

CUTICLE MICROMORPHOLOGY OF AGATHIS SALISBURY

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Cuticle micromorphology from all 21 species of the Southern Hemisphere conifer genus *Agathis* Salisbury was studied with scanning electron microscopy. External and internal features of abaxial and adaxial cuticles are characterized for the three recognized sections of the genus. External cuticle surfaces of all species are undulating and exhibit Florin rings and stomatal plugs, with most species being hypostomatic. Sunken stomata of various orientations occur in discontinuous rows and have three to nine subsidiary cells, four being the common number, and bilobed polar extensions. Epidermal cells are usually rectangular, but vary considerably even on one leaf. The cuticle on guard and subsidiary cell surfaces is smooth to striated and pitted and can be useful in identifying taxa. Distinguishing characters useful at the levels of genus, section, and species are outlined. Micromorphological features distinguishing *Agathis* from *Araucaria* include the undulating epidermal cell surfaces, the presence of Florin rings, stomatal orientations, and bilobed polar extensions. Subsidiary cell number, shape, and morphology and stomatal orientations are the best characters to use when distinguishing fossil araucarian cuticles from those of broad-leaved podocarps.

Introduction

The family Araucariaceae Strasburger contains two extant genera, *Agathis* Salisbury and *Araucaria* de Jussieu, that are mostly confined to the Southern Hemisphere. The family probably was more diverse and widespread during the Mesozoic, when *Araucaria* extended well into the Northern Hemisphere (Stockey 1982; Stockey et al. 1992b). The fossil record of *Agathis*, so far, can only be confirmed in the Southern Hemisphere (Florin 1963; Stockey 1982; Cantrill 1989). Leaves of extant species of *Agathis* were studied with light microscopy (LM) by Florin (1931), Cookson and Duigan (1951), Carr and Carr (in Hyland 1977), and Cantrill (1989).

Cuticle micromorphology of external surfaces of some *Agathis* species was studied with scanning electron microscopy (SEM) by Page (1980). Later, Stockey and Taylor (1981) examined three species using SEM of both internal and external cuticle surfaces. Since these studies, SEM has been used sporadically to compare fossil *Agathis* species to a limited number of extant taxa (e.g., Bigwood and Hill 1985; Cantrill 1989).

In this article we use SEM to characterize the micromorphology of both internal and external cuticles of all 21 species of the genus *Agathis*. Species delimitation in this group of closely related taxa has been notoriously difficult (Whitmore 1980; Whitmore and Page 1980). Taxonomy of the genus is examined in light of cuticle micromorphology, and these data are used to establish generic characters and distinguish the genus from *Araucaria* and the broad-leaved podocarps. The usefulness of these data for paleobotanical investigations is elucidated.

Material and methods

Leaves from all 21 species of the genus *Agathis* were examined from preserved or herbarium material (table 1). Leaves collected in 1977 and 1981 showed no cuticular differences between herbarium material and leaves preserved in FPA (5 mL formaldehyde, 5 mL propionic acid, 90 mL 50% ethanol). The only difference observed was the absence of stomatal plugs on some dried herbarium material. Some plugs are usually present in this material, but most probably were lost when the leaves were pressed and dried.

Cuticles were prepared by cutting the leaf into sections with the leaf margin intact, leaving both abaxial and adaxial epidermis attached (Stockey and Ko 1986). All preparations were immersed in 20% chromium trioxide solution for 96 h (Alvin and Boulter 1974). All other protocol for preparation follows Stockey and Ko (1986).

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

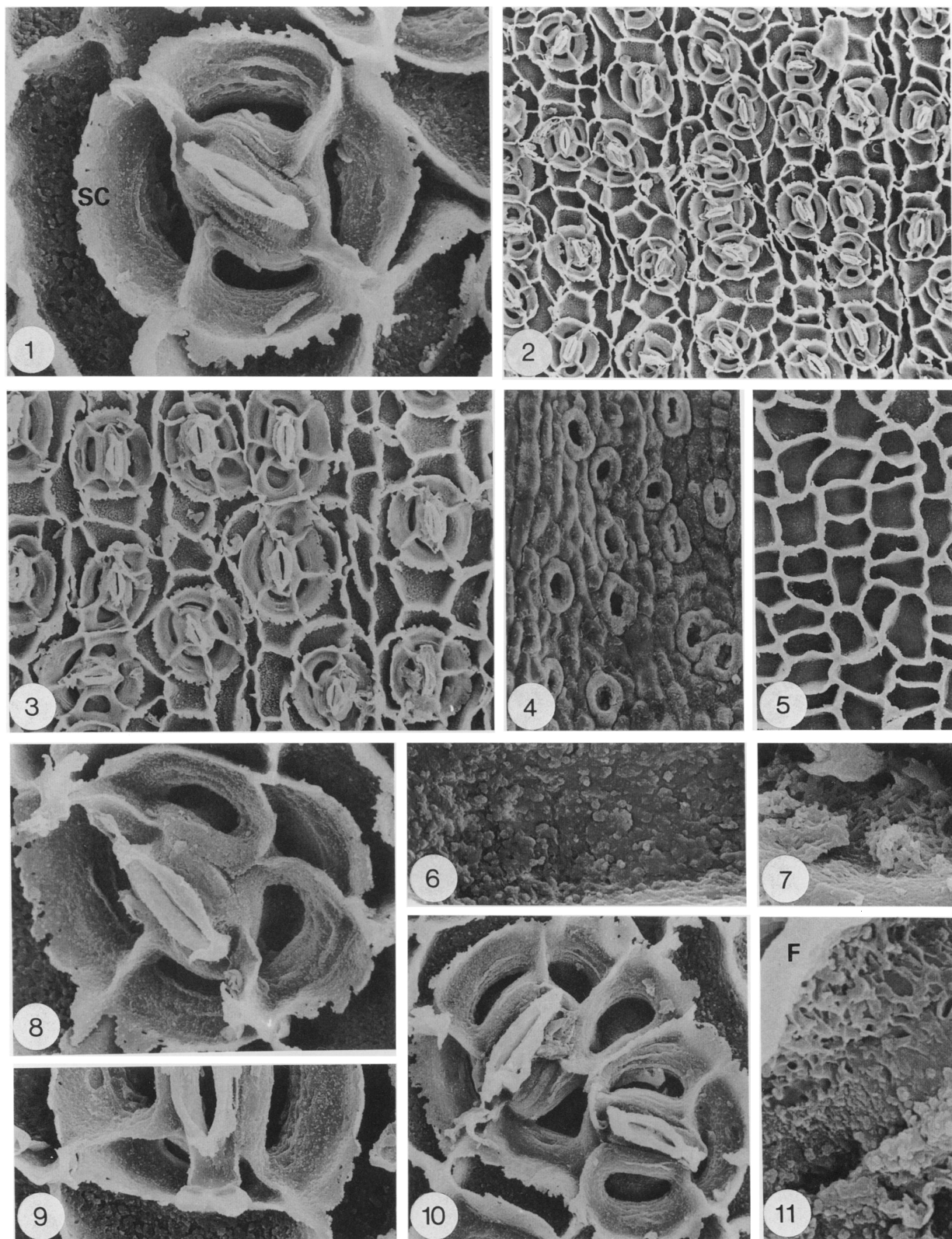
We found that in some species cuticular thickening extended to the level of the hypodermis, and clean cuticles showing only the first cell layer were difficult to obtain. Descriptions disregard what is obvious extraneous debris on cuticle surfaces. Photographs were taken with the long axis of the leaf parallel to the long axis of the plate, and stomatal orientations are given with respect to that axis. Classification follows that of de Laubenfels (1988). We have chosen to list the species in alphabetic order to eliminate any preconceived ideas about what cuticular features were characteristic of the sections. Because of the closeness of these taxa to one another and the lack of taxonomic consensus as to the major divisions within the genus, we preferred to later assess the rela-

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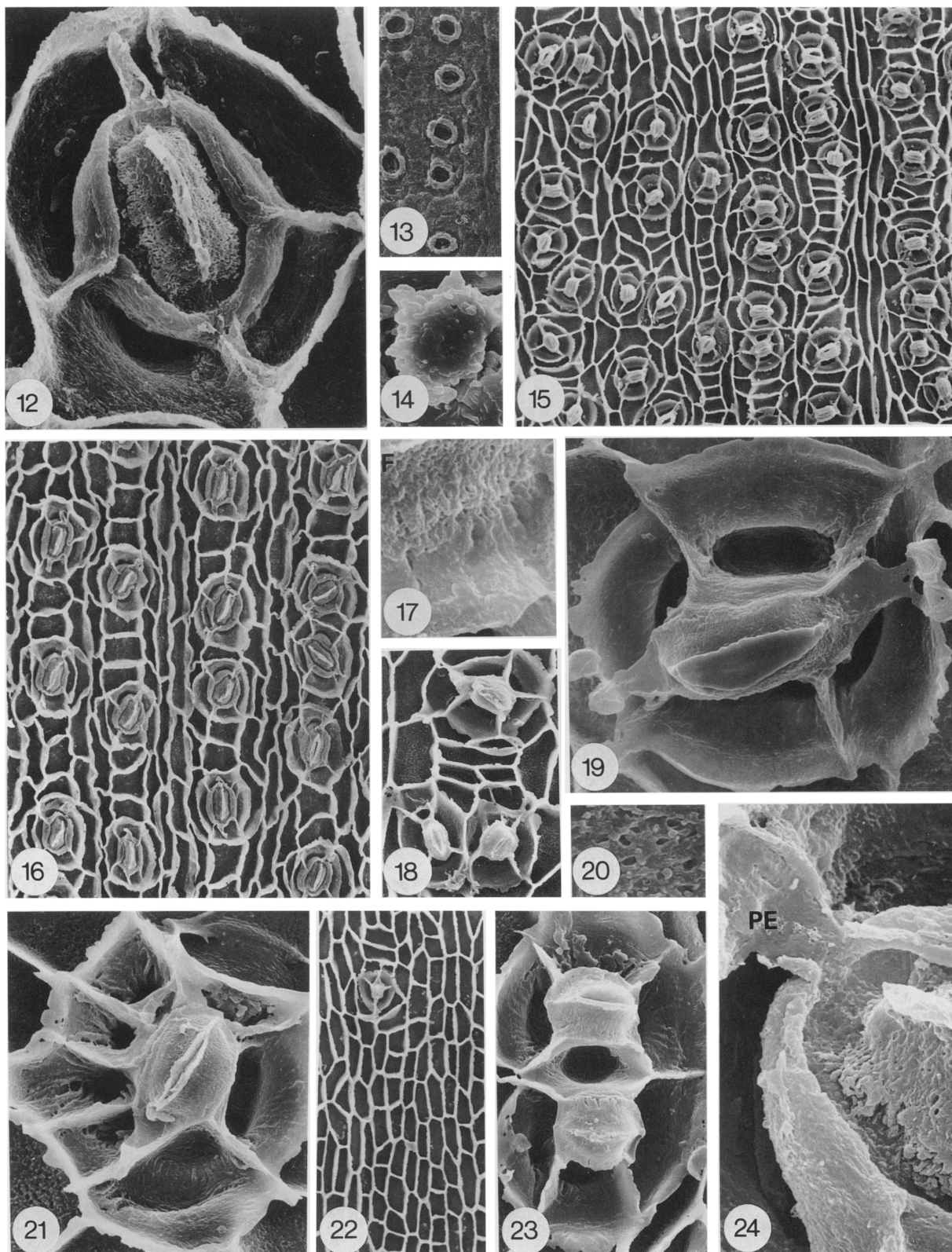
Table 1
AGATHIS SALISBURY

