Xeromorphic Leaf Types

Evolutionary Strategies
and Tentative Semophyletic Sequences

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Synopsis

In order to achieve a versatile and more profound understanding of xeromorphic structure, a detailed anatomical study of leaves from a number of South American xerophytes was undertaken. Ecophysiological and leaf ontogenetic viewpoints were incorporated as well as attempts from a semophyletical angle to look into the background or history of the characters under discussion. Ecophysiological considerations concerned adaptations for withstanding night frosts, drought and overheating. Other topics studied were water absorption from and loss to the atmosphere, and water flux and storing in the apoplast, as well as stomatal distributions and the occurrence and function of air-filled lacunae and various types of trichome. Morphological features included marginal involution, deflexion and revolution, dorsiventrality, the cataphyll-foliage leaf relation, prophyll-spines, microphylly and the cushion life form.

The discussion concerns problems of multiple adaptation, the meaning of xeromorphism, types of convergent evolution, semophylesis in relation to evolutionary canalization, and finally the delimitation of xeromorphic leaf types. Species treated in detail belong to the genera: *Acantholippia, Anarthrophyllum, Chuquiraga, Junellia, Mulinum* and *Perezia.*

Key words: Xeromorphy, ecophysiological anatomy, involution, deflexion and revolution, convergences, semophylesis, evolutionary canalization.

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1. Introduction

Like entire organs, morphological and anatomical features have a history. But how does one trace the origin or the evolution of a particular structure? Without evidence from fossil records we are restricted to making comparisons with structures in existing taxa. Genetical experiments can reveal important facts about the heritable background of a character, and the coincidence of the character with some environmental factors may often lead to essential clues. However, information of this kind can hardly tell us how and when the complex of genes responsible for the character came into existence. Thus so far the semophylesis (origin and further development) of a particular structure is bound to be hypothetical.

Xeromorphic features rarely occur as single characters. Usually several adaptive characters constitute a complex. They have probably evolved concomitantly as responses to a particular environment and have been forced to operate as a network of interdependent structures and functions during their emergence. The complexity of xeromorphic features appears staggering if one considers that, according to much experience, each character in the network, is governed by multiple and generally several additive genes. At any rate it is necessary to treat xeromorphic features as parts of a syndrome consisting of ecophysiologically co-operating structures.

With a broader understanding of structure in view, a synthesis of many scientific branches would seem required. However, I found myself compelled to concentrate my efforts on anatomical observations combined with some leaf ontogenetic investigations. An attempt was made to reach some kind of viewpoint by summarizing a number of short monographs about very different but still clearly xeromorphic leaves. The results presented here are mostly based on material (fixed in alcohol) collected during an expedition to West Argentina in 1955–56 (cp. *Böcher, Hjerting & Rahn* 1963–72), in the following quoted as *BHR*.

2. Partial or complete inverse dorsiventrality

Inverse dorsiventrality (or bifaciality) in leaves occurs as soon as one tissue stratum is reversed in relation to its placing in the classical type of dorsiventrality with adaxial palisades, abaxial spongy parenchyma and stomata preferably in the abaxial epidermis. Thus, hyperstomatous leaves with the pores on the upper surface are considered as inverse, but if no tissue strata other than the epidermis is involved, the inverse dorsiventrality is partial.

Xerophyte leaves are mostly isolateral, cylindrical or normal dorsiventral. The leaves in *Empetrum nigrum,* which were studied thoroughly by *Hagerup* (1946), must be classified as dorsiventral, but during ontogenesis they become hollow. The abaxial epidermis with the stomata lines a central cavity that has a narrow fissure as its opening. True hyperstomatous leaves are not frequent and need comment. The ecological conditions favouring an inversion of the position of the stomata are not obvious. However, it is evident that specially many cases of inversion in leaves can be established among high-montane (alpine) species.

One arctic-alpine species should be considered in this connection: *Silene acaulis,* which is devoid of stomata on its abaxial leaf sides *(Warming* 1920: 261). It is a well known cushion plant with very short internodia and densely spaced small but not particularly xeromorphic leaves. The position of the stomata may be connected with the fact that the cushions become filled with remains of dead leaves, forming a spongy mass that makes it difficult for the leaves to get access to air from below. Another typical cushion plant from the arctic areas is *Diapensia lapponica.* In

this species, however, one finds very typical dorsiventrality and all stomata are on the lower surfaces *(H. E. Petersen* 1908: 147). When the leaves of *Diapensia* die, they remain for a long time on the stems in the interior of the cushions. There is no formation of a spongy mass but the air has easy access to the stomata on the undersides of the leaves exposed to the light.

The structural difference between these two cushion plants makes it evident that an unimpeded access of air to at least one leaf surface is fundamental. In the chasmophytic genus *Dionysia (Primulaceae)* semophyletic reductional series have been described by *Wendelbo* (1961, 1971). These start with laxly tufted species with many flowers and end with xeromorphic species forming dense tufts or cushions with small imbricate leaves and single sessile flowers. Two of the most extremely xerophytic species from sunny cliff faces in Afghanistan were studied anatomically. The densely imbricate leaves are here hyperstomatous with all stomata placed in grooves in the adaxial concave leaf sides. The compactness of the leaves is very pronounced. The primary function of stomatal grooves here may therefore be to ensure the access of air to the pores. The abaxial sides of the leaves are said to be »well protected«, which seems to mean that the epidermis has particularly thick walls.

Parkhurst (1978) discussed the adaptive significance of stomatal distribution and tried to explain the predominance of hypostomatous leaves over hyperstomatous ones. Among the possible explanations, he mentions that pores on the upper surfaces seem more likely to be blocked

by dust or rainwater and that upper surfaces exposed to the sun become slightly warmer than the undersides. The temperature gradient would imply a greater evaporation from a leaf having stomata facing the sun compared with one having shaded stomata.

High-montane or some few arctic species with hyperstomatous leaves probably enhance their photosynthetic rates because of the warming effect, and this may be further augmented owing to the reduced ventilation through leaves with one porous layer only. When the stomata close, e.g. in the evening, relatively warm air will be trapped in the intercellular spaces. This may be of importance, particularly in southern high-montane areas where even in the vegetation period night frosts resulting from radiant cooling are common.

Low night temperatures in the summer undoubtedly limit the ascent of many species to high altitudes. The deleterious effects (low temperature injuries) seem, however, to be counteracted by structural and physiological properties developed by the alpine plants. One such structure is the formation of dense cushions, another may be hyperstomatous leaf structure. The dense cushion life form increases in importance with altitude (*BHR* : 345 pvd).

Approaches to a hyperstomatous leaf structure were found in the high-Andean *Junellia uniflora*. The anatomy of this species was thoroughly studied in order to find adaptive features that might be connected with its rough habitat.

It should be emphasized that hyperstomatous leaf structure takes up an initial position in the semophyletic series of structures discussed in the first part of the present paper. On the other hand, the hyperstomatous type itself clearly does not occupy a basal level. All semophyletic sequences are ultimately series of adaptational steps. In the case of partial inverse dorsiventrality, the following steps seem essential:

1) Drought or low temperature, or both, involve a shortening of the internodia together with a leaf blade size and petiole reduction.
2) Internodial shortening implies imbricate or dense leaf insertion. Mutual shading of leaves reduces their photosynthetic activity. But small leaf blade sizes reduce the shadow effects.
3) Unimpeded access to light, heat and CO_2 makes a hyperstomatous structure profitable and preferable.

Studies on the genetical (ecotypical) variation in internodial lenghts and leaf blade sizes were presented in previous papers on *Clinopodium vulgare* and *Veronica officinalis (Böcher* 1944, 1976). Cultivated races of *Silene acaulis* with different cushion densities are illustrated in the paper on convergence (*Böcher* 1977).

Junellia uniflora (Phil.) Moldenke
Morphology. Densely caespitose, prostrate dwarf shrub (*Hauman* 1918 Plate 20, *BHR* Fig. 13). The lower parts of the cushions are dark, consisting of densely spaced, dichotomously divided, ascending shoot systems covered with dead leaves or leaf scars. In the uppper parts that are exposed to light, the small, decussate, living leaves are covered with strong stiff hairs and scattered glandular hairs. The youngest leaves are boat-shaped. Two leaves in a pair face one another with their concave adaxial side. They are almost upright and protected by the following pairs, which likewise approach an upright position on the stem. The internodia are very short.

Ecology. Recorded abundantly in wind-exposed, gravelly fell fields at altitudes between 2900 and 3700 m. The vegetation sites were frequently dominated by scattered tussocks of *Poa holciformis* and contained, e.g., *Cruckshanksia glacialis, Oxalis compacta* or *O. erythrorhiza* (Plate 1 in *Böcher* 1977) and *Viola sempervivum (BHR:* 310, 319 and 328).

Leaf ontogeny. Young leaves have an involute structure. They are almost V-shaped in cross sections and become slightly dorsiventral by developing particularly dense palisades on their adaxial sides. Glandular hairs are abundant between the initials of the rigid hairs (Fig. 2 A).

Leaf anatomy; epidermis. The densely spaced, stiff hairs are slightly curved. The glandular ones have stalks, 3–4 cells long, and 4-celled heads. They decrease in number in mature leaves. The stiff hairs are pointed and have thick outer walls composed of several cellulosic layers, and they are covered with a cuticle containing many warts. The hair tips do not stain with Sudan IV, while the same distal sections can be stained with Ruthenium Red, indicating the occurrence of pectic substances. The cytoplasm remains alive. The conspicuous nucleus is at first placed near the dilated base (Fig. 2B), but in fully grown hairs it is located near the swollen base, which is surrounded by normal epidermal cells. There are no suberized or cutinized basal short cells. The apparent free space in the thick wall may allow water, if absorbed in the tips, to flow to the basal part. A water flux in the opposite direction, involving an enhancement of the transpiration, appears less probable in this case. In structure the hairs resemble those in *Heliotropium arbainense* described by *Volkens* (1887 Plate VIII 10) and by him regarded as water-absorbing.

The epidermal outer cell walls are thick with many cellulosic layers that continue in many low ridges, in cross section resembling papillae (Fig. 1A, 2 C, D). The cells are covered with a rather thin cuticle. There is no cutinized layer, but a pectinaceous layer is easy to demonstrate between the double refractive cellulosic part and the cuticle (Fig. 2D). The ridges are most conspicuous in the middle parts of the abaxial surfaces (Fig. 2C). Here they appear stratified being composed of pectinaceous layers that are stained with Ruthenium Red and cellulosic layers that are stained, e.g., in Johansen's quadrup-

le stain. The intermittent wall sections off the anticlinal walls consist of pectinaceous material and are merely limited by the cuticle.

The stomata are numerous in the adaxial epidermis and are slightly raised. They occur scattered on both sides of the ribbed abaxial middle part, which is devoid of stomata. *Espinosa* (1933: 155) reports the same stomatal distribution in *J. uniflora* and furthermore in the high-Andean *J. minima* (occurring in Peru, Bolivia and Chile) and in *J. caespitosa* from lower altitudes in the Argentinian Andes (from 1600 to 2300 m above the sea, cp. also Fig. 6 in *BHR*). Another dense cushion plant is *J. erinacea,* which ascends to 2000 m in the Atuel Valley. It has needle-like leaves with a strong sclerenchyma strand beneath the midvein and is amphistomatous (see *Pyykkö* 1966: 506). Other amphistomatous species with needle-like leaves occurring at lower altitudes (e.g., in the Puna region) are *J. juniperina* and *J. asparagoides.*

Mesophyll and vascular bundles. The leaves of *J. uniflora* are isolateral, but at the middle vein they appear dorsiventral because of the broad chlorophyll-free bundle sheath extension that occupies the area beneath the strong schlerenchyma strand at the vein. Between the extension and the abaxial epidermis with the ridges is a subepidermal tissue, likewise without chloroplasts. This local hypodermis has thick collenchymatous walls containing much pectic substance. A similar layer was described by *Pyykkö* (l.c.: 506) in *J. erinacea* in which this author found two vascular bundles at the midvein. In fact, two phloem strands are shown, but one strong sclerenchyma strand and one bundle sheath. In *J. uniflora* the midvein also has two phloem strands on both sides of the large sclerenchymatous strand and the xylem often has two extensions that continue in commissural strands leading to the marginal veins (Fig. 1C).

Protection against drought, radiation and radiant cooling. Together with other high-Andean species, *J. uniflora* is able to withstand drought,
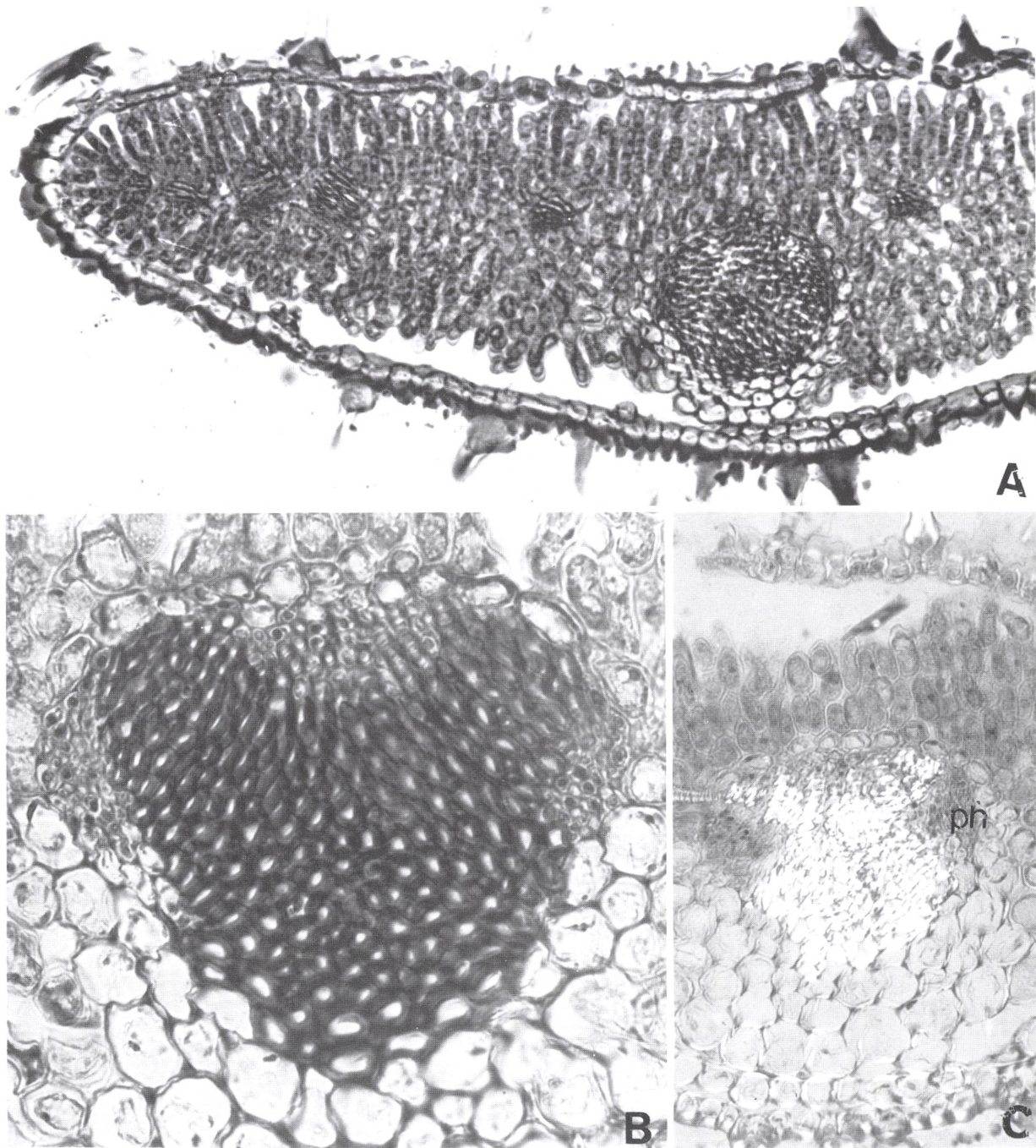
Fig. 1. *Verbena uniflora*. A. Transverse section of adult leaf. Johannsen's quadruple stain, semipolarized light. Adaxial, slightly raised guard cells, abaxial epidermal ridges and subepidermal cavities. (× 200). – B–C. Details of midrib with bundle-sheath extension, in C reaching the abaxial hypodermal and epidermal cell layers. – B. Fast green-Safranin. (× 500). – C. Polarized light. Xylem, sclerenchyma and hypodermal layer showing up, ph phloem strand. (× 320).
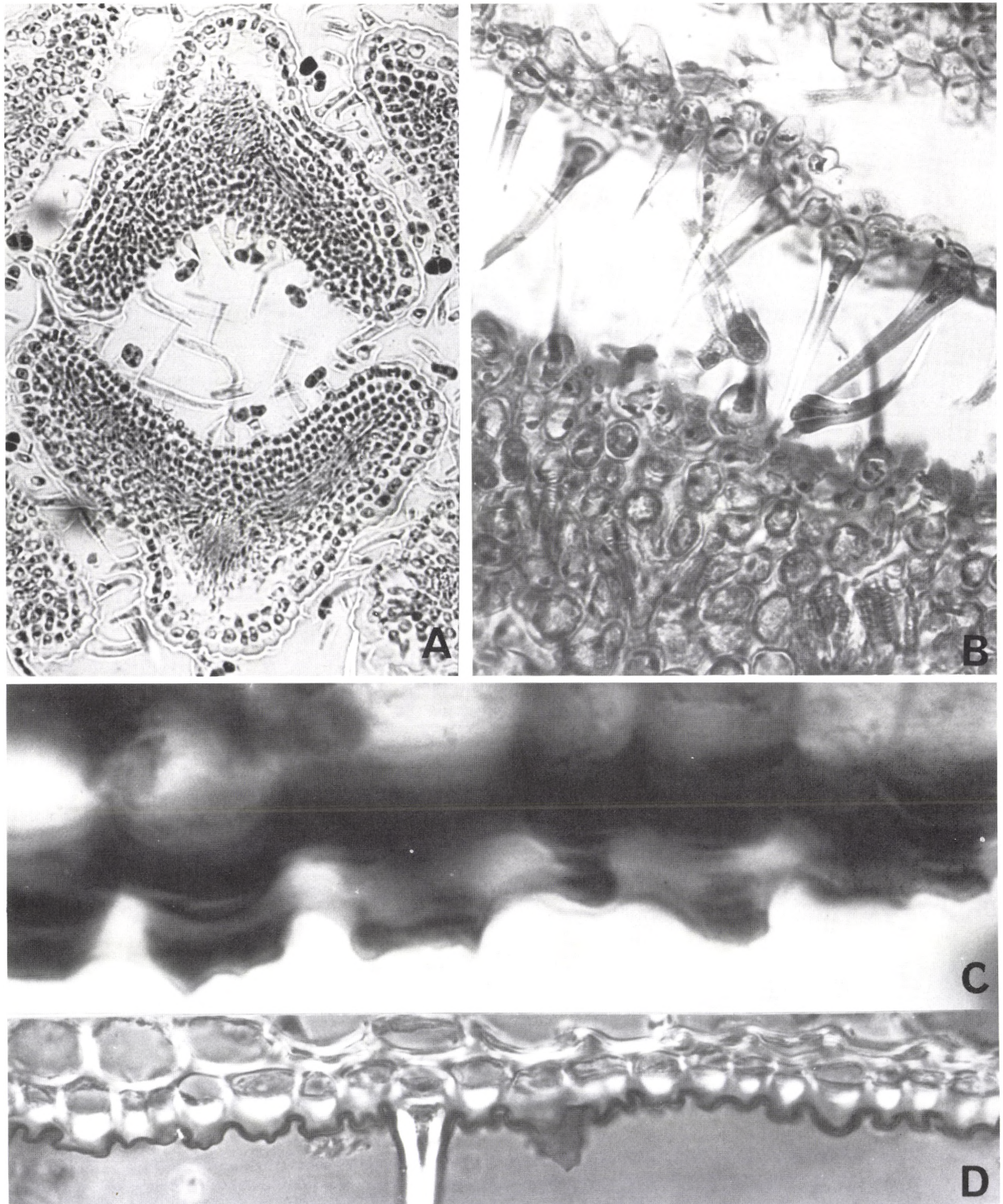
Fig. 2. *Verbena uniflora*. A. Youngest, uppermost leaves showing early formation of abaxial cavities and many glandular hairs. (×
200). – B. Space between two younger leaves with many rigid, thick-walled hairs, bright in semipolarized light and with sub-basal
nuclei near swollen bases. Fast green-Safranin. (× 500). – Middle part of abaxial epidermis, outer walls and ridges stained with
Johansen's quadruple stain, intervening pectic lamellae and cuticle unstained. (× 2000). – Epidermis treated with Sudan IV in
polarized light. Cuticle stained, interior thick cellulose part showing up, pectic isotropic part not. Walls at base of rigid hair
appear bright. (× 256).

nightly recurrent frosts, and daily, intense ultraviolet radiation. It is difficult to ascertain how this is possible. The most essential or vital parts in need of protection are the assimilating mesophyll, the leaf primordia and the shoot apices. It is problematic to point out morphological and anatomical features that imply frost hardiness or subdue ultraviolet radiation and water stress.

J. uniflora produces flattened cushions in which the shoots frequently become at least partly subterranean. *Hauman* (1918) mentioned *J. uniflora* together with *Adesmia subterranea* and *Oxalis bryoides* as examples of species with this type of growth, which he regards as an adaptation to withstand strong winds, but the dense insertion of short decussate leaves and many branched stems in the cushions may also provide the plant with some protection against low-temperature injuries. Most important is undoubtedly the occurrence of many cavities with stagnant air. Such spaces, which have an insulating effect, are produced not only between older parts of the cushion shoot system but also in the young parts carrying the actively assimilating leaves: 1) Between the bivalve-shaped uppermost leaf pairs (Fig. 2A), 2) between the imbricate leaves that never reach one another because of the stiff hairs on their surfaces (Fig. 2B), 3) internal lacunae. Early stages in leaf development already show schizogenous lacunae formed on both sides of the abaxial bundle-sheath extension and above the hypodermal layer (Fig. 2A). In adult leaves these lacunae are much widened, but cellular connections between the central vein and the abaxial epidermis are usually maintained (Fig. 1A). The lacunae are probably air-filled being connected with the intercellular space system in the leaves. Similar lacunae located near abaxial surfaces were described in *Dryas* by *Jessen* (1913), in *Arctostaphylos alpina* by *H. E. Petersen (1908b),* in *Viscaria alpina* by *Warming* (1920: 259–260) and by *Espinosa* (1933, Fig. 7–8) in two Andean species of *Azorella.* According to *Espinosa,* many species of *Azorella*

have larger cavities with the same position and formed by a tearing up of the cells. His pictures show some wall remains at the margins of the cavities. Similar remains are at least difficult to ascertain in *Junellia,* where the lacunae can be traced back to the youngest leaves and seem largely to be schizogenous. The position of the lacunae is predetermined, but their size under natural conditions is presumably considerably smaller than in the preparations.

The stagnant air in the cavities will be heated up on sunny days. The day microclimate near the soil surface is generally warmer than in the atmosphere above, but frosts are common near the soil surface on cold nights. In *Junellia uniflora* the stomata are to a great extent placed on the adaxial sides. When open their position counteracts the air flow through the leaves. Their closure at sunset may slow down the heat loss from the intercellular spaces. However, it is still a question how the plant can resist frost damages on cold nights. Even when the cavities and lacunae have absorbed much heat, they will hardly be able to effectively diminish the nightly heat loss by the trapping of the heat received during the day. However, the plant probably contains water in the veins and in the apoplast of, e.g., the thick sclerenchymatous fiber strands at the central veins. Thus water heated up during the day might act as a heat reservoir, which during the dark period would slowly lose heat to the green tissues, thereby neutralizing the effects of a strong radiant cooling of the ambient air.

By slowing down cell division and growth, intense ultraviolet radiation probably becomes a problem for plants growing at high altitudes. In *Junellia uniflora* the leaves may be sheltered by their position and mutual coverage and by the many hairs. The ribbed epidermal surface may furthermore cause some reflectance.

The characters of *J. uniflora* that deviate from those of other species of the genus from less elevated areas can be summarized as follows:

The cushion growth is much denser. The stomata are slightly raised and much more numerous on the adaxial sides. Epidermal, low ridges are developed. A hypodermal cell layer in connection with the bundle-sheath extension is better developed. Lacunae are formed near the abaxial side on both sides of the bundle-sheath extension. The leaf type is principally isolateral, but the species approaches partial inverse dorsiventrality because the stomata are concentrated on the adaxial side.

3. The occurrence of continuous abaxial sclerenchyma in relation to inverse dorsiventrality

Abaxial sclerenchyma and inverse dorsiventrality seem to be mutually linked, and also linked with some special habitat requirements and a dense, almost imbricate leaf spacing. Plants with abaxial sclerenchyma (or sclerenchymatous, or very thick-walled abaxial epidermis) are particularly common in high-montane, arid areas in the southern hemisphere. Good examples are found in *Azorella lycopodioides* and *filamentosa (Domin* 1908 Fig. 8, *Espinosa* 1933 Fig. 7–8). Other examples are mentioned by *Espinosa* in *Pycnophyllum,* by *Pyykkö* (1966 Fig. 98) in *Colobanthus,* by *Diels* (1897 Fig. 6A) in *Helichrysum coralloides,* and by *Spinner* (1936 Fig. 3) in *Tafalla thyoides.* A striking example pictured by *Espinosa* is *Chuquiraga atacamensis,* to which can be added *C. ruscifolia,* mentioned in detail below.

The anatomical structure in *Chuquiraga ruscifolia* clearly does not represent a primitive stage. Within the genus (to *Asterales, Mutisieae)* there are three sections. *Acanthochuquiraga* is characterized by pairs of prophyll spines. It is a character that also occurs in other genera in the *Mutisieae;* thus, e.g., in *Barnadesia (Troll* 1939: 1915–16). These spines are conspicuous, e.g., in *C. oppositifolia (Hauman* 1918 Plate 23, 1), *C. straminea (Cabrera* 1939 Fig. 28), but short in, e.g., *C. avellanedae.* However, they are absent from the sections *Ruscifolia* and *Unguis-cati* which, on the other hand, have developed a defence by spiny leaf apices. In species with prophyll spines there are no abaxial sclerenchyma plates, but the species have some sclerenchymatous areas along the leaf margins and at the vascular bundles. Their leaves are isolateral and amphistomatous. *Chuquiraga huaminpinta,* occurring at altitudes

between 4400 and 5500 m in Peru, clearly forms a transition to species with hyperstomatous leaves. Prophyll spines are still present and the leaves have short petioles and sclerenchyma at the midvein and along the margins, but, according to *Spinner* (1936: 13), the number of stomata per mm^2 decreases from 85 on the adaxial side to 30 on the abaxial side. Species in the *Ruscifolia* section with an abaxial sclerenchymatous tissue constitute an important step in the structural evolution of the genus. Once this structure was established, perhaps as an adaptation to night frosts (see below), the evolutionary process probably became irreversible.

Chuquiraga ruscifolia Don
Ecology. The material was collected at the type locality between Villavicencio and Uspallata (altitude: 2350–2500 m, BHR No. 2131 see Fig. 3A). The species was co-dominant in dry rocky vegetation characterized by *Adesmia uspallatensis, Mulinum spinosum* coll. and containing, e.g., *Baccharis thymifolia, Tetraglochin alatum* and *Fabiana denudata (BHR:* 304). The species is distributed in the mountains of West Argentina in the provinces of La Rioja and Mendoza.

Morphology. A low, densely branched shrub with almost sessile, 4–6 mm long, glossy, mucronate, densely spaced leaves that are decurrent (Fig. 3A). The sheath part of the leaves almost half-way encircles the internodium below. Upright, long hairs are developed at the junction of sheath and blade (Fig. 5A). The adaxial leaf margins are raised so that the leaves become almost boat-shaped.

