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Tracheoid Idioblasts in Chenopodiaceae: A Review and New Observations on *Salicornia virginica*

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Tracheoid idioblasts in the Chenopodiaceae have been reported in about 30 species of *Salicornia* and *Arthrocnemum*. These cells vary in size, shape, wall pattern, abundance, and spatial relation to vascular bundles. Most investigators have reported, or shown them to be unattached to vascular bundles. Tracheoid idioblasts in our examples of *Salicornia virginica* L., from two California coastal sites and a coastal site in Washington, were never connected to vascular bundles. The cortex of flowering and vegetative shoots contained helical-walled tracheids, whereas reticulate and pitted cells occurred only in flowering shoots. Elongate spicular cells with 2° walls were found in both types of shoot, just outside of the stele.

INDEX DESCRIPTORS: Chenopodiaceae, *Arthrocnemum*, *Salicornia*, tracheoid idioblasts.

Idioblasts have been defined simply as cells conspicuously different from surrounding cells. Among the many examples of idioblastic cells in plants (Foster, 1956), those that simulate tracheids are of special interest. These cells have been given several different names: lignified idioblasts (Warming, 1909), spiral cells (De Fraine, 1912), tracheoid idioblasts (Foster, 1956), tracheoidal idioblasts (Arnott, 1960), spirally thickened sclereids (Tölken, 1968), and tracheoidioblasts (Anderson, 1974). We prefer to call them tracheoid idioblasts. Such cells become elongate and develop a helical or reticulate secondary wall, but they are either only tenuously connected to a vascular bundle, or they are completely unattached. Warming (1909, p. 126) summarized the early reports of tracheoid idioblasts from several angiosperm taxa, and Foster (1956) and Dickison (1973) have shown additional examples.

In the dicot family Chenopodiaceae, tracheoid idioblasts and sclereids have frequently been described in *Salicornia* and *Arthrocnemum*, two genera consisting of succulent halophytes of inland and coastal salt water or alkaline areas. Such cells have not been described from other genera of this family. There has been considerable variation reported from these two genera concerning size, shape, wall patterns, and abundance of idioblasts, as well as their attachment to, or separation from, vascular bundles (Table 1). In this paper we have collated the results of previous studies and have added some original observations on these cells in *Salicornia virginica* L.

MATERIALS AND METHODS

Vegetative and flowering shoots were collected from three Pacific coast locations: (1) Aquatic Park, Berkeley, Alameda County, California (vegetative only), (2) Tomales Bay State Park, Marin County, California (vegetative and flowering) and (3) a salt marsh area along the coast, Pacific County, Washington (flowering only). Identifications were made in the field using the manual of Munz and Keck (1959). All collections were fixed in formalin-acetic acid-alcohol (Sass, 1958), dehydrated in an ethanol-xylene series, and embedded in 56° mp Fisher Tissue-prep. Tracheoid idioblasts were usually damaged when sections were cut at 8-12 μm; better results were obtained at 25 μm thickness. Sections were stained with Johansen's safranin (Johansen, 1940) and either chlorazol black E in 100 percent ethanol or fast green in 95 percent ethanol, and mounted in piccolyte. Additional stem and leaf material was cleared and stained by the method of Shobe and Lersten (1967). Photomicrographs were taken on a Leitz ortholux microscope fitted with an orthomat camera.

OBSERVATIONS

Salicornia species have small, almost scale-like, succulent leaves. Figure 1 shows a cleared leaf of this type from *S. virginica*. The numerous large tracheoid idioblasts are not attached to vascular bundles, although at this plane of focus a few at the upper end appear attached. Enlarged views of similar areas from other leaves (Figures 2, 4) show clearly that these cells are not connected (arrows indicate ends of representative vascular bundles).

Leaves seen in longitudinal section show the relationship of tracheoid idioblasts to adjacent cells in more detail (Figures 3, 5). They commonly abut on the epidermis, but we did not see any that occupied the place of a substomatal chamber just beneath a stomatal apparatus. The arrow in Figure 5 indicates a true substomatal chamber.

