

Morphological and anatomical investigations of *Aretiastrum magellanicum* (Hombr. & Jacq.) Skottsbo.

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Summary: In addition to former investigations of the genus *Aretiastrum* Graebn., we analyse *Aretiastrum magellanicum* (Hombr. & Jacq.) Skottsbo. because it differs from the other species in its pappose fruits. The peculiar combination of features, including the pulvinate growth form which is characteristic for all the species, seems to be a strong argument in favor of preserving the generic status. The pulvinate growth form presents an excellent advantage to survive in the High Andes and the subantarctic climate.

Keywords: Valerianaceae, Valeriana, *Aretiastrum magellanicum*, morphology, anatomy, taxonomy, flora of South America, Andes

Aretiastrum magellanicum (Hombr. & Jacq.) Skottsbo. (*Valeriana magellanica* Hombr. & Jacq.) differs from the other species of *Aretiastrum* Graebn. in its fruits being crowned by a pappus. Since the systematical status of *Aretiastrum* Graebn. – as a distinct section of *Valeriana* or as a separate genus – has been discussed frequently, we took the chance of studying this species in its natural habitats during a visit to Argentina and Chile and collected material for detailed studies, completing former investigations (WEBERLING & UHLARZ 1977).

Materials and methods

Living and herbarized material was collected in November 2005 during a field trip in Tierra del Fuego:

Aretiastrum magellanicum (Hombr. & Jacq.) Skottsbo., Kungl. Svenska Akad. Handl. N.F. 56: 132, 1916 (*Valeriana magellanica* Hombr. & Jacq. ex Decaisne in D'Urville, Voy. au Pôle Sud 2: 54, tab. 16 B, 1853)

Weberling 10998, Tierra del Fuego, SW slope of the top of Cerro Shenolsh (54°23'17" S; 67°41'57" W), 550 m s.m., cushion-plant formation on eolic weathered marine sedimentary rocks (sandstone) of Paleocene age, leg. F. & H. Weberling & Th. Stützel 20.11.05; Weberling 11002, Tierra del Fuego, Ea. San Julio, W slope of the top of Cerro Mesa Oeste (53°41'10" S; 68°27'53" W), 230 m s.m., cushion-plant formation on eolic weathered sandstone of Miocene age, leg. F. & H. Weberling & Th. Stützel 21.11.05; Weberling 11005, Tierra del Fuego, Ea. El Salvador, W slope on the top of Cerro Cañón (53°38'27" S; 68°32'40" W), 330 m s.m., cushion-plant formation on eolic weathered sandstone of Miocene age, leg. F. & H. Weberling & Th. Stützel 21.11.05.

This material will be deposited in Munich [M]. Additional to the herbarium material studied by WEBERLING & UHLARZ in 1977, the following specimens of *A. magellanicum* were analysed:

ARGENTINA: Tierra del Fuego, Ea. Vicuña, an sonnigen Schutt- und Felshängen, 200 m s.m., 13.11.1930, A.Donat 321 [SI]; Depto. Río Grande, Ea. El Salvador, 20.11.1971, 250 m s.m., O.Boelcke, M.N.Correa & B.Piccini 15105 [BAA, BA]; Ea. Sarmiento, R.N.P. Goodall 4381 [INTA]; Prov. St. Cruz, Depto. Güer

Aike, Ea. La Verdadera Argentina, Cerro de la Virgen, ladera *N.S. Arroyo*, *O. Boelcke*, *R Gomez Moore*, Casco Estancia, 800 m s.m., 50°50'S, 72°14'W, 18.4.1977 [BAA]; Sierra Chica, Páramo Andino, 05.02.1978, *J. Ambrosetti et al. 1048* [MERL 28331]; Sierra Chica, Río Turbio, 05.02.1978, *J. Ambrosetti et al. 1050* [MERL 28334].

By mistake some of these specimens were (and in some herbaria possibly still are) determined as *Valeriana sedifolia* d'Urv. (*Aretiastrum sedifolium* [d'Urv.] Graebn.).

CHILE: Volcan Chillan, *O. Zöllner 908*, Dez. 1957 [ULM]; Tierra del Fuego: ½ Camino Puerto Clarenceia – Cerro Sombrero, *Otto Magens 1108*, 17.02.1958 [B]; (Yacimiento) Chillan [Cerro Sombrero], *Otto Magens 1421a*, 15.2.1958 [B 10 1001700].

