Comparative Morphology of the New Zealand Species of *Pseudopanax* and *Nothopanax*

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Abstract

ON comparison of leaves, inflorescences, flowers, nodal structure and wood histology the New Zealand species of *Nothopanax* and *Pseudopanax* fall into five groups. Tables of description of the secondary wood are given for one member of each group (*N. edgerleyi, N. colensoi, N. lineare, P. lessonii, P. crassifolium*), and that containing *N. edgerleyi* is considered the most primitive. *N lineare* is intermediate between this group and that typified by *P. crassifolium.* It is suggested that all five groups should be treated as sections of a single genus.

INTRODUCTION

GENERA in the Araliaceae are not well defined. Their limits depend very largely upon the number of carpels in the gynaecium and the degree of union of their styles (Bentham and Hooker, 1867). These features serve to divide New Zealand's woody araliads (apart from one species of *Meryta* and one of *Schefflera*) between two genera—*Pseudopanax* C. Koch in which there are five carpels, and the styles are short and more or less wholly connate, and *Nothopanax* Miq. in which there are typically two carpels and the styles, though sometimes fused basally, have free recurved tips. However, these criteria almost break down in certain cases—in *N. lineare* there are often five carpels, and only the well-developed free limbs of the styles (Cheeseman, 1914, Pl. 71) place the species in *Nothopanax,* while in *P. discolor, P. lessonii* and *P. gilliesii* the style tips are free, and in *P. discolor* they are widely divergent when the fruit is mature (Cheeseman, 1914, Pl. 74). Cheeseman (1914, Pl. 71) has suggested that more attention to vegetative characters might lead to a more natural grouping of the species, and the particular object of this investigation was to ascertain whether, in conjunction with external morphology, details of wood histology and nodal structure would prove of taxonomic value.

On the basis of leaf-form two well-defined subdivisions can be made in either genus as in Cheeseman's (1925) keys thus:—

Leaves similar in juvenile and adult plants, palmately compound:

(a) *Nothopanax colensoi, N. arboreum, N. laetum, N. sinclairii*—these with the deletion of *N. sinclairii* will be termed the *colensoi* group.

(b) *Pseudopanax lessonii, P. discolor, P. gilliesii*—the *lessonii* group.

Heterophyllous, leaves simple in both juvenile and adult plants but larger, narrower and (except in *P. chathamicum*) excessively coriaceous in the juvenile:

(c) *Nothopanax lineare*—the *lineare* group.

(d) *Pseudopanax crassifolium, P. ferox, P. chathamicum*—the *crassifolium* group.

In addition *Nothopanax* contains heterophyllous species in which the juvenile leaves are palmately-compound, but the adult leaves are simple:

(e) *Nothopanax edgerleyi, N. simplex, N. anomalum*—constituting with the addition of *N sinclairii* the *edgerleyi* group.

(*N. parvum* and *N. macintyrei* are excluded because they appear to be hybrids—Cockayne and Allan, 1934, p. 33.)

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To a considerable extent these subdivisions based on leaf form are justified florally—(b) includes all the species of *Pseudopanax* with free style tips; (c) is the only species which combines an ovary almost or quite of the *Pseudopanax* type with well-developed free style limbs; and in (d) fall all the *Pseudopanax* species with the styles connate to the tips even in fruit. Form and position of the inflorescence are also substantially uniform in each subdivision provided one change is made—a transfer of *N. sinclairii* to a position beside *N. simplex* since it lacks the large terminal compound umbels that are a conspicuous feature of *N. colensoi, N. arboreum,* and *N. laetum.* This change is supported by Cheeseman's (1925, p. 636) comment that these two species are scarcely separable apart from the retention of the 3–5 foliate condition in mature foliage of *N. sinclairii.* Moreover, it will be shown that when this change is made the resulting groups are consistent anatomically.

ANATOMY

In histology of the secondary wood all species proved to have the following features in common:—

1. Large, simple, elliptical pits between vessels and rays or parenchyma, tending to a scalariform arrangement. Solereder (1908), Hoar (1915), Record (1919, 1934), Dadswell & Record (1936), Record & Hess (1943) and Metcalfe & Chalk (1950) record a similar type of pitting for other members of the Araliaceae.
2. Scanty, paratracheal, vertical parenchyma in strands 3–8 cells high. Metcalfe & Chalk (1950) found this in other genera of the Araliaceae.
3. Fibres with few, scattered, simple or indistinctly bordered pits. The fibres are, therefore, the libriform wood fibres of Reinders (1935) & Bailey (1936) or the fibre-tracheids with reduced borders of Bailey (1936) and the International Association of Wood Anatomists (1937).
4. Septate fibres with relatively large simple pits, often not numerous, but very numerous in *P. lessonii.* Record & Mell (1924) state that septate fibres always have simple pits and record them in the Araliaceae, as also do Solereder (1908) and Dadswell and Record (1936).

