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THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

THE COMPARATIVE MORPHOLOGY OF THREE CYLINDROPUNTIAS

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

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THE COMPARATIVE MORPHOLOGY OF THREE CYLINDROPUNTIAS

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THE COMPARATIVE MORPHOLOGY OF THREE CYLINDROPUNTIAS

CHAPTER I

INTRODUCTION

In the system used by Britton and Rose (1920) the Cactaceae are segregated into three tribes: (1) Pereskieae with no glochids, but with deciduous leaves and stalked flowers; (2) Opuntieae with glochids, small ephemeral leaves, and sessile flowers; and (3) Cereeae with no glochids, usually no leaves, and unstalked flowers with definite tubes. Britton and Rose list seven genera in the Opuntieae subdividing the genus Opuntia into three subgenera; Cylindropuntia (stems cylindroidal or circular in cross section), Tephrocactus (all of the South American species of Opuntia with short, oblong, or globular joints), and Platyopuntia (branches composed of flattened joints). They further subdivide Cylindropuntia into 13 series. Grusonia is listed as a separate genus at the end of the tribe. At one time Baxter (1932) proposed making a section (Grusonia) in Opuntia to accommodate O. bradtiana, O. kunzei, and O. santamaria. These three taxa, which have at some time or other been considered congeneric in Grusonia, are

the ones I am using for this comparative study. They probably would no longer be considered a well-defined section and most surely not a separate genus.

Synonomy

Opuntia bradtiana (Coult.) K. Brandegee was described by Coulter as a species of Cereus in April 1896. In December 1896 Reichenbach provided a description of Grusonia cereiformis, which is considered to be a synonym of Opuntia bradtiana. Brandegee and Weber transferred these species to Opuntia in 1897 and 1898, respectively. Britton and Rose returned O. bradtiana to Grusonia in 1920 and listed O. cereiformis as a synonym. Baxter (1932) and Marshall and Bock (1941) think the species should be retained in Opuntia.

Opuntia stanlyi var. kunzei (Rose) L. Benson (1969) was first described in 1908 as O. kunzei. In 1935 Baxter described Grusonia wrightiana from Arizona and in 1937 it was transferred to Opuntia by Peebles. This incomplete synonomy lists only what seems pertinent to my discussion. Some authors consider these two to be distinct while others regard them to be conspecific. Since the taxonomic status of the two is poorly understood I am arbitrarily using the older of the two specific epithets (i.e., O. kunzei) in this paper.

Opuntia santamaria (E. M. Baxter) Wiggins (1964) was discovered by Gates in 1931, but was not officially

described until 1934 when Baxter described it as Grusonia santamaria.

CHAPTER II

MATERIALS AND METHODS

All of the Opuntia bradtiana materials, including seeds and plants, were collected in late March 1967, June 1967, and late March, 1968 at two sites in Coahuila, Mexico: one was two miles west of the highway 40 Paila-Parras junction, the other was 6-8 miles east of Cuatro Ciénegas on highway 30. The O. kunzei plants were sent to me by Superintendent Matt H. Ryan from the Organ Pipe Cactus National Monument, Arizona. Fruits and seeds were collected in the same approximate location by Paul Whitson of the University of Oklahoma. The only live material I was able to locate of O. santamaria came from Mr. Ted Hutchison, Riverside, California and was from the Gates collection. However, Dr. John Thomas, curator of the Dudley Herbarium, Stanford University, loaned me the preserved type specimen of O. santamaria.

Treatment of O. bradtiana seeds for germination has been described previously (Hamilton, 1970). The only pretreatment used for O. kunzei was scarification with sandpaper. No seeds of O. santamaria were available.

Pre-germination embryos were stained with a 0.1% solution of tetrazolium chloride to provide contrast for photographic purposes. For serial sections all plant materials were fixed in Craf V, dehydrated in a dioxan series (Sass, 1958), and embedded in Paraplast (60 C). Sections were cut at 8-10 μ and stained with safranin (Sass, 1958) and fast green (Boke, 1952) or with a quadruple stain (safranin, crystal violet, fast green, and gold orange) (Conant, 1950). Some roots were stained in hematoxylin instead of safranin. Other materials were cleared according to a Debenham (1939) technique. Materials for maceration were treated with a 1:1 solution of 10% nitric acid and 10% chromic acid, stained with safranin, and mounted in glycerine. Starch and protein were identified by tests with IKI (iodine-potassium iodide) and mercuric bromo-phenol blue (Mazie, Brewer, and Alfert, 1953), respectively.