Species	Material examined	Source	Herbarium and voucher
Section <i>Agathis</i> de Laubenfels:			
<i>A. atropurpurea</i> Hyland	H	So. of Atherton, Queensland	NY de Laubenfels P469
<i>A. borneensis</i> Warburg	H	Borneo	NY bb29197 Neth. Ind. For. Serv.
<i>A. celebica</i> (Koord.) Warburg	H	Celebes, Manado	NY bb31503 Neth. Ind. For. Serv.
<i>A. corbassonii</i> de Laubenfels	H	New Caledonia	UAPC-ALTA McPherson 5262
<i>A. flavescens</i> Ridley	H	Malaysia, N. Malaya	MARSSJ 1498 de Laubenfels
<i>A. kinabaluensis</i> de Laubenfels	H	Malaysia, Sabah	NY de Laubenfels P644
<i>A. lenticula</i> de Laubenfels	H	Malaysia, Sabah	NY 9973 Abbe, Abbe, Meijer, and Lampangi
<i>A. macrophylla</i> (Lindley) Masters	H	Fiji, New Hebrides	NY 7 G. E. Petersen, NY 707 S. F. Kajewski
<i>A. montana</i> de Laubenfels	H	New Caledonia	MARSSJ Cherrier in MacKee 38381
<i>A. moorei</i> (Lindley) Masters	H, P	New Caledonia	NY 1A G. E. Petersen
<i>A. orbicula</i> de Laubenfels	H	Sarawak	NY de Laubenfels P614
<i>A. philippinensis</i> Warburg	H	Philippines	NY 412 H. N. Whitford, NY 163 T. E. Borden
<i>A. spathulata</i> de Laubenfels	H	New Guinea	NY de Laubenfels P489
Section <i>Rostrata</i> de Laubenfels:			
<i>A. australis</i> Salisbury	H, P	New Zealand, Queensland	UAPC-ALTA Stockey 1007, NY 265 Philson, Doore and Earle
<i>A. endertii</i> Meijer Drees	H	Sarawak	S 8879 E. F. Bruniig
<i>A. ovata</i> (Moore ex Vieillard) Warburg	H, P	New Caledonia	UAPC-ALTA McPherson and Stockey 3963
Section <i>Prismobracteata</i> Meijer Drees:			
<i>A. labillardieri</i> Warburg	H	New Guinea	NY bb30676, bb30660, Neth. Ind. For. Serv.
<i>A. lanceolata</i> Lindley ex Warburg	H, P	New Caledonia	UAPC-ALTA McPherson and Stockey 3967, Stockey 1008, NY 1609, 1609a Buchholz
<i>A. microstachya</i> J. F. Bailey et C. T. White	H	Queensland	NY 101 Wood Tech. Dept., Qld. For. Serv.
<i>A. robusta</i> (C. Moore et Mueller) F. M. Bailey	H, P	Queensland	NY 16 C. J. Trist
<i>A. silbai</i> de Laubenfels	H	New Hebrides	NY 374 G. Bourdy 374

Note. H = herbarium specimen; P = preserved specimen.



Figs. 1–11 *Agathis atropurpurea*. Fig. 1, Inner view, abaxial cuticle, region of stomatal apparatus, with four subsidiary cells (SC); $\times 850$. Fig. 2, Inner view, abaxial cuticle, stomatal rows; $\times 145$. Fig. 3, Inner view, abaxial cuticle, stomata, showing variable subsidiary cell number; $\times 250$. Fig. 4, Outer view, abaxial cuticle, showing Florin rings around stomata and undulating epidermal cell surfaces; $\times 170$. Fig. 5, Inner view, adaxial cuticle, showing epidermal cell wall flanges; $\times 210$. Fig. 6, Inner view, adaxial cuticle on epidermal cell surface; $\times 2,100$. Fig. 7, Outer view, abaxial cuticle, showing stomatal plug morphology; $\times 2,300$. Fig. 8, Inner view, abaxial cuticle, stomatal apparatus with five subsidiary cells; $\times 850$. Fig. 9, Inner view, abaxial cuticle, showing bilobed polar extension; $\times 900$. Fig. 10, Inner view, abaxial cuticle, showing two stomata sharing eight subsidiary cells; $\times 550$. Fig. 11, Inner view, abaxial cuticle on guard cell surface; $\times 4,500$; F = flange of cuticle between guard cells.



Figs. 12–24 *Agathis australis*. Fig. 12, Inner view, abaxial cuticle, adult foliage, region of stomatal apparatus, with four subsidiary cells; $\times 925$. Fig. 13, Outer view, abaxial cuticle, adult foliage, showing Florin rings and undulating epidermal cell outlines; $\times 115$. Fig. 14, Outer view, abaxial cuticle, juvenile foliage, showing stomatal plug; $\times 1,300$. Fig. 15, Inner view, abaxial cuticle, juvenile foliage, showing stomatal rows; $\times 165$. Fig. 16, Inner view, abaxial cuticle, adult foliage, showing stomatal rows; $\times 130$. Fig. 17, Inner view, abaxial cuticle, juvenile foliage, showing cuticle on guard cell surface; $\times 3,500$. Fig. 18, Inner view, abaxial cuticle, juvenile foliage, stomatal row, with large and small stomatal apparatus; $\times 350$. Fig. 19, Inner

tionships of these taxa. All stubs are deposited in the University of Alberta Paleobotanical Collection (UAPC-ALTA). Specimens jointly collected by McPherson and Stockey (table 1) were studied from duplicates of those housed at the Missouri Botanical Garden, St. Louis (MO).

Results

AGATHIS ATROPURPUREA (FIGS. 1–11)

Adult leaves were taken from a tree in the rain forest of the Queensland Mountains, south of Atherton at 1,130 m (table 1). Leaves are oval-lanceolate to oblong-elliptic (Silba 1986), 3–7 cm long and 0.5–2.0 cm wide, with short petioles (Hyland 1977). Stomata were observed only on abaxial surfaces.

The external cuticle surface is distinctly undulating, with epidermal cell outlines clearly visible (fig. 4). Stomata are sunken and surrounded by Florin rings (Buchholz and Gray 1948). Stomatal plugs are rare in the pressed herbarium material; however, when present they are composed of very short rods (fig. 7).

Inner cuticle surfaces show crowded stomata in discontinuous rows with stomata oriented perpendicular, parallel, and obliquely to the long axis of the leaf (figs. 2, 3). The stomatal apparatus varies in shape depending on its proximity to others (figs. 2, 3, 10), with most isolated stomata being nearly circular in outline (fig. 1). Four subsidiary cells are most common, but five and six may be present, usually a result of the division of lateral subsidiary cells (figs. 2, 3). Unusual shapes of the stomatal apparatus occur when subsidiary cells are shared (fig. 10). Due to the crowded nature of stomata, subsidiary cells are often in contact with one another (fig. 2). In one specimen (fig. 8), one of the lateral encircling cells also appears to be incorporated into the stomatal apparatus.

Cuticle on the outer cell wall flange of subsidiary cells is thick and irregular (figs. 1, 3, 8, 10). The surface of subsidiary cells is slightly pitted, with horizontal striations common (figs. 1, 8). A deep groove occurs in this cuticle surface where each subsidiary cell extends toward the leaf surface (figs. 1, 8–10).

The cuticular flange between guard cells is thick and slightly granular (figs. 8, 11). Polar extensions occur and are distinctly bilobed when over a polar subsidiary cell (fig. 9). When stomata are oblique-

ly oriented, however, polar extensions are confluent with subsidiary cell wall flanges, and the bilobed nature of the extension is not visible (fig. 1). The cuticle on the guard cell surfaces is rugose and pitted near the stoma (fig. 11), with a longitudinal crease present near the subsidiary cell wall flange (fig. 1). The flange of cuticle between guard and subsidiary cells is thick and rugose (figs. 1, 10).

Epidermal cells are irregular in shape, often broader than long on adaxial surfaces (fig. 5). Cells are more elongate between stomatal rows (fig. 2), but due to crowding many irregular shapes result (figs. 2, 3). Epidermal cell wall flanges are straight to curving but on abaxial surfaces appear irregular because of cuticle extension to the hypodermal level (fig. 3). Cuticle on the epidermal cell surfaces is rugose (fig. 6).