Leaf anatomy. Epidermis. When young the
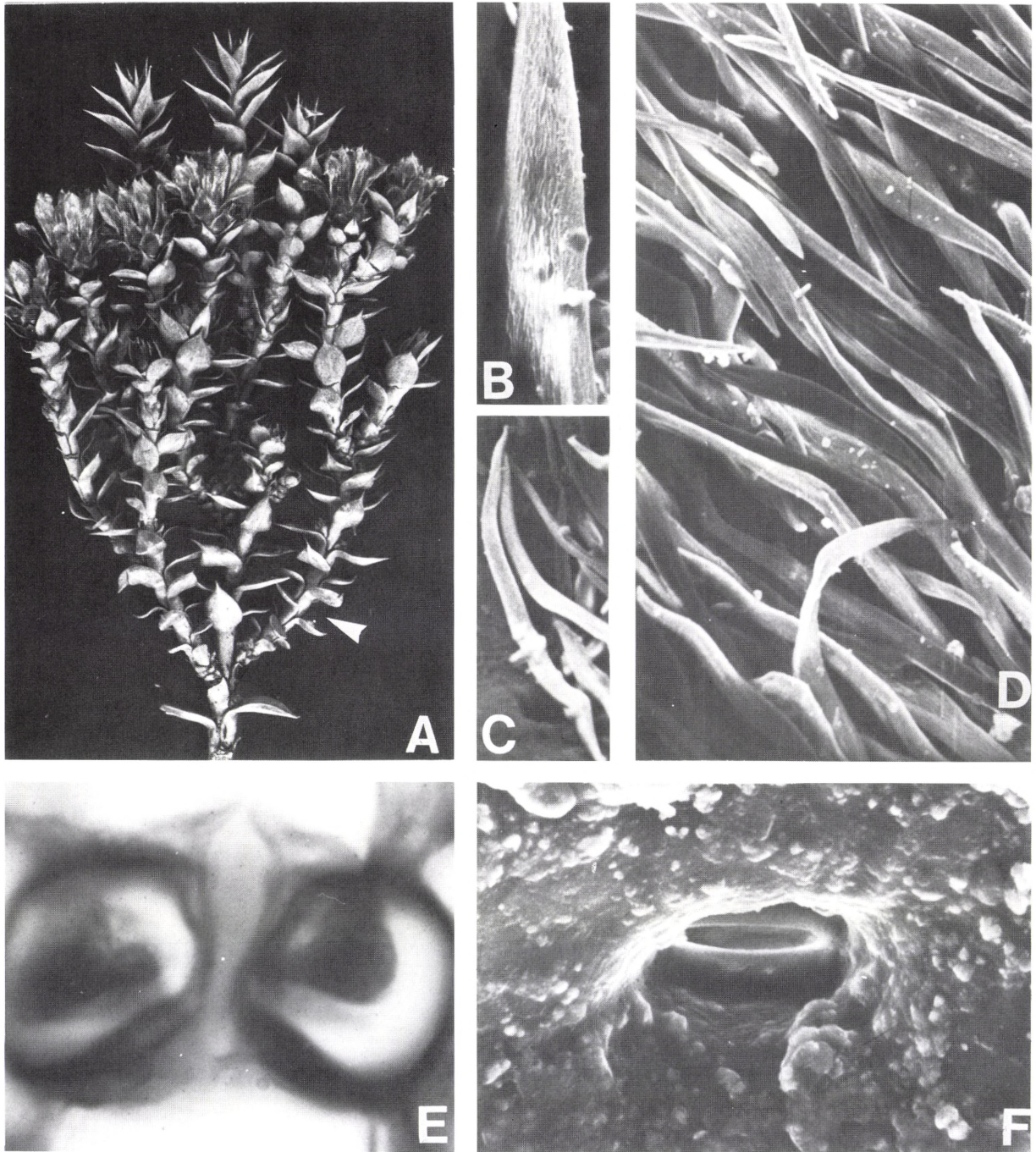
Fig. 3. *Chuquiraga ruscifolia*. A. Part of flowering specimen. White arrow points to basal sheath, encircling the stem half-way. (× 1.5). – B–D. Hair cover on adaxial surface of young leaf, SEM. (× 1500 (B), × 300 (C), × 450 (D)). – E. Stomatal pore with outer ledges on guard cells. Johansen's quadruple stain. (× 2000). – F. Stomatal opening and epicuticular wax pattern, SEM, (× 1500).
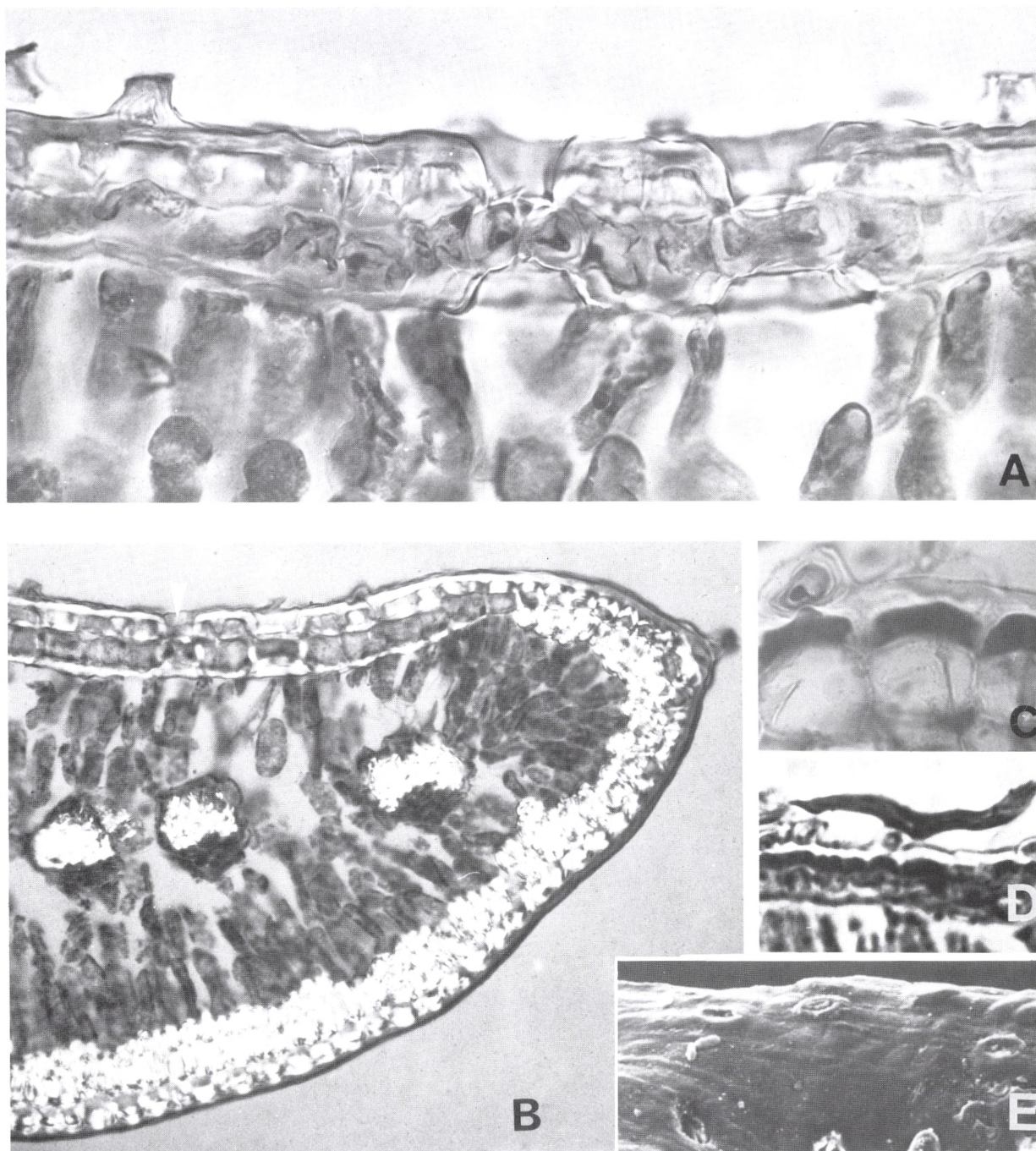
Fig. 4. *Chuquiraga ruscifolia.* A. Cross section of adaxial epidermis with two stomata and two hair bases. (× 500). – B. Cross section of leaf in polarized light. Abaxial and marginal sclerenchyma, xylem and adaxial epidermal walls showing up. White arrow indicating position of stoma. (× 200). – C. Part of adaxial epidermis. Cuticular layer unstained, cellulosic part dark red because of some kind of impregnation (Johansen's quadruple stain). Hair base with three wall layers and remains of nucleus. (× 500). – D. The two arms in a hair reacting with the quadruple stain. (× 200). – E. SEM of adaxial surface of adult leaf with hair bases or scars of same. (× 300).

adaxial leaf surfaces are covered with adpressed two-armed hairs (T-hairs), which have their arms oriented parallel with the leaf axis. The two pointed arms rest upon a short upright, living hair base cell. The latter has a cutinized wall, while the horizontal ones are not cutinized. They appear bright in polarized light and remain unstained with Sudan IV and Fluoroglucinol-HCl, but are easily stained with Neutral Red. SEM reveals that the surface of such T-hairs exhibits a network of elongate meshes (Fig. 3B). Similar hairs of the Malpighian type were described by *Schwabe* (1950) in *Doniophyton anomalum,* which, according to *Pyykkö* (l.c.: 520), has beneath the midvein a sclerenchymatous plate similar to that found in *Chuquiraga ruscifolia.*

During the growth of the epidermal cuticular layer in C. *ruscifolia* the basal hair cells become isolated from the epidermal cells beneath, and this results in a shedding of the horizontal part. The cutinized collars around the basal cells remain and appear in SEM as roundish warts (Fig. 4E). At a time when the leaves grow and need admission of ample water with dissolved solutes, these hairs may enlarge the water-evaporating surface, but they also protect the young leaves against too strong irradiation. A similar, early-shed, T-shaped hair type has recently been thoroughly studied by *Heide-Jørgensen* (1979) in *Hakea.*

Fully grown leaves which have almost lost the hairs develop a thick cuticular layer in their outer walls. This probably protects the plant against injurious water losses. The surface is granulated by epicuticular wax, and the outer part of the cuticular layer contains abundant intracuticular wax, having a type of birefringence opposite to that of the cellulose layer beneath. The wax-incrusted part takes up about one third of the cutinized wall. The cuticular flanges in the anticlinal walls are conspicuous. Also the abaxial epidermis has cutinized outer walls with a wax layer that is not so thick as that in the adaxial epidermis. The interior walls here remain unstained with Sudan IV except the parts facing the substomatal cavities. These wall sections are intensely stained with Sudan IV and the same is the case with the guard cells next to the apertures. The stomata have a recessed position and the guard cells have protruding outer ledges (Fig. 3E). The sheath part of the leaves has an epidermis of narrow cells that on their outturned sides have thick, cutinized outer walls and cutinized flanges. The walls in the two subepidermal cell layers are similar (Fig. 5C).

On axillary buds, and in the junctions between blade and sheath, long, non-cutinized hairs abound (Fig. 5A). These hairs have basal cutinized short cells with conspicuous nuclei.

Mesophyll and sclerenchyma. The mesophyll is arranged as in isolateral leaves with two almost equal palisade layers on both sides of the veins in the middle part (Fig. 4B). Some sclerenchymatous cells occur on the abaxial side of the middle vein. In some leaves green cells were locally replaced by swollen parenchymatous cells resembling those that occur as a continuous tissue in the major part of the sheath area.

Sclerenchyma occurs as two (-three) hypodermal cell layers and continues in the subepidermal layers in the sheath (Fig. 5C). The sclerenchyma is dense, without intercellular spaces and impedes a formation of stomata outside. The restriction of the stomata to the upper surface prevents air flow through the leaf, a feature which effects a temperature rise in the leaf during sunny hours. During cold nights, on the other hand, the location of the sclerenchyma may protect the leaf against frost damage, which is often said to set in at leaf margins and leaf tips (cp. *Treschow* 1970). By apoplastic storing of water the thick walls of the sclerenchyma may be able to accumulate heat during the day and on cold nights transfer it to the green tissue above.

The boat-shaped blades seem able to collect water (e.g., dew) on their surfaces and conduct it to the axils. The non-cutinized hairs (Fig. 5A)
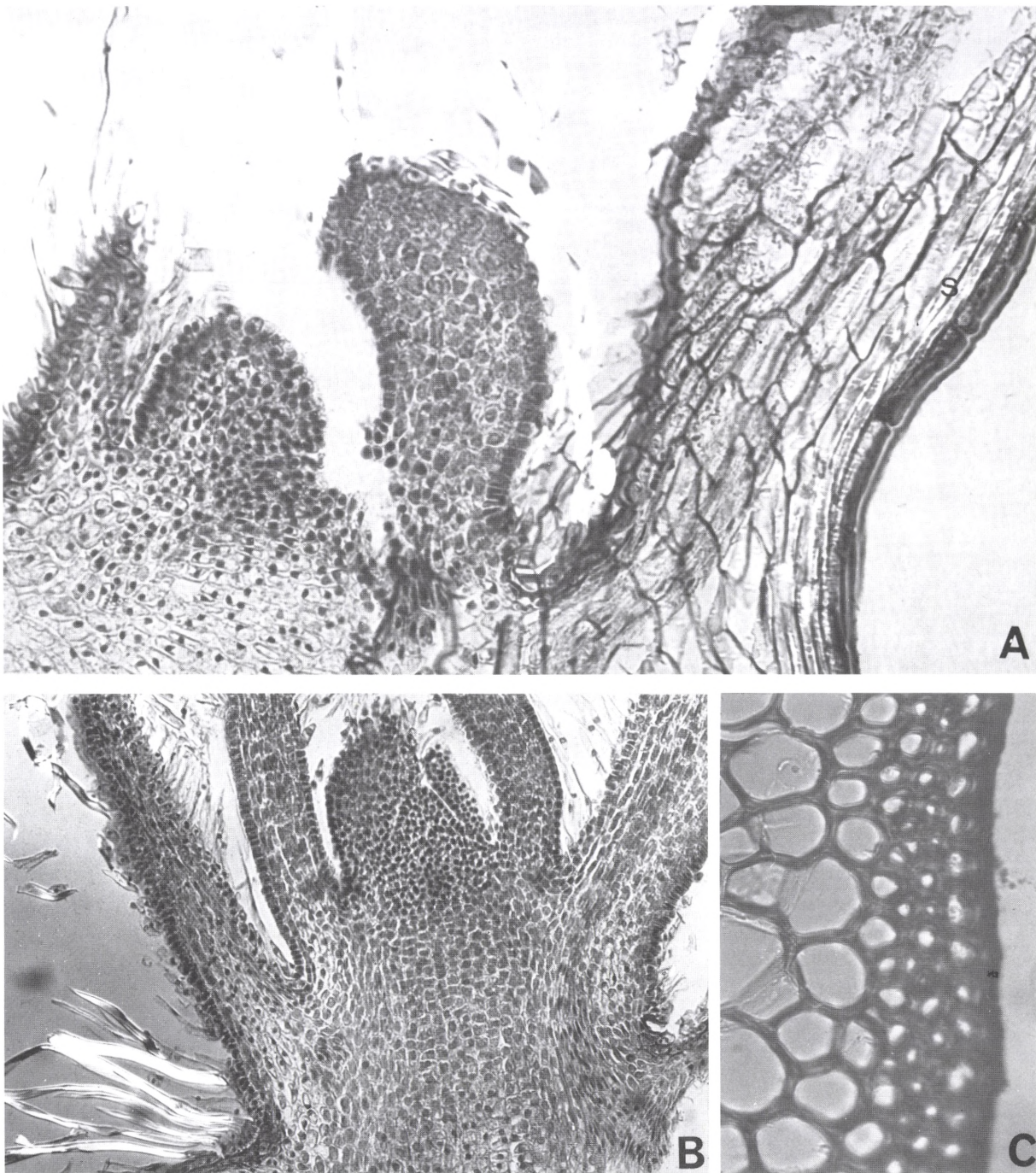
Fig. 5. A. Longitudinal section of axillary bud and leaf base in *Chuquiraga ruscifolia*. Long apical hair cells on bud scales bright in semipolarized light. s abaxial sclerenchyma. Fast green-Safranin. (× 200). – B. Terminal bud and bases of upper leaves in *Chuquiraga hystrix* showing similar long hairs at the leaf bases. (× 100). – C. Cross section of basal sheath part in *Chuquiraga ruscifolia*. Sudan IV stains walls in epidermis and subepidermal sclerenchyma. The parenchyma of wider cells is assumed to be water storing. (× 320).

may absorb it and conduct it to the sheath. Here the cells look like water-storing parenchyma (Fig. 5C), and they are protected against water loss by the cutinized subepidermal layers. Towards the axis the parenchyma borders the cortex of the stem. The outer cortex is a rhytidome with alternating phellem and sclerenchymatous layers. Thus the parenchyma is surrounded by cutinized or suberized cells, but small veins with tracheids locally traverse the cortex and reach the parenchymatous mantle.

Chuquiraga atacamensis Kuntze has a similar leaf anatomy *(Espinosa* l.c. Fig. 13), although the hair cover seems composed of simple, not T-shaped hairs. The leaves are slightly longer and with a longer spiny apex *(Gaspar* l.c. Fig. lG). The species has a more northerly distribution in Chile and in the provinces of Salta and Jujuy in Argentina, where it occurs at altitudes of between 3400 and 4000 m and grows in semideserts on sandy soils, sometimes near salt lakes and together with, e.g. *Sporobolus rigens (Ruthsatz* 1977: 127, 142).

4. The emergence of species with involute, "inverted ericoid" leaves

Among the Argentinian species of *Chuquiraga,* involution takes place in species of the sections *Ruscifolia* and *Unguis-cati.* Thus, *C. punensis* has long narrow mucronate leaves which at their bases clasp the stem, but distally become increasingly involute *(Gaspar* 1945 Fig. 3). Among the other species *C. hystrix* still has a conspicuous adaxial groove (Fig. 6A), but in *C. erinacea* and *C. rosulata* the involution is more advanced. The entrance to the groove may here be difficult to ascertain and the leaf apices become acicular (Fig. 11). In all three species stomata are confined to the adaxial side. The involution may therefore have an effect similar to the revolution of the leaf margins observed in the so-called "ericoid" leaves.

The semophyletic development in the genus *Chuquiraga* is governed by adaptive forces. An ecological and a morphological evolution took place concomitantly. *Espinosa* (1932) distinguishes between three morpho-ecological types: 1) A lowland type with stalked, rather thin, large leaf blades, 2) an Andean Paramo-Puna type with small, leathery, short-stalked leaves terminating in spines (e.g., *C. ruscifolia),* and 3) a southern (Patagonian) semidesert type with sessile, spiny, involute leaves. The species belonging to the latter type may – with the leaf structure of *C. ruscifolia* in mind – have evolved from ancestors that were adapted to high-Andean conditions, while the most primitive members may be connected with subtropical or low-montane habitats.

Chuquiraga hystrix Don
A southern Patagonian species ranging from Catamarca to Chubut. In Neuquén this is an important element of the Monte vegetation (cp. *BHR:* 221).

Morphology. Fig. 7 A–C. An about 1 m tall very branched shrub with strong spiny 19–25 mm long leaves having an adaxial hair-covered groove (Fig. 6A). The species deviates from the other species with involute leaves by the occurrence of a palisade tissue along the abaxial sclerenchyma. The inverse type of dorsiventrality is here almost complete.

Leaf ontogeny. The involution in the primordia starts early. The marginal meristems turn upwards, but the initials are not clearly demarcated. Thus, the rolling up is not a later occurring, sudden change in the marginal growth. Almost at the same early time when the involution starts, the many-layered hypodermal sclerenchyma is differentiated. Young sclerenchymatous cells early attain long pit canals that become conspicuous in polarized light (Fig. 7E). In longitudinal sections, maturing sclerenchyma appears not far from the well-defined basal intercalary meristem and may therefore have been established already by the apical meristem. On the adaxial sides parenchyma with young chloroplasts occurs below the epidermis. Guard cell precursors and cells that grow out as hairs abound. The primordia are enveloped by hairs which issue from cells formed in the upper part of the basal intercalary meristematic zone and in the apical meristem. Some of the enveloping hairs become long and straight (Fig. 7D). They have a shorter basal cell and a single long hair cell. Other hairs have a distal part that swells and finally becomes empty. Their walls are bright in polarized light. Both types are shed at an early stage. These
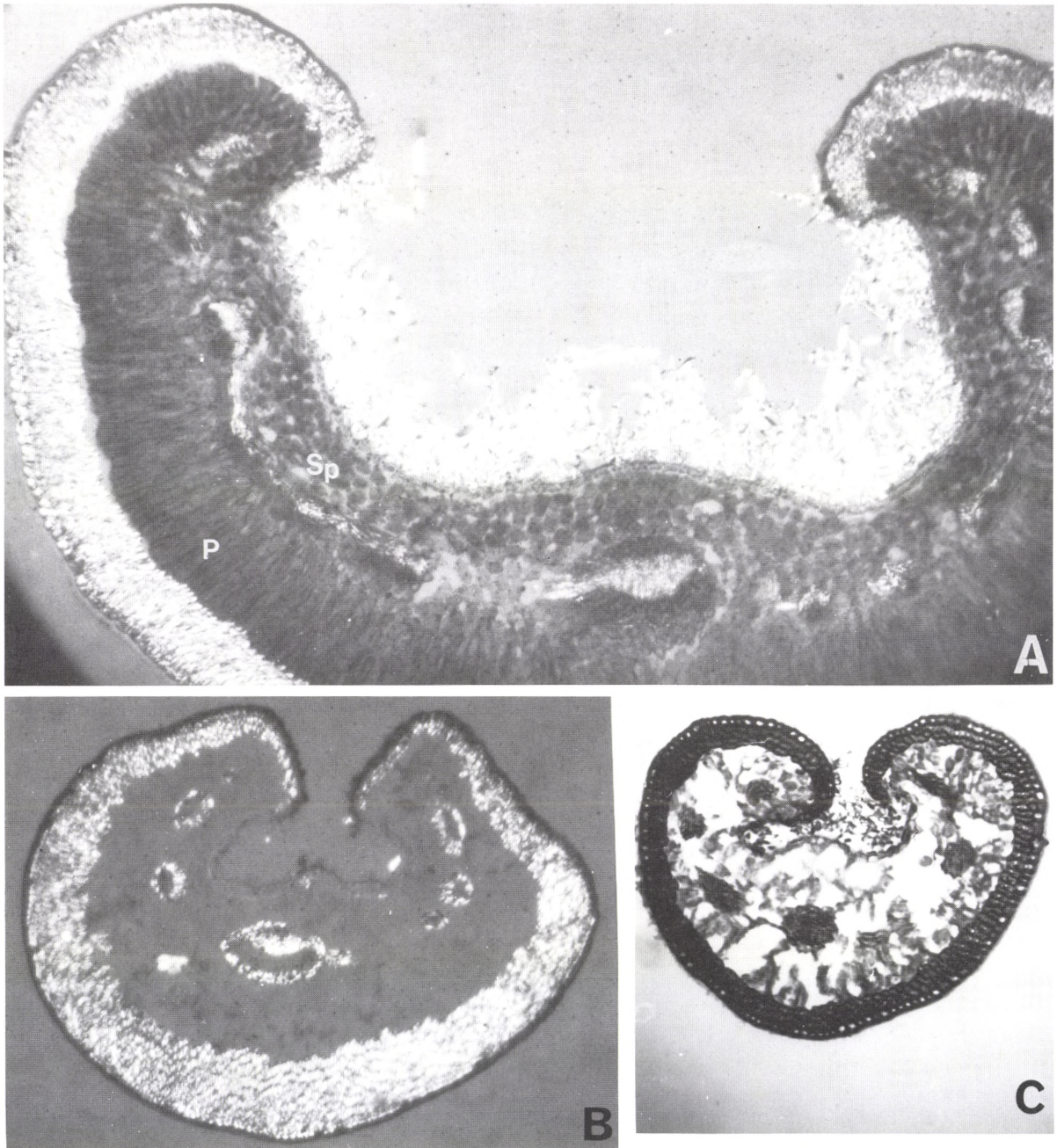
Fig. 6. Cross sedtions of involute leaves in *Chuquiraga.* – A. *C. hystrix,* inverse dorsiventrality conspicuous (p palisade tissue, sp spongy parenchyma). Hairs, xylem, sclerenchyma and abaxial epidermis show up in polarized light. – B. *C. rosulata.* Sclerenchymatous bundle sheaths and very thick abaxial sclerenchyma. Sudan IV stains cuticle and cuticular layer in epidermis outside groove. – C. *C. erinacea,* quadruple staining. A–C (× 200).
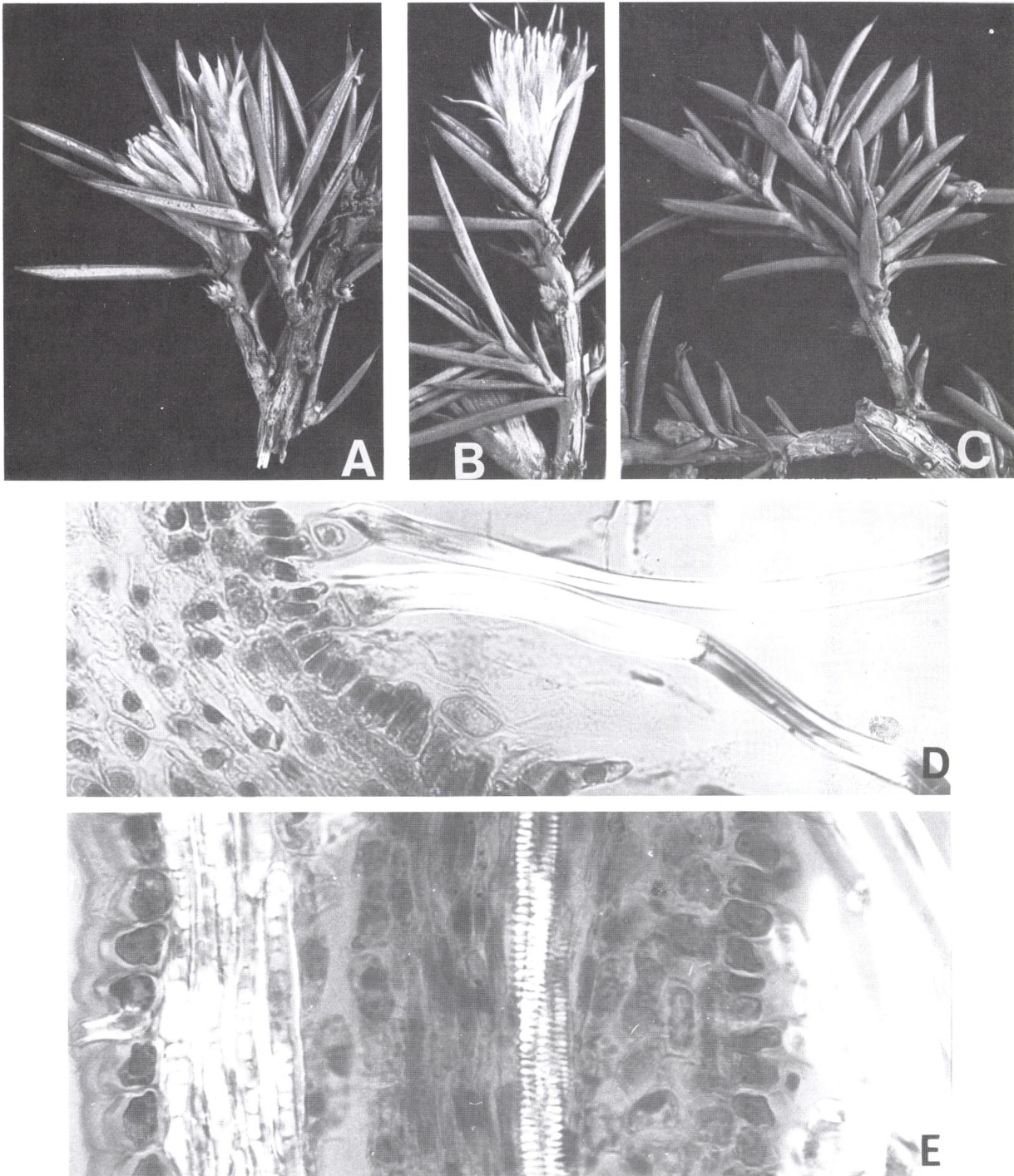
Fig. 7. *Chuquiraga hystrix.* A–B. Flowering specimen from Estancia El Sosneado, Atuel Valley (BHR No. 1394). – C. Specimen with slightly shorter leaves from Arroyo de la Manga near the Atuel Valley (BHR No. 919). A–C (× 1.5). – D. Adaxial epidermis in leaf primoridum. Long apical anisotropic hair cells and basal short isotropic cutinized cells. (× 500). – E. Longitudinal section through young leaf. Semipolarized light. From left: Abaxial epidermis with single hair base, sclerenchyma (bright) with pit canals, mesophyll with bundle (xylem bright) and adaxial epidermis with numerous long hairs. (× 320).
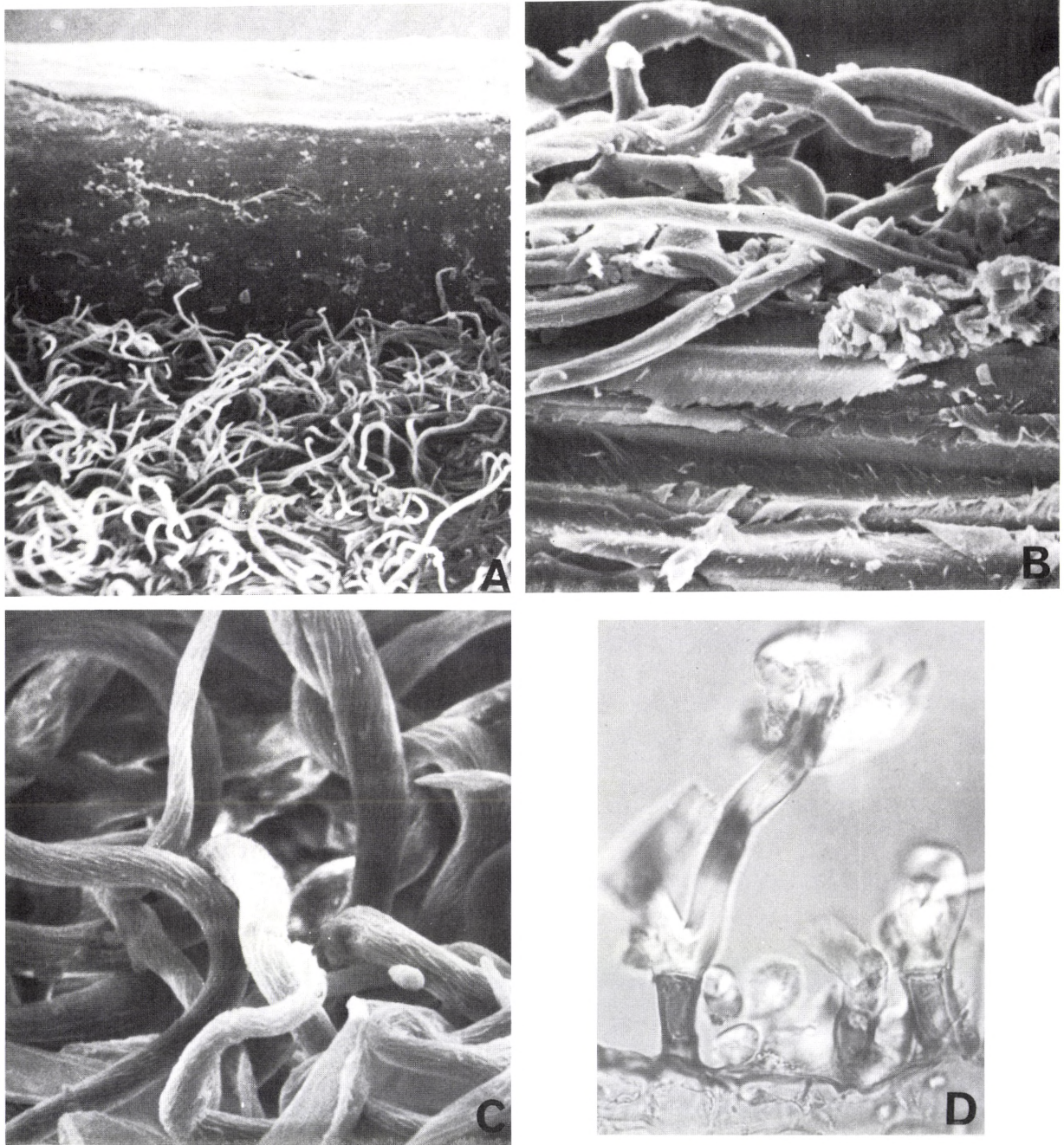
Fig. 8. *Chuquiraga hystrix.* Hair cover in adaxial groove. – A–C. SEM in A showing margin of leaf with scars from hairs which are shed and surface of felt. (× 150). – C. Detail showing surface of hairs. (× 1500). – D. Hair base and bipartite upper part. Sudan IV and semipolarized light. (× 500).
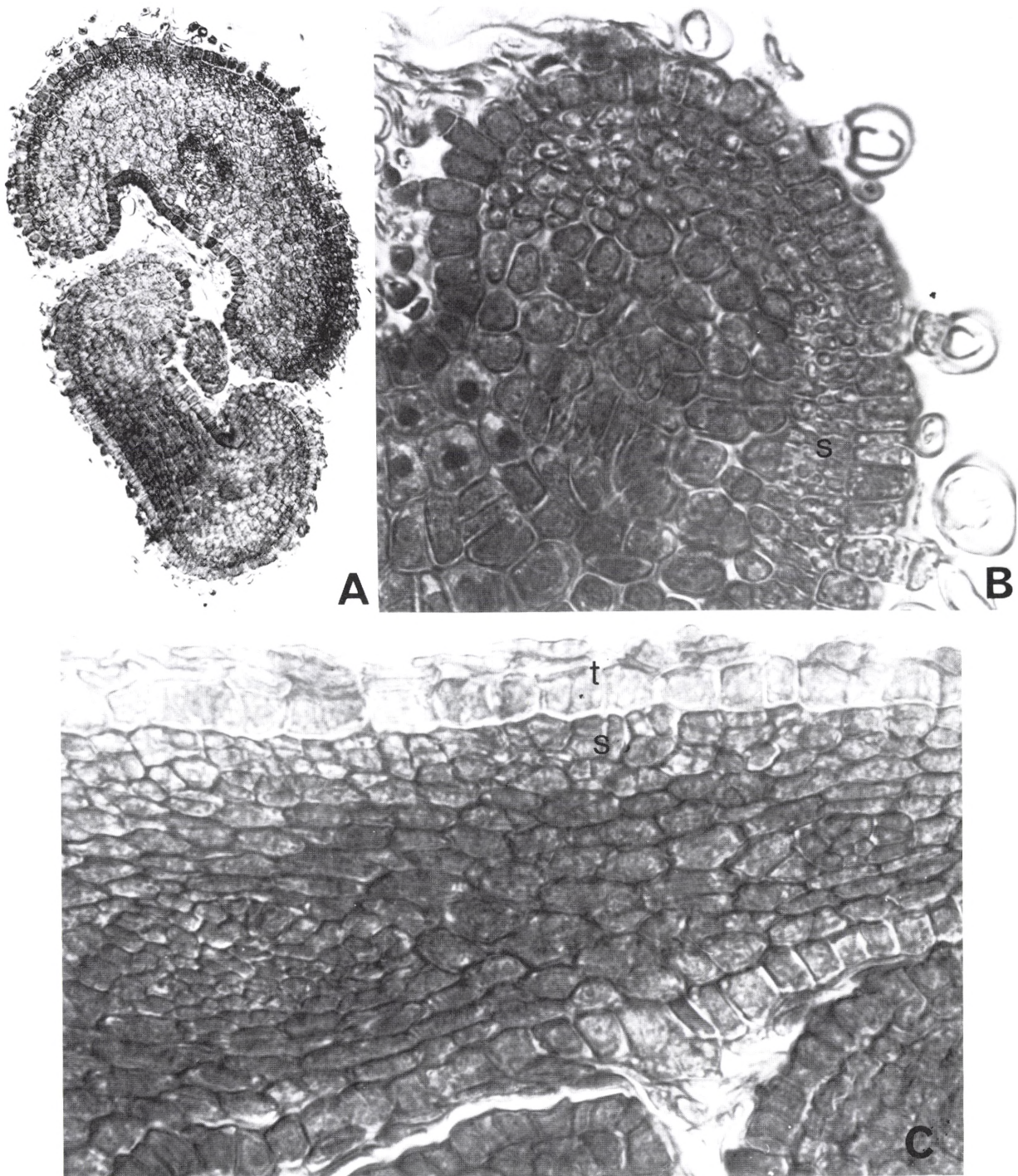
Fig. 9. *Chuquiraga hystrix.* Leaf primordia, cross sections. – A. Two youngest leaves showing early involution and (the upper leaf) differentiation of abaxial sclerenchyma and midrib. (× 100). – B. Part of the same at higher magnification showing sclerenchyma (s) and epidermis with young temporary hairs that swell distally. (× 500). – C. Slightly older primordium showing production of T-sheaped hairs (t), on both surfaces. The layer of abaxial sclerenchyma indicated by s. Initials of T-hairs on adaxial surface are seen below at spaces between the primordia. (× 640).

