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CUTICLE MICROMORPHOLOGY OF *PRUMNOPITYS* PHILIPPI (PODOCARPACEAE)

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Cuticle micromorphology of leaves from all 10 species and one variety of the conifer genus *Prumnopitys* Philippi (Podocarpaceae) was studied with scanning electron microscopy. Both herbarium and preserved specimens were examined and showed no differences in micromorphology. External and internal features of abaxial and adaxial cuticles are characterized for all 10 species and compared to other known podocarps. External cuticles exhibit undulating surfaces that may reflect underlying epidermal cell outlines, Florin rings, and stomatal plugs. Stomata have two to seven subsidiary cells, often with polar subsidiary cells lacking. There is a crease in subsidiary cell cuticle near the guard cells that corresponds to the Florin ring externally. Cuticle on subsidiary cells usually shows an irregular outer wall flange, granular to pitted surface, and horizontal and/or vertical striations. Polar extensions occur in all species but are less pronounced in section *Sundacarpus*. A rolled flange of cuticle occurs between guard cells and subsidiary cells and can be extensive in some taxa. Epidermal cell outlines are sinuous in most species; however, this character is variable within the genus. Epidermal cell surfaces are generally granular and pitted. Cuticle micromorphology supports the separation of *P. amara* into a separate section (or even separate genus) from the other taxa in the genus and indicates the reevaluation of *P. montana* var. *meridensis* as a separate species of the genus.

Introduction

The genus *Prumnopitys* Philippi contains 10 species that range from Australia and New Caledonia to New Zealand and from Chile to Venezuela and Costa Rica (de Laubenfels 1988). For many years this genus was treated as section *Stachycarpus* of the genus *Podocarpus* (e.g., Buchholz and Gray 1948*b;* Gray and Buchholz 1951). In recent years, however, most authors treat this group of species as a separate genus within the Podocarpaceae (de Laubenfels 1969, 1972, 1978, 1988; Silba 1984, 1986; Woltz 1986). The genus *Prumnopitys* contains small to large trees up to 60 m tall that grow in moist forest habitats (de Laubenfels 1978, 1988). *Prumnopitys* like *Podocarpus* species have one vein per leaf, with helically arranged, bifacially flattened leaves. Leaves lack a hypodermis and may have a decurrent base with a twist near the stem so that leaves appear distichous (de Laubenfels 1988). There is one resin canal adaxial to the vein in the leaf as opposed to several in the genus *Podocarpus,* and they lack an enlarged basal receptacle below the ovules (Silba 1984).

The genus is divided into two sections: section *Prumnopitys* and section *Sundacarpus* (de Laubenfels 1988). Section *Sundacarpus* contains one species, *P. amara* (Blume) de Laubenfels, that is found in Sumatra and the Philippines to northeastern Queensland and New Ireland (de Laubenfels 1988; Page 1988). Page (1988) has suggested that this species be separated from the genus and has placed it in the genus *Sundacarpus* (Buchholz et Gray) Page.

In this article we examine micromorphological features of all 10 species and one reported variety of the genus *Prumnopitys,* using scanning electron microscopy (SEM). One species, *P. ferruginoides* (Compton) de Laubenfels, previously examined by Stockey and Ko (1988), was reexamined here using a larger sample size for comparison with the other taxa. The seven of the 10 extant species of the genus were studied at the light microscope level by Greenwood (1987). Fossils attributed to the genus were studied by Greenwood (1987), using light microscopy, and Pole (1992), using SEM.

Because of the complex relief of many gymnosperm cuticles, SEM provides more detail than possible with the light microscope (Stockey and Ko 1986; Wells and Hill 1989). Micromorphological similarities are assessed to determine which characters can be used most consistently for taxonomic purposes. The usefulness of micromorphological cuticular features in distinguishing these taxa is examined and comparisons are made between these and other known fossil and extant podocarps.

Material and methods

Leaves of all species were examined from herbarium material (table 1). In addition, preserved specimens of *P. ferruginoides* were also used. No cuticular differences were observed in leaves preserved in FPA (5 mL formaldehyde, 5 mL propionic acid, 90 mL 50% ethanol) and dried herbarium specimens.

Leaves were sectioned with the leaf margins intact, leaving both abaxial and adaxial epidermis attached for cuticle examination. All leaves were rehydrated in water for 24 h and then immersed in 20% CrO_3 (chromium trioxide) solution for 96 h (Alvin and Boulter 1974; Stockey and Ko 1986). From two to 10 leaves per species were examined with SEM, depending on available sample size.

Cuticles were washed in distilled water, air dried, and mounted on stubs with silver conductive paint. Both inner and outer surfaces of leaves were examined by SEM. Specimens were sputter-coated with 150 Å Au on a Nanotek Sputter Coater and examined with a Cambridge Stereoscan 250 at 20 kV.

All stubs are deposited in the University of Alberta Paleobotanical Collection (UAPC-ALTA). Stomatal distribution was determined by the examination of the external surfaces of several leaves. Descriptions disregard what is obvious debris on cuticle surfaces. All photographs are taken with the

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Table 1

PRUMNOPITYS PHILIPPI MATERIAL EXAMINED

Species	Herbarium	Voucher	Source
Section *Prumnopitys:*			
P. andina (Poep. ex Endlicher) de Laubenfels	P	Woltz 1982	Mission, Chile
P. exigua de Laubenfels	NY	Hawkes 4390	Valle Grande, N. Bolivia
P. ferruginea (D. Don) de Laubenfels	HO	E/0963	New Zealand
P. ferruginoides (Compton) de Laubenfels	MO	McPherson & Stockey 3960C	Mt. Dzumac, New Caledonia
P. harmsiana (Pilger) de Laubenfels	P	de Laub. 767	Colonia Tovar, Venezuela
P. ladei (Bailey) de Laubenfels	P	de Laub. P460	Mt. Spurgeon, Queensland
	CBG	Nursery 788 7904993	Aust. Nat. Bot. Gard., Cook District, Queensland
P. montana (Humb. et Bonpl. ex Willd.) de Laubenfels var. *montana*	P	Veillon, 100870	Parama de la Negra, Tachira, Venezuela
P. montana var. *meridensis* Buchholz et Gray	P	Woltz	Parama de la Negra, Venezuela
P. standleyi (Buccholz et Gray) de Laubenfels	P	Budowski 160470	Turrialba, Volcan de Poas, Costa Rica
P. taxifolia (Sol. ex D. Don) de Laubenfels	P	Molloy	Ahuriri, Canterbury, New Zealand
Section *Sundacarpus:*			
P. amara (Blume) de Laubenfels	P	Woltz	Coastal N.E. Queensland

long axis of the leaf parallel to the long axis of the plate, and stomatal orientations are given with respect to that axis.

Results

SECTION *PRUMNOPITYS*

PRUMNOPITYS ANDINA (FIGS. 1–10)

Adult leaves were collected at 1500–2000 m near Mission, Chile (table 1). Leaves are linear, bright green adaxially and glaucus underneath, straight or only slightly falcate, 15–24 mm long × 1.5–2.0 mm wide, with an inconspicuous midrib and a short petiole (Buchholz and Gray 1948*b;* Silba 1986). Stomata were observed only on abaxial surfaces.

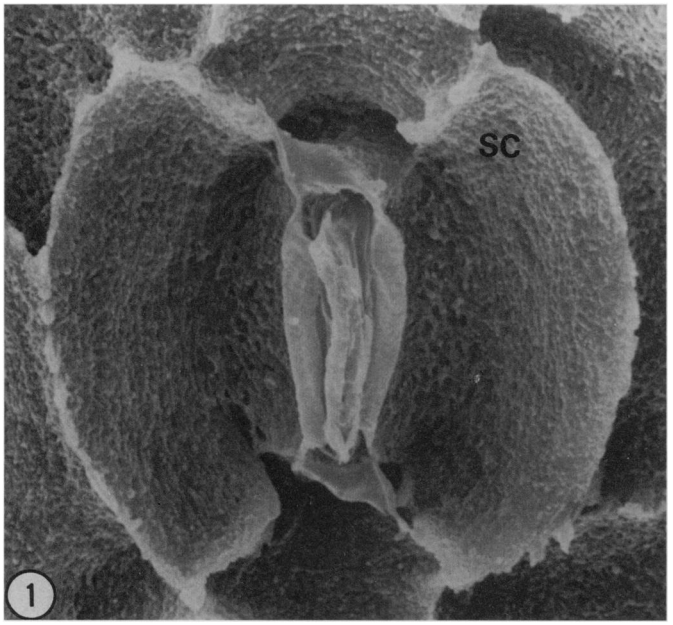
The external cuticle surface is undulating and covered with epicuticular waxes (table 2, fig. 4). Because of this covering, epidermal cell outlines are indistinct. Stomata are sunken and surrounded by Florin rings (fig. 4; Buchholz and Gray 1948*a*). Stomatal plugs are present and are composed of slender rods (figs. 4, 5).

Inner cuticle surfaces show stomata in indistinct rows oriented parallel to the long axis of the leaf (figs. 2, 3, 8, 10). Horizontal rows of stomata are as common as vertical rows (figs. 2, 8). The stomatal apparatus varies in shape depending on its proximity to others and the presence or absence of polar subsidiary cells (figs. 1–3, 8, 10). Two or three subsidiary cells are most common; however, up to six have been observed (table 3, figs. 2, 3). Commonly, polar subsidiary cells are absent and cells in this position show the same micromorphology as the surrounding epidermal cells (fig. 3). Lateral subsidiary cells have very broad flanges, and surfaces are sometimes striated (figs. 1, 10). Subsidiary cells from adjacent stomata are often in contact with one another, and unusual shapes result from crowding (figs. 3, 8, 10). Crescent-shaped encircling cells can occur when there is one cell between two adjacent stomata (figs. 3, 8).

Cuticle on the outer cell wall flange of subsidiary cells is thin and irregular and at nearly the same level as the epidermal cell wall flanges (figs. 1, 10). The surface of subsidiary cells is granular and pitted with striations (figs. 1, 9, 10). Horizontal striations occur on some stomata near the groove that corresponds to the position of the Florin ring on the outer surface. These grooves are not as distinct as they are in other species of *Prumnopitys.* Vertical striations have also been observed on some subsidiary cells (fig. 10).

The cuticular flange between guard cells is fairly thick (figs. 1, 9). Ribbon-like polar extensions occur that are more pronounced when over a subsidiary cell wall flange (fig. 1). The cuticle on guard cell surfaces is smooth to slightly granular, with a distinct ridge in the polar region (fig. 9). A rolled flange of smooth to slightly granular cuticle extends from the subsidiary cell partially over the lower surface of the guard cell (figs. 1, 9).

Epidermal cells are irregular in shape on abaxial surfaces but generally rectangular in outline when isolated from the stomata and more elongate between sto-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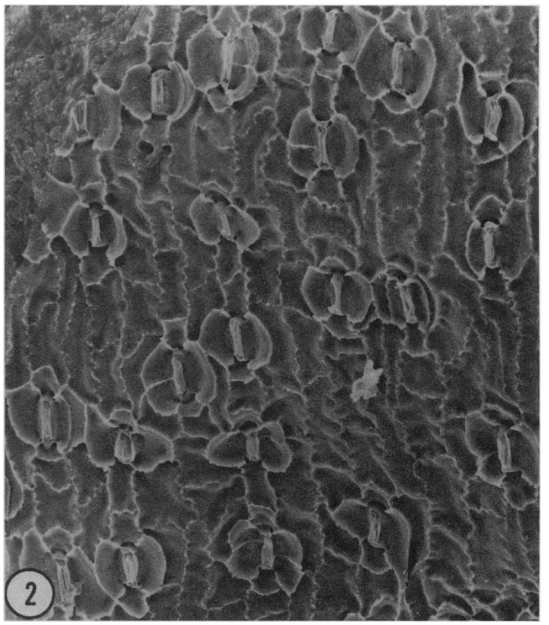
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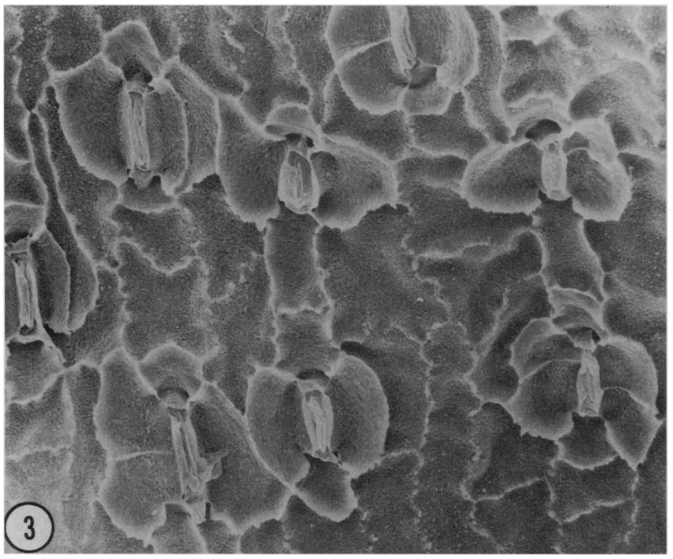
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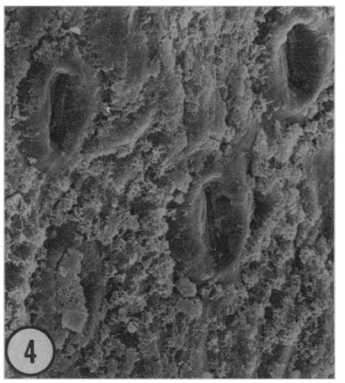
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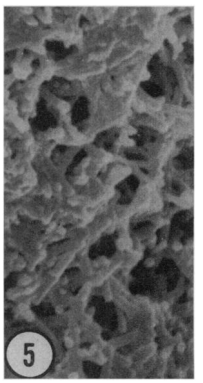
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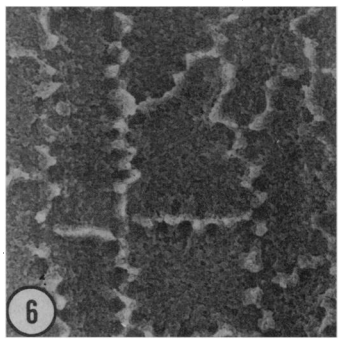
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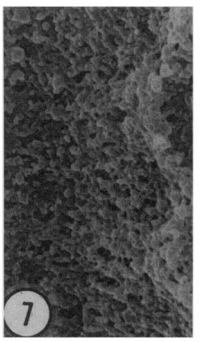
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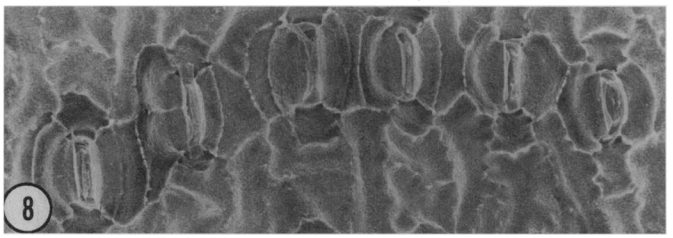
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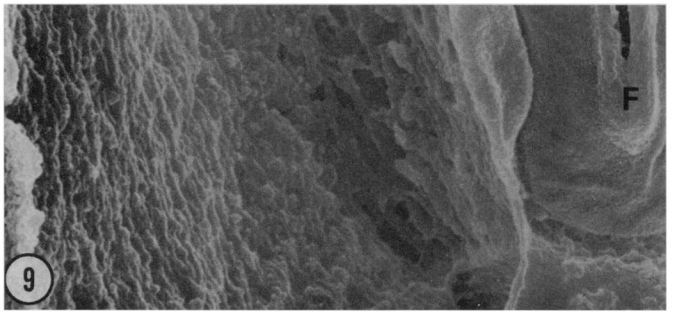
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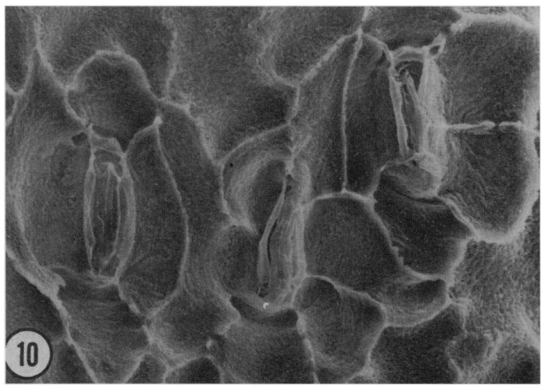
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Table 2

EXTERNAL CUTICULAR FEATURES ON LEAVES OF *PRUMNOPITYS* PHILIPPI

Species	Leaf dimensions (length × width, mm)	Stomatal plug components	Stomatal distribution[a]
P. andina	15–24 × 1.5–2.0	Slender rods	H
P. exigua	10–15 × 2	Rods	H
P. ferruginea	13–25 × 2	Short, slender rods	H
P. ferruginoides	9–18 × 2.5–3.5	Rodlike to globular	A
P. harmsiana	8–27 × 2.0–4.5	Slender rods	H
P. ladei	12–16 × 2.5–4.0	Short rods	A
P. montana var. *montana*	10–18 × 2.5–3.5	Short rods	H
P. montana var. *meridensis*	13–18 × 2.0–3.0	Fused rods	H
P. standleyi	12–18 × 2.5–3.5	Short rods	A
P. taxifolia	20–30 × 2	Solid rugose layers	H
P. amara	50–150 × 9–15	Globular	H

[a] H = hypostomatic; A = amphistomatic.

matal rows (table 3, fig. 2). Adaxial epidermal cells are generally rectangular (fig. 6). Epidermal cell wall flanges are sinuous on both leaf surfaces. Cuticle on epidermal cell surfaces is rugose and pitted (figs. 6, 7).