AGATHIS AUSTRALIS (FIGS. 12–24)

Both juvenile and adult leaves of this species were examined. Adult leaves were taken from a large tree at 90 m elevation, Bay of Islands, New Zealand, and at the forestry station at Imbil, Queensland (table 1). Juvenile leaves range from 5 cm to 10 cm long and 4 cm wide. Adult leaves are ovate-lanceolate, 1.5–6.0 cm long by 1.0–1.5 cm wide, with short petioles (Silba 1986). Stomata were found occasionally on adaxial surfaces of juvenile leaves but are mostly concentrated on abaxial surfaces in both leaf types (fig. 22).

The external cuticle surface is moderately undulating with the underlying cell structure (fig. 13), visible but not as pronounced as in *A. atropurpurea* (see fig. 4). Stomata are sunken and surrounded by Florin rings. Stomatal plugs are composed of solid irregular blocks (fig. 14).

Inner cuticle surfaces show stomata in discontinuous rows with varied orientation (figs. 15, 16), as in *A. atropurpurea*. Stomata oriented perpendicular to the long axis of the leaf are more prevalent in juvenile foliage (fig. 15), while parallel orientations are more common in adult leaves (fig. 16). Oblique orientations are most common in adult foliage (fig. 16). The stomatal apparatus is slightly variable in shape even when isolated, but also varies, as in *A. atropurpurea* when subsidiary cells are in contact with one another or shared (figs. 15, 16, 18, 23). Four subsidiary cells are most common, but as few as three and as many as seven may occur (figs. 12, 15, 16, 18, 21). Most of the higher numbers of subsidiary

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view, abaxial cuticle, juvenile foliage, showing region of stomatal apparatus, four subsidiary cells, and bilobed polar extensions; $\times 1,400$. Fig. 20, Inner view, adaxial cuticle on epidermal cell surfaces of juvenile foliage; $\times 2,700$. Fig. 21, Inner view, abaxial surface, juvenile foliage, stomatal apparatus with seven subsidiary cells; $\times 950$. Fig. 22, Inner view, adaxial surface, juvenile foliage, showing one stomatal apparatus and epidermal cell outlines; $\times 140$. Fig. 23, Inner view, abaxial cuticle, juvenile foliage, showing two stomata sharing a subsidiary cell; $\times 875$. Fig. 24, Inner view, abaxial cuticle, adult foliage, showing cuticle on guard cell surface and bilobed polar extension (PE); $\times 2,300$.

cells arise from the division of lateral subsidiary cells.

Cuticle on the outer cell wall flange of subsidiary cells is thick, with a relatively irregular outline (fig. 12). In juvenile leaves this flange thins and becomes more irregular since the cuticle extends to the hypodermal level (figs. 19, 21). The cuticle of subsidiary cells in both foliage types shows a deep groove where the cell extends to the leaf surface (figs. 12, 19, 21). The surface of the subsidiary cell cuticle, however, differs in adult and juvenile foliage. In adult leaves the surface is slightly granular (fig. 12); in juvenile leaves it is smoother, and vertical striations are often present (figs. 19, 21, 23).

The cuticular flange between guard cells is usually thin, with an irregular surface in adult leaves (figs. 12, 24) and a slightly smoother surface in juvenile leaves (figs. 17, 19, 21). Bilobed polar extensions occur in both leaf types (figs. 19, 24). These are not usually visible without close examination due to their delicate nature and their absence when the polar region coincides with a subsidiary cell wall flange (fig. 12). The cuticle on guard cells is pitted and more rugose toward the subsidiary cell wall flanges (figs. 17, 24) in both leaf types. There is a distinct groove in the guard cell cuticle in both leaf types (figs. 17, 24). This groove, however, is more pronounced in adult leaves (fig. 12), and the flange between guard and subsidiary cells is inrolled in this area.

Epidermal cells are basically rectangular in shape and more regular than those seen in *A. atropurpurea* (figs. 16, 22). They are shorter within a stomatal row than between rows (figs. 15, 16). Epidermal cell wall flanges are straight to curving in juvenile leaves and slightly sinuous in adult foliage. Cuticle on epidermal cell surfaces is rugose and pitted (fig. 20).

AGATHIS BORNEENSIS (FIGS. 25–33)

Adult leaves come from Moeara Tewa Sirek, Borneo, at an altitude of 50 m (table 1). They are ovate with an acute apex, measure 6–12 cm long by 2–3.5 cm wide, and taper to a 5-mm petiole (de Laubenfels 1988). Stomata were observed only on abaxial leaf surfaces.

The external cuticle surface is undulating, but distinct cell outlines are not always visible (fig. 28), as in *A. atropurpurea*. Stomata are sunken and Florin rings are present (fig. 28). Occasionally stomata are plugged with cuticular material (fig. 29). Presumably, these were nonfunctional. Stomatal plugs also occur, as in the other *Agathis* species; however, those in *A. borneensis* are unusual in that they are composed of elongated tubelike structures (fig. 30).

Inner cuticle surfaces show crowded stomata in discontinuous rows (figs. 26, 33). In many cases there are few intervening epidermal cells. Stomata are oriented in all directions; however, per-

pendicular and oblique orientations are more common than parallel (fig. 33). The stomatal apparatus varies in shape depending on its proximity to others (fig. 27). The majority of single stomata, however, have a nearly circular to elliptical stomatal apparatus (fig. 26). Four subsidiary cells are most common, but five and six also have been seen, making this species conservative for the genus (figs. 25–27).

Cuticle on the outer wall flange of subsidiary cells is thick and somewhat irregular (figs. 25, 27). The subsidiary cell cuticle is pitted and more rugose toward the guard cells (fig. 25). There are vertical striations on subsidiary cell cuticle surfaces (fig. 27), as are seen in juvenile foliage of *A. australis*. A deep groove occurs in this cuticle surface where a part of each subsidiary cell extends toward the leaf surface (figs. 25, 27). The subsidiary cell cuticle may be very rugose closer to the surface of the leaf.

The cuticular flange between guard cells is thin and slightly granular, sometimes irregular (fig. 25). Bilobed polar extensions occur when over a polar subsidiary cell (fig. 25). There is often a groove down the center of the polar extension, but the globular ends are usually absent when the extension is situated over a subsidiary cell wall flange (fig. 27). The cuticle on guard cell surfaces is rugose and pitted toward the subsidiary cells, similar to the situation in adult foliage of *A. australis*. There is also a thickened rolled edge of cuticle that abuts the subsidiary cells (fig. 25). In some instances there is an irregular edge on this cuticular flange (fig. 27).

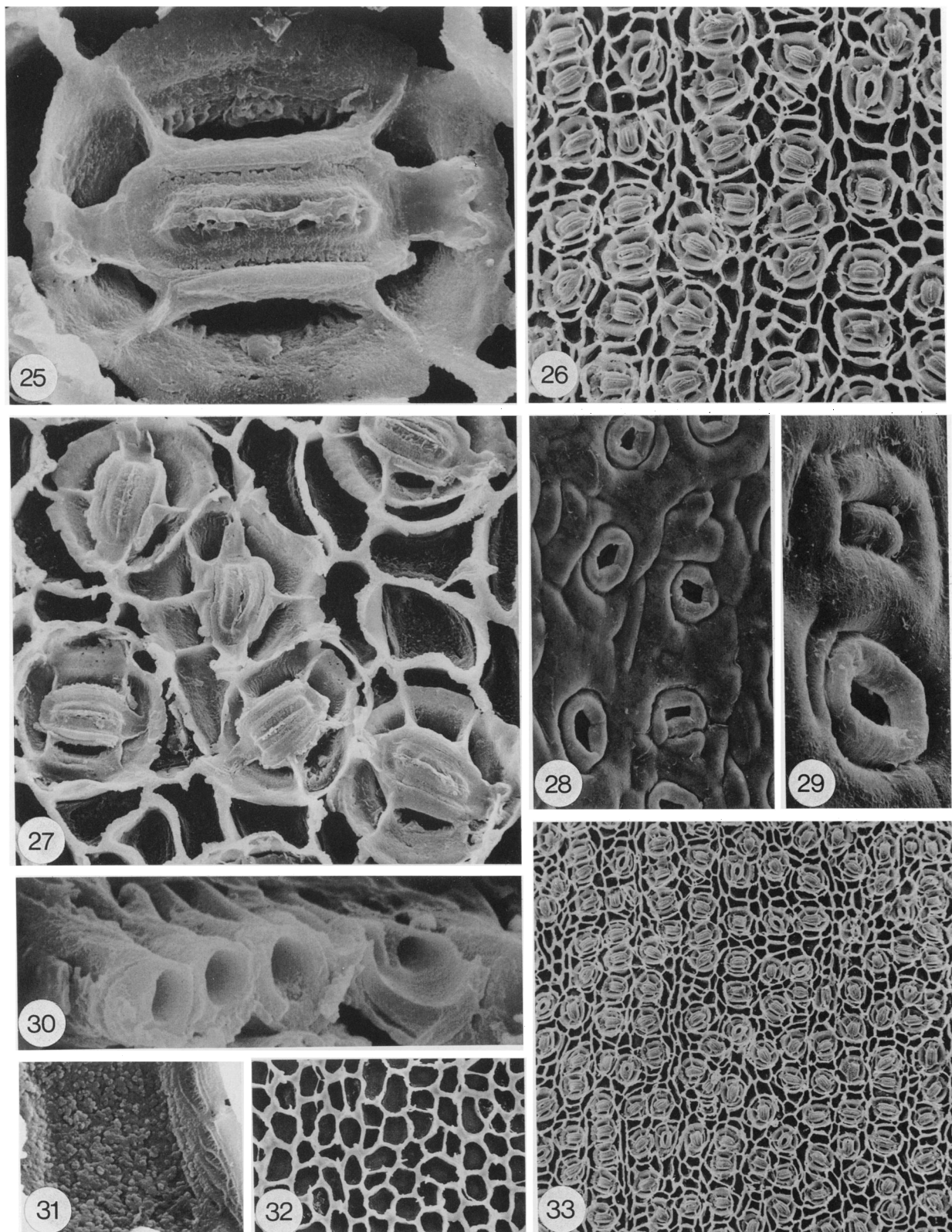
Epidermal cells on adaxial leaf surfaces are rectangular to nearly square or slightly irregular (fig. 32). Those on abaxial surfaces are irregularly shaped and broad within a stomatal row and rectangular and more elongate between stomatal rows (figs. 26, 33). Epidermal cell wall flanges are straight to slightly curving. Cuticle on epidermal cell surfaces is rugose (fig. 31).