hairs may have two functions: 1) By their transpiration to secure a sufficient water supply during the early growth period, 2) to protect the young photosynthetic tissues from too strong radiation.

Leaf anatomy. The hairs on the adult leaves become restricted to the adaxial grooves. They are related to the T-hairs with a cutinized basal cell carrying two arms which, however, curl and become entangled (Fig. 8D). The hairs produce a thick felt that can project from the opening of the groove. The curling parts have a surface structure similar to that described for *C. ruscifolia.* The hair initials are a row of three cells, one on a level with the other epidermal cells, one median cell develops into the basal cell with cutinized wall, while the third is spindle-shaped and develops into the upper curling part (Fig. 9C). The number of palisade cell layers is 3–4. Between the palisades and the adaxial epidermis is a loose tissue resembling a spongy parenchyma. (Fig. 6A sp. 10B) In some of the material the palisade cells become replaced by swollen parenchymatous cells, which are empty and acquire suberized walls. The remaining mesophyll seems at this stage to remain alive, and the same is the case for the phloem in the bundles. The formation of swollen suberized cells may be a kind of localized withering. The abaxial sclerenchyma is composed of 4–6 layers of thick-walled, lignified cells. Also the abaxial epidermis has thick, lignified walls and a thick cuticular layer. Thus, the green cells in the center of the leaves may sometimes suffer from insufficient access to light or insufficient water supply and may consequently die.

Chuquiraga erinacea Don

A wide-ranging West Argentinian species occurring from Tucumán to Chubut. It is particularly common in shrub steppes near salt lakes *(BHR:* 61–65, *Werner* 1972: 79, *Ruthsatz* 1977).

Morphology Fig. 11. It is a 0.7–1.5 m tall, branched shrub with densely spaced, 4–14 mm

long acicular, inverted ericoid leaves *(Cabrera* 1971: Fig. 307, *Roig* 1971: Fig. 102). The groove is wider at the basis of the leaves and almost closed near the apex, which terminates in a mucro.

Leaf ontogeny. In transverse sections the primordia are crescent-shaped and resemble cataphylls. The abaxial epidermis and the sclerenchymatous hypoderm develop and ripen first. The parts which later constitute the mesophyll appear from the beginning as a network of chloroplast-containing cells separated by a system of intercellular spaces.

Leaf anatomy. The main structure is derived from an isolateral leaf type such as that in, e.g., *C. ruscifolia.* The mesophyll is loose, composed of branched cell rows arranged between the veins and the abaxial sclerenchyma or the adaxial epidermis with the stomata (Fig. 6C). The hypodermal sclerenchyma consists of 2–4 cell layers which, at the entrance to the furrows, decrease to 2–1 rows and disappear in the cavity (Fig. 11D). The latter widens considerably inside the entrance forming pockets on both sides of the outwards bulge of the midvein. The stomata are densely spaced in the epidermis that lines the central cavity (Fig. 11B). They are not sunken, but effectively protected by a dense hair cover. The hairs are T-shaped, their two arms often being twisted and arranged parallel to the bottom of the furrow (Fig. 12). The T-hair basal cells and even some epidermal cells become a red colour after treatment with Sudan IV. Vacuoles in the photosynthetic cells and in the phloem also react with this dye, an observation indicating that lipids may have been produced during the photosynthesis.

Chuquiraga rosulata Gaspar

Another West Argentinian species that was described and depicted by *Gaspar* (1945: 170–71) and *Cabrera* (1971 Fig. 309). It is recorded from typical Monte vegetation by *Roiz Leal* (1961: 106) and *BHR:* 212.
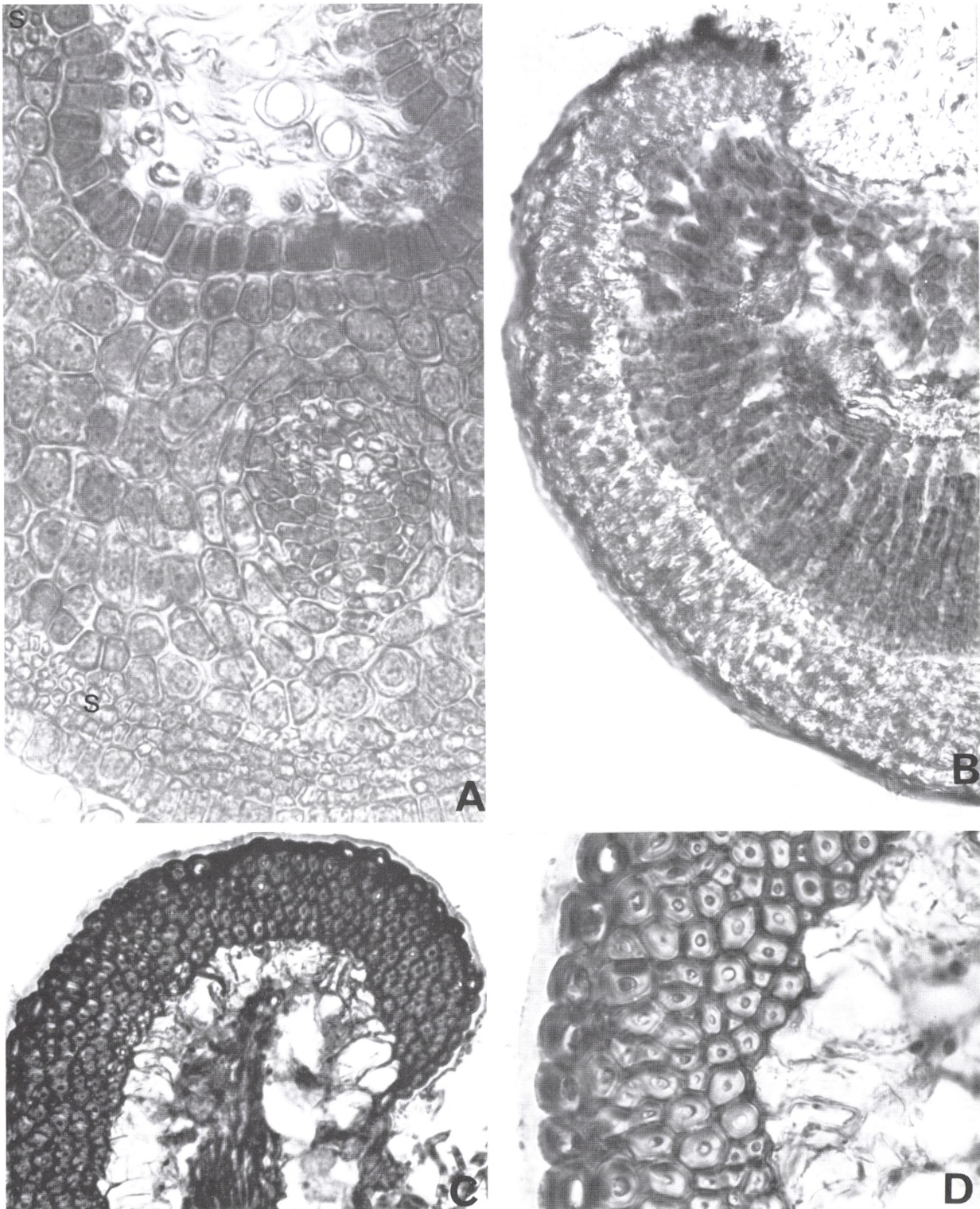
Fig. 10. *Chuquiraga hystrix.* Leaf development and differentiation. – A. Central part of primordium with midvein, abaxial sclerenchyma (s) and adaxial epidermis covered with temporary hairs. (× 500). – B. Leaf margin in adult leaf, all hairs on adaxial side are shed, palisade tissue between veins and sclerenchyma. (× 200). – C–D. Replacement of palisade tissue with swollen empty cells having suberized walls (Johannsen's quadruple staining). (× 200 (C), × 500 (D)).
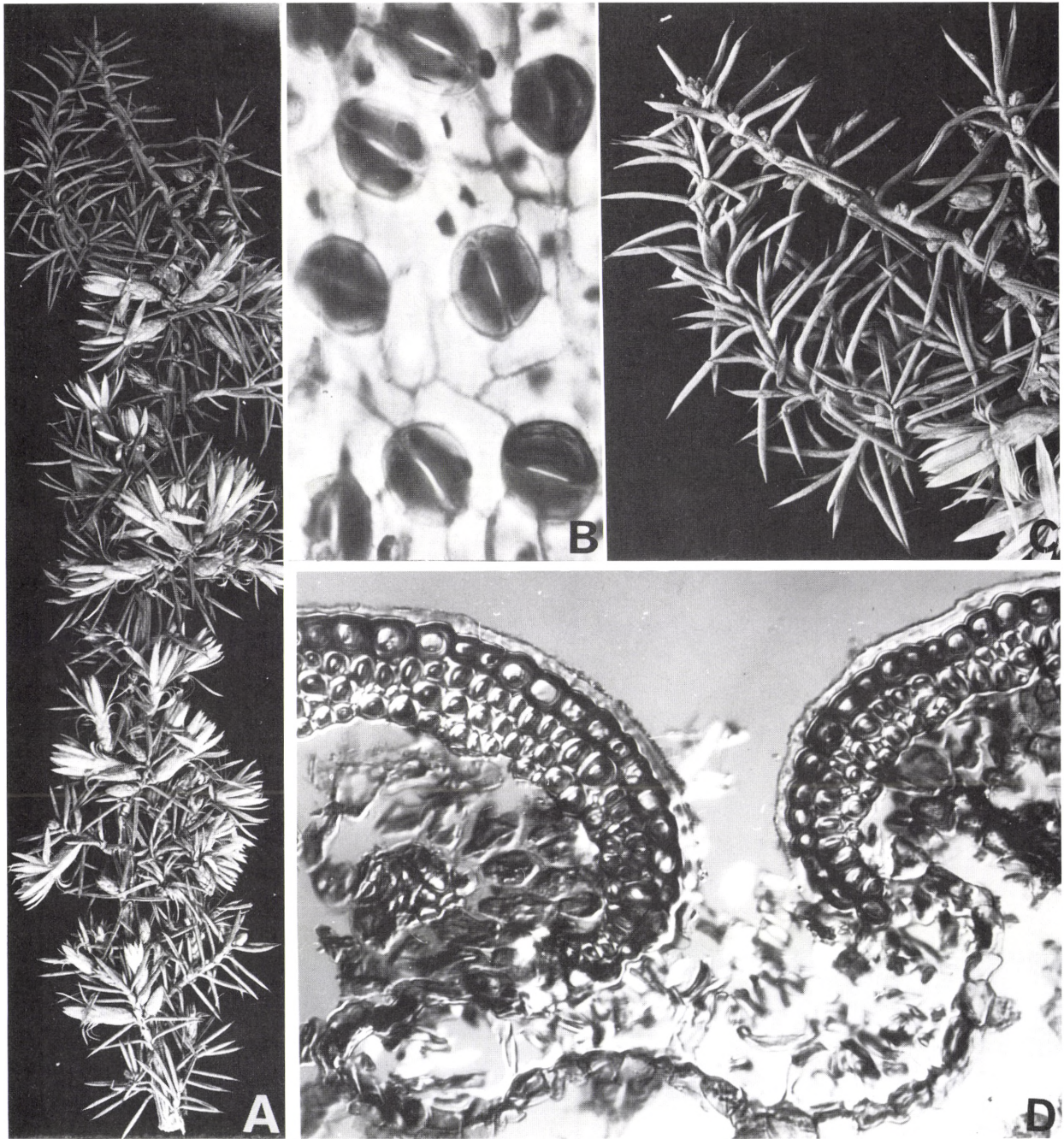
Fig. 11. *Chuquiraga erinacea.* A and C. Details of flowering specimen, A × 0.7, C × 1.5. – B. Surface of adaxial bottom of groove with stomata. (× 500). – D. Transverse section of groove and surroundings showing thick cuticular layer, lignified epidermal cells and 2–4 layers of sclerenchyma cells. Interference contrast. (× 320).
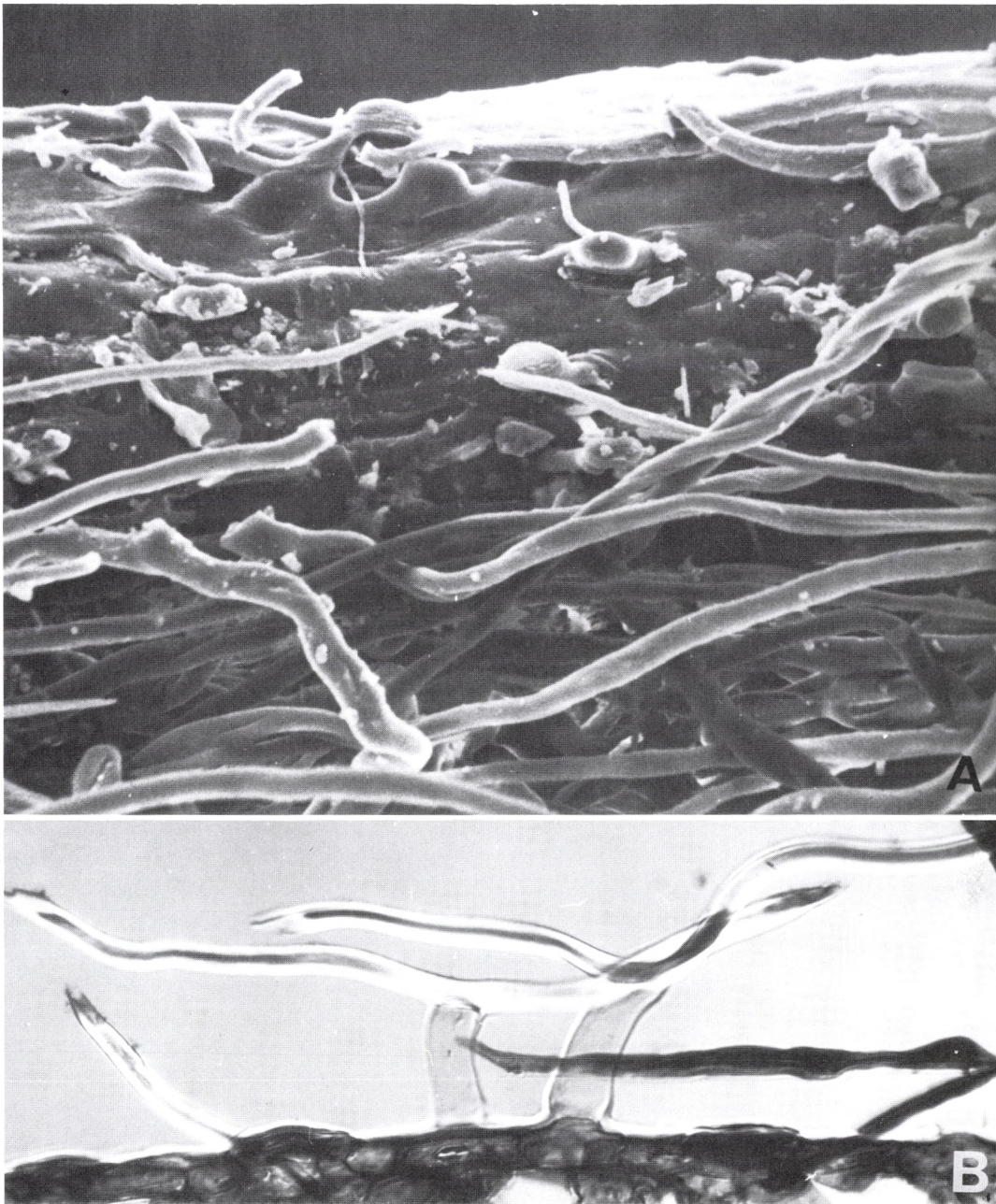
Fig. 12. *Chuquiraga erinacea.* A. SEM of margin and outer part of groove showing twisting of hair arms and wart-like remains after shed hairs. (× 750). – B. Epidermis in bottom of groove with T-hairs in polarized light. Uppper parts of T-hairs show up, one T-end is pointed, the other end appears broken and may represent the last formed part of the terminal T-hair cell. (× 500).
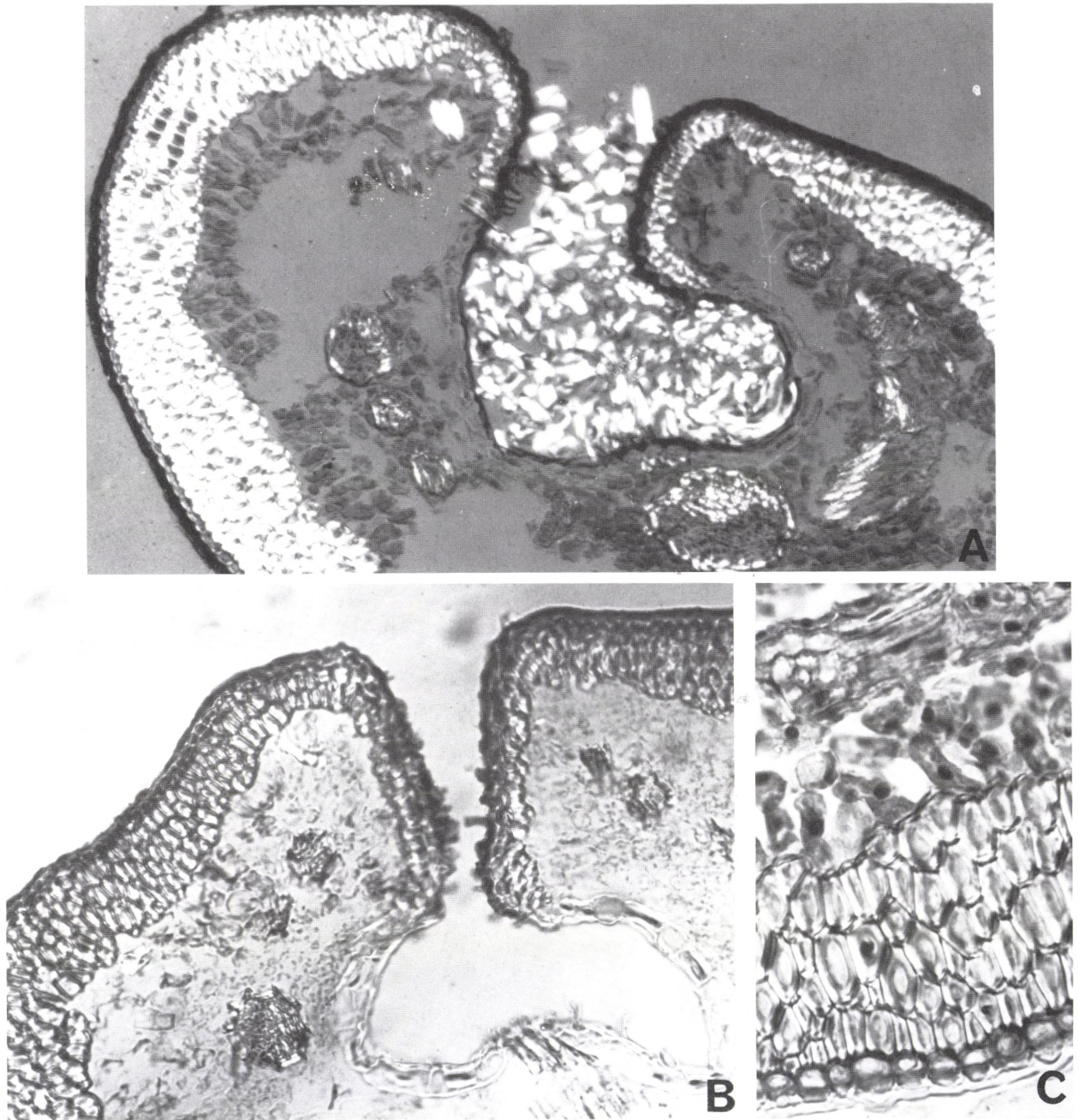
Fig. 13. *Chuquiraga rosulata.* Cross sections of leaves. – A. In polarized light and after staining with Sudan IV. Epidermal cells not or slightly birefringent. (× 200). – B. Leaf with particularly narrow entrance to groove. (× 200). – C. Central part of abaxial side showing loose palisade-like cells above five rows of sclerenchyma. Johansen's quadruple staining, semipolarized light. (× 500).

Leaf antomy. The material collected south of Mendoza resembles that of an unnamed species described by *Pyykkö* (1966: 519). The leaves correspond to those in *C. erinacea* in most characters. Transverse sections show that they are sometimes almost triangular and furnished with a number of sclerenchymatous cells in the bulge above the central vein. In *C. rosulata* all veins are surrounded by a sclerenchymatous bundle sheath (Fig. 13A). The entrance to the groove appears to be narrower, and the scleren-chyma lining the entrances usually consists of one cell layer only. On the other hand, there are five cell layers in the sclerenchyma at the median part of the abaxial side. The abaxial epidermis often has many unlignified cells. The mesophyll cells adjacent to the abaxial sclerenchyma approach a palisade cell structure (Fig. 13C). The hairs are related to T-hairs, but their arms are so twisted that the T-structure is difficult to establish.

5. Involute xeromorphic leaves or leaflets with adaxial grooves in the Fabales

Involute structure in mature leaves is rare among the dicotyledons, but not uncommon in, e.g. *Poales.* In the *Mutisieae (Asterales)* we have just described some particularly good examples and tried to understand how they came into existence through an evolution governed by changes in the environment. We do not know why involution of leaves, or formation of adaxial grooves, are so rare compared with revolute leaves with abaxial grooves protecting the stomata. The answer may be that it has been a selective advantage to utilize an adaxial, light-exposed, extended lamina to attain the most profitable photosynthesis, and, as pointed out by *Parkhurst* (1978), the placing of stomata on the abaxial sides counteracts the blocking of pores by dust, rainwater, etc. The normal dorsiventral leaf structure with adaxial palisades and abaxial stomata is most common in plants inhabiting arctic, temperate and wet tropical environments. Isolateral or cylindrical structure, on the other hand, seems favoured in dry subtropical regions (see Table 1 in *Parkhurst* (l.c.)), while odd inverse dorsiventral structure may be more exceptional and not a general phenomenon in some subtropical high mountains. The many examples of revolute leaf margins and ericoid leaf types occurring in widely distant families result from the fact that the plants in question are derived from ancestors with normal dorsiventral leaves.

Among the xerophytes from South America involution of leaflets seemed to take place in the genus *Anarthrophyllum,* which consequently was studied more carefully. However, in order to understand the strange and isolated leaflet structure in this genus, it was thought appropri-

ate to search for involute leaf structure in other genera in the *Fabales.* One of the best examples was mentioned by *Reinke* (1897) in the tribe *Podalyria.* This is regarded as a primitive group by systematists. The genus *Dillwynia* contains *D. ericifolia* with needle-like leaves which on their adaxial side have a narrow groove where the stomata occur sheltered by many hairs. These leaves are inverse dorsiventral with palisades at the abaxial side, while spongy mesophyll surrounds the groove. This structure is repeated in *D. juniperina* and *D. cinerascens.* In the latter the groove has a narrow entrance. *Flachs* (1916) classified *Dillwynia* leaves as showing a transition to inverse dorsiventrality. *Reinke* (l.c.) also mentioned adaxial grooves with stomata in *Eutaxia virgata* and *Pultenaea aristata* and *echinata;* the latter have densely spaced, needle-like leaves with concave adaxial sides containing all the stomata. According to *Reinke, Pultenaea* contains other species with normal dorsiventral leaves. Thus an evolution from flat and dorsiventral structure to inverse structure has taken place here in a group of related taxa.