PRUMNOPITYS EXIGUA (FIGS. 11–21)

Adult leaves of this species were collected near Valle Grande, northern Bolivia, at 2600 m (table 1). Leaves are semilinear, straight to slightly falcate, sessile, somewhat narrowed at the base, 10–15 mm long × 2 mm wide, with a weak groove above the midrib (Silba 1986). Stomata have been observed only on abaxial surfaces.

The external cuticle surface is undulating and shows some evidence of epicuticular wax (figs. 14, 15, 17). Underlying epidermal cell outlines can be seen in many cases (fig. 14), unlike the situation in *P. andina.* Stomata show very distinct Florin rings that are slightly depressed into the cuticle surface (table 2, fig. 14). The close proximity of underlying stomata can also be seen by the presence of what appear to be two pairs of guard cells surrounded by a common ring (fig. 17). Stomatal plugs are present and are composed of rodlike components (figs. 15, 16).

Inner cuticle surfaces show very crowded stomata in discontinuous vertical rows (fig. 13). Many stomata are in lateral contact (fig. 13), as is seen in *P. andina,* but this character is not so pronounced in *P. exigua.* Three and four subsidiary cells are most common; however, these are usually divisions of lateral subsidiary cells (table 3, figs. 11, 12, 19). As in *P. andina,* polar subsidiary cells may be absent, but this is not as obvious because of the straight epidermal cell wall flanges on abaxial surfaces. In *P. andina,* epidermal cells have a very sinuous outline, and when they occur in the place of a subsidiary cell (e.g., fig. 3), the contrast between these cells is marked.

Cuticle on the outer cell wall flange of subsidiary cells is thick and irregular (figs. 11, 19, 21). Cuticle on subsidiary cell surfaces is pitted and slightly granular and has numerous vertical striations (figs. 11, 19, 21). Pitting is more pronounced near the surface of the leaf where the groove that corresponds to the external position of the Florin ring is more distinct (figs. 19, 21) than in *P. andina.*

The cuticular flange between guard cells is relatively thin (figs. 11, 21). Ribbon-like polar extensions, often with a central raised area corresponding to the line of separation between the guard cells, are pronounced and have a smooth to slightly granular surface (figs. 11, 19, 21). Cuticle on guard cell surfaces is granular, with a distinct ridge in the polar region and a continuous groove laterally (figs. 11, 21). A rolled flange of relatively smooth cuticle extends from the subsidiary cell, partially over the lower surface of the guard cell, as in *P. andina,* and often obscuring this cuticle surface (fig. 19).

Epidermal cell outlines are sinuous and generally rectangular on adaxial leaf surfaces (fig. 18). Cell shapes are more variable on abaxial surfaces but are usually rectangular and more elongate between stomatal rows (table 3, figs. 12, 13). Epidermal cells are less obviously sinuous on abaxial surfaces when SEM is used because of the thickness of the cuticle and the large epidermal cell wall flanges (fig. 12). Cuticle on epidermal cell surfaces is rugose (fig. 20).

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Figs. 1–10 *Prumnopitys andina.* Fig. 1, Inner view, abaxial cuticle on stomatal apparatus; × 2000. Fig. 2, Inner view, abaxial surface, showing stomatal rows; × 255. Fig. 3, Inner view, abaxial surface, showing variable subsidiary cell number; × 450. Fig. 4, Outer view, abaxial surface, showing rugose cuticle on epidermal cell surfaces, Florin rings, and stomatal plug; × 400. Fig. 5, Outer view, abaxial surface, showing stomatal plug components; × 6000. Fig. 6, Inner view, adaxial surface, showing shallow, undulating, epidermal cell wall flanges; × 475. Fig. 7, Inner view, abaxial cuticle on epidermal cell surface; × 2750. Fig. 8, Inner view, abaxial surface, showing a horizontal stomatal row; × 350. Fig. 9, Inner view, abaxial surface, cuticle on stomatal apparatus; × 5000. Fig. 10, Inner view, abaxial surface, showing stomata with irregular subsidiary cells of varying number; × 700. *F,* flange of cuticle between guard cells; *SC,* subsidiary cell.

Table 3

INTERNAL CUTICULAR FEATURES (μm) ON LEAVES OF *PRUMNOPITYS* PHILIPPI

Species	Stomatal dimensions (average polar × lateral)	Number of subsidiary cells	Epidermal cell dimensions (length × width)		Epidermal cell surface
			Between stomatal bands	Within stomatal bands	
P. andina	52 × 45	2 common; 3 common; 4, 5, 6 occur; polar cells absent	70 × 13	33 × 19	Rugose and pitted
P. exigua	51 × 40	3 common; 4 common; polar cells usually absent	44 × 10	20 × 19	Rugose and pitted
P. ferruginea	51 × 48	4 common; 5 common; 6 rare; polar cells present	38 × 17	40 × 26	Smooth to slightly granular
P. ferruginoides	49 × 37	4 common; 2–6 occur; polar cells usually lacking	77 × 24	35 × 33	Smooth with globules of variable size
P. harmsiana	40 × 34	2 common; 3–6 occur; polar cells absent	42 × 14	31 × 20	Very rugose and pitted
P. ladei	37 × 34	4 common; 5 occur; polar cells often present	30 × 13	16 × 18	Pitted and granular; finely granular on abaxial surfaces
P. montana var. *montana*	51 × 36	2 common; 3 common; 4–7 occur; polar cells often absent	43 × 21	32 × 22	Very pitted and rugose, more pronounced adaxially
P. montana var. *meridensis*	28 × 27	2 common; 3 common; 4, 5 occur; polar cells often absent	34 × 16	20 × 15	Finely pitted and granular
P. standleyi	41 × 35	4 common; 2–6 occur; polar cells often absent	44 × 15	18 × 15	Granular and pitted
P. taxifolia	40 × 31	4 common; 2–6 occur; polar cells absent or present	28 × 12	16 × 20	Granular to pitted; few large pits on adaxial surface
P. amara	47 × 32	4 common; 2–6 occur; polar cells present or absent	124 × 49	36 × 39	Granular and pitted

PRUMNOPITYS FERRUGINEA (FIGS. 22–30)

Adult leaves were collected from South Island, New Zealand (table 1). Leaves are dark green adaxially and yellowish abaxially, 1.3–2.5 cm long × 2 mm wide, slightly falcate with a narrow midrib, bluntly acute apex, and short petiole (Silba 1986). Stomata were observed only on abaxial surfaces.

The external surfaces of leaves are undulating and lack any obvious epicuticular waxes (fig. 25). Stomata are surrounded by slightly sunken Florin rings (table 2, figs. 25, 26). Epidermal cell rows are visible on the undulating cuticle surface, but individual underlying epidermal cells are difficult to distinguish (fig. 25). Stomatal plugs are present and are composed of slender short rods (figs. 26, 27).

Inner cuticle surfaces show stomata in indistinct rows (fig. 23), as is seen in *P. andina*. Horizontal rows of stomata are most commonly observed (fig. 23). Stomata are oriented parallel to the long axis of the leaf (figs. 23, 24). They are most often isolated from one another and are separated by at least one epidermal cell (figs. 23, 24). The stomatal apparatus is oval to nearly circular in outline, and polar subsidiary cells are usually present (figs. 22, 24, 28). Four or five subsidiary cells are most common, with six sometimes observed (table 3, figs. 22, 24, 28).

Subsidiary cell wall flanges are broad and the outer cell wall flange is thick and irregular (figs. 22, 28). The cuticle on the surface of subsidiary cells is slightly granular on the outer flange and distinctly granular and pitted near the groove that corresponds to the position of the external Florin ring (fig. 30). The groove in the subsidiary cell cuticle is more pronounced in this species than in the *Prumnopitys* species previously described. Vertical striations also occur on subsidiary cell surfaces in *P. ferruginea* (figs. 22, 28, 30), as in the two previously described species.

The cuticular flange between guard cells is relatively

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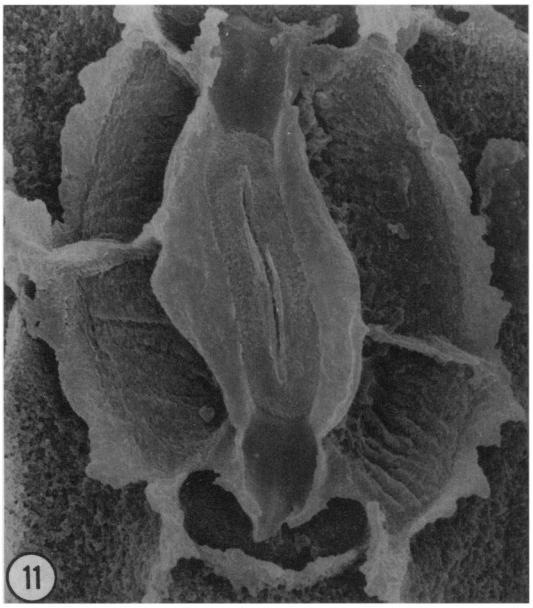
Figs. 11–21 *Prumnopitys exigua*. Fig. 11, Inner view, abaxial cuticle on stomatal apparatus with four subsidiary cells and prominent polar extensions; × 1600. Fig. 12, Inner view, abaxial surface, showing variable subsidiary cell number; × 475. Fig. 13, Inner view, abaxial surface, showing crowded stomatal rows; × 200. Fig. 14, Outer view, abaxial surface, showing Florin rings and undulating epidermal cell surfaces; × 350. Fig. 15, Outer view, abaxial surface, showing double Florin ring and stomatal plug; × 950. Fig. 16, Outer view, abaxial surface, showing stomatal plug components; × 7000. Fig. 17, Outer view, abaxial surface, showing double sunken Florin ring surrounding two pairs of guard cells; × 575. Fig. 18, Inner view, abaxial surface, showing sinuous epidermal cell outlines; × 300. Fig. 19, Inner view, abaxial surface, stomatal apparatus with four striated subsidiary cells, prominent polar extensions, and a large rolled flange of cuticle on guard cell surfaces; × 1200. Fig. 20, Inner view, abaxial cuticle on epidermal cell surface; × 1400. Fig. 21, Inner view, abaxial cuticle on stomatal apparatus; × 3250. *F*, flange of cuticle between guard cells; *PE*, polar extension; *SC*, subsidiary cell.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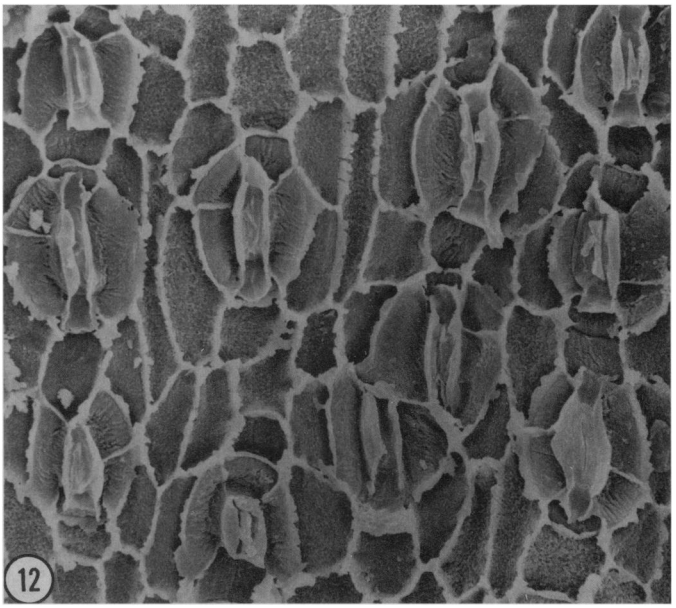
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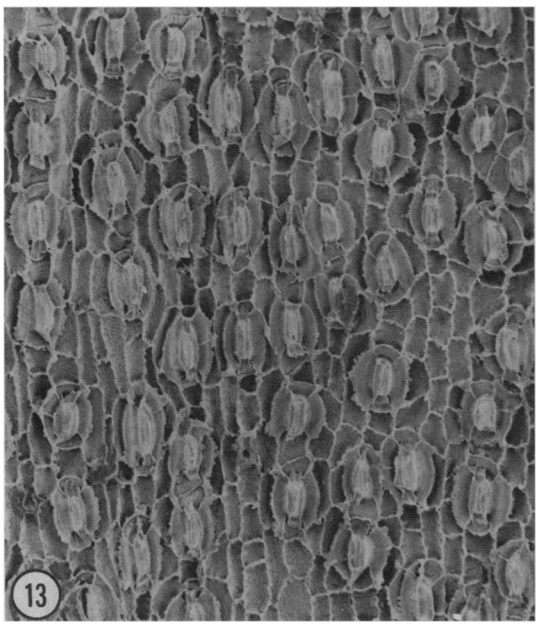
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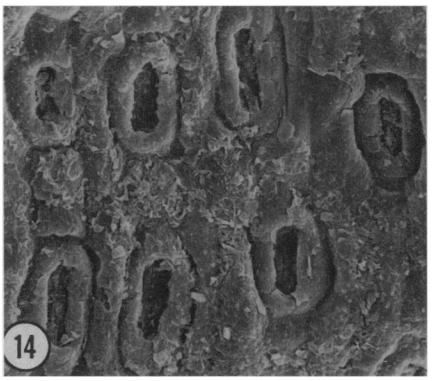
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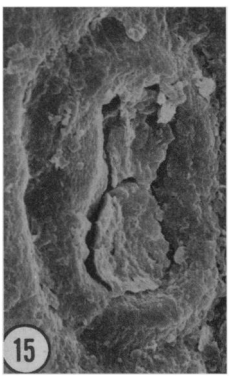
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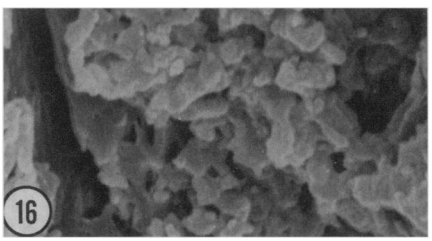
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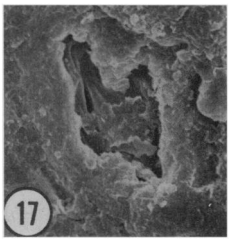
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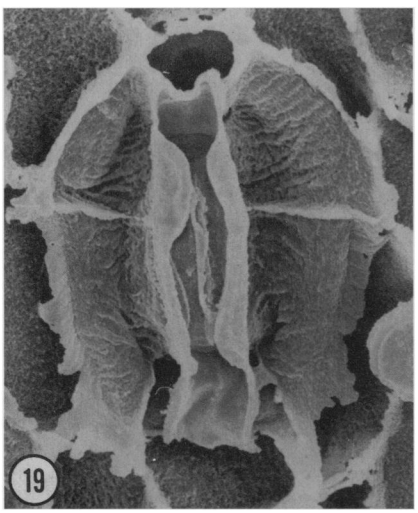
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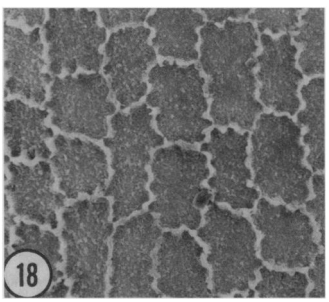
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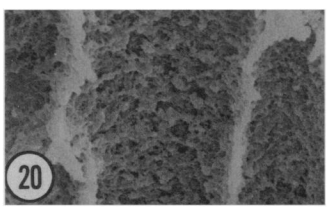
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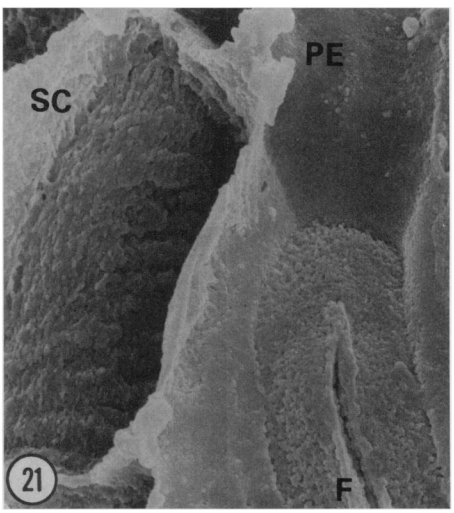
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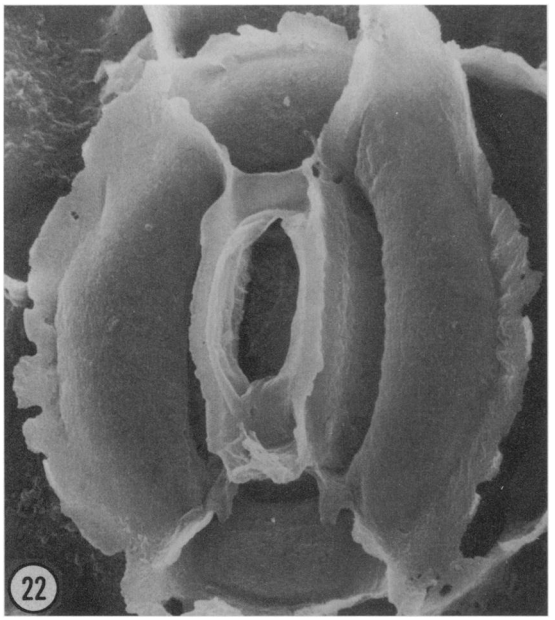
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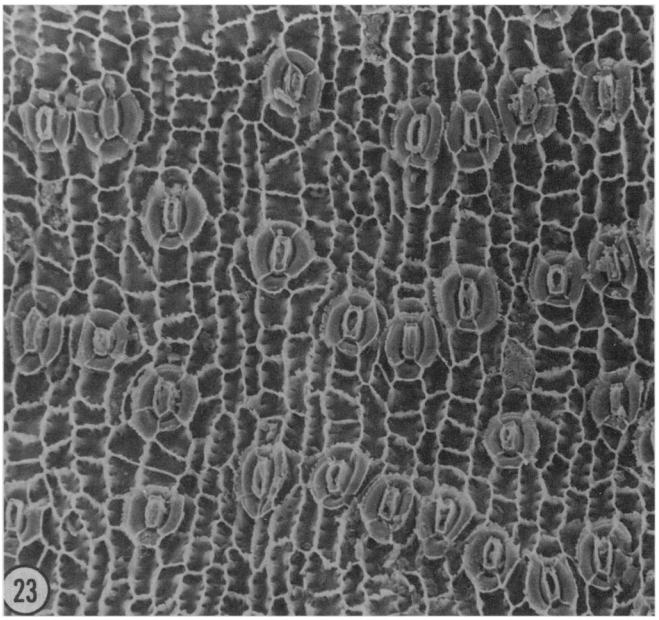
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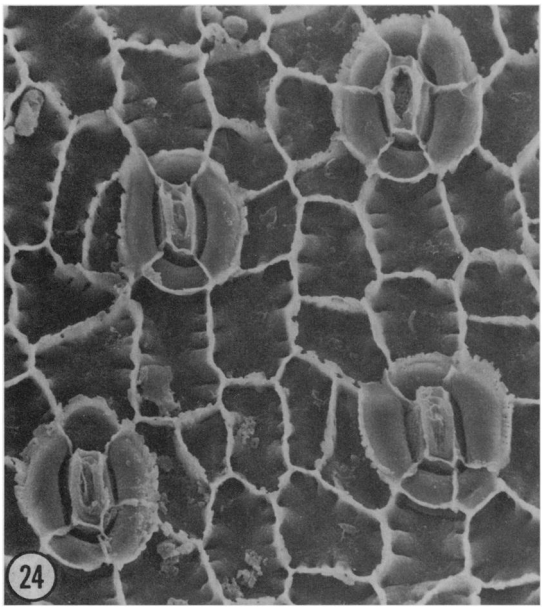
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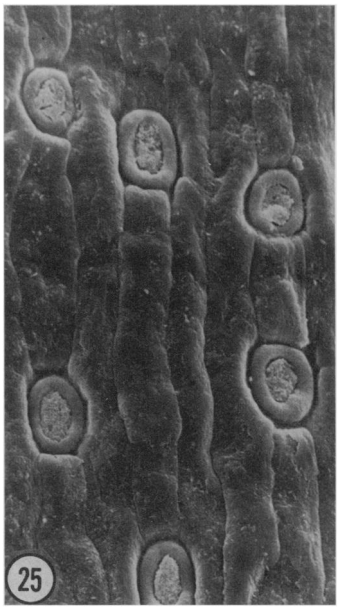
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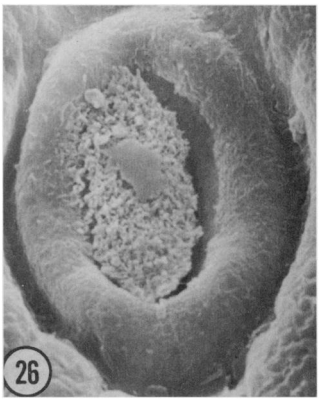
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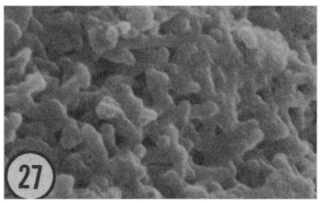
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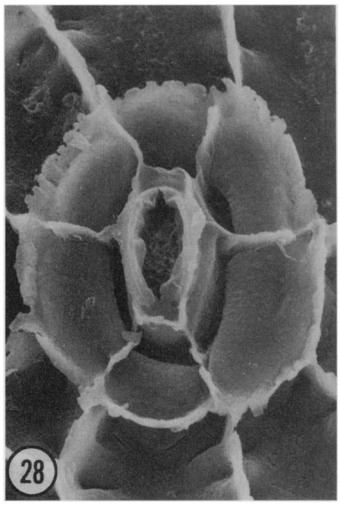
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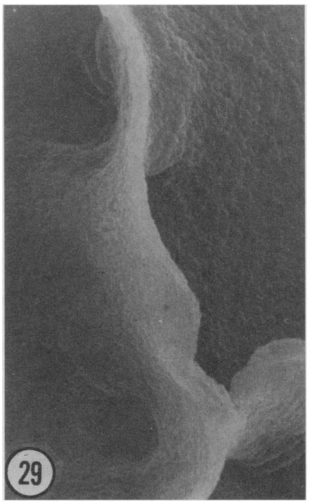
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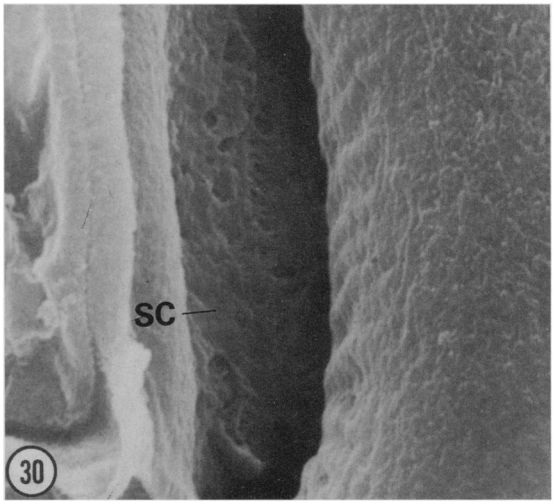
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thin and irregular (figs. 22, 28). Polar extensions are ribbon-like, short, slightly thicker over a subsidiary cell wall flange (figs. 22, 28, 30). The cuticle on guard cell surfaces is smooth to slightly granular, with a distinct ridge in the polar regions (figs. 22, 30). A flange of slightly granular cuticle extends from the subsidiary cell partially over the lower surface of the guard cell (figs. 22, 30). This flange may be slightly rolled but is not as extensive as in the previously described *Prumnopitys* species.

