

FIGURE 1. Map showing the geographical distribution of *Nothotsuga* in China (courtesy of Fu & Jin, 1992).

tional outlines are usually rounded and sometimes angular. Bordered pits are 18 (16–19)  $\mu\text{m}$  in diameter, almost exclusively uniseriate or occasionally irregular in the wider earlywood tracheids. Pit membranes have a centrally thickened torus with a more or less smooth edge. The pit membranes have thickened bars radiating from the torus. Pit apertures are rounded in earlywood, lenticular in latewood with axial or radial orientation. Tracheids have a warty layer lining the inner surface of the secondary wall and in the pit chambers. Trabeculae are absent.

Axial parenchyma are scarce and diffuse, arranged on the margin of the growth rings with a tendency to form a discontinuous line. Cross-sectional outlines are angular, nearly isodiametric in earlywood, radially flattened in latewood. The end walls of the cells are pitted and mostly nodular. Individual axial parenchyma cells are 162 (112–263)  $\mu\text{m}$  in length, 29 (22–34)  $\mu\text{m}$  in tangential diameter. Cells are commonly filled with dark-colored contents.

Normal and traumatic vertical resin canals are present. Normal resin canals are elongated and usually occur singly or in a pair in the boundary of latewood (Fig. 2). The number of normal resin canals is extraordinarily low in the juvenile region, but increases with age in the mature region. The size of normal resin canals also changes significantly with age, the oldest canals being the largest. The epithelial cells of normal resin canals are thick-walled, with six cells (5–9) per canal. Traumatic resin canals are characteristically cystlike and form short tangential series or are solitary in the boundary between earlywood and latewood

(Figs. 3, 4). Their epithelial cells are also thick-walled, but they are distinguishable on account of their large size and large number of epithelial cells. Transverse resin canals are not observed.

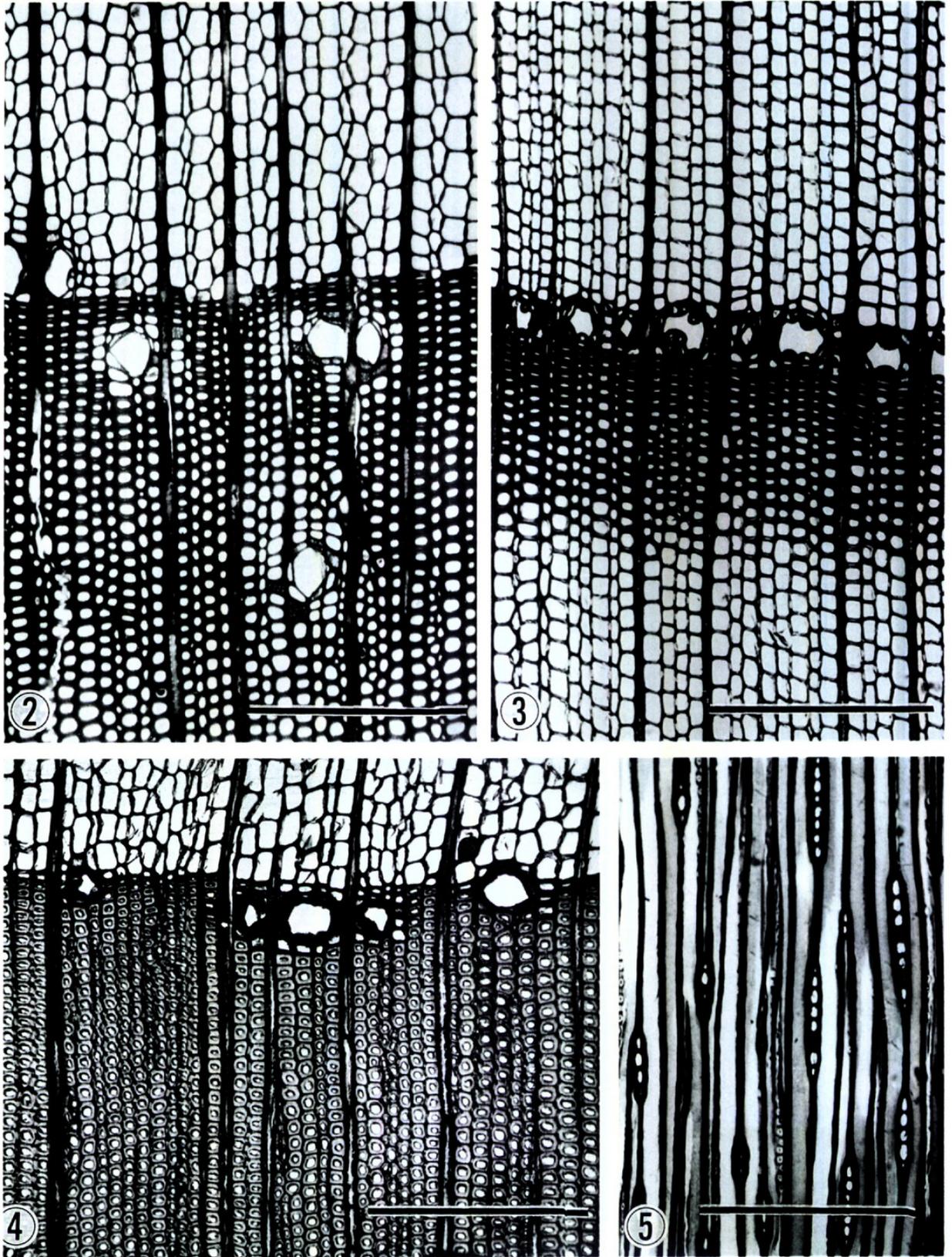
Rays are uniseriate, rarely biseriate, 23 (2–35) cells high, 31 rays per  $\text{mm}^2$  in tangential section (Fig. 5). Rays are composed of ray parenchyma and poorly developed ray tracheids (Fig. 6); the latter only occur in the margin rows of the ray. The horizontal walls of ray parenchyma are thick and strongly pitted. The end walls of ray parenchyma cells are thin without indentures or occasionally with small nodules (Fig. 7). Cross-field pits are taxodioid and cupressoid, with two or four pits per cross field (Fig. 8). Square or rectangular crystals are visible in lumina of the ray parenchyma.

