The Structure of the Wood of East Indian Species of *Pinus*.

By PERCY GROOM, M.A., D.Sc., F.L.S., and W. RUSHTON, A.R.C.S., D.I.C.

(PLATES 24 & 25.)

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IN India there are five native species of *Pinus*, whose names and distribution are :—

1. *PINUS EXCELSA*, Wall. A five-needed species with the vascular bundle single (haploxylic) in the leaf, a deciduous sheath of scales on the dwarf-shoot, and a terminal umbo on the cone-scale. It is definitely *temperate* and non-xerophilous in distribution, as it grows in the Western Himalayas at altitudes between 6,000 and 12,000 feet.

2. *PINUS GERARDIANA*, Wall. A three-needed species, haploxylic, with a deciduous leaf-sheath, and a central umbo on the cone-scale. It is definitely *xerophilous* in distribution, as it occurs in dry parts of the Western Himalayas, sometimes on dry, rocky slopes, and extends into Afghanistan ; its range of altitude is from 5,000 to 11,000 feet.

The remaining three species have diploxylic needles ; their leaf-sheaths are not deciduous ; their cone-scales have a central umbo each.

3. *PINUS LONGIFOLIA*, Roxb. This three-needed species lives largely in sub-tropical or even tropical climates, and is at least often xerophilous in habitat. In the drier Western Himalayas it ranges from 1,500 to 7,500 feet ; while in the moister Eastern Himalayas, for instance in Sikkim, it occupies dry southern slopes at altitudes between 1,000 and 3,000 feet. Webber describes the tree as sometimes growing on rocks in hot and dry woodlands.

4. *PINUS KHASIA*, Royle. This three-needed species is more Eastern in distribution and occurs in the Khasia and Naga Hills, also in Burma, at altitudes varying from 2,500 to 7,000 feet. According to J. D. Hooker it is not found in the wettest regions of the Khasia Hills where the annual rainfall may reach 600 inches. He describes the species as occurring in less wet places, for instance at an altitude of 6,000 feet on "moors" whose flora is distinctly temperate ('Himalayan Journals'). In Burma it occurs in dry hill-forests, according to Kurz. In the absence of adequate statistics as to soil and climate one surmises that this species can grow in habitats of considerable variety, in moist or moderately dry places in a temperate or subtropical, or perhaps even tropical climate.

5. *PINUS MERKUSII*, *Jungh. & de Vriese*. This two-needed species is tropical in distribution. Occurring in Burma and the Malay Peninsula at altitudes varying from 300 to 3,500 feet, as well as in Sumatra and elsewhere. Apparently it can grow in dry or moist places, occurring, for instance, in very hot dry forests in the Shan Hills (according to H. N. Thompson).

A number of problems present themselves in regard to the structure of the wood of these species.

In the first place, what light is shed on their affinities? Or, as regards habitat, do the species growing under tropical or xerophilous conditions show any corresponding structural features in their wood? and are these correlated with the histological structure of the leaves? Incidentally we found ourselves faced with the problem as to the nature of "Sanio's bars" and markings on the radial walls of the wood-tracheids.

This paper is divided into two parts, the first of which gives the general conclusions and summary of results, the second part contains the special description of the different species.

GENERAL CONCLUSIONS.

The structure of the wood of all five species conforms with that of typical species of *Pinus* in the following features. There is a heart-wood. Annual rings are distinct, as the spring-tracheids have wider lumina and thinner walls than the more compressed summer- ("autumn"-) tracheids. The radial walls of the tracheids bear bordered pits, which are smaller and scantier in the summer-wood and have narrower orifices. There are longitudinal resin-ducts, the epithelium of which is thin-walled and develops thyloses. The medullary rays are of two kinds: *uniseriate*, which are one cell thick, and *pluriseriate*, which are several cells in thickness but taper towards the upper and lower margins, where they are one cell thick, so that in tangential section these rays are *fusiform*. These latter, so-called fusiform rays, include a resin-duct. Some of the medullary rays of all species have ray-tracheids, or parenchyma or both.

(a) Annual Ring.

The species *Pinus longifolia* shows double annual rings (Pl. 24. fig. 18).

(b) Size of Tracheids.

The tracheids are shortest in the xerophilous *Pinus Gerardiana*, 3 mm., attain a length of 4 mm. in *P. excelsa* and *P. longifolia*, and 4.6 mm. in *P. Khasya*, and the relatively great length of 7 mm. in the tropical *P. Merkusii*. This last species also has by far the widest spring-tracheids, whose radial and tangential diameters are about 68.5 and 45 μ respectively

and often exceed these dimensions. The species whose spring-tracheids come next in width are likewise pines growing often in subtropical or even tropical climates, namely *P. longifolia* ($53.5\ \mu$ and $39.5\ \mu$), and *P. Khasya* ($52\ \mu$ and $25\ \mu$), which grows in places among tropical plants in Burma. The temperate *P. excelsa* and the xerophilous *P. Gerardiana* have much narrower spring-tracheids, the respective diameters being $38.5\ \mu$ and $37.5\ \mu$ in the former, and $34\ \mu$ and $29\ \mu$ in the latter.

These distinctions suggested to one of us an enquiry into the effect of environment and systematic affinity on the width of spring-tracheids of species of *Pinus*. A separate paper * deals with this, but the main results are given here.

Pinus Gerardiana has the narrowest spring-tracheids either because it is xerophilous or because it belongs to the sub-section Para-Cembra, group "Parrya." The observed mean diameter of its spring-tracheids was $31.5\ \mu$ —those of the four haploxylic American species † with the narrowest spring-tracheids varied from 24 to $33\ \mu$.

Pinus excelsa has broader spring-tracheids, either because it is not xerophilous or because it belongs to the section "Cembra" and group Strobilus. The observed mean diameter of the spring-tracheids was $38\ \mu$. Those of the American species belonging to the same group varied from 41.5 to $45\ \mu$.

Pinus longifolia, *P. Khasya*, and *P. Merkusii* have widest tracheids because they are sub-tropical or tropical in distribution with sufficiency of moisture.

In the case of the rather xerophilous *P. longifolia*, as in those of American species of sub-tropical distribution in a moist climate, the periodically or permanent dry nature of the superficial soil is not associated with narrowness of spring-tracheids. The mean diameter of its spring-tracheids ($46.5\ \mu$) may be compared with those of two sub-tropical American species, *P. clausa* ($48\ \mu$) and *P. palustris* ($49\ \mu$), growing on dry sand in a moist climate. The sub-tropical and perhaps tropical *P. Khasya*, in which the observed mean diameter of the spring-tracheids was 43.5 , practically agrees with the sub-tropical and tropical *P. cubensis* ($44\ \mu$) that grows in South Carolina and the West Indies.

Finally, the most tropical Asiatic species *P. Merkusii* has the widest spring-tracheids ($56.5\ \mu$), just as is the case with the most tropical American species *P. tropicalis* ($50.8\ \mu$).

* Percy Groom, "An Enquiry into the Significance of Tracheid-width in Coniferæ," ined.

† In comparing the figures with those given by Penhallow for American species, it must be pointed out that we measured the widest of the spring-tracheids, but we do not know whether Penhallow followed the same procedure or took the mean diameter of all the spring-tracheids.

Thus from the diameters of the spring-tracheids in these last three forms we can form no conclusion as to the amount of water required by them in the substratum, though analogies with the American species indicate a considerable rainfall. On the other hand, they suggest a means of obtaining collateral evidence as to the climate under which fossil pines grew.

From the structure of the leaves of *P. longifolia* and *P. Merkusii* we should conclude that stomatic transpiration can be vigorous, as stomata are present on the outer (lower) face as well as the flanks.

(c) Shapes of Ordinary Tracheids.

The tracheids running longitudinally in the wood belong to two main types: (i.) ordinary long, more or less prosenchymatous tracheids; and (ii.) much shorter, "septate" or parenchymatous tracheids, whose terminal walls are transverse. The latter, which especially occur in the vicinity of the resin-ducts, will be described in connexion with these.

The majority of ordinary tracheids, whether they be the relatively thin-walled well-pitted spring-tracheids, or the thick-walled fibro-tracheids of the summer-wood, are straight and have more or less tapering, sharp or rounded ends. When abutting on a medullary ray the end may fork, or bend so as to run for some distance along the ray and thus form a transition towards a ray-tracheid, or may bend even through an angle of 180° , or finally may end squarely and abruptly against a ray-tracheid. These ends of the tracheids may bear pits in contact with the ray-tracheid, therefore on the terminal, or, in a sense, tangential walls.

But *Pinus Khasya* and *P. Merkusii*, also show bundles of tracheids which, though not connected with medullary rays, yet are bent towards their ends, the curvature being mainly in a radial plane, so that in extreme cases these are seen cut transversely in longitudinal, especially tangential, sections. On the bent parts of these tracheids bordered pits are abundant on the tangential walls and even on the blunt terminations. As these bundles frequently form a radial sheet only one tracheid in thickness, in transverse section they are denoted by a radial series of tracheids with tangential bordered pits in the spring-wood or summer-wood.

(d) Arrangements of Bordered Pits on the Radial Walls.