Epidermal cells are nearly rectangular in outline, with sinuous cell wall flanges that may show buttressing (figs. 24, 29). Horizontal striations are present on these buttresses (fig. 29). Epidermal cells between vertical lines of stomata are more elongate than those bordering stomata (fig. 23). Cuticle on both abaxial and adaxial epidermal cell surfaces is smooth to slightly granular (table 3, fig. 29) and not distinctly pitted as on some other species.

PRUMNOPITYS FERRUGINOIDES (FIGS. 31–42)

Adult leaves were collected along the Mount Dzumac Road from Dumbéa Valley in New Caledonia (table 1). Leaves are linear to oval, slightly concave abaxially, 9–18 mm long × 2.5–3.5 mm wide, with a faint midrib, a rounded apex with a mucronate tip, and a very short petiole (de Laubenfels 1972). Micromorphology of these leaves was first described by Stockey and Ko (1988), and our description here adds some variability based on a larger sample size.

The external cuticle surface shows undulations resulting from the underlying epidermal cells and lacks any visible epicuticular wax (table 2, figs. 34, 35). Stomata were observed on both abaxial and adaxial surfaces. Florin rings occur on abaxial surfaces and may be distinctly raised or just slightly raised from the cuticle on epidermal cell surfaces (figs. 34, 35). Stockey and Ko (1988) suggested that sometimes these rings occurred in slight depressions. We have also found that they can occur in chains, with a raised area that corresponds to the position of epidermal cells in a stomatal row (fig. 34). Both kinds of micromorphology can occur on different areas of the same leaf. Stomatal plugs occur on both leaf surfaces and are composed of rodlike to globular components (figs. 35, 38).

Internal cuticle surfaces show widely spaced stomata in discontinuous rows (figs. 32, 33). Stomata are oriented parallel to the long axis of the leaf, and horizontal stomatal rows have not been observed (figs. 32, 33, 36). From two to six subsidiary cells are present. Four subsidiary cells are most common but five and six also occur (table 3, figs. 31, 33, 36, 37, 41, 42). In some cases, polar subsidiary cells are lacking and short cells with epidermal cell micromorphology occur in this position (figs. 33, 36). Lateral subsidiary cells usually have broad crescent-shaped or winglike flanges when two cells are present (fig. 31). The shape of the stomatal apparatus varies according to the number of subsidiary cells present (figs. 31, 41, 42). Occasional crescent-shaped encircling cells occur near some stomata (figs. 33, 37).

Cuticle on the outer lateral subsidiary cell wall flanges is thick and irregular (fig. 31). The surface of subsidiary cell cuticle is very rugose and pitted, with a large crease near the guard cells that corresponds to the external position of the Florin ring (figs. 31, 40, 42). Horizontal striations can occur in this groove (fig. 40) and vertical striations are also present on subsidiary cell wall surfaces (figs. 31, 40, 42).

The cuticular flange between guard cells, as Stockey and Ko (1988) report, is thick to thin and, as is seen here, can be rugose (figs. 31, 40, 42). Ribbon-like polar extensions are quite pronounced in this species and often show a bifurcation (fig. 31). The cuticle on guard cell surfaces is rugose to pitted, with a prominent polar ridge (figs. 31, 40). The flange of cuticle between subsidiary cells and guard cells is thick and rugose and can be somewhat rolled (fig. 40).

Epidermal cells are variable in shape and are more elongated between stomatal rows (table 3, figs. 32, 33). Cell wall flanges are not sinuous (figs. 32, 33, 36, 37), as in the previously described species of *Prumnopitys*. Cuticle on both epidermal cell surfaces is smooth, with small globules of variable size, but lacks the pitted appearance of many of the other *Prumnopitys* species (figs. 31, 39).

PRUMNOPITYS HARMSIANA (FIGS. 43–52)

Adult leaves were collected from Colonia Tovar, Venezuela (table 1). Leaves are spirally arranged, lanceolate, linear, 0.8–2.7 cm long × 2.0–4.5 mm wide, and have a slight ridge above the midrib, lack a petiole, and have a spinelike apex (Silba 1986). Stomata have only been observed on abaxial surfaces.

The external cuticle surface is undulating, with underlying epidermal cell rows visible (fig. 46). Large amounts of epicuticular wax have not been observed. Stomata are sunken and surrounded by Florin rings that are at about the same level as the surrounding epidermal cells (table 2, figs. 46, 47). Occasionally a double Florin ring occurs (fig. 47). Stomatal plugs are

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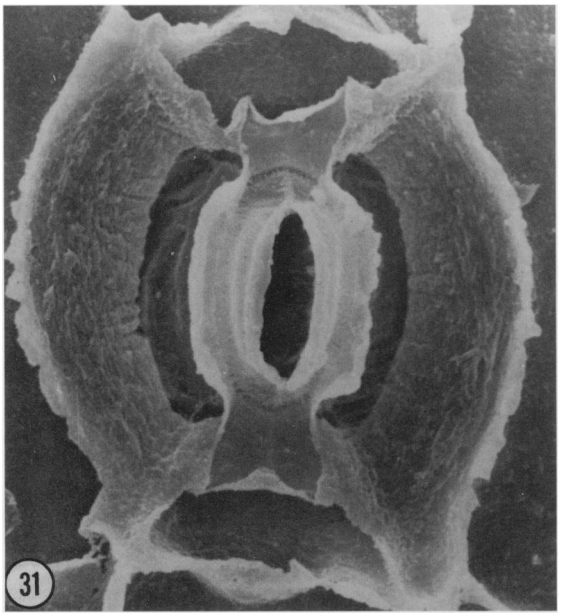
Figs. 22–30 *Prumnopitys ferruginea.* Fig. 22, Inner view, abaxial cuticle on stomatal apparatus with four subsidiary cells; × 1400. Fig. 23, Inner view, abaxial surface, showing stomatal rows and sinuous epidermal cell outlines; × 160. Fig. 24, Inner view, abaxial surface, showing variable subsidiary cell number; × 475. Fig. 25, Outer view, abaxial surface, showing Florin rings, stomatal plugs, and undulating epidermal cell surfaces; × 2700. Fig. 26, Outer view, abaxial surface, showing Florin ring and stomatal plug; × 1250. Fig. 27, Outer view, abaxial surface, stomatal plug components; × 7250. Fig. 28, Inner view, abaxial surface, showing stomatal apparatus with six subsidiary cells; × 700. Fig. 29, Inner view, abaxial surface, showing cuticle on epidermal cell surfaces; × 2300. Fig. 30, Inner view, abaxial surface, showing cuticle on guard and subsidiary cell surfaces; × 3750. *SC,* subsidiary cell.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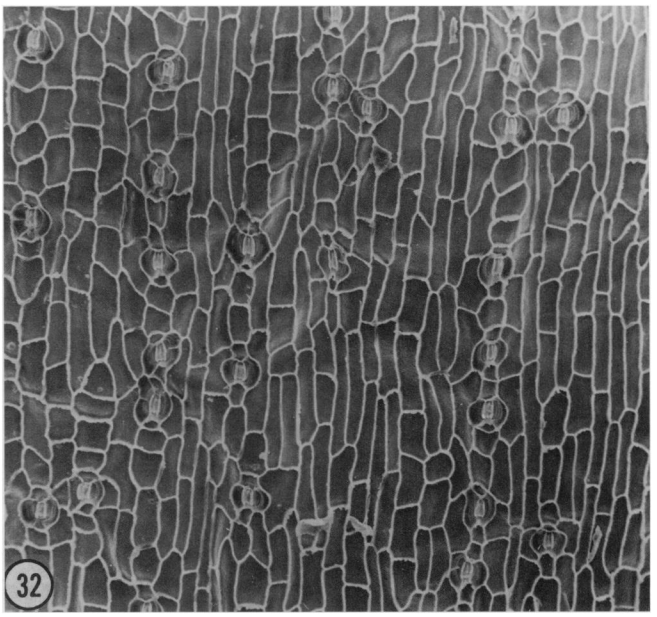
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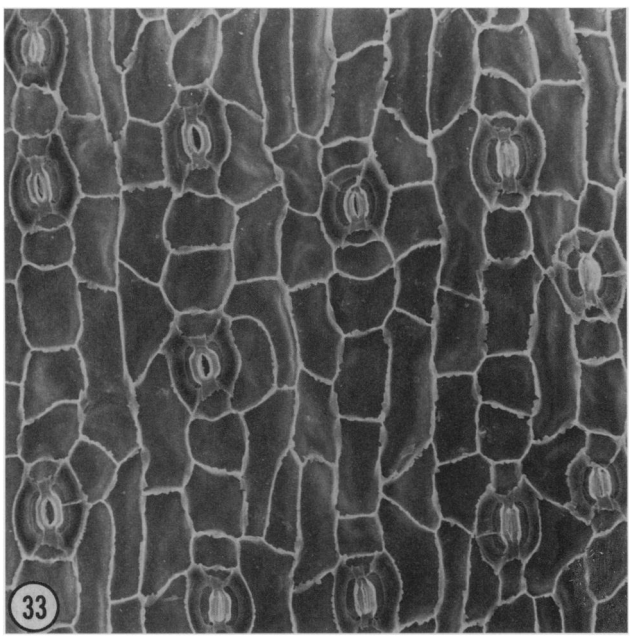
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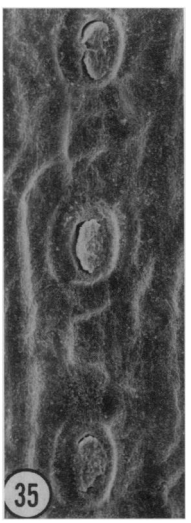
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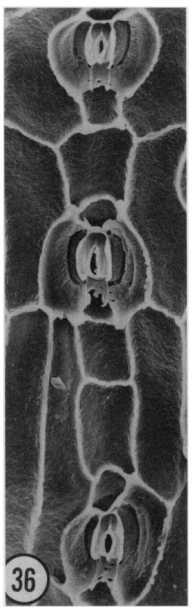
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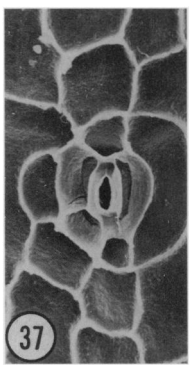
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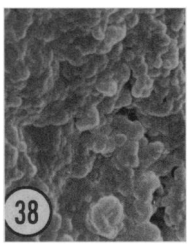
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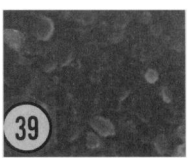
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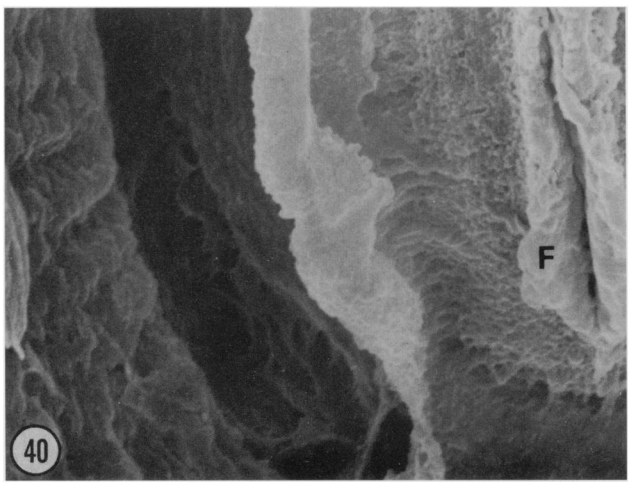
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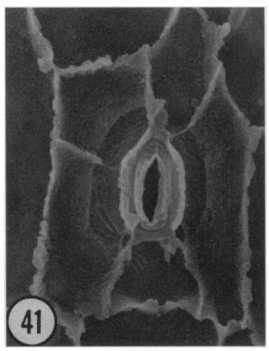
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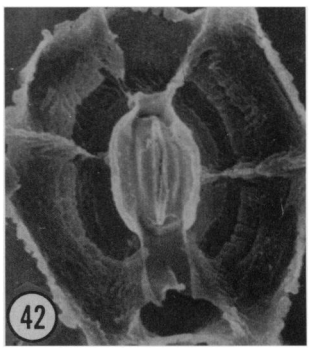
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present and have slender rodlike components (figs. 47, 49).

