 m; in the north sector of Tenerife, Canary Islands. Another distributioal map can be seen in Voggenreiter's (1974) publication.

Representative specimens. Spain. Canary Islands. Tenerife. Bajamar, 7 May 1933, *Asplund s.n.* (G, K, S); Tacoronta, 7 May 1933, *Asplund s.n.* (G, S); Taganana, *Bornmuller 659* (GH); El Bufaclero, May 1846 *Bourgeau 441 p.p.* (BH, BM, E, K, LE, LY), Feb 1847, *Bourgeau 441 p.p.* (K); Realejo, 25 Jun 1855 *Bourgeau 441 p.p.* (BM, C, G, GH, JE, K, LE, LY); near San Andres, *Evans 345* (OS); Masca, *Evans 377* (OS); between Bajamar and Punta Hidalgo, *Liu 2518* (OS); Cruz de Afur to Taganana, *Liu 2556* (OS); between San Andres and El Bailadero, *Liu 3145* (OS); El Medano, *Liu 3208* (OS); El Socorro, *Mulford 158* (RNG); San Juan del La Ramble, 20 Apr 1923, *Wall s.n.*(S).

Aeonium canariense var. *canariense* hybridizes with *A. cuneatum* (Praeger 1929). The name *A.* x *bramwellii* Rowley (Jacobsen & Rowley 1973) was not validly published because no type was indicated. *Sempervivum* x *exsul Bornmuller, a garden hybrid, possibly resulted from a cross between A. ciliatum* (or *A. urbicum*) and this variety (Praeger 1929, 1932).

10b. *Aeonium canariense* var. *palmense* (Webb *ex* Christ) H.-Y. Liu, *comb. nov. Aeonium palmense* Webb *ex* Christ, Bot. Jahrb. Syst. 9:112. 1888. *Sempervivum palmense* (Webb *ex* Christ) Christ, Bot. Jahrb. Syst. 9:161. 1888. *Sempervivum christii* Praeger, Trans. & Proc. Bot. Soc. Edinburgh 27:204. 1925. *Sempervivum canariense* L. subsp. *christii* (Praeger) Burchard, Biblioth. Bot. 98:128. 1929. TYPE: Spain, Canary Islands, La Palma, collector and date unknown (lectotype here designated: FI!; isolectotype: FI!). Two specimens with identical labels are in the Webb herbarium, and the one with ample material was chosen as the lectotype.

Sempervivum canariense L. subsp. *longithyrsum* Burchard, Biblioth. Bot. 98:1287. 1929. *Aeonium longithyrsum* (Burchard) Svent., Ind. Sem. Hort. Acclin. Plant. Arautapae (Orotava) 1968/69:45. 1969. TYPE: Spain, Canary Islands, Hierro, Collector and date unknown (type specimen not located; the diagnosis may bave been based on living material only).

Rosettes cup-shaped. Leaves with glandular hairs mostly 0.3-0.5 mm long and up to 1 mm long, and often with portions of margin strongly undulate. Inflorescence 40-60 cm long, 15-30 cm diam. Sepals 8-10, 4-6 mm long, 2-3 mm wide; petals lanceolate, 7-10 mm long, 2-3 mm wide, pale to light yellowish green; stamens with interpetalous ones 5.5-6.5 mm long, with antipetalous ones 5-6 mm long, with filaments greenish; nectariferous glands usually mushroom-shaped, 0.7-1 mm tall, 0.7-0.8 mm wide, yellowish, at apex rounded.

Phenology. Flowering from March to August.

Distribution. (Fig. 19). Common on rocks, soil banks, and cliffs, in fairly dry habitats; 0-1250 m; on La Palma and the north sector of Hierro, Canary Islands. The distribution of this variety on La Palma was previously studied by Voggenreiter (1973).

Representative specimens. Spain. Canary Islands. Hierro. Fuente de Tinco, *Evans 210* (OS); El Golfo, Rogues de Salmona, *Gillie 2610* (BH); S. S. W. Valverde, *Gillie 2785* (BH); El Golfo, Belgara Alta to Las Lapss, *Lems 6105* (MICH); Sabinosa, *Lems 6109* (MICH); Frontera, *Liu 3285* (OS). La Palma. Santa Cruz, Barranco Madeira and Barranco Carmen, *Bornmuller 2354* (G, GH, JE, LE, MO, WRSL); El Time, *Evans 298* (OS); Barranco Carmen, 1 Jun 1913, *Sprague and Hutchinson s.n.* (K); La Galga, *Liu 2668* (OS); Barranco del Rio, 10 Jun 1892, *Murray s.n.* (K); Barranco Madeira, May 1901, *Murray s.n.* (K); Santa Cruz, Mar 1928, *Praeger s.n.* (K).

Named for the island of La Palma, where this variety was first found.

Leaves of *Aeonium canariense* var. *palmense* often undulate at the margin from the middle portion to the base, which is rare in other varieties.

Christ (1888) submersed all Canarian species of *Aeonium, Aichryson* and *Greenovia* under *Sempervivum*. Thus, he simultaneously applied the name *S. palmense* to two taxa. One had been published as *Aeonium palmense* Webb *ex* Christ and the other as *Aichryson palmense* Webb before. Praeger (1925a) provided the name *S. christii* for *A. canariense* var. *palmense* when he treated *Aeonium* as a part of *Sempervivum*.

Burchard (1929) separated plants growing on Hierro as A. canariense subsp. *longithyrsum*, from those found on La Palma which he called *A. canariense* subsp. *christii*, and he added a short note indicating that the former has larger rosettes and inflorescences. No further information was provided. Praeger (1932) and Sventenius (1969) considered that this brief note did not constitute a valid publication. Also, Sventenius (1969) provided a Latin description for the La Palma plants. However, according to the ICBN a short diagnosis clearly does meet the requirement of valid publication, and hence *A. canariense* subsp. *longithyrsum* must be treated as a valid published name dated from Burchard (1929). Burchard's published notes may have been based on his field observation on the Canary Islands, and he may not have collected specimens. No original material has been found despite much effort of searching in all the herbaria where Burchard's specimens were presumably deposited. The author's field observations reveal that populations on Hierro and La Palma are indeed somewhat differentiated, with plants on Hierro slightly larger, more coarsely pubescent, and strongly viscid and balsamiferous. However, the above characters overlap between these two island populations, and in the author's opinion, they are best treated as a single taxon.

This variety hybridizes with *A. valverdense* and *A. hierrense* on Hierro (Praeger 1929), and with *A. arboreum* var. *holochrysum, A. davidbramwellii, A. goochiae, A. nobile*, and *A. sedifolium* on La Palma (Praeger 1929; Santos 1983; Bañares 1986). The name *A.* x *lambii* Bramwell & Rowley for the first hybrid (Jacobsen & Rowley 1973) was not validly published since no type was indicated and no Latin description or diagnosis was given. Also, the names *A.* x *jacobsenii, A.* x *junionae*, and *A.* x *santosianum* (Jacobsen & Rowley 1973) were not validly published because no nomenclatural type was indicated. The name *A. nogalesii* Bañares is a valid name for hybrid *A. canariense* var. *palmense* x *sedifolium*, and *A. wildpretii* is a valid name for hybrid between *A. arboreum* var. *holochrysum* and this taxon.

10c. *Aeonium canariense* var. *subplanum* (Praeger) H.-Y. Liu, *comb. nov.* *Aeonium subplanum* Praeger, J. Bot. 66:221. 1928. TYPE: Spain, Canary Islands, Gomera, 1924, *R. L. Praeger s.n.* [herbarium specimen made in 1925] (lectotype, here designated: K!).

Sempervivum canariense L. subsp. *latifolium* Burchard, Biblioth. Bot. 98:128. 1929. TYPE: Spain, Canary Islands, Gomera, collector and date unknown (type specimen not located; the diagnosis may have been based on living material only).

Rosettes often flattish. Leaves loosely imbricate, often transversely elliptic in upper one third, 3-7 cm wide, oblong in lower two-thirds, 1.2-2 cm wide, with multicellular trichomes 0.3-1 mm long. Inflorescence 18-30 cm long, 15-28 cm diam. Sepals 10-12, 3.5-5.5 mm long, 1.5-2 mm wide; petals lanceolate, 7-10 mm long, 2-2.5 mm wide, pale to light greenish yellow; stamens with interpetalous ones 7.5-9 mm long, with antipetalous ones 7-8 mm long, with filaments whitish; nectariferous glands depressed ovate, c. 0.6 mm tall, 0.8 mm wide, yellowish, at apex slightly emarginate.

Phenology. Flowering from March to August.

Distribution. (Fig. 19). Common on rocks, soil banks, and cliffs, in fairly dry to moist habitats; 200-1000 m; on Gomera, Canary Islands.

Representative specimens. Spain. Canary Islands. Gomera. near Arure, *Aldridge 1080* (BM); Chejelipes, 12 May 1976, *Elven s.n.* (O); La Laja, 12 May 1976, *Elven s.n.* (O); above Hermigua, near El Reji, *Gillie 2633* (BM); Barranco above San Sebastian, 6 Mar 1961, *Humuel s.n.* (S); Cruz del Tierno, *Kunkel 18369* (G); El Cedro, above Hermigua, *Lems 2304* (MICH); above Hermigua, *Lems 6106* (MICH); Valle de Arriba, *Liu 2623* (OS); near San Sebastian, *Liu 3105* (OS); Barranco de San Sebastian, 23 May 1894, *Murray s.n.* (K); between Agulo and Valle Hermoso, 20 May 1899, *Murray s.n.* (K).

The varietal epithet refers to the nearly flattened leaf rosettes.

Under most circumstances, the best characters to identify *Aeonium canariense* var. *subplanum* are the leaf rosette and leaf shape. Leaves in this variety, when mature, are usually transversely elliptic on the upper one-third and narrowly oblong to linear on the lower two-thirds, while those of its vicarious relatives are obovate to oblanceolate without sudden expansion in the upper portion. The rosettes of *A. canariense* var. *subplanum* are flattish in nature, but may form a disc to cup-shape when brought into cultivation (pers. obser.) Plants of *A. canariense* var. *canariense* occasionally become more or less flattened in the eastern end (Anaga region) of Tenerife and maybe mistaken for var. *subplanum.*

In Praeger's (1928) original description, he mentioned that several plants were brought into cultivation from his two trips to the Canary Islands in 1924 and 1927. Authough Praeger did not mention any specimen or specific date of collection in the protologue, the specimen at Kew (dated 1925) apparently was made from one of the plants he brought back in 1924 and may be regarded as part of the original material. This sheet is herein designated as the lectotype.

This variety hybridizes with *A. castello-paivae, A. decorum, A. lindleyi* var. *viscatum,* and *A. saundersii* (Praeger 1929; Bañares 1986). The name *A.* x *castelloplanum* (Jacobsen & Rowley 1973) for the first hybrid was not validly published because no type was indicated. The valid name *A.* x *beltranii* is for *A. decorum* x *canariense* var. *subplanum.* For nomenclatural discussions on hybrids between this variety and the latter two taxa, see under those two entries.

10d. *Aeonium canariense* var. *virgineum* (Webb *ex* Christ) H.-Y. Liu, *comb. nov. Aeonium virgineum* Webb *ex* Christ, Bot. Jahrb. Syst. 9:111. 1888. *Sempervivum virgineum* (Webb *ex* Christ) Christ, Bot. Jahrb. Syst. 9:161. 1888. *Sempervivum canariense* L. subsp. *virgineum* (Webb *ex* Christ) Burchard, Biblioth. Bot. 98:127. 1929. TYPE: Spain, Canary Islands, Gran Canaria, Barranco de La Virgen, Mar 1846, *E. Bourgeau 356* (lectotype, here designated: FI!; isolectotype: BM! C[2] CGE! E! FI[2]! G[5]! GH[2]! K! LE! MO! WRSL!). Three specimens with identical labels are in the Webb herbarium, the more ample sheet has been chosen as the lectotype.

Rosettes cup-shaped. Leaves sometimes with reddish to yellowish tinge, with multicellular trichomes mostly 0.6-0.9 mm and up to 1.3 mm long, and with margin occasionally undulate on some portions. Inflorescence 15-45 cm long, 12-30 cm diam. Sepals 6-9, 3-5 mm long, 1.5-2.5 mm wide; petals lanceolate, 7-8.5 mm long, 1.5-2 mm wide, yellow-green; stamens with interpetalous ones 6-7 mm long, with antipetalous ones 5-6.5 mm long, with filaments yellowish; nectriferous glands widely depressed ovate, 0.7-1 mm tall, 0.5-1 mm wide, greenish, at apex expanded and slightly emarginate.

Phenology. Flowering from March to June.

Distribution. (Fig. 19). Common on rocks, soil banks, and cliffs, in fairly dry habitats; 0-1000 m; on the north side of Gran Canaria, Canary Islands.

Representative specimens. Spain. Canary Islands. Gran Canaria. Barranco Calabozo, *Borgen 46* (O); Poso de La Plate, Apr 1846, *Bourgeau 357* (MO); Barranco de La Virgen, 26 Apr 1855, *Bourgeau s.n.* (G, K, LY); Monte Doramas, May 1962, *Esteve s.n.* (MAF); near Moya, *Evans 31, 36, 37* (OS); Caboo Verde, 4 Apr 1980, *Fernandez s.n.* (C, G, L); Barranco de Banaderos, 24 Apr 1897, *Gelert s.n.* (C); Cuesta de Silva, 2 May 1897, *Gelert s.n.* (C); W of Puerto de La Cruz, 8 May 1957, *Larsen s.n.* (C); Buen Lugar, below Firgas, *Lems 6131* (MICH); near Moya, *Liu 2695, 3060* (OS); Cueva Corcho, *Liu 3034* (OS); Barranco Suaje, 20 May 1894, *Murray s.n.* (K); Guia, Feb 1906, *Pitard s.n.* (G, LY, MA, MO); Barranco Los Propios, 23 Feb 1965, *Sunding s.n.* (O); Barranco de Los Tilos, 16 Mar 1966, *Sunding s.n.* (O).

Named from Barranco de La Virgen, where this variety was first collected.

Besides characters used in the key, *A. canariense* var. *virgineum* can be distinguished from its related varieties by the smaller rosettes (usually less than 25 cm diam.), and more rigid and red-tinged leaves.

This variety hybridizes with *A. percarneum* (Praeger 1929; Kunkel 1972). The putative hybrid is intermediate between two parents and the name *A.* x *lemsii* Kunkel has been published for this hybrid.

11. *Aeonium tabuliforme* (Haw.) Webb & Berth., Hist. Nat. Iles Canaries 3(2.1):185. 1840. *Sempervivum tabuliforme* Haw., Suppl. pl. succ. 69. 1819. [as tabulateforme] TYPE: Spain, Canary Islands, Tenerife, near Taganana, 15 May 1984, *H.-Y. Liu 3153* (neotype, here designated: OS!). The orthographic error of epithet *"tabulaeforme"* is corrected to *"tabuliforme" here.*

Sempervivum complanatum A. DC. in Lem., Jard. fleur. 1: misc. 35. *t. 1.* 1851. TYPE: introduced from Buenavista, Tenerife, Canary Islands by Webb, cultivated in Botanical Gardens in Geneva (type specimen not located; the description was said to be based on living material, and perhaps no herbarium specimen was prepared).

Aeonium berthelotianum Bolle, Bonplandia 7:239. 1859. *Sempervivum berthelotianum* (Bolle) Christ, Bot. Jahrb. Syst. 9:191. 1888. TYPE: Spain, Canary Islands, Tenerife, San Juan de La Rambla, 7 Jul 1855, *E. Bourgeau 1291* (lectotype, here designated: G!; isolectotype: C[2]! F! G[2]!).

Aeonium macrolepum Webb *ex* Christ, Bot. Jahrb. Syst. 9:112. 1888. *Sempervivum macrolepum* (Webb *ex* Christ) Christ, Bot. Jahrb. Syst. 9:161. 1888. TYPE: Spain, Canary Islands, Tenerife, Taganana, collector and date unkown (type specimen not located; no herbarium specimen has been found in the Webb herbarium).

Biennial to perennial terrestrial herbs. Stems very short, rarely with visible stems to 25 cm tall, unbranched or occasionally caespitose, 0.5-1.5 cm diam., erect, glabrate. Leaf rosettes 9-40 cm diam.; phyllotaxy 8/21. Leaves closely imbricate, obovate to oblanceolate, 4-20 cm long, 2-4 cm wide, oblate to transversely rhombic on the upper one third to the upper one fourth, then gradually attenuate towards the base, very narrowly obtriangular in cross-section, 3-6 mm thick, pale to grass green, glabrate, puberulent when young, at base cuneate, at apex rounded to mucronulate, at margin ciliate with multicellular trichomes 0.5-2 mm long. Inflorescence 15-30 cm long, 12-30 cm diam.; peduncles 12-30 cm long; pedicels 2-20 mm long. Sepals 7-9, elliptic, 3-4 mm long, 1.5-2 mm wide, at apex acute; petals narrowly elliptic, 6-7 mm long, 1.5-2 mm wide, pale yellow, puberulent on abaxial surface, at apex acute; stamens with interpetalous ones 5.5-6.5 mm long, with antipetalous ones 5-6 mm long, filament glabrous, whitish, anthers yellow; nectariferous glands oblong, 1-1.5 mm long, 0.3-0.5 mm wide, whitish, at apex truncate or slightly emarginate; carpels with ovaries 2.5-3.5 mm long, 1.5-2 mm diam., puberulent adaxially, with styles 2.5-3 mm long. Chromosome number, $n = 18$.

Phenology. Flowering from May to August.

Distribution. (Fig. 19). Common on crevices of rocks, soil banks, and cliffs, in fairly moist habitats; 0-850 m; in the north sector of Tenerife, Canary Islands.

Representative specimens. Spain. Canary Islands. Tenerife. Santa Ursula, 10 May 1933, *Asplund s.n.* (S); San Juan de La Rambla, 7 Jul 1846, *Bourgeau 412 p.p.* (BM, C, E, F, G, GH, K), 7 Jul 1855, *Bourgeau s.n.* (G, K, JE, LY), *Bramwell 2105* (TFC); Teno, above Punta Morro del Diablo, *Elven 13129* (O); El Fraile, near Buenavista, *Lems 6103* (MICH); between El Palmar and Buenavista, *Liu 2576* (OS); near Buenavista, *Liu 2577* (OS); El Socorro, *Mulford 157* (RNG); Icod de Los Vinos, Jun 1890, *Murray s.n.* (BM, G, K); Los Silos, May 1928, *Praeger s.n.* (K); between San Juan de La Rambla and Realejo, *Sventenius 225* (BH); Icod, 28 Apr 1923, *Wall s.n.* (S).

Named for its flattish, table-like rosettes.