Anarthrophyllum is referred to *Genisteae* where involute leaf structure is an exception. The South African *Lebeckia microphylla* has small narrow tripartite leaves with leaflets which have a groove on their adaxial side but are otherwise of isolateral structure. They possess three bundles with strong sclerenchyma on the abaxial sides *(Reinke* l.c.: 51). This species thus greatly resembles the South American *Anarthrophyllum.* Both belong to the subtribe *Crotalariinae.* Here we also find the large South African genus *Aspalatus* monographed by *Dahlgren* (1960). Ac-

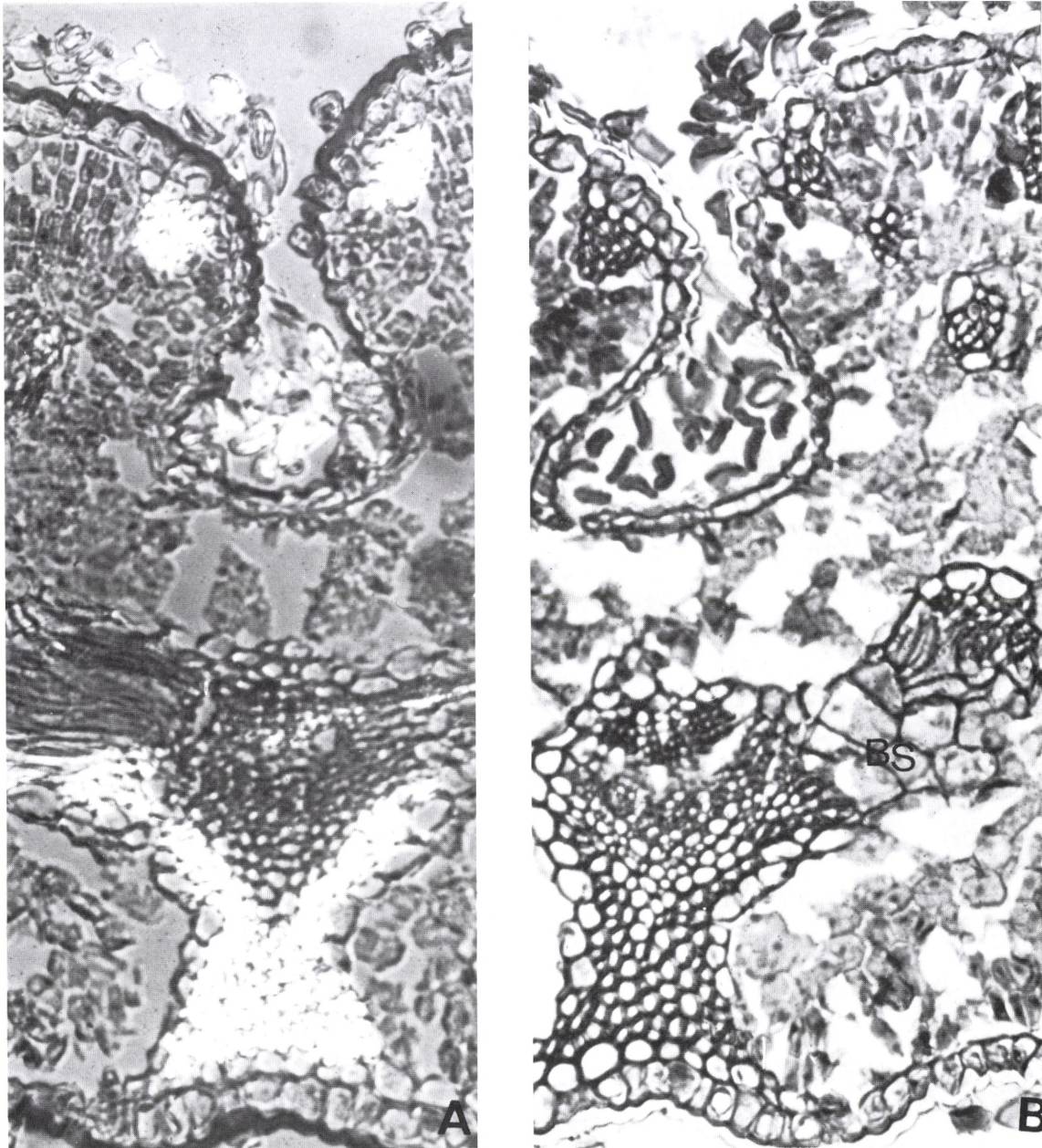Fig. 14. *Anarthrophyllum rigidum.* Transections of leaflets. – A. In polarized light after staining with Sudan IV. Sclerenchyma at midrib and hairs in groove bright. Cutinized epidermal layer stained. – B. Stained with Fast green-Safranin. Sclerenchyma and hair cells stained, cutinized layer unstained. Bundle sheaths surrounding sclerenchyma and accompanying commissural strand between midrib and small vein. A–B (× 200).

cording to this author very few or no species of *Aspalathus* have involute leaves. *A. diffusa* approaches the structure having inflexed leaf margins around the upper woolly side (l.c. 343–46). According to *Levy* (1902), who studied the anatomy of *Aspalathus,* only one species with triangular, needle-like leaves, *A. triquetra,* has the stomata confined to the adaxial surface.

Reinke (l.c.: 70) considered the *Crotalariinae* to be primitive, having properties resembling those of the ancestors of the *Genisteae.* The *Anarthrophyllum* leaf, therefore, is probably not just a result of a recent adaptive evolution. On the contrary, the adaxial groove may be a character selected long ago. The forces which created the groove were perhaps active when genera such as *Dillwynia* in the *Podalyria* tribe emerged. However, as pointed out by *Dormer* (1946: 150), both *Anarthrophyllum* and *Aspalathus* probably represent specialized members of the *Crotalariinae.*

In *Anarthrophyllum* the adaxial groove was present in all species studied by *Sorarú* (1974: 456–58). The groove can be short as in *A. andinum* or short and narrow as in *A. catamarcense,* or deep and wide as in *A. subandinum.* The latter has clearly typical involute leaflets and not merely an adaxial groove. In *A. rigidum* (including *A. brevistipula)* the morphology and anatomy of the leaves vary from one collection to another (see *Sorarú* l.c. Fig. 2) and *Pyykkö* (1966, Fig. 104)). Below two species of *Anarthrophyllum* are described in greater detail, viz. *A. rigidum* and *A. patagonicum.* They agree in the main structure of the leaflets, but are in many ways entirely different. Both species, however, have tripartite leaves. In the Chilean *A. andicolum (=A. juniperinum)* the leaves are reduced to one leaflet (see *Reinke* l.c. Fig. 36).

Anarthrophyllum rigidum (Gill.) Benth. & Hook.
A 0.8–1.6 m tall, densely branched shrub occurring in Chile (Prov. Curicó) and West Argentina (from Mendoza to Chubut and Santa Cruz). Its type of habitat is not so dry and exposed as that

in which *A. patagonicum* occurs (details in BHR: 282–283 and Fig. 122–125). However, the different ecological requirements of the two species are only reflected to a limited extent in their leaf structure.

Morphology. The leaves are trifid and densely covered with adpressed hairs pointing towards the apices of the leaflets which terminate in small spines. At their bases the leaves have a short sheath or ochrea formed by the two lanceolate stipules and the petiole. The latter is 2–3 (-5) mm long, while the leaflets reach 7–13 (-20) mm (*Sorarú* l.c. Fig. 7 i-k). The petiole and stipules were misinterpreted by *Pyykkö* (l.c.: 492). The petiole is green and would be an ellipsoidal phyllode if there were no leaflets. The leaflets approach a cylindrical structure although with adaxial grooves.

Leaf ontogeny. At a very early stage the leaflet primordia attain the groove (Fig. 15A). This is not a matter of simple involutions. The grooves appear to be congenital depressions between two equal lobes. In the early stages a strong promotion of the abaxial sides takes place. The hairs on this side appear almost mature, while the cells bordering the groove are embryonic (Fig. 15 B-C). The abaxial bundles with their sclerenchyma strands are also established at an early stage. The primordia develop inside the ochrea.

Leaf anatomy. The stipules behave like cataphylls. Their abaxial surfaces have large epidermal cells with thick cuticular layers and abundant hairs. Their adaxial sides have smaller epidermal cells, thin cuticular layers and scattered stomata. Below the abaxial epidermis follows a continuous hypodermal layer and mesophyll.

The petioles are furnished with strong central bundles. In cross sections the central bundle is almost surrounded by a horseshoe-shaped sclerenchymatous strand with the opening facing the adaxial side (Fig. 15F). Anatomically this petiole strand resembles strands described in *Indigofera* or *Myroxylon (Metcalfe & Chalk* 1950). In *Anarthrophyllum* strong lateral bundles furth-
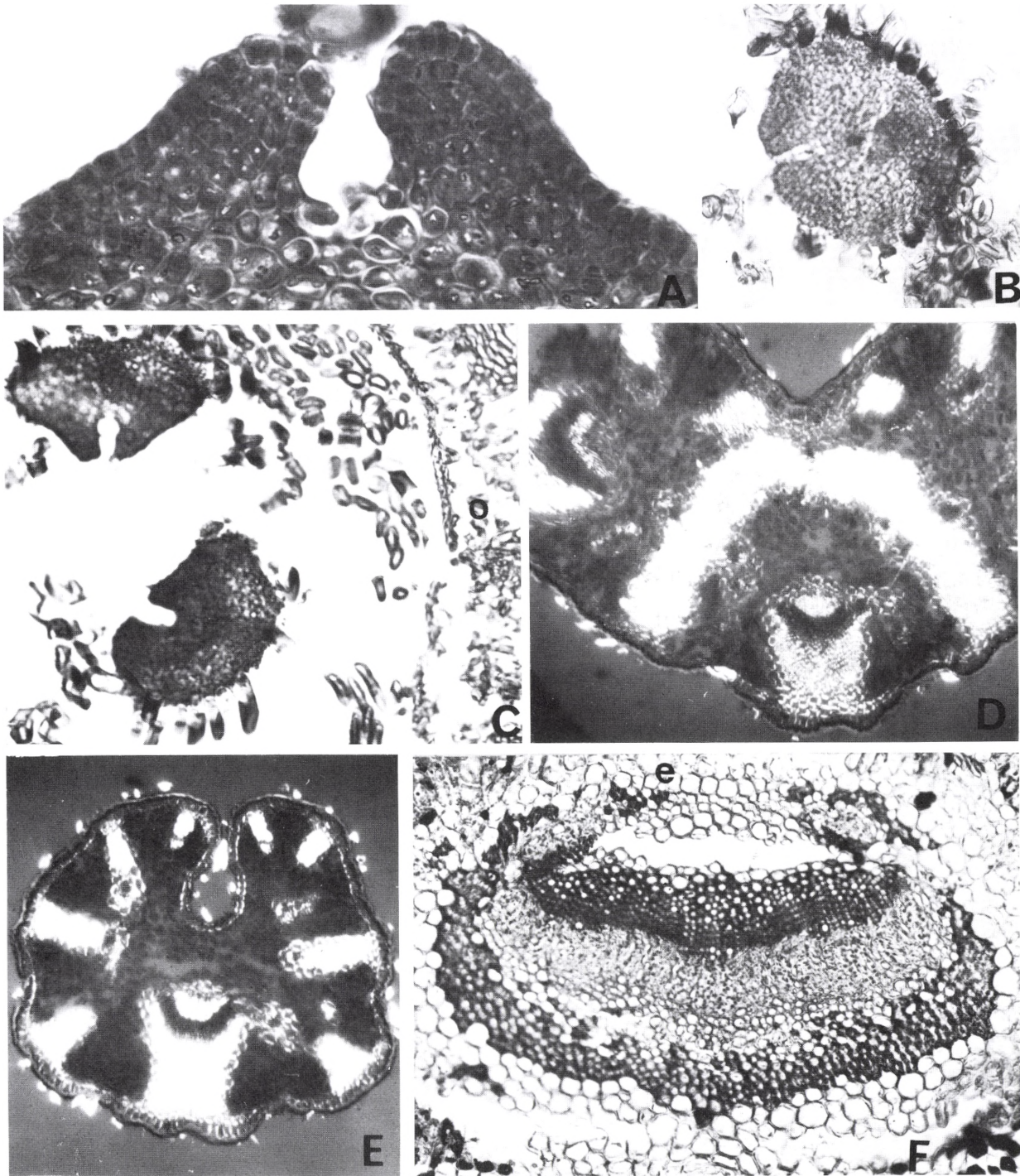
Fig. 15. *Anarthrophyllum rigidum.* A–C. Leaflet primordia. Cross sections. – A. Adaxial groove, crystals formed in most cells. Johansen's quadruple staining. (× 500). – B. Sudan IV stains basal cells in hairs on abaxial side. (× 100). – C. Two of the three primordia inside sheath-like ochrea (O). Johansen's quadruple stain. (× 100). – D. Junction of two leaflets with sclerenchymatous area shaped like a horseshoe. Polarized light. (× 100). – E. Leaflet in polarized light illustrating compartmentation of green tissues. (× 100). – F. Cross section of main bundle in petiole. e endodermis. Xylem and sclerenchyma stained dark reddish after treatment with Fluoroglucinol-HCl. (× 200).

er occur along the ends of the ellipsoidal body, while a number of small accessory bundles is developed in the surrounding parenchyma. Here the photosynthetic cells resemble palisades. They occur on both sides, but in a continuous layer on the adaxial side only. On the abaxial side the green tissue is interrupted by collenchyma, which accompanies the sclerenchyma at the central bundle.

Already in the upper part an intricate branching of the bundles takes place. The two lateral bundles proceed into the two lateral leaflets, but, after branching, the central bundle also furnishes the lateral leaflets with strong bundles. Concomitantly the accompanying sclerenchyma branches and some of the strands fuse and form large sclerenchymatous junctions at the base of the leaflets. Single bundles (or veins) with sclerenchymatous escort issue from these junctions and proceed into the lateral leaflets. In cross sections the junctions at one level form a pretzel-like figure which, however, soon disintegrates into smaller strands, while the junction alters its shape and forms a revolute horseshoe (Fig. 15D). The two bundle branches running into the lateral leaflets are in the middle of the openings in the pretzel and later on in both sides of the revolute horseshoe. The junctions, although corresponding to leaf articulations in other genera, appear to be firm and inflexible in the case of *Anarthrophyllum.* The central bundle in the petioles has a bundle sheath of large cells. The radial walls of the sheath cells are traversed by conspicuous, densely spaced plasmodesmata. This indicates that symplastic transport of substances can take place in the bundle sheath cells across the petioles. No wall structures resembling Casparian strips were ascertained.

Leaflets. Each leaflet receives one abaxial central bundle supported by sclerenchyma, which in cross section has an outline resembling the letter X. In cross sections of smaller lateral bundles the supporting sclerenchyma has a triangular outline (Fig. 14A, 15E). The few small interstitial veins are without sclerenchymatous support (Fig. 14B). All bundles are provided with bundle sheaths of wide cells without chloroplasts. In some of the smallest veins single bundle-sheath cells deviate, their walls having distinct trabeculae. The strong sclerenchyma strands at the bundles support the leaflets as beams which impede bending of the mesophyll. The mesophyll is rather uniform, but the peripheral cells are palisade-like. Stomata occur between the sclerenchymatous bundle areas as well as in the groove. Thus the leaf is amphistomatous, but air flow through the leaves is probably limited because the mesophyll has rather narrow intercellular spaces. The stomatal pores have front ledges and small front cavities. The walls facing the aperture have minute dentiform projections. The stomata in *A. catamarcense (Sorarú* l.c. Fig. 3) resemble those in *A. rigidum.* The three leaflets in the latter have a median groove which in the primordia appears glabrous but later becomes filled with hairs pointing to the apices. The entrances to the grooves are narrowed from the beginning. They continue right down to the top of the petiole and constitute an almost closed pipeline in which water may be able to flow by capillarity.

Hairs. The numerous hairs consist of three cells all containing nuclei: A basal cell on the level of the epidermis and usually smaller than the normal epidermal cells, a short oblique central cell surrounded by a thick cutinized layer and a long, pointed apical cell (Fig. 16). The latter has many cellulosic layers and is covered by a thin cuticle with minute cuticle warts. A large nucleus is placed near its base. In structure the hair somewhat resembles those described above in *Junellia uniflora.* There is occasional shedding of the apical pointed cell. Afterwards a cutinized scar is left. The base of the apical cell leaves a circular cellulosic mark that shows up in polarized light. (Fig. 16J). The part that can be shed has a cross wall at its base with a conspicuous pit field resembling a strainer. It is compo-
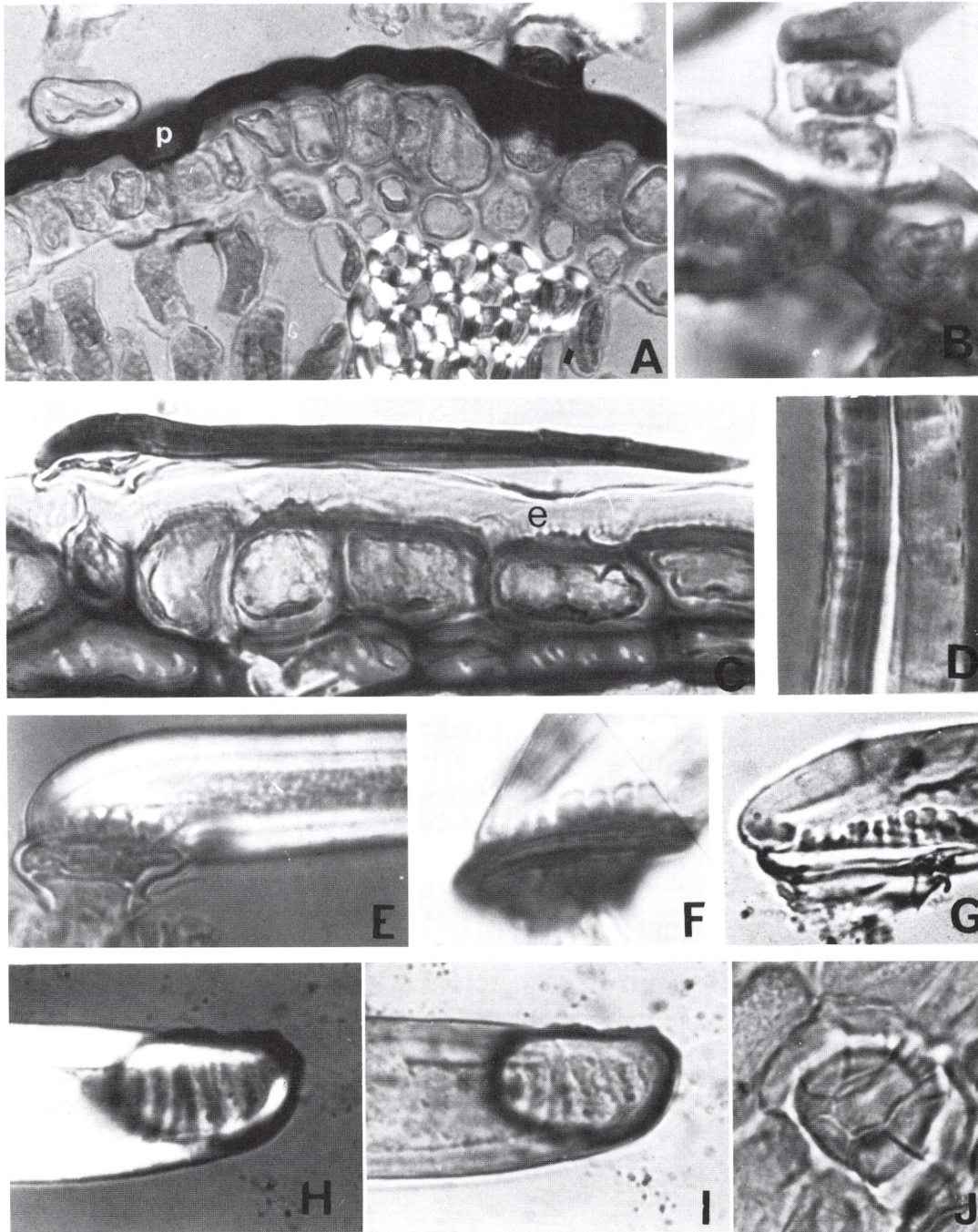
Fig. 16. *Anarthrophyllum rigidum.* A. In polarized light after staining with Sudan IV. Slightly sunken stoma (p), interior of guard cells has cutinized surfaces. At (p) distal part of hair with thin cuticle surrounding cellulosic part and the cell lumen. Bundle sheath cells between epidermis and sclerenchyma. (× 500). – B. Two basal hair cells with nuclei. (× 800). – C. Entire hair (dark reddish in Johansen's quadruple stain) with basal cell and cytoplasmatic connection to small epidermis cell below. Ectodesmata at (e). Many pits in subepidermal layer, which is part of a bundle sheath (cp. A). (× 500). – D. Distal part of hair cell showing cellulosic layers and small cutinized warts. Hair lumen white. (× 2000). – E–I. Basal wall in hair cell showing trabeculae separated by lengthy pits. E and H in polarized light, F, H and I stained with Sudan IV, G after enzymatic treatment, interference contrast. (× 800). – J Paradermal section of scar after shedding of apical hair cell. The cellulosic basal part visible as is the birefringent circle. Dark radiating pit canals to surrounding epidermal cells. (× 640).

sed of a number of rod-shaped outgrowths (trabeculae) separated by lengthy pits. The trabeculae are lined with cytoplasmic material, which disappears after enzymatic treatment (Fig. 16G). The proximal parts of the trabeculae are cutinized (Fig. 16H). Numerous pits into the surrounding epidermal cells occur around the scars. A thin strand connects the short basal hair cell with the small epidermal cell beneath (Fig. 16C). The water absorbing hairs in *Diplotaxis harra* described by *Volkens* (1887: 31–32) and *Haberlandt* (1904: Fig. 83) are remarkably similar in structure. *Hare* (1943) described the water absorbing function of the long, much twisted and interwoven hairs on leaves of *Senecio cottonii* growing in the mist at high altitudes on Kilimanjaro. The basal cells in the hairs have thin walls but prominent nuclei and are surmounted by two or more thick-walled cells devoid of contents at maturity. The cross walls are thick and perforated, resembling the basal walls in the hairs of *Anarthrophyllum*. *Hare* adds that drops of water applied to the felt-like cover of the abaxial leaf sides in *Senecio cottonii* are readily absorbed and that the water possibly passes on to the tissues of the leaves. The T-hairs in *Spartocytisus* described by *Lyshede* (1977), and by him regarded as water-absorbing, are also remarkable. The short bulge outwards opposite the long, pointed part in the *Anarthrophyllum* hair (Fig. 16C,G) may represent a reduced T-hair arm, and the interspaces between the trabeculae may correspond to the canals in the thick basal walls in the hairs of *Spartocytisus (Lyshede* l.c. Fig. 4).

Anarthrophyllum patagonicum Speg.

This species is a hemispherical cushion plant with 3 leaflets terminating in stronger spines. It is an »Igelstrauch« (hedgehog-shrub) attaining the same life form as, e.g. *Mulinum spinosum*, which is dominant on the Patagonian steppe (cp. Fig. 18).

Leaf morphology. The trifid leaves have 5–10 (-15) mm long mucronate leaflets. The stipules are long and also mucronate *(Soraru* l.c. Fig. 11N). The adaxial grooves are wider than in *A. rigidum* and not narrowed at the entrances.

Leaf anatomy. The mucronate leaflet apices have single, often horseshoe-shaped sclerenchyma strands that represent continuations of the five main sclerenchyma strands at the bundles (Fig. 17). Transections of the leaflets presented by *Pyykkö* (l.c. Fig. 102) and *Soraru* (l.c. Fig. 1A) do not agree well with regard to the adaxial groove, which is much wider in the material depicted by the latter author. The grooves in the material studied by me correspond to those in *Soraru's* material.

The anatomical leaf characters distinguishing *Anarthrophyllum rigidum* from *patagonicum* concern the width of the groove, the system of bundle-sheath cells, the shape of the sclerenchyma strands, and the median hair cells, which are bulbous in *A. patagonicum.* Both species have stomata in and outside the grooves and thick epidermal cuticular layers with much wax in the walls just outside the cellulosic interior wall layers.

The bundle-sheath system in the two species exhibits an interesting difference. The bundle-sheath cells are clearly much wider in the less xeromorphic *A. rigidum.* In *A. patagonicum,* on the other hand, wider bundle-sheath cells are confined to a row bordering the abaxial epidermis. The sheath cells here spread in a fan shape and thereby make contact with the epidermis over a longer distance. These locally wider subepidermal sheath cells may function like those in bundle-sheath extensions, hence in the extravascular translocation system in the leaf (cp. *Wylie* 1952). In *A. patagonicum* the function may be that of transferring water and solutes, preferably taking place in the apoplast. Considering the density of hairs with long living cells, and suggesting water permeability of the walls in the apical hair cells, an apoplastic transfer of water to and from the epidermis with its hair cover does not seem unlikely.
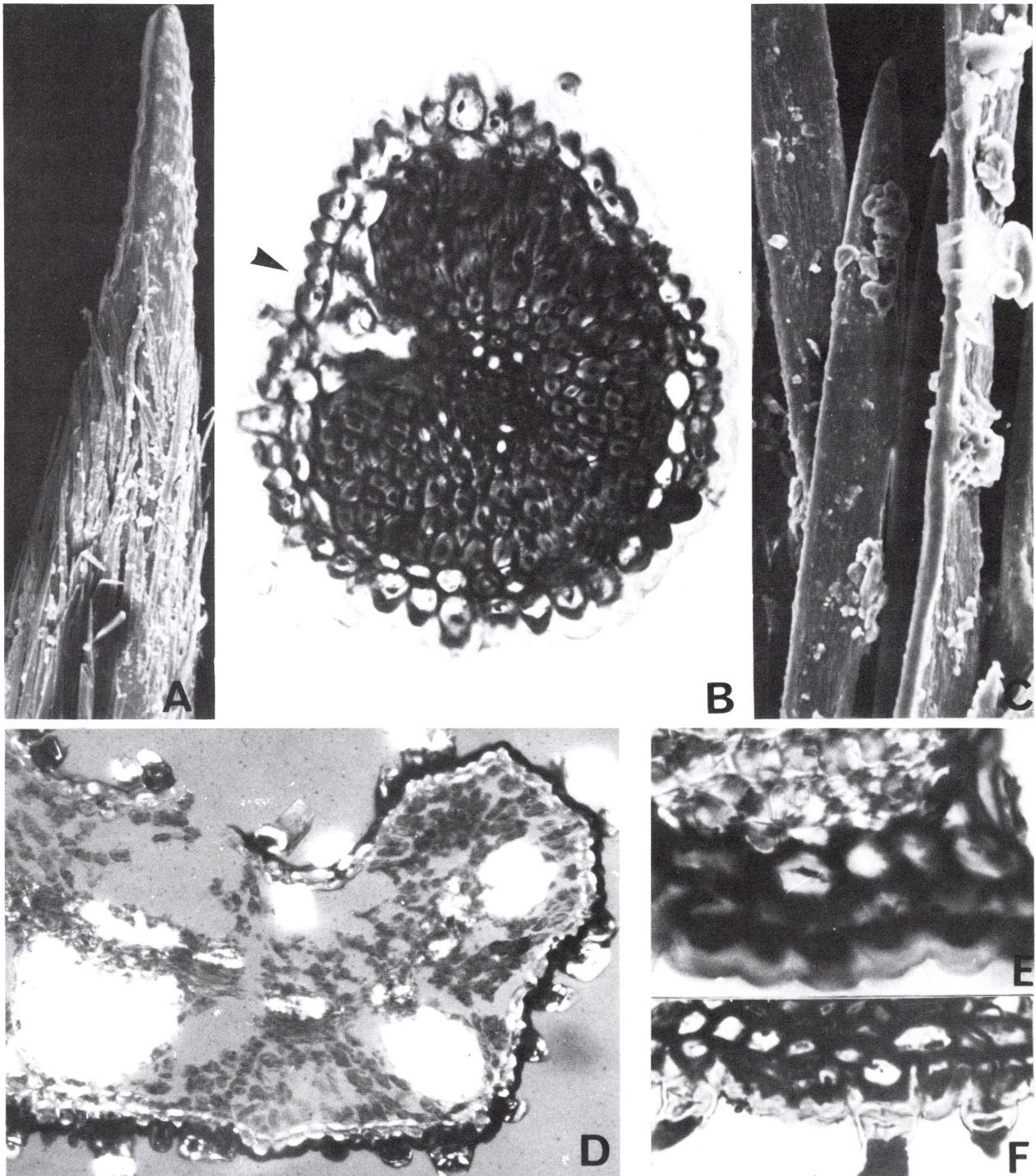
Fig. 17. *Anarthrophyllum patagonicum.* A. Mucronate leaflet apex with many adpressed hairs and uppermost part of groove (dark), SEM. (× 100). – B. Cross section of apical mucronate part. Johansen's quadruple stain. Black arrow points to continuation of groove. (× 320). – Flattened distal parts of hairs, SEM. (× 1000). – D. Cross section of leaf with unsually wide adaxial groove. Sudan IV staining of cuticle and cuticular layer as well as of basal hair cells. Sclerenchyma, xylem and distal long parts of hairs bright in polarized light. One central bundle (midrib) and two lateral ones. (× 200). – E–F. Bundle-sheath extension developed as a localized hypodermal layer inserted between the bundle sclerenchyma and the epidermis (in F having three hairs). Johansen's quadruple staining. (E × 320, F × 200).

According to *Sorarú* (Fig. 3), the sheaths are composed exclusively of small cells in, e.g. *A. catamarcense*. Thus the development of bundle sheaths in *Anarthrophyllum* varies. In *Aspalathus, Levy* (1901) mentions 22 out of 79 species with well developed bundle sheaths ("Parenchymscheiden"). This difference between the two genera ought to be studied more closely and considered in relation to the ecology of the species.

To ascribe a clear ecological significance to the adaxial grooves in *Anarthrophyllum* is impossible. In *A. patagonicum* the number of stomata inside the grooves is slightly higher than outside. Thus the grooves probably have a limited function as an antitranspirent arrangement. In *Chuquiraga* the involution, on the other hand, may have great effect against water losses.