Features of wood anatomy which serve to differentiate the species groups are set forth in Table I The number of leaf-trace gaps at the node is also included in this table. As Viguier (1909) has observed, the nodal structure is the same whether the leaves are juvenile or adult.

Table I requires some amplification. The tangential banding of the vessels confers a true ring-porous condition in *N. arboreum* and *N. anomalum* (Fig. 4) through the concentration of these bands towards the inner edge of the growth-rings, but in *N. colensoi, N. laetum, N. simplex* and *N. sinclairii* the bands are not thus concentrated—*N. colensoi* (Fig. 2) for example has two or three bands of vessels in each ring. *N. edgerleyi* has a wholly diffuse arrangement of the vessels (Fig. 1), and, together with *P. lessonii, P. crassifolium,* and *P. ferox,* lacks growth-rings. As appears commonly to be the case (Metcalfe & Chalk, 1950, p. xlviii), clearly defined growth-rings, true ring-porosity and tangential banding are characters not correlated with any others that have well-established phylogenetic significance, but all the woods possessing spiral thickenings, with the exception of *N. edgerleyi,* have proved partially or truly ring-porous.

Frost has shown (1930 a, b, c) that scalariform pitting and scalariform perforations are primitive features of the vessel elements, and that in evolution towards the advanced features of alternate pitting and porous perforations the pitting specialises more rapidly than the perforations. The New Zealand araliads illustrate this well. If the four stages of evolution in perforation and in pitting (Table II) are regarded as equivalent, it is apparent that almost every species has achieved a stage in evolution which for pitting is one in advance of that for perforation. But

Table I.—HISTOLOGY OF SECONDARY WOOD AND NODAL TYPE.

Group Feature	*edgerleyi*	*colensoi*	*lessonii*	*lineare*	*crassifolium*
Vessel arrangement	Scattered, in small clusters, chains or radial groups, or tangentially banded	Tangentially banded clusters	Radially aligned	Irregular clusters	Large clusters and radial groups
Vessel perforation	Scalariform	Simple	Mostly simple	Mostly scalariform	Mostly simple
Tertiary spirals	Present	Present	Absent	Absent	Absent
Intervascular pitting	All or mostly scalariform	Alternate	Mostly scalariform	About 50% scalariform	Mostly alternate
Fibre wall thickness	Thin	Thin	Thick	Mod. thick	Thick
Multiseriate Rays: Height Width Type	 Low Narrow Slight-mod heterogeneous	 Low Medium Almost homogeneous	 High Medium Heterogeneous	 High Medium Heterogeneous	 High Broad Markedly heterogeneous
Approx. % uniseriate rays	10%	1%	25%	40%	20%
Leaf gaps at node	3	9–16	5–7	3–5	5

Table II.—PERFORATIONS

Scalariform	Scalariform * –porous	Porous-oblique	Porous-transverse
N. edgerleyi	*N lineare*	*N. laetum*	Nil
N. simplex	*P. lessonii*	*N. colensoi*	
	P. discolor		
N. anomalum	*P crassifolium*	*N. arboreum*	
	P. ferox		
N. sinclairii	*P. chathamicum*		

* Mainly scalariform in *N lineare,* the remainder mainly porous.

Table III.—PITTING.

Scalariform	Mainly Scalariform	Mainly Alternate	Alternate
N. edgerleyi	*N. simplex*	*N. lineare*	*N. laetum*
	N sinclairii	*P. crassifolium*	*N. colensoi*
	N. anomalum	*P. ferox*	*N arboreum*
	P. discolor	*P. chathamicum*	
	P lessonii		

P. lessonii and *P. discolor,* like *Cheirodendron* (Record and Mell, 1924) are anomalous in sometimes retaining scalariform pitting in an element whose end wall has become porous.