Inner cuticle surfaces show crowded stomata in discontinuous rows (figs. 44, 45). Stomata are oriented parallel to the long axis of the leaf (figs. 44, 45). The shape of the stomatal apparatus is usually elliptical, depending on its proximity to others (figs. 43–45, 50). Often subsidiary cells of one stomatal apparatus are in contact with those in the neighboring row (figs. 44, 45, 50). Subsidiary cell number varies from two to six, with two the most common (table 3, figs. 44, 45). It is often difficult to distinguish polar subsidiary cells from the surrounding polar epidermal cells. At the poles, cells are closer to the external cuticle surface (i.e., they appear more deeply sunken internally) than the subsidiary cells (figs. 43, 50). In some cases the polar cells are distinctly epidermal, while in other cases the distinction is not so clear-cut. Lateral subsidiary cells have broad, irregular flanges that form crescent-shaped cuticle morphology when only two laterals occur (fig. 43). Often the lateral subsidiary cells divide, resulting in three or four lateral cells (figs. 44, 45, 50).

Cuticle on the surface of subsidiary cells is rugose and pitted, with a shallow groove near the guard cells that corresponds to the Florin ring externally (fig. 43). Slight horizontal striations may appear on this cuticle (fig. 52), but these are not pronounced as in some of the other species.

The cuticular flange between guard cells is fairly thin and slightly rugose (fig. 52). Ribbon-like polar extensions occur that may extend out into a very thin tip (figs. 43, 50, 52). Cuticle on guard cell surfaces is smooth to just slightly granular, with slight polar ridges (fig. 52). A rolled flange of smooth to slightly granular cuticle extends from the subsidiary cell partially over the lower surface of the guard cell (fig. 43). These cuticular flanges are sometimes large, as in *P. andina* and *P. exigua.*

Epidermal cells are generally rectangular but can be variable in shape depending on their proximity to the stomata (figs. 44, 45, 51). Cell wall flanges are distinctly sinuous, as in *P. andina* and *P. ferruginea* (figs 44, 45, 51). Cuticle on both abaxial and adaxial surfaces is very rugose and pitted (table 3, fig. 43, 48, 51).

PRUMNOPITYS LADEI (FIGS. 53–62)

Adult leaves were collected from Mount Spurgeon, Queensland, and also were obtained from the Australian National Botanic Gardens from a clone of a specimen that originated from around the Cook District, Queensland (table 1). Leaves are spirally arranged, usually lack a petiole, and are 1.2–1.6 cm long × 2.5–4.0 mm wide, with obtuse apices (Silba 1986). Stomata have been observed on both surfaces but are more numerous on abaxial surfaces.

The external cuticle surface is undulating, with some underlying epidermal cells visible (fig. 56). Very distinct, slightly sunken Florin rings occur around the sunken stomata (table 2, figs. 56–58). Stomatal plugs are present and may be porous or may have solid surfaces (figs. 57, 58). Plugs like those in most other *Prumnopitys* species have short rodlike components (fig. 59).

Inner cuticle surfaces show widely spaced stomata (fig. 54). Sometimes discontinuous vertical rows are seen (these are more common on abaxial surfaces; fig. 55), but stomata also appear in nearly horizontal rows, perpendicular to the long axis of the leaf (fig. 54). Stomatal orientation is parallel to the long axis of the leaf (figs. 54, 55). Stomata are usually nearly elliptical to almost square in outline, depending on their proximity to other stomata and the width of subsidiary cells (figs. 53, 61, 62). The common number of subsidiary cells is four; however, five also occur (table 3, figs. 53–55, 61). Two polar and two lateral subsidiary cells are common, but in some instances it is hard to tell polar subsidiary cells from epidermal cells in this position (fig. 53, top).

Cuticle on the outer subsidiary cell wall flanges is thick and irregular and often has large pits near the edge (figs. 53, 61, 62). On subsidiary cell surfaces, cuticle is smooth to slightly rugose, usually with vertical striations present (figs. 53, 61). There is a deep groove in the subsidiary cell cuticle near the guard cells that conforms to the position of the Florin ring externally (figs. 53, 62).

The cuticular flange between guard cells is usually thick, irregular, and slightly granular (figs. 53, 61, 62). Large, flat, ribbon-like polar extensions with occasional large pits and a central ridge occur in this species (figs. 53, 61, 62). The cuticle on guard cell surfaces is smooth to slightly granular, with a prominent polar ridge that can sometimes be seen as a complete elliptical ridge when the flange between guard and subsidiary cells is not covering this zone (figs. 53, 62). The flange of cuticle between guard cells and subsidiary

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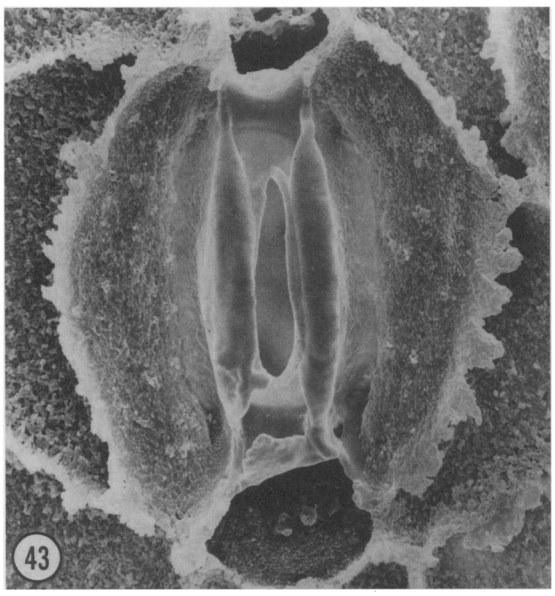
Figs. 31–42 *Prumnopitys ferruginoides.* Fig. 31, Inner view, abaxial cuticle on stomatal apparatus with four subsidiary cells and prominent polar extensions; × 1800. Fig. 32, Inner view, abaxial surface, showing stomatal rows; × 150. Fig. 33, Inner view, abaxial surface, showing stomata with variable subsidiary cell number; × 250. Fig. 34, Outer view, abaxial surface, showing Florin rings linked by a raised area that resulted from epidermal cells within a stomatal row: × 550. Fig. 35, Outer view, abaxial surface, showing Florin rings, stomatal plugs, and undulating epidermal cell surfaces; × 425. Fig. 36, Inner view, abaxial surface, showing stomatal row; × 400. Fig. 37, Inner view, abaxial surface, stomatal apparatus with several encircling cells; × 400. Fig. 38, Outer view, abaxial stomatal plug components; × 4250. Fig. 39, Inner view, adaxial cuticle on epidermal cell surface; × 6500. Fig. 40, Inner view, abaxial cuticle on stomatal apparatus; × 7000. Fig. 41, Inner view, abaxial surface of stomatal apparatus with five irregularly shaped subsidiary cells; × 700. Fig. 42, Inner view, abaxial surface, showing stomatal apparatus with six subsidiary cells; × 900. *F,* flange of cuticle between guard cells.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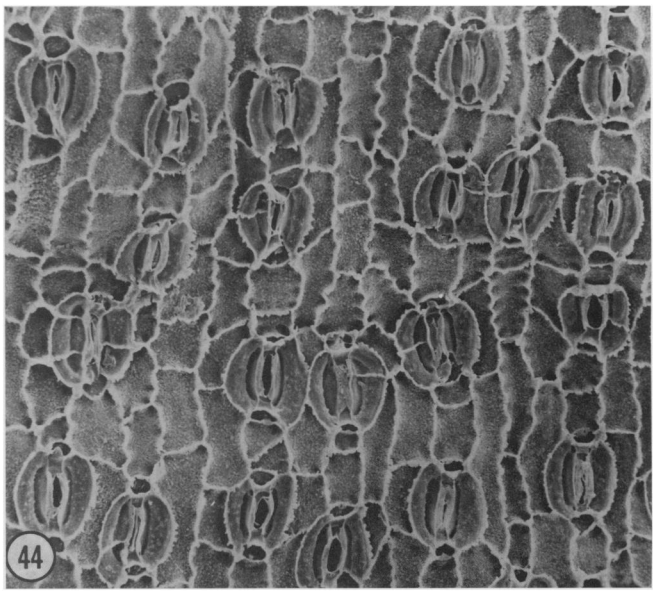
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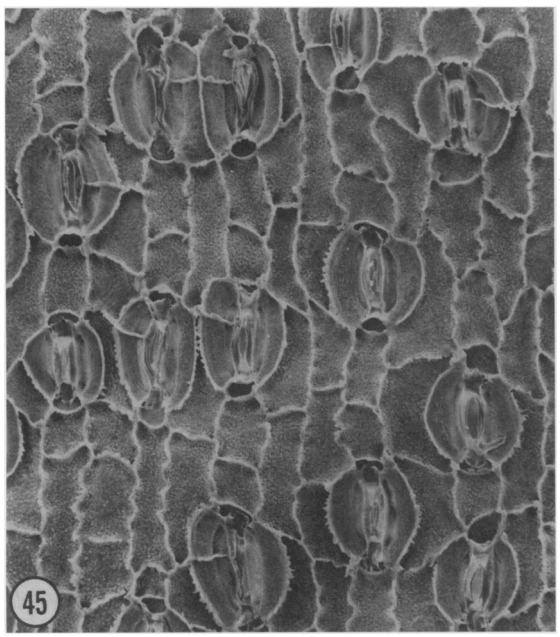
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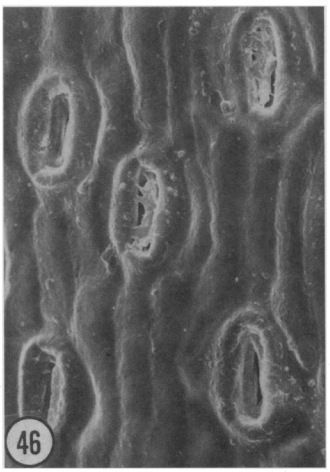
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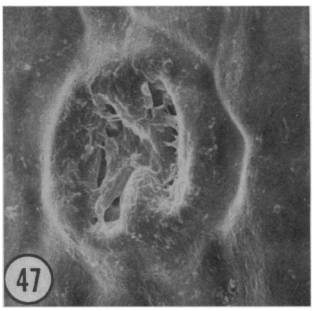
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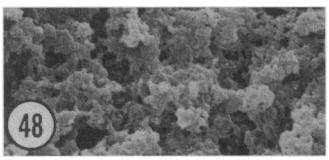
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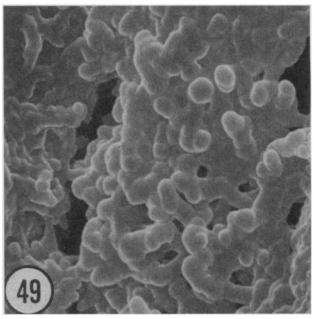
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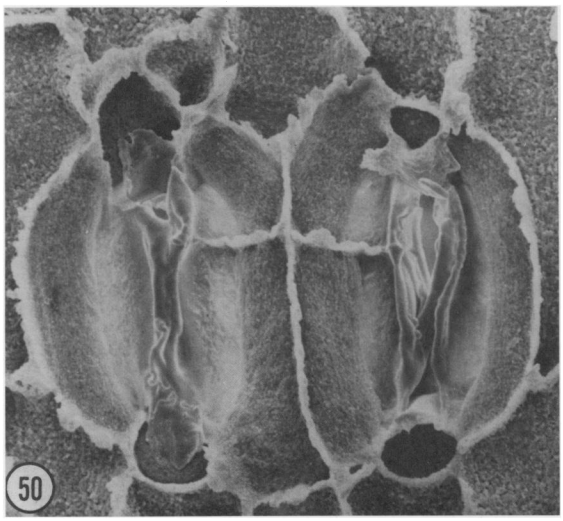
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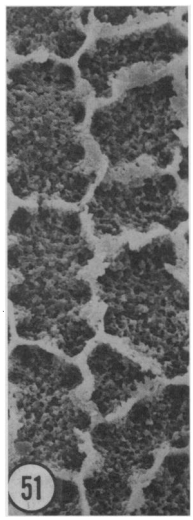
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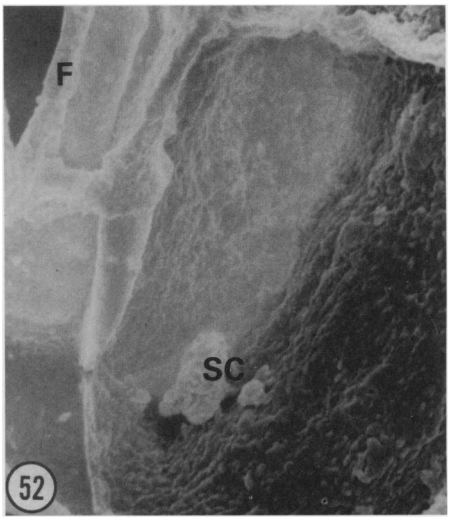
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cells is rugose and rolled, as in most *Prumnopitys* species (figs. 53, 62).

Epidermal cells are usually rectangular but are shorter than in most *Prumnopitys* species, even between stomatal rows (table 3, figs. 54, 55). Some irregular shapes occur, especially near the stomata (figs. 54, 55). Epidermal cell outlines are sinuous (fig. 55), but the thickness of the cuticle often masks this sinuousness with the SEM at low magnifications (fig. 54). Cuticle on epidermal cell surfaces is pitted and granular (fig. 60), but it is more finely granular on abaxial surfaces.

Prumnopitys montana var. *montana* (figs. 63–73)

Adult leaves were collected from Paramo de la Negra, Tachira, Venezuela, at 2400–2800 m (table 1). Leaves are spirally arranged and spread out distichously; they are linear, sometimes falcate, and 10–18 mm long × 2.5–3.5 mm wide, with acute or mucronate apices and short petioles with a distinct groove above the midvein (Buchholz and Gray 1948*b*). Stomata have only been observed on abaxial surfaces.

The external cuticle surface is undulating, with underlying epidermal cell outlines sometimes visible (fig. 66). Small amounts of epicuticular wax have been observed on external leaf surfaces (fig. 66). Stomata are surrounded by slightly sunken Florin rings (table 2, fig. 66). Stomatal plugs are present and are composed of small rods (fig. 67).

Inner cuticle surfaces show crowded stomata in discontinuous rows (figs. 64, 65). The shape of the stomatal apparatus is generally elliptical, but irregular shapes sometimes occur from crowding (fig. 64). Two or three lateral subsidiary cells are most common, but further divisions are possible (figs. 63–65, 69, 71, 72). As few as two (fig. 64) and as many as seven (table 3, fig. 72) subsidiary cells have been seen, making this the most variable species with respect to subsidiary cell number. Often polar subsidiary cells are absent (fig. 64), as in other *Prumnopitys* species.

Cuticle on the outer cell wall flange of subsidiary cells often has a longitudinal groove near the thick, irregular edge (figs. 63, 71). The surface of subsidiary cell cuticle is rugose, with prominent vertical striations in many stomata (figs. 63, 65). Deep grooves occur in subsidiary cell surfaces that correspond to the external position of a Florin ring, and the cuticle surface is more rugose and pitted in this area (figs. 63, 71, 73).

The cuticular flange between guard cells is relatively thin and smooth to slightly rugose (figs. 63, 71, 73). Long, ribbon-like polar extensions are present, sometimes showing a central ridge (figs. 63, 71). Cuticle on guard cell surfaces is slightly rugose (fig. 73), with a prominent ridge in the polar regions (figs. 63, 73). A rolled flange of smooth to slightly rugose cuticle extends between guard and subsidiary cells and sometimes completely encloses the guard cells (fig. 71). In one instance, cuticle with the characteristic outline of a stomatal apparatus was found that lacked guard cell cuticle (fig. 69). A similar situation was reported in *Agathis kinabaluensis* de Laubenfels and *A. robusta* (C. Moore et Mueller) F. M. Bailey (Araucariaceae) by Stockey and Atkinson (1993).

Epidermal cell outlines on abaxial surfaces are nearly rectangular, but variable shapes occur near the stomata (figs. 64, 65). On adaxial surfaces, epidermal cells are short and wall flanges are not sinuous (fig. 68). Cell wall flanges are sinuous on abaxial surfaces (figs. 64, 65). Cuticle on epidermal cell surfaces is very pitted and rugose on both sides of the leaf, but it is more pronounced on adaxial surfaces (table 3, figs. 65, 70, 71).

Prumnopitys montana var. *meridensis* (figs. 74–83)

Adult leaves were collected at Paramo de la Negra, Tachira, Venezuela, at 2500–3000 m (table 1). This variety was erected by Buchholz and Gray (1948*b*), based on the smaller-sized seed, with a pair of partially fused spinelike projections. Leaves have an open adaxial groove along the midvein. Buchholz and Gray (1948*b*) felt that it may be a distinct species, and since material of this variety was available to us, we decided to examine the cuticle micromorphology to see what characters, if any, differ from those seen in *P. montana* var. *montana.*

Externally, leaves show a smoother surface than those of *P. montana* var. *montana.* The outlines of underlying epidermal cells can be seen externally, and sunken Florin rings are less distinct (table 2, figs. 77, 78) than those reported for *P. montana* var. *montana.* The presence of a small amount of epicuticular wax is the same for both species (figs. 66, 78). Stomatal plugs occur and are composed of fused rods (fig. 78). Stomata were only found on abaxial surfaces.

