STUDIES ON FOLIAR SCLEREIDS IN DICOTYLEDONS.

IV. STRUCTURE AND DEVELOPMENT OF SCLEREIDS IN THE LEAF OF *TERNSTROEMIA JAPONICA* L.

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Recent studies of Foster (1947), and Rao (1951*a*) have emphasised the importance of studying the ontogeny of sclereids in order to know whether terminal sclereids originate from procambial cells in the developing veinlets or from adjacent cells of the ground meristem. The present paper describes some observations on the ontogeny of the foliar sclereids of *Ternstroemia japonica* L.

Leaf material of *Ternstroemia japonica* was collected from different places near Coonoor. Vegetative buds as well as young and old laminae were fixed in formalin-acetic-alcohol. In addition dry specimens were secured from a number of herbaria. The fixed material was dehydrated and embedded in paraffin according to the customary methods. Sections were stained by Foster's method (1934). The leaves of herbarium specimens were cleared and macerated as outlined by Subramanyam and Rao (1949).

Distribution of Sclereids in the Mature Lamina.—In agreement with the observations of Solereder (1908), the present study has revealed the existence of 'branched sclerenchymatous cells' in the mesophyll of *Ternstroemia japonica.* These are remarkable on account of the variation in their form and structure. Besides the polymorphic form of the adaxial sclereids, cleared portions of the laminae showed an abundance of apparently terminal, sub-terminal and diffuse sclereids. A noteworthy feature is the regular pattern of their distribution. Three categories were found: (i) Adaxial sclereids showing an intimate relation with the vascular bundles; (ii) abaxial sclereids in the lacunate spongy tissue; and (iii) sclereids in the parenchymatous part of the mid-rib.

The adaxial sclereids exhibit various trends resulting in symmetrical or sometimes asymmetrical forms. They vary greatly both in size and form (Figs. 15–22), from unbranched forms to stellately branched ones. The latter show long arms, sometimes forked and occupying considerable portion of the palisade and spongy regions. Whatever their form, some of the sclereids exhibit a close association with the foliar veins (Figs. 4–9).

Unlike the adaxial sclereids, the sclereids in the abaxial region of the lamina are situated in the midst of well-developed air-spaces with their arms lying free in the lacuna. Sclereids of this type have been reported in a large number of angiosperms and have been described quite recently in the leaf of *Trochodendron aralioides* (Foster, 1945*a*). A transection of the mature leaf shows the presence of idioblastic abaxial sclereids at various levels in the spongy parenchyma. They do not exhibit as much variation as the adaxial sclereids. All of these have a more or less stellate form with radiating arms of limited growth (Figs. 23–28). These diffuse sclereids do not show any connection with the vascular bundles.

In the parenchyma of the mid-rib region, the sclereids are more densely aggregated. They are abundant on the abaxial side of the mid-rib region. Their arms are short or drawn out and they exhibit an irregular form. Sometimes their arms come in close proximity to the foliar bundle.