CHAPTER III

OBSERVATIONS AND DISCUSSION

Each of the three species has a relatively restricted distribution. However, all grow in similar habitats where annual rainfall is usually less than eight inches. Opuntia bradtiana appears to be endemic to the Chihuahuan desert of north central Mexico in Coahuila, Chihuahua, and Durango (Gold, 1965, 1966, 1967). Opuntia kunzei is found in the Sonoran desert of southwestern Arizonia and northern Sonora. Opuntia santamaria, as far as I can determine, is located only on Magdalena Island, Baja California, also part of the Sonoran desert. Baxter (1932) suggests that these taxa were at one time much more widespread within their triangular boundaries (Fig. 16) and that they are the remnants of a dying group which has been replaced by evolving forms of cylindric and clavate types.

Gross Morphology

Opuntia bradtiana is a low growing, much branched cactus with trailing stems that are spiny, terete, and ribbed (Fig. 1). Britton and Rose report that the plant grows as high as two meters, but I think this is greatly

exaggerated. The plants in Fig. 1 are approximately 40 cm tall and this is characteristic of the large population near Cuatro Ciénegas, Coah. The plants grow in dense, almost impenetrable thickets in some areas. Stems and joints can be readily detached. Cut stems are extremely mucilaginous, with a bland, not unpleasant taste. Areoles are borne at the tops of tubercles which coalesce early in the seedling stage into vertical rows of ribs. They bear wool and many stout, unsheathed, white, glassy spines (Fig. 12) The smooth, acicular spines are slightly flattened and older ones are often brown-tipped. Opuntia bradtiana is usually considered to have glochids only in flowering areoles, but I find them in other areoles also. Usually one small, deciduous leaf subtends each areole. Flowers, which open in late May or early June, terminate the branches and are yellow. The ones I saw opened only during the middle of the day. Fruits are 28 mm long and 13 mm wide, very spiny, and heavily ribbed (Fig. 10, 13). They seem to be either sterile or the food source of some animal since viable seeds are difficult to find. The plants seem to propagate mostly by fallen stems coming in contact with the ground and rooting.

Opuntia kunzei is also a low growing, much branched cactus (Fig. 2), but instead of having trailing stems like O. bradtiana, it grows in a clump formation with stems rarely over 35 cm tall. The terete stems are rigidly joined and can be removed from the plant only with great difficulty.

Cut stems do not appear as mucilaginous as O. bradtiana and, to me, have a slight lemon taste. Dead stems exhibit a heavy, reticulated woody structure while those of O. bradtiana are not at all woody. Areoles are also borne at the tops of large tubercles, but tubercles in O. kunzei never completely coalesce into vertical rows of ribs. Areoles bear little wool, but do have many stout, tan spines some of which are as long as five cm. Spines are strongly flattened, subulate, and with roughened margins (Fig. 14). Spines on young joints (late spring and early summer) are spectacular in coloring--a bright rose-red with white tips. Not all stems (or even clumps) add new growth each year. Flowering areoles have large glochids. Usually one small, deciduous leaf subtends each areole. Flowers are at the end of branches, but do not necessarily terminate them. They bloom in May and June and are yellow, as are the persistent spiny, fleshy fruits of the plant (Fig. 15). These fruits (approximately 60 mm x 22 mm) give much evidence of being eaten by animals, but it seems to be the fleshy part that the animals prefer instead of the seeds. Viable seeds are plentiful in early spring in Organ Pipe Cactus National Monument. Seeds are tan-yellow and approximately twice the size of those of O. bradtiana.

Opuntia santamaria is a low moderately branched cactus, usually growing no more than 50-60 cm. As in O. kunzei new joints grow from near the base of the plant

and dead stems exhibit a similar reticulated woody structure, but of much lighter weight. Stems and joints (Fig. 3) are much more easily removed from the plant than those of O. kunzei, very mucilaginous when cut, and have a bland taste. Areoles are borne at the tops of tubercles which coalesce into slightly spiral ribs. Areoles are rather close together on the joints, giving the appearance of an Echinocereous. They contain wool, caducous glochids only when young (Marshall and Bock, 1941), and many slightly flattened subulate spines. The rigid spines (Fig. 11) are brownish-red and much shorter and more delicate than those of O. bradtiana and O. kunzei. They may occasionally be sheathed or only sheathed in youth. Flowers, at the apex of the previous year's joints, are greenish-yellow to sulfur-yellow, with the innermost perianth parts rose tinged along the midvein and margins. They are reported to turn red with age. They bloom in southern California in June (Shreve and Wiggins, 1964). I have not seen mature seeds and fruits and have found no description of seeds, but, according to Baxter (1934) the fruits are green, rather flattened, strongly ribbed, and with a much depressed umbilicus.