#### BARK DESCRIPTION

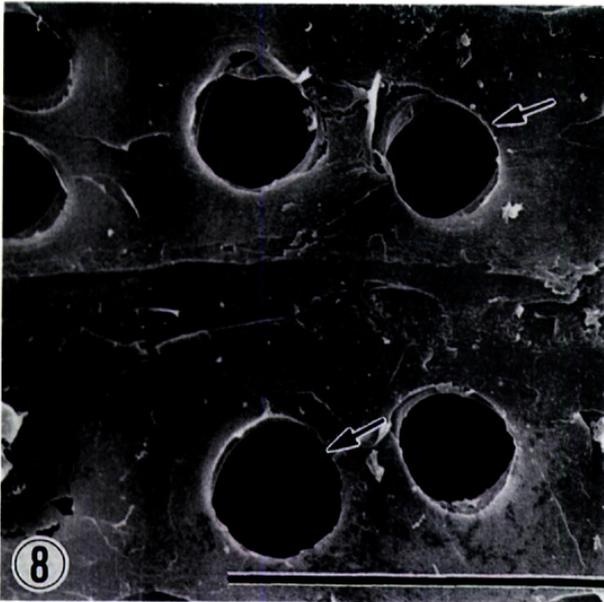
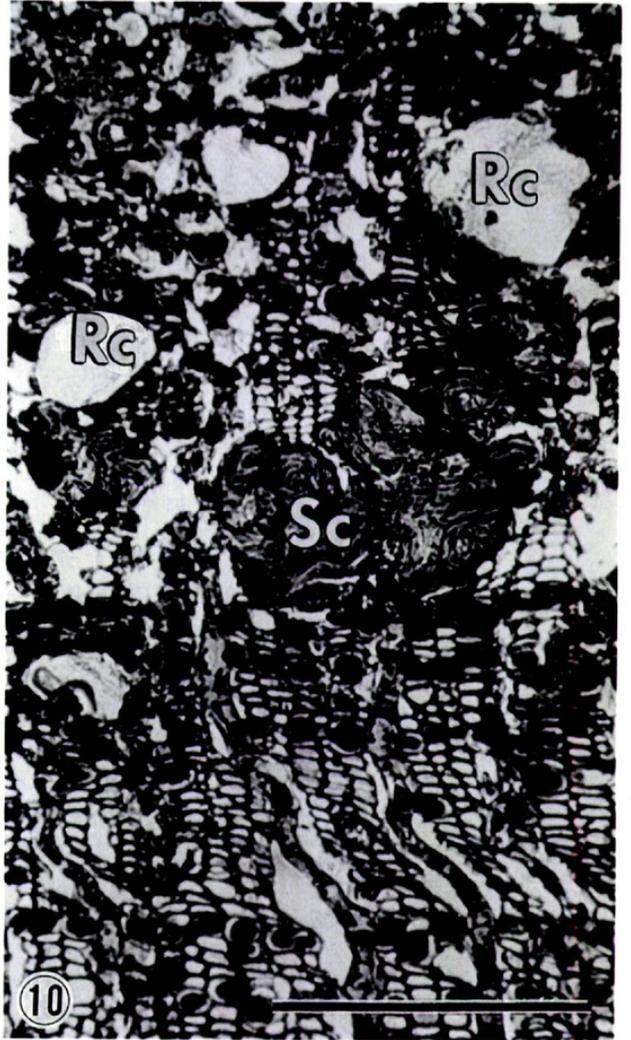
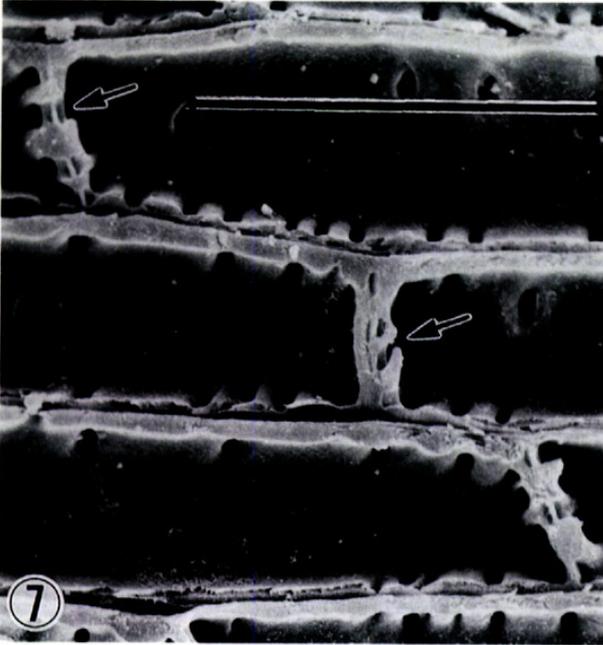
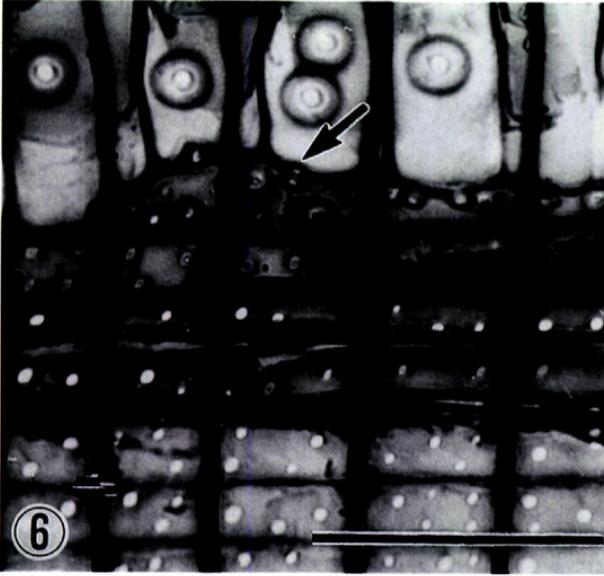
The phloem consists of sieve cells, axial parenchyma, ray parenchyma, resin cavities, and sclereids. Sieve cells and axial parenchyma appear randomly arranged, while sclereids occur in irregular radial rows.

Sieve cells appear rectangular in the transverse section of the functional zone; however, they are crushed by sclereids and rays in the nonfunctional zone. Sieve areas are 8 (3–12)  $\mu\text{m}$  diam., mostly in the radial walls in single files.

Axial parenchyma cells are rectangular to isodiametric in transverse section and rectangular in longitudinal section. They are mostly filled with tannin. Square or rectangular crystals are located in some parenchyma cells but are sometimes absent in the non-functional phloem.