AGATHIS CELEBICA (FIGS. 34–44)

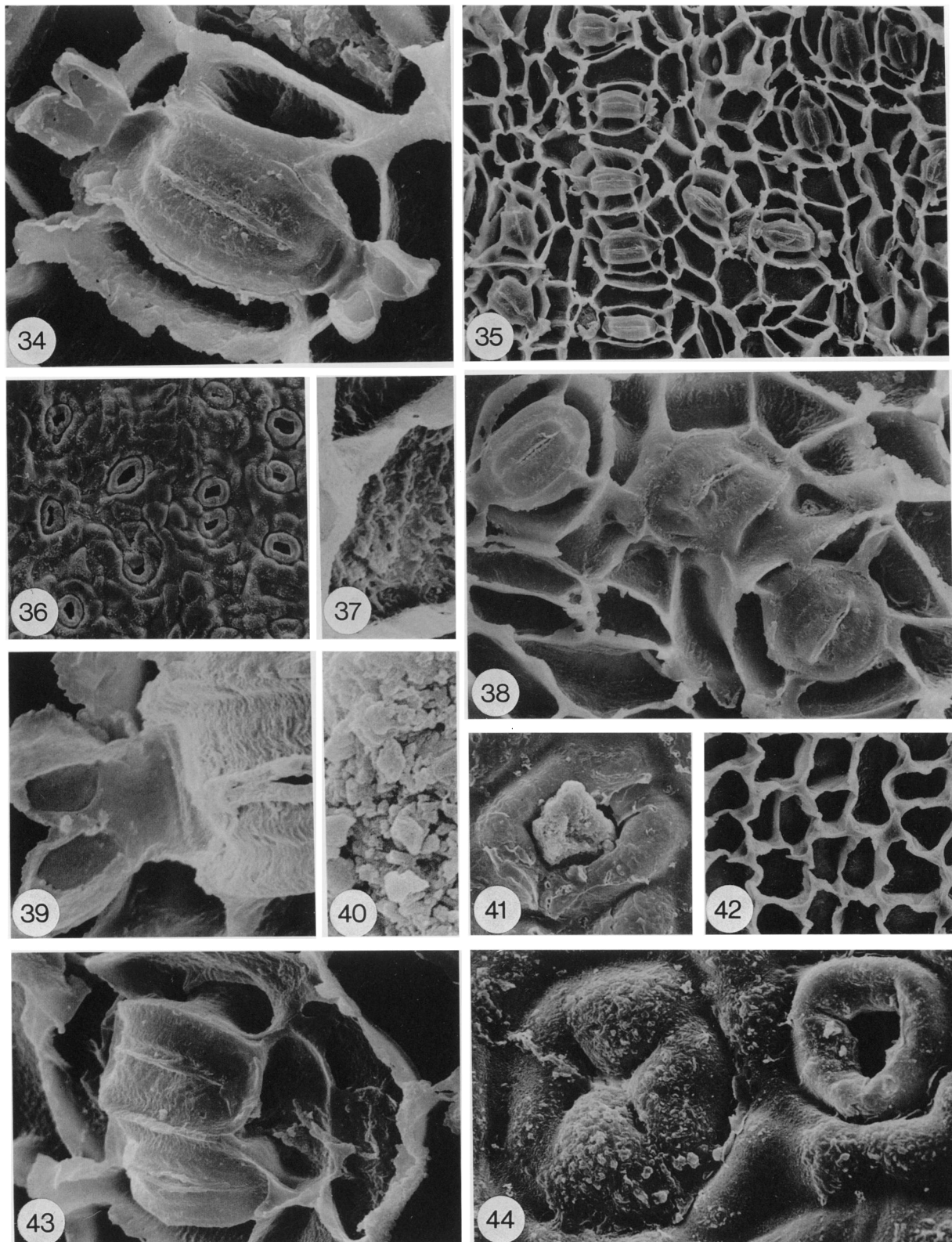
Adult leaves come from Manado, in the Celebes, at 550 m (table 1). They are 6–8 cm long by 2–3 cm wide and taper at the apex and at the base to a 5–10-mm petiole (de Laubenfels 1988). Stomata were observed only on abaxial surfaces.

The external cuticle surface is undulating, with outlines of underlying epidermal cells visible (fig. 36). Distinct Florin rings, that are sometimes irregularly shaped, occur in this species (figs. 36, 41, 44). In some instances stomata appear to be almost completely occluded by the Florin ring (fig. 44); in others a stomatal plug is present (fig. 41) that is composed of small blocks or cubes (fig. 40).

Inner cuticle surfaces show stomata in discontinuous rows of varying orientation. The shape and size of the stomatal apparatus vary widely in



Figs. 25–33 *Agathis borneensis*. Fig. 25, Inner view, abaxial cuticle, region of the stomatal apparatus, showing four subsidiary cells and bilobed polar extensions; $\times 1,300$. Fig. 26, Inner view, abaxial cuticle, stomatal rows; $\times 160$. Fig. 27, Inner view, abaxial cuticle, showing variable subsidiary cell numbers and irregularly shaped stomatal apparatus; $\times 500$. Fig. 28, Outer view, abaxial cuticle, showing Florin rings and undulating epidermal cell surfaces; $\times 270$. Fig. 29, Outer view, abaxial cuticle, showing plugged stoma and typical stoma with Florin ring; $\times 700$. Fig. 30, Outer view, abaxial cuticle, showing hollow tubular components of stomatal plug; $\times 4,250$. Fig. 31, Inner view, adaxial cuticle, showing epidermal cell surface; $\times 1,600$. Fig. 32, Inner view, adaxial cuticle, showing epidermal cell outlines; $\times 160$. Fig. 33, Inner view, abaxial cuticle, showing crowded stomata; $\times 80$.



Figs. 34–44 *Agathis celebica*. Fig. 34, Inner view, abaxial cuticle, region of the stomatal apparatus, showing four subsidiary cells with overarching bilobed polar extensions; $\times 1,350$. Fig. 35, Inner view, abaxial cuticle, discontinuous stomatal rows; $\times 270$. Fig. 36, Outer view, abaxial cuticle, showing Florin rings and undulating epidermal cell outlines; $\times 170$. Fig. 37, Inner view, adaxial cuticle on epidermal cell surfaces; $\times 1,600$. Fig. 38, Inner view, abaxial cuticle, showing a group of stomata of different sizes, the central one of which shows nine subsidiary cells; $\times 700$. Fig. 39, Inner view, abaxial cuticle on guard cell surfaces and prominent bilobed polar extension; $\times 2,500$. Fig. 40, Outer view, abaxial cuticle morphology of stomatal plug; $\times 8,000$. Fig. 41, Outer view, abaxial cuticle, showing stoma with Florin ring and plug; $\times 950$. Fig. 42, Inner view, adaxial cuticle on epidermal cells; $\times 375$. Fig. 43, Inner view, abaxial cuticle, showing two adjacent pairs of guard cells sharing common subsidiary cells; $\times 1,200$. Fig. 44, Outer view, abaxial cuticle, showing large, nearly closed stoma and typical Florin ring around smaller stomatal apparatus; $\times 950$.

this species, especially when subsidiary cells of adjacent stomata are shared or abut one another (figs. 38, 43). In one specimen we observed a double stomatal apparatus with four guard cells completely sharing a ring of subsidiary cells (fig. 43). In this specimen one of the encircling cells also has become part of the whole stomatal apparatus sharing a common outer wall with the lateral subsidiary cells (fig. 43). This species is also the most variable with respect to subsidiary cell number. Although four is the common number (fig. 34), as few as three and as many as nine subsidiary cells can occur per stomatal apparatus (fig. 38).

Cuticle on the outer cell wall flange of subsidiary cells is thick, with an irregular outline and probably extended to the hypodermal level (figs. 34, 38). The surface of subsidiary cells is slightly granular and shows longitudinal striations, as in *A. borneensis* and juvenile *A. australis* (figs. 34, 38, 43). The deep groove in this cuticle is not as pronounced as in the other *Agathis* species (figs. 34, 38).

The cuticular flange between guard cells is usually thin and slightly granular (figs. 34, 38, 39, 43). Bilobed polar extensions occur that usually extend beyond the subsidiary cell boundaries (figs. 34, 39). As in other *Agathis* species, these polar extensions often lack lobes when they coincide with a subsidiary cell wall flange (fig. 38). Cuticle on guard cell surfaces is rugose and slightly pitted toward the stoma (fig. 39). A longitudinal crease occurs in this cuticle surface near the subsidiary cell wall flange, and the edge of the flange closest to the subsidiary cells is slightly inrolled (figs. 34, 38, 39, 43).

Epidermal cells are rectangular to square in outline on adaxial leaf surfaces (fig. 42). On abaxial surfaces, cell shapes are irregular but are slightly more elongate between stomatal rows and broader than tall within a row (fig. 35). Epidermal cell flanges are straight to curving and on abaxial surfaces show irregular margins because of cuticle extension to the hypodermal level (fig. 35). Cuticle on epidermal cell surfaces is rugose (fig. 37).