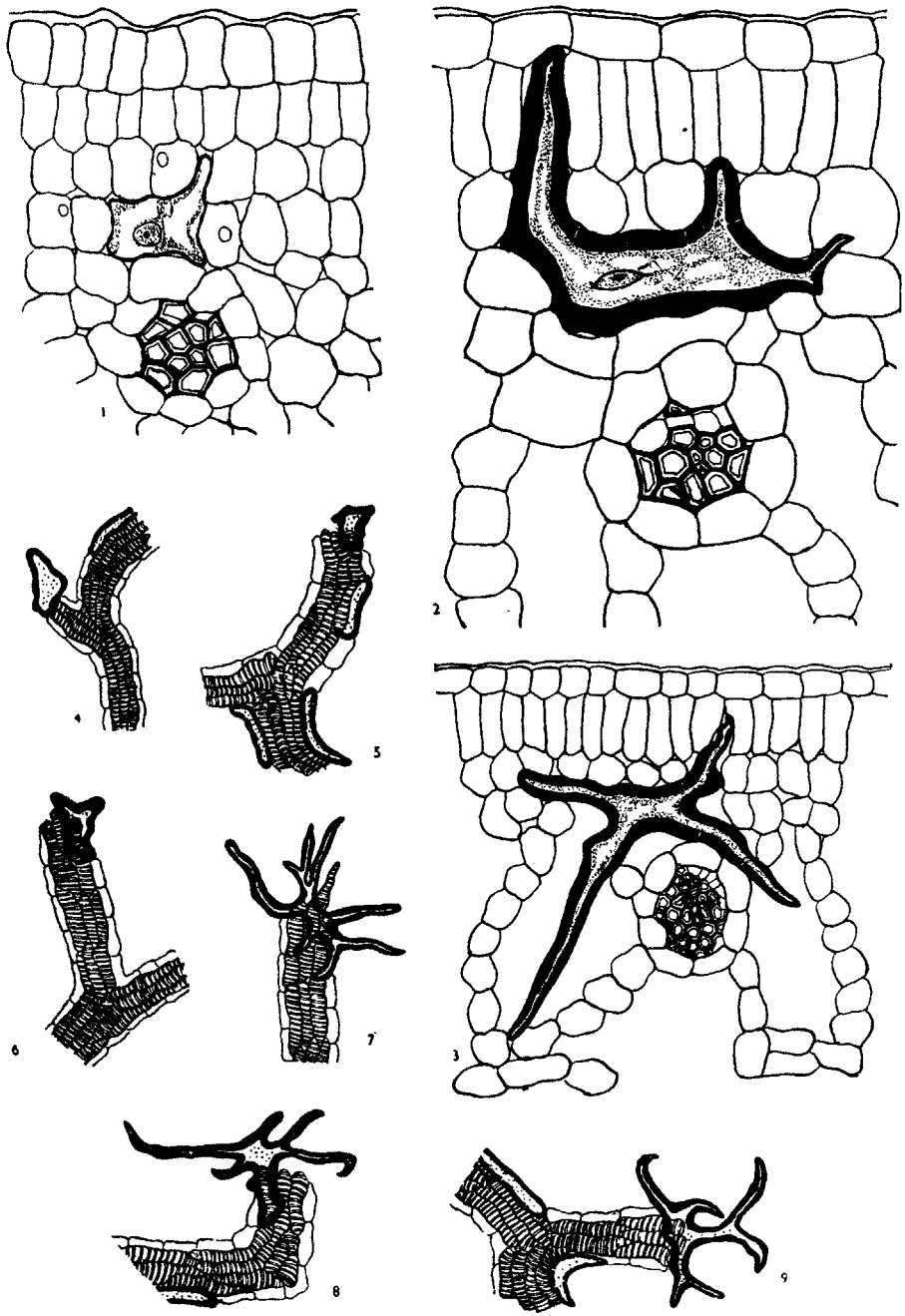

FIG. 1. Transection through submarginal portion of young lamina with very young sclereid initial showing adaxial and abaxial processes. ×450.

,, 2. More advanced stage. Note the conspicuous nucleus and the proximity of the sclereid to the vascular bundle. ×450.

,, 3. Transection of mature lamina showing pseudoterminal sclereid. Note the sharp abaxial processes lying in proximity to the vein-bundle. ×225.

FIGS. 4–9. Sclereids from cleared portions of mature lamina showing their proximity to veinlets. ×125.

Structurally, the adaxial sclereids show a vigorous growth and have a broad lumen in the centre which narrows towards the arms and finally becomes much reduced. The cell wall is homogeneous and free from spicules. The abaxial sclereids are similar to the adaxial, but they are less vigorous in growth and their arms are shorter. The sclereids of the mid-rib region present a strong resemblance to adaxial ones, but they are 'cell forms' of limited variation. The processes lie in small air-spaces and exhibit the same structural features.

Sclereids of the Mid-rib Region.—As in a previous study (Rao, 1951*a*) developmental stages of the sclereids were traced from sections of young leaves selected from unfolding leaf-buds. The unexpanded young lamina is composed of closely packed cells and neither sclereid initials nor air-spaces are distinguishable. Transections of the expanding laminae exhibit a slight tissue differentiation in the abaxial part and in the ground parenchyma of the mid-rib region. The sclereid initials appear first on the adaxial and abaxial sides of the mid-rib. They are either isolated or appear in groups of 3 to 5. They are polyhedral in shape with a large central nucleus and radiating strands of cytoplasm (Figs. 10–11). Small air-spaces now appear, especially in the abaxial region of the mid-rib. Thus the sclereids initials and air-spaces originate at about the same time. In the next phase of development the walls of the sclereid initials become slightly thicker and throw out plug-like processes in all directions. The mode of growth is intercellular. As noted by Sterling (1947), Foster (1944) and Rao (1951*a*), the sclereid arms show a strong tendency to make their way towards an air-space. The entry of the arms into the air-space seems, however, to stop their further growth. The cell wall now thickens considerably and the lumen of cell is almost entirely obliterated in the arms.