In the *colensoi* and *edgerleyi* groups the fibres have thin walls and wide lumina so that in cross sections they are often indistinguishable from wood parenchyma The fibres of the *lessonii* group are much thicker-walled (Fig. 5).

The rays (Figs. 3 and 6) are all of Kribs' (1935) class "Heterogeneous II" since both uniseriates and multiseriates are present, and all species have rectangular, vertically elongated cells in some at least of the uniseriates, while the multiseriates have procumbent central cells and elongated or cubical marginal cells. This is the ray type most commonly associated with the types of vessel that are present (Kribs, 1935, p. 551).

A table of description along the lines suggested by Rendle & Clarke (1934a, b) has been prepared for one species in each group (Table IV). From each of four adult trees of each of these species five samples were collected at various heights, always including several growth-rings close to the bark so as to cover the sapwood. From appropriate preparations of each sample a fixed number of measurements (usually 25) was made at random.

TABLE IV.—SECONDARY WOOD IN NOTHOPANAX AND PSEUDOPANAX.

Means ± standard deviations. Total numbers of measurements (in parentheses).

Species Character	*N. edgerleyi*	*N. colensoi*	*P. lessonii*	*N. lineare*	*P. crassifolium*
Vessels					
Int. diam. (μ) (500)	26.81 ± 9.05	27.39 ± 15.05	36.43 ± 8.50	19.14 ± 6.27	25.70 ± 8.90
Length (μ) (500)	656.80 ± 140.88	590.60 ± 134.88	700.20 ± 169.63	614.55 ± 136.00	708.50 ± 159.63
No. per mm² (40)	186 ± 42	126 ± 54	83 ± 19	149 ± 38	133 ± 9
Fibres					
Wall thickness (μ) (500)	2.31 ± 0.67	2.46 ± 0.78	4.07 ± 1.02	3.11 ± 1.10	3.78 ± 0.91
Length (μ)	769.55 ± 142.50	731.73 ± 210.25	874.80 ± 193.63	738.10 ± 183.88	971.85 ± 230.88
Proportional elongation (%)	17	23	25	20	37
Rays (in L.T.S.)					
* No per mm	4.6 ± 1.5	3.8 ± 1.0	5.0 ± 1.0	6.5 ± 2.0	5.0 ± 1.0
§ Concentration (500)	18.97 ± 4.5	24.4 ± 6.7	34.66 ± 4.5	29.27 ± 5.0	31.74 ± 6.2
Multiseriates Height (μ) (500)	563.85 ± 299.50	552.35 ± 234.88	858.11 ± 372.14	899.50 ± 256.63	891.88 ± 312.12
Width (μ) (500)	55.78 ± 18.19	84.28 ± 29.68	85.68 ± 16.48	82.98 ± 32.41	103.23 ± 36.56
Width (No. of cells) (100)	4.01 ± 0.98	5.15 ± 1.40	4.38 ± 1.28	4.51 ± 1.08	6.14 ± 1.92
Uniseriates (%)	8.2	1.05	22.6	42.3	18.7
Height (No. of cells) (100)	3.4 ± 2.0	2.3 ± 1.3	4.8 ± 2.8	3.6 ± 2.0	3.3 ± 2.0

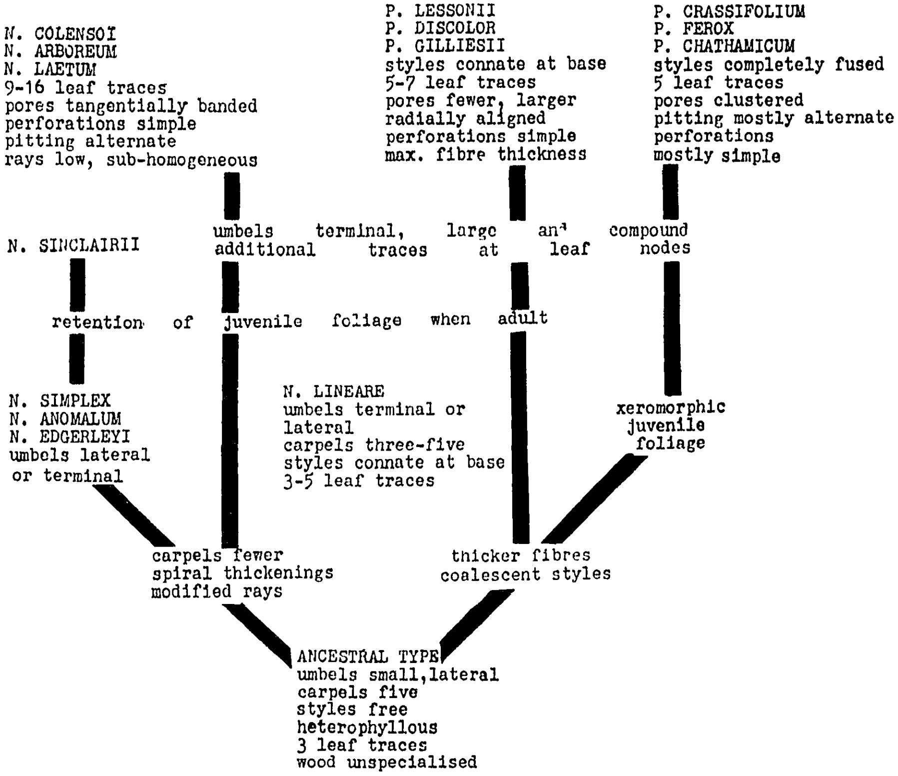
* Along the horizontal diameter of the field.