Aeonium tabuliforme is closely related to *A. canarience* var. *subplanum*, and can be distinguished from the latter by its glabrate and closely imbricate leaves with longer (usually 1.5-2 mm long) marginal hairs, pale yellow petals, and conspicuous oblong nectariferous glands. The habit of the above two taxa resembles that of *A. glandulosum*, from which they both differ in floral and leaf morphology and in geographical distribution. *Aeonium canariense* var. *subplanum* and *A. tabuliforme* are Canarian endemics whereas *A. glandulosum* is a Madeiran endemic. *Aeonium glandulosum* has rosettes flattish to cup-like, leaves pubescent, leaf margins with bead-shaped unicellular trichomes and very short multicellular trichomes, inflorescences

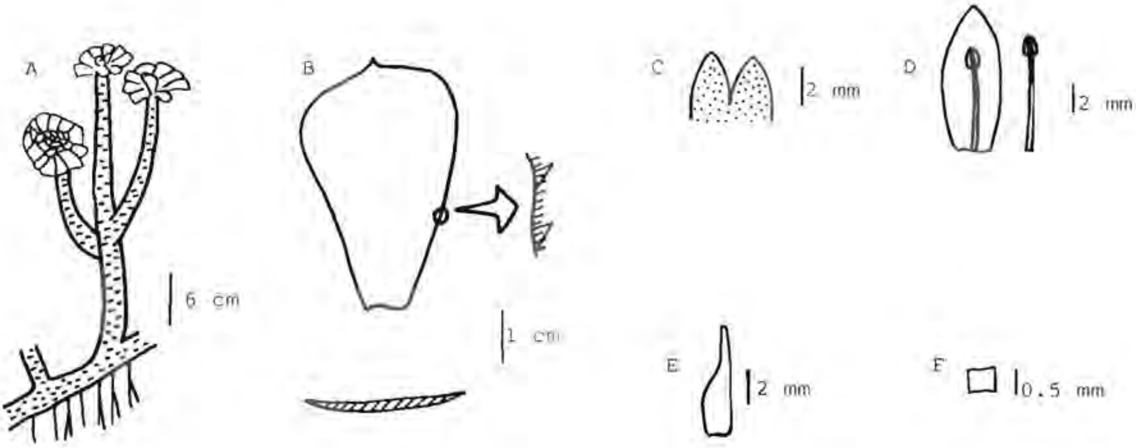


Fig. 20. *Aeonium korneliuslemsii*. A, habit; B, leaf; C, sepals; D, petal and stamens; E, carpel; F. nectariferous gland.

broader than long, corolla yellow, and nectariferous glands subquadrate.

No type material of *Aeonium tabuliforme* has been located. It is either that the description may have been based on living material only, as hinted in the original description stating it to be cultivated in Chelsea gardens, England, or that the specimen may have been destroyed by H. Fielding, who bought Haworth's herbarium and threw away most of the specimens (see discussion under *A. spathulatum* for a similar case). Haworth stated that this species had been introduced from Madeira, but this is surely a mistake because the taxon is not known from that island (Fig. 19). *Aeonium glandulosum* is native to Madeira and has a very similar morphology and could be the source of confusion, but the original description was clearly suggested *A. tabuliforme*. In view of the confusion and to avoid any possible future nomenclatural problem, a neotype has been selected.

A fasciated form is common in cultivation and called "cristatum".

See under *A. lindleyi* var. *lindleyi* for detail of hybridization with *A. tabuliforme*. It has been suggested that *A. tabuliforme* might have hybridized with *A. urbicum* (Praeger 1929), but no material has been seen.

IV. *Aeonium* sect. *Aeonium*. TYPE: *Aeonium arboreum* (L.) Webb & Berth.

Sempervivum L. sect. *Aeonium* (Webb & Berth.) Webb *ex* Christ *Holochrysa* Christ, Bot. Jahrb. Syst. 9:118. 1888; *stat. tax. non indic. Aeonium* sect. *Holochrysa* (Christ) Praeger, Acc. Sempervivum 152. 1932. TYPE: *Aeonium holochrysum* Webb & Berth. (see under *Aeonium arboreum* (L.) Webb & Berth. var. *holochrysum* H.-Y. Liu).

Aeonium Webb & Berth. sect. *Euaeonium* A. Berger in Engl., Nat. Pflanzenfam. ed. 2, 18a:431. 1930; nom. illeg.

Perennial terrestrial subshrubs. Leaf rosettes with the central portion flattened, the young leaves arising tightly against the older leaves. Leaves green, or rarely purple, may or may not with brownish stripes, abaxially mottled with several irregular, longitudinal tannic stripes at midrib, at margin with conical unicellular trichomes. Inflorescence a panicle, terminal, pyramidal, with bracts decreasing in size. Flowers with petals yellow.

12. *Aeonium korneliuslemsii* H.-Y. Liu, *sp. nov.* TYPUS: Morocco. Cape Cantin, 5 Dec 1935, *J. Gattefosse s.n.* (holotyype: MO!; isotype: K!)

Ab *A. arboreum* atque *A. balsamiferum* foliis obovato-spathulatis, puberulis, truncatis vel rotundatis differt.

Perennial terrestrial subshrubs. Stems erect, up to 1.5 m tall, fruticose with acrotonic branches; branches often in groups, 1-2 cm diam., suberect to ascending, green to light brown to grayish brown, glabrous, smooth; bark slightly fissured; leaf scars distinct, narrowly transversely rhombic-obtriangular, 2.5-6 mm wide and 0.5-1 mm tall; bundle scars visible. Leaf rosettes 5-17 cm diam.; phyllotaxy 8/21. Leaves obovate to obovate-spathulate, 4-9 cm long, 2-3 cm wide, narrowly transversely rhombic to very shallowly obtriangular in cross-section, 1.5-3 mm thick, recurved, occasionally slightly undulate, pale green to yellowish green, puberulent with multicellular trichomes c. 0.04 mm long, abaxially with few bright green tannin stripes in midrib, at base cuneate, at apex truncate to rounded, at margin ciliate with straight or curved conical unicellular trichomes 0.4-1 mm long. Inflorescence 5-20 cm long, 5-18 cm diam.; peduncles c. 12 cm long; pedicels 3-8 mm long, puberulent. Sepals 7-9, obovate, 1.3-2 mm long, 1.1-1.5 mm wide, green, sparsely puberulent to puberulent, at apex acute to rounded, often minutely toothed; petals elliptic, 4.5-6 mm long, 1.5-2.5 mm wide, yellow, glabrous, at apex acute to emarginate, at margin entire; stamens with the interpetalous ones 3-6 mm long, with the antipetalous ones 2.5-5.5 mm long, glabrous, with anthers yellow; nectariferous glands quadrate-cuneate, 0.5-0.8 mm long, 0.4-0.6 mm wide, pale yellow, at apex emarginate to cordate; carpels with ovaries 2-3 mm long, c. 1.3 mm diam., glabrous, with styles c. 2 mm long. Chromosome number, $n = 36$. Fig. 20.

Phenology. Flowering from December to May.

Distribution. (Fig. 21). Common on coastal rocks; S.W. Morocco.

Representative specimens: Morocco. Cape Rhir, 4 Apr 1926, *Lid s.n.* (O), *Nordhagen s.n.* (BG); S.W. Morocco, 1875, *Mardochai s.n.* (LY); no locality, Apr 1932, *Mauricio s.n.* (BM).

This new species is named after K. Lems (1931-1968), Dutch-American botanist who studied the evolution of growth forms of *Aeonium*.

Aeonium korneliuslemsii is closely related to *A. arboreum* and A. balsamiferum and can be distinguished from the latter two species by its broader and elliptic petals and its pale yellow, obovate to obovato-spathulate leaves with truncate to rounded apex.

Praeger (1925, 1932) considered this species to be conspecific with *Aeonium arboreum* and indicated that Morocco was the "home" of cultivated *A. arboreum*. As indicated above, they are different in many aspects, and all specimens from Morocco studied by the author, including several cultivated ones, belong to *A. korneliuslemsii*.

13. *Aeonium balsamiferum* Webb & Berth., Hist. Nat. Iles Canaries 3(2.1):192. 1840. *Sempervivum balsamiferum* (Webb & Berth.) Webb & Berth. *ex* Christ, Bot. Jahrb. Syst. 9:161. 1888. TYPE: Spain, Canary Islands, Lanzarote, collector and date unknown (holotype: FI!).

Perennial terrestrial subshrubs. Stems erect, up to 1.5 m tall, fruticose with acroramous branches; branches often in

Fig. 21. Distribution of *Aeonium* section *Aeonium* in Morocco and the eastern Canary Islands.

group, 0.8-2 cm diam., suberect to ascending, brown to grayish brown to gray, glabrous, smooth; bark slightly fissured; leaf scars indistinct to distinct, narrowly transversely rhombic-obtriangular, 3-9 mm wide and 0.5-2 mm tall; bundle scars visible. Leaf rosettes 7-18 cm diam., with the center generally flattened; phyllotaxy 8/21. Leaves narrowly obtrullate- to obtrullate-spathulate, 3-7 cm long, 1.5-3.5 cm wide, transversely linear in cross-section, 1.5-3 mm thick, arcuate, generally recurved, occasionally undulate, grayish green, occasionally with brownish stripes at and near the margin of upper portions, glabrous, at base cuneate, at apex mucronate, at margin ciliate with curved unicellular trichomes 0.5-1 mm long. Inflorescence 15-25 cm long, 14-20 cm diam.; peduncles 8-15 cm long; pedicels 2-12 mm long, glabrous. Sepals 7-8, triangular, 1.7-2 mm long, 1.1-1.4 mm wide, yellowish-green, glabrous, at apex acute to acuminate; petals lanceolate, 6-8 mm long, 1.2-1.5 mm wide, yellow, glabrous, at apex acuminate, at margin entire; stamens with the interpetalous ones 6-7.5 mm long, and with antipetalous ones 5.5-6.5 mm long, glabrous, with anthers yellow, nectariferous glands guadrate-cuneate, c. 0.5 mm long, 0.6 mm wide, yellow, at apex cordate; carpels with ovaries c. 3 mm long, 1 mm diam, glabrous, with styles c. 3.5 mm long. Chromosome number, $n = 18$.

Phenology. Flowering from April to July.

Distribution. (Fig. 21). Common on cliffs; in north and central parts of Lanzarote, Canary Islands; usually associated with *Aeonium lancerottense*. Cultivated and naturalized in Fuerteventura, Canary Islands.

Representative specimens. Spain. Canary Islands, Fuerteventura, Antigua, *Evans 23* (OS). Lanzarote: near Haria, *Liu 2637* (OS); no detailed locality, Jun 1926, *Praeger s.n.* (K).

Named after its strong balsamiferous odor.

Aeonium balsamiferum is closely related to *Aeonium arboreum* and *A. korneliuslemsii*, and it can be distinguished from these two by the strong balsamiferous odor and glabrous and grayish yellow leaves mottled with numerous abaxial cream lines.

14. *Aeonium arboreum* (L) Webb & Berth., Hist. Nat. Iles Canaries 3(2.1):185. 1840. *Sempervivum arboreum* L. Sp. Pl. 464. 1753. *Sedum arboreum* (L.) Hegi, Ill. Fl. Mitt.-Eur. 4(2):518. 1921. TYPE: Hortus Siccus Jachimi Burseri XVI(1):52 (lectotype, here designated: UPS: IDC 1064.114: III.4). Burser's specimen is chosen because it is the only specimen found directly relevant to Linnaeus (see discussion).

Sempervivum mutabile W. Schlecht *ex* Breiter, Hort. breiter. 472. 1817. *Aeonium arboreum* f. *foliis purpureis* Praeger, Acc. Sempervivum 160. 1932; nom. illeg. TYPE: garden plants, cultivated in Berlin and Saxony(not located; the description may have been based on living material only).

Aeonium manriqueorum Bolle, Bonplandia 7:241. 1859. *Sempervivum manriqueorum* (Bolle) Christ, Bot. Jahrb. Syst. 9:118. 1888. TYPE: Spain, Canary Islands, Gran Canaria, collector and date unknown (not located; the description may have been based on living material only). Bolle's herbarium is at B, and no type specimen has been found there.

Sempervivum arboreum var. *atropurpureum* hort. *ex* G. Nichols., Ill. dict. gard. 3:461. 1887. *Aeonium arboreum* var. *artopurpureum* (hort. *ex* G. Nichols.) hort. *ex* A. Berger in Engl., Nat. Pflanzenfam. ed. 2, 18a:431. 1930. TYPE: garden plants (not located).

Sempervivum arboreum var. *variegatum* G. Don, Gen. Hist. 123. 1834. *Aeonium arboreum* var. *variegatum* (G. Don) hort. *ex* A. Berger in Engl., Nat. Pflanzenfam. ed. 2, 18a:431. 1930. TYPE: cultivated in gardens (not located).

Aeonium arboreum f. *folis variegatis* Praeger, Acc. Sempervivum 160. 1932; *nom illeg.*

Perennial terrestrial subshrub, occasionally epiphytic. Stems erect, up to 2 m tall; branches often in groups, suberect to ascending, 1-3 cm diam., light brown to grayish-brown to gray, smooth or sometimes with bud scars elevated; bark slightly fissured; leaf scars distinct, narrowly transversely rhombic-obtriangular, 3-8 mm wide and 0.5-3 mm tall. Leaf rosettes 10-25 cm in diam. in the growing or wet season, with very small rosettes usually less than 5 cm diam. in the dry season, with the center flattened; phyllotaxy 8/21. Leaves obovate-oblanceolate, 5-15 cm long, 1-4.5 cm wide, transversely linear in cross-section, 1.5-3 mn thick, straight or slightly recurved, occasionally slightly undulate, green to purple, nitid, usually variegated with purplish brown lines on the midrib portion and on or near the margin of the upper portion, or with whitish margin, and abaxially mottled with several irregular, interrupted tannic stripes on the midrib, at base cuneate, at apex acuminate, with margin ciliate with curved conical unicellular trichomes 0.3-1 mm long. Inflorescence dense, conical to ovoid to hemispherical, 7-30 cm long, 7-15 cm diam., puberulent; peduncles 5-20 cm long; pedicels 2-12 mm long. Sepals 9-11, triangular, 2-3.5 mm long, 1.1-1.4 mm wide, 'at apex acuminate; petals narrowly oblong to lanceolate, 5-7 mm long, 1.5-2 mm wide, yellow, glabrous, at apex acuminate; stamens with interpetalous ones 5.5-6.5 mm long, with antipetalous ones 5-6 mm long, glabrous, with anthers yellow; nectariferous glands quadrate-cuneate, 0.5-1.2 mm wide and 0.5-1.5 mm tall, at apex cordate and crenulate; carpels with ovaries 2-3.5 mm long, 0.5-1 mm diam., with styles 1.5-2.5 mm long. Seeds c. 0.7 mm long, 0.2 mm wide.

Named for its shrubby habit.

The nomenclatural starting-point of *Aeonium arboreum* is Linnaeus (1753). No type material was found in Linnaeus's own herbaria in London, Paris, Stockholm, or Uppsala; or in Clifford's herbarium at BM. Linnaeus might have used garden material since this species was cultivated in the Uppsala Botanical Garden at that time (Juel 1919). That no specimen exists in Linnaeus's own herbarium perhaps may be due to the difficulty and/or inconvenience of pressing succulents. According to Stearn (1957), Linnaeus examined Burser's herbarium at Uppsala, consisting of 23 volumes of herbarium collections named and arranged in accordance with the *Pinax* of Caspar Bauhin, and used it to cite names from the Pinax. The diagnostic polynomial of *A. arboreum* in the *Pinax* was cited as a synonym in Species Plantarum. One specimen, sheet 52 of volume 16(1) in the Burser's herbarium (Hortus Siccus Joachimi Burseri), belongs to this species, and was examined and determined as *Sempervivum arboreum* by Linneaus (Savage 1937). Since no other competing specimen is found in any other herbarium, Burser's specimen is herein designated as the lectotype.

A fasciated form is common in cultivation.

14a. *Aeonium arboreum* var. *arboreum*

Inflorescence ovoid, 10-25 cm long; pedicels pubescent. Sepals pubescent; petals entirely yellow; nectariferous glands 0.5-0.8 mm wide and tall. Chromosome numbers, n = 18, 36.

Phenology. Flowering from October to April.

Distribution. (Fig. 22). Common on cliffs, rocks, roofs, soil banks, and occasionally on trees; 200-1200 m; on Gran Canaria, Canary Islands. The tetraploid ones are cultivated worldwide and naturalized in California, Mexico, Mediterranean region, South America, and New Zealand.

Representative specimens. Spain. Canary Islands. Gran Canaria. 1 km N of San Mateo on road to Teror, *Evans 7* (OS); San Francisco de Javiar, *Evans 225* (OS); above San Mateo, *Evans 226* (OS); 2 km S of Utiaca, *Evans 227* (OS); N of Utiaca, *Evans 233* (OS); 6 km E of Temisas, *Evans 256* (OS); above San Bartolome de Tirajana, *Evans 266* (OS); El Gallego, 24 Oct 1963, *Hulten s.n.* (S); Bandama, *Kunkel 19341* (G); Tafira, *Lems 2121* (MICH); Tentenguada, *Liu 2678* (OS), *Liu 3027* (OS); Caldera de Bamdama, Jan 1928, *Praeger s.n.* (K); Barranco de Guiniguada, 19 Feb 1965, *Sunding s.n.* (O).

Aeonium arboreum var. *arboreum* can be separated from its related varieties by puberulent pedicels and sepals, and by its inconspicuous nectariferous glands of the flowers.

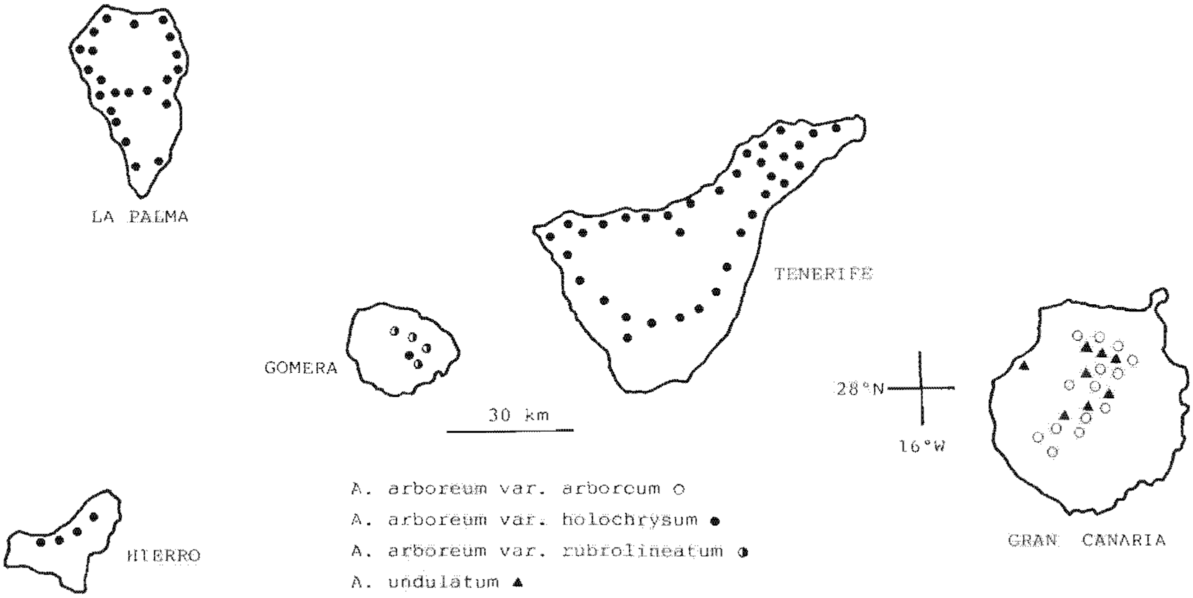


Fig. 22. Distribution of *Aeonium* section *Aeonium* in the western Canary Islands.