The bordered pits are oval or circular in surface view in the spring-wood, where they are ranged in one row, with occasional pairs, in *P. excelsa* and *P. Gerardiana*, in one or two rows in *P. longifolia* and *P. Khasya*, and in one, two, or three rows or in peculiar nests, of 3 or 4 in *P. Merkusii* (Pl. 25. figs. 47, 48). The species that has triseriate pits is also the one that shows the greatest radial width of tracheid. But an examination of the statistics.

given by Penhallow (1907) shows that the number of longitudinal rows of bordered pits on the radial walls is not determined by radial width of lumen, as the haploxylic species are mainly uniseriate, and that paired or biseriate pits occur only in two haploxylic species with widest tracheids. But in the diploxylic species Penhallow's statistics show that the wide tracheids of *P. Tueda* and *P. palustris* have only uniseriate pits, whereas many with narrower tracheids have uniseriate or occasionally paired pits, or even 1-2-seriate pits. Systematic affinity undoubtedly is one of the determinant factors. In the Indian species the point worthy of note is that *P. excelsa* and *P. Gerardiana* show the uniseriate arrangement prevalent in the haploxylic species. As is well-known, in one and the same species width of tracheid may appear to determine the number of rows, because in the summer-wood (of all the Indian species also) the radial pits are uniseriate.

(e) **Sanio's Rims.**

The radial walls of the spring-tracheids of the secondary wood of *Pinus* show certain narrow, transverse, or more or less curved strips that appear lighter than the rest of the wall and generally stain less deeply than this when treated with certain solutions (phloroglucin and hydrochloric acid, or safranin) which stain lignified membranes. (Sometimes, when sections deeply stained with safranin are decolorized, differentiated by clove oil, and mounted in Canada balsam, these bands are on the other hand the parts that retain the stain most deeply.)

Now Sanio showed that in *Pinus sylvestris* the differentiation of bordered pits is preceded by the delimitation of certain oval or elliptical patches bounded above and below by curved bow-like lines. According to Sanio it is only within such oval patches that bordered pits arise; hence he termed each patch a "primordial pit" and we term it "the primary pit-area." In such an area Sanio showed that one bordered pit, or two side by side, may arise, but usually the primary pit-area in the spring-tracheids is not completely covered by the pit or pits; there remains behind a margin above and below. According to Sanio's work it is these unoccupied margins of the primary areas that coincide in position with the above-mentioned bands that are seen in radial section. Consequently the name "Sanio's rims" may be given to the structures causing the band-like appearance. According to Sanio sometimes a bordered pit does occupy the whole of the primary pit-area, and with this fact may perhaps be correlated the absence of any distinct Sanio's rims in a number of cases. When the primary pit-areas are in contact, the two contiguous Sanio's rims are naturally "fused" and form a band that is transverse and single, except possibly at the two lateral edges where the natural curvature of each original boundary of the area causes the band to fork. When, on the other hand, the primary pit areas

are farther apart, they are separated by a stretch of wall that gives the full reactions of lignified membranes, and Sanio's rims are bands confined to the neighbourhood of the pits. In *Pinus excelsa* there is additional evidence that the structure at least of the inner layer of the radial wall centres round the pit-areas bounded by Sanio's rims: for when two uniseriate pits are at some distance apart the space intervening between them is occupied by the two narrow fringing curved bands (Sanio's rims), and between these by a stretch of wall showing striations which near the bands are curved in the same sense as these, but at increasing distances from the bands show decreasing curvature until midway between the two pits the striæ are straight and transverse. All the Indian species of *Pinus* show Sanio's rims. In *P. excelsa* and *P. Gerardiana* in the primary pit-area only one pit forms but occasionally two side by side may arise, whereas in the other three Indian species two pits are commonly produced side by side in one area. But *P. Merkusii* is unique among known living pines in that in one primary pit-area there may be produced either three pits side by side, or three forming a cluster, of which two are lateral and approximately side by side, while the third is median above or below, or finally four forming a cluster like the last except that there are two median, one above and one below (Pl. 25, figs. 43, 47, 48). Other deviations regarding the arrangements are described in the detailed description of *P. Merkusii*. Sometimes Sanio's rims completely surround the pit-bearing area, that is, also on the sides; in such a case they literally become a single fringe or margin (figs. 43, 46, 47).

The detailed structural relations in regard to these Sanio's rims were investigated in connexion with *P. Merkusii*. In radial sections with iodine and sulphuric acid the "rims" stain yellow; with ordinary hæmatoxylin they remain unstained; leaving sections in cupra-ammonium to dissolve out any cellulose, their staining properties are not changed materially. They are not composed of cellulose. They stain more deeply than the rest of the wall with iron-hæmatoxylin, with methylene-blue followed by immersion in 2 per cent. acetic acid, also with ruthenium-red. Treating radial sections with ammonium oxalate, or successively with 2 per cent. hydrochloric acid for half an hour and then boiling for two hours in 2 per cent. caustic soda, they do not stain with ruthenium-red or with methylene-blue and acetic acid. Therefore "Sanio's rims" are at least partly pectic.

Now the fact that a single straight band may be seen in radial section continuing across two or more tracheids, proves that the phenomenon is associated in some manner with the middle lamella. In tangential sections the appearance of these bands is seen to be due to a circular, or fusiform band-like, localized thickening of the middle lamella: where two successive superposed pits are close together the thickening between them is single, but where the pits are some distance apart there are two such thickenings, one

near each pit. The thickenings are seen to be separated from the actual pit by a short stretch of wall. These thickened parts of the middle lamella differ somewhat from the middle lamella elsewhere in chemical composition, for they do not stain crimson with phloroglucin and hydrochloric acid, whereas elsewhere the middle lamella is thinner and does stain more or less. Tangential sections stained in safranin and mounted in Canada balsam show these thickenings unstained and appearing like empty intercellular spaces, because their refractive index agrees with that of the balsam, whereas the rest of the middle lamella may be quite distinct. Stained with methylene-blue succeeded by 2 per cent. acetic acid or ruthenium-red (especially after being swollen by successive treatment with hydrochloric acid and ammonia) they stand out from the rest of the wall as more deeply stained parts of the middle lamella (fig. 38), though the other parts of this also frequently stain with ruthenium-red. In *transverse* section treated with ruthenium-red Sanio's rims are seen as deeply stained lines in the middle lamella of the radial walls, and contrast with the scarcely stained middle lamella in the tangential walls or in radial walls where the rims are lacking. (In our specimen a number of the tracheids in contact with medullary rays showed in transverse section the inner layers of the tangential walls, and sometimes of the radial walls, delignified and staining with ruthenium-red. Tangential sections showed that this is due to the occurrence of patches of pectic substance situated at the levels of the medullary rays. This localized pectic lining is due to the action of a fungus which is mainly distributed in the medullary rays into the adjoining tracheid, which run mainly in a tangential transverse direction.)

Combining the above given facts with Sanio's account of the development of pits in primary pit-areas, the following would therefore appear to be the truth. When young the actual marginal portion of the primary pit-area does not thicken by deposits of lignified wall so soon as it does elsewhere (except on the pit-closing membrane) but thickens by successive deposits of pectic substance until a stage is reached when lignified wall-substance is deposited even over the now thickened rims of the primary pit-area. Sanio's rims represent a system of rod-like or band-like pectic thickenings of the middle lamella running transversely in the radial walls and linked here and there by slightly curved longitudinal band-like similar thickenings (representing the lateral margins of the primary pit-areas).

In tracheids at the junction of the spring- and summer-wood, where the pits are uniseriate, Sanio's rims as seen in radial section are reduced to little crescent-shaped areas in a median position above and below each pit, and not as broad as the pit (fig. 44). In the summer-wood outside this critical layer Sanio's rims are not to be seen in radial section, even after staining with ruthenium-red. In tangential section the middle lamella here does not dilate

close to the pit ; it only broadens very slightly where it is forking just before passing into the wall of the pit-chamber ; moreover, the staining of the middle lamella with ruthenium-red is the same throughout and is rather light.

It is worthy of note that in staining radial sections with ruthenium-red or with methylene-blue, the part of Sanio's rim that stains most readily and deeply is frequently the part immediately beneath the centre of the pit, and when the Sanio's rims are dwindling in the outer spring-wood or inner summer-wood it is lateral or marginal parts that vanish first while the central parts remain.

As there appears to be some confusion concerning the meaning of the term "Sanio's bars" some comments may be made. In radial longitudinal sections of coniferous woods the appearance of transverse bands running across the tracheids is caused by three entirely different sets of structures :—

(i.) There are bars or rods stretching across the lumen from tracheid to tracheid and forming a continuous radial series, extending through a few tracheids or through one or more annual rings. Similar bars often extend across the lumina of sieve-tubes. In the wood these are lignified, but in the phloem they react as cellulose. C. Müller (1890) was the author of the name "Sanio's bars" and, as he explicitly stated, he coined the term to designate these structures as first discovered by Sanio in *Pinus sylvestris* (1873-4). In a radial section the individual rods are seen to form a continuous line and only one such series is seen, as a rule, in a single longitudinal radial section ; these rods then are limited in number.

C. Müller (1890), on the basis of his observations, formulated the proposition that Sanio's bars occur in all the sub-groups of the Coniferæ (including *Araucaria* and *Ginkgo*) and that they arise as folds of the radial walls. The proposition as to Sanio's bars has been incorrectly restated by Miss Gerry*.

(ii.) There are structures known as "resin-plates" arranged somewhat in the same manner as seen in radial section. They are found most frequently or exclusively in contact with medullary rays. In radial section they are generally deeper than Sanio's bars, usually clearly dilated against the tracheid wall, and often form a complete partition dividing the lumen of the tracheid into two chambers.