Aretiastrum sedifolium (d'Urv.) Graebn. (*Valeriana sedifolia* Dumont D'Urville, Fl. Iles Malouines, Mém. Soc. Linn. 4: 612, 1826). Hombr. & Jacq. ex Decaisne in D'Urville, Voy. au Pôle Sud 2, 53/54, tab. 16 a, 1853.

FALKLAND ISLANDS / ISLAS MALVINAS: *Dumont D'Urville*, Typus [G]; Top of Mount Adam, 715 m.s.m., 13.12.1907, *C. Scottsberg* [SGO 58721].

Taxonomic history of the genus *Aretiastrum*

From the Ecuadorian tableland of Antisana and Assuay HUMBOLDT et al. (1818: 324) described *Valeriana aretioides* – a species characterized by its suffruticose habit, pulvinate growth and imbricate small foliage leaves. The name of the species should remind of the peculiar growth form of *Aretia*, a genus of Primulaceae. For this reason CANDOLLE (1830: 633) united *Valeriana aretioides* and *V. sedifolia* in a separate section of *Valeriana*: „Cor. 4–5 fidae, tubo longo. Flores flavi, pauci intra folia suprema occultati. Folia imbricata crasso-coriacea integerrima. Caules fruticosi“. Then he continues: „unum genus proprium?“. Later SPACH (1841: 304) classified *Aretiastrum* as a separate genus, without giving any further comment. HÖCK (1897), as well as GRAEBNER (1906a) regarded it as section of *Valeriana*, mentioning the absence of a pappus as an important character.

Area of distribution, growth form and habitat

The seven species of the genus are growing in the High Andes ranging from Colombia to Ecuador, Peru and northern Bolivia, southern to Patagonia incl. Tierra del Fuego. *A. sedifolium* is only found on the Falkland Islands (Islas Malvinas). The large gap of about 3000 km between the northern (Bolivia) and the southern part (Patagonia) of the distribution area, which was known previously, has become smaller, since *A. magellanicum* was collected in central Chile (Volcán Chillan). The altitude of the localities ranges between 3500 to 4900 m s.m. in the northern Andes and 2500 m s.m. in central Chile and 550 m s.m. or even 230 m s.m. in Tierra del Fuego, where the conditions of living (except for the diurnal rhythm) are similar to those of the northern Andes. The specimens observed in Tierra del Fuego grew in 580 m s.m. on eolic weathered, marine, sedimentary sandstone rocks of Paleocene age (Cerro Shenolsh) or in 230 m s.m. and 330 m s.m. on eolic weathered sandstone of Miocene age (Cerros Mesa Oeste and Cañón).

All species described hitherto are pulvinate plants, characterized by RAUH (1939) as „radiate branched semiglobe-shaped cushions“ (Radialvollkugelpolster). This is shown here on *A. magellanicum*, forming a dense cushion of small rosettes of altogether 20 to 25 cm in diameter and about 2–3 cm in height (fig. 1). The plant was growing on the top of Cerro Shenolsh on

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Figure 1: *Aretiastrum magellanicum*, forming a dense cushion of small rosettes of altogether ca. 20–25 cm in diameter and about 2–3 cm high.



Figure 2: Cushion-plant formation on the top of Cerro Shenolsh, 550 m.s.m., Tierra del Fuego (Parador Yawen), with dense cushions of *Aretiastrum magellanicum* (Hombr. & Jacq.) Skotts. and others. In the background the Lago Yehuin, L. Cheepelmuth, Sierra de las Pinturas, and Sierra Bridges can be seen.



Figure 3: Cushion of *Aretiastrum magellanicum*, view from the inferior side.

sandstone which was partly uncovered by climatic influences and even exhibiting vestiges of aeolic weathering (fig. 2). A view from the inferior side (fig. 3) shows 6 more or less plagiotropous, vigorous woody branches, inserted on the vigorous primary axis in a very short distance. The short main axis of about 0.6 cm in diameter was firmly anchored in the stony soil by a vigorous tap root of > 0.7 cm in diameter and 60 cm (often much more) in length. All the vigorous primary branches appear to be „bifurcated“, because of an „acrotonous-hypotonic“ ramification in terms of RAUH (1939). Although the apical part of the primary branch is already dead, the two branches still bear densely imbricate leaves in their distal parts and show further ramification. Each of the branches starts growing with a relatively thin axis, which still can be observed at its insertion on the relative main axis. The primary thickening growth increases in acropetal direction, but during the development of the terminal inflorescence it decreases again. The axils of the uppermost leaves below the inflorescence bearing buds usually continue the ramification after fruiting of the inflorescence. This periodical acrotonic ramification of all branches results in the formation of dense cushions of rosettes, which are characteristic for *Aretiastrum*.