Inner cuticle surfaces show discontinuous rows of stomata that are not as crowded as those of *P. montana* var. *montana* (fig. 75). Stomata are oriented parallel to the long axis of the leaf, and occasional pairs of stomata have subsidiary cells that come in contact with

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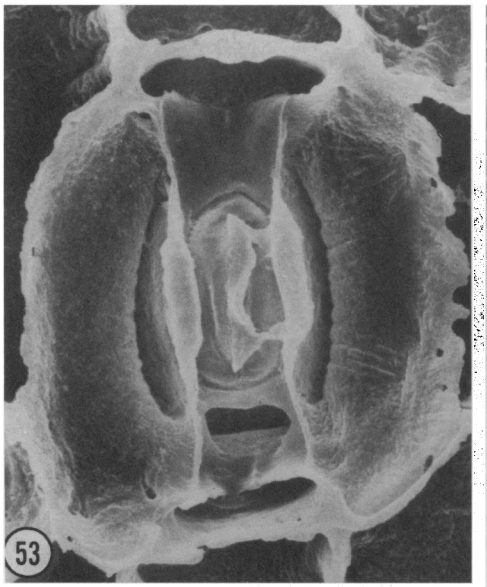
Figs. 43–52 *Prumnopitys harmsiana.* Fig. 43, Inner view, abaxial cuticle on stomatal apparatus; × 1750. Fig. 44, Inner view, abaxial surface, showing stomatal rows; × 300. Fig. 45, Inner view, abaxial surface, showing stomata with variable subsidiary cell numbers; × 375. Fig. 46, Outer view, abaxial surface, showing Florin rings, stomatal plugs, and undulating epidermal cell outlines; × 500. Fig. 47, Outer view, abaxial surface, showing double Florin ring surrounding two pair of closely spaced guard cells; × 750. Fig. 48, Inner view, adaxial cuticle on epidermal cell surface; × 2500. Fig. 49, Outer view, abaxial surface, showing stomatal plug components; × 4000. Fig. 50, Inner view, abaxial surface, showing two stomata with bordering subsidiary cells; × 1000. Fig. 51, Inner view, adaxial surface, showing sinuous cell outlines and very granular texture of wall surface cuticle; × 475. Fig. 52, Inner view, abaxial cuticle on stomatal apparatus; × 5000. *F,* flange of cuticle between guard cells; *SC,* subsidiary cell.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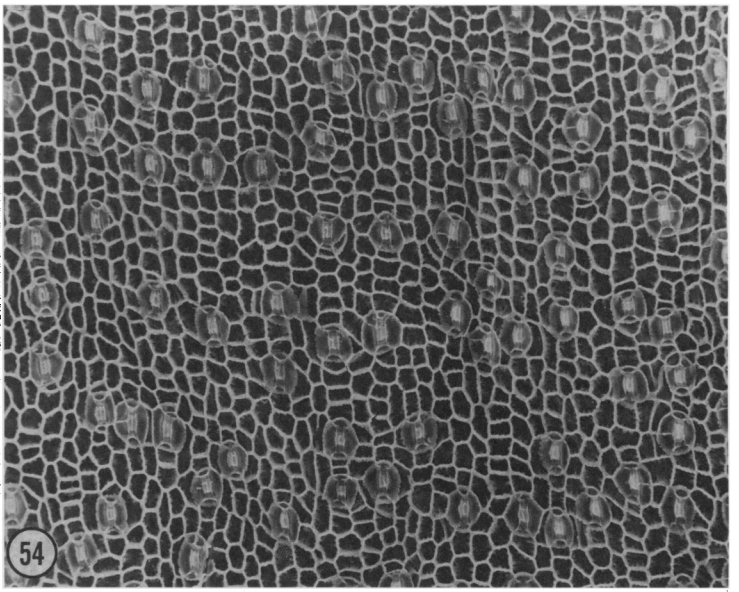
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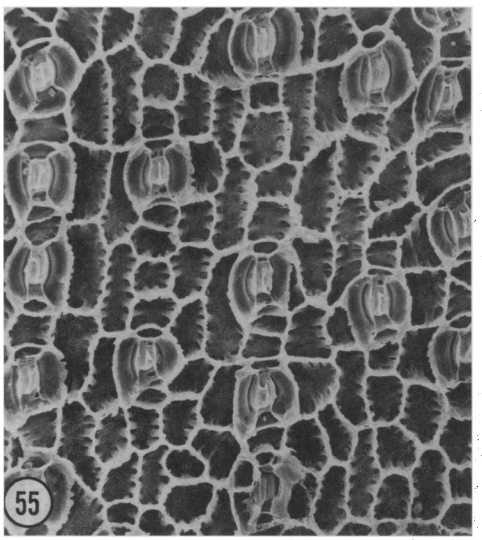
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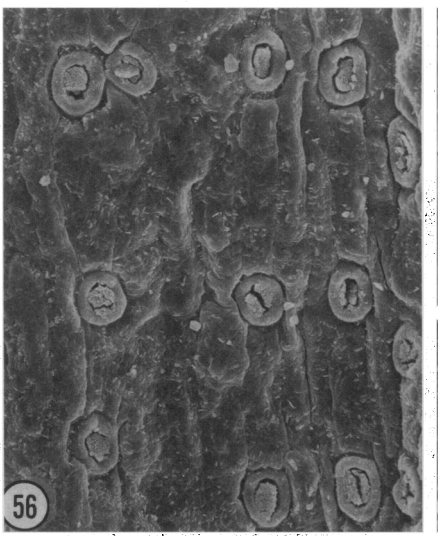
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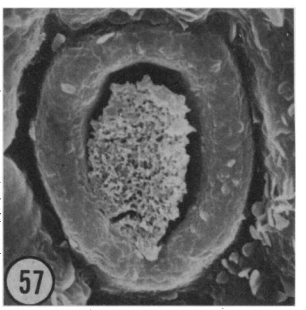
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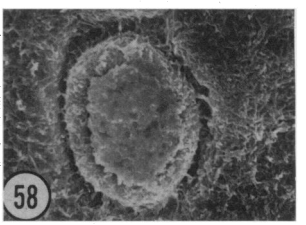
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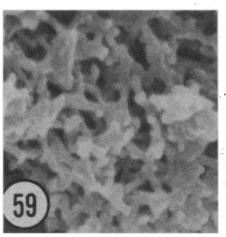
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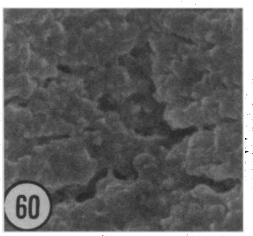
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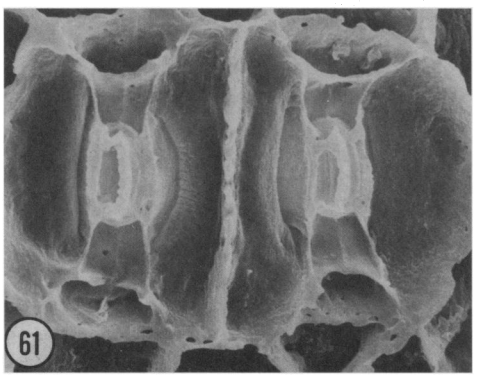
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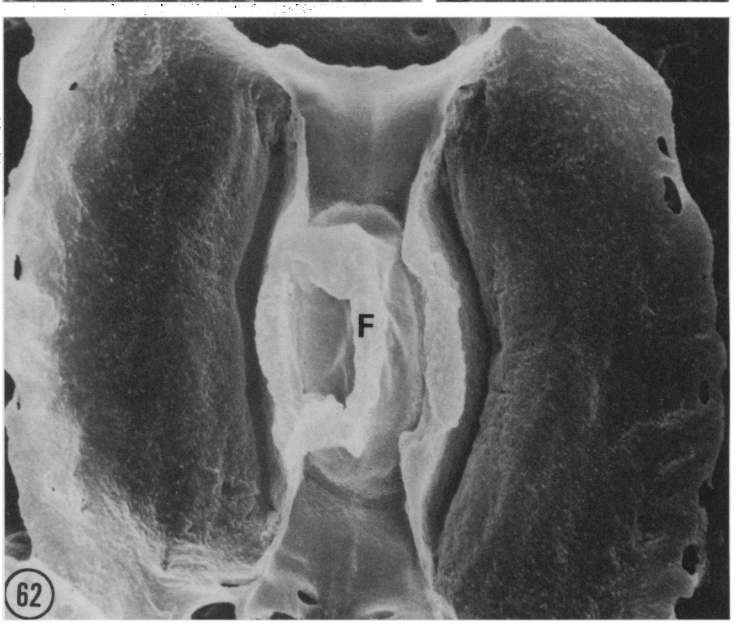
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one another (figs. 75, 79). The shape of the stomatal apparatus varies depending on the proximity of other stomata, but in general it is more circular in outline (figs. 74, 83) than in *P. montana* var. *montana,* where outlines are usually more elliptical. Two subsidiary cells are most common. but three regularly occur (table 3, figs. 74, 75, 83). Often polar subsidiary cells appear to be lacking and lateral subsidiary cells divide to form up to five subsidiary cells per stomatal apparatus (fig. 75).

Cuticle on the outer subsidiary cell wall flange is thin and irregular (figs. 74, 83), and in general cuticle is thinner than that in *P. montana* var. *montana.* The cuticle on the surface of subsidiary cells is very granular and rugose compared to that seen in *P. montana* var. *montana* (figs. 74, 81, 83). Horizontal striations occur on subsidiary cell surfaces (figs. 74, 83), unlike the prominent vertical striations in *P. montana* var. *montana* (fig. 63). Distinct grooves occur in the subsidiary cell cuticle near the guard cells resulting in the external Florin rings (figs. 74, 83).

The cuticular flange between guard cells is moderately thick and rugose (figs. 74, 81). Ribbon-like polar extensions also occur in this taxon and have a median ridge (figs. 74, 81, 83). They are quite extensive on some stomata and can have thin, pointed tips (fig. 83) as seen in *P. harmsiana* (fig. 50) and *P. montana* var. *montana* (fig. 63). The cuticle on guard cell surfaces is slightly granular, with a distinct polar ridge (fig. 81). The rolled flange of cuticle between guard and subsidiary cells is extensive, as in *P. montana* var. *montana,* and can cover the entire guard cell surface (figs. 76, 83).

Epidermal cells in this variety are much more elongate than those of *P. montana* var. *montana* (table 3). On abaxial surfaces, cells are very elongate (fig. 75) and their appearance is similar to juvenile foliage leaves of other conifers (Stockey and Taylor 1978; Stockey and Atkinson 1993; R. A. Stockey, personal observation). Adaxial epidermal cells are rectangular and more elongate than in *P. montana* var. *montana* and have a sinuous outline (fig. 82). Abaxial epidermal cells do not show this sinuousness (fig. 76). This is the opposite case of that seen in *P. montana* var. *montana,* where abaxial epidermal cell outlines are sinuous and adaxial cell outlines are not (figs. 64, 68). Cuticle on epidermal cell surfaces is finely pitted and granular (fig. 80) and less rugose than that seen in *P. montana* var. *montana.*

PRUMNOPITYS STANDLEYI (FIGS. 84–93)

Adult leaves were collected in Turrialba, Volcan de Poas, Costa Rica (table 1). Leaves are helically arranged or in two subopposite ranks, linear, sometimes falcate, 1.2–1.8 cm long × 2.5–3.5 mm wide, grooved above the midrib, with an acute or mucronate apex (Silba 1986). Stomata are observed on both leaf surfaces.

The external cuticle surface is undulating, but the cuticle surface is covered by irregular clumps of epicuticular wax (fig. 87). Florin rings are present, but these may also be partly obscured by the surface wax (table 2, fig. 87, 90). Stomatal plugs are present and are composed of small rods (fig. 88) that may be covered over with surface wax (fig. 87).

Inner cuticle surfaces show stomata in distinct ver-

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Figs. 53–62 *Prumnopitys ladei.* Fig. 53, Inner view, abaxial cuticle on stomatal apparatus with four subsidiary cells; × 2000. Fig. 54, Inner view, abaxial stomatal rows; × 150. Fig. 55, Inner view, abaxial surface, showing stomata and sinuous epidermal cell outlines; × 325. Fig. 56, Outer view, abaxial stomata with distinct Florin rings, stomatal plugs, and undulating epidermal cell surfaces; × 300. Fig. 57, Outer view, abaxial surface, showing Florin ring and porous stomatal plug; × 1900. Fig. 58, Outer view, abaxial cuticle, showing solid stomatal plug surface; × 900. Fig. 59, Outer view, abaxial surface, stomatal plug components; × 8000. Fig. 60, Inner view, adaxial cuticle on epidermal cell surface; × 5500. Fig. 61, Inner view, abaxial surface, showing two stomata with bordering subsidiary cells; × 1200. Fig. 62, Inner view, abaxial cuticle on stomatal apparatus, showing very wide lateral subsidiary cell wall flanges and ribbon-like polar extensions; × 3300. *F,* flange of cuticle between guard cells.

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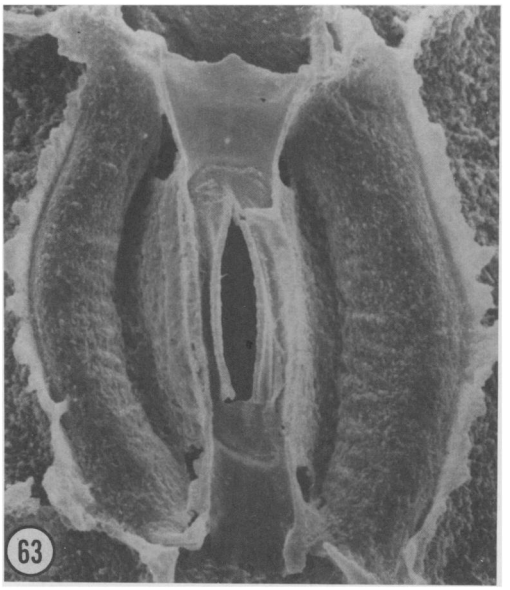
Figs. 63–73 *Prumnopitys montana* var. *montana.* Fig. 63, Inner view, abaxial cuticle on stomatal apparatus with two subsidiary cells and prominent polar extensions; × 1800. Fig. 64, Inner view, abaxial surface, showing stomatal rows; × 250. Fig. 65, Inner view, abaxial surface, showing stomata with variable number of subsidiary cells; × 500. Fig. 66, Outer view, abaxial surface, showing Florin rings and undulating epidermal cell outlines; × 300. Fig. 67, Outer view, abaxial stomatal plug components; × 4000. Fig. 68, Inner view, adaxial epidermal cell outlines; × 325. Fig. 69, Inner view, abaxial surface, showing stomata with bordering subsidiary cells, one with undeveloped guard cell cuticle; × 900. Fig. 70, Inner view, adaxial cuticle on epidermal cell surface; × 4000. Fig. 71, Inner view, abaxial surface, showing cuticle surrounding guard cell area; × 1900. Fig. 72, Inner view, abaxial surface, showing stomatal apparatus with seven subsidiary cells; × 1100. Fig. 73, Inner view, abaxial cuticle on stomatal apparatus; × 4750. *F,* flange of cuticle between guard cells.