Seedling Development

As mentioned above seeds of O. santamaria were not available, however those of O. bradtiana and O. kunzei are similar except for size and germination (Fig. 8) The mature off-white seeds of O. bradtiana are 2-3 mm in

diameter, 1.5 mm thick, essentially round and flattened. Immature seeds are somewhat reniform. The outer testa (Fig. 20) has druses in such abundance that this may account for the germination difficulties mentioned below. Seeds of O. kunzei are yellow-tan, 4-5 mm in diameter, 1.5-2 mm thick, also round and flat with a hard outer testa. There are only scattered druses in the testa (Fig. 21). Seeds of both taxa are typically "opuntioid" with a hard smooth arillus, an extension of the funiculus which completely surrounds the ovule and looks like a third integument. The central perisperm is surrounded by a large curved embryo with its two succulent cotyledons (Fig. 9). Cotyledons of both store protein whereas the perisperms store starch. Druses are found in the dry, ungerminated embryos of both taxa. This is rather surprising since druses are usually considered to be a waste disposal mechanism and a dry seed certainly has greatly reduced metabolism. Seeds of both become very mucilaginous when moistened, although seeds of O. bradtiana do not readily take up water and expand as do those of O. kunzei. Both have a small hilum near the micropyle. Seeds of O. kunzei germinated much more readily than those of O. bradtiana, which seemed to require a minimum of six weeks, usually much longer. Opuntia kunzei seeds germinated in 14 days following scarification with sandpaper. Many treatments were given O. bradtiana seeds to promote germination, but with little success.

Seedling development in both taxa is similar once the seed coat is ruptured. Initially, seedlings of O. kunzei (Fig. 4) seem more robust. Cotyledons shed the seed coat 4-5 days after germination. Hypocotyl elongation is rapid in both, reaching a peak at two weeks with O. kunzei measuring approximately 30 mm above ground and O. bradtiana measuring 26 mm. Measurements given are an average taken of 15 O. bradtiana and 10 O. kunzei seedlings. Most O. kunzei hypocotyls are thicker. By two weeks hairs are beginning to appear in the crotch of the cotyledons of both. Tubercles did not begin to be obvious until after three months (Fig. 5, 6) and those of O. bradtiana did not begin to coalesce until five or six months later. Epicotyls of young seedling are rather clavate, later becoming cylindric (Fig. 5, 6, 7). One small, green succulent leaf subtends each areole in O. bradtiana. In O. kunzei the leaf is usually red and seems, at this stage, to be much more ephemeral than that of O. bradtiana.

Glochids occur in areoles of O. kunzei seedlings, but I have found none in O. bradtiana. Opuntia kunzei seems to have fewer and smaller druses in all tissues than does O. bradtiana.

With the few exceptions noted above, seedling development of O. kunzei parallels that of O. bradtiana as described previously (Hamilton, 1970).

Mature Plant

No root material of O. santamaria was available but according to Baxter (1934) the roots are fibrous and woody as are those of most chollas. The only joint I had failed to root. Roots of O. kunzei have a heavy, woody primary root with many woody secondary and tertiary roots. This species grows readily in the greenhouse.

In both taxa cork is formed early in the seedling stage. At maturity roots have a thick cork layer with a one to several-celled layer of stone cork. Stone cork is rarely mentioned in recent literature dealing with cactus roots, but this type of cork cell is apparently found in the roots of many cacti, as well as in those of some species of Salix, Fagus, and Viburnum. Cork cells are usually tabular, thin-walled, suberized cells. Stone cork cells are tabular, thick-walled, lignified cells (Fig. 24, 25, 26). According to Wolf (1912) they arise from the same initial layer as the thin-walled type. Coutant (1918) describes and illustrates stone cork in two species of Opuntia but gives it no name. She says it is never more than three cells thick. In O. kunzei there are layers 7-8 cells thick. Occasionally the stone cork layers are interspersed with thin-walled cork layers, rather suggestive of annual growth increments (Fig. 24). Hemenway (1934) says that stone cork, as a wound response, becomes 3-6 times thicker than the thin-walled type and alternates with it.

Roots of O. kunzei are polyarch, usually with five xylem poles. Tracheary thickening seems to be only helical. Druses are small, rounded, and not nearly so abundant as in O. bradtiana. Abundant mucilage cells are found only in primary roots. Roots of O. bradtiana are also polyarch, usually with seven xylem poles, and what superficially appears to be a pith is immature xylem. Tracheary thickening also seems to be only helical. The stone cork layer is 1-4 cells thick (Fig. 26) and the cortical parenchyma has few intercellular spaces or mucilage cells. The roots abound with small, rounded druses which are readily observed and also tiny crystalline particles which are visible only under polarized light.

The epidermis of the mature stem of all three taxa is covered with a layer of cutin. This layer is so heavy in O. bradtiana that it gives the plant a definite greyish cast. In all three taxa there is a collenchymatous hypodermis of 2-7 cells. The cell layers just under the epidermis are nearly always so full of rounded druses that a surface view looks like a solid layer of druses with only small spaces between (Fig. 18). This does not hold true for all opuntias. In O. kleiniae, another cylindropuntia, the druses are comparatively far apart (personal observation).