Unlike most Valerianaceae the shoots of *Aretiastrum* seem to have an alternate phyllotaxis (fig. 5A). Cross sections of shoot tips are clearly ascribable to an oblique decussate phyllotaxis merging into a spirodecussate arrangement in *A. magellanicum*. The medial plains of the first leaf pairs do not intersect those of the next at a right angle, but show an acute respectively an obtuse angle. This kind of phyllotaxis is preserved in *Aretiastrum aschersonianum* (WEBERLING & UHLARZ 1977, fig. 6A), but proceeding one step further in *A. magellanicum*. The leaves of the same pair do not remain strictly opposite, but are displaced in a way approaching their margins on one side (spirodecussation, fig. 4). This stage can merge into a completely dispersed phyllotaxis – a

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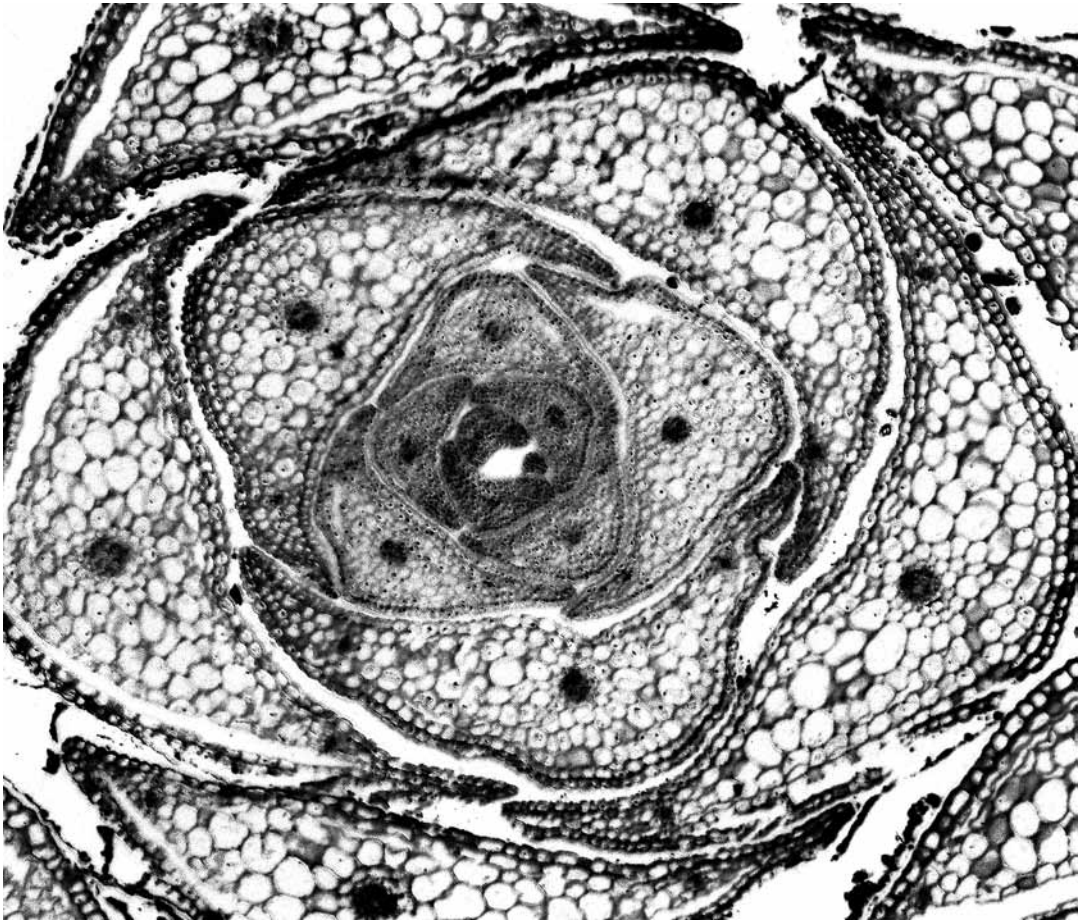