The Abaxial Sclereids.—With the development of sclereids in the mid-rib vertical air-spaces appear in the spongy tissue of the sub-marginal part of the leaf. It is during this phase of expansion of the spongy region that the abaxial sclereid initials become recognisable (Fig. 12). As in *Trochodendron aralioides* (Foster, 1945*b*) the sclereid initials originate at various levels of the septa which separate the air-spaces. At this stage the septal layer is composed of a vertical row of young spongy cells. As reported by Foster (1945*b*), Bloch (1946), Sterling (1947) and Rao (1951*a*) the idioblastic sclereid initials show a large nucleus with radiating strands of cytoplasm. The sclereid initial cells are mostly sub-spherical with thin cellulose wall. The enlargement of the sclereid initial coincides with the vertical and transverse expansion of the air-space. The first stage of the growth of the sclereid initial cell is the appearance of blunt processes, especially at the corners (Figs. 12–13). These processes make their way into the air-space. With the development of the processes the cytoplasm is thick around the nucleus but shows parietal disposition in the developing arms. The sclereid processes have a limited growth and occupy a small portion of the air-space. At maturity they possess a broad central lumen which narrows towards the arms (Fig. 14). As noted by Rao (1951*a*) the nucleus can be observed up to a late stage in the lignification of the sclereid (Fig. 14).

The Adaxial Sclereids.—The adaxial sclereid initials are initiated in the third layer beneath the upper epidermis (Fig. 1), at a somewhat later stage than the abaxial sclereids. At the time of their initiation the lamina shows a good degree of tissue maturation, with a well-organised cuticle and palisade region. The vascular bundles are also fairly well organised. At this phase of leaf expansion, the mesophyll cells beneath the palisade layer are closely packed without any air-spaces. On the contrary, the abaxial region of the lamina possesses clear vertical clefts and well-developed sclereid initials.

In the light of the occurrence of 'terminal sclereids' in *Mouriria huberi* (Foster, 1947), *Memecylon heyneanum* (Rao, 1951*b*), *M. Lushingtonii* and *Niehburia apetala* (Rao, in press) microtome sections of *Ternstroemia* were examined to see whether