Figs. 74–83 *Prumnopitys montana* var. *meridensis.* Fig. 74, Inner view, abaxial cuticle, one stomatal apparatus, showing three subsidiary cells; × 2500. Fig. 75, Inner view, abaxial stomatal rows; × 240. Fig. 76, Inner view, abaxial surface, showing stomata with elongate flanges of cuticle covering part of guard cell surface and prominent polar extensions; × 900. Fig. 77, Outer view, abaxial surface, showing stomatal rows, Florin rings, and undulating epidermal cell surfaces; × 260. Fig. 78, Outer view, abaxial surface, showing Florin ring and stomatal plug; × 1850. Fig. 79, Inner view, abaxial stomata with bordering subsidiary cells of varying shapes; × 800. Fig. 80, Inner view, abaxial cuticle on epidermal cell surface; × 4500. Fig. 81, Inner view, abaxial cuticle on stomatal apparatus; × 5750. Fig. 82, Inner view, adaxial epidermal cell outlines; × 320. Fig. 83, Inner view, abaxial surface, showing prominent polar extensions and flaps of cuticle surrounding the inner guard cell wall area; × 2900. *F,* flange of cuticle between guard cells; *PE,* polar extension; *SC,* subsidiary cell.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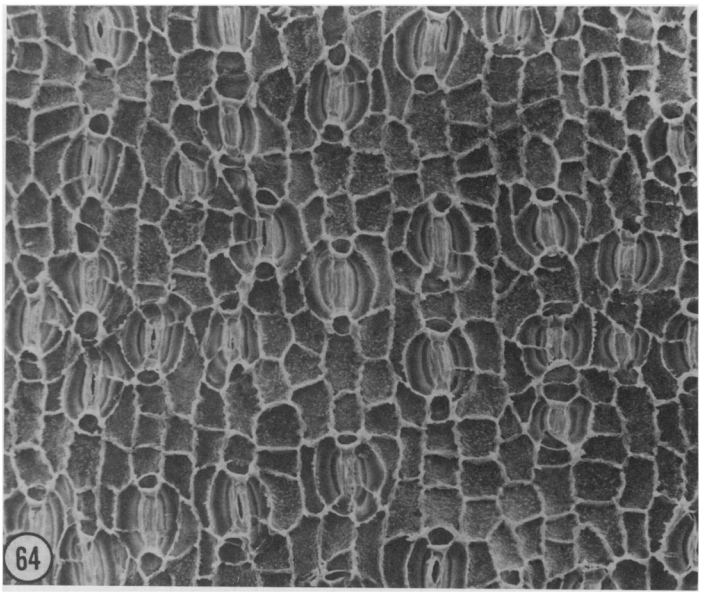
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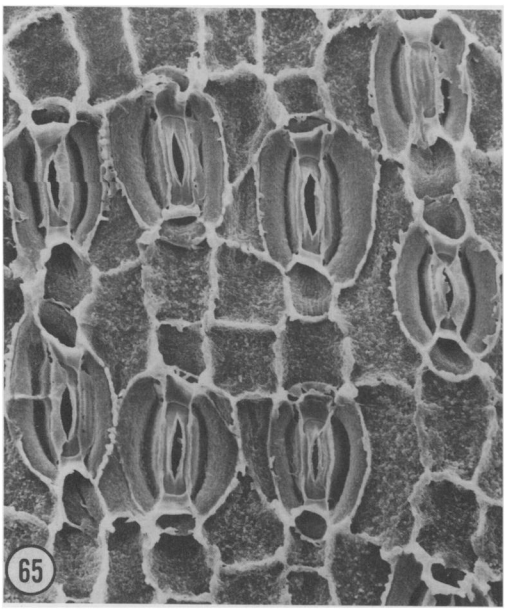
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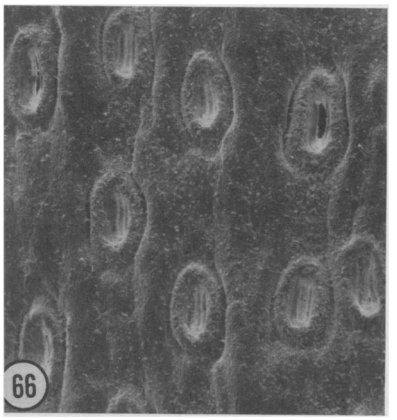
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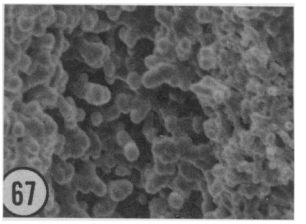
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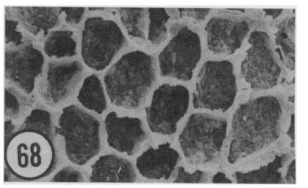
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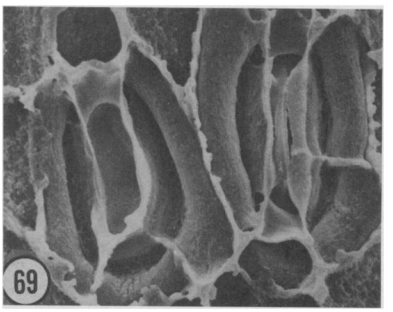
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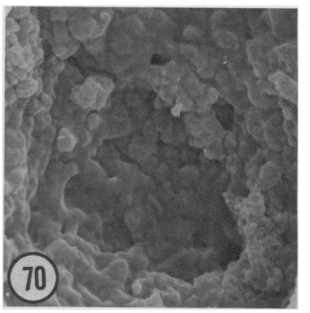
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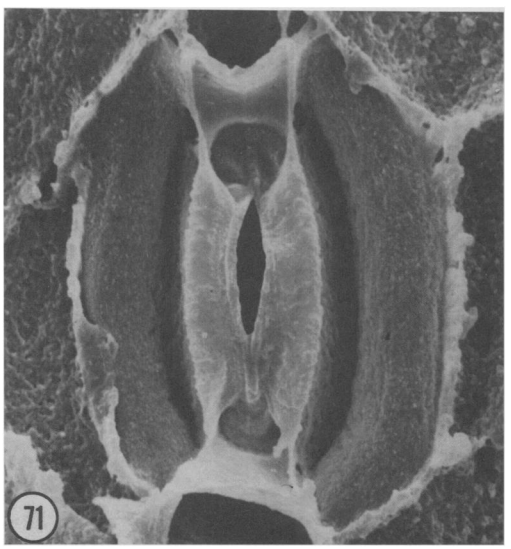
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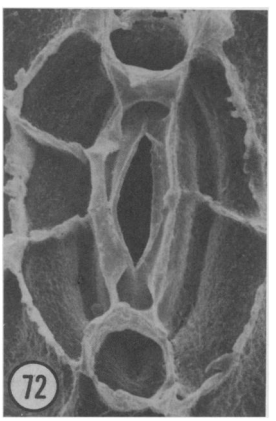
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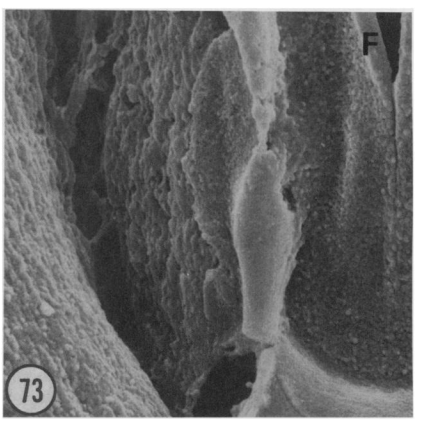
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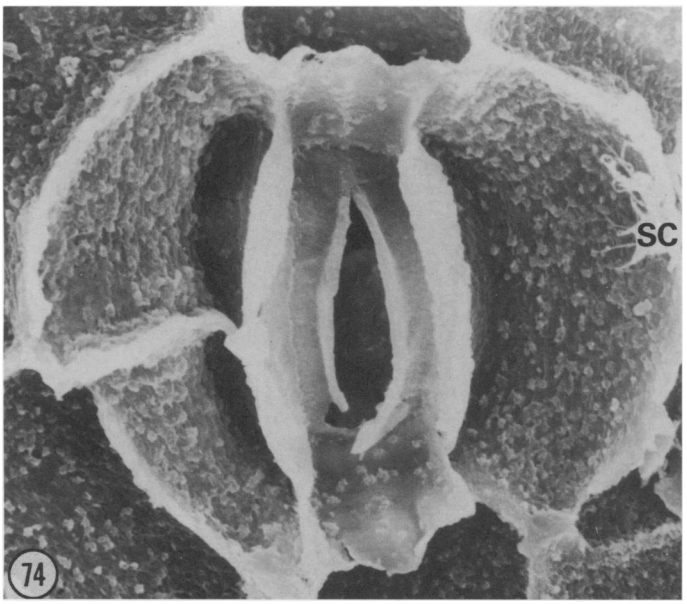
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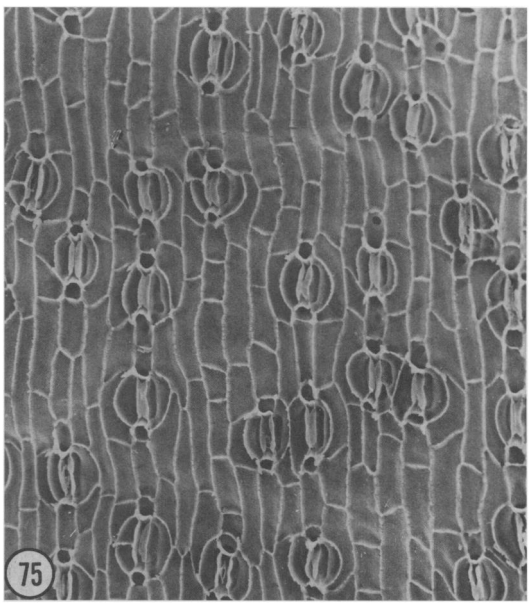
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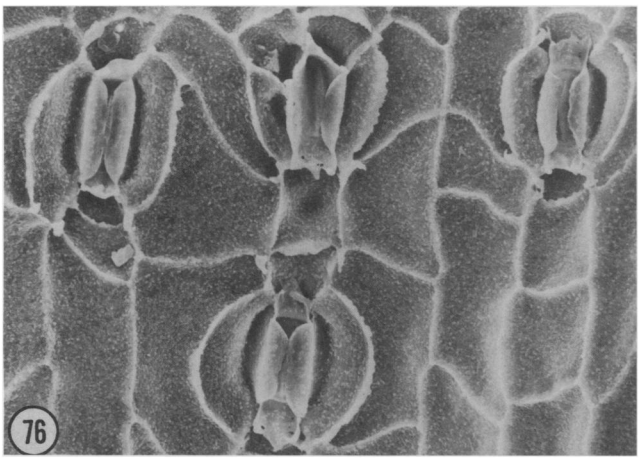
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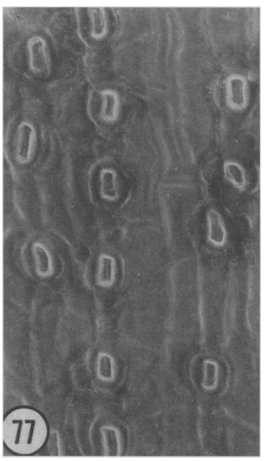
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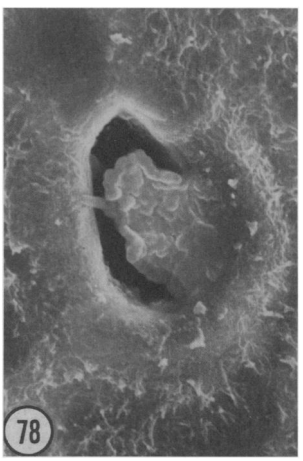
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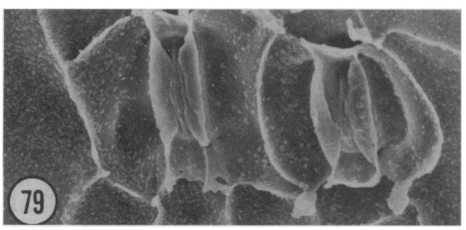
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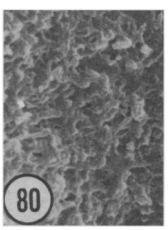
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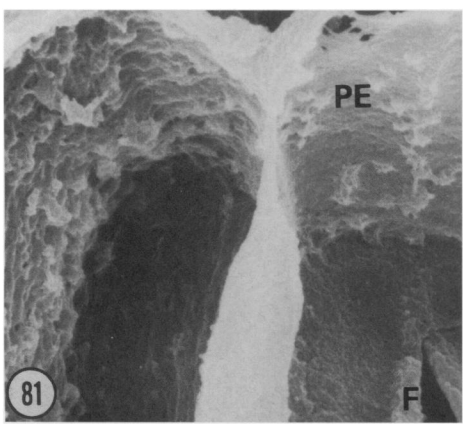
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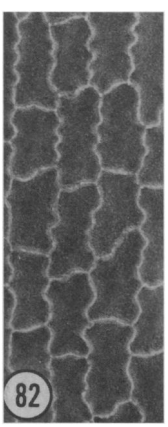
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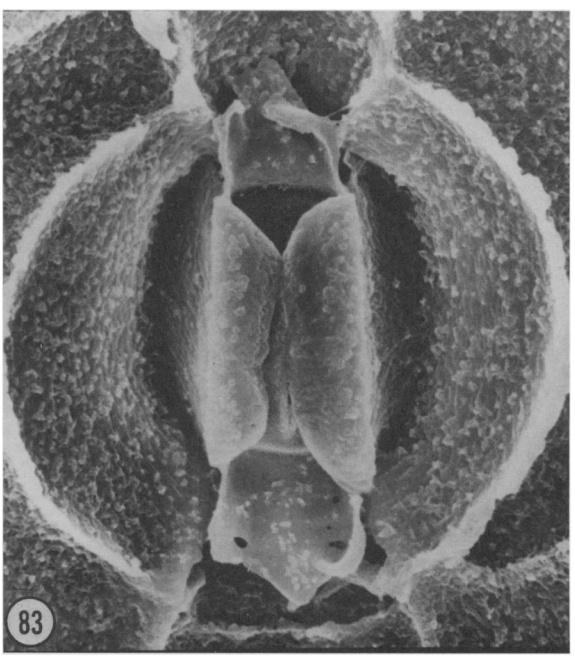
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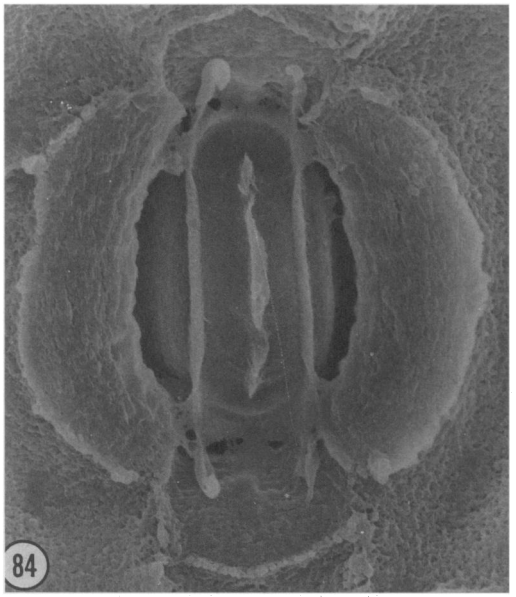
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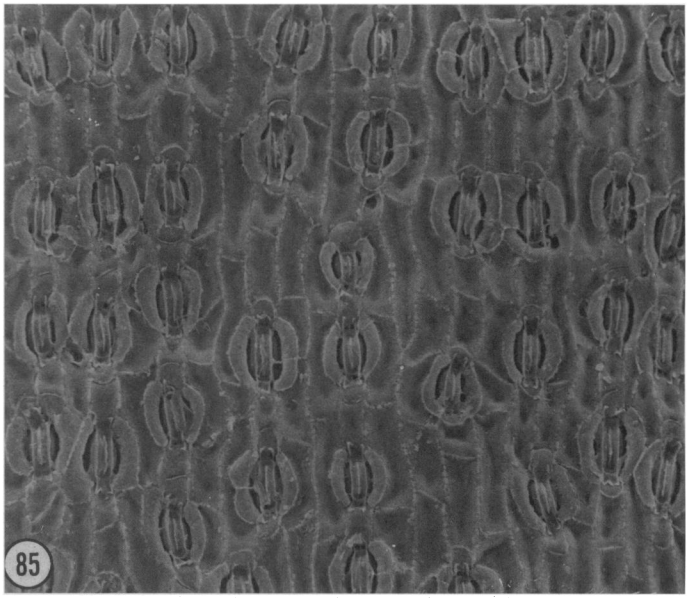
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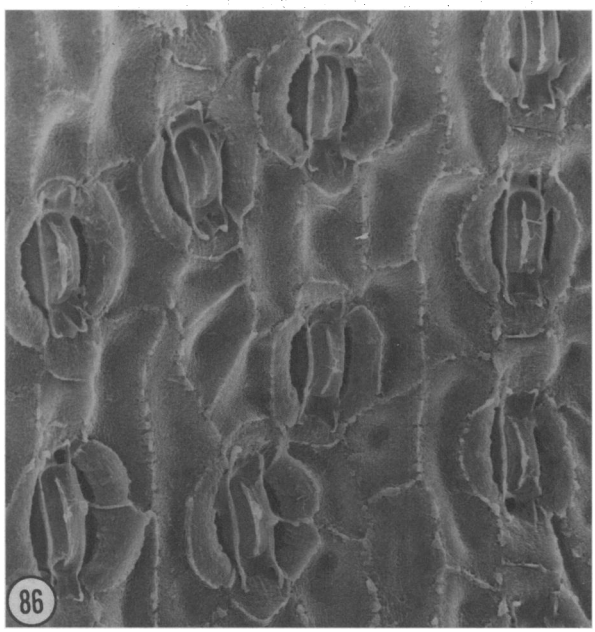
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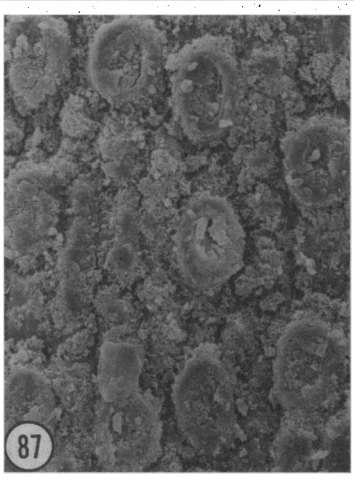
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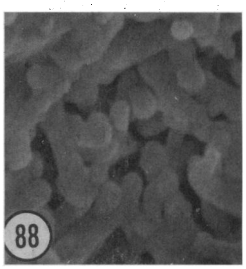
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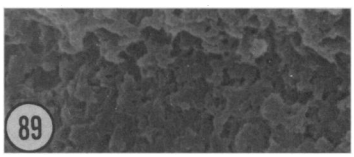
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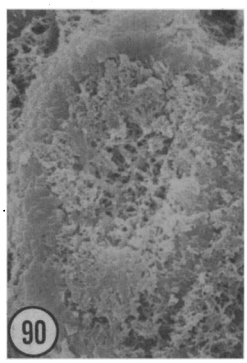
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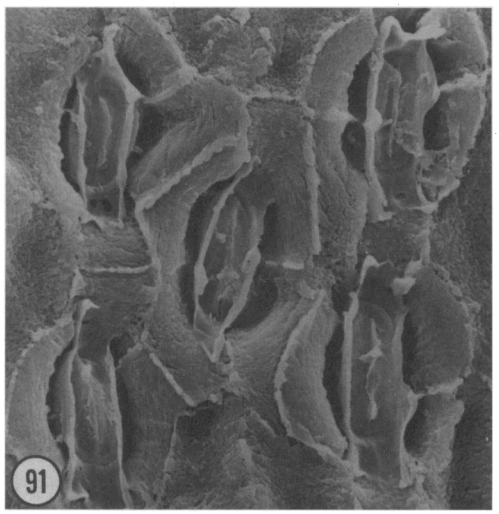
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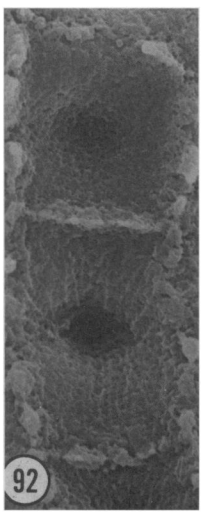
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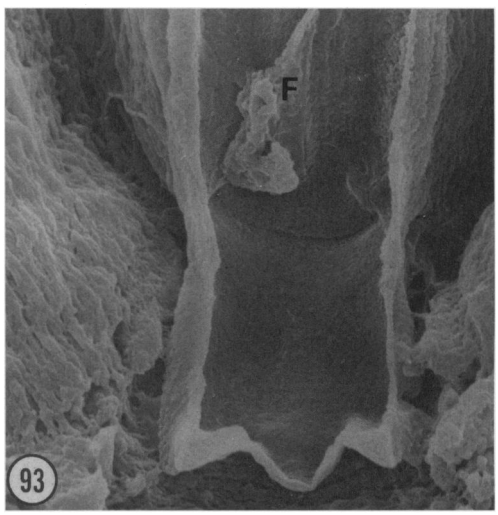
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tical rows and oriented parallel to the long axis of the leaf (fig. 85). Cuticle is thin and cell wall flanges shallow. The stomatal apparatus varies in shape depending on its proximity to others (fig. 91). As in many other *Prumnopitys* species, it is often difficult to distinguish polar subsidiary cells from epidermal cells in this position (figs. 84–86). The most common subsidiary cell number is four, with two to six observed (table 3, figs. 84–86, 91).