Sharply pointed to slightly rounded druses are also found scattered in the cortex, especially around the vascular tissue. Of the three taxa, O. santamaria has the

largest druses (Fig. 19). These are easily visible without magnification and occasionally measure 1 mm in diameter. The druses of O. bradtiana and O. santamaria fall into two definite types (stellate cortical and rounded hypodermal) and can be easily identified as such. They also seem to be much more abundant in all tissues and at all stages of growth than those in O. kunzei. Druses of O. kunzei are rather rounded in all tissues and comparatively small. Whether soil type or other external factors have anything to do with the differences noted, I cannot say. Rather unexpectedly, druses are nearly always found in abundance near areas of greatest meristematic activity.

Stomata of all three taxa (Fig. 17) are superficial, paracytic, and accompanied by a sub-stomatal chamber which extends through all layers of the hypodermis. Areoles of all three are usually subtended by one small succulent, terete, ephemeral leaf. The mesophyll of the leaves is not differentiated into palisade and spongy layers as in most dicotyledons. This agrees with Freeman's (1970) observations in O. basilaris and Boke's (1944) in O. cylindrica. The mesophyll cells are loosely organized with many intercellular spaces. The leaf is vascularized by one central bundle, composed solely of helical tracheary elements, but with its branches of short, tapered segments. Mucilage cells and druses are numerous.

Areoles are borne in the axils of leaves and give rise to spines, glochids, and trichomes. Near-terminal areoles of year-old joints may give rise to flowers. Opuntia bradtiana was originally described as having glochids only in flowering areoles, but this is not correct. Marshall and Bock (1941) say glochids are found in all areoles. I find them only occasionally on microslides of O. bradtiana and O. santamaria tubercles, but regularly on O. kunzei (Fig. 22). There is some difficulty in distinguishing spine, glochid, and leaf primordia, but mature organs are readily distinguishable (Fig. 23). The glochid basal meristem functions only a short time and the base does not become indurate. A spine becomes heavily sclerified and its base indurate and underlaid with several layers of cork (Fig. 23). Spines and glochids are not vascularized. Areoles are borne at the tops of prominent tubercles. Tubercles of O. bradtiana and O. santamaria coalesce into vertical or slightly spiral rows of ribs, while those of O. kunzei never seem to completely coalesce. These two characters, ribbed stems and absence of glochids on all but flowering areoles, were used earlier to separate the three taxa from other opuntias and put them in Grusonia.

According to Metcalfe and Chalk (1950) Opuntia is characterized by an unusual type of tracheid; a broad cell "with very thin walls, in shape midway between that of a barrel and that of a spindle; they are provided with

locular or spiral thickening ridges inserted on the thin wall by their narrow edge and project far into the cell lumen." These short, wide tracheids are prevalent in stems of all three taxa (Fig. 27) but not in roots. They are usually towards the pith of the plant with helical and annular elements nearest the hypodermis. The tracheids are non-storied in these three taxa but in another cylindropuntia (O. kleiniae) (personal observation) they are storied in tangential section. The vascular tissue occurs as a ring of separate vascular bundles around a compact pith.

Corollas of the three taxa are rotate. All three bloom in May or June with the flowers usually being borne singly near the top of the previous year's growth. Ovaries are spiny and strongly tuberculate.

CHAPTER IV

SUMMARY

There is no question in my mind that the three taxa are specifically distinct from one another and should be retained in the genus Opuntia as cylindropuntias. Other opuntias have a characteristic type of seed which is shared by O. bradtiana and O. kunzei. Seedling development likewise parallels that of other species (Wiggins and Focht, 1967) and differs from seedling development of cacti in other tribes (Meyrán, 1956).

All three taxa contain the barrel tracheids characteristic of opuntias and stone cork, which seems to be wide-spread throughout Cactaceae. Opuntia bradtiana and O. santamaria seem to be more similar to each other than does O. kunzei to either of the two. Opuntia bradtiana and O. santamaria contain an abundance of two distinct kinds of druses (stellate cortical and rounded hypodermal); O. kunzei has fewer druses of a single type. The tubercles of O. bradtiana and O. santamaria join to form true ribs, while those of O. kunzei do not. Glochids are scarce on O. bradtiana and O. santamaria, more abundant on O. kunzei.

The bland tasting mucilage of O. bradtiana and O. santamaria is much more abundant than the lemon tasting mucilage of O. kunzei. Opuntia bradtiana and O. santamaria occupy highly restricted ranges; O. kunzei, while somewhat restricted, is not nearly so much so as the other two.