§ Total ray widths across the diameter of the field expressed as a percentage of the diameter.

DISCUSSION

The species studied have not been shown to possess any structural features not hitherto recorded in the Araliaceae, but the five groups into which they fall when gross morphology of inflorescence, flower and leaf are considered have proved to differ widely in the degree of specialization of their wood and in nodal structure. According to the phylogenetic views advanced by Sinnot & Bailey (1914), Frost (1930 a, b, c) and Kribs (1935), the *edgerleyi* group, with its strictly trilacunate nodes, scalariform perforations, scalariform pitting and thin fibre walls, seems the most primitive. *N. edgerleyi* itself is unique in the wholly unspecialized diffuse arrangement of its vessels, and is also the only member of its group which has more than two carpels. The *colensoi* group is specialised in nodal structure, and in having alternately pitted vessels with porous-oblique end-walls, and almost homogeneous rays with uniseriates nearly eliminated. The *lessonii* group is rather less specialised in the node, vessel and ray, but the fibres are thick-walled and the vessels aligned radially in a characteristic manner. The *crassifolium* group is considerably specialised in all features except ray-type. *N. lineare* seems to be truly intermediate between the *crassifolium* and *edgerleyi* groups except that it has smaller vessels than any other of the species studied in detail. Cytological evidence of its origin as a hybrid between the diverging *crassifolium* and *edgerleyi* lines might well be sought.

Rattenbury (1956), from comparison of chromosome numbers, has concluded that *N. simplex, N. edgerleyi* and *N. anomalum* constitute the more primitive species group in *Nothopanax*. The evidence of wood histology supports this view. He suggests that *N. colensoi* and its allies are neotenous, retaining in the adult a leaf form which was formerly a transient feature of development. Nevertheless the



TEXT-FIG. 1 —Probable course of evolution of the New Zealand species of *Nothopanax* and *Pseudopanax*. *N. lineare* is considered to occupy an intermediate position between the *Nothopanax* and *Pseudopanax* series, but the question of its derivation is left open heterophyllous ancestry of *N. colensoi, N. arboreum* and *N. laetum* would seem to be remote, since they resemble one another closely and are far in advance of any member of the *edgerleyi* group. *N. sinclairii* however, although also exhibiting neoteny, would appear to be a recent derivative of *N. simplex.* A corresponding neoteny in the *Pseudopanax* line before the juvenile foliage became simple and xeromorphic may be postulated to account for the origin of the *lessonii* group. Probable phylogenetic relationships of the species are shown diagrammatically in Text-fig. 1. The exact position of *N. lineare* is doubtful. On the basis of floral morphology and nodal and wood structure, it would appear that it may have diverged from the *crassifolium* line earlier than the *lessonii* group. On the other hand, the possession of simple, xeromorphic, juvenile foliage relates it more closely to the *crassifolium* group, and suggests that it may show the relatively recent combination of *crassifolium* and *edgerleyi* characters by hybridisation.

All five groups of species might well be treated as subgenera of a single genus as they seem to be equivalent in status. However, allied species outside New Zealand would need to be considered before this step were taken. For the present, it does appear that the *lessonii* group are better placed in *Pseudopanax* than in *Nothopanax.* The only advantage not hitherto apparent in including *N. lineare* in *Pseudopanax* is that all species with thick-walled fibres and large rays would then be together. However, floral structure remains a substantial objection to this course.