In his 1932 monograph, Praeger separated the widely cultivated *Aeonium arboreum* from its wild progenitors by a more strict and upright habit, and shorter and cuneate leaf. He also suggested that the place of origin for this widely cultivated taxon was in Morocco. However, Moroccan plants belong to *A. korneliuslemsii*. Also the present study reveals that no character, including those mentioned by Praeger, can be used to separate consistently the cultivated from the wild ones, previously called *A. manriqueorum*. However, the cultivated *A. arboreum* is apparently only tetraploid ($n = 36$; Uhl 1961), and the wild populations are found to be diploid ($n = 18$) in this study. Autotetraploidy is known in *A. simsii* (Uhl 1961), and this apparently has also occurred in *A. arboreum* var. *arboreum*.

See under *A. simsii* for a discussion of hybrids with *A. arboreum* var. *arboreum*.

14b. *Aeonium arboreum* var. *holochrysum* *H.-Y. Liu, nom. nov. Sempervivum urbicum* Lindley, Bot. Register 7:*t.1741*. 1835; *non* Chr. Smith. *ex* Hornem. 1819. *Aeonium holochrysum auct. non.* Webb & Berth. TYPE: Bot. Register 7:*t.1741*. 1835. (the plate in Lindley's protologue is designated as lectotype).

Aeonium vestitum Svent., Addit. Flor. Cannar. 13. 1960. TYPE: Spain. Canary Islands. La Palma: Tijarafe, 25 Sep 1954, *E. R. S. Sventenius s.n.*, (holotype: ORT).

Inflorescence ovoid to conical, 7-30 cm long; pedicels glabrate. Sepals glabrous; petals yellow; nectariferous glands 1.1-1.5 mm wide and 0.8-1.2 mm tall. Chromosome number, $n = 18$.

Phenology. Flowering from November to June.

Distribution. (Fig. 22). Common on rocks and cliffs; 0-1500 m; in the Canary

Islands: Gomera, Hierro, La Palma, and Tenerife. Rare in Gomera and common on other three islands. Commonly associated with Euphorbia scrub. The distribution of this variety on Tenerife and La Palma was previously studied by Voggenreiter (1973, 1974).

Representative specimens. Spain. Canary Islands. Gomera. Roque Cano de Vallehermoso, *Bramwell 456* (RNG). Hierro. above Frontera, *Aldridge 1344* (BM); track from Jinama to Fuente de Tinco, *Evans 214* (OS), *Evans 215* (OS); 5 km W of Frontera, *Evans 218* (OS); 2 km N of San *Andres, Liu 3317* (OS); Riscos de Jinama, Mar 1906, *Pitard s.n.* (G, L, MO). La Palma. above San Antonio, *Evans 279* (OS); 5 km S of Las Caletas, *Evans 282* (OS); 2 km S of Los Sauces, *Evans 300* (OS); W of Barlovento, *Evans 303* (OS); La Galga, *Liu 2652* (OS), Mar 1928, *Praeger s.n.* (K). Tenerife. near Santa Ursula, 11 Mar 1933, *Asplund s.n.* (G, S); near Tacoronte, 17 Mar 1933, *Asplund s.n.* (S); Mesa de Mota, 3 Feb 1845, *Bourgeau 11* (BH, E, G, GH, LY), 4 Feb 1855, *Bourgeau s.n.* (C, F, G, GH, JE, W); San Jose, *Bramwell 584* (MO); La Orotava, Feb 1923, *Burchard s.n.* (E, F, G, S); 2 km N of El Socorro, *Evans 357* (OS); near La Victoria de Acetntejo, *Evans 362* (OS); 2 km below Vegas, *Evans 371* (OS); Valle de Masca, *Evans 376* (OS); San Juan de La Rambla, 2 Jan 1961, *Hummel s.n.* (S); Icod, *Kers and Wanntorp 4131* (S); Tejina, *Kunkel 14585* (G); W of Puerto de La Cruz, Jun 1957, *Larsen s.n.* (C); above Guimar, *Liu 2584* (OS); La Questa, Jan 1906, *Pitard s.n.* (G, L, LY, MO); Orotava, Mar 1925, *Praeger s.n.* (K); Montaneta de La Horca, *Sventenius 134* (BH, S).

Named for its entirely yellow flowers.

In the original description of *Aeonium holochrysum*, Webb and Berthelot (1840) stated that the calyx was pubescent. Praeger (1932) suggested that this statement was a mistake and described the calyx as glabrous. In Webb herbarium there are two specimens on the same sheet with the name *A. holochrysum*, and both do show pubescent sepals which are clearly not a characteristic feature of the current taxon. (The specimen on the right side of the sheet in the Webb herbarium, which has puberulent sepals and ovoid-shaped inflorescence has been selected as the lectotype to fit the original description.) As mentioned above, Webb and Berthelot's name *A. holochrysum* is not applicable to the current taxon. However, because of the wide use of the epithet, the epithet was used for this variety but treated as a new name.

Sventenius (1960) established a new species, *A. vestitum*, for some plants on La Palma with marcescent leaves on the older stems and with relatively small inflorescences (to 15 cm tall whereas "ordinary" plants of var. *holochrysum* have inflorescence 15-30 cm tall). Similar features have been observed from some plants on the Teno region of Tenerife. Some of these plants retain marcescent leaves on old stems for a long time even long under cultivation. A continuous variation in both inflorescence and marcescent leaf characters throughout La Palma and Teno region of Tenerife was observed. These features may simply a response to the dryer environments of those two areas, hence no formal recognition seems warranted.

This variety hybridizes with *A. davidbramwellii* on La Palma (Praeger 1929, Santos 1983, Bañares 1986; all treated *A. davidbramwellii* as *A. ciliatum*). The hybrid is similar to this variety, but its leaves are dark green, red margined, and 3-4 mm thick. The name *A. x kunkellii* Bramwell & Rowley (Jacobsen s Rowley 1973) for this hybrid was not validly published because no type was indicated. *Aeonium arboreum* var. *holochrysum* is also reported to hybridized with *A. canariense* var. *palmense* and *A. spathulatum* (see under those taxa).

14c. Aeonium arboreum var. *rubrolineatum* (Svent.) H.-Y. Liu, *comb. nov.*
Aeonium rubrolineatum Svent.

Biol. Inst. Nac. Invest. Agron. 10(23):299. 1954. TYPE: Spain, Canary Islands, Gomera. Roque de Agando, 20 May 1945, *E. R. S. Sventenius s.n.* (holotype: ORT).

Inflorescence hemspherical to ovoid, 8-15 cm long, often without leaves when blooming; pedicel glabrate. Flowers parts with reddish veins and sometimes also with reddish bases and margins; sepals glabrous; petals yellow to pale yellow with reddish variegation; nectariferous glands 0.7-1.4 mm wide and 0.7-1.1 mm tall. Chromosome number, n = 18.

Phenology. Flowering from May to November.

Distribution. (Fig. 22). Common on soil banks and cliffs; 0-1200 m; on Gomera, Canary Islands, especially common in the SW sector of the island.

Representative specimens. Spain. Canary Islands. Gomera. N of Alajero, *Evans 191* (OS); 1 km S of Arure, *Evans 194* (OS); 5 km below Arure, *Evans 196, 197* (OS); Fortaleza, *Evans 199* (OS); 2 km S of Tunel de Hermigua, *Evans 417* (OS); above Alajero, 11 Sep 1957, *Gillie s.n.* (BH); Roque Agando, *Kunkel 18319* (G); Valle Gran Rey, *Lems 7185* (MICH); Barranco de Argaga, *Lems 7307* (MICH).

Named for the reddish-veined flowers.

The petal color of Aeonium arboreum var. *rubrolineaturm* ranges from bright yellow with pale reddish veins, to very pale yellow with strong reddish veins, bases, and margins. A few reddish-tinged individuals occasionally have some young leaves arising suberect in rosettes. The leaves of this variety also usually fall off during to flowering period. The combination of the above two characters is found also in most species of section *Leuconium*. As *Aeonium arboreum* var. *holochrysum* also grows on the same island and differs mainly in the two characters mentioned above, it is possible that var. *rubrolineatum* originated from hybridization between *A. arboreum* var. *holochrysum* and one of the species of section *Leuconium* (most likely *A. urbicum*) on the same island. Additional studies are needed to verify this hypothesis. The pollen stainability of var. *rubrolineatum* ranges from 96-98%, which suggests that it might not be of hybrid origin, at least not recently, although high pollen viability (95%) has been observed in hybrids in *Aeonium*, and even in a crassulaceous intersubfamily hybrid (Uhl 1976.)

15\. *Aeonium undulatum* Webb & Berth., Hist. Nat. Iles Canaries 3(2.1): 197. 1841. *Sempervivum undulatum* (Webb & Berth.) Webb & Berth. *ex* Christ, Bot. Jahrb. Syst. 9:161. 1888. TYPE: Spain, Canary Islands, collector and date unknown; cultivated in Webb's own garden at Milford, England (not located in the Webb herbarium, the description may have been based on living material only).

Aeonium youngianum Webb & Berth., Hist. Nat. Iles Canaries 3(2.1): 197. 1841. *Sempervivum youngianum* (Webb & Berth.) Webb & Berth. *ex* Christ, Bot. Jahrb. Syst. 9:161. 1888. TYPE: Spain, Canary Islands, collector and date unknown; cultivated in Webb's own garden at Milford, England (not located in the Webb herbarium; the description may have been based on living material only).

Perennial terrestrial subshrubs, occasionally epiphytic. Stems up to 2.5 m tall, unbranched or fruticose with basiramous branches; branches 1-3 cm diam., suberect, green to pale brown to gray, glabrous, smooth; bark slightly fissured; leaf scars distinct, narrowly transversely rhombic, 3-9 mm wide and 0.5-3 mm high; bundle scars visible. Leaf rosettes 10-30 cm diam., with the center flattened; phyllotaxy 8/21. Leaves oblanceolate-spathulate to oblong-spathulate, 6-18 cm long, 3-5 cm wide, transversely linear in cross-section, 1.5-3 mm thick, often undulate, dark green, often with brownish margin, at least with brownish apex, occasionally variegated with few brownish pigmented lines on either surface, glabrate, at base cuneate, at apex acute with a point, at margin ciliate with curved conical unicellular trichomes 0.5-2 mm long. Inflorescence 12-50 cm long, 12-40 cm diam.; peduncles 5-20 cm long; pedicels 1-8 mm loŋg, glabrous. Sepals 9-12, obovate, 1.5-1.8 mm long, 0.8-1 mm wide, glabrous, at apex retuse; petals oblong-lanceolate, 6-8 mm long, 1.2-1.5 mm wide, yellow, glabrous, at apex retuse; stamens with interpetalous ones 6-7 mm long, with antipetalous ones 5.5-6.5 mm long, glabrous, with anthers yellow; nectariferous glands quadrate-cuneate, 0.6-0.8 mm wide, 0.2-0.3 mm tall, yellow, at apex emarginate; carpels with ovaries c. 3 mm long, 1 mm diam., glabrous, with styles c. 2 mm long. Chromosome number, $n = 18$.

Phenology. Flowering from April to May.

Distribution. (Fig. 22). Common on banks and cliffs, occasionally epiphytic on trees; 300-1500 m; on Gran Canaria, Canary Islands.

Representative specimens. Spain. Canary Islands. Gran Canaria. Cumbre Tenteniguada, 22 Apr 1846, *Bourgeau 738* (BM, G, K); 2 km S of Utiaca, *Evans 229 (OS); San Mateo, Kunkel 17278* (G); Tenteniguada, *Lems 6209* (MICH); Los Tilos, *Lems 7791* (MICH); near Lagunetas, *Liu 3051* (OS); Barranco de La Virgen, 13 May 1892, *Murray s.n.* (K); Tenor, 21 May 1894, *Murray s.n.* (BM); Tenteniguada, Mar 1928, *Praeger s.n.* (K), Jul 1928, *Praeger s.n.* (K); Mountain Montanon, 15 Mar 1966, *Sunding s.n.* (S).

Named for the undulate leaves.

Aeonium undulatum is unique among all species of *Aeonium* by having basitonic branching. New branches arise from near or below the ground, which sometimes give a clumped appearance.

This species hybridizes with *A. simsii* (see discussion under this taxon) and *A. percarneum* (Praeger 1929). The binominal, legitimate name for the hybrid between *A. percarneum* and *A. undulatum* is *A. x bollei* Kunkel (1972).

V. *Aeonium* sect. *Megalonium* A. Berger in Engl., Nat. Pflanzenfam. ed. 2, 18a:429. 1930. TYPE: *Aeonium nobile* (Praeger) Praeger

Aeonium sect. *Nobilia* Praeger *ex* A. Berger in Engl., Nat. pflanzenfam. ed. 2, 18a:429. 1930; *pro. syn.* under sect. *Megalonium*

Perennial terrestrial subshrubs. Stems unbranched. Leaves pale yellowish-green, glabrate, sticky when young, very thick, rounded at the margin, with or without very few conical unicellular trichomes; young leaves arising suberectly, without tightly against the older ones. Inflorescence a panicle, flat-topped to very broadly dome-shaped; flowers red.

Named for its large and thick leaves.

16. *Aeonium nobile* (Praeger) Praeger, Proc. Roy. Irish Acad. 38B:477. 1929. *Sempervivum nobile* Praeger, Trans. & Proc. Bot. Soc. Edinburgh 29:208. 1925. TYPE: Spain. Canary Islands. La Palma: 6 km N of Santa Cruz, Feb. 1924, *R. L. Praeger s.n.* (not located).

Perennial terrestrial subshrubs. Stems up to 60 cm tall, unbranched or rarely with acroramous branching, 1-3 cm diam., erect, brown to grayish brown, glabrous, usually rough; bark fissured; leaf scars distinct, narrowly transversely elliptic, 5-15 mm wide and 1-5 high; bundle scars usually indistinct. Leaf rosettes 15-60 cm diam., phyllotaxy 5/13. Leaves obovate, 7-30 cm long, 4-20 cm wide, narrowly transversely

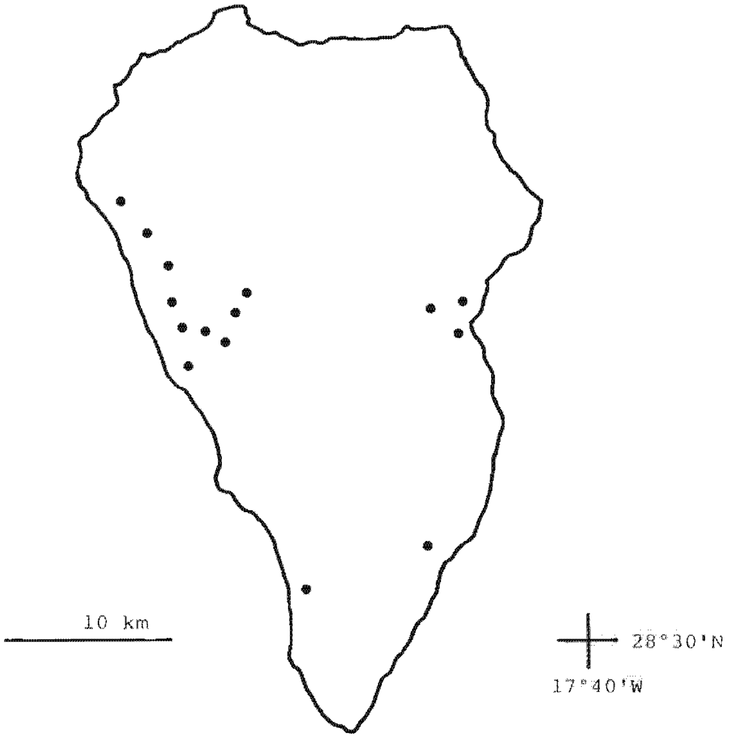


Fig. 23. Distribution of *Aeonium* section *Megalonium (Aeonium nobile).*

elliptic, 6-12 mm thick, slightly recurved, yellowish-green, occasionally with few irregular brownish lines, especially on the adaxial midrib regions, viscid when young, glabrate, at base cuneate, at apex acute with a point, at margin ciliate with straight conical unicellular trichomes c. 0.5 mm long, sometimes trichomes scanty or missing when mature. Inflorescence flat-topped to broadly dome-shaped, 20-40 cm long, 30-60 cm diam., peduncles 0-5 cm long; pedicels 1-2 mm long, puberulent. Sepals 7-9, 2-3 mm long, 1-1.5 mm wide, green, variegated with numerous reddish lines, puberulent, at apex acuminate; petals lanceolate, 3-5 mm long, 1-1.5 mm wide, suberect, very pale yellow, variegated with numerous reddish lines, glabrous, at apex acuminate; stamens with interpetalous ones 4-6 mm long, with antipetalous ones 3-5 mm long, glabrous, withish with reddish tinge, tapering, with anthers yellow; nectariferous glands quadrate, c. 0.5 mm tall and 1 mm wide, yellow, at apex cordate; carpels with ovaries 2-3 mm long, 1 mm diam., glabrous, with styles 2-3 mm long. Chromosome number, $n = 18$.

Phenology. Flowering from March to July.

Distribution. (Fig. 23). On dry slopes, banks, and cliffs; 0-750 m; throughout La Palma of the Canary Islands except absent from the NE corner of the island.

Representative specimens. Spain. Canary Islands. La Palma. 6 km N of El Time, *Evans 296* (OS); Barranco de Las Angustias, *Evans 306* (OS); Barranco de Las Angustias, *Lems 5802* (MICH); between La Ladera and Los Llanos, *Liu 2648* (OS); 12 km S of Grafia, *Liu 3266* (OS); Barranco de Los Gomeros, Mar 1928, *Praeger s.n.* (BM, K), *Pickering 122* (BM).

Named for its imposing appearance.

Praeger (1932) indicated that the original description of *A. nobile* was based on a specimen collected in 1924. In this case, a herbarium specimen was clearly made, but no place of deposit was mentioned. The author has failed to locate this in the herbaria where Praeger deposited his Canarian specimens (DBN and K). It is believed that such a specimen may be misplaced.

This species is a very large succulent with leaves up to 12 mm thick at the central point of the leaf of a well-watered plant. Its dark red flowers are unique in the genus. A close examination shows that the dark red color results from numerous reddish stripes on pale yellow petals with two marginal reddish lines as in *A. glutinosum*. Thus, it provides a clue to its relationship. *Aeonium glutionosum* and *A. nobile* both have dull-green and sticky leaves marked by a few unicellular trichomes and brownish stripes.

This species hybridizes with *A. davidbramwellii* (Praeger 1929; Bañares 1986), and with *A. canariense* var. *palmense (see under this taxon). The binominal hybrid name A.* x *splendens* Bramwell & Rowley (Jacobsen & Rowley 1973) for the former hybrid is not a valid name since no type was indicated.

VI. *Aeonium* sect. *Pittonium* A. Berger in Engl., Nat. Pflanzenfam. ed. 2, 18a:428. 1930. TYPE: *Aeonium glutinosum* (Aiton) Webb & Berth.

Perennial terrestrial subshrubs. Stems often reticulate on the young, green regions. Leaves forming a lax rosette with leaves remaining some distance down the stem; young leaves suberect, not forming a flattish rosette center. Inflorescence a terminal panicle, with bracts decreasing in size. Petals yellow.

Named for the sticky mucilage found in the type species of this section.

17. *Aeonium glutinosum* Webb & Berth., Hist. Nat. Isles Canaries 3(2.1):185. 1840. *Sempervivum glutinosum* Aiton, Hort. kew. 2:147. 1789. TYPE: Madeira. 1777, *F. Masson s.n.* (holotype: BM!)