AGATHIS CORBASSONII (FIGS. 45–56)

Adult leaves come from a tree 13 m tall from Mandjelia, above Pucbo, New Caledonia, at an elevation of 500 m (table 1). They are linear or slightly ovate, blunt, narrowing to a large basal petiole, 45–70 mm long and 6–11 mm wide, with a glaucous abaxial surface (de Laubenfels 1972). Stomata have only been observed on abaxial surfaces.

External cuticle surfaces are very undulating and clearly show outlines of the underlying epidermal cells (fig. 48). Stomata are sunken and prominent Florin rings are present (figs. 48, 50). Stomatal plugs occur and are composed of very short rods or globules (figs. 49, 50).

Inner cuticle surfaces show crowded but usually separate stomata that are oriented in all directions, with perpendicular orientations being the most common (figs. 46, 47). The stomatal apparatus is usually elliptical and sometimes almost circular (figs. 45, 47, 56). Occasionally stomata in one row have subsidiary cells that abut one another (fig. 55). Four subsidiary cells are most common, but from three to six occur (figs. 45, 47, 56). In stomata with three subsidiary cells, one of the polar cells is missing (fig. 56). In those with five or six, these usually result from the division of a lateral subsidiary cell (fig. 47).

Cuticle on the outer cell wall flange of subsidiary cells is thick and slightly irregular when the cuticle extends to the level of the hypodermis (figs. 45, 56). The surface of subsidiary cell cuticle is distinctly pitted and shows horizontal striations (fig. 45) like those reported in *A. atropurpurea*. Grooves in this cuticle are not deep as in most of the other *Agathis* species.

The cuticular flange between guard cells is relatively thick and rugose (figs. 45, 53, 54, 56). Polar extensions are distinctly bilobed (figs. 45, 53) but are not usually visible when they coincide with a subsidiary cell wall flange (fig. 56). Cuticle on guard cell surfaces is rugose and narrow (figs. 45, 53, 54). A distinct groove occurs in this cuticle surface as in other *Agathis* species (figs. 45, 54). The flange of cuticle between guard and subsidiary cells is not very pronounced (fig. 45).

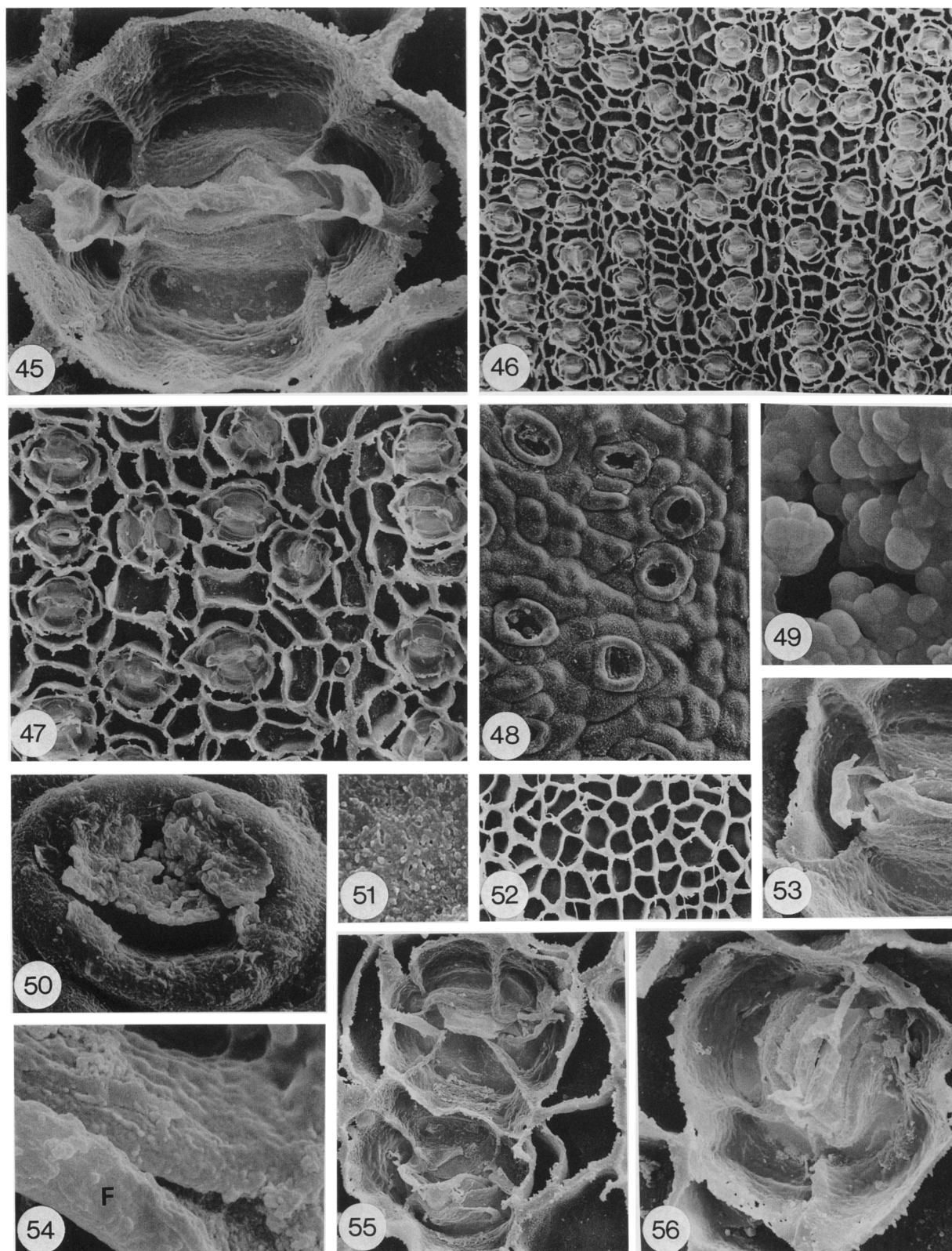
Epidermal cells on adaxial surfaces are rectangular to square (fig. 52). On abaxial surfaces cells are rectangular and more elongate between stomatal rows and of variable shape, but usually broader than long within rows (figs. 46, 47). Epidermal cell wall flanges are straight to curving. The tops of the flanges are irregular on the abaxial surface where the cuticle reaches the level of the hypodermis (fig. 47). Cuticle on epidermal cell surfaces is rugose to pitted (fig. 51).

AGATHIS ENDERTII (FIGS. 57–67)

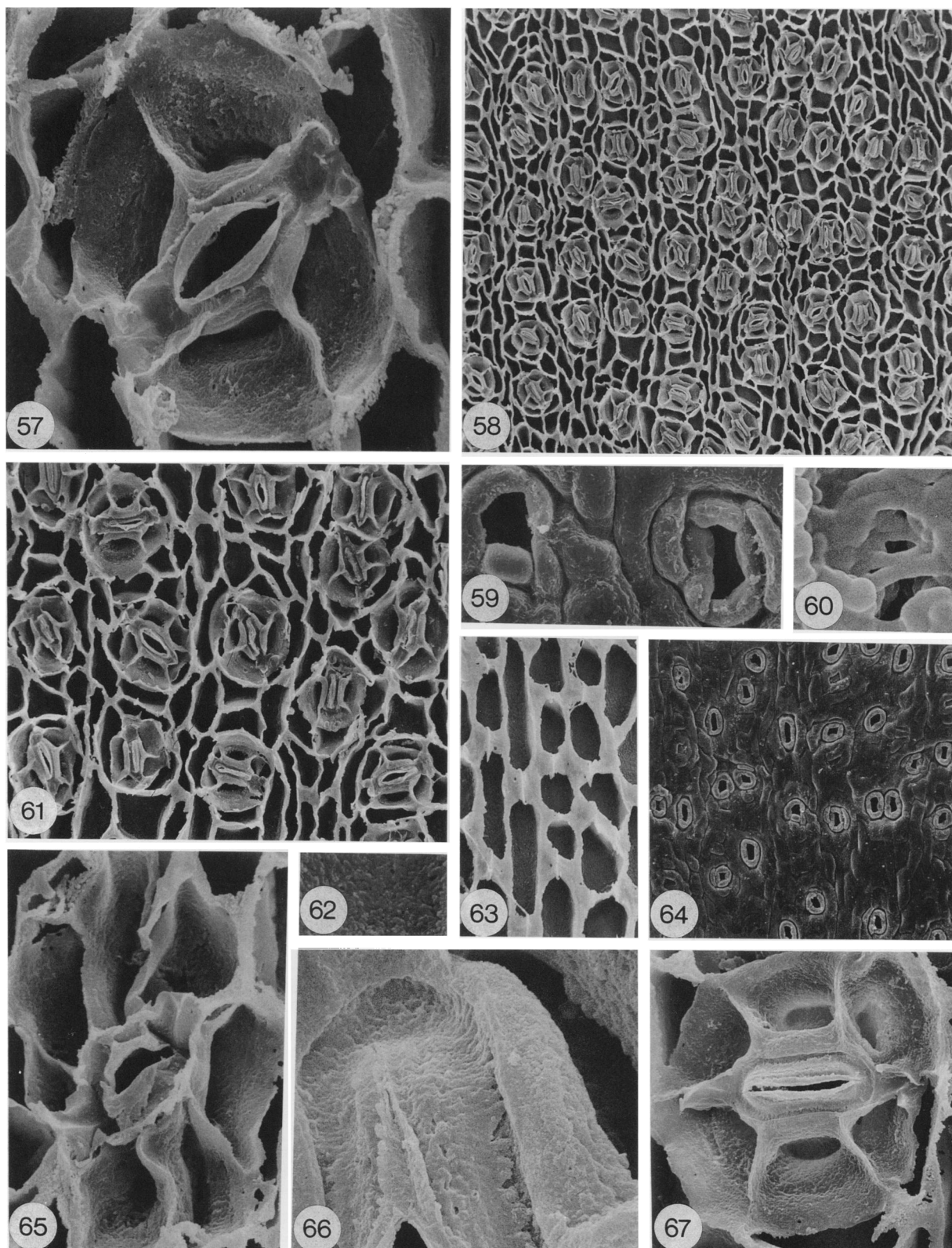
Adult leaves were collected at 2,400 m on the Merurong Plateau, Bintulu, Sarawak (table 1). They are ovate, slightly acuminate, or occasionally in the smaller leaves round and blunt, 3.5–7 cm long and 1.8–3.2 cm wide, and taper at the base to a 4–7-mm petiole (de Laubenfels 1988). Stomata were only observed on abaxial surfaces.