The cuticle on the outer subsidiary cell wall is thin and irregular and on approximately the same level as the epidermal cell wall flanges (fig. 84, 86). The surface of subsidiary cells is granular and pitted, with both horizontal and vertical striations (figs. 84, 86, 91, 93). Deep grooves occur in subsidiary cell wall surfaces closest to the guard cells, and cuticle is more rugose in this area (figs. 84, 86, 91, 93).

The cuticular flange between guard cells is thick and irregular (fig. 84) and can be granular (fig. 93). Ribbon-like polar extensions occur and are sometimes very thin (fig. 84). As in most *Prumnopitys* species, the polar extension may have two arms and a central pointed area (fig. 93). If the center of the polar extension is broken or very thin, these extensions can appear bilobed (fig. 84), a characteristic of species of the genus *Agathis* Salisbury (Araucariaceae) (Stockey and Atkinson 1993). However, the cuticular knobs are not as consistent or rounded as in *Agathis* and are easily distinguished from those in that genus. The cuticle on guard cell surfaces is slightly granular, with a distinct polar ridge (fig. 93). A rolled flange of slightly granular cuticle extends between the subsidiary cells and guard cells (figs. 84, 93), but this flange is not as pronounced as in some other *Prumnopitys* species.

Epidermal cell outlines are generally rectangular between stomatal rows but irregular in shape around stomata (figs. 85, 86). Epidermal cell wall flanges are very shallow and extremely pitted to discontinuous and do not appear striated (figs. 86, 91, 92). Cuticle on epidermal cell surfaces is granular and pitted (table 3, figs. 89, 92). Occasionally epidermal cells show a central depression in the cuticle where the cells extended closer to the leaf surface (figs. 86, 92).

Prumnopitys taxifolia (figs. 94–102)

Adult leaves were collected at Ahuriri, Banks Peninsula, Canterbury, New Zealand (table 1). Leaves are linear, with a prominent midrib, and 2.0–3.0 cm long × 2.0 mm wide with prominent petioles (Silba 1986). Stomata have only been observed on abaxial surfaces.

The external cuticle surface is very rugose and is covered with epicuticular wax (fig. 97). The underlying epidermal cell patterns sometimes can be seen, and slightly sunken Florin rings are present (table 2, figs. 97, 98). Stomatal plugs occur as solid layers of rugose material (fig. 98).

Inner cuticle surfaces show crowded stomata in discontinuous rows that are oriented parallel to the long axis of the leaf (figs. 95, 96). The shape of the stomatal apparatus is usually elliptical to nearly circular but can vary depending on its proximity to others (figs. 94–96, 100). Because of crowding, subsidiary cells of stomata from adjacent rows are often in contact with one another (figs. 95, 100). Subsidiary cell number is usually four, with two to six observed (table 3, figs. 94–96, 100). Polar subsidiary cells are present in most of the stomata of this taxon, unlike many of the other *Prumnopitys* species (fig. 94). However, they can be lacking on some stomata (figs. 95, 96).

Cuticle on outer lateral subsidiary cell wall flanges is thick and irregular (fig. 94). The surface of subsidiary cell cuticle is rugose, with vertical striations sometimes visible (figs. 94, 102). There is a very deep crease with numerous pits in the subsidiary cell cuticle near the guard cells, corresponding to the external Florin ring (fig. 102).

The cuticular flange between guard cells is thick and slightly rugose (figs. 94, 102). Ribbon-like polar extensions occur and may show a bifurcation (figs. 94; 96, bottom right; 102). Cuticle on guard cell surfaces is granular to rugose, narrow, with a prominent polar ridge, and often obscured by the rolled flange of cuticle between guard cells and subsidiary cells (figs. 94, 102). This rolled flange is slightly rugose but not as extensive as in some *Prumnopitys* species (fig. 102).

Epidermal cells on both leaf surfaces have sinuous wall flanges (figs. 95, 96, 101). Cells are nearly rectangular between stomatal rows, but vary in shape when near the stomata (table 3, figs. 95, 96). On abaxial surfaces epidermal cells are usually elongate and parallel to the long axis of the leaf, but occasionally cells are separated by a nonsinuous cross wall (what was probably a later division of the epidermal cell) and are oriented with their long axes now perpendicular to the long axis of the leaf (fig. 101). Cuticle on both epidermal cell surfaces is granular to pitted, sometimes with a few larger channels on adaxial surfaces (fig. 99).

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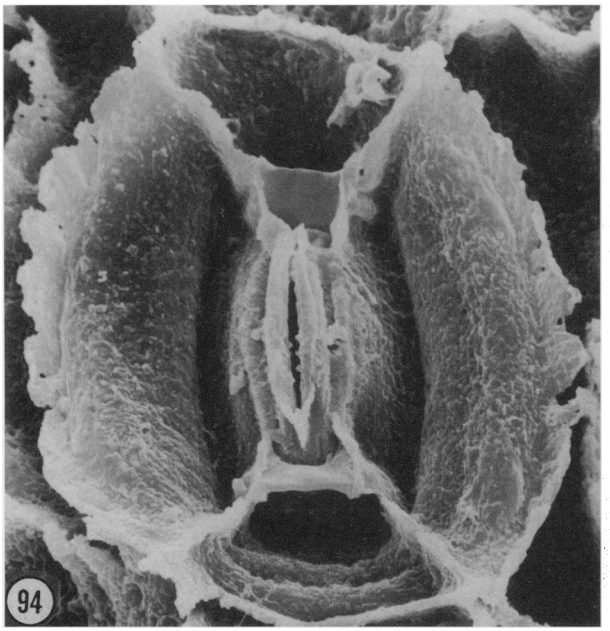
Figs. 84–93 *Prumnopitys standleyi.* Fig. 84, Inner view, abaxial cuticle on stomatal apparatus with four subsidiary cells; × 1550. Fig. 85, Inner view, abaxial surface, showing stomatal rows and low relief; × 250. Fig. 86, Inner view, abaxial surface, showing stomata with variable subsidiary cell number; × 475. Fig. 87, Outer view, abaxial surface, showing Florin rings, stomatal plugs and epicuticular waxes overlying epidermal cell outlines; × 275. Fig. 88, Outer view, abaxial stomatal plug; × 11,000. Fig. 89, Inner view, cuticle on adaxial epidermal cell surface; × 1700. Fig. 90, Outer view, abaxial surface, showing Florin ring and stomatal plug; × 1100. Fig. 91, Inner view, abaxial surface, showing group of five stomata with bordering subsidiary cells of variable shape and number; × 750. Fig. 92, Inner view, abaxial cuticle on epidermal cell surfaces, showing central depressions; × 1300. Fig. 93, Inner view, abaxial cuticle on stomatal apparatus, showing prominent polar extension; × 3500. *F,* flange of cuticle between guard cells.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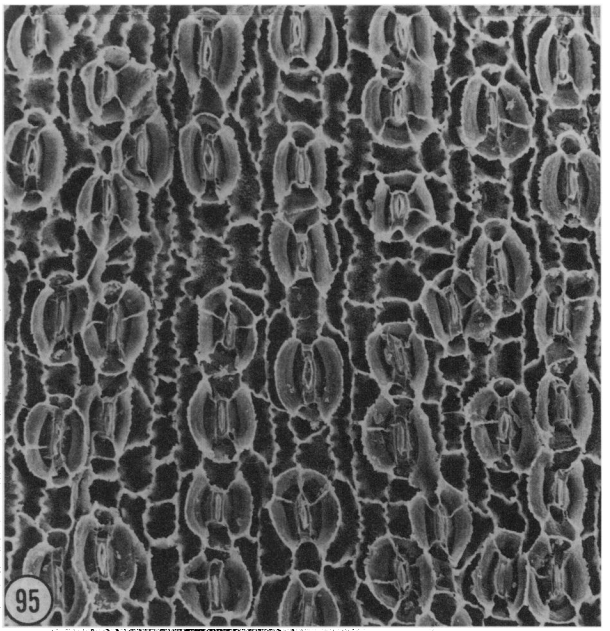
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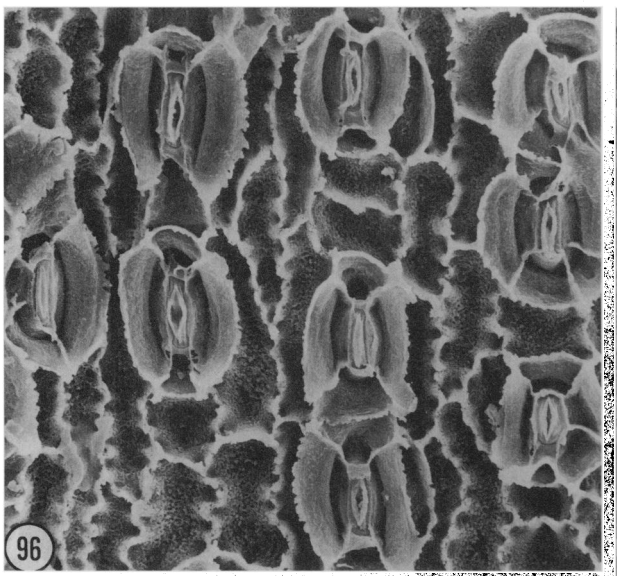
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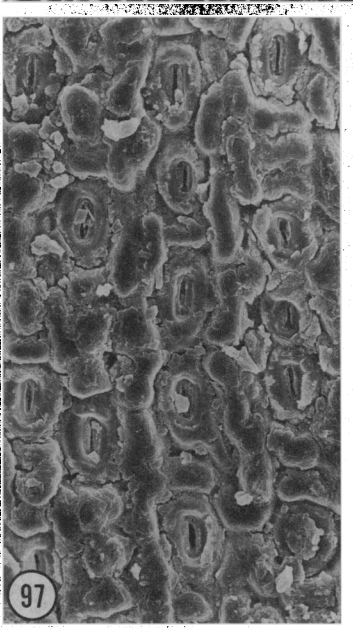
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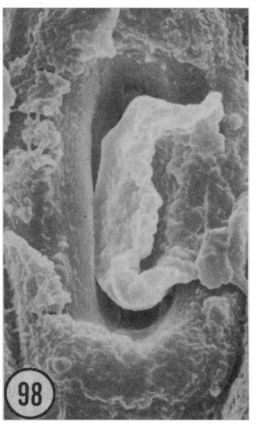
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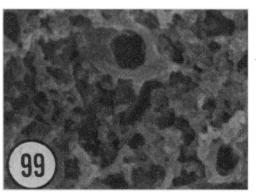
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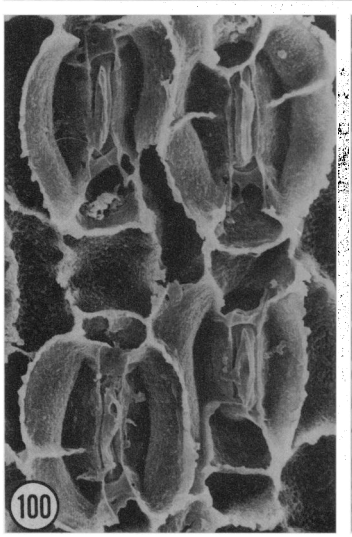
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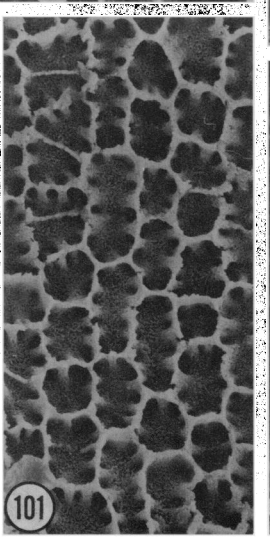
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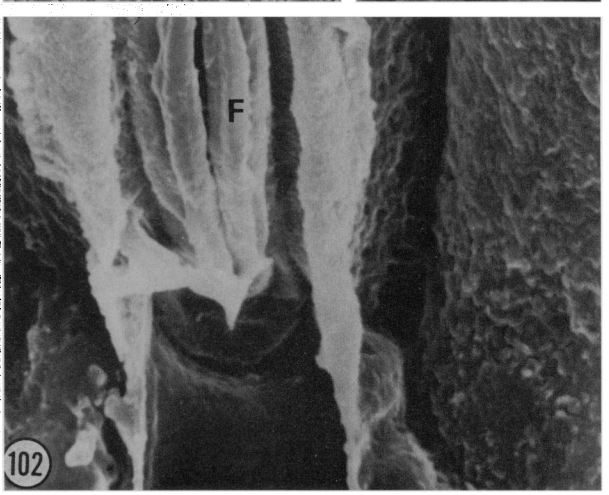
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SECTION *SUNDACARPUS*

PRUMNOPITYS AMARA (FIGS. 103–114)

Adult leaves were collected in northeastern Queensland (table 1). Leaves are linear to elliptic, distichously flattened, 5–15 cm long × 8–15 mm wide, with a distinct groove over the midvein (Silba 1986; de Laubenfels 1988; Page 1988). Stomata were only observed on abaxial surfaces.

External cuticle surfaces are relatively smooth to slightly undulating, with slightly sunken Florin rings (table 2, figs. 104, 108). There is very little epicuticular material, and thick stomatal plugs were not observed, although some small globular components of a plug were observed in one specimen (fig. 108).

Internal cuticle surfaces show very shallow cell wall flanges (figs. 105, 106). Stomata are widely spaced in discontinuous rows and seldom come in contact with one another (figs. 105, 106, 113). Stomata are oriented parallel to the long axis of the leaf, and horizontal stomatal rows have not been observed (fig. 105). Four subsidiary cells are most common, although from two to six have been observed (table 3, figs. 103, 105–107, 110, 112, 113). As in other *Prumnopitys* species, polar subsidiary cells can be lacking and elongate epidermal cells can occur in this area (fig. 107). The shape of the stomatal apparatus is generally elliptical to nearly circular, depending on the number of subsidiary cells present (figs. 103, 106).

Cuticle on the outer subsidiary cell wall flanges is thin and relatively smooth (fig. 103); however, these outer flanges are often so shallow that the surrounding sinuous epidermal cell outlines sometimes are prominent (figs. 110, 112). The surface of subsidiary cell cuticle is smooth to slightly granular, with a shallow, centrally located groove that corresponds externally to the Florin ring and occasional vertical striations (figs. 103, 110, 112, 114). Horizontal striations can occur in this groove (fig. 114).

The cuticular flange between guard cells is relatively thin and irregular (figs. 103, 114). Polar extensions are not common and appear to be short, ribbon-like, and delicate (fig. 103). The cuticle on guard cell surfaces is narrow and slightly granular, usually partially covered by the rolled flange of cuticle between guard and subsidiary cells (figs. 103, 112, 114), and shows a prominent polar ridge, as in most *Prumnopitys* species (fig. 114). The flange of cuticle between guard and subsidiary cells is rugose (figs. 103, 114).

Epidermal cells show two distinct morphologies on abaxial and adaxial surfaces. Abaxial cuticles show the most sinuous epidermal cell outlines of any *Prumnopitys* species (figs. 105–107). Cells are more elongate between stomatal rows (table 3, fig. 106). On adaxial cuticle surfaces, epidermal cell wall flanges are not sinuous and are very elongate and rectangular (fig. 109). The epidermal cell surface cuticle is granular and pitted on both leaf surfaces (fig. 111).

Discussion

With this study of *Prumnopitys* we are now able to characterize the cuticle micromorphology of all 10 species within the genus and to distinguish the two major sections. The genus itself is characterized by undulating outer cuticle surfaces that may reflect epidermal cell outlines; slightly sunken Florin rings; stomatal plugs; discontinuous stomatal rows with stomata oriented parallel to the long axis of the leaf; from two to seven subsidiary cells, with polar subsidiary cells often absent or difficult to distinguish from the surrounding epidermal cells; granular subsidiary cell surfaces with a crease or groove near the guard cells that corresponds to the external Florin ring; ribbon-like polar extensions; slightly granular guard cell cuticle with a prominent polar ridge; rolled cuticle flanges between guard and subsidiary cells; and usually granular epidermal cell surfaces.