Perennial terrestrial subshrubs. Stems up to 1.5 m tall, 0.7-2 cm diam., fruticose with acroramous branches, erect; branches often in groups, usually overtopping the parental one, ascending or decumbent, green to brown to grayish-brown, sticky, glabrous, smooth; bark fissured irregularly; leaf scars distinct, far apart on the young branches, transversely linear to narrowly transversely rhombic-trullate, 6-12 mm wide and 0.5-1.5 mm tall; bundle scars often indistinct. Leaf rosettes 12-22 cm diam., with glutinous coating near the center; phyllotaxy 5/13. Leaves obovate-spathulate, 7-12 cm long, 3-5.5 cm wide, transversely linear-obtriangular in cross-section, 2-4.5 mm thick, slightly folded and arcuate, dull pale green to fresh green, usually with brownish pigmented stripes on the midrib near the apex, and sometimes variegated with few irregular brownish pigmented stripes on either surface, sticky at least when young, glabrate, at base cuneate, at apex acute, at margin ciliate with very few scanty to numerous straight to curved conical unicellular trichomes c. 0.5 mm long. Inflorescence very lax, 15-40 cm long, 15-30 cm diam., sticky, pale yellow with chocolate-brown lines, with later branches away from the axil of bracts; peduncles 10-25 cm long; pedicels 2-10 mm long, puberulent. Sepals 8-10, oblong-ovate, 2.5-3.5 mm long, 1.6-2 mm wide, variegated with reddish stripes on some sepals, puberulent, at apex acute; petals oblong-ovate to oblong-lanceolate, 5-7 mm long, 2-3 mm wide, yellow, abaxially variegated with marginal reddish stripes, glabrous, at apex antipetalous ones 4-5 mm long, glabrous, with filaments tapering, with anthers yellow; nectariferous

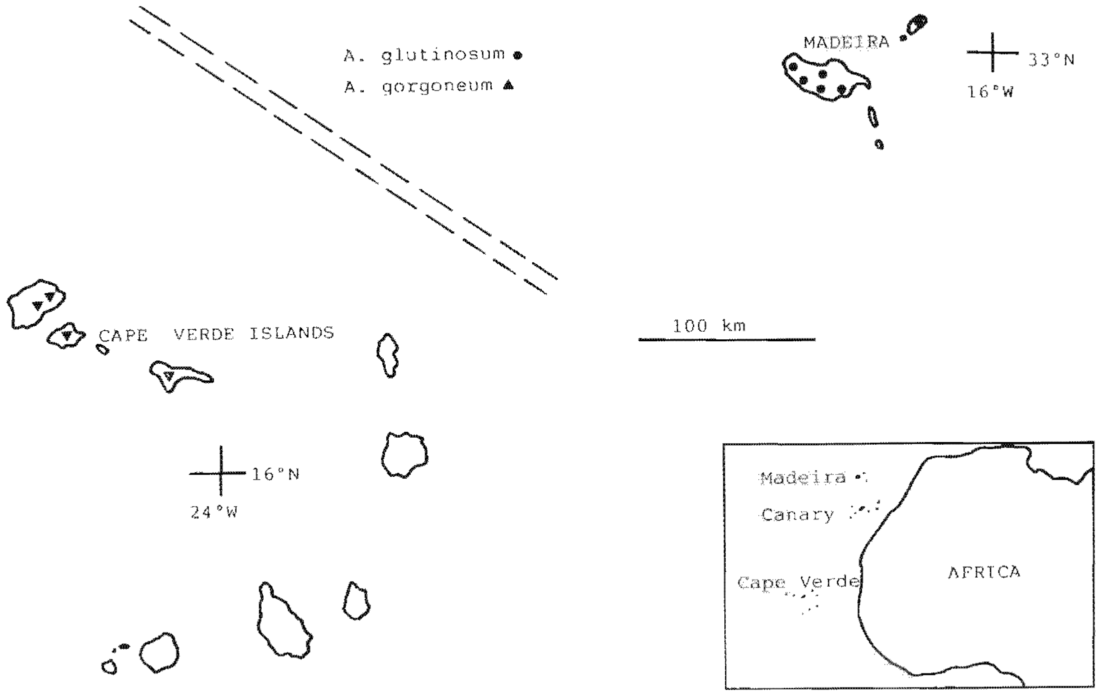


Fig. 24. Distribution of *Aeonium* section *Pittonium* in Macaronesia.

glands cuneate-quadrate, 0.5-0.8 mm wide and 0.4-0.5 mm tall, yellow, at apex emarginate; carpels with ovaries 2-2.5 mm long, 1-1.5 mm diam., glabrous, with styles 1-3 mm long. Chromosome number, *n* = 18.

Phenology. Flowering from May to August.

Distribution. (Fig. 24). On cliffs, ravines, rocks, and rocky banks; 0-1500 m; Madeira archipelago, especially common on the south side of Madeira.

Representative specimens. Portugal. Madeira. Funchal, 11 Jul 1900, *Bornmuller s.n.* (JE, WRSL); above Funchal, Aug, 1905, *Bornmuller s.n.* (GH); between Pau Bastiao and Fajo do Cedro Gordo, *Hampshire 8* (BM); Ridge E of Pico do Facho, *Hampshire 132* (BM); Ponta do Gargjau, *Hampshire 170* (BM); Ponta Delgada, 25 Jul 1968, *Hansen s.n.* (C); Ribeira Brava, Lems 7555 (MICH); near Funchal, *Liu 2703* (OS); Porto Moniz, *Liu 3326* (OS); Serra de Agua, 2 Jul 1957, *Malmberg s.n.* (H); Ribeira de S. Jorge, 8 Jul 1866, *Mandon s.n.* (W); near Funchal, 11 Jun 1895, *Murray s.n.* (MO); Road to Curral from S Antonio, *Pickering 45* (BM); E of Areiro, *Rustan 85* (O); E of Camara de Lobos, *Rustan 95* (O).

Named for its sticky nature.

Aeonium glutinosum is distinct in this section, and can be separated from the remaining species by its extremely sticky surfaces, brownish streaked and scatter-teethed leaves, and extremely lax inflorescence.

The growth form of *Aeonium glutinosum* varies from subsessile rosettes to much branched subshrubs. In a general way these habit difference are correlated with habitat. Subsessile rosettes are associated with cliff habitats, and few branches are produced. In this respect, it resembles *A. cuneatum*, and the species were actually placed closely in Praeger's 1932 treatment (they are different in all other aspects, however). The stem of *A. glutinosum* is also visible when it is subsessile. The suberect and branched condition is associated with open and flat rocky habitats, whereas the short-stemmed, much branched, and sprawling condition is found in intermediate habitats, *i.e.*, banks, ravines, and ruggy rocky areas.

Aeonium glutinosum hybridizes with *A. glandulosum* (see under this taxon), and possibly with *Greenoria aurea* (Praeger 1932).

18. *Aeonium gorgoneum* J. A. Schmidt, Beitr. Fl. Cap Verd. Ins. 258. 1852. *Sempervivum gorgoneum* (J. A. Schmidt) J. A. Schmidt *ex* Cout., Herb. Gorg. Cat. 1:285. 1914. TYPE: Cape Verde Islands, San Antonio, Mar 1851, *J. A. Schmidt s.n.* (type specimen not located). No type material of this species has been found in J. A. Schmidt's herbarium at C, GOET, HBG, and W.

Perennial terrestrial subshrubs. Stems up to 2 m tall, fruticose with acroramous branches; branches usually in groups, 0.5-1.5 cm diam., ascending, green to yellowish-orange to grayish-brown, glabrous, smooth; bark fissured irregularly; leaf scars distinct to indistinct, usually apart, narrowly transversely to transversely elliptic-rhombic, 4-9 mm wide and 1-4 mm tall; bundle scars usually indistinct. Leaf rosettes 9-20 cm diam.; phyllotaxy 5/13. Leaves oblanceolate-spathulate to spathulate, 5-10 cm long, 1.5-3 cm wide, narrowly transversely rhombic in cross-section, 3-6 mm thick, green, strong glaucous, often with reddish margin and midrib line, glabrous, at base cuneate, at apex mucronate, at margin ciliate with straight to curved conical unicellular trichomes c. 0.5 mm long. Inflorescence pyramidal, 5-8 cm long, 7-10 cm diam.; peduncles 5-8 cm long; pedicels 1-8 mm long, glabrous. Sepals 8-10, elliptic, 2-3 mm long, 0.8-1 mm wide, often variegated with red, glabrous, at apex acuminate; petals oblong-lanceolate, 5-6 mm long, 1-1.5 mm wide yellow, variegated with red, glabrous, at apex acuminate and sometimes recurved; stamens with interpetalous ones 5-6 mm long, with antipetalous ones 5.5-6.5 mm long, with filaments glabrous, slightly tapering, with anthers yellow; nectariferous glands quadrate, 0.6-0.8 mm long, 0.3-0.5 mm wide, at apex crenulate; carpels with ovaries c. 3 mm long, c. 1.5 mm diam., glabrous, with glands, with styles c. 2 mm long. Seeds c. 0.5 mm long, 0.2 mm diam. Chromosome number, $n = 18$.

Phenology. Flowering from October to February.

Distribution. (Fig. 24). On rocks and cliffs, 300-1300m; in San Antonio San Nicolau, and San Vicente of the Cape Verde Islands.

Representative specimens. Cape Verde Islands. San Antonio. Lombo do Mar, near Ribeira de Adriao, *Rustan & Brochmann 1330* (O); Ribeira do Paul, *Sunding 2677* (O); Cova, *Sunding 3485* (O); Ribeira das Pedras, *Sunding 3534* (O); upper part of Ribeira das Pedras, *Sunding 3539* (O). San Nicolau. Monto Gordo, 9 Dec 1953, *Lindberg s.n.* (H); Agua des Patas, *Sunding 3749* (O); Monte Gordo, *Sunding 3794* (O). San Vicente. Mt. Verde, 29 Dec 1974, *Gilli s.n.* (W), *Sunding 262* (O).

Named from an old designation of the Cape Verde Islands.

The occurrence of *Aeonium* species in the Cape Verde Islands is another example of a Macaronesian phytogeographical distribution (Sunding 1979). *Aeonium gorgoneum* does not have any close relative, and its extremely glaucous leaves and reddish leaf margin distinguish it from the remaining species of the same section.

It leaf characters relate this species to section *Leuconium*, but its yellow flowers and pyramidal inflorescence relate it to section *Aeonium*. Most of the combined features mentioned above in this species are also seen in other species of section *Pittonium*, and this may suggest that sections *Aeonium*, *Leuconium*, and *Pittonium* might have evolved from the similar stock with a divergence of two former section in the Canary Islands.

19. *Aeonium leucoblepharum* Webb *ex* A. Rich., Tent. fl. abyss. 1:314. 1848. *Sempervivum chrysanthum* Hochst. ex Britten in Oliver, Fl. trop. Afr. 2:400. 1871; *nom. superfl. Aeonium chrysanthum* (Hochst. *ex* Britten) A. Berger in Engl., Nat. Pflanzenfam. ed. 2, 18a:432. 1930. *Sempervivum leucoblepharum* (Webb *ex* A. Rich.) Hutch. & E. A. Bruce, Bull. Misc. Inform. 1941:89. 1941. TYPE: Ethiopia, *G. H. W. Schimper 838* (lectotype, here designated: P!; isolectotype: G! FI! K! W!; paralectotype: *R. Ouartin, L. Dillon & Petit s.n.*, P!).

Sempervivum chrysanthum var. *glandulosum* Chiov., Nuovo Giorn. Bot. Ital. n. s. 25:154. 1918. *Aeonium leucoblepharum* f. *glandulosum* (Chiov.) Praeger, Acc. Sempervivum 166. 1932. *Aeonium leucoblepharum* var. *glandulosum* (Chiov.) Cuf. Enum. pl. Aethopiae 22. 1969. TYPE: Ethiopia, Soira, 5 Dec 1905, *G. Dainelii and O. Marielli s.n.* (holotype: FI!).

Perennial terrestrial subshrubs. Stems up to 2 m tall, fruticose with acroramous branches, erect to decumbent; branches usually in groups, 0.7-2 cm diam., ascending to decumbent, pale green to light brown, with leaf base marks on pale green portion, glabrous, smooth; bark fissured irregularly; leaf scars distinct, very shallowly obtriangular, 4-8 mm wide and 1-1.5 mm tall; bundle scars distinct. Leaf rosettes 10-20 cm diam.; phyllotaxy 5/13. Leaves oblanceolate- to obovate-spathulate, 5-12 cm long, 1.5-3.5 cm wide, narrowly transversely elliptic in cross-section, 2-5 mm thick, slightly recurved, yellowish-green to dark green, usually with reddish tinge on abaxial surface, sometimes with reddish margins, and sometimes variegated with brownish pigmented stripes on abaxial surface, glabrate, at base cuneate, at apex acuminate, at margin ciliate with straight or curved conical unicellular trichomes 0.4-1 mm long. Inflorescence ovoid to dome shaped, 8-18 cm long, 8-15 cm diam.; peduncles 3-15 cm long, sometimes with tannic stripes; pedicels 1-6 mm long, very sparsely puberulent to densely puberulent with multicellular trichomes less than 0.1 mm long, sometimes with tannic stripes. Sepals 7-10, ovate, 1.7-3.5 mm long, 1-2.1 mm wide, sometimes variegated with red (or orange) at margin, and sometimes with tannin stripes, very sparsely puberulent to pubescent, at apex acute; petals elliptic-lanceolate, 6-8 mm long, 1.8-2.3 mm wide, yellow, sometimes variegated with red, glabrous, at apex retuse; stamens with interpetalous ones 6.5-8 mm long, with antipetalous ones 6-7.5 mm long, with filaments glabrous to sparsely puberulent, with anthers yellow; nectariferous glands quadrate, 0.4-0.7 mm tall, 0.5-1 mm wide, yellow, at apex emarginate to obcordate; carpels with ovaries 2.5-4 mm long, 1.5-2 mm diam., glabrous, with styles 2-3 mm long. Chromosome number, $n = 18$.

Phenology. Flowering from September to April.

Distribution. (Fig. 25) Common on rocks, banks, and cliffs; 2000-3500 m; in Yemen and eastern Africa (Ethiopia, Somalia, Kenya, and Uganda).

Representative specimens. Ethiopia. Begemder. Simen national park, *Heinonen 1092* (H); Simien mountain, *Nievergelt 1149* (EA); Balageze river valley, *Selassie 664* (ETH). Gojjan. Debre Markos Awraja,

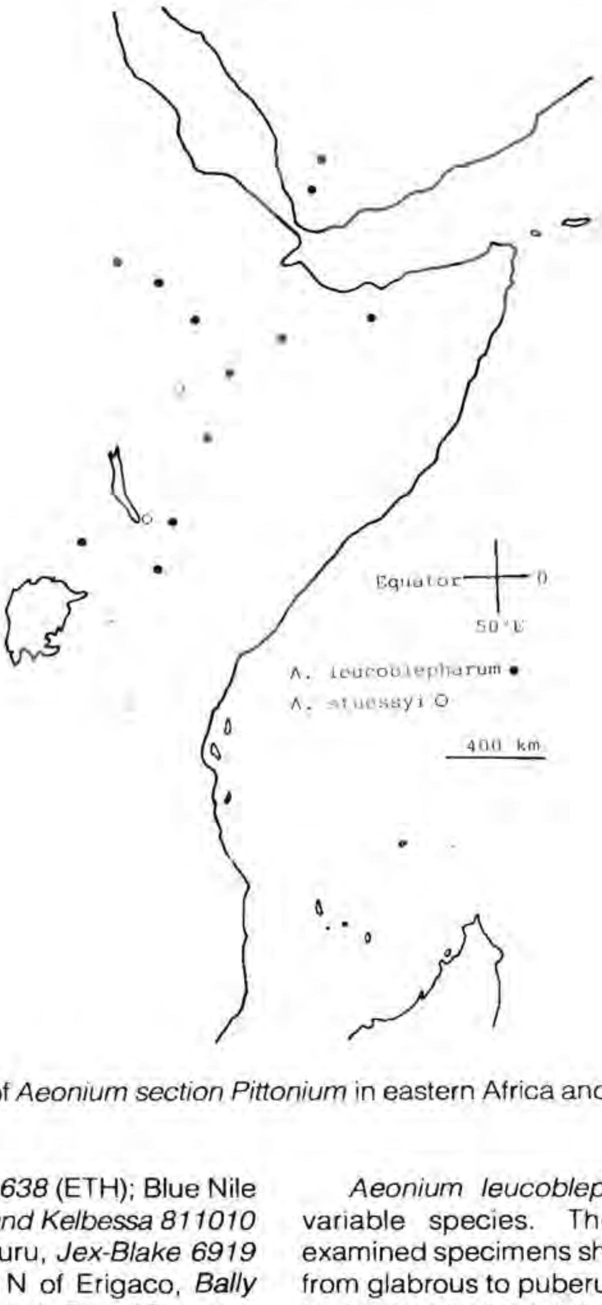


Fig. 25. Distribution of *Aeonium section Pittonium* in eastern Africa and Yemen.

Mesfin and Kagnew 1638 (ETH); Blue Nile Gorge, *Puff, Mantell, and Kelbessa 811010* (ETH). Kenya. Samburu, *Jex-Blake 6919* (K). Somalia. 18 mi N of Erigaco, *Bally 10356* (EA, K); Gaah Libah Forest Reserve, *Bally 11790* (K); *Bally and Melville 16213* (EA, G, K). Uganda. Karamoja District, Sogolimen Peak, *Bally 12733* (K). Yemen. Ascent to Sumara pass, *Lavranos 15996* (E, MO); Naguil Sumara, *Lavranos 16227* (K); W Spur of Jebel Sumarah, *Radcliffe-Smith and Henchie 4699* (K).

Named for the white cilia on the leaf margins.

Aeonium leucoblepharum is a very variable species. The sepals in the examined specimens show great variation from glabrous to puberulent, and this may be the result of hybridization between this species and *A. stuessyi*, or perhaps the result of local populational genetic drift due to isolation. Much more study, especially on living material, is needed to resolve this question. Besides the sepal vestiture, three populations worth further comments. The Uganda specimen is with densely glandular-pilose inflorescence; the Somalia specimens are with dull green leaves; and the specimen from Jebel Sumarah of

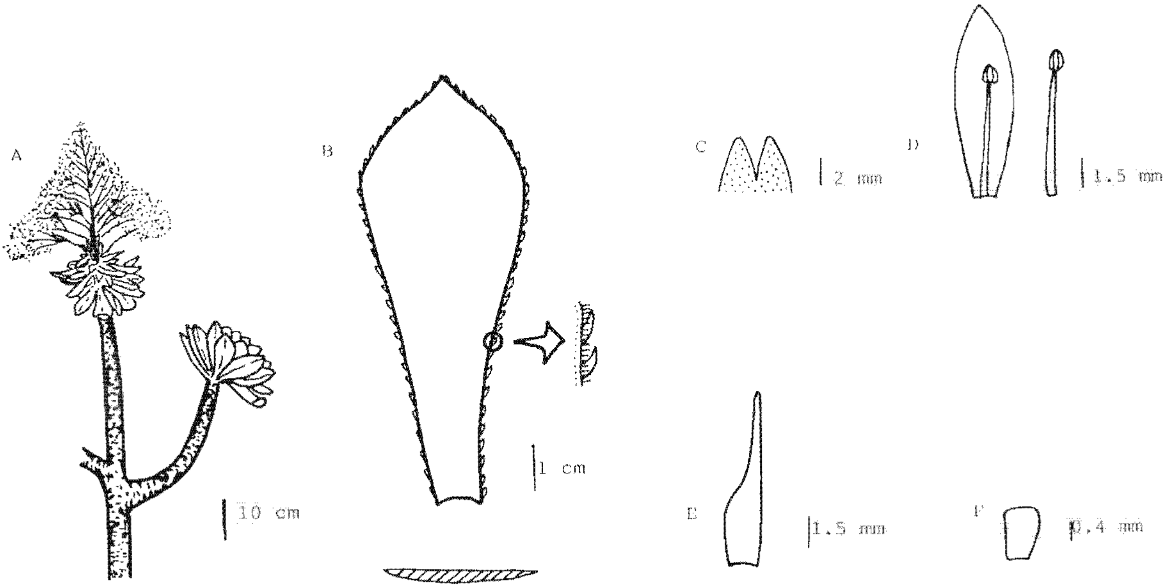


Fig. 26. *Aeonium stuessyi*. A, habit; B, leaf; C, sepals; D, petal and stamens; E. carpel; F, nectariferous gland.