(iii.) There are certain markings which form a pattern on the radial walls of the tracheids, especially in the spring-wood. The markings are largely in the form of transverse bands, but contrast with the other bands seen in radial section in that in every spring-tracheid numerous bands are visible,

* Gerry, in *Ann. Bot.* xxiv. (1910) pp. 119-123.

and in that they do not usually continue in the same straight line through a number of tracheids. These bands are the structures that we term "Sanio's rims."

Not in any one among these three kinds of markings in the wood is the bar, plate or band composed of cellulose.

Miss Gerry, working with Professor Jeffrey, in her paper on the "bars of Sanio," was obviously not dealing with "Sanio's bars" but with the structures that we term Sanio's rims. She describes them as "bars" or "folds" of cellulose and specifically mentions their presence in *Pinus*. In this genus we have shown that these bands are not ridges, bars, or folds projecting into the lumen, but occur at regions of the wall where this is no thicker than elsewhere, and that each consists of a locally thickened peptic middle lamella overlaid by lignified layers. The evidence of the cellulose nature of these bands provided by Miss Gerry is quite inadequate, since the sole fact given by her in support of her statement is that the bands stain with hæmatoxylin. We entirely failed to make these structures stain with this dye excepting in the form of iron-hæmatoxylin, which of course may be readily deposited as a stain in peptic bodies and particularly in the middle lamella of wood. Hence it remains to be seen if these bands are composed of cellulose in any of the Coniferæ.

(f) **Structure of the Bordered Pits on the Radial Walls.**

In the spring-wood the bordered pits on the radial walls are larger and generally have broader orifices. In the summer-wood the orifices are more or less fusiform and more approximating to the vertical oblique, and may be continued out with long oblique furrows arranged in a steep spiral.

(g) **Bordered Pits on the Tangential Walls.**

Only two Indian species, *P. excelsa* and *P. Gerardianá*, regularly show pits on the tangential walls of all the outer summer-tracheids.

Tangential pits are known to occur sporadically in narrow annual rings of various Abietinæ (see Strasburger). They occur in *P. longifolia*, *P. Khasya*, and *P. Merkusii*, in spring-wood or summer-wood, but in the last two species they are abundant especially in the spring-wood in the radially deflected bundles of tracheids already described, though the annual ring was broad in our specimen of *P. Khasya*. Small bordered pits occur on the tangential walls on the radially outer and inner sides of the tracheids around the resin-ducts, at least in some Indian species of *Pinus*, e. g., *P. Gerardiana* and *P. excelsa*.

(h) Other Structural Features of the Tracheids.

As regards the thickness of tracheid-wall and size of lumen the transition from spring-wood to autumn-wood is, as would be anticipated, gradual in the haploxylic *P. excelsa* and *P. Gerardiana*, and more sudden in the diploxylic *P. longifolia* and *P. Merkusii*, but unexpectedly is gradual in the diploxylic *P. Khasya*. As seen in radial section the walls of the tracheids are very clearly thicker, against the medullary rays than elsewhere.

Radial lignified bars, "Sanio's bars," stretching across the lumina of a series of tracheids were seen in several of the species. The bars seen in transverse section were hollow, and mostly cylindrical, but close to the attachment to the tracheid-wall the bar may deepen so that the contours of it and its cavity are vertically elongated (Pl. 24. fig. 22).

"Resin-plates" occur in some of the Indian pines, e. g., *P. excelsa*.

(i) Resin-Ducts

In all the Indian pines except *P. Gerardiana* the resin-ducts are most abundant in the outer part of the annual ring, but in that species they are most numerous in the middle part of the ring and are unusually uneven in distribution, being locally scanty.

P. longifolia and *P. Khasya* are marked by great development of the ducts; in the former the ducts are very wide (diameter .2 mm.), and solitary or in pairs, mostly in the outer and middle parts of the annual ring. *P. Khasya* has very numerous ducts ranged usually in groups of 2-4.

The species show the following types of cells associated with the ducts (figs. 2, 20, 31, 42).

- (i.) Thin-walled epithelium lining the duct.
- (ii.) Thin-walled, more elongated parenchyma.
- (iii.) Thick-walled, still more elongated parenchyma, the walls of which bear numerous simple pits.
- (iv.) Parenchyma-tracheids, much shorter than ordinary tracheids, with bordered pits on all their walls, including the terminal transverse walls.

(k) Medullary Rays.

Except in *P. excelsa* thin-walled parenchyma, as well as thick-walled, occurs in the medullary rays. This species has only the latter.

In all Indian pines ray-tracheids, both marginal and internal (so-called "interspersed"), occur. In the haploxylic species *P. excelsa* and *P. Gerardiana* the ray-tracheids bear no denticulations on their walls, or in the latter species such denticulations are scantily and feebly suggested. The three diploxylic species all have denticulate ray-tracheids.

The marginal ray-tracheids assume various forms including shapes transitional towards bent ordinary wood-tracheids (figs. 11, 12, 34, 41). Similar peculiar forms have been described by W. P. Thompson (1910). In *P. excelsa* long marginal ray-tracheids with a narrow tapering lumen (fig. 11) were seen in connexion with ray-tracheids that approximated in form to those characteristic of "*distended medullary rays*." There occur uniseriate rays of this latter type entirely composed of peculiar lobed, vertically dilated ray-tracheids, whose connexion with one another is slight or possibly even lacking (fig. 10).

Where the medullary rays cross a resin-duct the ray-tracheids, or thick-walled parenchyma, do not (as is usually stated in regard to *Pinus*) necessarily give way to thin-walled parenchyma, though such a change sometimes does take place. Possibly the determinant factor is the distance of the medullary ray from the actual resin-duct, and the nature of the cell that it crosses; if crossing a parenchyma-tracheid for instance the ray-tracheid would probably persist across the duct.

Details concerning the shape and size of the pits of the various kinds of ray-cells are given in the special descriptions of the different species.

(l) **Conclusions as to the Systematic Affinities and Ecological Structure.**

Pinus excelsa and *P. Gerardiana*.

P. excelsa and *P. Gerardiana* agree in the following features: the leaf is haploxylic, the scaly sheath of the dwarf-shoot is deciduous, the transition from the spring-wood to summer-wood is gradual, the outermost tracheids in the summer-wood have tangential pits and the ray-tracheids have feeble or no denticulations. For these reasons both belong to one and the same great subdivision of *Pinus*. But in *P. excelsa* the needles are in tufts of five, the cone-scale has a terminal umbo and the ray-parenchyma has large apparently simple pits in the lateral walls. This species therefore belongs to the sub-section *Cembra* (Parlatore), and since its cone-scales are thin and the cones long it belongs to the group *Strobus*. But, according to Penhallow, in the species constituting the sub-section *Cembra* the upper walls of the ray-parenchyma cells are thin: if this be correct, *Pinus excelsa* stands apart from all these. As regards width of spring-tracheids the American species belonging to the Section *Haploxyton* that most closely approach it likewise belong to the group *Strobus*.

Pinus Gerardiana differs from *P. excelsa* in that its cone-scale has a central umbo and is thick, its leaves are in tufts of 3, and hence it is separated, for instance by Koehne, from *Cembra* as a member of the sub-section *Para-Cembra*. H. Mayr (1890) noted that the small clearly half-bordered pits on the lateral walls of the ray-parenchyma ally it with the other species constituting

this sub-section. It agrees with typical members of the Haploxyton Section in its uniseriate pits on the radial walls of the wood-tracheids.

In altitudinal range there is not much difference between *P. excelsa* (6,000–12,000 ft.) and *P. Gerardiana* (5,000–10,000 ft.), but the latter alone is xerophilous in habitat: and its leaf has a much thicker cuticle and the hypoderma has thicker walls. The greater development of transfusion-tissue in *P. Gerardiana* perhaps might be associated with the greater thickness of the leaf, but Max Scheit (1883) concluded that the amount of transfusion-tissue varies directly with the external influences promoting transpiration, and the great development of the resin-ducts in this species recalls the extensive production of ethereal oil glands in the leaves of plants in dry hot places.

Pinus longifolia, *P. Khasya*, and *P. Merkusii*.

These three species agree not only in the diploxylic nature of the leaves, the persistent nature of the sheath of the dwarf-shoot, and the possession of a central umbo on the thick cone-scale, but also in that the transition from spring-wood to summer-wood is sudden (except in *P. Khasya*), the outermost tracheids of the annual ring do not universally bear pits on the tangential walls, the pits on the radial walls of the spring-tracheids are often 2-seriate, and the ray-tracheids are denticulate.

As already pointed out, these three species that frequently grow under subtropical or even tropical conditions are, like the sub-tropical American pines, the species possessing the widest spring-tracheids, despite of the fact that *P. longifolia*, and apparently sometimes the other species, live in situations that are at least temporarily dry. As regards leaf-structure all three have stomata on all their faces. *P. longifolia*, the most clearly tending to xerophily, has the thickest cuticle (though not so thick as *P. Gerardiana*), and *P. Khasya* has the thinnest. *P. Merkusii* has the most numerous lines of stomata, as its twelve lines of stomata imply that these are about .2 mm. apart on the average; whereas in *P. Khasya* and *P. longifolia*, with 10 and 8 stomatic lines respectively, these are on the average .26 mm. apart. In the more xerophilous *P. longifolia* the endodermis has markedly thickened outer walls, in *P. Merkusii* this is less marked, while in *P. Khasya* there is no indication of such thickening. All three species contrast with the haploxylic Indian species in the feebler development of the tissue separating the endodermis from the vascular tissue. The sub-endodermal layer forms a fenestrated cylinder of transfusion-tissue, in addition to this there is usually only one layer of complementary tissue, excepting in *P. longifolia* where there is a disproportionate development of mechanical tissues 1–3 cells thick. The xylem is well developed in all three species. The two three-needed species have merely two marginal resin-ducts, whereas *P. Merkusii* also has a median one against the outer face: in all three cases the ducts are against

the hypoderma. All these facts collectively seem to indicate that these three species of *Pinus* live in a region of considerable annual rainfall, but can endure a considerable season of drought.