FIGURES 2-4. Transverse sections of wood.—2. Normal resin canals in the mature portion of wood.—3. Traumatic resin canals forming a tangential series in the juvenile portion of wood.—4. Solitary and tangential arrangement of traumatic resin canals in the mature portion of wood. FIGURE 5. Tangential section of mature wood. Scale bars in 2, 3, 4 and 5 = 20  $\mu$ m.



Phloem rays are usually uniseriate, although not infrequently some biseriate rays occur. In height they are 22 (2–28) cells or approximately 700  $\mu\text{m}$ . There are about 23 (12–26) rays per  $\text{mm}^2$  tangentially as measured on the cross section; short rows of erect marginal cells are occasionally found in a few of the phloem rays.

Resin cavities are seen in the outer part of inner bark (Fig. 9). They occur singly or in groups of two or three and are abundant in old bark. Some of the larger cavities are found to 120–150  $\mu\text{m}$  diam. and 150–180  $\mu\text{m}$  in axial extent, whereas some of the cavities lack definite borders surrounding them. In prepared slides, they are often filled with a whitish slimy substance.

Sclereids are roundish or polygonal with very narrow lumina in cross section and irregular in longitudinal section. They are invariably filled with brown tannins or resin substances. The walls are lignified, birefringent, and seem to be made up of polylamellate layers. In young twigs sclereids are distributed singly or in masses of 2–4 cells, while they are groups of 5–8 aggregated in “cigar-shaped” or fusiform profiles in old stems.

The periderm consists of 2–3 layers of phelloderm, one layer of phellogen, and alternate layers of thin-walled phellem cells and thick-walled cells, which are probably originated from phelloderm (Fig. 10). Both types of phellem cells show similar shape in outline. They are 14 (12–18)  $\mu\text{m}$  and 22 (20–25)  $\mu\text{m}$  in radial and tangential dimensions, respectively. The thick-walled cells are characterized by narrow lumina and distinct simple pits, while the thin-walled cells are rather uniform in thickness and with large lumina. Both types of cells contain a resinous substance. Phelloderm cells are arranged in definite radial rows, rectangular to isodiametric in transverse section and radial section. They are sometimes merged into parenchyma cells of secondary phloem tissues.

#### DISCUSSION

As noticed by Page (1988), this genus occupies a position linking with several other genera of Pinaceae. For example, the shoot and pulvinus form, twig layout, number of resin canals, a sunken midrib in the leaves, and pendulous leading shoots are

close to those of *Tsuga* (Yao & Hu, 1982; Page, 1988), while its female cones more closely resemble *Keteleeria* or *Abies* in erect habit, *Pseudotsuga* in size, shape, structure, and number of scales (Napp-Zinn & Hu, 1989; Hu et al., 1989), and *Larix* in exserted, simple bracts and in long, leafy cone peduncles (Farjon, 1990). Further, the unusual grouping of the male cones into clusters appears to link it also with *Pseudolarix* and, more distantly, perhaps with *Cathaya* (Hu et al., 1976; Hu & Wang, 1984; Page, 1988). Because most of its characteristic features are intermediate between *Keteleeria* and *Tsuga* (Gaussen, 1966), it has been considered by van Campo-Duplan & Gausen (1948) to be a recent hybrid between the two genera. Based on fossil evidence of *Palaeotsuga*, plants of probable nearest affinity with *Tsuga longibracteata* occurred in the Pliocene of both Japan and Russia (Miki, 1954; Karavaev, 1958). Page (1988) and Frankis (1988) argued that it was not a modern hybrid.

In studying the wood structure of *Tsuga-Keteleeria longibracteata*, Yu (1956) found no normal vertical resin canals and no important structural diversities between *Tsuga-Keteleeria* and *Tsuga*. Thus, he concluded that there was no necessity of raising the species to the rank of genus. His point of view was also accepted by Cheng & Fu (1978) in compiling the *Flora Reipublicae Popularis Sinicae*.