Growth habits of O. kunzei and O. santamaria are similar in that branching is basal in both, resulting in a clump formation, while in O. bradtiana the stems trail along the ground and branch at joints. Flowers of the three taxa are essentially yellow and borne near the top of the previous year's growth. Dead stems of O. kunzei and O. santamaria exhibit the woody structure expected in a cholla, but those of O. bradtiana seem to decompose completely.

ILLUSTRATIONS

1. Opuntia bradtiana.
2. O. kunzei.
3. O. santamaria type specimen.
4. O. kunzei--one day above ground. X 4.
5. O. bradtiana--15 weeks. X 1 1/5.
6. O. bradtiana--26 weeks. X 1 1/2.
7. O. kunzei--30 weeks. X 1 1/2.

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ILLUSTRATIONS

8, 9. Opuntia bradtiana (top) and O. kunzei (bottom)--seeds and embryos. X 2 1/2.

10. O. bradtiana--cut dried fruit. X 1 1/2.

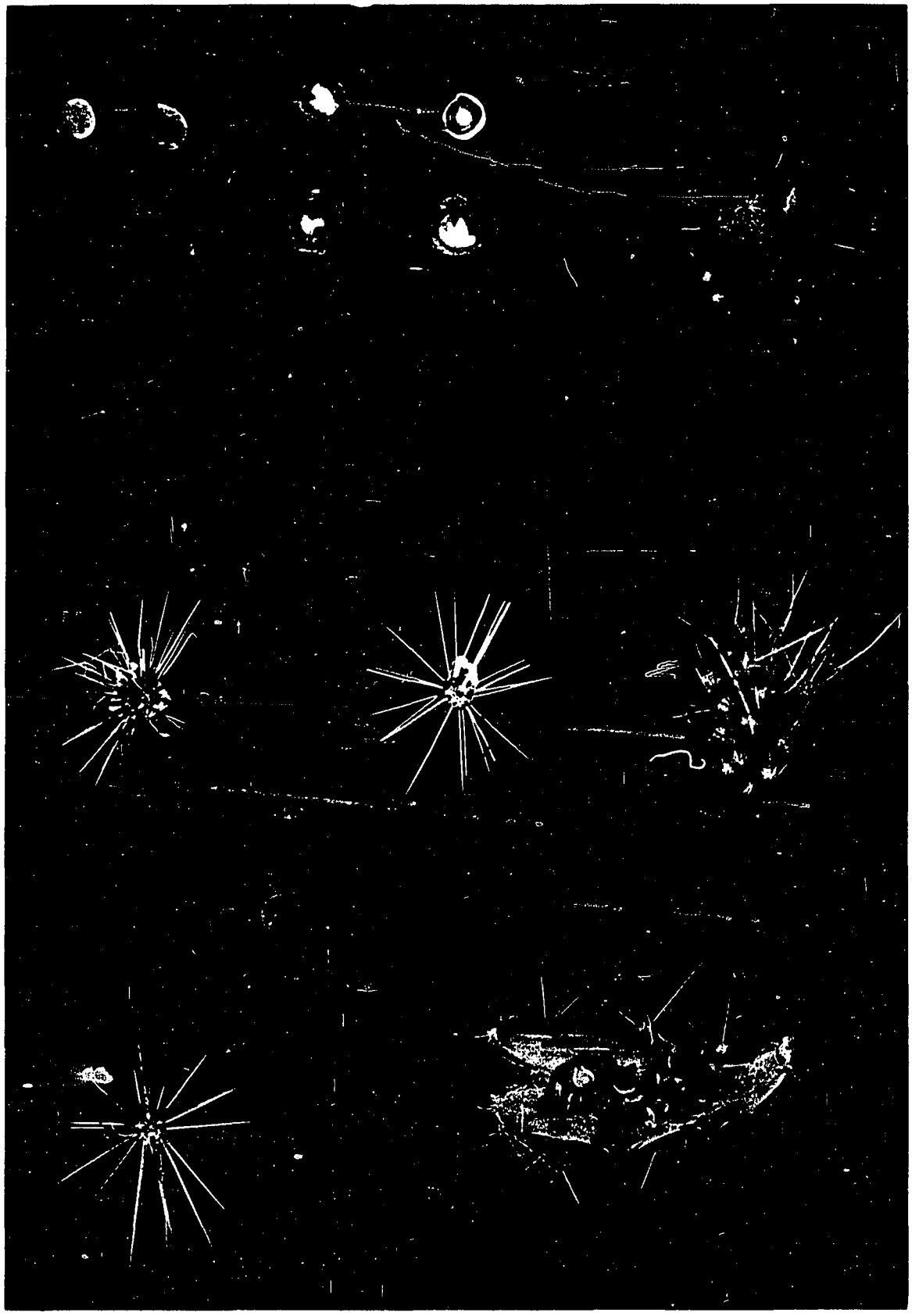
11. O. santamaria--areole with spines. X 1.