Figure 4: Cross section through a shoot of *Aretiastrum magellanicum*, showing the transition from oblique decussation to spirodecussation.

development, which can be observed in *Stangea*, *Belonanthus* and several High Andean species of *Valeriana* (RAUH & WEBERLING 1960; D. & F. WEBERLING 1981; LÖRCHER & WEBERLING 1982; LÖRCHER 1990).

The foliage leaves of *Aretiastrum* are small, only few millimeters long, dilated at the base and more or less broadly connated across the nodes. The broad basis distally passes over in a broadly linear, lanceolate, ovate or triangular, often coriaceous leaf blade, which can be basally slightly constricted into a broad petiolar zone. The latter applies to the leaves of *A. magellanicum* (fig. 5 B), which are 4 mm long, the lamina being 2 mm in diameter, ovate-rhombic in outline, tapering basally into a “petiolar zone” of 1.6 mm in diameter, the entire free part of the leaf is shortly fimbriate. The basal connate zone is only 0.2–0.3 mm high. Within this connate zone the marginal parts of the neighbouring leaves consist of three layers or the upper and lower epidermis only.

In preceding investigations (WEBERLING & UHLARZ 1977) the anatomical structure of the leaves within the genus *Aretiastrum* proved to be rather uniform. This also includes the structure of the lamina of *A. magellanicum*. It is amphistomatic (fig. 6 A, B), which corresponds to the equifacial structure of the mesophyll. In cross sections it does not show a differentiation in a palisade and a spongy parenchyma. It exhibits a tissue with large intercellular spaces and ribbons formed by