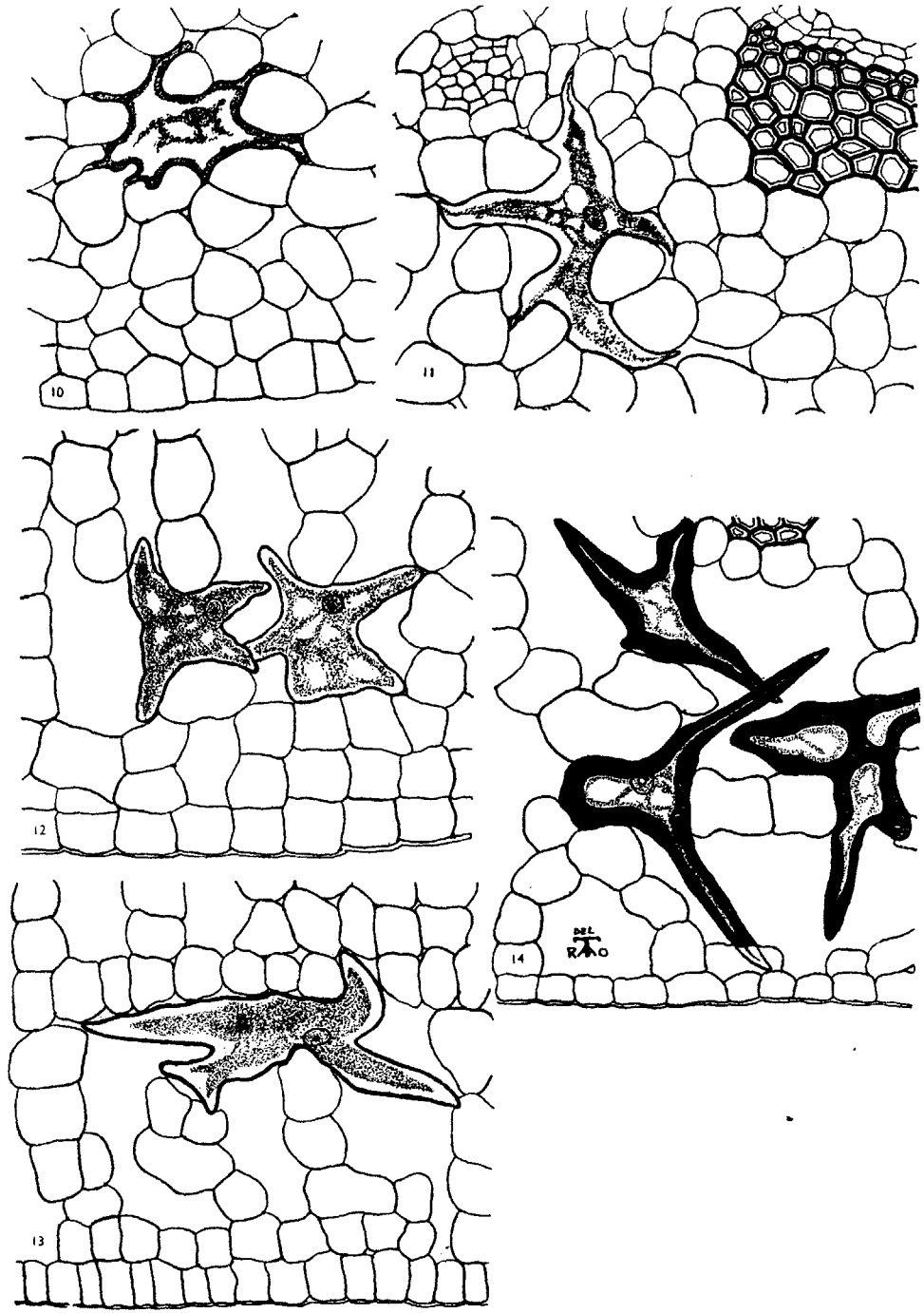

FIG. 10. Sclereid initial in the midrib portion. ×450.

,, 11. Sclereid initial showing prominent processes. Note approximation of adaxial process to vascular bundle. ×450.

FIGS. 12-13. Transections of young laminae showing early stages in ontogeny of abaxial sclereids. Note the prominent processes protruding into the developing and expanding air-clefts. ×450.

FIG. 14. More advanced stage of abaxial sclereid showing a prominent nucleus and cell wall with pit-canals. ×450.

the sclereid initials are differentiated at the tips of the procambial strands. As in *Diospyros* it was confirmed that the adaxial sclereid initials originate just above the vascular bundle and not from the same procambial strand.

The adaxial sclereid initial, which is more or less rectangular in transection, shows plug-like processes at the corners (Fig. 1). These processes elongate in all possible directions; sometimes entering the air-spaces of the spongy tissue. In all cases the growth is intercellular. By virtue of their close juxtaposition with the vascular bundle, they exhibit a prevailingly terminal or sub-terminal position (Figs. 2–3). The sclereid initial shows a prominent nucleus with radiating strands of cytoplasm. The mature adaxial sclereids possess a homogeneous cell-wall and pit canals. The nucleus can be recognised for a long time. In later stages, it becomes pear-shaped, a feature also seen in the growing sclereids of *Olea* (Rao and Kulkarni, 1952), *Memecylon* (Rao, 1951*b*), *Linociera intermedia* and *Niehburia apetala* (Rao, in press).

Conclusion.

The present study shows that sclereid initials in different regions of the leaf do not differentiate simultaneously. The first to appear are the sclereids of the mid-rib region; these are followed by those of the spongy region; and finally, the adaxial part. As noted in *Trochodendron* (Foster, 1945*b*), the origin of the sclereid initials is not limited to the early phases of tissue maturation.

Regarding the relation between air-spaces and sclereid initials, the sclereid initials of the spongy region form processes which project freely into the adjoining air-space. The arms of the adaxial sclereid initials, on the other hand, grow vigorously in an intercellular fashion, although, sometimes they grow further and penetrate into the air-spaces of the spongy tissue (Fig. 3).

The arms of the sclereids in the mid-rib region may also work their way towards the adjacent air-spaces. The air-space seems to arrest the further growth of the arms, since in the absence of an air-space the arms grow more vigorously.

As in *Diospyros discolar* (Rao, 1951*a*) and *Linociera intermedia* (Rao, in press) the apparent terminal position of adaxial sclereids is due to a close juxtaposition of the sclereids to the vein-ends. These pseudo-terminal sclereids exhibit much variation and pronounced growth. The significance of this is so far unknown.

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Summary.