As regards features of systematic significance, *P. Merkusii* is perhaps the most interesting abietineous plant in existence from the point of view of structure of wood, which shows possible relations to the araucarian type of pitting on the radial walls. So far it is the only existing conifer known to have these pits arranged in the cluster-like manner already described. In certain Cordaites (*C. Newberryi*) the pits are arranged in clusters which in the successive tracheids of a radial row form a radial series, so as to present the appearance of the possibility that the grouped pits correspond to the position of contiguous medullary rays. The pits forming one group or cluster are more numerous than in *Pinus Merkusii*. Gothan (1910) describes and figures a fossil conifer, *Cedroxylon transiens* (Gothan), whose wood shows in some of the tracheids typical araucarian pitting, and in other tracheids little clusters of 3-4 pits, very similar to those of *P. Merkusii*. He regards this clustered arrangement as the first step in the change from an araucarian type of pitting towards the abietinean condition. If this "star-like" (as Gothan terms it) arrangement is thus a transitional stage between the two conditions, *P. Merkusii* completes the picture by providing a type that has the typical abietinean pitting and the clustered "star-like" arrangement, so that the stages between the two extremes are now known. *P. Merkusii* also shows appearances that may be interpreted as transition between the alternate (araucarian) and opposite (abietinean) arrangement of these pits (fig. 46). So far as we are aware no other living conifer, outside the Araucariaceæ, has triseriate pits in the radial walls of the spring-tracheids: the pits are not arranged alternately as in the araucarian type, but are opposite.

SPECIAL DESCRIPTION OF THE SPECIES.

PINUS GERARDIANA (Wall.).

Pinus Gerardiana, the Himalayan edible pine, a species with its leaves in 3-needled tufts, is clearly xerophilous in distribution, as it occurs in the "inner dry and arid West Himalaya" (Gamble, 1902), at altitudes varying from 5,000-10,000 ft., also in Afghanistan, Kafristan, and in the Hariab district (7,000-11,000 ft.), moreover the species is social on "dry steep rocky slopes" (Gamble). The thick leaf is xerophytic in structure, for the epidermis has very thick walls, including thick cuticle and cuticular layers; the stomata are sunk, and there is a thick-walled hypoderma. Despite this xerophilous distribution and xerophytic structure the bark is "very thin, grey, smooth, and cracked only in very old trees" (Gamble). Europe, however, supplies an analogue in *Betula alba*, whose habitat is often dry.

A. MACROSCOPIC FEATURES (naked eye).

The heart-wood is light brown. The annual rings were 17 to the inch in our specimen, 13 in Stewart's specimen (Gamble). The transition from the spring-wood to summer-wood in the same annual ring is gradual. The relative proportions of the spring-wood and summer-wood varied widely in different annual rings: the latter forming from $\frac{1}{3}$ to more than $\frac{1}{2}$ of the ring. The medullary rays are invisible in transverse section but show as thin darker bands on the radial section. The resin-ducts, just visible in transverse section, are noticeable on the longitudinal section as dark lines; their distribution in the annual ring is uneven, as they are scattered and often locally scanty, though generally more numerous in the later spring-wood and early summer-wood, they are not lacking from the inner and outer boundaries.

B. MICROSCOPIC STRUCTURE.

Tracheids.

In transverse section the spring-tracheids are square or oblong-rectangular, with the slightly longer axis radial or tangential. The gradual decrease in radial diameter and in thickness of wall in the summer-wood culminates in the outermost tracheids, which are very compressed thick-walled fibro-tracheids.

The following are measurements of typical tracheids:—

	Width of Lumen.		Thickness of Wall.	
	Radial.	Tangential.	Radial.	Tangential.
Inner spring-tracheid	34 μ	29 μ	3.5 μ	3.5 μ
Outermost summer-tracheid. .	8 μ	21 μ	6 μ	8 μ

Length of tracheid 3 mm.

The tracheids show three sets of deviations from normal shape as regards their ends:—

1. Where they terminate against a medullary ray the straight end may be rectangular-truncate or forked, but the end may bend radially inward. Bordered pits occur on the bent part or truncate end.
2. Here and there the tracheids bend radially inwards at their ends and dovetail, and on the dove-tailing terminal portions there are pits on the tangential walls in the spring-wood.
3. In the vicinity of resin-ducts rectangular parenchyma-tracheids occur.

The bordered pits on the radial walls are uniseriate though occasionally they occur in pairs. In contour the pit-chamber is oval or circular (fig. 6), the former especially often in the spring-wood, whilst the aperture in the inmost spring-wood is circular or slightly oval with the longer axis transverse; but travelling outwards in the ring the aperture becomes gradually oblique or even vertical (Pl. 24. fig. 8), broadly lenticular, not becoming narrow lenticular except perhaps in the outermost layer. Moreover, the pointed ends of the aperture are continuous with oblique line-like furrows which may be continuous with like ones from higher and lower pits, so that the spiral arrangement of the pit-apertures is very evident. (It is possible that these line-like furrows are not natural to the wood in the tree, but are due to desiccation and consequent fracture.) The longitudinal distance apart of the pits in the spring-wood is very variable in tracheids. Sanio's rims are distinct.

The outer summer-tracheids also possess on their tangential walls smaller, more irregularly arranged, bordered pits, which are scanty and uniseriate in some tracheids, and more numerous and up to triseriate in others. They are most numerous in the outermost two or three layers, but occur in the latest five series of tracheids. In any case they occupy a relatively small area of the wall, and agree in structure and approximately in size with the pits on the radial walls of the summer-tracheids: the outline of the chamber is circular and that of the orifice is lenticular (fig. 7).

Resin-Ducts.

The ducts attain a diameter of $120\ \mu$ and their epithelial cells a radial width of $14\ \mu$. The flattened epithelial cells give rise to numerous occluding thyloses. Around these are two layers of rather flattened parenchyma with somewhat thicker pitted walls, which are longer and have their thinnest walls towards the resin-epithelium. These are succeeded on the outside by parenchymatous cells which are oblong rectangular in longitudinal section and have thicker walls; and these in turn by parenchyma-tracheids of similar shape with relatively thin walls and few bordered pits which occur on the end walls as well as on the lateral, including tangential walls in summer-wood and spring-wood (fig. 2). The lengths of measured parenchyma-tracheids were $\cdot 114$, $\cdot 25$, $\cdot 27$, and $\cdot 5$ mm., in comparison with 3 mm. the approximate length of the ordinary tracheids. Thus around the resin-ducts there are cells showing transitional stages from epithelial parenchyma to typical tracheids.

Medullary Rays.

The linear usually uniseriate rays vary in height from 1 to 24 cells. The fusiform rays attain a height equivalent to 30 cells, but some of them are shallower than the tallest uniseriate rays.

In addition to ray-tracheids, there are two kinds of parenchyma-cells, thick-walled and thin-walled.

Each *thick-walled parenchyma-cell* is radially elongated and in length equal to the radial diameters of 4–6 tracheids in the spring-wood and about 8 tracheids in the summer-wood. In tangential view the lumen is an upright oval, and the general contour is vertically oblong with rounded angles in uniseriate rays, but the contour is more rounded near the central parts of the fusiform rays. Their end walls are oblique or transverse. On the lateral walls the pits are very small, half-bordered (*Picea*-like) and circular in contour, but their orifices opening into the tracheids are lenticular and oblique. These pits are not nearly so tall as the height of the ray-cell, on the walls of which they are ranged in one or two tiers, and there are 2–3, usually two pits in each tier to the radial width of each tracheid, but only 1–2 in the summer-wood—therefore, as a whole, 2–5 in the spring-wood (fig. 4). In the summer-wood the apertures are much elongated and oblique (fig. 3). The upper and lower walls, as well as the end walls, the latter especially near the margins, have rounded pits.

The *thin-walled parenchyma-cells* are enlarged radially with straight transverse or oblique, or bow-like terminal walls, which are devoid of special thickenings or pits.

The *ray-tracheids* have transverse or oblique ends, bordered pits on all their walls, and are devoid of denticulations or very feebly and scantily denticulate in the case of the marginal ray-tracheids.

The *uniseriate rays* (fig. 5) are nearly entirely composed of thick-walled parenchyma and ray-tracheids, mainly the former. The latter are very largely marginal, but some internal ray-tracheids occur in smaller or larger numbers. Where the ray passes a resin-duct and comes in contact with the parenchyma surrounding this, thin-walled parenchyma partially replaces the thick-walled, but there are also a few thick-walled parenchyma-cells which are continuous with similar ones or with ray-tracheids. This change is quite local and the ray assumes the original structure after passing the duct.

Occasionally *biseriate rays* devoid of resin-ducts may be seen.