Yemen is with caespitose habit. However, due to poor or incomplete preservation of above specimens, the formal recognition of the variability is not warranted at the present stage.

This species is closely related to *A. stuessyi* and can be separated from the latter by its glabrate leaves. Geographically, *A. leucoblepharum* is more northern and eastern except the questionable Uganda population. Ecologically, *A. leucoblepharum* is terrestrial whereas *A. stuessyi* is basically epiphytic.

There are two specimens in Richard's herbarium at Paris with the handwritten name of this species. *Schimper 838* was chosen as the lectotype since it was listed as "*Sempervivum chrysanthum* Hochst. in *pl. Schimp. Abyss.* sect. II. 838" in the original publication and definitely a type.

20. *Aeonium stuessyi* H.-Y. Liu, *sp. nov.*
TYPUS: Tanzania, Arush National Park, *D. Vesey-FitzGerald 6398* (holotype: EA!; isotype: K!)

Ab *A. leucoblepharum* foliis viscidis, puberulis differt.

Perennial epiphytic subshrubs. Stems up to 2 m tall, fruticose with acroramous branches; branches usually in groups, 1-2 cm diam., ascending to decumbent, green to yellowish green to grayish-brown, glabrous, smooth; bark fissured irregularly; leaf scars distinct, narrowly transversely elliptic, 3-9 mm wide and 0.5-2 mm tall; bundle scars indistinct. Leaf rosettes 10-20 cm diam.; phyllotaxy 5/13. Leaves oblanceolate- to obovate-spathulate, 5-12 cm long, 2.5-3.5 cm wide, narrowly transversely rhombic-obtriangular, 3-5 mm thick, sometimes with a central adaxial shallow groove, straight or slightly incurved with the apex recurved, yellowish-green to dark green, usually with reddish margin, puberulent, with multicellular trichomes 0.06-0.1 mm long, at base cuneate, at apex acute to acuminate, at margin ciliate with straight or curved conical unicellular trichomes 0.4-1 mm long. Inflorescence 8-18 cm long, 8-18 cm diam.; peduncles 3-15 cm long; pedicels 1-6 mm long, sparsely puberulent. Sepals 7-11, 2-3 mm long, 1.5-2 mm wide, green, sometimes variegated with reddish midvein, sparsely puberulent; at apex acute to retuse; petals obovate-elliptic, 7-8 mm long, 1.5-2.5 mm wide, yellow, variegated with reddish lines, glabrous, at apex retuse; stamens with interpetalous ones 6.5-7.5 mm long, with antipetalous ones 7-8 mm long, glabrous, with anthers yellow; nectariferous glands quadrate, 0.6-1.1 mm tall, 0.5-1 mm wide, yellow, at apex crenulate; carpels with ovaries 3.5-5 mm long, 1.5-2.5 mm diam., glabrous, with styles 2.5-3.5 mm long. Chromosome number unknown. Fig. 26.

Phenology. Flowering from August to April.

Distribution. (Fig. 25). Common on trees, occasionally on rocks; in the highlands of East Africa (Ethiopia, Kenya, and Tanzania), 2000-3000 m.

Representative specimens. Ethiopia. near Ankobar, *Ash 2354* (EA, ETH, MO); Wofasha forest, *Mooney 6992* (EA, ETH). Kenya. Mathews Range, *Aicher s.n.* (EA).

Named after Tod F. Stuessy, professor of Botany at the Ohio State University, who introduced the author to the world of *Aeonium*.

Aeonium stuessyi is related to *A. leucoblepharum* (see that species discussion for difference).

VII. *Aeonium* sect. *Leuconium* A. Berger in Engl., Nat. Pflanzenfam. ed. 2, 18a:429. 1930. LECTOTYPE (here designated): *Aeonium ciliatum* Webb & Berth.

Aeoniom sect. *Urbica* (Christ) Praeger, Acc. Sempervivum 166. 1932. *Sempervivum* L. sect. *Aeonium* (Webb & Berth.) Webb *ex* Christ *Urbica* Christ, Bot. Jahrb. 9:118. 1888; *stat. tax. non indic.* TYPE: *Aeonium urbicum* (Chr. Smith *ex* Hornem.) Webb & Berth.

Perennial terrestrial subshrubs. Stems monocaulous or acroramously branching; surface reticulate, with distinct leaf scars and cicatrices. Leaf rosettes lax, with the center not flattened, young leaves arising suberectly. Leaves at margin often reddish and with conical unicellular trichomes. Inflorescence a terminal panicle, usually dome-shaped, with bracts decreasing in size along inflorescence axes. Petals white, rarely pale yellow, often with pink streaks on the central region.

Named for the white petals.

Taxa within this section have complicated relationships and usually have more than two or three closely related taxa. Although some taxa might be better reduced to varietal rank, it is difficult to resolve this problem with current available data. Hence, no change for these taxa has been recommended at this time.

21. *Aeonium lancerottense* (Praeger) Praeger, Acc. Sempervivum 190. 1932. *Sempervivum lancerottense* Praeger, Trans. & Proc. Bot. Soc. Edinburgh 29:207. 1925. TYPE: Spain, Canary Islands, Lanzarote, near Haria, 1924, *R. L. Praeger s.n.* (type specimen not located at DBN and K, where Praeger's Canarian specimens were deposited; the description may have been based on living material only).

Perennial terrestrial subshrubs. Stems up to 60 cm tall, fruticose with acroramous branches; branches at interval, 7-15 mm thick, ascending, pale brown to silver gray to silver, glabrous, rough; adventitious roots common; bark fissured irregularly, with reticulate lines slightly elevated, leaf scars transversely depressed trullate to obtrullate, 3-8 mm wide and 1-3 mm tall. Leaf rosettes 10-18 cm diam.; phyllotaxy 8/21. Leaves obovate to oblanceolate-spathulate, 5-9 cm long, 1.5-4 cm wide, narrowly transversely semi-elliptic with upper side flattened or

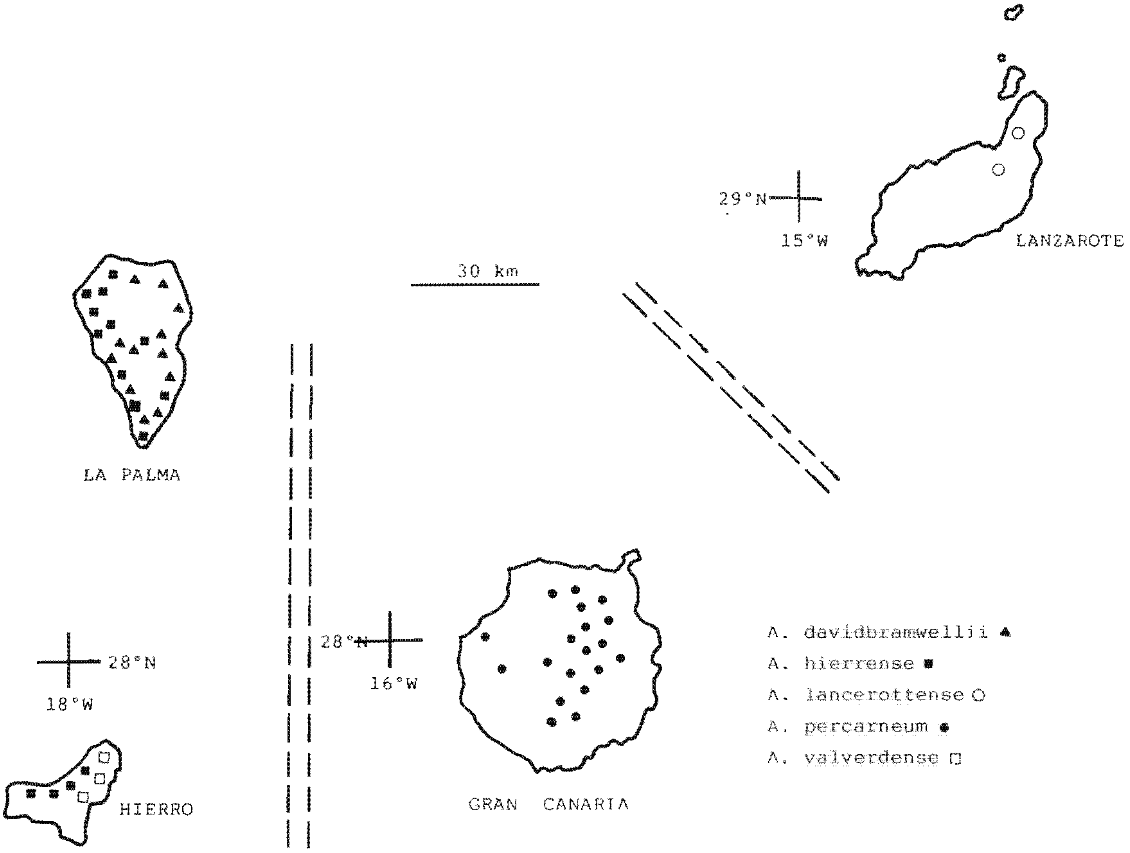


Fig. 27. Distribution of *Aeonium* section *Leuconium* in Gran Canaria, Hierro, Lanzarote, and La Palma (the Canary Islands).

slightly concave in cross-section, 3-6 mm thick, often slightly folded near the apex, green to yellowish green, often with reddish tinge abaxially, and with reddish line near the apex adaxially, glabrate, glaucous, at base cuneate, at apex caudate, at margin weakly denticulate with wrinkly conical unicellular trichomes at the denticulate tips. Inflorescence dome-shaped, 8-30 cm long, 8-25 cm diam.; peduncles 6-20 cm long; pedicels 1-3.5 mm long, glabrous. Sepals 7-8, triangular, 1.7-3 mm long, 1-1.5 mm wide, puberulent to glabrate, at apex acuminate, sometimes variegated with pinkish lines on veins; petals linear-lanceolate, 6-9 mm long, 1-1.5 mm wide, whitish, median portion variegated with pink, glabrous, at apex acuminate; stamens with interpetalous ones 6-8 mm long, with antipetalous ones 5-6 mm long, with filaments glabrous, whitish, tapering, with anthers yellow to pinkish; nectariferous glands quadrate, 0.5-0.7 mm long, 0.5 mm wide, whitish, at apex cordate; carpels with ovaries 2.5-3 mm long, 1.5 mm diam., glabrous, with styles 3-4 mm long, sometimes marked with few pinkish lines. Seeds c. 0.5 mm long, 0.2 mm diam. Chromosome number, $n = 18$.

Phenology. Flowering from March to July.

Distribution. (Fig. 27). Common on rocks, rocky slopes, and crevices, usually along streams or near water source; 200-600 m; in the north sector of Lanzarote, Canary Islands.

Representative specimens. Spain. Canary Islands. Lanzarote. 25 m below Mirador de Haria, *Evans 400* (OS); cliffs of Famara, *Evans 410* (OS); at the road S of Haria, 6 Feb 1961, *Humnel s.n.* (S);

Mozaga near San Bartolome, *Lems 7665* (MICH); near Haria, *Liu 2636* (OS); 120 ft above Haria, 8 Apr 1954, *Pickering s.n.* (BM, F).

Named for Lanzarote, where it is endemic.

Aeonium lancerottense can be distinguished from the remaining members of section *Leuconium* by its silver stems, weakly denticulate leaves, and weakly developed conical trichomes at the leaf margins. *Aeonium lancerottense* resembles *A. haworthii* and *A. percarneum.* Besides the characters mentioned above, *A. lancerottense* can be distinguished from *A. haworthii* by its compact, dome-shaped inflorescence (not very lax or hemispherical), and rather smooth stem, and from *A. percarneum* by its smaller, glabrous petals and stamens.

22. *Aeonium haworthii* Salm-Dyck *ex* Webb & Berth., Hist. Nat. Isles Canaries 3(2.1):193. 1840. *Sempervivum haworthii* Salm-Dyck, Hort. dyck. 253. 1834; *nom. nud. Sempervivum haworthii* (Webb & Berth.) Salm-Dyck *ex* Christ, Bot. Jahrb. Syst. 9:118. 1888. TYPE: Spain, Canary Islands, Tenerife, Buenavista, collector and date unknown; cultivated in Webb's own garden at Milford, England (type specimen not located in the Webb herbarium; the description may have been based on living material only).

Perennial terrestrial subshrubs. Stems up to 60 cm tall, fruticose with acroramous branching; branches c. 0.4 cm diam., slender, ascending or pendent, tortuous, brown to gray, glabrate, more or less smooth to rough, surface with reticulate lines slightly crackered; adventitious roots abundant; bark fissured, fissures mainly longitudinal and along the leaf bases; leaf scars transversely elliptic, c. 2 mm wide and 1 mm tall. Leaf rosettes 6-11 cm diam.; phyllotaxy 5/13. Leaves obovate, 3-5.5 cm long, 1.5-3 cm wide, depressed obovate in cross-section, 2.5-4 mm thick, sometimes slightly folded near the apex, green, weakly to strongly glaucous, glabrate, at base cuneate, at apex acute to caudate, at margin ciliate with curved conical unicellular trichomes 0.4-0.8 mm long. Inflorescence lax, hemispherical, 6-16 cm long, 6-16 cm diam.; peduncles 1-15 cm long; pedicels 2-12 mm long, glabrous. Sepals 7-9, triangular, 3-4 mm long, 1.5-2 mm wide, green, sometimes orange-red, variegated glabrous, at apex acuminate; petals lanceolate, 7-9 mm long, 1.2-1.8 mm wide keeled, pale yellow to whitish, pinkish, variegated, glabrous, at apex acuminate, at margin serrulate; stamens with interpetalous ones 7-8 mm long, with antipetalous ones 5.5-7 mm long, with filaments whitish to pinkish, tapering, glabrate to sparsely puberulent, with anthers pale yellow, pinkish to whitish; nectariferous glands quadrate, c. 0.8 mm wide and 0.5 mm tall, at apex obtuse to cordate; carpels with ovaries c. 3.5 mm long, 1.5 mm diam., glabrous, with styles c. 3.5 mm long, glabrate to sparsely puberulent. Seeds 0.4 mm long, 0.2 mm diam. Chromosome number, $n = 36$.

Phenology. Flowering from April to July.

Distribution. (Fig. 28). Common on rocks and dry cliffs; 0-1000 m; in the eastern and western end (Anaga and Teno regions) of Tenerife, Canary Islands.

Representative specimens. Spain. Canary Islands. Tenerife. Barranco de Buenavista, *Aldridge 1651* (BM, MO, RNG); Los Silos, 8 May 1933, *Asplund s.n.* (G, S); Buensvista, 19 May 1846, *Bourgeau 739* (G, GH); 2 km W of Buenavista, *Evans 387* (OS), *Evans 394* (OS); near Carrizal Alto, *Liu 2573* (OS); El Palmar, *Liu 2574* (OS); Masca, Liu 3179B (OS); Taganana, 17 Jul 1858, *Lowe s.n.* (LE); Chamorga and path to Casillas, *Lems 7432* (MICH); Palmar, 1 Jun 1901, *Murray s.n.* (BM).

Named after Adrian H. Haworth (1768-1833), British gardener and entomologist.

No type material has been found during a personal visit to the Webb herbarium (FI), where Webb deposited most of his specimen, nor in other herbaria which were obtained on loan. The name was used as a garden name before Webb and Berthelot validly published it. It first appeared as *Sempervivum haworthii* in a garden list prepared by Salm-Dyck in 1834.

Aeonium haworthii is unique in section *Leuconium* by having petal color varying from yellow to white. In this species the yellow petals are usually associated with strongly glaucous leaves, whereas white petals are associated with weakly glaucous leaves. This variation suggest that *A. haworthii* connects section *Leucnnium* with sections *Aeonium* and *Pittonium*. This connecting position and its restricted and disjunctional distribution on the oldest regions of Tenerife, suggest that *A. haworthii* may possibly be a relic species and near to the ancestor of section *Leuconium*. Its tetraploid chromosome number, however, suggests that it is a chromosomally derivated taxon.

Aeonium haworthii closely resembles *A. castello-paivae* and *A. decorum*. These three species are smaller, much branched, and have tortuous branches in comparison to other *Leuconium* species. Also, these three species tend to have the largest flowers within section *Leuconium*. *Aeonium castello-paivae* can be distinguished from *A. haworthii* by its glabrate stem (not puberulent), limp leaves, and greenish-white petals (neither pink-variegated nor pale yellow to white). *Aeonium decorum* can be further distinguished by its strongly cracked surface reticulate pattern on the stem away from the cicatrices (slightly tuberculated and adjacent to cicatrices in *A. haworthii*, and smooth and adjacent to cicatrices in *A. castello-paivae*), and puberulent leaves (not glabrate). In addition, *A. decorum* can be distinguished from *A. castello-paivae* by its firm, and often reddish leaves. Also, *A. castello-paivae* and *A. decorum* differ from *A. haworthii* by having puberulent stamens and carpels.

Aeonium haworthii also resembles *A. lancerottense*, and the former can be distinguished by its tuberulated ,stem surface (not smooth), entire and strongly ciliated leaf margin (not denticulate and very weakly ciliated), and strongly branched stems (usually with more than 30 branches per individual in *A. haworthii* and less than 10 branches in *A. lancerottense).*

This species hybridizes with A. sedifolium (see discussion under this taxon), *A. ciliatum*, *A. urbicum*, and *Greenovia dodrentalis* (Praeger 1929). Praeger (1929) suggested that there was an extensive hybridization among *A. ciliatum*, *A. haworthii*, and *A. urbicum*, but it is difficult to estimate the extent. These three species are extremely similar to each other and the variational range of each species has still not been fully understood due to their perennial habit and the absence of leaves during the flowering period (when collection are usually made). The names *Aeonium* x *hawbicum* Bramwell & Rowley, *A.* x *tenensis Bramwell & Rowley, and A.* x *teneriffae* Bramwell & Rowley (Jacobsen & Rowley 1973) were not validly published because of no type and/or no Latin diagnosis. x *Greenonium rowleyi* Bramwell (Jacobsen & Rowley 1973) and x *Greenonium lambii* Voggenreiter (1975), both designated for the intergeneric hybrid, were not validly published too because no type was indicated.