In both genera the strong sclerenchymatous strands or plates of mainly abaxial position have undoubtedly influenced the semophyletic development and made leaf involution or adaxial groove formation one of the possible structural endings. However, these endings are entirely different. In *Chuquiraga* the continuous plate impedes gas exchange through the abaxial tissues and each leaf constitutes one photosynthetic compartment. In *Anarthrophyllum*, on the contrary, there is a conspicuous radial compartmentation of the green tissues, effectuated by strong but isolated sclerenchyma strands reaching the abaxial epidermis and one deep adaxial groove (Fig. 15 E).

6. Development of spiny tripartite leaves from involute primordia

Leaf morphology and phylogeny (semophylesis) in the *Apiales* were already studied by *Domin* (1909). According to this author (p. 142), the great morphological leaf variation in the genus *Azorella* is of fundamental importance for the understanding of the semophyletic lines leading to the different leaf types in the family. *Azorella* is so closely related to *Mulinum* that *Reiche* (1902) finds it difficult to keep these two genera apart. Both belong to the primitive group *Hydrocotyloideae,* which has many representatives in the Andes.

Reductions of the petiole and in the number of lobes in the blades in *Azorella* appear from the summary in *Domin* (l.c. 140–141). The figures in his Plates II–III show that the leaf margins are sometimes involute, thus in the very deviating *Azorella ameghinoi* as well as in *A. apoda* and *Bolax gummifera. Espinosa* (1932 Fig. 7) illustrates a striking example of an involute leaf in *Azorella filamentosa.* The number of segments or lobes in *Azorella* – leaves varies between 3 and 7. Very characteristic of *Azorella,* and of *Mulinum,* are the leaf sheaths that are grown together and ciliated along the margin. Many species of *Azorella* have closely inserted leaves overlapping each other, sometimes scale-like, thus, e.g., in *A. selago* studied by *Ternetz* (1902). *A. lycopodioides,* an important cushion plant in Tierra del Fuego, approaches *Mulinum* in having tripartite leaves with narrow, spiny segments. Some species of *Mulinum,* on the other hand, approach *Azorella* in having broader and not spiny lobes or segments, thus *M. patagonicum, M. echegarayi* and *M. pauciflorum.* The latter was discussed and illustrated by *Constance* (1965: 279). The great

morphological diversity in the leaves of *Azorella* from Ecuador appears strikingly from the work of *Mathias & Constance* (1976: 6–16).

A semophyletic lineage leading to the spiny group of *Mulinum* would probably start with species with palmately three- to five-lobed leaves. An evolution of this kind would involve an increasing amount of sclerenchyma at the main bundles, reductions of the mesophyll and a change from palmately lobed or almost three- to five-foliate leaves to a trifid structure with narrow, spiny segments.

Mulinum spinosum (Cav.) Pers.
This important Patagonian species is one of a complex or aggregate of closely related microspecies. My material includes typical *M. spinosum* from Tierra del Fuego *(Hjerting, Søgaard & Ødum (75–203)),* which at present is cultivated in Copenhagen, and *M. ovalleanum* Phil., collected in 1955 in the upper part of the Atuel Valley. The latter forms denser cushions than *M. spinosum* (Fig. 81 in *BHR),* but its anatomical structure is only slightly different.

Morphology. Forms large hemispherical, not very dense cushions. The leaves are 3 (-5) partite with spiny segments. In the lateral segments the lamina approaching the middle segment are narrower than the out-turned lamina. The middle vein protrudes, while the lamina on both sides are slightly concave, forming two runnels. There are no petioles, but the narrow part resembles one. The plants are glabrous, but the sheaths have long-ciliated margins (Fig. 19A).

Leaf sheath and hair-like excrescences. The leaf primordia appear densely packed inside sheaths
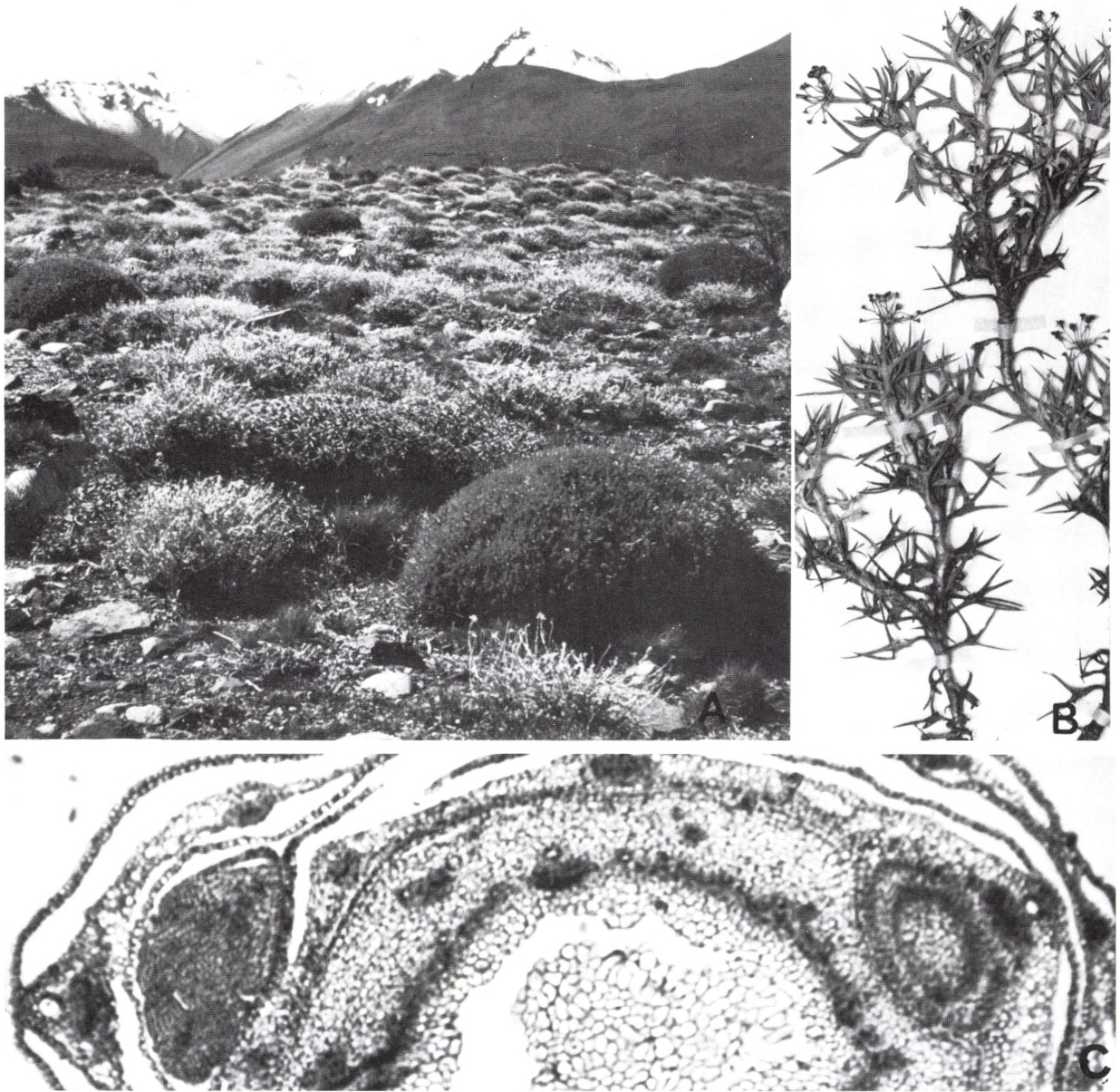
Fig. 18. A. Patagonian steppe vegetation in the middle part of the Atuel Valley, Argentinian Andes, Mendoza Province. *Anarthrophyllum patagonicum* forming dense hemisphercical cushions covered with yellowish-red flowers (4 dark specimens in the picture). The vegetation occurred on a gravelly, exposed plain and contained much *Senecio psammophilus, Stipa chrysphylla, Maihuenia* sp. and *Mulinum ovalleanum*. – B. Parts of flowering cushion of *Mulinum spinosum* (Salado Valley, alt. 2100 m. BHR No. 1453). (× 0.5). – C. Cross section of stem of *Mulinum spinosum*. Two axial buds. The oldest (on the left) is seen at higher magnification in Fig. 20A. The stem section shows pith and an almost continuous cambium. Johansen's quadruple staining. (× 50).
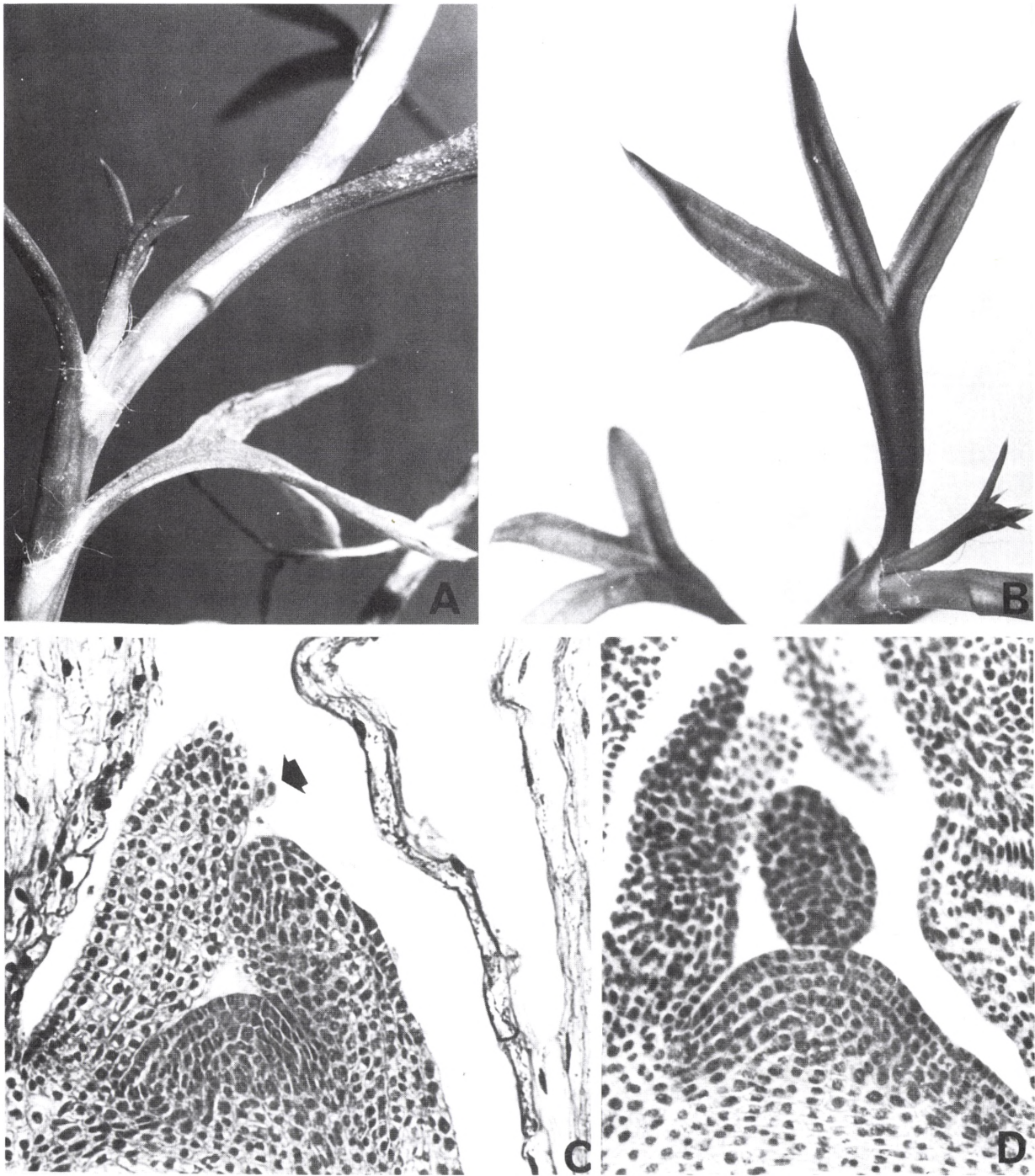
Fig. 19. *Mulinum spinosum* from Tierra del Fuego cultivated in Copenhagen. – A–B. Sheathing ciliated leaf bases and axillary shoots. – B shows a leaf with four segments. – C. Young axillary bud with apical meristem and developing leaves, arrow points to small body detached from adjacent sheath initial. On the right, curly epidermal layer covering air-filled cavity on the adaxial sheathing side of leaf. – D. Apical meristem of main shoot with leaf primordium which shows branching off of two segments. C–D (× 200).

which thus enclose a kind of bud. Two successive internodia with their primordia are encircled by their sheaths. Longitudinal sections through the shoot apex show that tips of leaf primordia and particularly sheath primordia continue in hair-like cell rows, which are inclined to ligate smaller parts at their upper endings. The hair-like excrescences may be related to emergences covering the leaves in *Azorella ameghinoi (Domin* l.c. Plate III 8) and they resemble the barbules in *Begonia (Mayewski* 1872) and the villi in *Papaver,* described by *Netolitzski* (cp., *Uphof & Hummell* 1962). The small bodies which become isolated are proliferations of the epidermis and the subepidermal layer. In *Mulinum* the epidermis appears biseriate. In cross sections of buds the excrescences and the small isolated bodies are seen between the primordia and along the sheath margins where they are discharged. They are composed of 2–3 (-5) cell rows, have rather thick cell walls which appear bright in polarized light, and they frequently have papillose or striated cuticles similar to the cuticles in the outer epidermal cells.

At the very early stage (e.g., in the axillary bud, Fig. 22A) subepidermal lacunae are formed. Sheathing cataphylls always have large lacunae which, probably being air-filled, contribute to the insolation of the primordia. The epidermal layers of sheathing leaves, facing stems and the primordia which they enclose, soon become loose with large, air-filled spaces behind. Below the ciliated sheath margin the epidermal layers become transversely wrinkled (cp. Fig. 20C-D) probably because cell stretching does not take place concurrently with that in the sheath parenchyma behind the lacuna. The epidermal cells of the interior sheath side have rather thick, irregularly lengthwise striated walls. Water gathering on the leaf blade surfaces will probably run in the two adaxial furrows and may be conducted to the sheath. However, a few experiments concerning water supply to leaf surfaces did not show clearly whether water can be absorbed in

the sheaths. The cuticle covering the adaxial epidermal sheath cells has discontinuous cutin lamellae probably interspaced with pectinaceous substances and may be penetrable for water (cp., *Slatyer* 1960: 367). The many hair-like excrescences between the primordia may have different functions. They have heavily stained cell nuclei. The small bodies that are liberated form a kind of polishing powder, which may be of importance when the primordia grow and become displaced.

Leaf ontogeny. The youngest primordia found in small buds (e.g., that in Fig. 22A) are bowl-shaped and obcordate with two upright lobes in cross sections. Initials for vascular bundles are found in the terminal parts of the lobes. In the abaxial part there is one such initial with a young secretory duct. In the later stages there is a pattern of primordia arranged inside sheaths wedging their lobes promiscuously, but always with narrow interspaces where the excrescences occur. Primordia which are cut at the bases below the point of branching are still bowl-shaped and involute and have five conspicuous secretory ducts in connection with initials of vascular bundles. The middle parts of such primordia are occupied by parenchyma (Fig. 22B below). In transverse sections of the primordia the three distal sections in the leaves appear more or less triangular with three lobed adaxial sides. At the center each section has an initial sclerenchyma strand (Fig. 22B). The central cells in such strands are clearly wider and resemble pit parenchyma at first, but their walls lignify and increase finally in thickness. Following the same primordium through several successive sections, it becomes evident that the two lateral lobes in the proximal part are bent so that they cover the adaxial central part of the primordium (Fig. 23 A). Proximal to the point of branching of the primordium, deep, narrow clefts are formed. (Fig. 23B). Concomitantly, pectic intercellular substances increase in the parenchyma between the clefts and the surface (Fig. 23C).
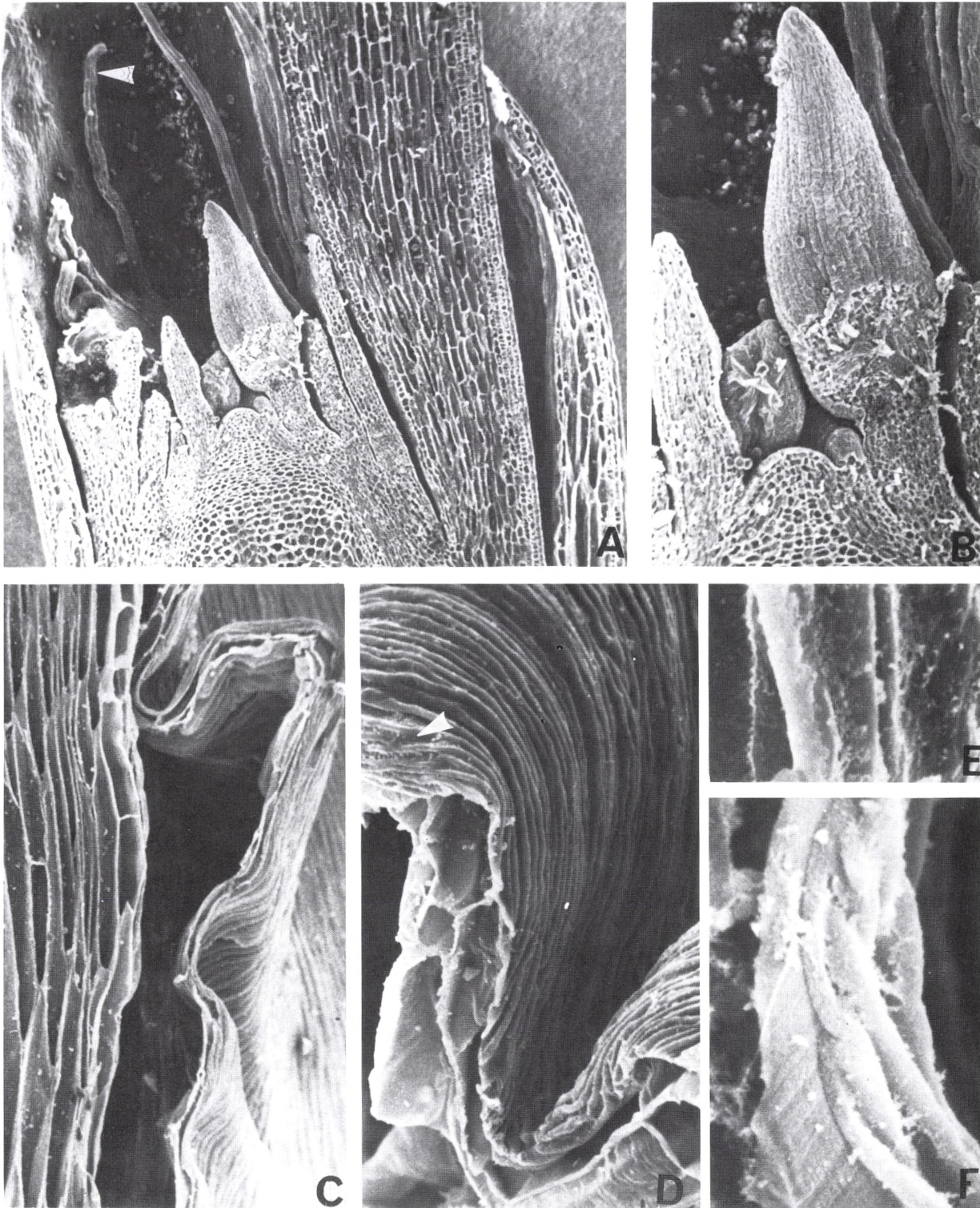
Fig. 20. *Mulinum spinosum.* A–B. SEM of apical meristem and leaf primordia. White arrow pointing to hair-like outgrowth from sheathing leaf, A × 70, B × 135. One segment in the larger primordium in B, facing the observer, has been cut off. – C–F. SEM of undulating adaxial loose biseriate epidermis of sheath just beneath its upper margin (cp. Fig. 19 A–B), C × 135, D × 675. White arrow pointing to area where the cuticular ridges appear connected with minute, transversely arranged anastomoses. E–F × 4500. E. Surface of convex part, two parallel ridges at anticlinal furrow (cp. * in Fig. 21 A), loosened interior wall with minute fibrillar thickenings. – F. Surface of concave part near bottom; cuticular ridges showing plaiting and anastomoses.
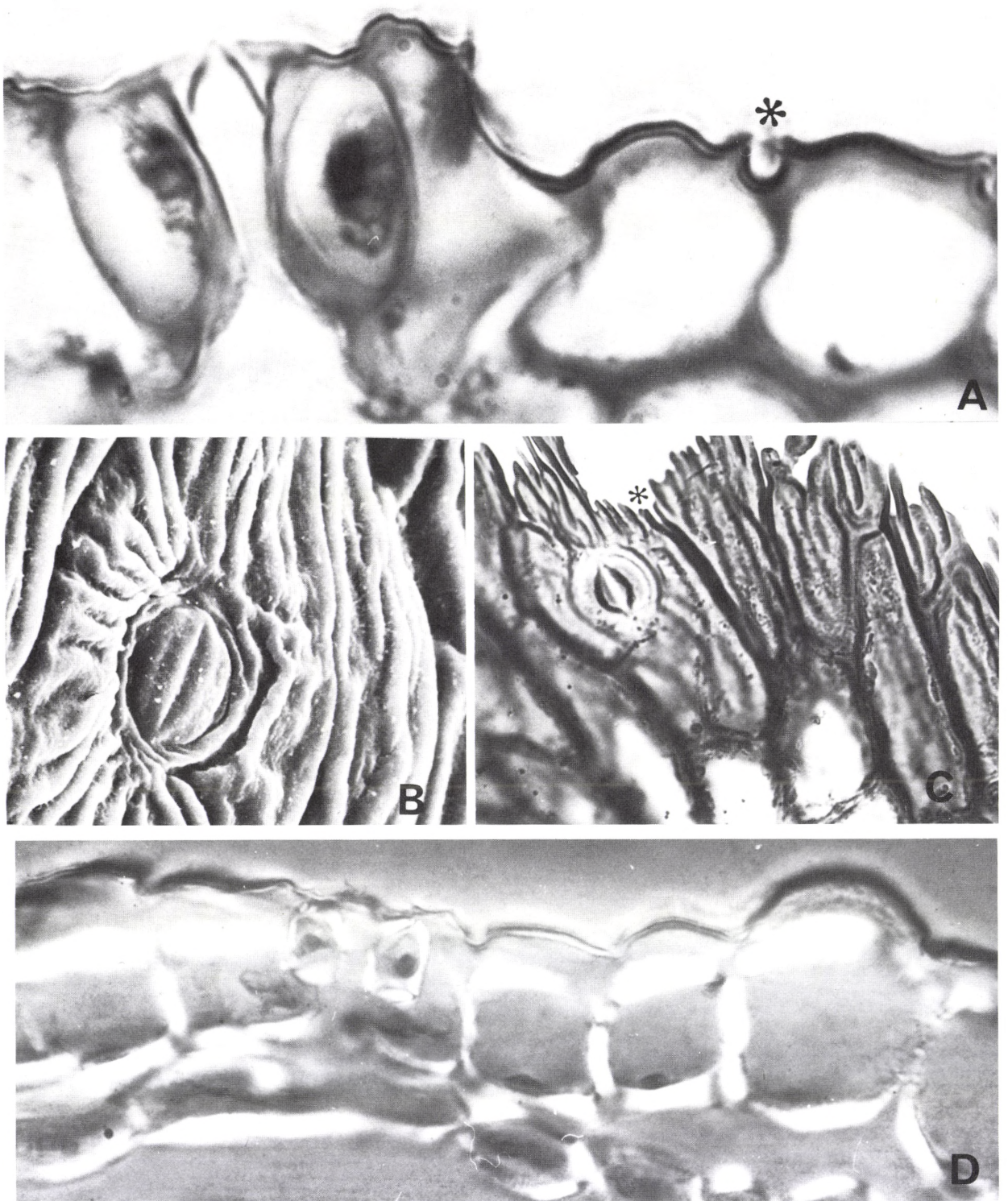
Fig. 21. *Mulinum spinosum*. A. Outer epidermal layer with stomatal pore and outer ledges. Cuticle stained with Sudan IV. Anticlinal furrow * (× 2000). – B. SEM of stoma in upper part of sheath. Many anastomoses between cuticular ridges. (× 1350). – C. Paradermal view of epidermis with one stoma and many ridges stained with Sudan IV. Anticlinal furrow * (× 500). – D. Biseriate epidermis in polarized light. One stoma. Cellulosic walls bright, pectinaceous outer walls beneath cuticle not so. (× 800).
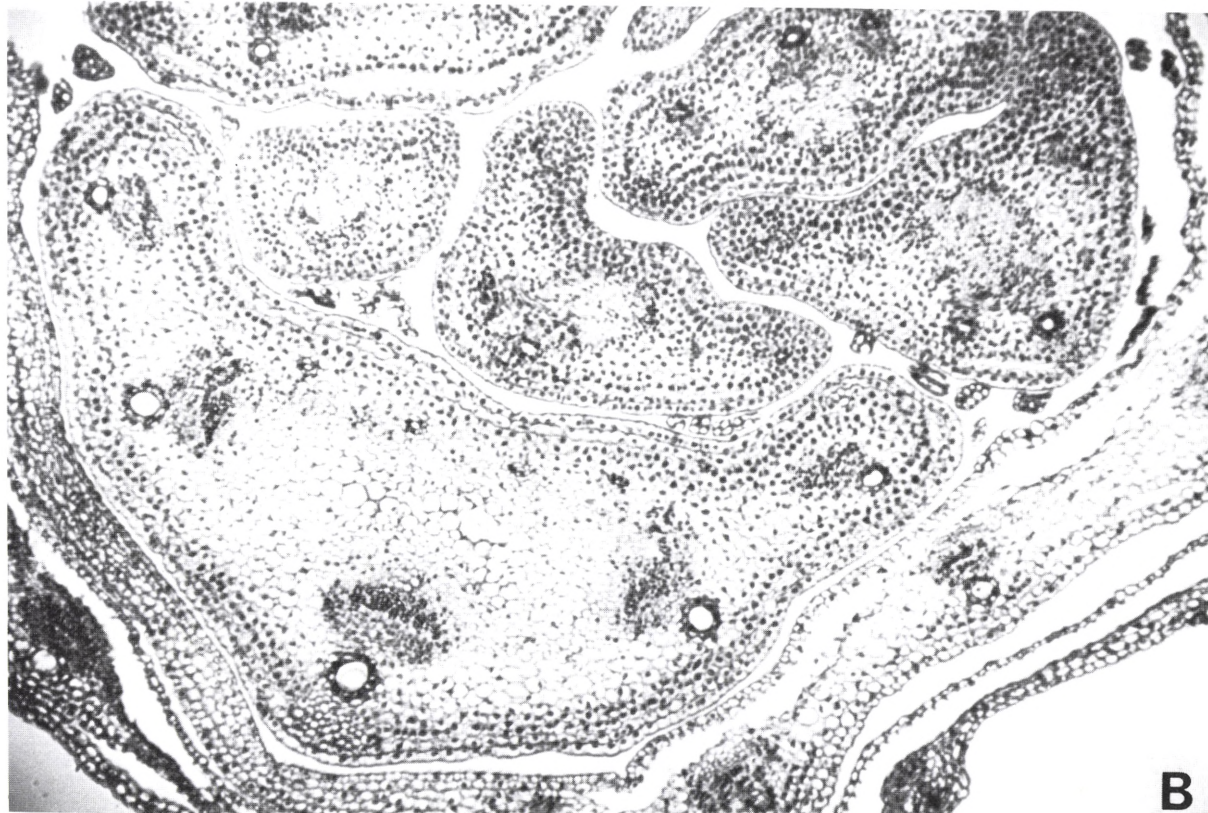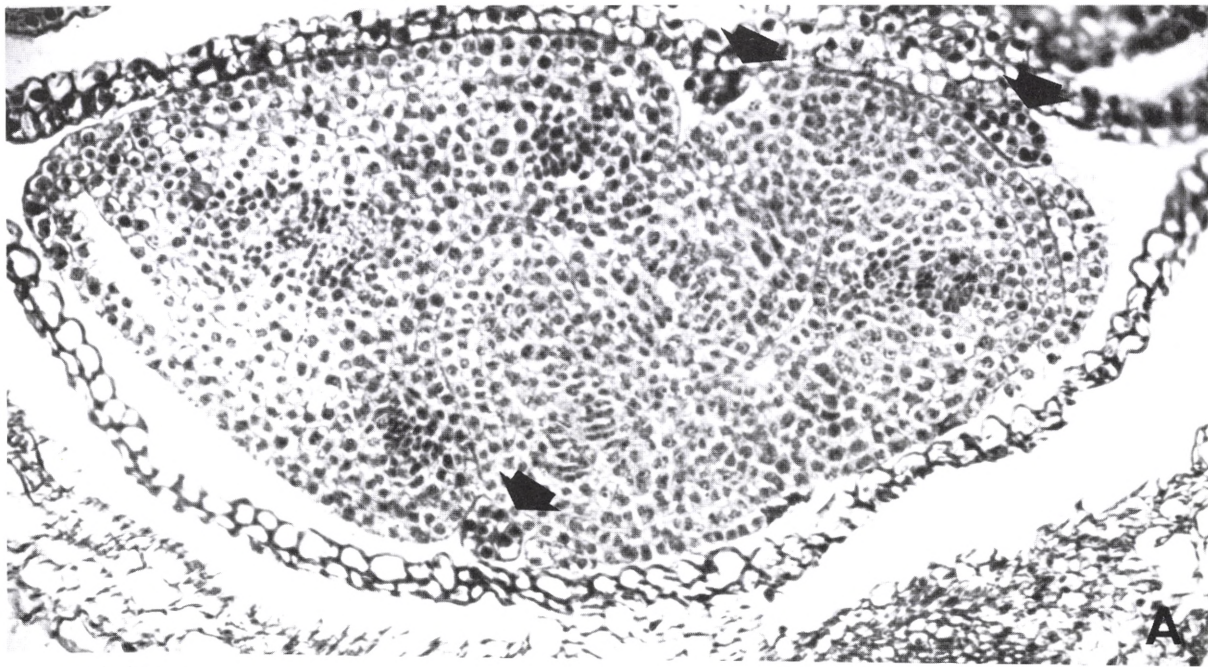
Fig. 22. *Mulinum spinosum.* A. Axillary bud (cp. Fig. 18 C). Arrows pointing to small bodies at the point of being detached from enveloping sheaths. One cordate basal leaf primordium is differentiated on left side of bud and already has a subepidermal abaxial space and three bundle initials. (× 200). – B. Part of older stage. Cross sections of leaf primordia and several hair-like bodies in interspaces. The largest primordium (below) shows the basal part, the other primordia are leaf sections with trilobate adaxial surfaces and initials of central sclerenchyma strand (× 64)

Just distal to the point of branching, the free segments are somewhat different. The middle segment is flatter and symmetrical, while the two lateral ones are more irregular and asymmetrical (Fig. 23B) as in the mature leaf, Fig. 19B. Meristematic regions develop inside the epidermal layers on both sides of the separating clefts. From these marginal meristems, the growth activity soon results in a less asymmetrical structure in the lateral segments. The interesting tissue decomposition at the endings of the clefts indicates that the leaf type is derived from a more palmately lobed leaf, and that it gets its deep incisions (and acicular segments) late in the ontogenesis.