The *fusiform rays* (fig. 1) in tangential section are often slender, sometimes being one cell in thickness except in the central part where the resin-duct is. In tangential section the resin-duct is bounded by a wall of about four thin-walled flattened epithelial cells (which grow inwards to form thyloses). These are ensheathed by a single layer of similar cells, which on the flanks are in contact with the wood-tracheids. These in turn are succeeded by a little collection of thin-walled wider parenchymatous ray-cells, usually in two tiers, but among them may be an isolated, thick-walled parenchyma-ray cell. The thinner portions of the ray, which are biseriate towards the centre

and uniseriate towards the margins, are mainly composed of thick-walled parenchyma, with one or two tiers of marginal ray-tracheids.

Hence apart from or surrounding the resin-ducts, both types of rays are composed of thick-walled parenchyma, with a smaller number of marginal ray-tracheids, together with sporadic thin-walled parenchyma and internal ray-tracheids.

PINUS EXCELSA, Wall.

This five-needed species belongs distinctly to the temperate climate, as its range of altitude in the Himalayas is from 6,000 to 12,000 ft. Its area stretches from Afghanistan to Bhutan.

As this species is widely grown in Europe the appearance of the wood is familiar, but for the sake of completeness a brief description of the structure of this is given.

A. MACROSCOPIC FEATURES (naked eye).

The wood is light in colour, the sapwood being whitish and the heartwood a light red. In each annual ring the spring-wood gradually merges into the summer-wood with no sudden transition. The annual rings vary in width from $\frac{1}{4}$ to about $\frac{1}{30}$, or less, of an inch (in our Indian specimen the mean thickness was $\frac{1}{27}$ of an inch). The medullary rays are visible to the naked eye as yellow lines in the heart-wood. Resin-ducts are numerous in the outermost spring-wood and especially in the summer-wood.

B. MICROSCOPIC STRUCTURE.

Tracheids.

Spring-wood formed the greater part of the annual rings in our specimen : for instance, in one ring the radial row of tracheids was constituted of 28–30 forming the spring-wood, and 5–8 forming the summer-wood. In transverse section the inner spring-tracheids are mostly square or rectangular-oblong with a longer radial diameter. The transition to summer-tracheids is very gradual, and only a few of the outermost of these show marked shortening of the radial diameter. Below are given measurements of typical tracheids, whose length is 3·4–4 mm.

	Width of Lumen.		Thickness of Wall.	
	Radial.	Tangential.	Radial.	Tangential.
Spring-tracheids ..	38·5 μ	37·5 μ	3·4 μ	3·4 μ
Summer-tracheids..	11·5 μ	28·5 μ	4·4 μ	4·4 μ

According to Gamble's statistics the wood of *Pinus excelsa* is lighter in weight and less hard than that of *Pinus Gerardiana*: this is due to the thinner walls of both spring- and summer-tracheids, and perhaps to the smaller percentage of summer-wood in the former.

The tracheids have pointed ends except where they end abruptly on medullary rays. In the spring-wood the numerous pits on the radial walls are nearly entirely uniseriate, but occasionally paired. They are oval and transversely elongated or circular, with a transverse oval or nearly circular orifice. The torus is ragged at the edges and the membrane radially striated. Large simple pit-like structures occur between some of the bordered pits (fig. 16). In the summer-wood the pits on the radial walls are uniseriate, less numerous, and circular in outline, with steeply oblique and even nearly vertical orifices (fig. 15). Sanio's rims are narrow but quite distinct in the spring-wood.

In the outer summer-wood on the tangential walls there are present numerous small scattered bordered pits. These are most abundant in the outermost layer of the tracheids, but may be seen in the outer three layers. They are circular in outline, with nearly vertical elongated fusiform apertures (fig. 14).

Radial bars, "Sanio's bars," occur scantily: each is usually a cylindrical rod with a minute canal in its centre.

Tracheids with the so-called "resin-plates" occur against some of the medullary rays.

Resin-Ducts.

Each resin-duct has a flattened layer of thin-walled epithelial cells, which are broadly brick-shaped in longitudinal tangential view. In our specimen all the resin-ducts were blocked by numerous large thyloses. Around the epithelium are parenchymatous cells whose form varies with the distance from the epithelium. The cells adjoining this are elongated brick-shaped with thin walls, and large rounded simple pits. Outside these the cells are longer, narrower, and still square-ended; their walls are thicker and lignified, and the simple pits are smaller; against the tracheids the pits are half-bordered. Finally there are parenchyma-tracheids whose terminal walls are transverse or somewhat oblique; these have small bordered pits on all their walls. The parenchyma extends farther in a tangential direction towards a medullary ray than towards the reverse side; moreover, this production of wood-parenchyma in contact with the medullary ray may be continued on the side of the latter that is distant from the duct.

Medullary Rays.

The uniseriate rays are distinctly shallower than the fusiform rays, as they vary from 1-12 cells in height, whereas the latter rays are often equivalent to 18 or 19 cells in height.

Apart from the resin-producing epithelium the parenchyma shows two extreme forms, and ray-tracheids occur. Some of the uniseriate rays are composed solely of ray-tracheids.

In particular some rays, so-called "*distended rays*," consist solely of a line of ray-tracheids of characteristic shape. In such rays each tracheid on the radially inner end is blunt or tapers to a more or less fine point, it widens in an outward direction and divides at its widest region into two or three marked lobes arranged in a vertical plane. In the case of two-lobed tracheids, the ends of the next tracheid dovetails with the two lobes; in the case of the three-lobed tracheids, the medium lobe may be continuous with the beginning of the next ray-tracheid, or the successive ray-tracheids are not in contact (fig. 10). More or less similar ray-tracheids occur marginally on other uniseriate rays that include parenchyma (fig. 11).

In normal rays the *ray-tracheids* are mainly marginal though internal ray-tracheids do occur, and their radial continuity is sometimes disturbed by the intercalation of ray-parenchyma. Sometimes there occur very long slender ray-tracheids whose lumen locally is reduced to a thin line (fig. 12). The ray-tracheids show bordered pits on all their walls, and are devoid of denticulations.

The *ray-parenchyma* is composed of rather thick-walled cells elongated radially and having simple pits on all their walls. On the radial walls the typical broader ones have large oval pits elongated radially; in the spring-wood to the radial width of one wood-tracheid there is one pit, which nearly stretches across the whole height of the cell, or occasionally two or three pits: when there are three the pits are in two tiers (fig. 9). In the summer-wood there is still one pit to the radial width of each tracheid, but the pit area is fusiform and steeply oblique towards the lumen and slit-like towards a tracheid. The end wall bears a few large pits, so that it belongs to Penhallow's "locally thickened type." The other parenchyma-cells are usually shallower, their pits are smaller and more crowded together so that the thick portions of the wall form bars which are linked to form a reticulum. These latter cells appear to be specially numerous close to the resin-ducts of the wood of the medullary ray. The parenchyma-cells often bulge into the lumen of the contiguous tracheid to form thyloses (fig. 17) (in sections the pit-closing membranes often also dip into the cavity of the parenchyma-cell itself).

In the *fusiform rays* the resin-duct is walled by a flattened epithelium (whose cells in our specimen had produced many thyloses). Surrounding this are thin-walled parenchymatous cells elongated radially (in our specimen on the flanks of the ray these were very much flattened as if crushed). Above and below in tangential section occur two or three tiers of triseriate or biseriate thick-walled parenchyma-cells, which in turn are succeeded by

4-6 similar cells forming a uniseriate series; sometimes the marginal cells, or rarely some internal cells, are ray-tracheids. The ray-tracheids are not abundant (fig. 13).

The *uniseriate rays* are mainly composed of ray-parenchyma, whose cells in tangential section are vertically elongated, with an oval lumen and an oblong-oval contour; these outlines are disturbed by the bulging in or out of the large pit-closing membrane. In some of these rays ray-tracheids are numerous (fig. 17). The length of the ray-parenchyma cell is equal to the radial width of 4-6 wood-tracheids in the radial spring-wood, and 2-4 in the summer-wood.

PINUS LONGIFOLIA, Roeb.

Pinus longifolia, the chir or long-leaved pine, is a three-needled species whose geographical distribution is interesting. According to Gamble (1902) and Brandis (1907) the tree flourishes in sub-Himalayan tracts and outer Himalayas. In the drier western region extending from Afghanistan to Nepal, it forms extensive pure forests at altitudes ranging from 1,500 to 6,500 and occasionally 7,590 feet, but does not grow in the inner valleys. In the *moister* eastern region it is less common, is often mixed with *Shorea robusta*, and in Sikkim is usually on dry southern slopes at altitudes between 1,000 and 3,000 feet. Thus this pine shows greatest success in regions that are least moderately dry, and Gamble points out that transplants will not endure a wet soil. In the drier western region its thick rough bark suggests the xerophyte and the light-demanding plant, in the *moister* eastern regions its bark is thinner. The suggestion has been made that its limited distribution in the eastern region is due to the rainfall being too heavy. The deep tap-root confers an ability to obtain moisture in dry places, and its capacity in this direction is doubtless enhanced by its power of flourishing as a sub-deciduous tree; for Gamble described the chir pine as more or less deciduous, while according to Brandis its needles remain on the trees for two or three years. In addition to its moderately xerophilous tendency this pine is exceptional in that it naturally occurs within the limits of the tropical climate, and "will thrive in the Indian plains, even at Calcutta" (Gamble, *loc. cit.*). Thus some interest also attaches to the structure of the leaves and wood.