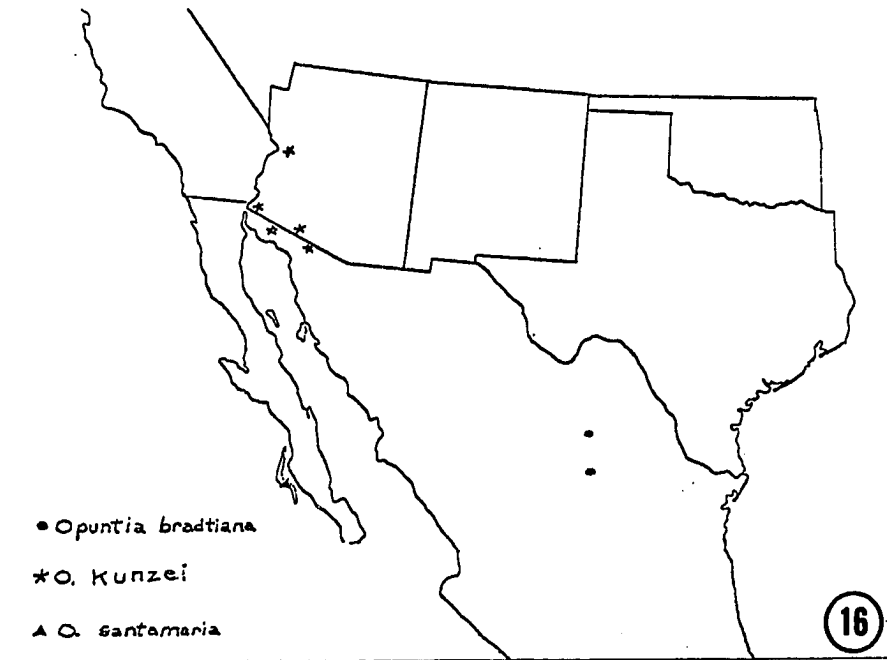
12. O. bradtiana--areole with spines. X 1.

13. O. bradtiana--spiny fruit. X 1 1/2.

14. O. kunzei--areole with spines. X 1.

15. O. kunzei--fresh cut fruit. X 1.

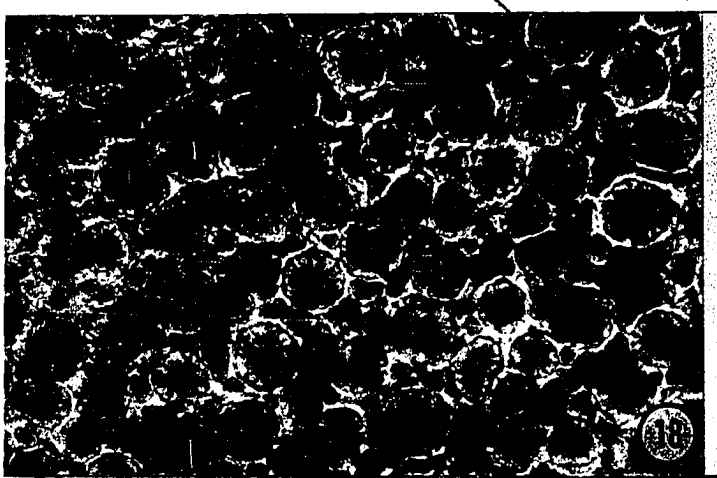




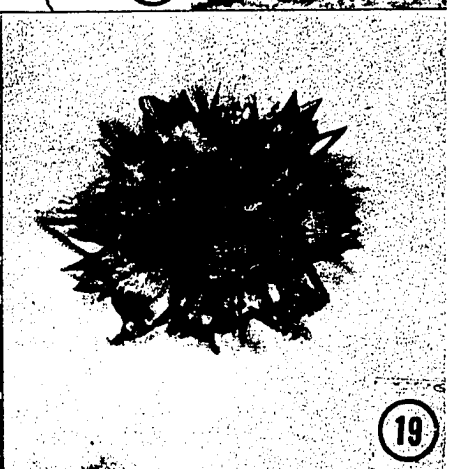
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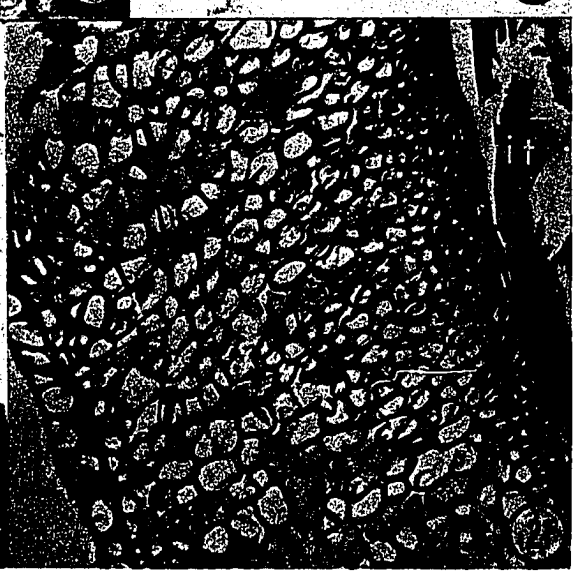