The external cuticle surface is moderately undulating, with some underlying epidermal cells visible (fig. 64). Stomata are sunken and prominent Florin rings present (figs. 59, 64). Rings may be irregularly shaped or broken, and in some cases lateral encircling cells extend to the surface and flank the Florin ring (figs. 59, 64). Stomatal plugs are present and composed of short rods (fig. 60).

Inner cuticle surfaces show crowded stomata of various orientations, with oblique being the most common (figs. 58, 61). The stomatal ap-



Figs. 45-56 *Agathis corbassonii*. Fig. 45, Inner view, abaxial cuticle, area of the stomatal apparatus, showing four subsidiary cells; $\times 1,100$. Fig. 46, Inner view, abaxial cuticle, stomatal rows; $\times 90$. Fig. 47, Inner view, abaxial cuticle, showing stomata with varying orientations and numbers of subsidiary cells; $\times 200$. Fig. 48, Outer view, abaxial cuticle, showing Florin rings and undulating epidermal cell surfaces; $\times 200$. Fig. 49, Outer view, abaxial cuticle, stomatal plug morphology; $\times 5,750$. Fig. 50, Outer view, abaxial cuticle, showing Florin ring and stomatal plug; $\times 1,150$. Fig. 51, Inner view, adaxial cuticle on epidermal cell surface; $\times 1,900$. Fig. 52, Inner view, adaxial cuticle, showing epidermal cell outlines; $\times 150$. Fig. 53, Inner view, abaxial cuticle, showing bilobed polar extension; $\times 900$. Fig. 54, Inner view, abaxial cuticle on guard cell surface and rugose flange (F) between guard cells; $\times 4,750$. Fig. 55, Inner view, abaxial cuticle, showing two stomatal apparatusi in contact; $\times 500$. Fig. 56, Inner view, abaxial cuticle, region of the stomatal apparatus, with three subsidiary cells; $\times 850$.



Figs. 57–67 *Agathis endertii*. Fig. 57, Inner view, abaxial cuticle, region of the stomatal apparatus, showing four subsidiary cells with broad flanges and bilobed polar extensions; $\times 850$. Fig. 58, Inner view, abaxial cuticle, stomatal rows; $\times 110$. Fig. 59, Outer view, abaxial cuticle, showing dissected Florin ring and epidermal and encircling cell outlines; $\times 525$. Fig. 60, Outer view, abaxial cuticle, stomatal plug morphology; $\times 6,000$. Fig. 61, Inner view, abaxial cuticle, showing stomata with varying orientations and subsidiary cell numbers; $\times 220$. Fig. 62, Inner view, abaxial cuticle on epidermal cell surface; $\times 1,550$. Fig. 63, Inner view, abaxial cuticle, showing epidermal cell outlines; $\times 310$. Fig. 64, Outer view, abaxial cuticle, showing Florin rings, undulating epidermal cell surfaces, and plugged stomata (arrows); $\times 105$. Fig. 65, Inner view, abaxial cuticle, region of the stomatal apparatus, with seven subsidiary cells; $\times 825$. Fig. 66, Inner view, abaxial cuticle on guard cell surfaces; $\times 3,100$. Fig. 67, Inner view, abaxial cuticle, region of the stomatal apparatus, showing six subsidiary cells; $\times 700$.

paratus varies in shape depending on the number of subsidiary cells present and its proximity to other stomata. Most are elliptical in outline (figs. 57, 58, 61, 67). Four subsidiary cells are most common, but from five to seven also occur (figs. 57, 61, 65, 67). Larger numbers are the result of the division of lateral subsidiary cells.

Cuticle on the outer subsidiary cell wall flange is thick and irregular and extends to the level of the hypodermis (fig. 57). The surface of subsidiary cell cuticle is slightly rugose and pitted with some indications of lateral striations; however, these are not pronounced (figs. 57, 65, 67). A deep groove occurs in some subsidiary cell cuticles (fig. 57); in others it is not so pronounced (fig. 67).

The cuticular flange between guard cells is thick and granular (figs. 57, 66). Bilobed polar extensions occur that are often broken or lack lobes when over a subsidiary cell wall flange (figs. 57, 65, 67). There is often a longitudinal groove down the center of the extension (fig. 65). Cuticle on guard cell surfaces is rugose to slightly pitted toward the subsidiary cell wall flange (fig. 66). A longitudinal crease occurs on this surface and the flange between guard and subsidiary cells is slightly inrolled and rugose (fig. 66).

Epidermal cells are square to rectangular in outline on adaxial surfaces (fig. 63). On abaxial surfaces, cells are elongate between stomatal rows and irregular, often broader than long within a row (figs. 58, 61). Epidermal cell wall flanges are relatively straight. Edges of the flange are irregular on both cuticles as they extend to the hypodermal level (figs. 61, 63). Cuticle on epidermal cell surfaces is rugose (fig. 62).

AGATHIS FLAVESCENS (FIGS. 68–77)

Adult leaves come from the Pahang Mountain Plateau, Cunon Tahan, Malaya (table 1). They are ovate, often wider before the middle, 3–4 cm long and 1–2 cm wide, rounded and blunt at the apex, tapering at the base to a 3–5-mm petiole (de Laubenfels 1988). Stomata have only been observed on abaxial surfaces.

The external cuticle surface is undulating, with outlines of underlying epidermal cells sometimes visible (fig. 71). Stomata are sunken and surrounded by Florin rings that may be slightly irregular in shape (figs. 71, 72). Stomatal plugs are present and are composed of very short rods (figs. 72, 73).

Inner cuticle surfaces show stomata in discontinuous rows with variable orientation, perpendicular and oblique being the most common (figs. 68–70). The stomatal apparatus varies in size and shape depending on its proximity to others (figs. 69, 70), with most being circular to elliptical (fig. 68). Four subsidiary cells are most common, with five to seven also present (figs. 68–70). Subsidiary cells within a row are often in contact with one another (figs. 69, 70).

Cuticle on the outer cell wall flange of subsidiary cells is thick and irregular (figs. 68, 70). The surface of subsidiary cell cuticle is pitted, with slight horizontal striations present (figs. 68, 70). A groove also occurs in this cuticle surface that sometimes appears deep and other times more shallow (figs. 68, 70).

The cuticular flange between guard cells is thin and granular (figs. 68, 75, 77). Bilobed polar extensions occur when over a polar subsidiary cell (figs. 68, 75), but the bilobed nature is not visible when the extension is broken or coincides with a subsidiary cell wall flange (fig. 70). The cuticle on guard cell surfaces is rugose and pitted toward the stoma, with a longitudinal crease as in other *Agathis* species (figs. 68, 70, 77). The flange of cuticle between guard and subsidiary cells is slightly inrolled or not very pronounced (figs. 68, 70, 77).

Epidermal cells are irregular in shape. On adaxial surfaces they vary from square to rectangular or triangular and are sometimes broader than long (fig. 76). Cells are usually more elongate between stomatal rows on abaxial surfaces and broader than long within a row (fig. 69). Epidermal cell wall flanges are relatively straight and epidermal cell surfaces are pitted (fig. 74).

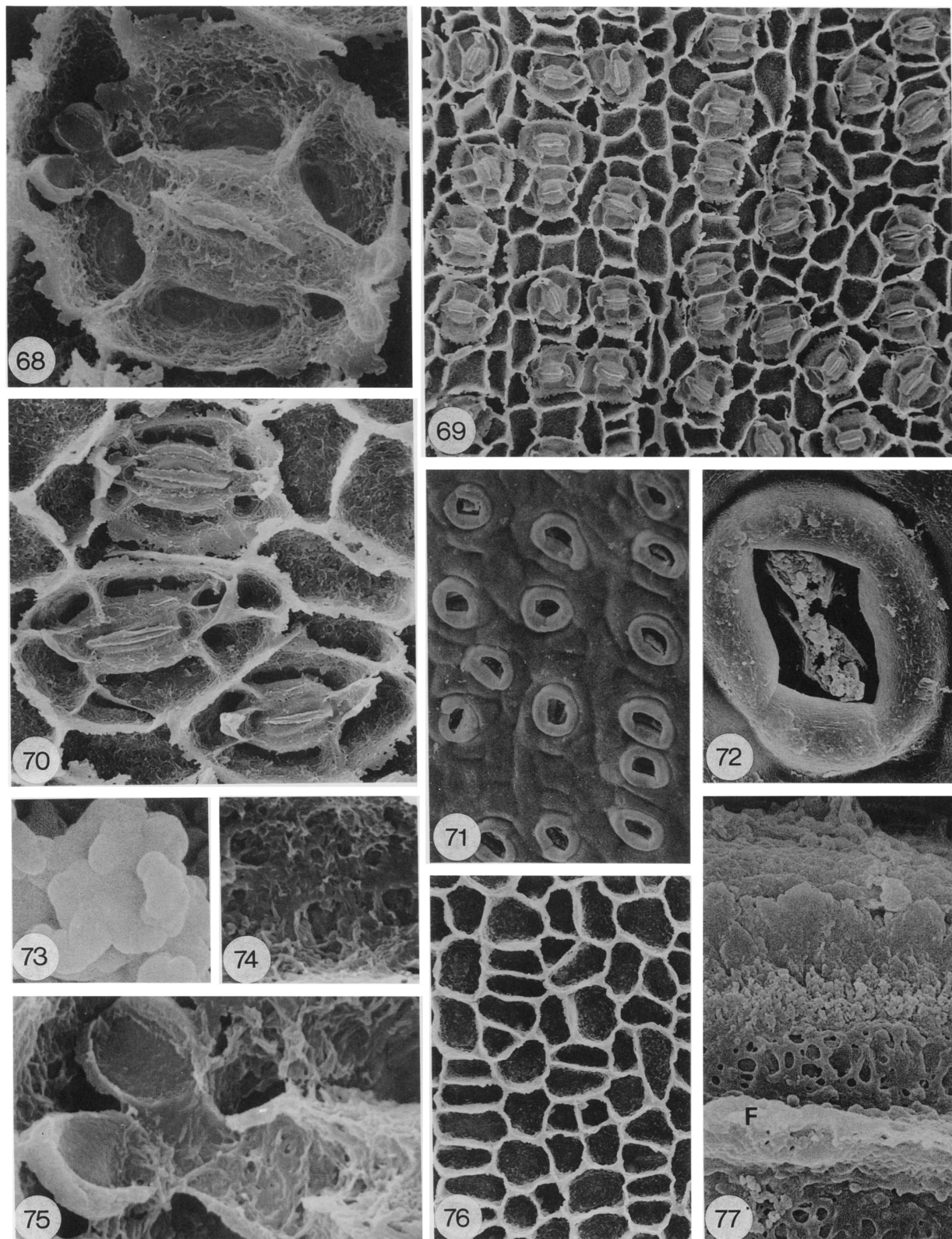
AGATHIS KINABALUENSIS (FIGS. 78–87)