A. MACROSCOPIC FEATURES (naked eye).

The light coloured sap-wood contrasts with the red- or pink-brown heart-wood. Annual rings and resin-ducts are very distinct to the naked eye. The number of rings to the inch radius varies according to Gamble from 2 up to 20; in our specimen there were 9. In each annual ring the summer-wood is rather abruptly marked off from the spring-wood. There is considerable variation in the proportions of the spring- and summer-wood forming one annual ring; in our specimen the summer-wood formed a

fraction of the annual ring varying from one-half to one-eighth. The medullary rays are visible in transverse section, especially in the summer-wood and darker heart-wood, as light-coloured lines, and in radial section as slightly darker narrow bands. The resin-ducts are clearly visible and especially striking in longitudinal views as brown lines. They occur in the spring-wood and summer-wood, but appear to be more numerous in the middle and outer parts of the annual ring than in the inner. Their number appears to be independent of the relative amount of spring- and summer-wood.

B. MICROSCOPIC STRUCTURE.

Tracheids.

The transverse section of the tracheids in the earliest spring-wood tends to be oblong rectangular with the long axis radial; further out this changes to square, and ultimately in the summer-wood to rectangular with the long axis tangential. The change in size of lumen and thickness of wall is shown in the following table.

	Width of Lumen.		Mean thickness of Walls.	
	Radial.	Tangential.	Radial.	Tangential.
Early spring-tracheid . .	53.5 μ	39.5 μ	3.4 μ	3.4 μ
Late summer-tracheids .	10.5 μ	22.5 μ	8 μ	9.6 μ

Typical length of tracheid 4 mm.

Thus the outermost summer tracheids vie with fibres in thickness of wall and smallness of lumen.

Our specimen regularly showed "double annual rings." The spring-tracheids somewhere near the middle of the true annual ring rather abruptly give way to two or three layers of compressed tracheids with thicker walls and smaller lumina. Outside this belt the tracheids more or less completely assume the form of spring-tracheids with larger lumina and with walls either as thin as those in the spring-wood or considerably thicker. Outside this zone in turn more or less sudden thickening of the walls marks the beginning of the true summer-tracheids (fig. 18).

The walls as seen in radial section widen markedly in contact with the medullary rays.

The ends of the tracheids are more or less sharp, or bluntly rounded, except when they end abruptly on a medullary ray; when ending thus

on a ray-tracheid the transverse terminal wall has one or more bordered pits. With this exception and the sporadic occurrence of pits on the tangential and terminal walls, the bordered pits are confined to the radial walls, where in the spring-wood they are uniseriate or biseriate or both in the same tracheid (fig. 26). In each primary pit-area there may be one bordered pit or two collateral ones. Here the bordered pits are circular or oval with the longer axis transverse and the orifices circular, or widely fusiform and with the longer axis directed transversely, obliquely or nearly vertically. In the summer-wood the scantier and smaller pits are circular with a narrow fusiform, nearly erect orifice (fig. 21).

The peculiar structure shown in figure 22 and superficially resembling a deformed bordered pit is a transverse section of a radial bar (Sanio's bar) which stretches across the lumen of the tracheid and perhaps increases in height near its attachment to the tangential wall.

Resin-Ducts.

The resin-ducts may be solitary or paired, and in the latter case separated by only a few layers of flattened thin-walled parenchyma. The ducts have an unusually wide cavity (the width of which attained $\cdot 2$ mm., while the radial width of the epithelial cells was 13μ). The cells composing the one-layered epithelium in longitudinal section are short, broad, often elongated transversely and hexagonal in form.

This layer may be wholly or partially enveloped in a sheath of flattened parenchyma.

Surrounding these cells is thin-walled parenchyma, whose cells are brick-shaped, and elongated longitudinally. Such cells are often particularly developed on the side towards the nearest medullary ray, with whose parenchyma they are continuous.

Typical parenchyma-tracheids occur in contact with this parenchyma, and with thick-walled copiously parenchyma-cells that have numerous simple pits (fig. 20).

Medullary Rays.

The uniseriate rays vary in height from 1–25 cells, while the fusiform rays vary from a height shorter than the highest uniseriate up to equal to 30 cells.

In the rays, apart from resinous epithelium, there are three kinds of cells : thick-walled and thin-walled parenchyma, also ray-tracheids.

The *thick-walled parenchyma-cells* are much more abundant than the thin-walled. Each cell is brick-shaped with a transverse or oblique terminal wall. The length equals the radial width of 6–8 tracheids in the spring-wood, and

9-10 in the summer-wood. All the walls are pitted. On the lateral (radial) walls the pits are of moderate size but not nearly equalling the height of the cell; they are arranged in one or two horizontal series, with 1-3 pits in each series. The outline of the pit is usually very broadly lenticular, with the long axis nearly horizontal or oblique, or nearly circular, but the thickening on the two sides is not exactly similar, so that the pits often show a double outline, the aperture or area being often slightly narrower on the tracheid-side (fig. 24). This distinction is more marked in the summer-wood where the orifice on the tracheid side is narrowly fusiform and nearly erect, and in a vertical direction often longer than the diameter of the chamber, while on the side away from the tracheid the pit orifice is shaped as in the spring-wood (fig. 23). The terminal walls have coarse reticulate thickenings, so that oval, fusiform, or circular pits result. In tangential section, the cell-lumen is mostly oval with the long axis erect in uniseriate rays (fig. 25), but more rounded in fusiform rays. They do not bulge into the adjoining tracheids like thyloses.

The *thin-walled parenchyma-cells* have unpitted terminal walls, which are transverse and bow-like. Towards the tracheid on the radial walls their pits often resemble those of the thick-walled parenchyma, but often are so much larger that in the spring-wood there may be only one pit to the radial width of a tracheid, and this one pit stretches across the whole height of the parenchyma-cell. In the summer-wood the slit-like orifice is often longer than the circular chamber. The upper and lower walls are not pitted. The occurrence of large pits and relatively small bordered pits on the radial walls of ray-parenchyma of one and the same pine, is of special interest in relation to the classification of the genus and the systematic position of *P. longifolia*.

The *ray-tracheids* show bordered pits on all walls. The walls of the marginal tracheids bear denticulations, which sometimes nearly meet across the lumen and are more pronounced in the summer-wood than in the spring-wood. The terminal walls are transverse or oblique. Internal ray-tracheids occur and have curved terminal walls; some are unusually wide and others narrow.

The *uniseriate rays* are usually composed of thick-walled parenchyma (fig. 25) with or without ray-tracheids, but in some cases thin-walled parenchyma forms a considerable part of the ray. Where the ray crosses a resin-duct, thick-walled, starch-containing parenchyma is often but not always replaced by thin-walled, slender brick-shaped cells with more elongated pits on the side walls and entire transverse walls. Neither are ray-tracheids always replaced across the duct by parenchyma, for very slender ray-tracheids are to be seen crossing the duct.

Here and there occur *rays* that are *biseriate* in the middle and uniseriate at the margins, and are devoid of resin-ducts.

A typical *fusiform* ray (fig. 19) consists in the centre of a resin-duct, surrounded by a flattened epithelium, around which in turn is a second similar layer. Above and below succeed (about four) tiers of wide thin-walled starch-containing parenchyma, arranged in a biseriate manner. Next to these are several (2-5) tiers of thick-walled starch-containing parenchyma, arranged in a uniseriate manner. The ray is completed at its margin by 1-3 tiers of uniseriate ray-tracheids. Internal ray-tracheids may interrupt the tiers of thick-walled parenchyma. Less frequently the thin-walled parenchyma is more abundant: for instance, one ray in tangential section consisted successively of 1 tracheid, 2 uniseriate thick-walled parenchyma-cells, 4 uniseriate and two tiers of 2-3-seriate thin-walled parenchyma-cells, 2 layers of flattened cells around the duct, 1 3-seriate and 1 2-seriate and 1 1-seriate tiers of thin-walled parenchyma-cell, a solitary thick-walled parenchyma-cell, and 2 uniseriate ray-tracheids.

PINUS KHASYA, *Royle*.

This three-needled thick-barked species occurs in the Khasia and Naga Hills, as well as in several regions in Burma, at altitudes varying from 7,000 feet to the comparatively low one of 2,500. By Kurz it is described as growing in Burma in dry hot woods forming pure forests or mixed with trees belonging to the "upper dry forests." These pine-woods are well-lighted, rich in epiphytes (especially orchids and lichens), but very poor in lianes. The epiphytes suggest considerable atmospheric humidity at least periodically. The tree thus seems capable of living on dry sunny sites and in a climate ranging from temperate to sub-tropical or even tropical. On the Khasia Hills it does not grow in the regions of very great rainfall (Hooker).

A. MACROSCOPIC FEATURES (naked eye).

The light-coloured "pale brown to red" (Gamble) wood shows distinct annual rings, which in our specimen are somewhat sinuous. In a specimen of which Gamble gives the measurements there were six annual rings to the inch radius; ours showed 3·2. The transition from the spring-wood to the summer-wood is gradual, and the distinction between these two is not great. The numerous resin-ducts of this very resinous wood are most abundant in the outer half of the annual ring, in fact they are almost lacking from the inner third or half: in longitudinal views they form well-marked brown stripes. The medullary rays faintly suggested by ill-defined radial striation in the cross-section, form a delicate silver grain on the radial section.

B. MICROSCOPIC STRUCTURE.

The interesting features in the microscopic structure of the wood are :—

- i. There are unusually complete arrangements for the conduction of water in various directions in the body of the wood ; for the tracheids may have bordered pits on all their walls.
- ii. Some of the tracheids assume unwonted forms.
- iii. The resin-ducts and associated parenchyma are very richly developed.