Greenwood (1987) suggested that *Prumnopitys* was mostly characterized by sinuous epidermal cell outlines. While this is true in most cases, a few species do not follow this pattern. *Prumnopitys ferruginoides* from New Caledonia (Stockey and Ko 1988) does not show particularly sinuous epidermal cell wall flanges on either leaf surface. *Prumnopitys montana* var. *meridensis* has relatively straight wall flanges on abaxial surfaces, and *P. amara* has straight epidermal cell wall flanges on the adaxial leaf surfaces. Pole (1992) further suggested that epidermal cell sinuousness could not be used as a character to distinguish leaves of *Podocarpus* from those of *Prumnopitys* since sinuous epidermal cells also occur in the former genus. Since the large genus *Podocarpus* has not been completely examined using cuticle micromorphology, it is difficult to say at the present time which characters may be reliably used to distinguish the two genera. Pole (1992) suggested that the stomata are in well-defined and well-spaced uniseriate rows in *Podocarpus,* while this is not the case in *Prumnopitys.* However, our data indicate that such rows may in fact occur in some species, e.g., *P. ferruginoides* and *P. amara.*

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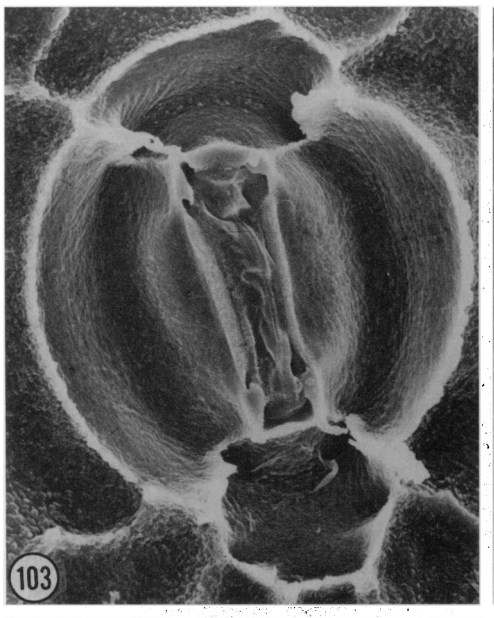
Figs. 94–102 *Prumnopitys taxifolia.* Fig. 94, Inner view abaxial cuticle on stomatal apparatus with four subsidiary cells; × 2200. Fig. 95, Inner view, abaxial cuticle, showing stomatal rows; × 270. Fig. 96, Inner view, abaxial surface, showing stomata with variable subsidiary cell numbers; × 500. Fig. 97, Outer view, abaxial surface, showing epidermal cell outlines, Florin rings, and stomatal plugs; × 300. Fig. 98, Outer view, abaxial surface, showing Florin ring and stomatal plug; × 1900. Fig. 99, Inner view, adaxial surface, showing pitted cuticle on epidermal cell; × 3750. Fig. 100, Inner view, abaxial surface, showing stomatal apparatuses with bordering subsidiary cells of variable shape and number; × 950. Fig. 101, Inner view, adaxial surface, showing nearly rectangular epidermal cells with undulating wall flanges; × 325. Fig. 102, Inner view, abaxial cuticle on surface of stomatal apparatus; × 4500. *F,* flange of cuticle between guard cells.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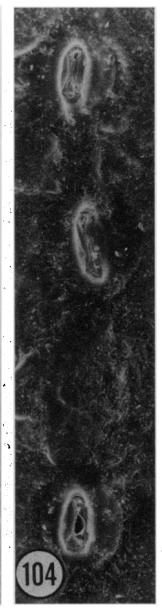
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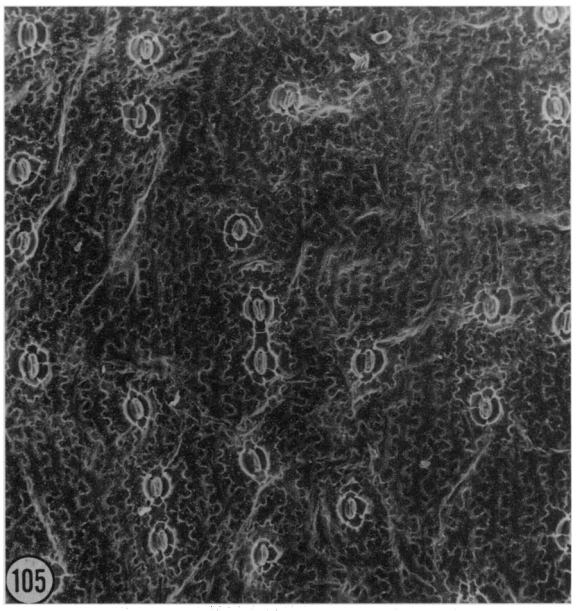
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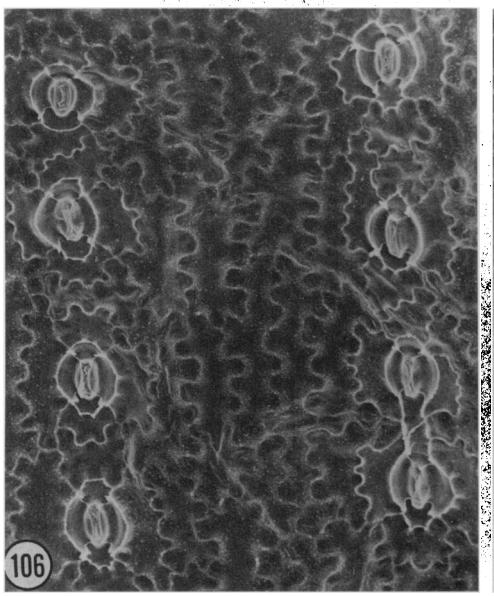
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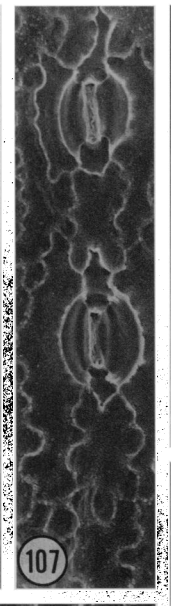
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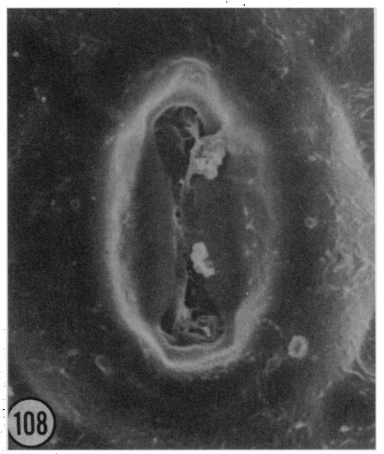
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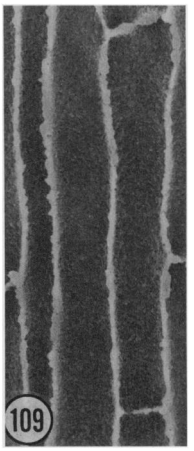
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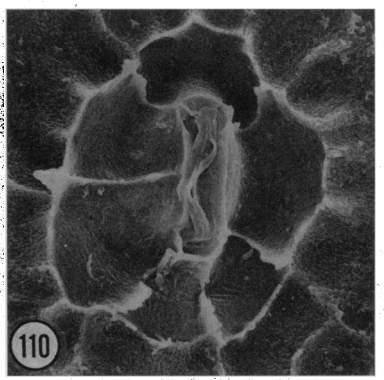
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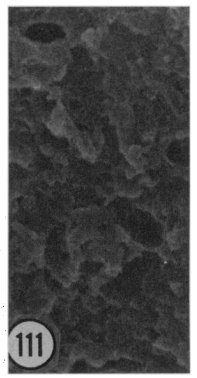
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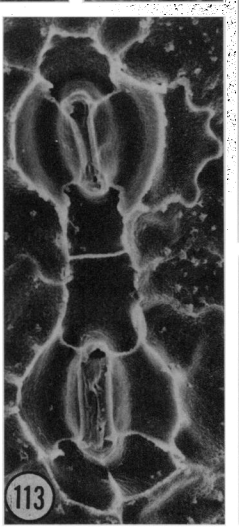
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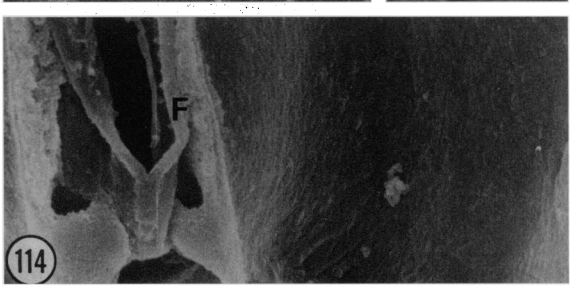
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The section *Sundacarpus,* i.e., *Prumnopitys amara,* can be distinguished micromorphologically from the other species of the genus by its very thin cuticular flanges on the epidermal cell surfaces. The undulating epidermal cell walls (found only on abaxial surfaces) are more pronounced than in the other taxa. Polar extensions are less pronounced. Adaxial epidermal cells are very elongate when compared to those of section *Prumnopitys.* These data support Page's (1988) separation of this taxon into a distinct genus, *Sundacarpus.* In addition, the cuticle on epidermal cell surfaces has scattered, deep, lens-shaped pits not seen in other *Prumnopitys* species. These pits and the elongated epidermal cells on adaxial surfaces are characteristic of juvenile foliage of other conifers such as *Araucaria* de Jussieu (Stockey and Ko 1986) and *Agathis* Salisbury (Stockey and Atkinson 1993) of the Araucariaceae. Enlarged pits, however, have also been seen in adult foliage of *Falcatifolium* (Stockey et al. 1992) of the Podocarpaceae.

Cuticle on the guard and subsidiary cell surfaces has been shown to be diagnostic for some conifer species, e.g., *Araucaria* (Stockey and Ko 1986). However, in the genus *Prumnopitys,* cuticle on the guard cell surfaces is remarkably similar. The flange of cuticle between the guard cells and subsidiary cells is very large and can cover the guard cell surfaces in *P. montana* var. *montana* and *P. montana* var. *meridensis,* and nearly covers the surface in *P. exigua* and *P. harmsiana.* One of the most important characters useful in distinguishing some species is the cuticle on epidermal cell surfaces. But in general, a combination of characters may be useful for any one species, such as the usual number of subsidiary cells; type of striations on the subsidiary cell surfaces; sinuousness of epidermal cells; shape of the stomatal apparatus; lengths, shapes, and thicknesses of polar extensions; and amount of stomatal crowding. We have not tried to distinguish species based on epicuticular waxes, since even the time of collection of the leaves may affect their appearance (Morvan 1982, 1987). All species of *Prumnopitys* have stomatal plugs, and most appear to be composed of rodlike components; but again, because of the changes that can occur in these waxes, we have not used these data to distinguish species.

Prumnopitys montana var. *montana* and *P. montana* var. *meridensis,* while they show many similarities, can be distinguished from one another on the basis of cuticle micromorphology. In *P. montana* var. *meridensis,* Florin rings are less distinct (show a lower relief) and leaf surfaces are generally smoother. Internally, the variety shows stomatal rows that are less crowded than in *P. montana* var. *montana,* and the shape of the stomatal apparatus is more circular and subsidiary cell surfaces are more granular. Prominent vertical striations on subsidiary cells of *P. montana* var. *montana* are not seen in the *P. montana* var. *meridensis.* Epidermal cell shapes are more sinuous on abaxial surfaces in *P. montana* var. *montana,* but more sinuous and elongate on the adaxial surface in *P. montana* var. *meridensis.* Short, nearly square epidermal cell outlines on adaxial surfaces in *P. montana* var. *montana* readily distinguish the two taxa (cf. figs. 68 and 82). We suggest that the status of *P. montana* var. *meridensis* probably needs to be reexamined. Buchholz and Gray (1948*b*) suggested that the variety might be regarded as a distinct species based on external morphological characters. These two taxa are more different from each other in cuticle micromorphology than from some of the other species of *Prumnopitys.*

Fossil podocarp leaves that have been included in the genus *Prumnopitys* are known from Australia and Tasmania (Townrow 1965; Greenwood 1987; Pole 1992). Greenwood (1987) described *P. lanceolata* Greenwood from the Eocene Alcoa Anglesea open-cut brown coal in Victoria, Australia. Leaf arrangement in this species is similar to *P. taxifolia,* and leaf shape and size are similar to *P. andina, P. ferruginea, P. taxifolia,* and *P. ferruginoides* (Greenwood 1987). The fossil species is amphistomatic, while *P. andina* and *P. taxifolia* are hypostomatic. Townrow (1965) reports that stomatal distribution in *P. ferruginea* is variable in cultivation. Greenwood (1987) and Stockey and Ko (1988) report amphistomatic leaves in *P. ferruginoides.* We have found amphistomatic leaves in *P. ferruginoides, P. ladei,* and *P. standleyi* in this study (table 2). Leaves of these species are those that are helically arranged and not distichous; this indicates that the positions of stomata in many conifers are a reflection of how the leaf is borne on the stem and are not necessarily of taxonomic value by themselves (R. A. Stockey, personal observation).

Greenwood (1987) compared the nonsinuous epidermal cell outlines in the fossil *P. lanceolata* to those in *P. ladei* and *P. ferruginoides.* In our study, we observed sinuous cell outlines in *P. ladei.* He further mentions that strongly sinuous epidermal cell walls are "erratically developed" in *P. amara* and *P. montana.*

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Figs. 103–114 *Prumnopitys amara.* Fig. 103, Inner view, abaxial cuticle on stomatal apparatus with three subsidiary cells and one polar epidermal cell; × 1700. Fig. 104, Outer view, abaxial surface, showing Florin rings with low relief; × 250. Fig. 105, Inner view, abaxial surface, showing discontinuous stomatal rows; × 120. Fig. 106, Inner view, abaxial surface, showing stomatal rows and sinuous epidermal cell outlines; × 250. Fig. 107, Inner view, abaxial surface, showing irregularly shaped polar cells on two stomata; × 320. Fig. 108, Outer view, abaxial Florin ring; × 1600. Fig. 109, Inner view, adaxial epidermal cell wall flanges; × 650. Fig. 110, Inner view, abaxial cuticle on stomatal apparatus; × 2750. Fig. 111, Inner view, adaxial cuticle on epidermal cell surface; × 6500. Fig. 112, Inner view, abaxial surface, showing stomatal apparatus with four possible subsidiary cells, showing irregular outer wall flanges; × 1400. Fig. 113, Inner view, abaxial surface, showing two adjacent stomata with varying subsidiary cell numbers; × 600. Fig. 114, Inner view, adaxial cuticle on epidermal cell surface; × 6500. *F,* flange of cuticle between guard cells.

In our study, we have observed that only one leaf surface of each of these species lacked sinuousness (see discussion above). Greenwood (1987) concluded that *P. lanceolata* was most closely comparable to *P. ladei* and *P. ferruginoides.* Without the benefit of SEM with Greenwood's material, we feel that these leaves most closely resemble *P. ferruginoides,* especially when epidermal cell shapes are considered.

The second species described by Greenwood from the Alcoa Anglesea open-cut was referred to *P. tasmanica* (Townrow) Greenwood (1987). These leaves are also amphistomatic and were believed to be helically arranged but distichously flattened (Townrow 1965). Greenwood's material has larger leaves than Townrow's original type material. Epidermal cell shapes in the holotype from the Eocene of Buckland, Tasmania (Townrow 1965, fig. 2*c*) appear similar in shape to *P. ferruginoides,* while those described by Greenwood (1987) approach the shapes in *P. standleyi.* Clearly, further work is needed on these and similar specimens.

Pole (1992) described two species from the Eocene of Tasmania, *P. portensis* Pole and a fossil similar to *P. montana. Prumnopitys portensis* is amphistomatic and has strongly sinuous epidermal cell outlines and an asymmetrical leaf shape. Pole (1992) reports this leaf shape in *P. taxifolia* and *P. ferruginea.* Asymmetry also occurs in *P. exigua* and *P. standleyi,* where leaves are reported as slightly falcate (Silba 1986). In our observation, these *P. portensis* leaves most closely resemble *P. ferruginea* in the region of the stomatal apparatus and *P. harmsiana* and *P. ferruginea* in epidermal cell shape as well as cuticle on the epidermal cell surfaces. Four distinct subsidiary cells are present in the fossil material (Pole 1992), and few species of *Prumnopitys* (*P. ferruginea, P. ladei,* and *P. taxifolia*) show regular polar subsidiary cells, although these may be absent in the latter two species. However, the absence of polar subsidiary cells is very common in the genus as a whole.

The fossil referred to as *Prumnopitys* cf. *P. montana* by Pole (1992) shows very similar-appearing cuticle on the stomatal apparatus to *P. montana* var. *montana* observed in this study, even in having a longitudinal striation or groove on the outer flange of the subsidiary cell cuticle (Pole 1992, fig. 78, and our fig. 63). Epidermal cell outlines, however, are more elongate in the fossil leaves than those that we have observed (cf. Pole 1992, figs. 76, 81, to our figs. 64, 68).

Pole (1992) further described a species of *Podocarpus, P. sinuatus,* also from the Eocene of Hasties, Tasmania. Epidermal cell walls are very sinuous, similar to what we observed on abaxial surfaces of *Prumnopitys amara* (sect. *Sundacarpus*). Unfortunately, only one fossil specimen was reported. The polar extensions illustrated by Pole (1992, fig. 59), however, are much more elongate than what we observed in *P. amara,* and the subsidiary cell wall flanges are more frilled in the fossil. Further observations of the genus *Podocarpus* and more fossil specimens are needed before the affinities of this species can be determined.

Characters that are most useful in distinguishing the genus *Prumnopitys* as a whole include epidermal cell shapes, texture of cuticle on epidermal cell surfaces, the lack of polar subsidiary cells on some stomata but not others on the same leaf, slightly sunken Florin rings, and the flange of cuticle between guard and subsidiary cells. The species within the genus show quite a lot of variability in some of these features. Further observations of the genus *Podocarpus,* in particular, are needed before this genus can be fully resolved in the fossil record.

Acknowledgments

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