23. *Aeonium urbicum* (Chr. Smith *ex* Hornem.) Webb & Berth., Hist. Nat. Iles Canaries 3(2.1):194. 1841. *Sempervivum urbicum* Chr. Smith *ex* Hornem., Enum. pl. hort. hafn. suppl. 60. 1819. TYPE: Spain, Canary Islands, Tenerife, Urbicum [Laguna],

1815, *Chr. Smith s.n.* (holotype: not located, but presumably at C; isotype: BM!).

Sempervivum retusum Haw., Philos. Mag. Ann. Chem 1:125. 1827. *Sempervivum urbicum* var. *retusum* (Haw.) DC, Prodr. 3:411. 1828. TYPE: cultivated plant, introduced from Tenerife, Canary Islands in 1824 (not located, the description may have been based on living material only, or the specimen may have been destroyed by H. Fielding; see discussion under *A. spathulatum).*

Perennial terrestrial subshrubs. Stems up to 2 m tall, unbranched or rarely with acroramous branches, 1.5-3 cm diam., erect, pale brown to gray, glabrous; with surface reticulate lines smooth; bark smooth or slightly fissured; leaf scars transversely depressed obtrullate, 5-8 mm wide and 1-2 mm tall. Leaf rosettes 15-32 cm diam.; phyllotaxy 8/21. Leaves obovate-oblanceolate to oblanceolate, 8-18(-25) cm long, 3-4.5(-5.5) cm wide, narrowly transversely oblong in cross-section, 4-7 mm thick, green, glaucous, glabrate, at base cuneate, at apex apiculate, at margin ciliate with more or less straight conical unicellular trichomes 0.5-1 mm long. Inflorescence dome-shaped, 15-75 cm long, 10-45 cm diam.; peduncles 3-15 cm long; pedicels 2-6 mm long, glabrous. Sepals 8-10, triangular, 2-3 mm long, 1-1.5 mm wide, sometimes variegated with reddish margin, glabrous, at apex acuminate; petals lanceolate, 7-10 mm long, 1.2-2 mm wide, whitish, median portion pink-variegated, glabrous, at apex acuminate; stamens with interpetalous ones 7-10 mm long, with antipetalous ones 6-8 mm long, with filaments glabrous, whitish, tapering, with anthers pale yellow to whitish; nectariferous glands quadrate, c. 1 mm tall and wide, whitish, at apex cordate; carpels with ovaries 3.5-4.5 mm long, c. 2 mm diam., glabrous, with styles 4-6 mm long. Seeds c. 0.5 mm long, 0.2 mm diam. Chromosome number, $n = 18$.

Phenology. Flowering from April to October.

Distribution. (Fig. 28). Common on rocks, cliffs, walls, and roofs; 0-1900 m; on Tenerife and Gomera, Canary Islands.

Representative specimens. Spain. Canary Islands. Gomera. Fortaleza de Chipude, *Lems 7363* (MICH). Tenerife. Valle de Orotava, 29 Apr 1933, *Asplund s.n.* (G, S); Montes de Anaga, 16 May 1933, *Asplund s.n.* (G); Tegueste, *Bornmuller 656* (GH); Santa Cruz, *Bornmuller 2349* (GH, JE, LE, MO, W, WRSL); Laguna, Apr 1845, *Bourgeau 76* (BM, E, G, LE, LY, WRSL), 16 Jun 1855, *Bourgeau 1290* (BM, C, F, G, GH, JE, W); Palmar, *Burchard 329* (E, F, G, S); Montana de Taco, *Ehrendorfer, Fischer, Krendl, and Niklfeld 4* (W); Barranco del Infierno, 19 May 1977, *Gilli s.n.* (W); 2 km S of El Roque, *Evans 373* (OS); 1 km from Tamaimo, *Evans 384* (OS); Icod de Los Vinos, *Hansen 83* (C); Puerto de La Cruz, *Hansen 1055* (C); slope to the sea at Garachico, 22 Oct 1971, *Hansen s.n.* (C); above Los Silos, 21 May 1957, *Larsen s.n.* (C); trail to Masca, *Lems 7381* (MICH); near Mirador Cruz del Carmen, *Liu 2541* (OS); between Santiago del Teide and Masca, *Liu 2563* (OS); Masca, *Liu 3174* (OS); Laguna, 10 Apr 1894, *Murray s.n.* (G), 10 Mar 1855, *Perraudiere s.n.* (G); Orotava, Mar 1925, *Praeger s.n.* (K).

Named after the town Urbicum (Laguna), where this species was first collected.

Christen Smith collected and distributed specimens of this species to several institutions in 1815. Smith died in the following year on a botanical expedition to the Congo and was not able to publish the new species. Hornemann (1819) published this species based on Smith's collection and designated herbarium name, but no specimen has been found at C (Hansen 1978) where Hornemann placed Smith's specimen. A specimen at British Museum was apparently a part of Smith's collection, and can be regarded as an isotype.

This species is closely related to *A. hierrense* and *A. ciliatum*. It can be distinguished from *A. hierrense* by its glabrous flowers. It differs from *A. ciliatum* by its smooth bark, glabrous flowers, and broader petals.

Populations in Gomera are slightly different from Tenerife populations by its thicker and more glaucous leaf.

See under the previous species and *A. sedifolium* for information about hybrids with *A. urbicum*. Praeger (1929, 1932) indicated that there is an extensive hybridization between *A. ciliatum* and *A. urbicum,* and this seems a quite common phenomenon in Anaga region.

24. *Aeonium gomerense* (Praeger) Praeger, Proc. Roy. Irish Acad. 38B: 473. 1929. *Sempervivum gomerense* Praeger, Trans. & Proc. Bot. Soc. Edinburgh 24:205. 1925. TYPE: Spain, Canary Islands, Gomera, Degollada de San Sebastian, 1924, *R. L. Praeger s.n.* (type not located at DBN and K where Praeger Canarian specimens were deposited; it is assumed that Praeger described the species from cultivated material).

Perennial terrestrial subshrubs. Stems up to 2 m tall, fruticose with acroramous branches; branches usually at intervals, 3-15 mm diam., slender, ascending or pendent, pale brown to gray, glabrous, rough, with surface reticulate lines slightly cracked; bark fissured; leaf scars transversely depressed obtrullate, 2-5 mm wide and 1-3 mm tall. Leaf rosettes 10-28 cm diam.; phyllotaxy 8/21. Leaves obovate to oblanceolate, 5-14 cm long, 2.5-4 cm wide, narrowly transversely rhombic in cross-section, c. 3-7 mm thick, green, glaucous, glabrate, at base cuneate, at apex acuminate and often recurved, at margin ciliate with more or less straight conical unicellular trichomes 0.5-1 mm long. Inflorescence dome-shaped, 15-40 cm long, 10-30 cm diam.; peduncles 10-20 cm long; pedicels 2-6 mm long, glabrous. Sepals 7-9, triangular, 3-4 mm long, 1-1.5 mm wide, glabrous, at apex acuminate; petals lanceolate, 8-10 mm long, 1.5-2 mm wide, whitish, with abaxial median portion green-variegated, glabrous, at apex acuminate; stamens with interpetalous ones 7-8.5 mm long, with antipetalous ones 6-7 mm long, with filaments glabrous, whitish, tapering, with anthers whitish; nectariferous glands quadrate, c. 0.7 mm tall and 1 mm wide, whitish, at apex cordate; carpels with ovaries c. 3.5 mm long, 1.5 mm diam., glabrous, styles c. 3.5 mm long. Chromcsome number, *n* = 18.

Phepology. Flowering from April to June.

Distribution. (Fig. 28). On rocks, dry cliffs, or among bushes, not common; 500-1100 m; on Gomera, Canary Islands.

Representative specimens. Spain. Canary Islands. Gomera. La Fortaleza, near Chipude, 6 Sep 1957, *Gillie s.n.* (BH); Barranco de La Villa, Degollada de San Sebastian, *Liu 3124* (OS).

Named after the island of Gomera, where it was first collected by Praeger in 1924.

There are only two populations found in Gomera, one near Fortaleza and another in Barranco de la Villa. Both places are called Degollada de San Sebastian. These two populations are extremely similar in their vegetative and reproductive parts, although the La Villa population is taller and with more lax branches. The population near Fortaleza grows abundantly with *A. decorum* and *A. urbicum* and approaches the intermediate form of those two species. This intermediate population and its

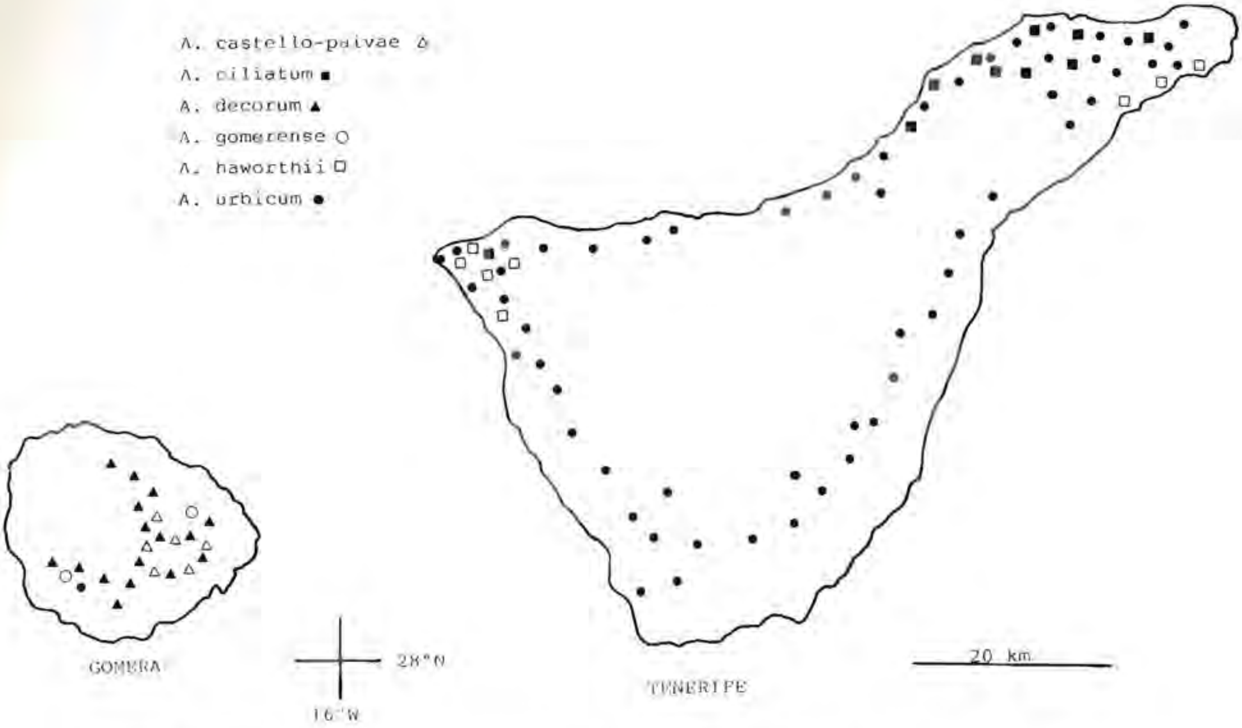


Fig. 28. Distribution of *Aeonium* section *Leuconium* in Gomera and Tenerife, the Canary Islands.

extreme rareness suggests it might be a hybrid. However, neither of *A. decorum* nor *A. urbicum* has greenish white petals and would be unlikely to produce a hybrid with such features. An experimental study is needed to test the hypothesis of hybrid origin. *Aeonium canariense* var. *subplanum* which has yellowish-green petals and in abundant near both locations of *A. gomerense*, should also be incorporated into any future hybridization study to learn what role it might have played, if any.

25. *Aeonium ciliatum* Webb & Berth., Hist. Nat. Iles Canaries 3(2.1):195. 1841. *Sempervivum ciliatum* Willd., Enum. pl. hort. reg. berol. 508. 1809; *non* Gilib. 1782. TYPE: Spain, Canary Islands, Tenerife, 1807, *P. Broussonet s.n.* (holotype: B; IDC 7440.651:IV.1; isotype: LE!).

Perennial terrestrial subshrubs. Stems up to 1 m tall, fruticose with acroramous branches; branches at intervals, 0.5-2 cm diam., ascending, pale brown to gray, glabrous, rough; adventitious roots Common; with surface reticulatre lines tubercular; leaf scars transversely elliptic, 3-5 mm wide and 1-3 mm tall, slightly elevated; bark fissured. Leaf rosettes 8-20 cm diam.; phyllotaxy 8/21. Leaves obovate- to oblanceolate-spathulate, 4-12 cm long, 2-5 cm wide, transversely depressed obtrullate in cross-section, 4-8 mm thick, often slightly folded near the apex, dark green to yellowish-green, glabrate, glaucous, at base attenuate-cuneate, at apex acute and often slightly recurved, at margin ciliate with conical unicellular trichomes 0.4-0.8 mm long. Inflorescence dome-shaped, 15-40 cm long, 10-35 cm diam.; peduncles 5-20 cm long; pedicels 2-4 mm long, puberulent. Sepals 7-9, triangular, 2.5-3 mm long, 1-1.5

mm wide, puberulent, at apex acuminate; petals lanceolate, 7-10 mm long, 1.2-2 mm wide, slightly keeled, whitish, abaxial median portion green-variegated, sparsely puberulent on abaxial surface, at apex acuminate; stamens with interpetalous ones 5-8 mm long, with antipetalous ones 4-6.5 mm long, with filaments sparsely puberulent, whitish, tapering, with anthers pale yellow to whitish; nectariferous glands quadrate, 0.6-0.8 mm tall and 0.8-1 mm wide, whitish, at apex cordate; carpels with ovaries 2.5-4 mm long, c. 1.5 mm diam, glabrous, with styles 2.5-5 mm long. Seeds c. 0.5 mm long, 0.2 mm diam. Chromosome number, $n = 18$.

Phenology. Flowering from March to July.

Distribution. (Fig. 28). Common on rocks, soil banks, and cliffs, especially common in the montane forest belt; 200-1000 m; in Anaga region and along northeastern coasts of Tenerife (rare in Teno region); Canary Islands. Voggenreiter (1974) has provided another distributional map for this species.

Representative specimens. Spain. Canary Islands. Tenerife. Los Silos, 8 May 1933, *Asplund s.n.* (S); Montes de Anaga, 16 May 1933, *Asplund s.n.* (S); Near Afur, *Evans 351* (OS); Masca, *Evans 375* (OS); between Las Canteras and Las Mercedes, *Lems 5527* (MICH); between Bajamar and Punta Hidalgo, *Liu 2519* (OS); near Taganama, *Liu 3152* (OS); Taganama, 1 Apr 1855, *Perraudiere s.n.* (GH, MO).

Named for the ciliated leaf margin, which is also common on most of the other *Aeonium* species.

Aeonium ciliatum is closely related to *A. percarneum* (see under that species for their differences), *A. davidbramwellii*, *A. gomerense*, and *A. urbicum*. *Aeonium ciliatum* can be distinguished from *A. davidbramwellii* by its tuberculate stems (not smooth), glabrate and deep-green leaves (not puberulent and often brownish), and glabrous carpels; from *A. gomerense* by its strongly corrugated stem surfaces (not rather smooth), deep-green and somewhat spathulate leaves (not light-green and much broader, somewhate obovate), puberulent flower parts (not glabrous); and from *urbicum* by its tuberculate, branched stems (not smooth and unbranched), pubescent sepals and anthers (not glabrous), and linear-lanceolate petals (not lanoeolate).

See under *A. haworthii and A. urbicum* for hybridization information.

26. *Aeonium percarneum* (R. P. Murray) Pit. & Proust, Iles Canaries 191. 1908. *Sempervivum percarneum* R. P. Murray, J. Bot. 37:201. 1899. TYPE: Spain, Canary Islands, Gran Canaria, Caldera de Bandama, 28 Apr 1892, *R. P. Murray s.n.* (lectotype, here designated: BM!; isolectotype: K[2]!; paralectotype: Caldera de Bandama, 10 May 1892, *R. P. Murray s.n.*, K[2]!; Guia, 20 May 1892, *R. P. Murray s.n., BM! E! K!).*

Sempervivum percarneum (R. P. Murray) Pit. & Proust var. *guiaense* Kunkle, Cuad. Bot. Canar. 28:59. 1977. TYPE: Spain, Canary Islands, Gran Canaria, Barranco de Guia, *G. Kunkle 17220* (holotype: BM!; isotype: G!).

Perennial terrestrial subshrubs. Stems up to 1.5 m tall, fruticose with acroramous branches, or rarely unbranched; branches in interval, 0.7-2 cm diam., ascending, light brown to gray, glabrous; with surface reticulate lines smooth; bark smooth or slightly fissured; leaf scars transversely depressed obtrullate, 3-13 mm wide and 1-4 mm tall. Leaf rosettes 8-20 cm diam.; phyllotaxy 8/21. Leaves obovate- to oblanceolate-spathulate, 4.5-10 cm long, 2-4 cm wide, transversely depressed obtrullate with the upper side concave in cross-section, 3-6 mm thick, more or less straight, dark green, with reddish margin, and usually with reddish tinge, glaucous, glabrate, at base cuneate, at apex caudate, at margin subentire to weakly denticulate with curved conical unicellular trichomes 0.5-1 mm long, or sometimes without trichomes. Inflorescence dome-shaped, 10-30 cm long, 10-25 cm diam.; peduncles 8-20 cm long; pedicels 1-3 mm long, puberulent. Sepals 8-10, triangular, 2-3 mm long, 0.8-1.5 mm wide, green, puberulent, at apex acuminate; petals lanceolate, 7-8 mm long, 1.2-1.8 mm wide, whitish, median portion pink-variegated, sparsely puberulent on abaxial surface, at apex acuminate; stamens with interpetalous ones 6-7 mm long, with antipetalous ones 5-6 mm long, with filaments whitish to pinkish, sparsely puberulent, with anthers yellow to whitish; nectariferous glands quadrate, 0.5-0.8 mm tall and wide, greenish, at apex cordate; carpels with ovaries 2-3 mm long, 1-1.5 mm diam., pinkish, glabrous, with styles 3-4 mm long. Seeds c. 0.6 mm long, 0.2 mm diam. Chromosome number, $n = 18$.

Phenology. Flowering from April to June.

Distribution. (Fig. 27). Common on rocks, and sometimes on roofs; 100-1300 m; on Gran Canaria, Canary Islands; often associated with *Euphorbia* scrub.

Representative specimens. Spain. Canary Islands. Gran Canaria. Barranco de Fataga, *Aldridge 1557* (BM, MO, RNG); Cuesta de Silva, 23 May 1933, *Asplund s.n.* (G, S); Caldera de Bandama, 20 May 1900, *Bornmuller s.n.* (GH); Barranco de Tirajana, *Burchard 324* (E, F, G, S); Caldera, *Cook 672* (F, MO); above Santa Lucia, *Evans 253* (OS); above Hotel los Ferciles, Tafira Alta, *Evans 255* (OS); Tafira, in Monte Sicoo, 24 Jun 1931, *Frey and Sova s.n.* (H); Custa Silva, 2 May 1897, *Gelert s.n.* (C); Cenobio, *Kunkel 11012* (G); Tafira Alta, *Kunkel 14315* (G); between Tenor and Valleseco, *Kunkel 17306* (G); Barranco Dolores, *Lems 7790* (MICH); Tentiniguada, *Liu 3025* (OS);

Named for the reddish tinge of the leaves.

Several of Murray's specimens with the name *Sempervivum percarneum* were found at BM, E, and K. All agree with the description and locality mentioned in Murray's (1899) paper, and should be treated as syntypes, a lectotype has been selected from them.