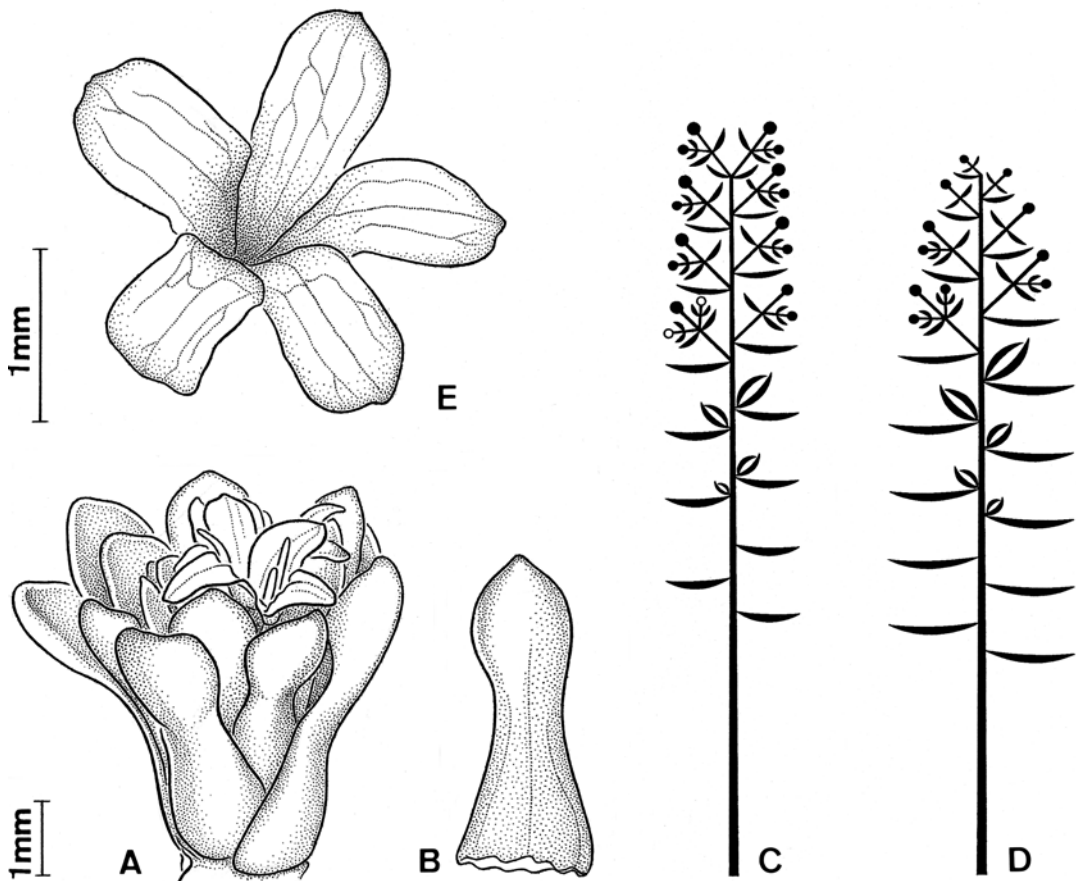


Figure 5: *Aretiasturm magellanicum*, (A) tip of a shoot terminating in a male inflorescence, (B) foliage leaf, diagrams of a richer (C) and a poorer (D) flowered inflorescence, (E) corolla of a male flower from above.

radiate elongated cells richly filled with chloroplasts, and a less extensive central tissue with only few chloroplasts. This tissue contains the main vascular bundle and two lateral bundles. They are surrounded by a parenchymatic bundle sheath (see fig. 6 A). Three bundles enter the axis.

As in the other species the epidermis cells are provided with strong walls and a considerably thickened cuticula. This applies especially to the tip of the leaf (fig. 6 C). The stomata are anomocytic, the stomatic cells are not accompanied by subsidiary cells. They are deeply sunken and provided with an outer and an inner ledge, similar to those shown in *A. aschersonianum* by WEBERLING & UHLARZ (1977, fig. 5 H). Like in *A. sedifolium* (WEBERLING & UHLARZ 1977, fig. 2 C), the peculiar annular collar surrounding the stomata, which WEBERLING & UHLARZ (1977) reported for *A. aschersonianum*, is missing. In the broad „petiolar“ zone preceding the lamina, a hypodermal layer of thick-walled cells is developed (figs. 4, 6 A).

As already reported by WEBERLING & UHLARZ (1977, fig. 8) and investigated in detail by LÖRCHER 1990: 37), *A. aschersonianum* shows an anomalous secondary growth, similar to other High Andean species of Valerianaceae. This is based on the activity of newly formed medullary cambia leading to a completely bipolar structure of the vascular bundles (see comprising internal xylem and phloem), whereas in other species only internal xylem is produced. As a consequence, the cross