Adult leaves were collected from a tree 25 m tall on Mount Kinabalu, Sabah, at 1,675 m (table 1). Leaves are ovate, apices slightly acuminate to round but blunt on smaller leaves, 3.5–7 cm long and 1.8–3.2 cm wide, tapering at the base to a 4–7-mm petiole (de Laubenfels 1988). Stomata have only been observed on abaxial surfaces.

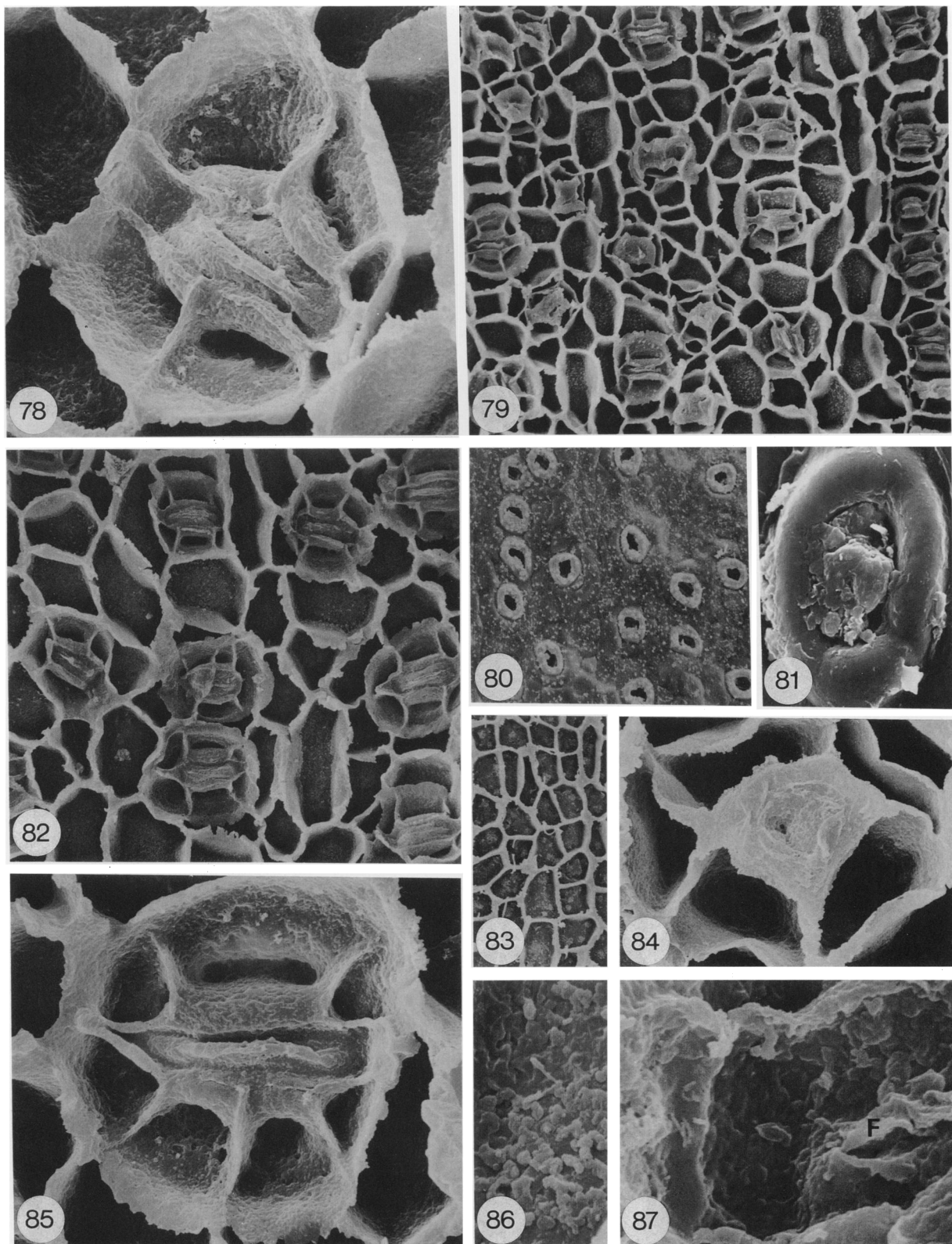
The external cuticle surface is slightly undulating; however, underlying epidermal cells are not obvious (fig. 80). Small surface platelets have also been observed on some leaves (fig. 80). Stomata are sunken and prominent Florin rings are present (figs. 80, 81). Stomatal plugs are present and appear to be composed of irregular blocks (fig. 81).

Inner cuticle surfaces show discontinuous stomatal rows with variable orientation, but perpendicular and oblique orientations are most common (figs. 79, 82). The stomatal apparatus is circular to elliptical in outline (figs. 78, 79, 82, 85). Four subsidiary cells are most common, but as few as three and as many as five occur (figs. 78, 79, 82, 85), with five resulting from the division of a lateral subsidiary cell. In several instances, what were probably aborted stomata occur (fig. 84). On these regions of the leaf, a circle of four cells occurs, with the general shape and size of subsidiary cells; however, the guard cell cuticle has very little in the way of distinct morphology. If guard cells do occur, there is no exit to a stoma.

Cuticle on the outer wall flange of subsidiary



Figs. 68–77 *Agathis flavescens*. Fig. 68, Inner view, abaxial cuticle, region of the stomatal apparatus, showing four subsidiary cells and bilobed polar extensions; $\times 1,100$. Fig. 69, Inner view, abaxial cuticle, stomatal rows; $\times 200$. Fig. 70, Inner view, abaxial cuticle, stomatal apparatus, with variable subsidiary cell numbers; $\times 625$. Fig. 71, Outer view, abaxial cuticle, showing Florin rings and undulating epidermal cell surfaces; $\times 220$. Fig. 72, Outer view, abaxial epidermis, Florin ring and stomatal plug; $\times 1,250$. Fig. 73, Outer view, abaxial cuticle, stomatal plug morphology; $\times 13,500$. Fig. 74, Inner view, abaxial cuticle on epidermal cell surface; $\times 2,000$. Fig. 75, Inner view, abaxial cuticle, bilobed polar extension; $\times 2,700$. Fig. 76, Inner view, abaxial cuticle, showing epidermal cell outlines; $\times 200$. Fig. 77, Inner view, abaxial cuticle on guard cell surfaces; $\times 6,250$; *F* = flange of cuticle between guard cells.



Figs. 78–87 *Agathis kinabaluensis*. Fig. 78, Inner view, abaxial cuticle, region of the stomatal apparatus, showing four subsidiary cells; $\times 1,100$. Fig. 79, Inner view, abaxial cuticle, stomatal rows; $\times 215$. Fig. 80, Outer view, abaxial cuticle, Florin rings and undulating epidermal cell surfaces; $\times 145$. Fig. 81, Outer view, abaxial cuticle, Florin ring and stomatal plug; $\times 1,150$. Fig. 82, Inner view, abaxial cuticle, stomatal rows and tall epidermal cell wall flanges; $\times 320$. Fig. 83, Inner view, abaxial cuticle, epidermal cell outlines; $\times 165$. Fig. 84, Inner view, abaxial cuticle, showing aborted stomatal apparatus; $\times 1,100$. Fig. 85, Inner view, abaxial cuticle, region of the stomatal apparatus, with five subsidiary cells; $\times 1,075$. Fig. 86, Inner view, abaxial cuticle on epidermal cell surface; $\times 1,900$. Fig. 87, Inner view, abaxial cuticle on guard cell surfaces and bilobed polar extension; $\times 4,400$.

cells is thick and irregular when it extends to the hypodermal level (figs. 78, 82, 85). The cuticle of subsidiary cells is rugose to pitted, with slight indications of longitudinal striations on some subsidiary cells (fig. 78). These, however, are not very pronounced. A deep groove occurs in this cuticle surface (figs. 78, 85).

The cuticular flange between guard cells is relatively thin and rugose (figs. 78, 85, 87). Polar extensions are bilobed (figs. 85, 87). The cuticle on guard cell surfaces is rugose (fig. 87). A longitudinal crease is present on this cuticle surface and the flange between guard and subsidiary cells is rugose and inrolled (figs. 78, 85, 87).