The conical unicellular trichomes on the leaf margins of *Aeonium percarneum* occasionally are missing. This condition was also observed in some populations of *A. castello-paivae*. In both cases, the leaf margin was entire, and not weakly denticulate as in *A. lancerottense*. Also, the trichomeless condition in both species are usually found in some, not all, leaves of an individual. The trichomeless population of *A. percarneum* in Guia was called var. *guiaense* previously.

Aeonium percarneum resembles *A. lancerottense* (see dissusion under *A. lancerottense* for their differences), *A. ciliatum*, *A. davidbramwellii*, and *A. urbicum*. *Aeonium percarneum* can be distinguished from *A. ciliatum* by its smooth stems (not tuberculate), purplish tinged leaves, pinkish petals, and puberulent and filiform filaments (not glabrous and tapering); from *A. davidbramwellii* by its much branched and taller stems, glabrate leaves, and by puberulent and filiform filaments; from *A. urbicum* by its often branched stems, purplish-tinged leaves, pubescent sepals, narrower and puberulent petals, and puberulent and filiform filaments. Occasionally, the stems of *A. percarneum* are unbranched and the leaves become green without typical purplish tinge; hence, an individual of that nature becomes monocarpic and can only be distinguished from *A. urbicum* by floral characters.

See under *A. simsii*, *A. canariense* var. *virgineum*, and *A. undulatum* for information about known hybridization.

27. *Aeonium decorum* Webb *ex* Bolle, Bonplandia 7:240. 1859. *Sempervivum decorum* (Webb *ex* Bolle) Christ, Bot. Jahrb. Syst. 9:161. 1888. TYPE: Spain, Canary Islands, Gomera, Barranco del Agua, 4 Apr 1845, *E. Bourgeau 141* (lectotype: FI!; isolectotype: BH! BM! G! K! LE! LY! WRSL!).

Perennial terrestrial subshrubs. Stems up to 60 cm tall, fruticose with acroramous branches; branches c. 0.6 cm diam., slender, ascending or pendent, tortuous, pale reddish green to whitish, glabrous, rough; adventitious roots abundant; with surface reticulate lines ribbed and cracked, away from cicatrices; bark slightly fissured; leaf scars transversely depressed obtrullate, 3-4 mm wide and 1-1.5 mm tall. Leaf rosettes 5-10 cm diam.; phyllotaxy 5/13. Leaves obovate-oblanceolate to oblanceolate, 2.5-5 cm long, 1-1.5 cm wide, depressed obovate in cross-section, 2.5-4.5 mm thick, often slightly folded near and recurved at the apex, dark green to yellowish-green, with reddish margin, and often with reddish tinge, glaucous, puberulent with multicellular trichomes 0.05 mm long or less, at base cuneate, at apex acuminate, at margin ciliate with few scattered unicellular trichomes c. 0.5 mm long. Inflorescence lax, cylindric, 8-30 cm long, 8-20 cm diam.; peduncles 10-30 cm long; pedicels 2-10 mm long, puberulent. Sepals 6-8, triangular, 3-4 mm long, 1-1.5 mm wide, green, red-variegated, puberulent, at apex acuminate; petals lanceolate, 7-8 mm long, 2-2.5 mm wide, whitish, with median portion pink-variegated, sparsely puberulent on abaxial surface, at apex acuminate; stamens with interpetalous ones 6-7 mm long, with antipetalous ones 5-6 mm long, with filaments sparsely puberulent, whitish, tapering, with anthers pale yellow to whitish; nectariferous glands quadrate, c. 0.5 mm tall, 1 mm wide, whitish, at apex crenulate; carpels with ovaries 2-3.5 mm long, c. 1.5 mm diam., pubescent, with styles 3-4 mm long. Seeds c. 0.5 mm long, 0.2 mm diam. Chromosome number, $n = 18$.

Phenology. Flowering from April to June.

Distribution. (Fig. 28). Common on rocks, dry cliffs, and walls; 100-900 m;on Gomera, Canary Islands.

Representative specimens. Spain. Canary Islands. Gomera. road from San Sebastian to Benchijigua, *Aldridge 1198* (MO, RNG); Valle Gran Rey, *Borgen 1751* (O); near Agando, *Charpin 18702* (G); Roque Agando, *Charpin 18703* (G); Barranco de Hondura, *Cuatrecasas 280* (MAF); below Arure, *Evans 195* (OS); Barranco de La Laja, *Evans 430* (OS); 1 km S of Arure on road to Valle Gran Rey, *Evans 441* (OS); near Chipude, *Kunkel 18332* (G); upper part of the Barranco de La Villa, *Lems 7215* (MICH); Barranco de Argaga, *Lems 7306* (MICH); Tagamiche, *Lems 7326* (MICH); Barranco de la Villa, *Lems 7330* (MICH); between Tagamiche to Arure, *Lems 7357* (MICH); near Agando, *Liu 2606* (OS); Barranco de La Laja, 28 May 1894, *Murray s.n.* (BM); Lomo de Fragoso, Mar 1906, *Pitard s.n.* (G, MO); 9.5 km from San Sesbastian, on the road to Hermigua, *Sunding 4248* (O); La Orilla between Arure and El Cercado, *Sunding 4305* (O).

Named for its attractive appearance.

Aeonium decorum is related to *A. castello-paivae* and *A. haworthii*, and possibly to *A. gomerense*. See under *A. haworthii* for a more detailed discussion of the differences among these taxa. *Aeonium decorum* can be distinguished from *A.* gomerense, its another relative, by its strongly cracked stem pattern around the leaf bases, by its puberulent leaves, and by its pinkish petals.

Aeonium decorum is reported to hybridize with *A. castellopaivae* and *A. canariense* var. *subplanum* (Bañares 1986). The binominal name *A.* x *castellodecorum* Bañares and *A.* x *beltranii* Bañares have been provided for these two hybrids

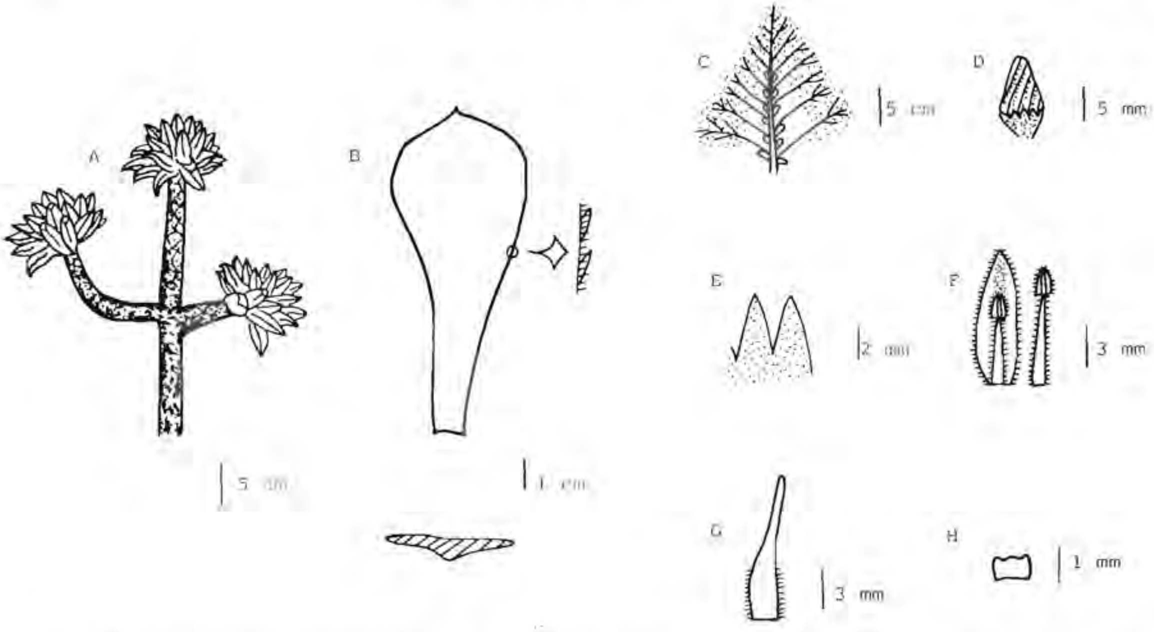


Fig. 29. *Aeonium davidbramwellii*. A, habit; B, leaf; C, inflorescence; D, bud; E, sepals; F, petal and stamens; G, carpel; H, nectariferous gland.

respectively.

28. *Aeonium davidbramwellii* H.-Y. Liu, *sp. nov.* TYPUS: Spain, Canary Islands, La Palma, near Cueva de Agua, *H.-Y. Liu 3261A* (holotype: OS!)

Ab *A. ciliatum* atque *A. percarneum* foliis puberuliis differt, a *A. valverdense* foliis purpurascentibus, obovato- vel oblanceolato-spathulatis differt.

Perennial terrestrial subshrubs. Stems up to 1 m tall, fruticose with acroramous branches, 7-25 mm diam.; branches at intervals, ascending, green to gray, glabrous; with surface reticulate lines smooth; leaf scars transversely depressed obtrullate, 3-6 mm wide and 1-2 mm tall; bark smooth or slightly fissured. Leaf rosettes 6-22 cm diam.; phyllotaxy 5/13. Leaves obovate to oblanceolate-spathulate, 3-12 cm long, 2-4 cm wide, very shallowly obtriangular in cross-section, 2-6 mm thick, sometimes slightly folded near the apex, dark green to yellow-green, with reddish margin, often with reddish or browish tinge on abaxial surface, puberulent with glandular hairs c. 0.1 mm long or less, at base attenuate-cuneate, at apex acuminate, at margin ciliate with conical unicellular trichomes c. 0.5 mm long. Inflorescence dome-shaped, 10-35 cm long, 8-25 cm diam.; peduncles 5-20 cm long; pedicels 1-3 mm long, puberulent. Sepals 6-8, triangular, 1.5-2.5 mm long, 1-2 mm wide, sometimes variegated with reddish margin, puberulent, at apex acuminate; petals lanceolate, 6.5-9 mm long, 1.5-2.5 mm wide, whitish, median portion green-variegated, sparsely puberulent on abaxial surface, at apex acuminate; stamens with interpetalous ones 6-8 mm long, with antipetalous ones 5-7 mm long, with filaments puberulent, whitish, tapering, with anthers pale yellow to whitish, puberulent; nectariferous glands quadrate, 0.5-1 mm tall and wide, whitish, at apex cordate; carpels with ovaries c. 3 mm long, 1.5 mm diam., pubescent, with styles 3 mm long. Chromosome number, $n = 18$. Fig. 29.

Phenology. Flowering March to June.

Distribution. (Fig. 27). Common on rocks, soil banks, and cliffs; 0-1000 m; on La Palma, Canary Islands.

Representative specimens: Spain. Canary Islands. La Palma. Santa Cruz, 30 Apr 1901, *Bornmuller s.n.* (G, GH, H, JE, MO, W); Fuencaliente, below Las Caletas, *Lems 7756* (MICH); 2 km S of Las Caletas, *Evans 286* (OS); 2 km from Jedey, *Evans 290* (O6); 6 km N of El Time, *Evans 294* (OS); between La Ladera and Los Llanos, *Liu 2649* (OS); Santa Cruz, May 1899, *Murray s.n.* (E); *Sunding 3092* (O).

This new species honors Dr. David Bramwell, Director of Jardin Canario, who has promoted botanical research in Macaronesia. The epithet "davidbramwellii" was selected because a name *A.* x *bramwellii* was published in 1973 by Rowley (Jacobsen & Rowley 1973). Although Rowley's name was not validly published because of failure to indicate a type, and therefore the epithet "bramwellii" could be used, but the new epithet in protologue preferable to avoid confusion.

This taxon has been referred to different species in the past. Praeger (1932) applied the name *Aeonium ciliatum* but indicated it might be deserving of varietal rank. Voggenreiter (1973) identified it as *A. gomerense* instead of *A. ciliatum*, but questioned its taxonomic status. Lems and Holzapfel (1974) believed it belonged to *A. percarneum* but also mentioned that it probably merits taxonomic recognition.

Aeonium davidbramwellii is related to *A. ciliatum*, *A. percarneum* (see under *A. ciliatum* and *A. percarneum* for discussion), *A. hierrense*, and *A. valverdense*. *Aeonium davidbramwellii* is very similar to *A. valverdene*, and can be distinguished from the latter by its purplish, narrower leaves (not brownish and less than 4 cm wide; also not with submarginal yellowish conical unicellular trichomes), often reddish sepals, and shorter petals. *Aeonium davidbramwellii* is extremely similar to *A. hierrense* in the field especially before the typical branching habit developed in *A. davidbramwellii*. When fully developed, *A. hierrense* can be easily separated from *A. davidbramwellii* by its pale green, strongly glaucous, spathulate (more lorate in *A. davidbramwellii*) and larger (usually more than 15 cm long) leaves with apex arcuate, and monocaulous stems.

This species, as *"A. ciliatum"*, has been reported to hybridize with *A. arboreum* var. *holochrysum*, *A. nobile*, *A. canariense* var. *palmense*, *A. spathulatum* and *A. sedifolium* (Praeger 1929; Santos 1983; Bañares 1986). Names *A.* x *kunkellii* Bramwell & Rowley, *A.* x *splendens* Bramwell & Rowley, and *A.* x *junionae* Bramwell & Rowley (Jacobsen & Rowley 1973) for the first three hybrids were not validly published since no types were indicated. However, *A.* x *cilifolium* Bañares is a valid hybrid name for *A. davidbramwellii* x *sedifolium*.

29. *Aeonium valverdense* (Praeger) Praeger, Proc. Roy. Irish Acad. 38B:484. 1929. *Sempervivum valverdense* Praeger, Trans. & Proc. Bot. Soc. Edinburgh 29:211. 1925. TYPE: Spain, Canary Islands, Hierro, Valverde, 1924 [herbarium specimen made in Feb 1925], *R. L. Praeger s.n.* (lectotype, here designated: K!).

Perennial terrestrial subshrubs. Stems up to 1 m tall, fruticose with acroramous branches; branches usually in groups, 1-2 cm diam., ascending, pale brown to gray, glabrous, rough; with surface reticulate lines smooth; bark fissured; leaf scars transversely depressed obtrullate, 4-8 mm wide and 1-2 mm tall. Leaf rosettes 12-25 cm diam.; phyllotaxy 5/13. Leaves obovate, 6-12 cm long, 4-6 cm wide, narrowly transversely elliptic-obtriangular in cross-section, 5-8 mm thick, green to yellowish-green, and with yellow and pink tinge, puberulent with multicellular trichomes c. 0.07 mm long or less, glaucous, at base attenuate-cuneate, at apex caudate and recurved, at margin ciliate with conical unicellular trichomes c. 1.2 mm long or less, often yellow with tannins, and often submarginal and adaxial. Inflorescence dome-shaped, 10-30 cm long, 10-25 cm diam.; peduncles 5-30 cm long; pedicels 2-4 mm long, puberulent. Sepals 7-9, triangular, 3.5-5 mm long, 1-1.5 mm wide, puberulent, at apex acuminate; petals lanceolate, 10-12 mm long, 2-2.5 mm wide, whitish, with median portion pink-variegated, puberulent, at apex acuminate; stamens with interpetalous ones 9-11 mm long, with antipetalous ones 8-10 mm long, with filaments puberulent, whitish, tapering, with anthers pale yellow; nectariferous glands quadrate, c. 0.6 mm tall and 1 mm wide, whitish, at apex cordate to crenulate; carpels with ovaries 4-5 mm long, c. 2 mm diam., puberuent, with styles 4-5 mm long, puberulent. Seeds c. 0.6 mm long, 0.2 mm diam. Chromosome number, n = 18.

Phenology. Flowering from April to May.

Distribution. (Fig. 27). Common on rocks and cliffs; 0-800 m; on Hierro, Canary Islands.

Representative specimens. Spain. Canary Islands. Hierro. track from Jinama to Fuente de Tinco, *Evans 214* (OS); 1 km E of Los Llanillos, *Evans 219* (OS); near Valverde, *Liu 3271* (OS); between Restinga and Taibique, *Sunding 3902* (O).

Named after the town of Valverde, Hierro, near which this species is abundant.

Aeonium valverdense is related to *A. davidbramwellii* (see under that species) and *A. hierrense*, and can be distinguished from the latter by its branched habit, brownish and puberulent leaves, smaller inflorescence (usually about half-sized, less than 25 cm tall), and longer petals (usually longer than 11 mm).

This species hybridizes with *A. hierrense*. Praeger (1929) indicated that there was extensive hybridization between these two species, but the present study provides no confirmation of this. Praeger left no specimens of this suspected hybrid. The author personal field work did reveal a few hybrid individuals, but no evidence for extensive hybridization has been found. *Aeonium valverdense* also hybridizes with *A. canariense* var. *palmense* (see under this taxon).

30. *Aeonium hierrense* (R. P. Murray) Pit. & Proust, Iles Canaries 191. 1908. *Sempervivum hierrense* R. P. Murray, J. Bot. 37:395. 1899. TYPE: Spain, Canary Islands, Hierro, Valverde, May 1899, *Murray s.n.* (lectotype, here designated: K!; isolectotype: BM!). Specimens at BM and K were both collected by R. P. Murray at the same time. The sheet at K has been selected as the lectotype because the label informtion is the same as that of the diagnosis in the protologue.

Perennial terrestrial subshrubs. Stems up to 1.2 m tall, unbranched or rarely with acroramous branches, 2-5 cm diam., erect, gray, glabrous; with surface reticulate lines flush with surface; bark smooth or slightly fissured; leaf scars transversely depressed obtrullate-obovate, 6-18 mm wide and 2.5-5 mm tall. Leaf rosettes 15-60 cm diam.; phyllotaxy 8/21. Leaves obovate to oblanceolate, (7-)10-30 cm long, (3-)5-8 cm wide, very shallowly obtriangular with adaxial side flattish or concave in cross-section, 3.5-7.5 mm thick, green, with reddish margin, and often with pinkish or purplish tinge, strongly glaucous, glabrate, at base cuneate, at apex caudate and often recurved, at margin ciliate with conical unicellular trichomes 1-2 mm long. Inflorescence dome-shaped, 15-50 cm long, 12-50 cm diam.; peduncles 5-25 cm long; pedicels 2-6 mm long, puberulent. Sepals 6-9, triangular, 2.5-3 mm long, 1-1.5 mm wide, puberulent, at apex acuminate; petals lanceolate, 7-9 mm long, 1.5-2 mm wide, whitish, with the median portion pink-variegated, puberulent on abaxial surface, at apex acuminate; stamens with interpetalous ones 7-9 mm long, with antipetalous ones 5.5-7 mm long, with filaments puberulent, whitish, tapering, with anthers pale yellow; nectariferous glands quadrate, c. 0.4 mm tall and 0.6 mm wide, whitish, at apex cordate to crenulate; carpels with ovaries c. 3.5 mm long, 1.5 mm diam., pubescent, with styles c. 3.5 mm long. Seeds 0.5 mm long, 0.2 mm diam. Chromosome number, $n = 18$.

Phenology. Flowering from April to May.

Distribution. (Fig. 27). Common on soil banks and cliffs; 200-1200 m on Hierro and 0-1000 on La Palma, Canary Islands.