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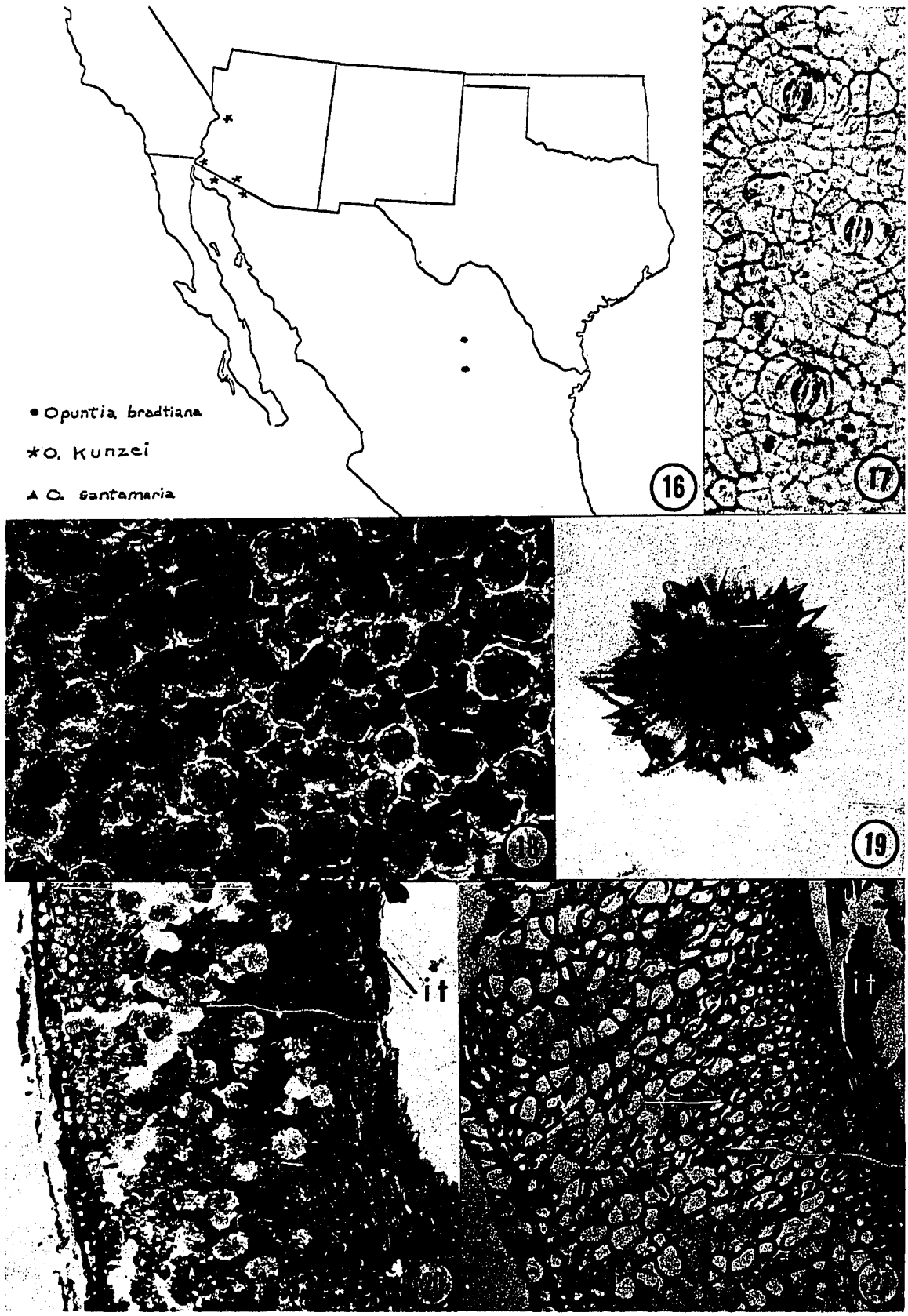


ILLUSTRATIONS

16. Distribution map.
17. Opuntia bradtiana--stomata in surface view. X 235.
18. O. bradtiana--hypodermal druses in surface view. X 150.
19. O. santamaria--cortical druse. X 118.
20. O. bradtiana--transverse section of seed coat showing abundant druses. X 150.
21. O. kunzei--transverse section of seed coat showing only a few scattered druses. X 150.