Abundant helical tracheoid idioblasts occurred in the leaf and the stem cortex of vegetative and flowering shoots of California examples, but they were sparse in flowering shoots of Washington examples. Figure 6 shows an enlarged view of one cell from a leaf. The helices, which appear dark here, were stained intensely red with safranin in the cleared preparation, indicating lignification. At this higher magnification, each band seems to be composed of smaller fibrillar units.

In flowering shoots only, we found abundant sclerified cells with either a reticulate or scalariform wall pattern (Fig-

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TABLE 1. SUMMARY OF INVESTIGATORS REPORTING IDIOBLASTS IN *Salicornia* AND *Arthrocnemum*

Taxon	*Investigator*	*[1]Spicular Cell*	*Pitted Idioblastic Tracheid*	*Helical Idioblastic Tracheid*	*[2]Contact with Vascular Tissue*
Salicornia					
disarticulata	De Fraine (1912)	No	[3]Yes	No	?
fruticosa	Duval-Jouve (1868)	?	?	Yes	No
fruticosa	Hultberg (1881-2)	Yes	No	Yes	No
fruticosa	Mangin (1882)	?	?	Yes	?
fruticosa	Chermezon (1910)	Yes	No	Yes	Mostly No
fruticosa	De Fraine (1912)	Yes	?	Yes	No
fruticosa	Mao (1933)	Yes	No	Yes	No
glauca	De Fraine (1912)	No	Yes	No	?
gracillima	De Fraine (1912)	No	[3]Yes	No	?
herbacea	Duval-Jouve (1868)	No	No	Yes	?
herbacea	Hultberg (1881-2)	Yes	No	Yes	No
herbacea	Dangeard (1888)	?	?	Yes	?
herbacea	Chermezon (1910)	Yes	No	Yes	Mostly No
herbacea	De Fraine (1912)	No	No	Yes	No
herbacea	Waisel (1972)	?	?	Yes	?
lignosa	De Fraine (1912)	?	[3]Yes	No	?
macrostachya	Duval-Jouve (1868)	?	[3]Yes	No	[4]No
macrostachya	Mangin (1888)	?	Yes	No	?
meyeriana	Moss (1954)	?	No	Yes	?
perennis	De Fraine (1912)	No	[3]Yes	No	?
perrieri	Moss (1954)	?	No	Yes	?
prostrata	De Fraine (1912)	No	No	Yes	No
pusilla	De Fraine (1912)	No	No	Yes	No
peruviana	Dangeard (1888)	?	?	Yes	?
ramosissima	De Fraine (1912)	No	No	Mostly No	No
virginica	Dangeard (1888)	?	?	Yes	?
virginica	Anderson (1974)	Yes	No	Yes	Mostly No
virginica	Lersten and Bender (1975)	Yes	[3]Yes	Yes	No
Arthrocnemum					
ambiguum	Dangeard (1888)	?	?	Yes	?
ambiguum	Baumgärtel (1917)	?	Yes	No	[4]Yes
arbuscula	Baumgärtel (1917)	?	Yes	No	[4]Yes
capensis	Tölken (1968)	?	Yes	No	?
coralloides	Baumgärtel (1917)	?	Yes	No	[4]Yes
decumbens	Tölken (1968)	?	Yes	No	?
fruticosum	Dangeard (1888)	?	?	Yes	?
glaucum	Baumgärtel (1917)	?	Yes	No	[4]Yes
Subg. *gymanthemum*					
(12 species)	Moss (1954)	Yes	Yes	Yes	?
indicum	Baumgärtel (1917)	?	Yes	No	[4]Yes
littoreum	Tölken (1968)	?	No	Yes	?
macrostachyum	Chermezon (1910)	?	Yes	No	?
macrostachyum	Baumgärtel (1917)	?	Yes	No	[4]Yes
mossianum	Tölken (1968)	Yes	Yes	No	?
perenne	Tölken (1968)	No	No	Yes	?
pillansii	Tölken (1968)	No	No	Yes	?
terminale	Tölken (1968)	No	Yes	No	?
xerophilum	Tölken (1968)	?	No	Yes	?