Representative specimens. Spain. Canary Islands. Hierro. between Valverde and Tinor, *Bornmuller 2353* (G, GH, JE, LE, MO, W); Valverde *Burchard 396* (E, F, G, S); 3 km below Tinor, *Evans 209* (OS); 1 km E of Los Llanillos, *Evans 219A* (OS); S. S. W of Valverde, 31 Jul 1957, *Gillie s.n.* (BH); between Tinor and Valverde, *Lems 6104* (MICH); Mirador Pinar, *Liu 3269* (OS). La Palma. La Galga, *Liu 2651* (OS); Neve de Agua, *Liu 3261A* (OS).

Named after the island of Hierro, where this species was first found.

Beside *A. davidbramwellii* and *A. valverdense* (see under these species), *Aeonium hierrense* is closely allied to *Aeonium urbicum* and *A. percarneum*. It can be distinguished from *A. urbicum* by the bigger stem diameter (usually more than 3 cm thick), the heaveily glaucous and red-tinged leaves, and the pubescent flowers. It differs from *A. percarneum* by its commonly unbranched and thicker stem, larger and wider obovate leaves, and tapering and pubescent filaments.

La Palma and Hierro populations differ in vegetative size, the latter is larger in stem diameter (usually more than 5 cm in diam.) and leaf size and thickness. The La Palma population, formely recognized as *A. urbicum* by Praeger (1932), although widely spread, is poorly collected and needs an additional study.

A fasciated form has been reported from Sabinosa (Praeger 1932).

See under *A. canariense* var. *palmense* and *A. valverdense* for information about hybridization.

31. *Aeonium castello-paivae* Bolle, Bonplandia 7:240. 1859. *Sempervivum castello-paivae* (Bolle) Christ, Bot. Jahrb. Syst. 9:161. 1888. TYPE: Spain, Canary Islands, Gomera, Hermigua and Valhermoso, 1856, *C. Bolle s.n.*; and cultivated in the botanical garden in Berlin (type specimen not located at B). It is assumed that the specimen was probably destroyed during the World War II or no herbarium specimen was made ever.

Sempervivum paivae R. Lowe, Bot. Mag. 82:*t.5593*. 1866. *Aeonium paivae* (R. Lowe) Lem., Pl. grasses 14. 1869. TYPE: Spain, Canary Islands, Gomera, Hermigua valley, no date, *Lowe s.n.* (holotype: K!).

Perennial terrestrial subshrubs. Stems up to 70 cm tall, fruticose with acroramous branches; branches 3-8 mm diam., slender, ascending or pendent, tortuous, green to pale brown to gray, puberulent below leaf rosettes, surface reticulation indistinct, more or less smooth; adventitious roots abundant; bark fissured in plates; leaf scars depressed obovate, c. 1 mm wide and 0.7 mm tall. Leaf rosettes 3-7 cm diam.; phyllotaxy 5/13. Leaves obovate-spathulate, 1.5-3.5 cm long, 0.8-2 cm wide, narrowly transversely elliptic in cross-section, 2-3 mm thick, occasionally slightly folded near the apex, pale green to yellowish green, and somtimes variegated with few reddish lines on the abaxial surface, glabrate, glaucous, at base cuneate, at apex acuminate to caudate, at margin ciliate with straight conical unicellular trichomes less than 0.2 mm long, sometimes without trichomes. Inflorescence lax, hemispherical, 6-20 cm long, 6-20 cm diam.; peduncles 7-25 cm long; pedicels 1-2 mm long, puberulent. Sepals 7-9, triangular, 2.5-3.5 mm long, 1.2-2 mm wide, green, puberulent, at apex acuminate; petals linear-lanceolate, 8-10 mm long, 1-1.5 mm wide, greenish-white, puberulent, at apex acuminate; stamens with interpetalous ones 6-7 mm long, with antipetalous ones 5-6 mm long, with filaments whitish to pinkish, puberulent, tapering, with anthers white to pale yellow; nectariferous glands quadrate, 0.8-1.5 mm wide and 0.7-1 mm tall, pinkish, at apex rounded or cordate; carpels with ovaries c. 3 mm long, 1.5 mm diam., pubescent, with styles c. 3 mm long, puberulent. Seeds c. 0.5 mm long, 0.2 mm diam. Chromosome number, $n = 18$.

Phenology. Flowering from March to August.

Distribution. (Fig. 28). Common on rocks, soil banks, and cliffs; 200-900 m; on Gomera, Canary Islands.

Representative specimens. Spain. Canary Islands. Gomera. 3 km S of Hermigua, *Evans 205* (OS); near tunel de Heligua, *Evans 416* (OS); above Vallehermoso, *Evans 435* (OS); Monte de Agua Hilva, 13 Aug 1931, *Frey and Sora s.n.* (H); above Hermigua, near El Rejo, 27 Aug 1957, *Gillie s.n.* (BH); El Tino, *Kunkel 18443* (G); vicinity of Monteforte, *Lems 2313* (MICH), *Lems 2316* (MICH); Barranco de Villa, *Lems 6107* (MICH); Hills E of Vallerhermoso, *Lems 7343* (MICH); Le Carbonnera, *Liu 2635* (OS); Barranco de La Villa, *Liu 3115* (OS); Degollada de San Sebastian, 25 May 1894, *Murray s.n.* (BM); Hermigua, 26 May 1894, *Murray s.n.* (BM, G).

Named after Barao do Castello de Paivae, Portuguese officer who promoted scientific activities on the Canary Islands in the 19th century.

Aeonium castello-paivae closely resembles A. haworthii and *A. decorum*. See discussion under *A. haworthii* for their distinguishing features.

See under *A. canariense* var. *subplanum*, *A. decorum*, and *A. lindleyi* var. *viscatum* for information about hybridization.

EXCLUDED AND DOUBTFUL TAXA

Aeonium aizoides (Lam.) A. Berger, in Engl., Nat. Pflanzenfam. ed. 2, 18a:427. 1930. *Sempervivum aizoides* Lam., Encycl. 3:290. 1789. TYPE: cultivated in Royal Botanical Garden at Roi, not located. = *Aichryson* x *domesticum* var. *aizoides* (Lam.) Praeger, Proc. Roy. Irish Acad. 38B:20. 1928.

Aeonium bethencourtianum Webb *ex* Bolle, Bonplandia 7:243. 1859. TYPE: Spain, Canary Islands, Fuerteventura, Handia, Jul 1845, *E. Bourgeau 737* (FI!). = *Aichryson bethencourtianum* Bolle.

Aeonium burchardii (Praeger) Praeger, Proc. Roy. Irish Acad. 38B:465. 1929. *Sempervivum burchardii*

Praeger, Trans. & Proc. Bot. Soc. Edinburgh 29:202. 1927. TYPE: Spain, Canary Islands, Tenerife, Valle de Masca, Jan 1923, *O. Burchard s.n.*, cultivated in Praeger's greenhouse in Britain (type not located). A hybrid between *Aeonium sedifolium* and *A. urbicum*, see discussion under *A. sedifolium* for more information.

Aeonium domesticum (Praeger) A. Berger in Engl., Nat. Pflanzenfam. ed. 2, 18a:427. 1930. *Sempervivum domesticum* Praeger, J. Bot. 65:211. 1927. TYPE: cultivated plant. = *Aichryson* x *domesticum* (Praeger) Praeger, J. Bot. 65:211. 1927.

Aeonium exsul Bornmuller, Repert. Spec. Nov. Regni. Veg. 13:2. 1912. TYPE: cultivated plant at Gottingen, lost in a war (Praeger 1932). = a possible hybrid between *A. ciliatum* and *A. canariense* (Praeger 1932).

Aeonium mascaense Bramwell, Bot. Macaronesica 10:58. 1982. TYPE: Spain, Tenerife, Masca, 26 Mar 1969, *D. Bramwell 1386* (JVC) = *A. sedifolium* x *haworthii* (see discussion under *A. sedifolium).*

Aeonium tortuosum (Aiton) A. Berger, in Engl., Nat. Pflanzenfam. ed. 2, 18a:427. 1930. *Sempervivum tortuosum* Aiton, Hort. Kew. 2:148. 1789. TYPE: cultivated plant. = *Aichryson tortuosum* (Aiton) Praeger, Acc. Sempervivum 104. 1932.

Aeonium webbii Bolle, Bonplandia 7:238. 1859. TYPE: Cape Verde Islands, San Vicente, *Bolle s.n.* (not located). Bolle's herbarium is at B, and there is no type specimen found there. No one has ever collected this species since its first discovery. It is believed that this could be a variety of *A. gorgoneum.*

LIST OF PUBLISHED HYBRIDS

This list includes all published binominal names and formulae of hybrids, following by the literature which that name or formula first appeared. Where in the taxonomic treatment the information about that hybrid can be obtained is also added. When a name has been changed, the accepted name is placed within a bracket immediately after that name.

Aeonium x *anagensis* Bramwell & Rowley, *sin typus* (Jacobsen & Rowley 1973); see under 1a. *A. lindleyi* var. *lindleyi.*

Aeonium x *beltranii* (Bañares 1986); see under 10c. *A. canariense* var. *subplanum.*

Aeonium x *bollei* Kunkel (Kunkel 1972); see under 15. *A. undulatum.*

Aeonium x *bramwellii* Rowley, *sin typus* (Jacobsen & Rowley 1973); see under 10a. *A. canariense* var. *canariense.*

Aeonium x *bravoanum* Bramwell & Rowley, *sin typus* (Jacobsen & Rowley 1973); see under 1b. *A. lindleyi* var. *viscatum.*

Aeonium x *burchardii* (Praeger) Praeger, *pro sp.* (Praeger 1925, as *Sempervivum burchardii* Praeger); see under 3. *A. sedifolium.*

Aeonium caespitosum [= *simsii*] x

canariense (Praeger 1928); see under 5. *A. simsii*.

Aeonium caespitosum [= *simsii*] x *manriqueorum* [misidentified; = *percarneumm*] (Burchard 1929); see under 5. *A. simsii*.

Aeonium caespitosum [= *simsii*] x *mauriqueorum* [= *arboreum* var. *arboreum*] (Praeger 1929); see under 5. *A. simsii*.

Aeonium caespitosum [= *simsii*] x *percarneum* (Praeger 1929); see under 5. *A. simsii*.

Aeonium caespitosum [= *simsii*] x *spathulatum* (Praeger 1932); see under 6. *A. spathulatum*.

Aeonium caespitosum [= *simsii*] x *undulatum* (Praeger 1929); see under 5. *A. simsii*.

Aeonium canariense [= *canariense* var. *canariense*] x *cuneatum* (Praeger 1929); see under 10a. *A. canariense* var. *canariense*.

Aeonium x *castellodecorum* Bañares (Bañares 1986); see under 27. *A. decorum*.

Aeonium castello-paivae x *decorum* (Bañares 1986); see under 27. *A. decorum*.

Aeonium castello-paivae x *subplanum* [= *canariense* var. *subplanum*] (Praeger 1929); see under 10c. *A. canariense* var. *subplanum*.

Aeonium castello-paivae x *viscatum* [= *lindleyi* var. *viscatum*] (Praeger 1929); see under 1b. *A. lindleyi* var. *viscatum*.

Aeonium x *castelloplanum* Bramwell & Rowley, *sin typus* (Jacobsen & Rowley 1973); see 10c. *A. canariense* var. *subplanum*.

Aeonium ciliatum x *haworthii* (Praeger 1929); see under 22. *A. haworthii*.

Aeonium ciliatum [= *davidbramwellii*] x *holochrysun* [= *arboreum* var. *holochrysum*] (Praeger 1929); see under 14b. *A. arboreum* var. *holochrysum*.

Aeonium ciliatum [= *davidbramwellii*] x *nobile* (Praeger 1929); see under 16. *A. nobile*.

Aeonium ciliatum [= *davidbramwellii*] x *palmense* [= *canariense* var. *palmense*] (Praeger 1929); see under 10b. *A. canariense* var. *palmense*.

Aeonium ciliatum [= *davidbramwellii*] x *sedifolium* (Bañares 1986); see under 3. *A. sedifolium*.

Aeonium ciliatum x *urbicum* (Praeger 1929); see under 23. *A. urbicum*.

Aeonium x *cilifolium* Bañares (Bañares 1986); see under 3. *A. sedifolium*.

Aeonium decorum x *subplanum* [= *canariense* var. *subplanum*] (Bañares 1986); see under 10c. *A. canariense* var. *subplanum*.

Aeonium x *floribundum* A. Berger (Berger 1930); see under 6. *A. spathulatum*.

Aeonium glandulosum x *glutinosum* (Praeger 1929); see under 9. *A. glandulosum*.

Aeonium goochiae x *palmense* [= *canariense* var. *palmense*] (Praeger 1929); see under 2. *A. goochiae*.

Aeonium x *hawbicum* Bramwell & Rowley, *sin typus* (Jacobsen & Rowley 1973); see under 22. *A. haworthii*.

Aeonium haworthii x *urbicum* (Praeger 1929); see under 22. *A. haworthii.*

Aeonium hierrense x *valverdense* (Praeger 1929); see under 29. *A. valverdense.*

Aeonium hierrense x *palmense* [= *canariense* var. *palmense*] (Praeger 1929); see under 10b. *A. canariense* var. *palmense.*

Aeonium holochrysum [= *arboreum* var. *holochrysum*] x *spathulatum* var. *spathulatum* [= *spathulatum*] (Bañares 1986); see under 6. *A. spathulatum.*

Aeonium x *holospathulatum* Bañares (Bañares 1986); see under 6. *A. spathulatum.*

Aeonium x *hybridum* (Haw.) Rowley (Rowley 1969); see under 6. *A. spathulatum.*

Aeonium x *jacobsenii* Bramwell & Rowley, *sin typus* (Jacobsen & Rowley 1973); see under 10b. *A. canariense* var. *palmense.*

Aeonium x *junionae* Bramwell & Rowley, *sin typus* (Jacobsen & Rowley 1973); see under 10b. *A. canariense* var. *palmense.*

Aeonium x *kunkelii* Bramwell & Rowley, *sin typus* (Jacobsen & Rowley 1973); see under 14b. *A. arboreum* var. *holochrysum.*

Aeonium x *lambii* Bramwell & Rowley, *nom. nud.* (Jacobsen & Rowley 1973); see under 10b. *A. canariense* var. *palmense.*

Aeonium x *lemsii* Kunkel (Kunkel 1972); see under 10d. *A. canariense* var. *virgineum.*

Aeonium x *lidii* Sunding & Kunkel (Sunding & Kunkel 1972); see under 5. *A. simsii.*

Aeonium lindleyi x *tabulaeforme* [= *tabuliforme*] (Praeger 1929); see under 1a. *A. lindleyi* var. *lindleyi.*

Aeonium x *lowei* Bramwell & Rowley (Jacobsen & Rowley 1973); see under 9. *A. glandulosum.*

Aeonium x *mascaense* Bramwell, *pro sp.* (Bramwell 1982); see under 3. *A. sedifolium.*

Aeonium nobile x *palmense* [= *canariense* var. *palmense*] (Santos 1983); see under 10b. *A. canariense* var. *palmense.*

Aeonium x *nogalesii* Bañares (Bañares 1986); see under 3. *A. sedifolium.*

Aeonium x *ombriosum* Bramwell & Rowley, *sin typus* (Jacobsen & Rowley 1973); see under 29. *A. valverdense.*

Aeonium palmensis [= *canariense* var. *palmense*] x *sedifolium* (Bañares 1986); see under 3. *A. sedifolium.*

Aeonium palmense [= *canariense* var. *palmense*] x *valverdense (Praeger 1929); see under 10b. A. canariense* var. *palmense.*

Aeonium palmensis [= *canariense* var. *palmense*] x *vestitum* [= *arboreum* var. *holochrysum*] (Bañares 1986); see under 10b. *A. canariense* var. *palmense.*

Aeonium percarneum x *virgineum* [= *canariense* var. *virgineum*] (Praeger 1929); see under 10d. *A. canariense* var. *virgineum.*

Aeonium percarneum x *undulatum* (Praeger 1929); see under 15. *A. undulatum.*

Aeonium praegeri Kunkel (Kunkel 1969); see under 5. *A. simsii.*

Aeonium rowleyi Bramwell, *sin typus* (Jacobsen and Rowley 1973); see under 6. *A. spathulatum.*

Aeonium rubrolineatum [= *arboreum* var. *rubrolineatum*] x *spathulatum* var. *spathulatum* [= *spathulatum*] (Bañares 1986); see under 6. *A. spathulatum.*

Aeonium x *sanchezii* Bañares (Bañares 1986); see under 6. *A. spathulatum.*

Aeonium x *sanctisebastianii* Bramwell & Rowley, *sin typus* (Jacobsen & Rowley 1973); see under 4. *A. saundersii.*

Aeonium x *santosianum* Bramwell & Rowley, *sin typus* (Jacobsen & Rowley 1973); see under 2. *A. goochiae.*

Aeonium saundersii x *subplanum* [= *canariense* var. *subplanum*] (Praeger 1929); see under 4. *A. saundersii.*

Aeonium sedifolium x *goochiae* (Santos 1983); see under 2. *A. goochiae.*

Aeonium smithii x *spathulatum* (Praeger 1929); see under 6. *A. spathulatum.*

Aeonium spathulatum x *ciliatum* [= *davidbramwellii*] (Santos 1983); see under 6. *spathulatum.*

Aeonium spathulatum x *Greenovia diplocycla* (Santos 1983); see under 6. *A. spathulatum.*

Aeonium x *splendens Bramwell & Rowley, sin typus* (Jacobsen & Rowley 1973); see under 16. *A. nobile.*

Aeonium subplanum [= *canariense* var. *subplanum*] *viscatum* (Praeger 1929); see under 1b. *A. lindleyi* var. *viscatum.*

Aeonium x *sventenii* Kunkel (Kunkel 1972); see under 5. *A. simsii.*

? *Aeonium tabulaeforme* [= *tabuliforme*] x *urbicum* (Praeger 1929); see under 11. *A. tabuliforme.*

Aeonium x *tabulicum* Bramwell & Rowley, *sin typus* (Jacobsen & Rowley 1973); see under 11. *A. tabuliforme.*

Aeonium x *tenensis* Bramwell & Rowley, *sin typus* (Jacobsen & Rowley 1973): see under 22. *A. haworthii.*

Aeonium x *teneriffae* Bramwell & Rowley, *sin typus* (Jacobsen & Rowley 1973); see under 23. *A. urbicum.*

Aeonium x *vegamorai* Bramwell & Rowley (Jacobsen & Rowley 1973); see under1b.*A. lindleyi* var. *viscatum.*

Aeonium x *velutinum* (N. E. Br) H.-Y. Liu, *comb. nov. Sempervivum velutinum* N. E. Br., Gard. Chron. 1901, ii., 318. 1901. TYPE: Kew Gardens, 3 Apr 1882, *N. E. Br. s.n.* (holotype: K!) Praeger (1928) listed *A. velutinum* as a synonym under *Sempervivum velutinosum*, so a combination is needed to fulfill the requirement of ICBN. See discussion under *A. simsii* for further information.

Aeonium x *wildpretii* Bañares (Bañares 1986); see under 10b. *A. canariense* var. *palmense.*

? *Aeonium aurea* x *Aeonium glutinosum* (Praeger 1932); see under 17. *A. glutinosum.*

Greenovia dodrentalis x *Aeonium haworthii* (Praeger 1929); see under 22. *A. haworthii.*

Greenovia dodrentalis x *Aeonium* ? *spathulatum* (Praeger 1929); see under 6. *A. spathulatum.*

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