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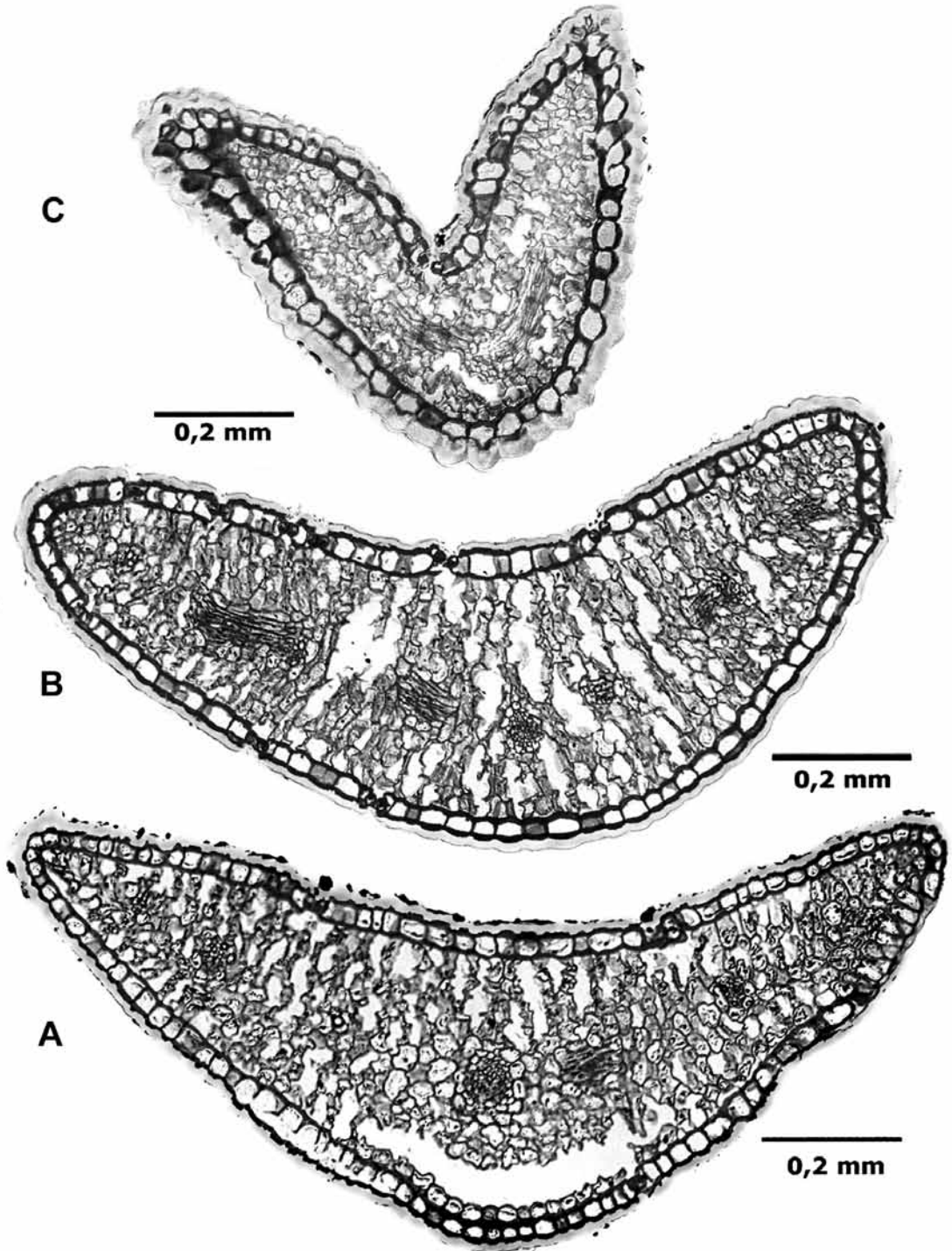


Figure 6: Cross sections through the lamina of a foliage leaves of *Aretiastrum magellanicum*, (A) transition between the "petiolar zone" and the lamina, showing the hypodermal layer, (B) lamina, (C) tip of a foliage leaf, showing the extremely thick cuticula.



Figure 7: *Aretiastrum magellanicum*, inflorescence with hermaphrodite flowers from above, showing the corollas with exserted styles and stamens.

section of vascular bundles of older rhizomes has an almost starlike shape. The independently formed medullary cambia join in ellipsoidal rings and form hadrocentric complexes. The same might be possible in *A. magellanicum*, because like in *A. aschersonianum* the older axis is surrounded by a thick mantle of periderm.

When the branches have reached a length of 1.5 or 2 cm, they usually end in a monothyrsic terminal inflorescence. Since in *Aretiastrum* the main axis of this inflorescence remains extremely short, the flowers are „hidden among the uppermost leaves“ (KILLIP 1937: 288) and the inflorescence sometimes does not comprise more than four flowers. However, the thyrsic ramification is well discernible, especially in *A. magellanicum*, which has the richest inflorescences within the genus. We found inflorescences containing up to 17 flowers arranged in triflorous or biflorous cymes, placed in the axils of linear bracts of 3 mm length and 1 mm in diameter (fig. 5 C, D).

As far as we could observe, *A. magellanicum* is polygamous-trioecious. Thus, there are bisexual, male and female flowers. The corolla of the bisexual flowers is somewhat larger than those of the male flowers, and infundibuliform. The three stamens and the style are distinctly exserted in anthesis, the style presenting a trifid stigma (fig. 7). The filaments are attached on the inner side of the corolla. That is also true for the male flowers, but the anthers remain at the entrance of the short campanulate corolla (fig. 8 D). These flowers also contain a short rudimentary style. In female flowers the campanulate corolla is slightly gibbose above its insertion (fig. 8 A). Unlike other species of the genus the fruits of *A. magellanicum* bear a pappus with 12 rays (fig. 8 B).