In the present study, we notice that there are normal resin canals in the wood. In the juvenile portion, few normal resin canals are sporadically observed and they might be missed where scarce. However, there is an increasing tendency towards more resin canals in mature wood, and they can readily be seen in the wood older than 30 years. We are uncertain why Yu (1956) found no normal vertical resin canals in the wood of *Tsuga-Keteleeria longibracteata*. He did not mention where the tree came from nor how old the tree was in his study, but we presume that he was looking for normal resin canals in the juvenile wood rather than in the mature wood.

At wounds, traumatic resin canals in *Nothotsuga* appear to be of sporadic distribution in addition to tangential series. Similar distribution patterns were

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FIGURES 6–8. Radial sections of wood.—6. Poorly developed ray tracheid (arrow).—7. SEM, Showing ray parenchyma with strongly pitted horizontal walls and nodular end walls (arrows).—8. SEM, showing taxodioid pitting in the cross-field (arrows). FIGURE 9. Cross section of inner bark. FIGURE 10. Cross section of outer bark, showing alternating arrangement of thin- and thick-walled phellem cells. Sc = Sclereids, Rc = Resin cavity. Scale bars in 6, 7 = 5  $\mu\text{m}$ ; in 8 = 1  $\mu\text{m}$ ; in 9 = 20  $\mu\text{m}$ ; in 10 = 30  $\mu\text{m}$ .

Table 1. Differences in wood and bark features among *Nothotsuga*, *Keteleeria*, and *Tsuga*. TGR: Transition of growth rings; NVRC: Normal vertical resin canals; Rc: resin cavities.

Features	<i>Keteleeria</i>	<i>Nothotsuga</i>	<i>Tsuga</i>
1. TGR	gradual	abrupt	abrupt
2. Ray tracheids	none	poorly developed	fully developed
3. Cross-field	taxodioid	taxodioid, cupressoid	cupressoid
4. NVRC	present	present	absent
5. Rc	present	present	absent

observed in *Keteleeria* by Bannan (1936), who studied the conifers quite extensively. He believed that the scattered distribution in *Keteleeria* differed from *Tsuga* and *Abies*, where the associated canals were almost invariably in tangential series. Although the relationship of the scattered canals to injury has not been determined, in this respect *Nothotsuga* resembles such genera as *Keteleeria*, *Larix*, *Pseudotsuga*, and *Picea*.

Resin cavities in the bark are believed to arise through modification of large-sized marginal ray cells or phloem parenchyma cells without further differentiation of border cells. Similar structure has been reported in *Abies* (Srivastava, 1963), *Larix*, *Picea*, *Pinus*, and *Pseudotsuga*, but not in *Tsuga* (Chang, 1954; Lotova, 1975).

The comparisons in Table 1 suggest that several structural features of *Nothotsuga* do not correspond well with any of the existing pinaceous taxa. In particular, a comparison with *Keteleeria*, one of the genera often considered a possible relative, illustrates the differences: the transition from earlywood to latewood in *Keteleeria* is gradual in contrast to the abrupt transition in *Nothotsuga*. Additionally, *Keteleeria* lacks ray tracheids (Greguss, 1955; Phillips, 1963) while *Nothotsuga* possesses ray tracheids. When comparing the structure of *Nothotsuga* with that of *Tsuga*, another genus most often assumed having close affinities, we also found some features that are not in agreement. In addition to possession of normal resin canals in the wood and resin cavities in the bark mentioned above, *Nothotsuga* is characterized by poorly developed ray tracheids occasionally on either side of rays, which differ from the fully developed ray tracheids in *Tsuga*. Furthermore, the cross-field pitting in *Nothotsuga* is mainly taxodioid, occasionally cupressoid or piceoid, while it is mainly cupressoid in *Tsuga* as noticed by Cheng (1980) and Ho et al. (1984).

The wood and bark structure described above indicates that *Nothotsuga* does not fit well in either *Tsuga* or *Keteleeria*. The presence of normal vertical resin canals in the wood, together with resin cavities in the bark of *Nothotsuga*, weighs heavily

against some of the earlier treatments where it was included within the genus *Tsuga*, for example, in the section *Heopeuce* Keng & Keng f. of *Tsuga* (Cheng & Fu, 1978). Some characters, particularly the occurrence of ray tracheid in the wood, also exclude *Nothotsuga* from the genus of *Keteleeria*. In conclusion, we support the view that *Nothotsuga* should be validated as a separate genus in the Pinaceae and put between *Keteleeria* and *Tsuga*.

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