Key to abbreviation:

it inner testa

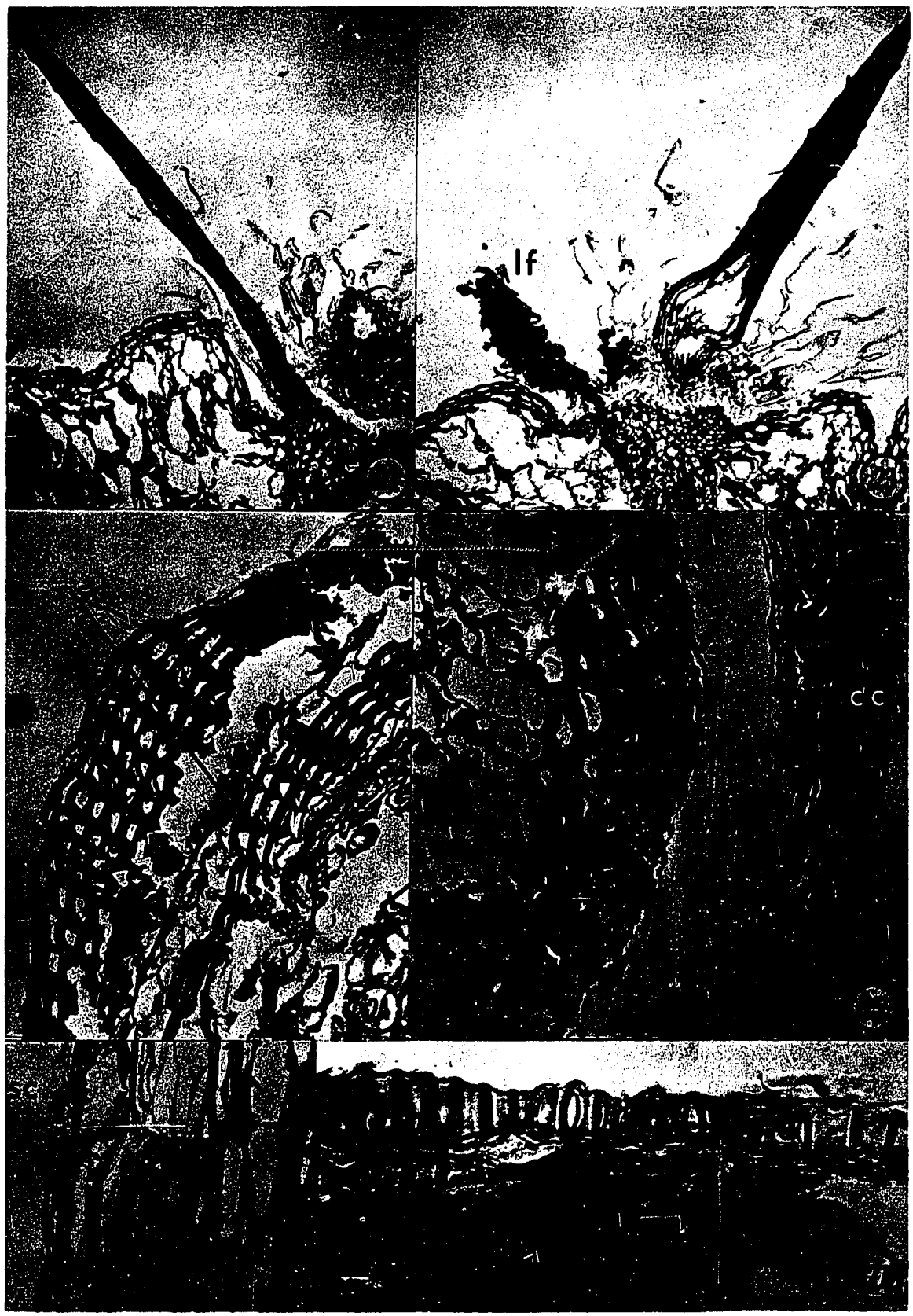

• Opuntia bradtiana
*O. Kunzei
▲ O. santamaria
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ILLUSTRATIONS

22. Opuntia kunzei glochid--longisection. X 90.
23. O. kunzei--longisection of leaf and spine. Note the cork layer under the spine. X 90.
24. O. kunzei--transection of mature root showing two distinct areas of stone cork separated by normal crushed cork cells. X 150.
25. O. santamaria--transection of stem showing layers of cork and stone cork peripheral to the druse-laden hypodermis. X 150.
26. O. bradtiana--longisection of mature root showing one layer of stone cork with regular cork on both sides. X 150.
27. O. santamaria--macerated material of barrel-type tracheids. X 240.

Key to abbreviations:

lf leaf
sc stone cork
cc crushed cork


If
CC

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