Tracheids.

In transverse section the spring-tracheids are wide and rectangular to hexagonal with the radial diameter exceeding the tangential. Passing outwards there is a very gradual shortening of the radial diameter, and thickening of the walls, until the outermost three or four rows of the summer-wood are flattened. The measurements are given below :—

	SPRING-WOOD.		SUMMER-WOOD.	
	Radial.	Tangential.	Radial.	Tangential.
Width of lumen	52 μ	25 μ	9.2 μ	19 μ
Thickness of wall	2 μ	2.5 μ	5 μ	5 μ

Mean length of the tracheid 4.6 mm.

In addition to tracheids of normal form, others occur with blunt rounded ends, and near the resin-ducts with transverse rectangular ends, also with feebly bilobed rounded ends. Here and there bundles of tracheids deviate from the straight course, portions of them run in a radial plane obliquely to the longitudinal axis, so that at spots not in contact with the medullary rays tangential longitudinal sections show transverse sections of tracheids (fig. 28). Where the ends of the tracheids abut upon medullary rays from above or below, some end bluntly, others bend and run radially transversely for shorter or longer distances and thus, so far as arrangement is concerned, form transitions between tracheids of the body of the wood and ray-tracheids. This transition is even more remarkably shown by those tracheids which bend into a medullary ray, so that their terminal portions run in a transverse radial direction and their terminal walls end directly against a terminal wall

of a ray-tracheid (fig. 34). Other tracheids push their ends between the ray cells, so that in tangential section such tracheids may be seen cut transversely.

The bordered pits are mainly on the radial walls. In the wider spring-tracheids they are uniseriate or biseriate with circular apertures (fig. 35). The biseriate pits are circular in outline or slightly flattened where the pits are in lateral contact. The chambers of the uniseriate pits are often elliptical in contour with the long axis transverse. In the narrow summer-tracheids the radial pits are much scantier, uniseriate, and have oblique narrow fusiform apertures (fig. 36).

In addition to the bordered pits on the radial walls there are others on the oblique lateral walls of tracheids that are hexagonal and pentagonal in transverse section, and on tangential walls of some tracheids (fig. 30). These tangential pits occur in the first place on tracheids that are contiguous with the parenchyma on the radially inner and outer sides of the resin-ducts.

Tangential pits also occur often, if not exclusively, in the bundles of bent tracheids already described, especially or solely near the ends of the obliquely directed portions. Here they are most abundant in the spring-wood though not absent from the summer-wood. Inasmuch as these bent tracheids form radial series and their bent ends are often at approximately the same level, in transverse sections the tangential pits are seen in radial rows. The occurrence of bordered pits on the tangential walls of species of *Pinus* that usually have none has been recorded (see Strasburger), but in such cases the tangential pits appear to be characteristic of unusually narrow annual rings, whereas in *Pinus Khasya* these radial bands of tracheids with tangential pits occur in wide annual rings.

Finally, bordered pits occur on the transverse or bluntly rounded walls of the same types of tracheids that have tangential pits, as well as on tracheids that end bluntly against ray-tracheids (fig. 29).

Sanio's rims are distinct in the spring-wood (fig. 35).

As seen in the radial section, the walls of the tracheids in contact with the medullary rays are thicker than elsewhere, as in the case with resin-tracheids of *Dammara*. As there is no question of resin-tracheids here, the thickening of the wall in *Dammara* may be connected with the proximity to the medullary ray and not with the existence of resin-plates.

Resin-Ducts.

The resin-ducts are most numerous in the outer half of the annual ring, where they tend to form a tangential series as seen in transverse section. Very few isolated ducts occur at the inner boundary of the annual ring. Outside this zone succeeds a spring-zone devoid of ducts.

The ducts in place of being solitary are usually clustered in groups of two, three or even more. Frequently a medullary ray divides the cluster, which often includes two kinds of ducts—normal wide ones and much narrower ones. The diameter of a large resin-duct measured was nearly 80μ and the radial diameter of the epithelium-cells nearly 18μ . The duct itself is walled by a single layer of flattened peripherally extended thin-walled cells which tend to be somewhat elongated in a longitudinal direction. Around these is a collection of thin-walled parenchyma which is more extensive than usual. These cells are more elongated than those walling the duct, and towards the surrounding tracheids are increasingly narrow and long, their walls not being lignified. Where a resin-duct is close to a uniseriate medullary ray, this parenchyma may also form a radial series on the distant side of the ray. Outside the thin-walled parenchyma there occur two other types of cells: thick-walled parenchyma and parenchyma-tracheids. Sometimes the latter are separated from the thin-walled parenchyma by the former (fig. 31). The thick-walled parenchyma-cells are elongated, and on their longitudinal walls occur numerous more or less broad or narrow fusiform simple pits, which are elongated transversely or obliquely. The parenchyma-tracheids are shorter than ordinary tracheids and their bordered pits are considerably smaller than those of the surrounding normal tracheids. Where a tracheid abuts on parenchyma the pit is half-bordered.

Medullary Rays.

The uniseriate rays may reach a height of twenty cells, and the fusiform scarcely exceed this or are shallower. Apart from the resinous epithelium, the rays are mainly composed of ray-tracheids and thin-walled parenchyma, though parenchyma with somewhat thicker walls is not entirely lacking.

The *ray-tracheids* are denticulate, bear bordered pits on all their walls; the terminal walls are transverse or oblique. The length of the ray-tracheid equals the radial width of 3–4 wood-tracheids in the spring-wood, and about 6 in the summer-wood.

The *thin-walled parenchyma-cells* mainly have transverse terminal walls, and in length are equal to the radial width of 5–6 tracheids in the spring-wood, and 3–4 in the summer-wood. On the lateral walls the pits are large and only little less high than the cell itself (fig. 27). There is usually one pit to the radial width of a tracheid, both in the spring-wood and the summer-wood, and in the latter the shape varies from oblong-oval with the long axis usually horizontal to oblique broadly fusiform. In the spring-wood the large pit may be divided into two or rarely into three or four small ones, whose contours are fusiform oval or nearly circular. Passing to the summer-wood, the aperture of the single large pit on the side towards the

tracheid gradually narrows and its long axis is increasingly erect (fig. 37) : while the aperture and contour on the side of the wall truly belonging to the parenchyma-cell remains broad, fusiform or nearly circular. Occasionally the pit-membrane bulges into the contiguous wood-tracheid. The terminal and upper and lower walls are devoid of pits. In tangential section the cells are, in the uniseriate rays, mostly vertically elongated, being oval-oblong, but more rounded in the fusiform rays.

Parenchyma-cells with slightly thicker walls occur. They differ from the thin-walled cells also in the occasional occurrence of pits in the terminal, upper, and lower walls.

The *uniseriate rays* show marginal and internal ray-tracheids, which may be replaced by parenchyma when crossing a resin-duct. The proportion of parenchyma and ray-tracheids varies. Some low rays are composed entirely of ray-tracheids ; in taller rays, too, ray-tracheids may preponderate (fig. 32).

The *fusiform rays* include a small resin-duct which is the central or nearer to the upper or the lower margin. Outside the epithelium is a somewhat similar layer of flattened thin-walled parenchyma, which here and there is interrupted by flattened cells which have thick lignified walls on the side distant from the epithelium. Above and below this tissue the ray is two cells in thickness, but there are only two biseriate layers of cells, which are parenchymatous, either thick-walled or thin-walled. Elsewhere the ray is uniseriate and composed of parenchyma and marginal and internal ray-tracheids (fig. 33).

PINUS MERKUSII, *Jungh. & de Vriese.*

In habitat this two-needed species is the most tropical in Asia, as it occurs in the Philippines and Cochin China, and stretches from Burma southwards to the Malay Peninsula, at altitudes varying from 300 to 3,500 feet, and reappears in Sumatra. As regards supply of moisture the tree appears to be capable of enduring considerable dryness, for it is found in hot dry forests on the Shan Hills, but judging from its distribution elsewhere the species also flourishes on sites where at least atmospheric moisture is abundant. The bark is thick.

A. MACROSCOPIC FEATURES (naked eye).

The yellowish-brown heart-wood shows very sharply marked annual rings, of which there were about eighteen to the inch radius in our specimen, and eleven in the specimens mentioned by Gamble. Thus, in spite of the tropical distribution, growth in thickness appears to be comparatively slow. The reddish-brown summer-wood is sharply and suddenly marked off from the

lighter yellowish-brown spring-wood of the same annual ring. The proportion between these two types of wood varies; in our specimen the summer-wood is about equal in quantity to the spring-wood, and is well developed in most annual rings, so that the wood is rather hard and heavy.

The resin-ducts are distinct in cross-section and more abundant in the summer-wood than in the spring-wood: they are marked as brown lines in longitudinal view.

B. MICROSCOPIC STRUCTURE.

Tracheids.

In transverse section the spring-tracheids are rectangular or feebly hexagonal, oblong, with the long axis radial. A marked feature of the spring-tracheids is the unusually large size of the lumina, associated with the moderate thickness of wall. This type of structure with radial elongation of the lumen persists throughout the spring-wood, and is correlated with the 1-3-seriate arrangement of the bordered pits on the radial walls. In the inner summer-wood not only are the walls thicker, but also in transverse section the lumen is rounded and approximately isodiametric or slightly shorter in a radial direction. The shortening of the radial diameter is most marked in the late summer-wood, so that the outermost two layers of tracheids have flattened lumina.