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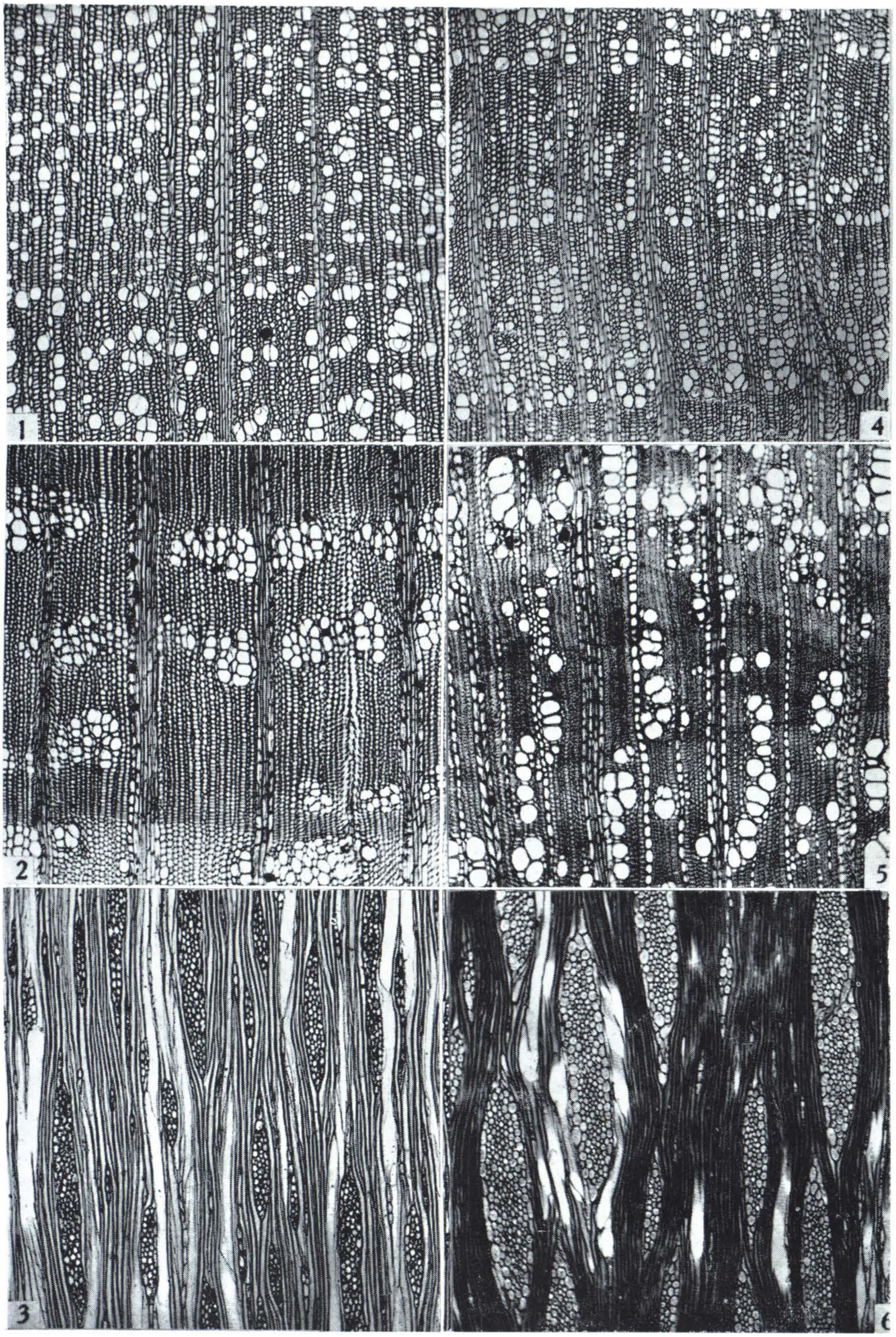

Secondary wood × 45.

FIG. 1.—T.S. *N. edgerleyi*. FIG. 2.—T.S *N. colensoi*. FIG. 3.—L.T.S. *N. edgerleyi*. FIG. 4.—T.S. *N. anomalum*. FIG. 5.—T.S. *P. lessonii*. FIG. 6.—L.T.S. *P. crassifolium*.

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