[1]Slender, elongate, non-pitted cells.

[2]Refers to helical idioblastic tracheids only.

[3]Flowering shoots only.

[4]Refers to pitted tracheids.

ure 7), or simple pits with crossed elongated apertures (Figure 8). These cells were also typically shorter and broader than the idioblasts with helical walls.

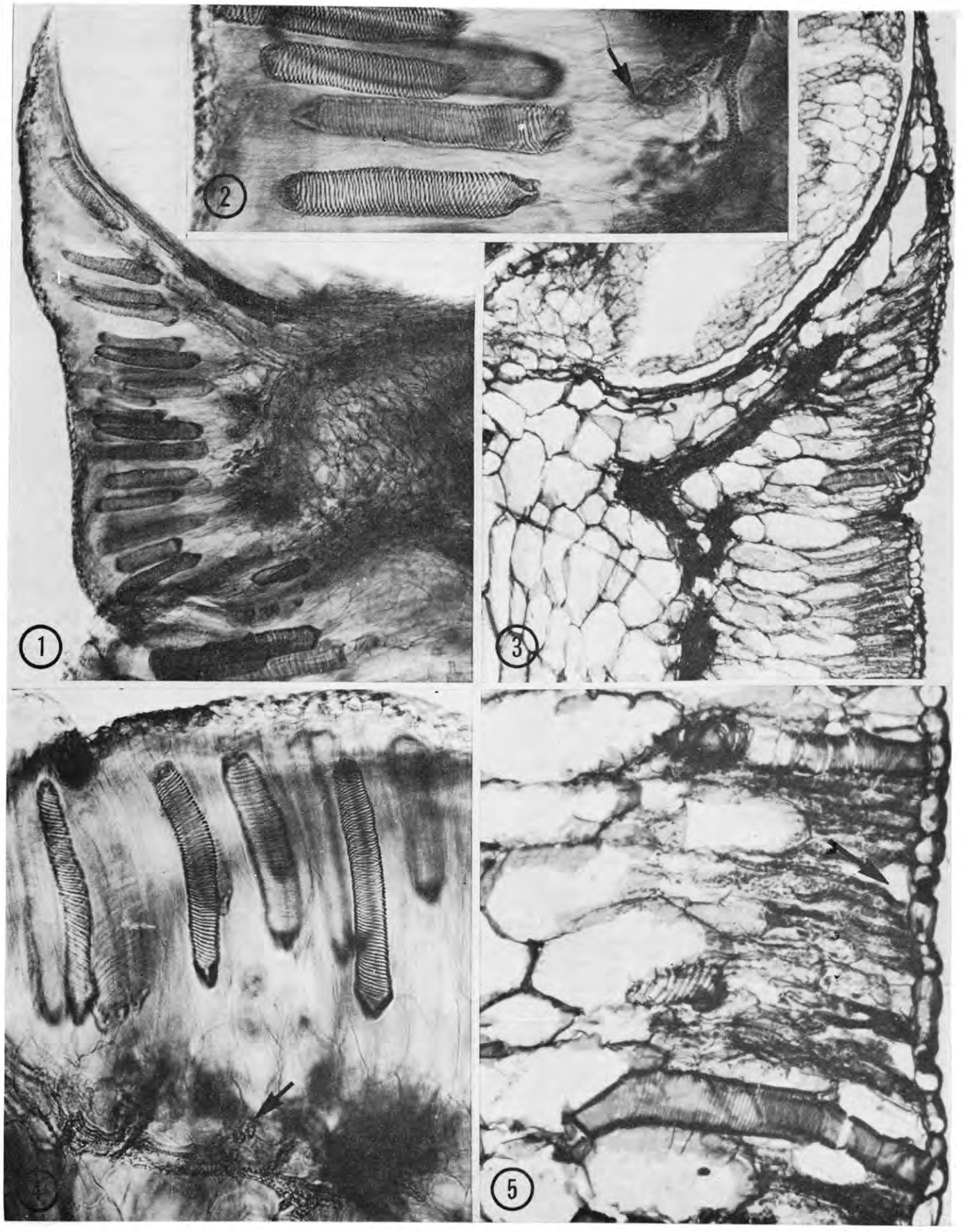
Figure 9 illustrates a portion of a stem cross-section. At right is the stele, with six vascular bundles and a hollow pith. Numerous small vascular bundles (two indicated by the two arrows at left) occur in the broad cortex. These bundles are part of a complex, anastomosing vascular network, which can be seen to some extent in longitudinal view in Figure 10. Fahn and Arzee (1959) have illustrated this network better in cleared whole stem segments of *S. fruticosa*. The two right arrows in Figure 9 indicate spicular cells, which are sclerenchyma fibers located just outside the stele. These cells can be seen in longitudinal view in Figure 10, which is from a thick slab of stem that has been cleared. The broad, dark, vertical stripe in the center is the stele, and the arrows indicate two of the four spicular cells at this level. Such cells are isolated laterally and vertically from other spicular cells.