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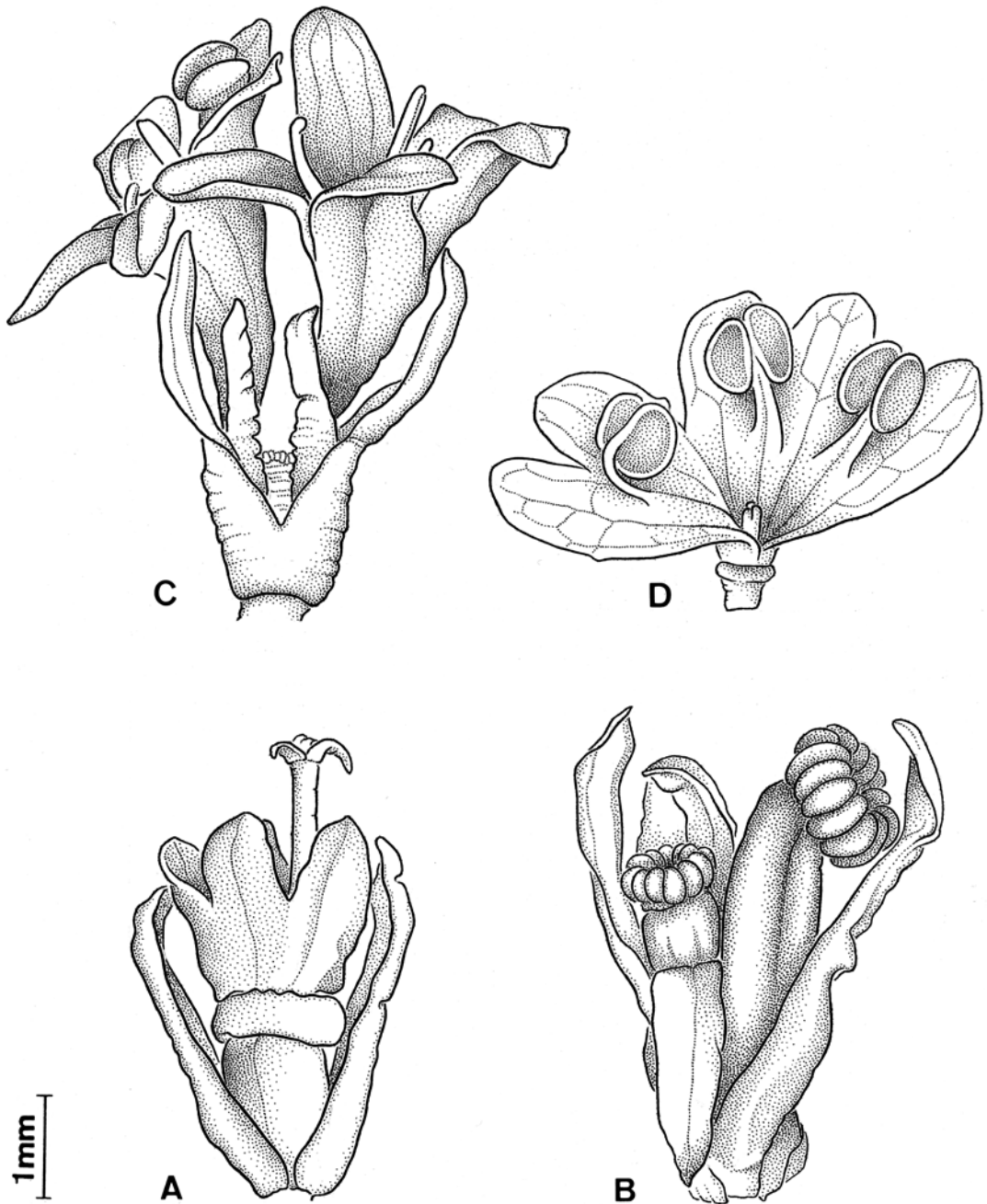


Figure 8: *Aretiastrum magellanicum*, (A) female flower with prophylls, (B) female partial inflorescence with young fruits, the larger one is 3.5 mm long (including the still involute pappus), (C) postanthesis male partial inflorescence, (D) young male flower with a rudiment of a style, the corolla measuring 2.5 mm in length.