The sclereids in the cleared leaf of *Ternstroemia japonica* show apparent terminal and diffuse distribution with reference to veinlets. The sclereid ontogeny has revealed that sclereid initials appear in three stages of tissue expansion. They are in fact transformed spongy cells and the apparent terminal position of some of the adaxial sclereids is due to juxtaposed and vigorous development near the veinlet. The study emphasises the need for ontogenetic study to prove the real relationship between procambial layer and the sclereid initials.

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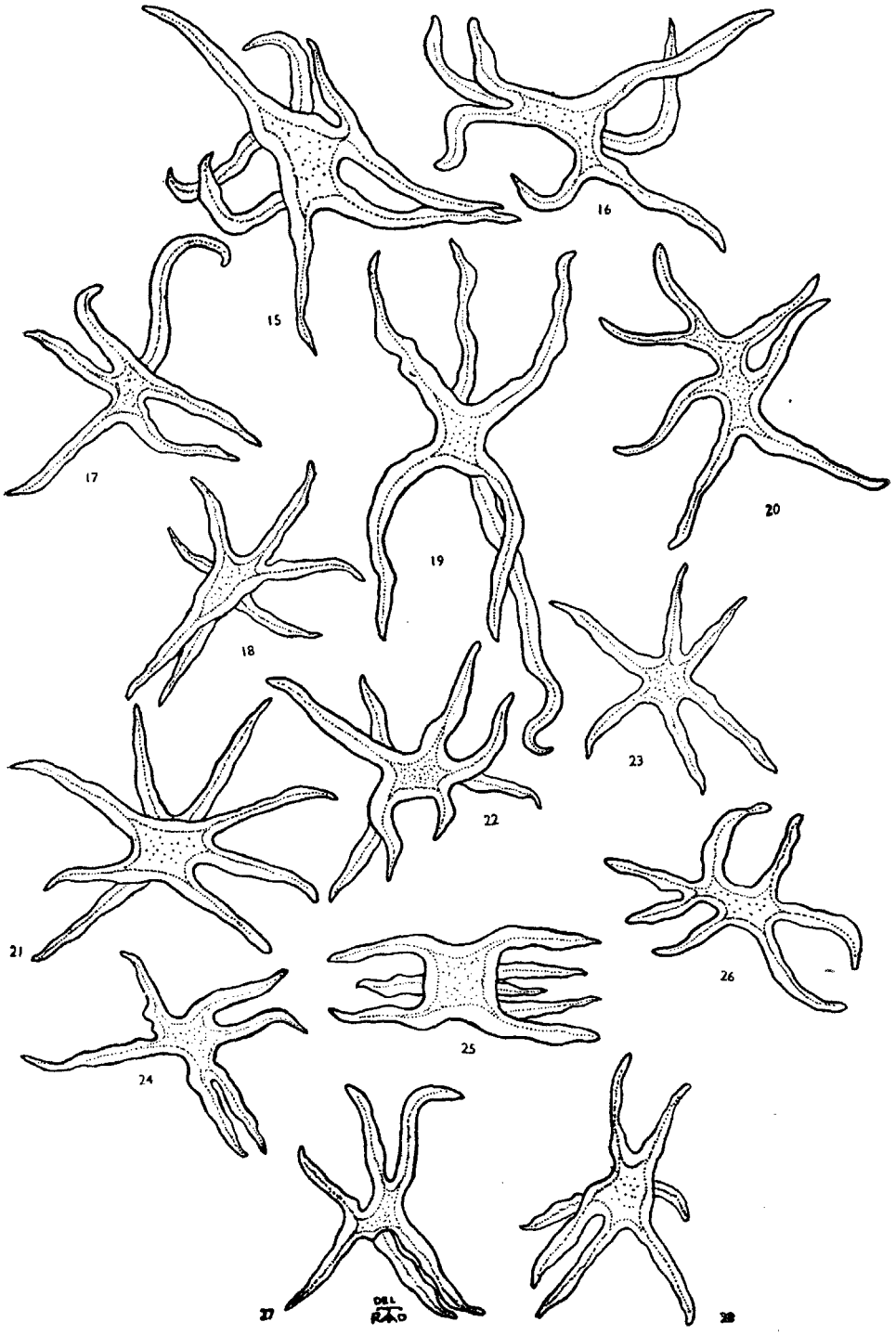

FIGS. 15–22. Polymorphic adaxial sclereids. ×225.
,, 23–28. Polymorphic abaxial sclereids. ×225.

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