DISCUSSION

We have seen eight previous references in which there are statements and/or illustrations bearing on the question of attachment of tracheoid idioblasts to vascular bundles. Duval-Jouve (1868) showed only unattached tracheoid idioblasts in his drawings. Hultberg (1881-82) referred to Duval-Jouve, and stated that in his own work on *Salicornia* he never saw tracheoid idioblasts connected to a vascular bundle. De Fraine (1912), on the basis of a study of 10 species, stated flatly that "Spiral cells are never directly connected with the vascular bundle system." Her figure, showing six unattached cells in a stem cross-section, supports this conclusion. Mao (1933) included several drawings of stem cross-sections of *Salicornia fruticosa*, each with numerous conspicuous tracheoid idioblasts. None of them were attached to vascular bundles. To these previously published observations we must add that we never saw a tracheoid idioblast attached to a vascular bundle in our examples of *S. virginica*.

There is, however, evidence that such cells sometimes do contact vascular bundles. Baumgärtel (1917) showed connections in a stem cross-section of *Arthrocnemum* sp. (A second figure, however, shows numerous idioblasts, none connected to vascular bundles.) Chermezon (1910) included a drawing

Figures 1-5. Idioblastic tracheids in *Salicornia virginica*. 1. Cleared scale-like leaf showing numerous idioblastic tracheids separated from vascular bundles. X77. 2. Enlarged portion of a cleared leaf to show idioblastic tracheids with spiral walls. Arrow indicates end of a vascular bundle. X210. 3. Longitudinal paraffin section of a leaf. Two idioblastic tracheids are shown. X92. 4. Enlarged portion of cleared leaf showing several idioblastic tracheids isolated from vascular bundles (arrow). X176. 5. Paraffin section of stem. Enlarged portion with two idioblastic tracheids seen in median longitudinal view. Arrow indicates a substomatal chamber. X210.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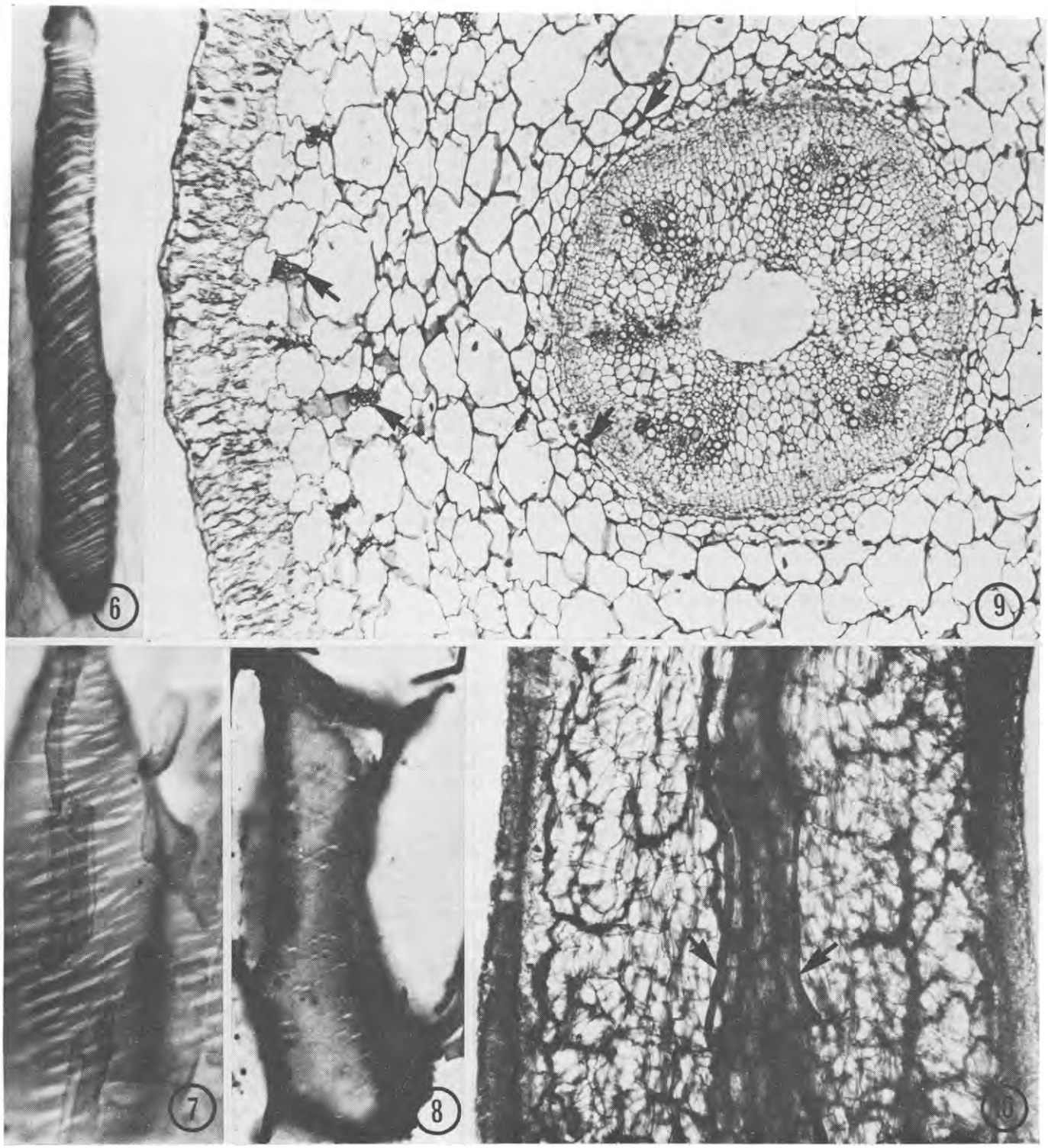

Figures 6-10. 6. Idioblastic tracheid enlarged from a cleared leaf. Spiral bands are subdivided into smaller fibrillar units. X462. 7. Broad tracheid with reticulate wall from bract of flowering shoot. X504. 8. Tracheid with simple pits from bract of flowering shoot. Pits have elongate apertures. X567. 9. Cross-section of vegetative stem. Stele at right has six vascular bundles and hollow pith. Right pair of arrows indicates two spicular cells just outside the stele. Several smaller bundles are scattered through the broad cortex (two indicated by left arrows). X92. 10. Longitudinal view of cleared stem segment. Arrows indicate two of the four spicular cells visible just outside the stele. X70.