The primordia belonging to the same stem section develop inside a sheathing cataphyll. Along its two margins, which almost reach each other, a number of small biseriate epidermal bodies are frequently detached. On its abaxial side the central vein has a large secreting duct and a collenchymatous strand near the epidermis. On the adaxial side is a broad sclerenchymatous area, which in most cases includes a schizo-lysigenous cavity formed by decomposition of parenchymatous cells contained in the sclerenchymatous area.

Anatomy of mature leaf sections. The outer epidermal layer includes the guard cells and acquires a thin continuous cuticle, while the interior layer becomes interrupted inside the stomatal pores in the outer layer. The two layers remain together and the many cavities are formed between the biseriate epidermis and the mesophyll. The outer layer has mucilaginous outer walls. Hence the cuticle loosens easily during preparation and may, if completely detached, also carry off the guard cells (Fig. 24A, c). The latter appear raised and are firmly connected with the cuticle. They are furnished with non-cutinized outer ledges (Fig. 21A). In polarized light the outermost walls have, inside the cuticle, thick isotropic layers of pectic material, but near the cell lamina they have equally

thick anisotropic cellulosic layers. Obviously, the pectic layer swells during the lifting of the cuticle, which is grooved lengthwise outside anticlinal walls. The cuticle is isotropic although appearing birefringent where it borders the pectic layer. Using Sudan IV only the cuticle is stained. The cuticle has many ribs running lengthwise and always grooves outside periclinal walls (Fig. 21A,C). The system of ribs continues in the leaf sheaths.

The epidermal structure resembles that described by *Ternetz* (1902: 7) in *Azorella selago.* Even though *Ternetz* speaks about an apparent two-layered epidermis, this species has abaxially a biseriate epidermis and a cuticle folded lengthwise. Furthermore, the two-layered, firmly coherent epidermal layers are stated often to be separated from the mesophyll by intercellular spaces.

The mesophyll in *Mulinum* is arranged as in isolateral leaves with palisades radiating from the central bundle area. On its abaxial side the central sclerenchymatous column is accompanied by the central main bundle and on its adaxial side by two additional bundles. All three bundles, the sclerenchymatous column and the central duct are surrounded by a common bundle sheath of tangentially stretched cells (Fig. 24 A). There are further small bundles in the two marginal lobes.

Pyykkö (1966: p. 500–501) mentions analyses of the leaves in *Mulinum leptacanthum* and *spinosum.* She found a biseriate epidermis in the former, but only one layer in the latter. In the picture (Fig. 105 p. 567) of *M. spinosum,* however, it is impossible to detect any kind of epidermis.

The large dimensions of the sclerenchymatous column are striking. The share of the xylem in the diameter of the column is small if one considers the number of palisades in the surrounding mesophyll. The many, large xylem strands in a similar looking species such as *Anarthrophyllum patagonicum* emphasize the
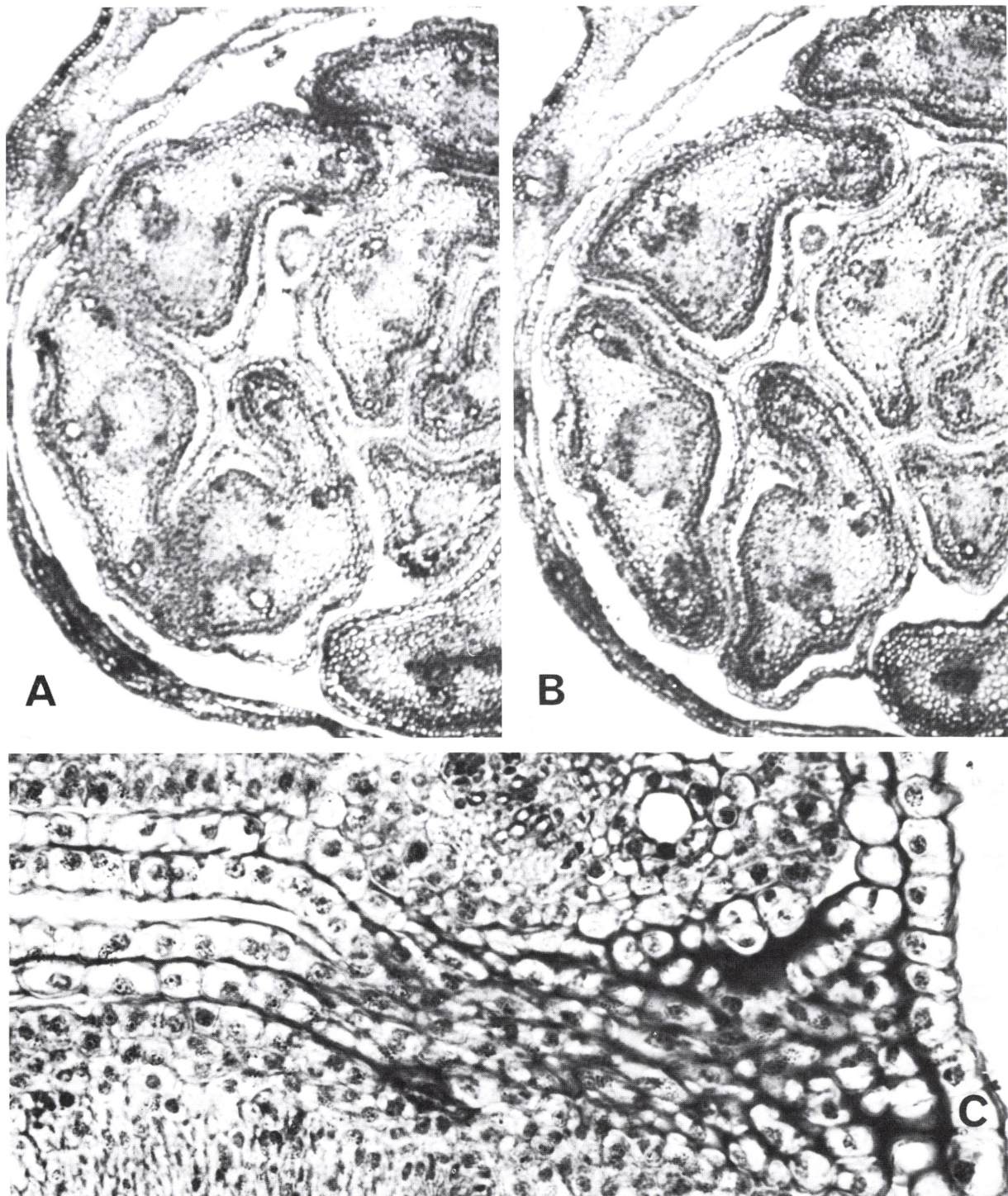
Fig. 23. *Mulinum spinosum*. A–B. Transverse sections of primordia surrounded by sheathing leaves. On the left in the figures, one leaf just below the point of division (A) and just above that point (B). (× 50). – C. Abaxial part of fissure between two leaf sections before the division. The tissue between the fissure and the adaxial epidermis (on the right) is in a stage of decomposition, intercellular pectic material occurs in great quantities. (× 320).
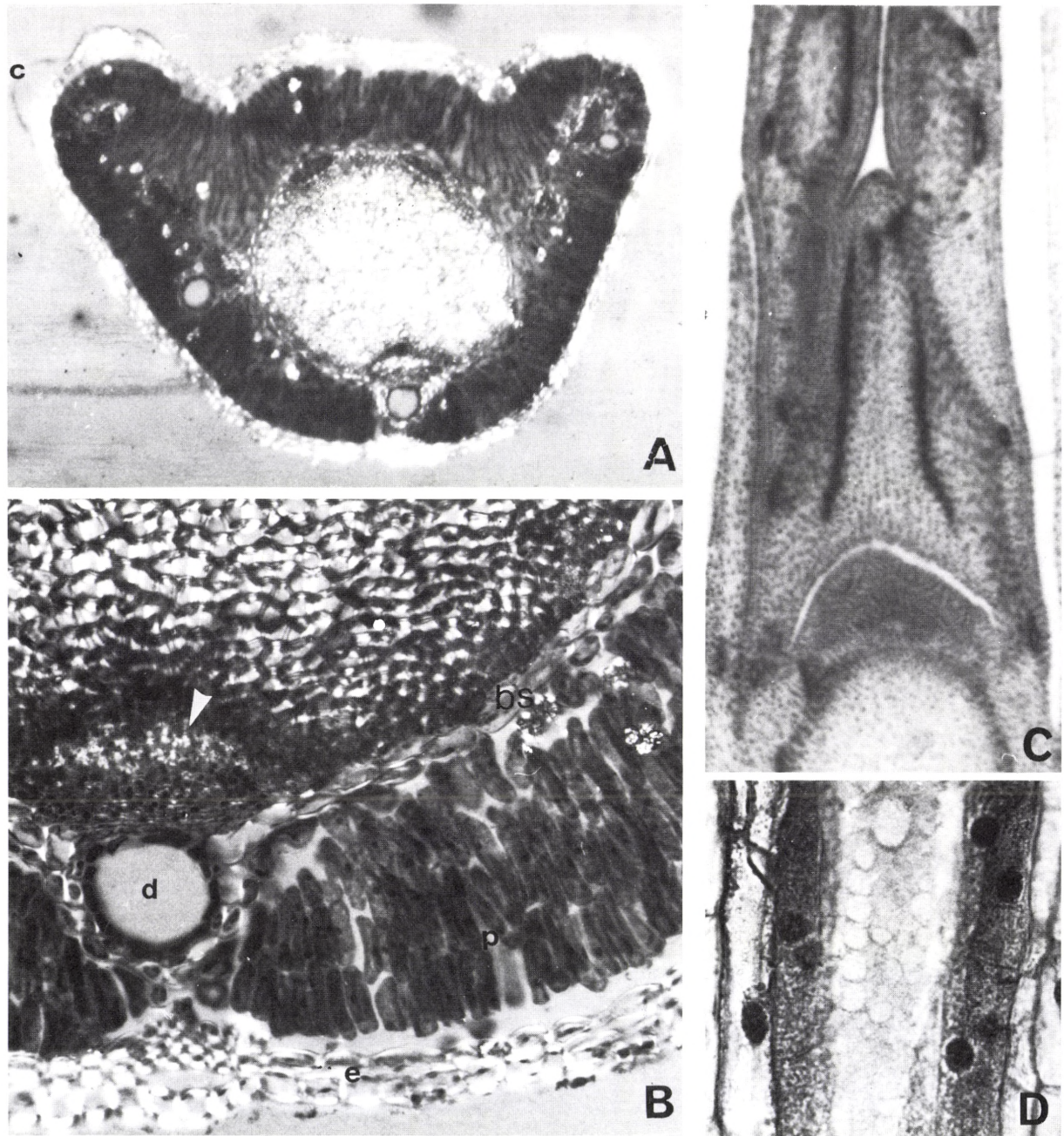
Fig. 24. *Mulinum ovalleanum* A–B, *Mulinum spinosum* C–D. A. Transverse section of terminal leaf segment in polarized light. Biseriate epidermis, sclerenchyma, xylem and druses showing up. c disengaged cuticle. * phloem. (× 50). – B. Abaxial part of leaf transect in semipolarized light. White arrow pointing to xylem. d secretorial duct, bs bundle sheath, p palisade tissue, e epidermal layers. (× 500). – C. Longitudinal section of axis with two successive apical meristems. Black lines are initial secretory ducts. Sheath on the right at the margin of the picture. (× 50). – D. Longitudinal section of small part of secretory duct. The secretory epithelian cells with dense cytoplasm and large nuclei. The contents in the duct have many lipid droplets. Fast green-Safranin. (× 500).

structural peculiarity of *Mulinum.* However, an under-supply of water in the green tissues hardly occurs, and this is probably because there is an apoplastic slow water flux in the sclerenchyma. Of course, the column terminates in a spine which must be strong and firm, but as long as it is surrounded by palisades, it may also conduct water. It appears not unlikely that the bundle sheath cells play a part in the transfer from apoplastic sclerenchyma to symplastic palisades.

7. Transition from involute cataphylls to deflexed foliage leaves

The counterpart to involute leaf structure is a revolute or deflexed structure. A bending backwards in a sharp curve of a leaf margin may be designated a deflexion. It may be related to a rolling downwards of the margn as in typical revolute leaves. Rolling of leaf margins in the *Ericales* has been discussed by *Hagerup* (1953) and *Hara* (1956). From a leaf ontogenetic point of view, it is not a uniform process. It can be the result of a gradual curvation of the leaf margins proper or of two abaxial pads which are developed near the margins (the *Phyllodoce* type described by *Hagerup).* In leaves which are deflexed, a third typ of ontogeny seems to occur, characterized by a synchronous growth and maturing on both sides of marginal incisions. The incisions are similar to those already described in the *Anarthrophyllum* leaflets. In the latter case, the resulting leaflets, however, resemble involute rolled leaves, while in deflexed (recurved) leaves the adult foliage leaf becomes similar to a revolute rolled one. The ecological advantages of rolling or bending leaf margins upwards or downwards are probably almost similar. However, previous evolutionary events may determine which direction the rolling or bending will take. In any case, both types of marginal development can be found in the same taxonomical group, thus, e.g., in the *Mutisieae.* A striking feature here is that a transition from involute to deflexed structure takes place in the same species if, as in *Perezia recurvata,* one compares basal cataphylls with later-formed foliage leaves (cp. Fig. 25).

The genus *Perezia* of the *Mutisieae* consists of herbaceous perennials with leaves in basal roset-

tes or imbricate. The leaves vary from pinnatifid with lobes terminating in spines *(P. pilifera)* to entire, lanceolate with dentate margins *(P. hunzikeri,* see *Cabrera* 1950 Fig. 1) and entire linear and slightly grooved on the adaxial side *(P. linearis, Cabrera* 1939, Fig. 38). In *P. lanigera* (= *sessiliflora)* the small, linear, mucronate leaves have revolute or deflexed margins *(Pyykkö* : 525) and resemble anatomically those in *P. recurvata* (see below).

Few species within the *Mutisieae* have revolute leaves. *Pyykkö* (l.c.) describes three species of *Brachyclados.* Her drawings (Figs. 46 and 100) indicate that the type of rolling corresponds to the common one found in, e.g., *Ledum* or *Loiseleuria* and in the South American *Chiliotrichum rosmarinifolium.*

It is difficult to imagine how an evolution could take place in *Perezia* from dissected broad leaf lobes of rosette herbs to loose cushion plants with small, entire and deflexed leaves. One possibility might be a reduction connected with a replacing of pinnatisect or lobed foliage leaves, with foliage leaves being transformed bracts or cataphylls. In *P. recurvata* a rather smooth transition from basal cataphylls to sheathing foliage leaves and further on to bracts can be ascertained. A reduction of this kind, however, does not involve a deflexion of the leaf margins as in *P. recurvata* and *P. lanigera.* The genes responsible for these deflexions may have disappeared from or been strongly modified in the majority of *Perezia* species. However, they clearly operate in the genera *Mutisia* (e.g., in *M. linearifolia, M. retrorsa* and *M. decurrens)* and *Nassauvia.*

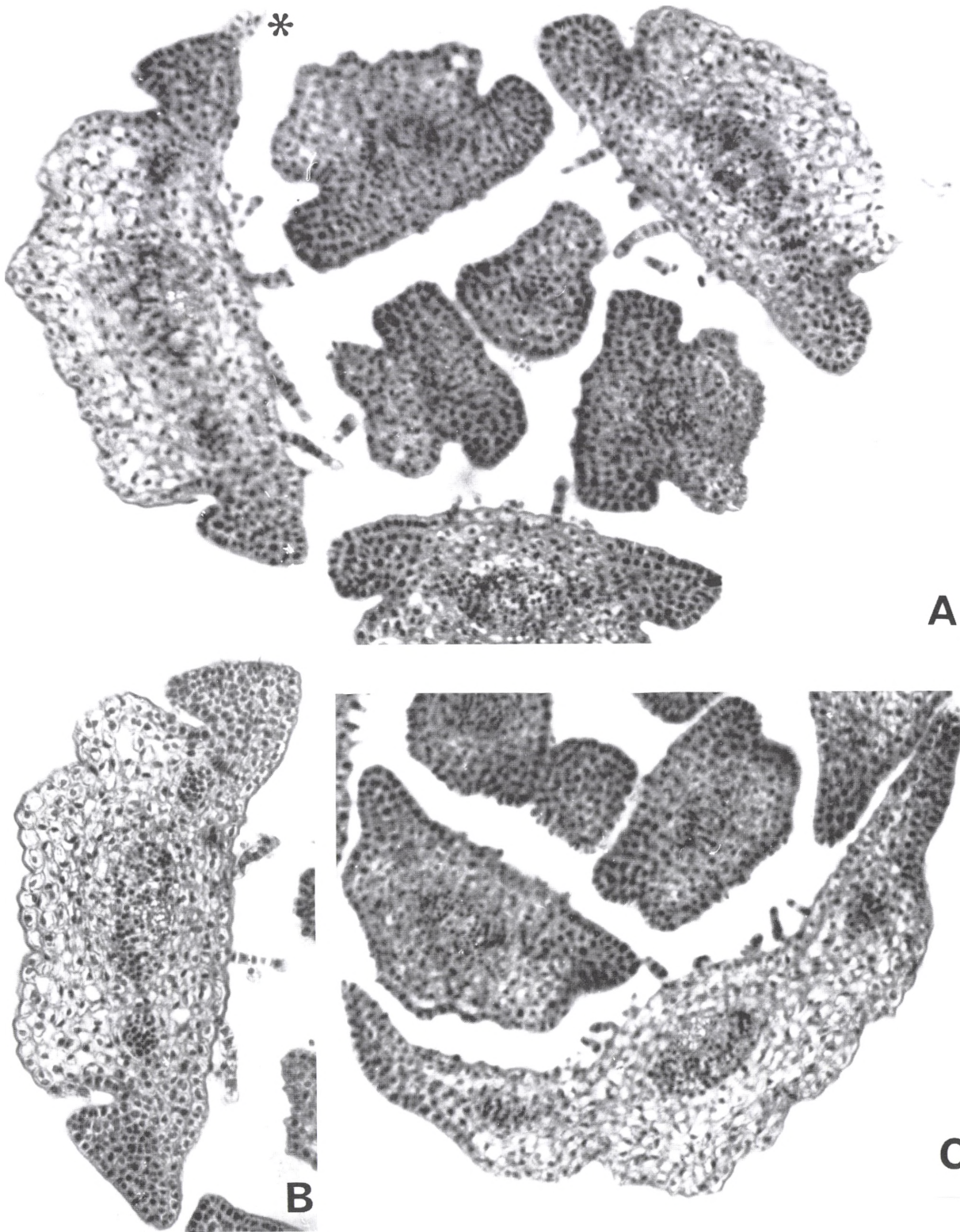The leaf structure in the latter was already

Fig. 25. *Perezia recurvata.* A–C. Transverse sections of bud showing leaf primordia in different stages of development. In the largest primordia the marginal incision is turned to the abaxial side (B). The first formed (lowest) primordium develops into an involute cataphyll (C bottom). * Initial to corner emergence. (× 200).

mentioned by *Goebel* (1893: 28–29). *Nassauvia nivea (N. nivalis* in *Pyykkö* 1966: Fig. 94) has many deep furrows between lengthwise ribs on the adaxial sides of the grass-like sheathing leaves. The furrows disappear in the sheathing parts. The stomata occur in the furrows and also on the abaxial surfaces. *N. pumila,* however, has almost needle-like leaves and two lengthwise furrows on the underside with many hairs, and all the stomata are concentrated here. According to *Goebel,* both species have disproportionately large sclerenchymatous strands. With respect to the amount of sclerenchyma, *Perezia recurvata* is much more moderate, but it has two abaxial furrows similar to those in *Nassauvia pumila.*

Perezia recurvata (Vahl) Less

P. recurvata is a widely distributed Patagonian herbaceous, loose cushion plant. The imbricate leaves are arranged in several single shoots, which often terminate in single heads. The bases of the stems are surrounded by sheathing cataphylls. It grows on Patagonian steppes (e.g., *Mulinum* or *Nassauvia axillaris* communities), but ascends to Andean steppes with *Adesmia* and *Stipa chrysophylla.* For further details, see *Cabrera* (1939 Fig. 393) and *BHR* (Fig. 25 and pp. 226–229, 319).

Stem anatomy. The eustele has first a ring of separate collateral bundles. Leaf traces occur at an early stage in the thick cortex, which is developed outside a typical endodermis with Casparian strips. Outside the main bundles, a number of schizogenous ducts is formed. The surrounding cortex cells have rather large central nuclei and keep much cytoplasm near to the ducts. The narrow cells separating the ducts have cross walls next to the endodermis, resembling those in endodermal cells. A vascular cambium arises and soon becomes continuous, producing additional vascular bundles between those first developed.

Leaf ontogeny. Leaves inserted near the base of the shoot are cataphylls with involute structure.

The first foliage leaves resemble cataphylls but acquire many multicellular hairs on the adaxial side (Fig. 25). The next leaves are typical foliage leaves and attain two incisions at the margins. At first the incisions are parallel to the adaxial surface, but at later stages they are turned and get a transverse position. The incisions, which contain initials for stomata and glandular hairs, finally develop into two cavities formed as deep furrows behind the abruptly deflexed leaf margins (Fig. 25B). *Perezia recurvata* thus exhibits a very peculiar type of leaf margin development, in fact there are no signs of a regular curvature of the margins. At the sharp corners between the adaxial surface and the flanks, regularly spaced emergences (cilia) occur. They are initiated as 3–4 rows of short cells, which later stretch considerably (Fig. 25A*). The dense spacing of the leaves resembles species of *Nassauvia* which, e.g., in *N. juniperina* and *N. abbreviata,* have sheathing involute leaf bases and ciliated margins.

Leaf anatomy. The foliage leaves have a sheathing basal part, concave on the adaxial sides and with numerous glandular hairs. The margins are fringed with sclerenchymatous, pointed emergences. On the abaxial sides of the blades there are two deep cavities or furrows on both sides of the central part with the middle vein. The cavities divide the blades into three parallel sections (Fig. 26A).

Epidermis. All stomata are restricted to the cavities where they occur together with uniseriate or biseriate glandular hairs. The epidermal cells have very thick outer walls except in the furrows. *Pyykkö* (1966) measured a thickness of 10–14 μ in the outer walls of the adaxial epidermis.

The thick walls have cytochemical properties of interest. The cuticle is thin but seems to contain an interior lamella which shows up in polarized light with a type of refringence opposite that of cellulose, and thus may be composed of wax. The cuticular layer next to the cuticle
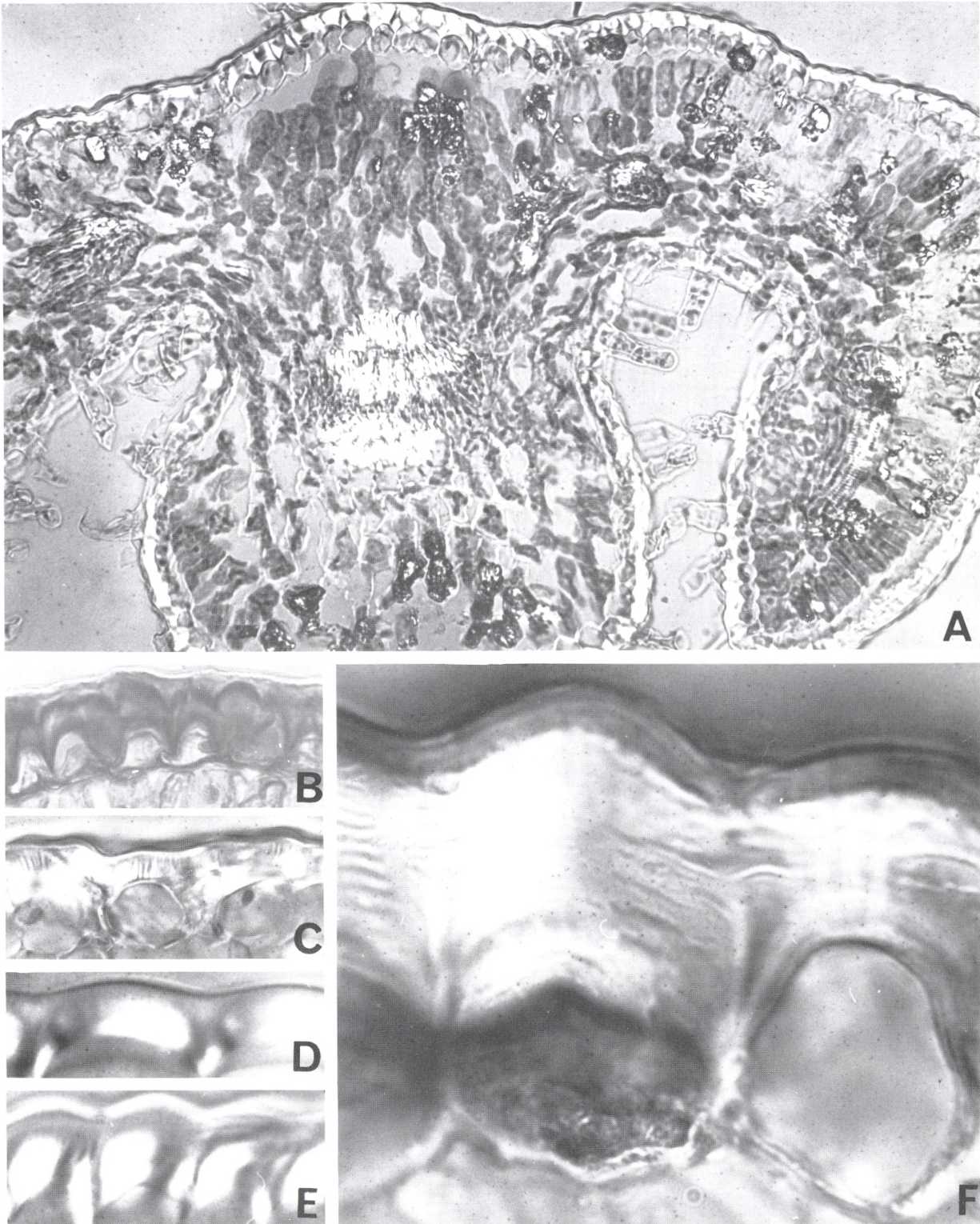
Fig. 26. *Perezia recurvata*. A. Cross section of mature leaf in semipolarized lght. Thick cellulosic epidermal walls, xylem and fiber strands and druses show up. (× 200). – B. Outer epidermal wall in semipolarized light. Fast green-Safranin stains pectinaceous, isotropic parts brownish-red. (× 500). – C. Many radiating isotropic lines appear in polarized light. (× 500). – D. Young and E older walls in polarized light. A birefringent layer is observed beneath the cuticle in E. (× 800). – Outer wall in mature leaf. Sudan IV and interference contrast showing lamellae and staining of layer beneath cuticle. (× 2000).

follows the outer surface. It is not thick and has no flanges in the anticlinal walls (Fig. 26 F). In young walls the interior cellulosic part next to the cell lumen shows up. Outside this part there is an isotropic layer, probably of pectinaceous substances, which in some preparations is stained brownish-red with Safranin (Fig. 26B). In old thick walls this layer is still demonstrable as a dark arch following the cell contour. Using Toluidine Blue the pectinaceous layers appear lamellate, while the interior layers next to the cell lumen are unstained. In polarized light, however, these layers are bright, which indicates that they contain much cellulose. The cellulosic part is traversed by numerous radiating, narrow, isotropic areas. Some of them are probably ectodesmata (Fig. 26C). The lamellate structure of the thick walls becomes conspicuous in the interference contrast microscope (Fig. 26F). The stratification is probably due to an alternate layering of chiefly pectinaceous and cellulosic material. The entire wall inside the cuticle is stained with Ruthenium Red. It is remarkable in a xerophyte to find the majority of the thick epidermal wall composed of chemically hydrophilic substances and no signs of cutinization or of lignification.