Ecological aspects

Our field observations as well as the studies of herbarium material show that *A. magellanicum* is a characteristic element of the South Patagonian cushion-plant formations of western slopes on the tops of South Patagonian hills, exposed to strong, cold and more or less continuous



Figure 9: Cushion-plant formation on the more sheltered side of the top of Cerro Shenols, 580 m.s.m. *Aretiastrum magellanicum* together with other cushion plants like *Azorella* sp. *Oreopolus macranthus* (Phil.) Ricardi, *Saxifraga magellanica* Poir. and a considerable number of plants with diverse growth forms.

westerlies. Above all: the most exposed flanks of rocky tops, visited by us, were nearly exclusively inhabited by cushion plants, and *A. magellanicum* forms a considerable part of them. These and other cushion plants are growing on the more sheltered side as well, together with a considerable number of plants of several growth forms (fig. 9). There is no doubt about it: the growth form as hemispherical „radiate branched semiglobe-shaped cushions“ (Radialvollkugelpolster: RAUH 1939), firmly nestled against the soil, provided with a deep reaching tap root, is useful to survive in this unfavourable climate. There is also the possibility of accumulation of water preserving humus in the interior hollow space, penetrated by adventitious roots attaining up to 8 cm length and 2 mm in diameter, while the dense packing of rosettes with small leaves, well protected by thick cuticles, inhibits an excessive transpiration.

This point of view has been confirmed by HAGER (1986) during investigations of cushion-plant formations in Patagonia. Although his investigations refer to dry East Patagonian communities, his statement “wind is the main factor for the distribution of cushion plants” (translated from German) is valid for the vegetation of Tierra del Fuego as well. Among the cushion plants occurring in the formations investigated, he also mentions *Valeriana magellanica* Hombr. [*Aretiastrum magellanicum* (Hombr. & Jacq.) Skottsbl.].

Discussion

Comparing our results on morphology and anatomy of *Aretiastrum magellanicum* with data obtained from former studies, including our own (WEBERLING & UHLARZ, 1977), it becomes evident that, regarding all the characters and the conformity of the growth forms, this species fits well into the genus, notwithstanding the presence of a pappus. Generally, the species, hitherto placed into this genus, can be distinguished by a well defined combination of structural properties: the distinct growth form as „radiate branched semiglobe-shaped cushions“, which enables the Patagonian as well as the High Andean species to survive in an unfavourable climate, the morphology and anatomy of the axes and leaves, being similar in their general features as well as in the structure of the few flowered thyrse inflorescences and the structure of the pollen grains (WEBERLING & UHLARZ 1977). Among the species of the genus *Valeriana* there are also cushion plants like *V. supina* L. or the Argentinian species *V. corynodes* Bors. and *V. descolei* Bors., but they do not show such a strictly regular architecture like the species of *Aretiastrum*. The only species, which does not fit in quite well, is *A. imbricatum* Killip, „an erect shrub, 10–25 tall“ (ERIKSEN 1989b: 11; also see WEBERLING & UHLARZ 1977: 219), because it differs in its white corollas. In *A. aschersonianum* Graebn. the number of corolla lobes can vary between 3 and 5.

Anatomically the axis of *A. aschersonianum* shows a scarce development of the vascular tissue (WEBERLING & UHLARZ 1977) and we discussed the question, whether under these conditions the water supply by the root system might be sufficient or a supplemental absorption of water by the leaves might take place. The latter was already reported for High Andean plants by WEBERBAUER (1906, 1911, 1945). This, of course, is not possible through the epidermis of a lamina covered by a thick cuticula. Later, however, we could verify that berberinsulfate – dissolved in water and applied to the surface of the plant – was transported into the vascular tissue, probably absorbed by the cells of the leaf-bases, which are thin-walled in *A. aschersonianum*, or by the adventitious roots (F. Weberling & L. Müller, unpubl.). In the axis of *A. magellanicum* the vascular bundles appear to be somewhat stronger than in *A. aschersonianum*, which corresponds with the vigorous development of its tap root.

In the description of the Valerianaceae in the ‘Flora Patagonica’ (BORSINI et al. 1999: 465–466) *Valeriana sedifolia* d’Urv. [*Aretiastrum sedifolium* (d’Urv.) Graebn.] is enumerated as a species growing in Islas Malvinas and in Tierra del Fuego. However, during our revision, all the specimens named for Tierra del Fuego turned out to belong to *Aretiastrum magellanicum*. Thus *Aretiastrum sedifolium* appears to be distributed exclusively in Islas Malvinas as already described by DUMONT D’URVILLE (1825).

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