The tracheids normally have typical rounded tips but occasionally show long tail-like continuations. On the medullary rays they terminate with blunt, flat ends or the terminal parts are bent, so that in extreme cases the curvature attains an angle of 180° ; thus in longitudinal tangential section transverse sections of these "wood-tracheids" are to be seen in contact with the medullary rays.

One remarkable feature in this typical pine is the extraordinary length of the tracheids, which often attain 7 mm. in length. The mean dimensions of the tracheids are shown in the succeeding table, and they show the very great size of the lumen of the spring-tracheids.

	SPRING-WOOD.		OUTER SUMMER-WOOD.	
	Radial.	Tangential.	Radial.	Tangential.
Width of lumen	68.5 μ	45 μ	10 μ	27 μ
Thickness of wall	4.9 μ	4.9 μ	6 μ	8.2 μ

The structure of the radial walls and the arrangement of the bordered pits.

have already been described in the general part of this paper. Here attention may be merely directed to the facts that Sanio's rims sometimes more or less completely surround the pit-bearing patch on the wall (figs. 43, 46, 47), also that they may be visible as oblique lines enclosing a single pit (fig. 46) and even separating two pits at the same level (fig. 48). As the pits become uniseriate near or in the summer-wood and the wall is thicker, Sanio's rims dwindle to mere crescents bounding the upper and lower margins of the pit, or one margin only (fig. 44). Proceeding farther out in the annual ring, even these vanish and no Sanio's rims are visible.

In the summer-wood the pits on the radial walls are scantier and are uniseriate.

The bordered pits on the radial walls of the spring-wood are oval or circular in outline, or slightly flattened where close to a neighbouring pit, and the aperture is circular in outline. But in the summer-wood although the pit is circular in outline the aperture is short, fusiform, and oblique or nearly vertical (fig. 49).

Pits are not entirely wanting on the tangential walls, for they occur both in the spring-wood and summer-wood, more especially near the slightly bent tapering ends of bundles of radially deflected bundles of tracheids, which recall the more extensively bent bundles of *Pinus Khasya*. Occasionally, tangential pits occur on the outer walls of the inmost layer of tracheids of the annual ring.

Bordered pits also occur on the rounded ends of some tracheids. Radial lignified bars, "Sanio's bars," stretching across the lumina of radial rows of tracheids also occur.

The walls of the tracheids, as seen in radial section, are thicker against the medullary rays than elsewhere.

Resin-Ducts.

The resin-ducts are fairly numerous and are almost confined to the summer-wood.

The thin-walled epithelium is surrounded by tissue composed of three kinds of cells :—

- i. More elongated parenchyma-cells, with somewhat thicker cellulose-walls, which bear large simple oval transversely extended pits.
- ii. Very elongated parenchyma-cells with lignified walls bearing obliquely-directed simple pits that are smaller than those on the thinner-walled parenchyma (fig. 42).
- iii. Parenchyma-tracheids whose lateral walls have bordered pits that are circular in outline but have long oblique fusiform apertures. Bordered pits occur also on the transverse terminal walls (fig. 42).

Medullary Rays.

The uniseriate rays attain a maximum height of 17 cells: the fusiform rays are relatively shallow, in fact not so tall as the highest uniseriate rays.

The ray-tissue includes, apart from the resin-ducts, three extreme types of cells: thin-walled and thick-walled parenchyma, and ray-tracheids.

The *parenchyma* is mainly of the thick-walled type. The terminal walls are more or less transverse and include a few rounded simple pits. On the lateral walls, to the radial width of one spring-tracheid there are 1-5 large pits, which are in one tier if 2-3 in number, and are in two tiers if 4-5. When, as is usual, there is only one tier of pits on the radial wall, the height of the pits is not much less than that of the cell. The pits vary in contour from oblong or radially elongated to circular or oval vertically elongated (fig. 50). In the summer-tracheids on the lateral walls there is only one pit to the radial width of one tracheid, and this pit has an oblique oval or a circular outline with a long, narrow, nearly vertical, fusiform aperture, towards the wood-tracheid (fig. 45). The upper and lower walls have numerous simple pits of rounded outline. In some of the rays markedly narrower and broader parenchyma-cells of this type are to be distinguished. The usual length of a cell is equal to the radial width of 4-5 spring-tracheids or 4-6 summer-tracheids. The lateral walls do not bulge into the contiguous tracheids. In tangential section the cell is oval, erect or circular (fig. 39).

The *thin-walled parenchyma-cells* are radially elongated with walls that are not pitted.

The *ray-tracheids* have denticulate walls, and their ends are straight and transverse or oblique, or are convex. The walls often are locally thickened to such an extent that in tangential sections the ray-tracheids present the appearance of fibro-tracheids (see fig. 39). Marginal and internal ray-tracheids occur, and the former often assume peculiar forms, especially in the summer-wood, as the terminal part emits a lateral process which either grows over the next ray-tracheid (fig. 41) or forms a more or less erect caecum. In the latter case the ray-tracheid in shape and direction is transitional towards a wood-tracheid that applies its bent end to a medullary ray. When passing a resin-duct the ray-tracheid may be replaced by a thick-walled parenchyma-cell, but ray-tracheids are also found crossing a resin-duct: possibly, in this and other species of *Pinus*, the change from ray-tracheid to parenchyma does not take place if the ray is passing a point at which parenchyma-tracheids are in contact with the ray, but does take place if the ray comes into direct contact with parenchyma around the duct.

The *uniseriate rays* vary considerably in composition. All four types of cells occur in them, and the ray-tracheids are internal as well as marginal. One ray for instance showed the following composition (the Roman numbers

representing the number of ray-tracheids, and the Arabic representing those of the thick-walled parenchyma): III, 3, IV. 4, III; another showed III, 3, III. Ray-tracheids are evidently well-represented. Some uniseriate rays are composed solely of thin-walled parenchyma and ray-tracheids. A marked feature of these rays is the large size of the intercellular spaces.

It was not possible to get perfect preparations of the *fusiform rays*, as these were all attacked by a fungus. The resin-duct was seen to be surrounded by thin-walled parenchyma, which extends for some distance towards the upper and lower margins, which were composed of ray-tracheids, or partly thick-walled parenchyma (fig. 40).

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EXPLANATION OF THE PLATES.

PLATE 24.

The magnification is 312, excepting in the cases of Fig. 17 ($\times 520$), Fig. 18 ($\times 140$), and Figs. 11 & 12 ($\times 240$ circa), Fig. 31 ($\times 72$).

Pinus Gerardiana.

- Fig. 1. Fusiform ray, tangential section.
 2. Parenchyma and parenchyma-tracheids adjoining resin-duct.
 3. Ray-parenchyma in summer-wood, radial section.
 4. Medullary ray in spring-wood, radial section.
 5. Uniseriate medullary ray, tangential section.
 6. Spring-tracheid, view of radial wall.
 7. Outer summer-tracheid, view of tangential wall.
 8. Summer-tracheid, view of radial wall.

Pinus excelsa.

- Fig. 9. Medullary ray in spring-wood, radial section.
 10. "Distended" medullary ray, radial section.
 11. Medullary ray with lobed marginal ray-tracheids, radial section.
 12. Medullary ray with very narrow ray-tracheids, radial section.
 13. Fusiform ray, tangential section.
 14. Outer summer-tracheid, view of tangential wall.
 15. Summer-tracheids, radial section.
 16. Spring-tracheids, view of radial walls.
 17. Uniseriate ray, tangential section of ray-parenchyma.

Pinus longifolia.

- Fig. 18. "Double annual ring," transverse section.
 19. Fusiform medullary ray, tangential section.
 20. Thick-walled parenchyma adjoining resin-duct and medullary ray, tangential section.
 21. Summer-tracheids, radial section.
 22. Tangential section showing a transverse section of a "Sanio's bar."
 23. Medullary ray in summer-wood, radial section.
 24. Medullary ray in spring-wood, radial section.
 25. Uniseriate medullary ray, tangential section.
 26. Spring-tracheid, radial section.

PLATE 25.

Pinus Khasya.

- Fig. 27. Medullary ray, radial section.
 28. Tangential section showing a wood-tracheid cut transversely.
 29. Radial section, showing pits on the terminal, radial, and tangential walls of tracheids.
 30. Summer-tracheid, showing pits on tangential and radial walls, tangential section.

- Fig. 31. Tissue adjoining resin-duct (which lay to the left), longitudinal section.
32. Uniseriate medullary ray, tangential section.
33. Fusiform medullary ray, tangential section.
34. Medullary ray, and bent wood-tracheids, in spring-wood, radial section.
35. Spring-tracheid, radial section.
36. Summer-tracheid, radial section.
37. Medullary ray, showing pits of ray-parenchyma, radial section.

Pinus Merkusii.

- Fig. 38. Wall of spring-tracheid, tangential section.
39. Uniseriate medullary ray, tangential section.
40. Fusiform medullary ray, tangential section.
41. Medullary ray with lobed marginal ray-tracheids, radial section.
42. Tissue adjoining resin-duct (which lay to the left), longitudinal section.
43, 46-48. Spring-tracheids, radial sections.
44. Late spring-tracheid or early summer-tracheid showing the last trace of Sanio's rims, radial section.
45. Medullary ray in summer-wood, radial section.
49. Summer-tracheid, radial section.
50. Medullary ray in spring-wood, radial section.
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