Mesophyll and vascular bundles. The mesophyll appears rather loose. The densest palisades are located beneath the adaxial epidermis and along the flanks. The number of druses in the palisade tissue is very high. The vascular supply of the photosynthetic cells takes place through a number of veins occurring between the large middle lobe vein and the main veins in the side lobes. All larger veins have bundle sheaths with Casparian strips. The largest middle lobe vein is supported by fibers (Fig. 26A).

8. Development of minute, trilobate, revolute leaves with dorsal inflexions

A leaf diminution combined with leaf margin revolution and a dense indumentum – i.a. with glands excreting volatile oils – together with a considerable increase of the thickness of the boundary layer may represent maximum adaptation for withstanding the water loss caused by transpiration. This particular combination is found in species belonging to the South American genus *Acantholippia (Verbenaceae).* One of the many striking characters in this genus is the development of fascicles of small leaves in the axils of similarly small sessile adjacent stem leaves. The leaves are mostly three-lobed and revolute and covered with many kinds of hair, among which some are glandular and emit a strong aromatic odor. The species in question form knobbly dwarf shoots, long shoots, often divaricately branched, and leafless shoots that terminate in woody spines and die. Similar knobbly shoot structures are found in certain species of *Junellia* (e.g., *J. seriphioides (Roig* 1970 Plate 70) and *J. tridactylites).*

According to the monographic treatment by *Moldenke* (1961: 326–328), *Acantholippia* is a small genus comprising five species only. *Acantholippia* is regarded as closely related to *Lippia,* but differs in its singular xerophilous habit and the copious endosperm. *Pyykkö* (1966: 505) examined anatomically one species of *Lippia* and two of *Acantholippia. Lippia juncea* is said to grow in dry forests and wooded steppes in Southern Argentina. It is a sparsely branched shrub with opposite, lanceolate leaves, 12–18 mm long and 3–7 mm broad with slightly revolute margins and distinctly keeled below. The leaves are amphistomatous and carry few, unicellular,

thick-walled hairs as well as short glandular hairs with small heads. *Lippia foliolosa* was examined anatomically by *Cabrera* (1961), who reports leaves with subrevolute margins, unicellular stiff hairs as well as glandular vesiculose unicellular hairs. The habits of the *Acantholippia* species deviate by short internodia and intricate branching with many twigs, which are often stiff, divaricate and spine-tipped. The minute-small leaves (1–6 mm long) are sometimes scattered and bear, as mentioned, fascicles of additional leaves in their axils.

The most striking habit is presumably that found in *A. riojana.* Its leaves were already described by *Goebel* (1893: 13–14, Plate XII, 1–4). The stem leaves are scale-like and adpressed, but the very small leaves on the branchlets are subglobose trilobate with irregularly incised lobes resembling the surface of a brain. The adaxial sides have a number of deep furrows. The lobes have thickened, revolute, glabrous margins. They are deeply 3-canaliculate beneath and densely pubescent in the furrows on both sides where the stomata also occur. According to *Goebel* (l.c.), this leaf type is probably derived from the more normal one found in *A. deserticola (A. salsoloides)* which has almost ericoid leaves but with a shallow furrow on the adaxial side above the middle vein (l.c. Fig. 5). *A. seriphioides,* to be mentioned below, is intermediate with regard to the morphology of the leaves.

Acantholippia seriphioides (A. Gray) Moldenke
A. seriphioides is an important inhabitant of the Argentinian semideserts, sandy areas and dry rocky areas. It ascends to 2600 m above sea level.

Details about its occurrence are found in *Molden-ke* (l.c.) and *BHR* (238–239, 244). The habit appears from a photograph in *Roiz Leal* (1961: 105) and a drawing in *Roig* (1970, Plate 72, 1). Anatomical details are mentioned by *Pyykkö* (1966: 505).

This is a small, depressed or prostrate, divaricately branched shrub. Its branches, often reaching 20–40 cm in length, are sometimes almost covered by loose sand. The species was easily recognizable because of its pleasant odor resembling that emitted by species of the *Lamiales* (e.g., *Calamintha, Thymus* etc.). The scent, the very irregular shoot structure and the revolute, trilobate leaves, largely arranged in clusters, made a closer study attractive.

Leaf ontogeny. Young leaves are borne in the axils of cataphylls or lobed foliage leaves. Shortly after their appearance, the foliage leaves acquire marginal abaxial incurvations and a median adaxial inflexion. The abaxial incurvations occur on both sides of a keel containing the midrib (Fig. 27). The adaxial inflexion is broad to start with, but during further development it narrows and finally becomes a deep furrow-like inflexion above the midrib, but often obliquely placed (Fig. 27 A). The middle lobe appears first, but very soon two lateral lobes are added. Both of these acquire revolute margins, and finally very strange leaf structures appear, suggesting a triple ericoid habit, but merely being transections of three adjacent lobes, a median and the two lateral ones. The rolling of the lateral lobes sometimes results in the formation of short cavities (Fig. 28 B). The isolation of the lateral lobes can be followed in successive sections. The lateral lobes are without prominent median keels and have no adaxial furrows.

Morphology. Fundamentally, the leaves are opposite, but the shoot structure shows many deviations from a regular decussate phyllotaxis. First, the two opposite leaves in a pair are often dissimilar, one being a crescent-shaped cataphyll or a leaf morphologically approaching a catap-

hyll, while its sister leaf is more like a foliage leaf. The development along the transverse axis at a right angle to the main axis between two sister leaves is often depressed or irregular mainly because of growth rate differences along the main axis.

At an early stage two sister cataphylls may be joined by their adaxial involute margins. Opposite buds develop in the axils (Fig. 29 C). The two cataphylls are not identical, one having, e.g., a conspicuously larger main bundle. The main axis cuts the basal rudimentary lateral axes in the two buds. The axes in the buds first carry two cataphylls, which are joined at the base near the main axis but in the direction away from the main axis acquire revolute margins as in foliage leaves. The next pair of smaller foliage leaves is placed on the main axis above the first cataphyll pair, but they are dissimilar; the leaf nearest to the axis which is the youngest remains small, while its sister leaf away from the axis is already differentiated with incurvations and soon acquires lateral lobes.

The morphological difference between the members of the leaf pairs is maintained for some time. The gradient along the main axis appears strikingly from Fig. 29. The emergence of oblique leaves, cataphyll-like near the axis and of foliage type at the ends away from the axis, is indicated by a white arrow.

Leaf anatomy. The strongly revolute structure appears from Fig 27A and 28A, which also show that the leaf is dorsiventral. However, palisades occur at the revolute margins as well as on the abaxial side of the central keel. Both areas receive much light, e.g., by reflection from the sand below. Most stomata are placed in the incurvations, thus also in the adaxial, narrow inflexion.

Epidermis. The cuticle is thin. It is heavily stained by Sudan IV, but it exhibits a very irregular surface with a number of low ridges above the periclinal walls and a number of cracks. In transverse sections it appears compos-
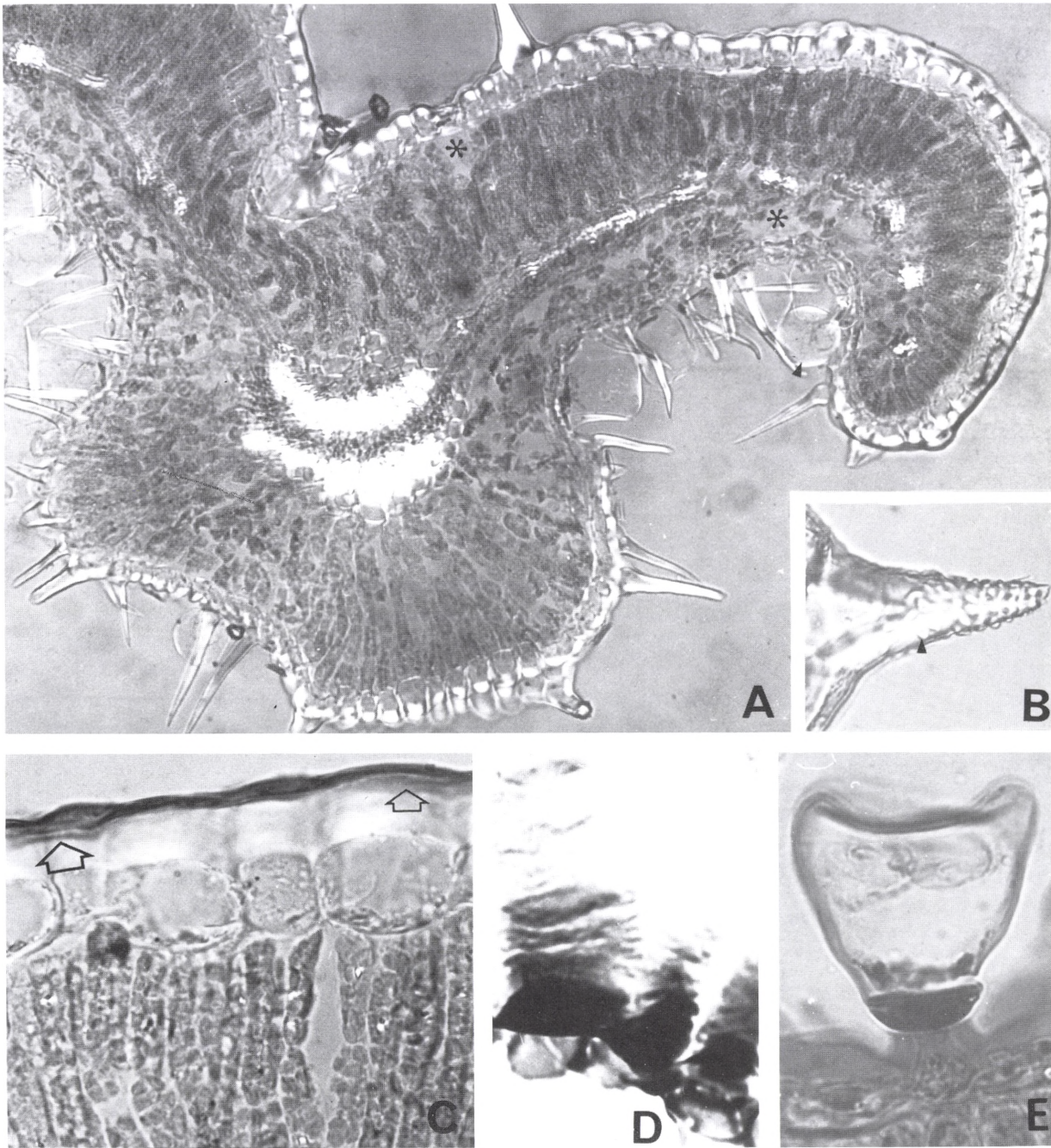
Fig. 27. *Acantholippia seriphioides*. A. Cross section of mature leaf in semipolarized light. Small black arrow pointing to wall in balloon hair. * substomatal chambers. (× 200). – B. Strong hair at left corner with many warts. Small black arrow pointing to pore (?) in wart. (× 640). – Outer epidermal wall and palisades in semipolarized light and stained with Sudan IV. Cuticle consisting of several layers separated by birefringent layers (open arrows). (× 640). – Outer mucilaginous part of wall after bursting of cuticle and swelling of pectinaceous wall layers, which becomes visible after treatment with Toluidine Blue. (× 640). – E. Balloon hair after staining with Fast green-Safranin. Basal cell deeply stained. (× 800).

ed of small flakes overlapping each other and occasionally leaving small, perhaps pectinaceous interspaces. The cuticle is unstained by Aniline Blue Black except for some short, flat, paradermal intrusions and a thin outermost coating which are stained. In polarized light some of the intercuticular intrusions and layers show weak birefringence (Fig. 27C, arrows).

The thick wall inside the cuticle stains with Aniline Blue Black. With this staining the wall adjacent to the cuticle shows some stainable protuberances, which, when considered in connection with the paradermal, flat intrusions and the outermost coating, indicate the occurrence of substances involved with a paradermal intrusive growth of the cuticle. The thick wall becomes heavily stained with Toluidine Blue. Should the coating burst locally during preparation, the wall material inside swells up exhibiting a number of irregularly anastomizing layers (Fig. 27D). This mucilaginous wall material acquires a bluish-violet tint, while the cellulose walls behind remain blue. With Ruthenium Red the entire wall is stained, but the outer mucilaginous part which swells up has a more intensively stained outer fringe that is divided into sections corresponding to the epidermal cells beneath.

According to its staining and birefringence, the interior part of the outer walls next to the cell lumina is cellulosic, but bright layers are also found in walls mainly containing pectinaceous substances. Thus the thick walls resemble those in *Perezia* and are composed of alternately mainly cellulosic and mainly pectinaceous substances. With dyes like Johansen's quadruple stain the entire wall inside the cuticle is stained but it does not react with Fluoroglucinol-HCl.

Epidermal cells exposed to much light are clearly arched and have few hairs (trichomes) in adult leaves. Abaxial sides, on the other hand, have a dense indumentum of many kinds of hair. In young leaves and stems all surfaces are covered so densely by hair that it becomes difficult to detect the guard cells. The four hair types are described in order according to their share in the indumentum.

Stiff spinous hairs. They are thick-walled, unicellular, retain their nuclei and cytoplasm for a long time, and resemble those described for *Junellia uniflora.* They issue from two adjacent, upright epidermal cells. The thin cuticle has numerous warts which at high magnification appear hollow, perhaps with a minute apical pore (Fig. 27B). The tips are stained by Ruthenium Red and Toluidine Blue. The cellulosic, many-layered wall is bright in polarized light but remains unstained by Safranin.

Glandular balloon hairs. They have a wineglass-shaped basal stipe cell with a wall stained by Sudan IV and Safranin. The upper cell swells, its nucleus degenerates, but granular cytoplasmic remains form an irregular cup-shaped body which is stained by Safranin (Fig. 29D). The thin wall that surrounds the secreted oil (probably ethereal) is cellulosic and easy to detect in polarized light. It is stainable with Toluidine Blue and Ruthenium Red. With Sudan IV it is possible – although difficult – to ascertain a thin, stainable lamella within the wall. The hairs resemble glands described by *Klug* (1926: Fig. 16) in *Mentha piperita* by the cutinized stipe, and the swollen part may have similar ring-shaped folds although not well demarcated (Fig. 27E, 28C). The balloon hairs in *Acantholippia* are probably related to the vesiculose, glandular hairs in *Lippia* described by *Cabrera* 1961.

Multicellular glands of the type found in the *Lamiales.* The head of secreting cells consists of about 5–10 cells. The secretion is collected beneath a common cuticle. The stipes have 2–3 cells.

Smaller glands usually issuing from two epidermal cells. They have a two-celled stipe and 2 or few cells in the secreting head (Fig. 28A).

The indumentum in this species is more comprehensive and denser than in most other xerophytes. At least two of the glandular hair types are responsible for the strong aromatic
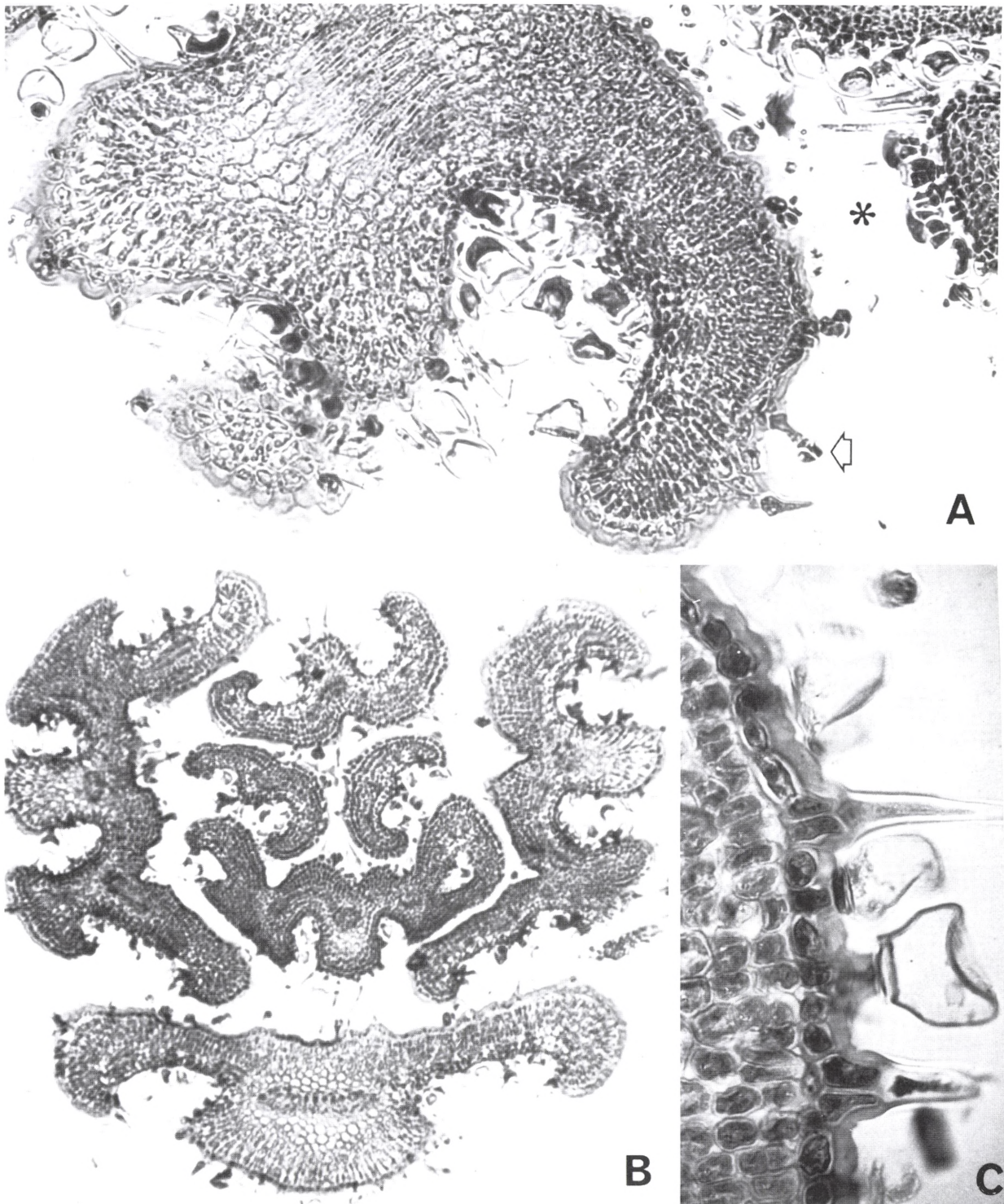
Fig. 28. *Acantholippia seriphioides.* A. Cross section of young leaves showing density and hair types in indumentum, the central keel with the middle vein and one lateral revolute part. Balloon hairs particularly frequent on abaxial sides. The asterisk placed outside areas with many glands of the Lamiales type,the open arrow points to one of the smaller glands (× 200). - B. Cluster of young leaves illustrating leaves with »triple ericoid« structure resulting from basal coherence of middle lobe and two lateral lobes. The central leaf, second from the bottom, appears to have a cavity owing to strong revolution of the margin. The two leaves above are turned in relation to the vertical axis cutting the cluster. The bottom leaf in the cluster had a sister leaf that was already divided into three separate lobes (omitted). (× 80). – C. Surface of young leaf with two stiff spinous hairs issuing from two upright epidermal cells. Two balloon hairs, the larger one with peripheral ring-shaped fold. (× 500).
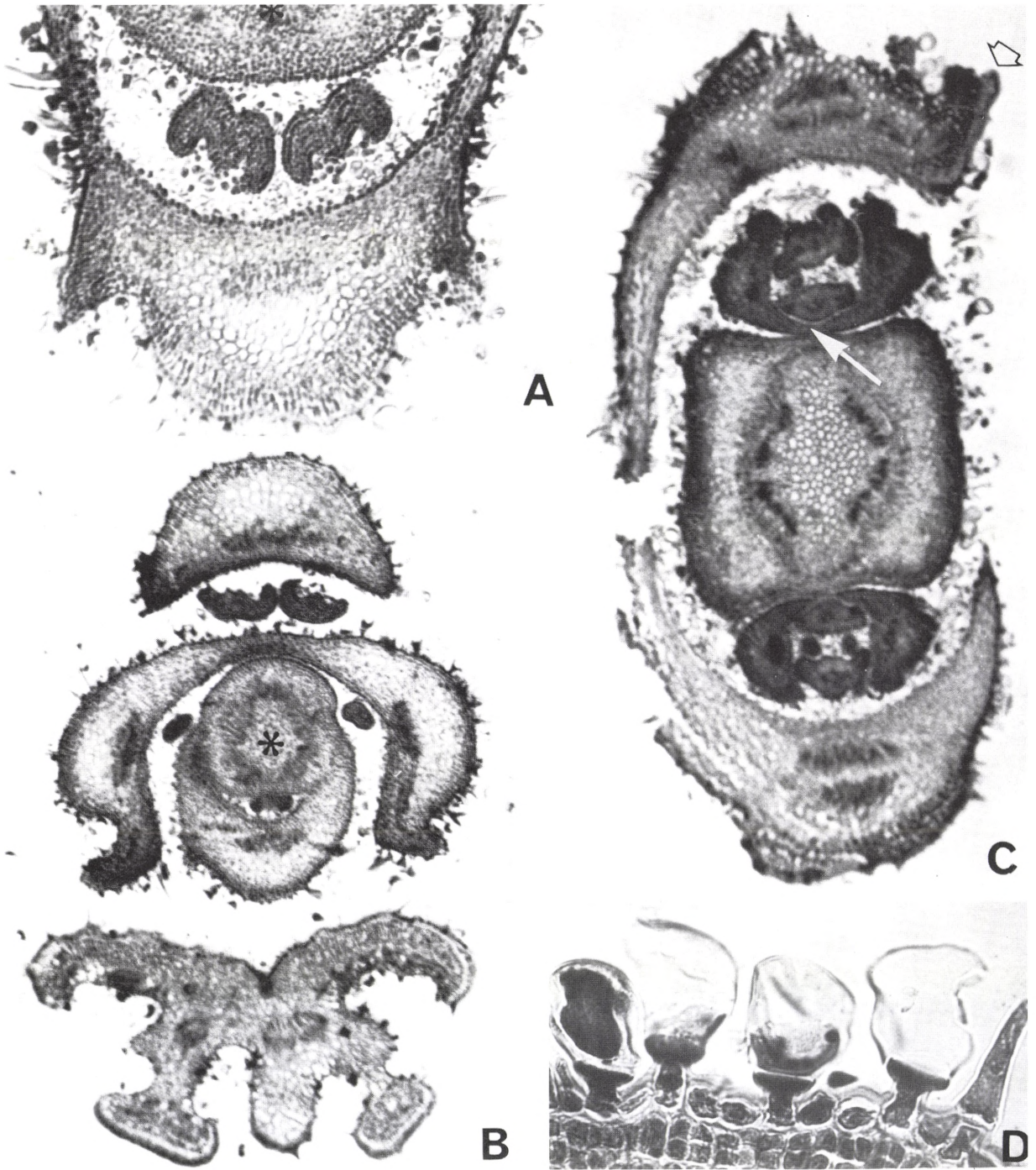
Fig. 29. *Acantholippia seriphioides*. A. Two leaf primordia on reduced axillary shoot (* the axis). The axis bears two opposite leaves, a crescent-shaped cataphyll (omitted) and a transistional leaf which is involute and connected with the margins of the cataphyll but at the same time shows marginal revolution as in mature leaves. (× 103). – B. Leaf cluster (its axis marked by an asterisk) illustrating irregular shoot structure. The cataphyll (top) has a sister leaf that is trilobate. The next leaf pair is still connected at the end near the top cataphylll. The two free ends, on the other hand, have revolute margins. The next leaf pair is crescent-shaped cataphylls. Small pairs of primordia are formed in all three leaf axils. (× 64). – C. Two opposite cataphylls (the top one transitional arrow pointing to revolute margin) supporting two axillary buds. Arrow pointing to adaxial connection between leaf pair (cp. A–B). Xylem in stem (dark) interrupted at vascular connections to the buds. (× 64). – D. Surface of young stem with balloon hairs farthest left with contents), and one young spinous hair still with cytoplasm and nucleus. Fast green-Safranin. (× 200).

odor. The ethereal oils produced by this and other xerophytes enhance the gas density in leaf air spaces and in the boundary layer of the leaf. This gives a higher resistance to evaporation from the cell walls and a lower transpiration. In young leaves the indumentum covers all surfaces and is particularly dense. When the leaves grow, a sufficient flux of water with dissolved solutes must be essential. In spite of many antitranspirent arrangements in *Acantholippia,* it is considered necessary for the plant to keep up transpiration rates to permit a sufficient supply of nutrients to the leaves. The many young hairs and the young mucilaginous epidermal cells may collectively have a hydathode function, and at the same time the cooling effect of the vaporization will prevent overheating of the developing photosynthetic tissues beneath.

9. Discussion and conclusions

1: Adequacy of terms for adaptive features. Concept of multiple adaptation

Already when defining a common term such as xerophyte we are faced with severe difficulties. Are xerophytes adapted to grow in dry habitats (soils), in dry climates or both? The word »dry« is ambiguous because it also covers physiologically dry soils such as those found in areas of permafrost. *Empetrum nigrum* is a xerophyte in spite of its ability to grow abundantly in Sphagnum bogs as well as in dry sand dunes. Several desert or steppe plants have subterranean water-storing organs, while the epigeic parts resemble mesophytes in structure (see, e.g., *Hoffmanseggia falcaria* (cp. *Roig* 1970 Fig. 50), *Tropaeolum incisum (BHR* Fig. 50)). Are they still xerophytes?

A xeromorphic structure enables a plant to withstand water stress, in many cases such structures are antitranspirent arrangements. Good examples are thick cuticular layers and sunken stomata, but *Larrea cuneifolia,* perhaps one of the most typical xerophytes, has raised stomata (cp. *Morello* 1955: 323). In this case, however, a thick resinous mass covers the surfaces, necessitating the elevating of the pores above this cover. Thick cuticular epidermal layers are absent in a typical xerophyte such as *Mulinum spinosum,* but here the epidermis is biseriate and its outer cell layer has mucilaginous walls covered with a thin cuticle. Thus, a thick cuticular layer is not a general xeromorphic character, nor are sunken or depressed stomata, but such characters are hardly found in mesophytes or hygrophytes.

We must be very cautious about using the term xeromorphic for single characters and admit that most vegetative characters found in a xerophyte should be looked upon as parts of a structural pattern comprehended as a xeromorphic syndrome. Leaves, although very important in water economy, should not be considered as single objects; they are part of the entire plant and may be missing in apophyllous xerophytes or be mesomorphic in another xerophyte that has developed water-storing, bulbous underground parts.

But what is the situation considering species that show clear adaptations to widely different ecological conditions? In such cases the syndrome – the ecophysiologically coupled complex of characters – would be difficult or impossible to overlook. In a paper on the salt steppe grass *Sporobolus rigens, Böcher & Olesen* (1978) introduced the adjective xero-halophytic to be able to discuss characters that are probably adaptive in two respects, and a similar attitude might be adapted in the present work concerning structural features of high-Andean species. These must in some way be adapted to xeric conditions as well as to recurrent nightly frosts. Such species possess hardiness against excessive drought, intense radiation and daily frosts in the vegetation period. They deserve a compound designation which, however, probably would be too long and impractical. In reality our understanding of the ecophysiological adaptations in such cases is so superficial that intricate new terms referring to ecological adaptation would be of very limited value. In the case of *Sporobolus* the authors try to distinguish between xerophytic, halophytic and xero-halophytic features. The latter is estimated to be the result of an evolutionary process

determined by an equal and synchronous influence of a dry and saline environment.

It is clearly problematic to assign a species to a particular ecological group by using a word such as, e.g., halophytic. A procedure of this kind may involve a masking of the range of adaptability of the species. In fact, the ecological demands of hardly any species can be adequately expressed by single words. We must admit that multiple adaptation is a reality and applicable to a majority of species. But such versatile adaptation is difficult to express and understand simply because it is the result of an interaction between different, simultaneously working selective forces. Moreover, terms such as xerophyte, xeromorphic, etc., are practical and perhaps inevitable, but they cover only a small share of our requirements for expressing different kinds of adaptation.

Among the adaptive trends in the Afro-Alpine flora, *Hedberg* (1964) mentions protection against radiation, low night temperatures, drought and solifluction. The responses of the plant to the high-montane factor complex are expressed in a number of life forms that immediately appear widely different. Considering that they have evolved under the same complex of factors, they must all in various ways be results of the Afro-Alpine multiple factor complex. They are not merely xerophytes or just freeze-tolerant, but – as they have many counterparts, e.g., in South American tropical-subtropical high mountains – they might be called »tropic-alpine«. A term of this kind would at least have the advantage, above all, of referring to the particular climatic conditions in tropical high mountains, and it would not point to just one type of adaptation within the multiple factor complex in question.

2: Xeromorphy in relation to degree of scleromorphy and cutinization

Ten different species have been described, all xerophytes, but very different with regard to leaf structure. One of the most striking differences concerns the amount of sclerenchyma. With regard to the importance of sclerenchyma, the species can be arranged in a sequence starting with the most sclerophyllous ones, thus: *Chuquiraga erinacea, C. rosulata, C. hystrix, C. ruscifolia, Anarthrophyllum patagonicum, A. rigidum, Mulinum spinosum, Junellia uniflora, Acantholippia seriphioides, Perezia recurvata.* The sclerenchyma is concentrated in peripheral parts in the first two genera, has a central position in *Mulinum* and *Junellia,* and is reduced to single strands at the main bundles in the last two, which are not sclerophyllous. Using the same sequence in considering the degree of cutinization of the outer epidermal cell walls, Nos. 1–6 have thick cuticular layers and often cuticular flanges beneath the cuticle, while Nos. 7–10 have no or only thin cuticular layers and no flanges. Instead they are furnished with a biseriate epidermis with mucilaginous walls *(Mulinum),* or single, thick walls composed of pectinaceous and cellulosic substances.

The decrease in the amount of sclerenchyma in the sequence is probably not parallel with a decrease in drought tolerance. *Acantholippia* is perhaps the most pronounced xerophyte of them all. However, in this case the small leaf size and the strong keels and the rolling render supporting sclerenchymatous strands superfluous. A short, small leaf having revolute margins and a strong keel is in no danger of being bent or broken, e.g., by heavy gales. Similar reflections would be applicable for xerophytes like *Empetrum nigrum, Cassiope tetragona* and many others which have short revolute leaves and hardly any sclerenchyma.

An apparent antagonism appears from the fact that xerophytes may have either thick cutinized outer epidermal walls or thick non-cutinized walls inside the cuticles. It is true that cutin or wax layers in outer walls may effectuate a reduced water permeability and thus contribute to a minimizing of the cuticular transpiration,

but nobody really knows how thick pecto-cellulosic walls function during water stress conditions. Moreover, when the cuticle itself loses water under xeric conditions, the surface of water contained in the cuticle will be reduced and thereby the water loss to the atmosphere. Also the replenishment of water in the cuticle from water contained in the thick wall layers beneath will be slowed down. Finally, one should always realize that the outer epidermal walls in xerophytes are certainly not decisive for the water economy as a whole. In the case of *Acantholippia seriphioides,* a deep-going taproot and a very reduced joint leaf surface covered with a dense indumentum may very well balance a relatively large cuticular water loss.

3: Water flux and storage in thick cell walls

The amount of water kept in the apoplast of thick walls varies according to the physico-chemical properties. In lignified walls the majority of microcapillaries is probably blocked by lignin, but some are estimated to remain open. The cell wall apoplast stores water: it has a »hydraulic capacitance« from which water can flow to other parts during periods of water stress. Thus thick walls are able to buffer adjacent living cells, e.g., epidermal or photosynthetic cells, protecting them from deleterious changes in their hydration. However, it is not known to what extent a resupply with water can take place if the water is too tenaciously held by the walls (due to matric forces (adsorption)).

Water contained in microcapillaries in thick walls is assumed to take part in the water movement, perhaps mainly as a buffer. In *Junellia* (Fig. 1) and *Mulinum spinosum* (Fig. 25) this is probably brought about indirectly by the occurrence of a bundle sheath enclosing xylem as well as the central sclerenchymatous columns. In the latter species the central parts of the sclerenchymatous tissue have maintained wider cell lumina, being almost parenchymatous, though thick-walled, and they may be more capable of storing water. The water-storing capacity of thick pectinaceous-mucilaginous outer epidermal walls is perhaps doubtful and ought to be elucidated experimentally.

In the case of species exposed to nightly frosts it was suggested that the thick walls in, e.g., sclerenchyma, might serve as heat sinks or small thermotanks because of the specific heat of the water which they contain. This hypothesis is also in need of reconsideration after experimental approaches.

Water absorption by hairs (as well as evaporation from such hairs) was discussed in the case of *Chuquiraga ruscifolia, Anarthrophyllum, Junellia uniflora* and *Acantholippia.* In all cases an apoplastic passway in the thick walls of the hair cells is assumed, but furthermore a large and probably active nucleus is shown to be present at the base of the hair cell. In some cases a basal cell with cutinized wall is inserted and this may contribute to a translocation of water from the apoplast to the symplast. In the case of *Chuquiraga ruscifolia,* the axillary, elongated hair cells are not cutinized, while the basal short cells are. Here a translocation to the symplast is necessary if water is going to be stored in the non-photosynthetic parenchyma that occurs in the sheath part beneath and inside layers of cutinized cells (Fig. 5). In the case of *Anarthrophyllum* the cutinized basal cells have pit fields in the transverse walls separating them from the hair cells (Fig. 16). The bundle sheaths and their extensions in *Anarthrophyllum* border the epidermis with its multitude of hairs. Thus an apoplastic water passway is established from the veins to the hairs and vice versa. At least to some extent this passway may be controlled by the protoplast in the hair cells and bundle-sheath extensions. Penetration of water through the cuticle of the hair cells may take place through pores in cuticle warts or at non-cutinized apices. In *Acantholippia* (and perhaps *Mulinum)* the cuticle appears to be composed of small flakes overlapping each other.

4: Analogous convergence resulting in the formation of cylindrical photosynthetic bodies

Various types of regressive evolution among xerophytes led ultimately to an abandonment of photosynthesis associated with broad, flat, petioled and protruding phyllomes. In this regressive line leaf-size reduction was an important stage. *Raunkiær* (1916, 1934) already realized that large leaf blades were encountered in tropical, moist climates, whereas small leaves characterized dry, cold climates. He proposed six leaf-size classes and treated them statistically as life forms. Leaf-size reduction can be ascertained within a single species. Small-leaved races of *Veronica officinalis* were found in open areas of cold, windy climates, while most large-leaved races came from protected woodlands *(Böcher* 1944). The ecological importance of microphylly has been discussed, i.a. by *Grieve & Hellmuth* (1970: 59). A series of increasing leaf-size reductions in a group of related taxa forms a semophyletic lineage. The main types of reduction resulting in cylindrical green bodies may be four:

a) Leaf blade disappearance
Several parallel evolutionary lines resulting in apophyllous species with photosynthetic stems have been analysed. Such switch plants may have leaves in juvenile stages or leaves during their first growing period each year. Later the leaves are shed and the green stems carry non-photosynthetic scale leaves or cataphylls only *(Böcher & Lyshede* 1968, 1972, *Böcher* 1972, 1975). Leaf blade disappearance with maintenance of the midrib region only occurs in *Sporobolus rigens (Böcher & Olesen* 1978).

b) Cylindrical leaves, leaflets or phyllodia
Reinke (1897) refers to cylindrical stem-like phyllodia in various leguminous species *(Viminaria denudata, Indigofera juncea).*

Cylindrical unifacial leaves are found in more than 20 species of the genus *Hakea (Flachs* 1916).

Recently, *Hakea suaveolens* has been taken up for renewed and modern studies *(Heide-Jørgensen* 1978, 1979).

Pyykkö (1966: 566) distinguishes an anatomical leaf type which she calls the *Mulinum leptacanthum* type. It has spiny leaves (leaflets or leaf sections) and abundant sclerenchyma. Plants with this type of leaf are, however, widely different. *Chuquiraga* sp. (probably *C. rosulata)* and *Anarthrophyllum rigidum* have abundant sclerenchyma, but it is located abaxially in involute arrangements and there is no central sclerenchymatous column. This, on the other hand, is present in *Mulinum* and in *Junellia erinacea (Pyykkö* l.c. Fig. 103).

c) Involution, deflexion and revolution (rolling) of leaf margins

Examples of revolute leaves are abundant. Such leaves are usually small and densely spaced. Permanent rolling in *Empetrum* has created an almost closed cylindrical body. The dense insertion in *Empetrum* gives rise to a shoot structure in which the shoot approaches a single although not continuous cylindrical body. This trend becomes even more evident in species where the leaves are adpressed to the stem. The South American *Berberis empetrifolia (Pyykkö* l.c. 481–482) shows a strong resemblance in leaf structure to *Empetrum* but deviates with respect to the adaxial epidermis, which is multiple with thick lignified cell walls. The West Mediterranean *Hypericum empetrifolia* has normal revolute leaves and deviates markedly from *Empetrum,* i.a. by having some stomata on the adaxial leaf sides.

Revolute amphistomatous leaf structure also occur in *Acantholippia seriphioides* where, however, stomata are confined to incurved and inflexed parts. In this genus a culmination in leaf size reduction, rolling of margins and formation of adaxial furrows is recorded in *A. riojana* where the dwarf branch leaves attain a surface shape resembling that of a brain.

Examples of permanent, involute rolled, mature leaves are found in numerous grasses (e.g., *Triodia irritans* cp. *Craig & Goodchild* 1977) and in some species of *Chuquiraga* mentioned in the present paper. This type of structure seems to be almost unique within the dicotyledons. *Gamocarpha poeppigii (Pyykkö* l.c. 512) belonging to the *Calyceraceae* is a perennial herb with isolateral, amphistomatous leaves and also deviating by involute structure.

d) Dense spacing af cataphyll-like green leaves
Among dicotyledons this type was probably first described in *Tamarix* by *Volkens* (1887 Plate V). It is strikingly developed in the *Flagriformis* section of the New Zealand genus *Hebe.* The species in question have scale-like leaves arranged in terete or sometimes tetragonous whipcordlike branches. In spite of a similar habit, the *Flagriformis* species deviate from one another in xerophytism. In *H. cupressoides* the stomata on the abaxial out-turned sides are raised, while in *H. armstrongii* they are depressed and the epidermal walls have very thick cuticular layers. In New Zealand these two species are connected with different habitat conditions and occur at different altitudes. The whipcord growth form, therefore, is not a response to one particular type of environment.

Type (d) is of particular interest. Dense leaf spacing is connected with cataphyll-like small leaves. According to *Napp-Zinn* (1973: 117), scale leaves are in many cases inverse dorsiventral. Dicotyledonous involute leaves are often sheathing, small and cataphyll-like. In the case of *Perezia recurvata* a transition from involute cataphylls to deflexed foliage leaves takes place (p. 50) and in *Acantholippia* opposite sister leaves may be classified as involute cataphylls and revolute foliage leaves (p. 56). *Chuquiraga* species with involute leaves have crescent-shaped primordia which also look like cataphylls. A development from primordia to foliage leaves is a matter of increase in size and maturing of the

photosynthetic tissues. The appearance of small, cataphyll-like involute leaves may be controlled by gene complexes regulating growth rate and the distribution of meristematic activities. On the other hand, the maintenance of cataphyll-like mature leaf blades is probably adaptive. Under certain environmental conditions genes affecting primordial development may be subject to mutation, recombination and selection, or their effect could be modified through the action of additional genes favouring a maintenance of a cataphyll-like structure. The result might be an apparent regressive evolution resembling a kind of neoteny.

The convergences leading to green cylindrical bodies instead of broad flat blades are end-results of long-time evolutions concomitant with changes from mesic to dry environmental conditions. A green, flat body oriented vertically to the sun remains much cooler than one which is exposed more at right angles, and a cylindrical almost stationary green body will never suffer from long-time exposure to sunbeams which continuously change their angles of incidence.

A hyperstomatous structure is clearly connected with imbricate leaf insertion and therefore it is at the same time a phenomenon common in plants with short internodia and overlapping leaves; thus, in the scale-like leaves of *Azorella selago* from the Kerguelen Islands *(Ternetz* 1902: 6) as well as in the very peculiar high-Andean *Viola* species of the *Rosulata* section. Both have dorsiventral leaves with a higher concentration of stomata on the adaxial sides. *Reiche* (1893) attributes the higher stomatal densities on the adaxial sides in *Viola atropurpurea* to the reduced contact with air at the abaxial surfaces. In *Chuquiraga atacamansis* and *ruscifolia* all such contact is made impossible by the continuous sclerenchyma plates.

5: Semophyletic sequences, evolutionary canalization and adaptive shifts
Semophylesis was introduced as a term by *Zim-*

mermann (1930, 1959) to cover the German »Merkmalsphylogenetik«. Unfortunately, it has been discussed as phylogeny of single characters. But when *Zimmermann* and *Meeuse* (1966) use the term semophylesis, they generally discuss very intricate structures, e.g., the reduction of toes in the legs of horses or the evolution of ovules from megasporangia. Such structures can hardly be treated as single characters. They depend on intricate gene complexes and gene interactions. Thus a semophyletic lineage should be comprehended as a continuous series of evolutionary events in which each step, being marked as a certain morphological-functional level, is a response to some kind of ecological change and therefore involves many interdependent cooperating genes. It is almost impossible to imagine semophyletic changes without concomitant changes in external environment and perhaps also changes in what *Stebbins* (1974) calls the internal phase, which implies interactions of genes present in the organism itself.

In *Chuquiraga* the changes resulting in the differentiation of the main sections were explained in relation to climatic alterations during territorial expansions and migrations. A change resulting in the *Ruscifolia* section was estimated to evolve as adaptations to Andean conditions, while another change leading to species of the *Unguis-cati* section was thought to be coherent with an alteration from Andean to xeric Patagonian conditions. There is, of course, no evidence for these hypothetical evolutionary lines, but the structural specializations support the semophyletic sequences. The absence of stomata on abaxial surfaces is a feature that determines a further development towards involution. We are faced with a process which very much resembles an evolutionary canalization as described by *Stebbins* (1974: 22–23). This author supposes an origin of higher taxonomic categories involving major adaptive shifts in which the most prominent character combinations were highly canalized, being produced by coordinated and inte-

grated interactions between many different genes.

The type of leaflet involution in *Anarthrophyllum* deviates considerably from the leaf blade involutions in *Chuquiraga*. Very few genera among the *Genisteae* show a similar structure. The South African *Lebechia* is perhaps the only example of a genus that approaches the *Anarthrophyllum* structure. In the latter genus several ecologically and morphologically different species all have an adaxial groove and the stomata are not confined to the groove. Thus, the structure of the leaflets with their fixed groove formation is best explained as a case of conservation of an organisation (cp. *Stebbins* l.c. p. 24). The groove is slightly modified according to differences in habitat. The whipcord structure in *Hebe* (section *Flagriformis)* is another good example of conservation of a characteristic structure.

It is difficult to imagine any further evolution in species groups with such fixed characters. Still, according to the views of *Stebbins,* xeromorphic features are at least sometimes changed into mesomorphic, but in the case of very stable life forms such as, e.g., the Cactus type of stem succulents he doubts that such drastic changes could happen. In the case of very specialized adaptations such as the needle-like, involute *Chuquiraga* leaves, I rather imagine that the species would become extinct, if an alteration towards mesic conditions took place. Yet, if an evolution away from a pronounced xeromorphic leaf structure really occurred, it would probably be initiated by drastic mutations affecting the juvenile stages, where a mature xeromorphic structure was not yet achieved.

6: Xeromorphic leaf types
Xerophytes constitute a very comprehensive and very disorderly biological group, but still a kind of life form. The term xerophyte only suggests that the plant is adapted to withstand drought. The term xeromorphic restricts the xerophyte

concept to a structure enabling drought resistance, but structure alone says nothing without the adjective »ecophysiological«. Leaves are crucial in most xerophytes, but as already emphasized they can, when considered separately, hardly reveal more than single aspects of the water economy of a plant.

Still, after studying a number of xeromorphic leaves, it appears possible to discuss a setting up of some structural types expressing important adaptational strategies – immediately realizing that any delimitation of "xeromorphic types" is done in order to facilitate a survey of a continuum.

It is obvious from the preceding that the most important characters implicate: (1) amount and distribution of sclerenchyma, (2) histochemistry of epidermal layers, (3) position (and protection) of stomata, and (4) density and composition of indumentum. The aim is to determine particularly common combinations of characters from the four groups.

(1) The presence of large quantities of sclerenchyma has already led to the designation sclerophyllous. Two subtypes of sclerophyllous xerophytes are described in the present paper, viz. one with sclerenchyma concentrated in peripheral layers (epidermal, hypodermal) and another with a sclerenchymatous central column.

(2) Epidermal-subepidermal layers are widely divergent with regard to cell wall texture and chemistry. In all cases they are covered with a continuous cuticle, but the peripheral cell layers beneath can have walls which are cutinized, cutinized and lignified, or pectinaceous and mucilaginous. The interior parts of the walls near the cell lumina are mostly cellulosic. A deviating species is one such as *Atamisquea emarginata,* which has an adaxial waterstoring epidermis (not described in detail in the present paper).

(3) Guard cells are usually depressed and often provided with outer ledges forming antechambers. In cases of a thick hair cover the guard cells may be elevated. This is also the case, and particularly so, in leaves which become covered with some kind of varnish produced by colleters or glaudular tissue compartments. Stomatal pores are furnished with antitranspirent arrangements such as antechambers and long, irregularly curved diffusion pathways; furthermore they are often concentrated in epidermal grooves or in cavities formed by involution, revolution or deflexion of leaf margins. Abaxial hair-covered stomatal crypts in flat dorsiventral leaves are described from the South American *Condalia microphylla* (Pyykkö 1966: 557) but occur in several unrelated genera *(Nerium, Banksia, Stephanotis, Dionysia)* giving a striking example of convergent evolution of an anatomical character.

(4) The indumentum varies from being nearly absent *(Mulinum)* to being a very dense hair cover and with great diversity of hair types *(Acantholippia).* The density decreases with the age of the leaves, but high densities in mature leaves are maintained in cavities or grooves. The ecophysiological significance of the various hairs has been estimated in each of the species mentioned in detail. In general, the indumentum in xerophytes seems to be of great importance and its function obviously varies from case to case, but it is by and large poorly understood.

Common combinations of characters are:

A. The sclerophyllous-cutinized type with peripheral sclerenchyma and a high degree of epidermal cutinization. Mostly very poor in glands, but having abundant covering hairs (e.g., T-hairs) with light-reflecting effects or other functions. Stomata sunken or protected in grooves or depressions.

B. The columnar sclerophyllous-non-cutinized type. Sclerophyll in central columns. In the case of *Mulinum* there is a two-layered mucilaginous epidermis, in species of *Junellia* a one-layered epidermis with thick cellulosic-pectinaceous outer walls. Stomata slightly raised or not sunken; not protected otherwise.

C. Non-sclerophyllous keeled, revolute or de-flexed type. Prominent keels or marginal recurvations substitute for sclerenchymatous strengthening systems. Epidermal cell walls are thick, pectinaceous (mucilaginous) and cellulosic. Stomata protected, slightly raised or not sunken. Hair cover often abundant and with many glands, sometimes producing ethereal oils.

D. Linear or small, not revolute or deflexed, not sclerophyllous but sticky type. The stickiness results from resinous substances covering the surface and produced by glands. This type is important (with many representatives). In the present paper no examples are discussed in detail because the type deserves separate treatment. Here the stomata are usually raised (see discussion p. 62 with comments on *Larrea cuneifolia*). Other good examples of species having leaves of this category are *Baccharis thymifolia, Chiliophyllum densifolium (BHR Fig. 20), Haplopappus rotundifolius, Gutierrezia spathulata, Adesmia guttulifera (BHR Fig. 34)*, and *Zuccagnia punctata*.

Among the apophyllous species mentioned in detail by *Böcher & Lyshede* (1972: 50–59), *Fabiana denudata* and *viscosa* clearly show the same strategy and exhibit highly elevated guard cells in the epidermis on assimilating stems. The stomata here expel the sticky cover like submarine periscopes. However, the leaves, which are shed early, have no protruding stomatal ledges. They are small, centric, non-sclerophyllous with thick non-cutinized outer walls.

Evidently the four types, A–D, do not cover all xeromorphic leaves, they only constitute important types of strategy. It is characteristic that those of type D have no or very few types of hair other than those producing resinous material, and that the leaves are not involute or revolute. Likewise, those of types A–C never have a sticky cover. The glandular hairs in *Acantholippia* produce ethereal oils, which increase the density of gas in the boundary layer and in the leaf air spaces and thus produce a higher diffusion resistance to water vapour evaporating from the cell walls. A resinous cover, however, may functionally resemble a thick cuticular layer in outer walls, and it probably substitutes for the anti-transpirent effects of cutinization and wax intrusions.

Literature

Burkart, A., 1943: Las Leguminosas Argentinas. – Buenos Aires.

Böcher, T. W., 1944: The Leaf Size of Veronica officinalis in Relation to Genetic and Environmental Factors. – Da. Bot. Ark. *11,* 7:

– 1975: Structure of the multinodal photosynthetic thorns in Prosopis kuntzei Harms. – Kgl. Da. Vid. Selsk. Biol. Skr. *20,* 8: 1–43.

– 1976: Experimental and cytological studies on plant species XIII Clinopodium vulgare L. – Bot. Tidsskr. *70:* 152–179.

– 1977: Convergence as an evolutionary process. – Bot. J. Linn. Soc. *75,* 1: 1–19.

– J. P. Herting & K. Rahn, 1963–72 (BHR): Botanical Studies in the Atuel Valley Area, Mendoza Province, Argentina. – D. Bot. Ark. *22,* 1–3: 1–358.

– & O. B. Lyshede, 1968: Anatomical studies in xerophytic apophyllous plants. I. Monttea aphylla, Bulnesia retama and Bredemeyera colletioides. – Kgl. Da. Vid. Selsk. Biol. Skr. *16,* 3: 1–44.

– & – 1972: Anatomical studies in xerophytic apophyllous plants. II. Additional species from South American shrub steppes. – Kgl. Da. Vid. Selsk. Biol. Skr. *18,* 4: 1–137.

– & P. Olesen, 1978: Structural and ecophysiological pattern in the xero-halophytic C4 grass, Sporobolus rigens (Tr.) Desv. – Kgl. Da. Vid. Selsk. Biol. Skr. *22,*3: 1–48.

Cabrera, A., 1939: Las Compuestas del Parque Nacional del Nahuel Huapi. – Rev. Mus. La Plata (Nuev. Ser.) *2.* Bot.: 227–396.

– 1961: Anatomy of some xerophilous plants of Patagonia. – Unesco. Arid Zone Res. *16:* 235–239.

– 1971: Compositae in Flora Patagonica. Ed. by Malvia Correa. Part VII. – Buenos Aires.

Constance, L., 1965: Some subtractions from the Umbellifera of South America. – Ann. Missouri Bot. Gard. *52:* 274–280.

Craig, S. & D. J. Goodchild, 1977: Leaf ultrastructure of Triodia irritans: a C4 grass possessing an unusual arrangement of photosynthetic tissues. – Austr. J. Bot. *25:*277–290.

Dahlgren, R., 1960: Revision of the genus Aspalathus I. – Opera Bot. Lund *4:* 1–393.

Diels, L., 1897: Vegetations-Biologie von Neu-Seeland. – Englers Bot. Jahrb. *22:* 202–300.

Domin, K., 1908–09; Morphologische und phylogenetische Studien über die Familie der Umbelliferen. – Bull. Intern. Acad. Sciences Bohème *13:* 108–152, *14:* 1–52.

Dormer, K. J., 1956: Vegetative morphology as a guide to the classification of the Papillionatae. – New Phytol. *45:* 145–161.

Espinosa, R., 1933: Ökologische Studien über Kordillerenpflanzen. – Englers Bot. Jahrb. *65:* 120–212.

Flachs, K., 1916: Über die Verbreitung des äquifazialen Blattbaues in der australischen Flora. – Diss. Univ. München. – Leipzig: 1–68.

Gaspar, F. C., 1945: Las especies Argentinas del género Chuquiraga. – Rev. Argent. Agron. *12:* 157–172.

Goebel, K., 1893: Die Vegetation der venezolanischen Paramos. – Pflanzenbiol. Schild. 2. Teil. – Marburg.

Grieve, B. J. & E. O. Hellmuth, 1970: Eco-physiology of Western Australian Plants. – Oecologia Plantarum *5:* 33–67.

Haberlandt, G., 1904: Physiologische Pflanzenanatomie. – Leipzig.

Hadley, N. F., 1976: Desert species and adaptation. – Amer. Scientist *60:* 338–347.

Hagerup, O., 1946: Studies on Empetraceae. – Vidensk. Selsk. Biol. Medd. *20,* 5: 1–49.

Hare, C. L., 1943: The arborescent Senecios of Kilimanjaro. A study of ecological plant anatomy. – Trans. Roy. Soc. Edinburgh *60:* 355–371.

Hauman, L., 1918: La Végétation des Hautes Cordillères. – Anal. Soc. Cient. Argent. *86:* 121–348.

Hedberg, O., 1964: Features of Afroalpine Plant Ecology. – Acta Phytogeogr. Suecia *49:* 1–144.

Heide-Jørgensen, H. S., 1978: The xeromorphic leaves of Hakea suaveolens R.Br. I. Structure of photosynthetic tissue with intercellular pectic strands and tylosoids. – Bot. Tidsskr. *72:* 87–103.

– 1978: The xeromorphic leaves of Hakea suaveolens R.Br. II. Structure of epidermal cells, cuticle development and ectodesmata. – Bot. Tidsskr. *72:* 226–244.

– 1979: The xeromorphic leaves of Hakea suaveolens. III. Ontogeny, structure and function of the T-shaped trichomes. – Bot. Tidsskr. (In press).

Jessen, K., 1913: Rosaceae. Structure and Biology of Arctic Flowering Plants. – Medd. om Grønland *37:* 1–126.

Klug, I., 1926: Über die Sekretdrüsen bei den Labiaten und Compositen. – Diss. Frankfurt a. M. – Darmstadt.

Levy, L., 1901: Untersuchungen über Blatt- und Achsenstructur der Genisteen Gattung Aspalathus und einiger verwandter Genera. – Beih. Bot. Centralbl. *10:* 311–366.

Lyshede, O. B., 1977: Structure and function of trichomes in Spartocytisus filipes. – Bot. Notiser *129:* 395–404.

Majewski, M. P., 1873: Evolution des barbules du Begonia manicata. – Bull. Soc. Imp. Nat. Moscou *45:* 241–282.

Mathias, M. & Constance, L. 1976: Umbelliferae in Harling & Sparre. Flora of Ecuador, no. 5. Stockholm.

Meeuse, A. O. J., 1966: Fundamentals of phytomorphology. – Ronald Press. New York.

Metcalfe, C. R. & L. Chalk, 1950: Anatomy of the dicotyledons. Vol. I and II. – Clarendon Press. Oxford.

Moldenke, H., 1961: Materials toward a monograph of the genus Acantholippia. – Phytologia *7:* 326–338.

Morello, J., 1955: Estudios botanicos en las regiones aridas de la Argentina. – Rev. Agronóm. Nordoeste Argent. *1,* 3 (Tucumán): 301–524.

Napp-Zinn, K., 1973: Anatomie des Blattes. – Handb. d. Pflanzenanat. 2 Aufl. II A l. – Berlin & Stuttgart.

Parkhurst, D., 1978: The adaptive significance of stomatal occurrence on one or both surfaces of leaves. – Journ. of Ecol. *66:* 367–383.

Petersen, H. E., 1908a: Diapensiaceae. Structure and Biology of Arctic Flowering Plants. I. – Medd. om Grønl. *36:* 139–154.

– 1908b: Ericineae (Pirolaceae, Ericaceae). Structure and Biology of Arctic Flowering Plants. I. – Medd. om Grønl. *36:* 75–154.

Pyykkö, M., 1966: The leaf anatomy of East Patagonian xeromorphic plants. – Ann. Bot. Fenn. *3:* 453–622.

Raunkiær, C., 1916: Om Bladstørrelsens Anvendelse i den biologiske Plantegeografi. – Bot. Tidsskr. *34:* 225–237.

– 1934: The Life Forms of Plants and Statistical Plant Geography. Oxford.

Reiche, K., 1893: Violae chilenses. Ein Beitrag zur Systematik der Gattung Viola. – Englers Bot. Jahrb. *16:* 405–452.

– 1902: Flora de Chile. III. Umbelliferas. Pp. 46–121.

Reinke, J., 1897: Untersuchungen über die Assimilationsorgane der Leguminosen. – Jahrb. wiss. Bot. *30:* 1–70.

Roig, F., 1971: Flora y vegetation de la reserva forestal de Nacuñan. – Deserta.-Ann. Inst. Invest. Zonas aridas y semiaridas. *1:* 25–232.

Roiz Leal, A., 1961: Un Oasis en el Desierto. – Bol. Estud. Geograf. Argent. *8, 32:*

Ruthsatz, B., 1099: Pflanzengesellschaften und ihre Lebensbedingungen in den Andinen Halbwüsten Nordwest-Argentiniens. – Dissertationes Botanicae *39.* – Vaduz.

Schwabe, H., 1950: Anatomia foliar de Doniophyton (Compositae). – Biol. Soc. Argent. *3:* 77–79.

Slatyer, R. O., 1960: Absorption of water by plants. – Bot. Rev. *26:* 331–392.

Solbrig, O. & G. H. Orians, 1977: The adaptive characteristics of desert plants. – American Scientist *65:* 412–421.

Sorarú, S. B., 1974: Revisión de Anarthrophyllum, genero Argentino – Chileno de Leguminosas. – Darwiniana *18:* 453–488.

Spinner, H., 1936: Stomates et altitude. – Ber. Schweitz. Bot. Ges. *46:* 12–27.

Stebbins, G.L., 1974: Flowering plants. Evolution above the species level. – Cambridge, Mass. 1–399.

Ternetz, Ch., 1902: Morphologie und Anatomie der Azorella selago Hook. fil. – Bot. Ztg. *60:* 1–20.

Treschow, M., 1970: Environment and plant response. – McGraw-Hill. New York.

Troll, W., 1939: Vergleichende Morphologie der höheren Pflanzen. I, 2. – Berlin.

Uphof, I. C. Th. & K. Hummel, 1962: Plant hairs. – Handb. d. Pflanzenanat. IV 5. – Berlin & Stuttgart.

Warming, E., 1920: Caryophyllaceae. Structure and biology of arctic flowering plants. II. Medd. om Grønl. *37:* 231–342.

Wendelbo, P., 1961: Studies in Primulaceae. I. A monograph of the genus Dionysia. – Acta Univ. Berg. Math. Nat. *3:* 1–83.

– 1971: On xeromorphic adaptations in the genus Dionysia (Primulaceae). – Ann. Naturhist. Mus. Wien *75:* 249–254.

Werner, D. J., 1972: Campo arenal, eine landschaftsökologische Detailstudie. – Biogeographica *1:* 75–86.

Zimmermann, W., 1930: Die Phylogenie der Pflanzen. – Jena.

– 1959: Die Phylogenie der Pflanzen. 2. Aufl. – Stuttgart.

Biologiske Skrifter

Biol. Skr. Dan. Vid. Selsk.

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