Epidermal cells are irregular in shape, varying from square to triangular and rectangular on adaxial leaf surfaces (fig. 83). Cells are more elongate and rectangular in shape between stomatal rows on abaxial surfaces and broader than long within a row (fig. 79). Epidermal cell wall flanges are straight to curving but may have irregular surfaces when they extend to the hypodermal level (fig. 82). Cuticle on the epidermal cell surfaces is rugose (fig. 86).

AGATHIS LABILLARDIERI (FIGS. 88–100)

Two different specimens from Bosniek and Seroei, New Guinea, from 250 m and 50 m, respectively, were examined (table 1). Juvenile leaves from Seroei were also examined (table 1). They are ovate and acuminate, 10 cm long and 6 cm wide (de Laubenfels 1988). Adult leaves are ovate to oval lanceolate, acute, 6–9 cm long and 2.0–2.4 cm wide, narrowing to a 5–7-mm petiole (de Laubenfels 1988). A few scattered stomata have been observed on adaxial surfaces of adult leaves; however, most are found on the abaxial surface.

The external cuticle surface is undulating, with many underlying epidermal cell outlines visible on the surface (figs. 89, 93). Stomata are sunken and Florin rings are usually present on both foliage types (figs. 93, 95). However, on some adult foliage areas occur in which the rings are plugged with cuticular material or broken up and obscured (fig. 89). Stomatal plugs are composed of rugose sheets of material (fig. 95).

Inner cuticle surfaces show discontinuous rows of stomata that in juvenile foliage are not in contact with one another (figs. 90, 92). Occasionally subsidiary cells of adjacent stomata are in contact with one another, altering the shape of the stomatal apparatus (fig. 91). Most stomatal apparatus are elliptical in outline with those of juvenile foliage being slightly more expanded (fig. 88) than those of adult leaves (fig. 100). Stomata are oriented in all directions; however, oblique and perpendicular orientations are most common (fig. 90). Four subsidiary cells are most common, with three or five occurring rarely (figs. 88, 92, 100);

five being the result of the division of a lateral subsidiary cell. One stomatal apparatus was found in which the lateral subsidiary cell apparently divided tangential to the apparatus (fig. 97).

Cuticle on the outer wall flange of subsidiary cells is thick and irregular in juvenile foliage (fig. 88) but smoother on adult leaves (fig. 100). The surface of subsidiary cells is slightly granular (figs. 88, 97, 100), with occasional pits on juvenile leaves (fig. 88). Longitudinal striations occur on subsidiary cell wall cuticle in both juvenile and adult foliage (figs. 88, 97, 100). A deep groove occurs in this cuticle on both leaf types but may be slightly more pronounced in adult foliage (figs. 88, 100).

The cuticular flange between guard cells is thin and rugose in both leaf types (fig. 98). Bilobed polar extensions occur commonly (figs. 88, 91, 92, 97, 100). The cuticle on guard cell surfaces is rugose (fig. 98), and often both a ridge and a crease occur on this cuticle (figs. 88, 97, 100). There is a thickened rolled edge of cuticle that abuts the subsidiary cells (figs. 88, 97, 100).

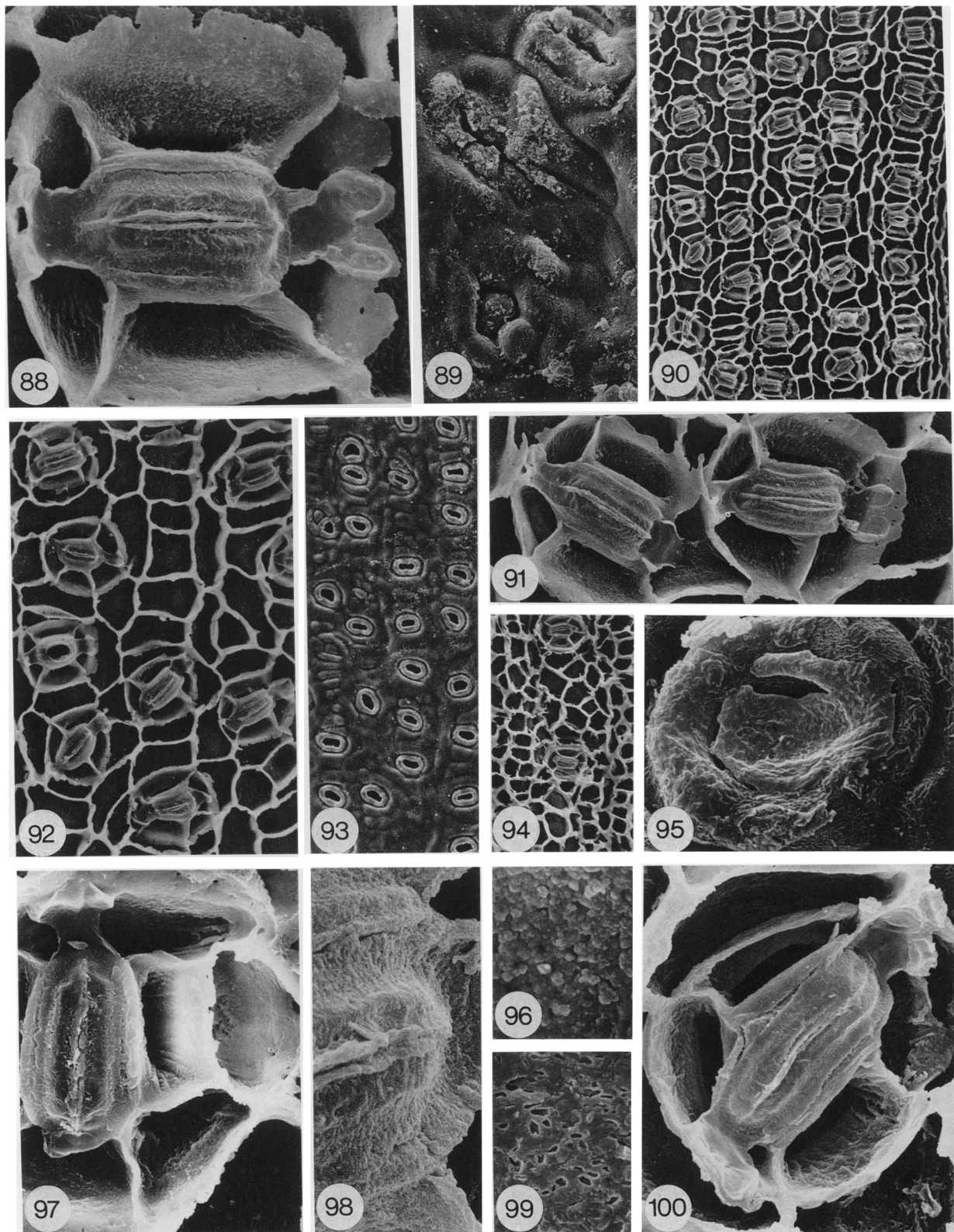
Epidermal cells on adaxial leaf surfaces are irregular in shape, from square to rectangular to polygonal, and appear just slightly larger when adjacent to the scattered stomata on this surface (fig. 94). On abaxial surfaces, epidermal cells are more elongate between stomatal rows and broader than long within a row (fig. 90). Epidermal cell wall flanges are straight to curving and extend slightly to the hypodermal level in juvenile foliage (fig. 92). Cuticle on epidermal cell surfaces is rugose in adult foliage (fig. 96) and rugose and pitted in juvenile leaves (fig. 99).

AGATHIS LANCEOLATA (FIGS. 101–113)

Both juvenile and adult foliage of this species was examined from greenhouse specimens and trees from along the road to Mount Dzumac and along the river north of St. Louis, in New Caledonia (table 1). Juvenile leaves are acuminate on a short petiole, 4.5–13 cm long and 4.4 cm wide, and grade gradually into the adult form (de Laubenfels 1972; Silba 1986). Adult leaves are oval-lanceolate with acuminate or rounded apices, 4–8 cm long and 1.6–3.2 cm wide, tapering to a large petiole 4 mm long (de Laubenfels 1972; Silba 1986). Stomata have only been observed on abaxial surfaces.

The external cuticle surface is moderately undulating, with underlying epidermal cell outlines sometimes visible (fig. 105). Stomata are sunken and Florin rings are present (fig. 105). Stomatal plugs are composed of short rods of material (fig. 109).

Inner cuticle surfaces show stomata in discontinuous rows on both leaf types; however, they are more widely spaced on juvenile foliage (figs. 102, 103). Stomata are mostly oriented obliquely



Figs. 88–100 *Agathis labillardieri*. Fig. 88, Inner view, abaxial cuticle, juvenile foliage, region of the stomatal apparatus, showing four subsidiary cells and bilobed polar extensions; $\times 1,350$. Fig. 89, Outer view, abaxial cuticle, adult foliage, showing plugged stomata and broken Florin rings; $\times 525$. Fig. 90, Inner view, abaxial cuticle, juvenile foliage, stomatal rows; $\times 130$. Fig. 91, Inner view, abaxial cuticle, juvenile foliage, showing adjacent stomata with subsidiary cells in contact; $\times 650$. Fig. 92, Inner view, abaxial cuticle, juvenile foliage, showing stomata with varying orientation and subsidiary cell number; $\times 260$. Fig. 93, Outer view, abaxial cuticle, juvenile foliage, showing Florin rings and undulating epidermal cell surfaces; $\times 130$. Fig. 94,

and perpendicular to the long axis of the leaf (figs. 102, 103). The shape of the stomatal apparatus is usually elliptical but can vary slightly when subsidiary cell wall flanges are in contact with one another (figs. 102, 110). Four subsidiary cells are most common, with as few as three and as many as five occurring on the leaf (figs. 101, 102, 110, 113).

Cuticle on the outer subsidiary wall flange is thick and irregular in both leaf types (figs. 101, 103, 113). The surface of subsidiary cells is rugose and sometimes shows a few pits (figs. 101, 113). There are vertical striations on subsidiary cells of juvenile foliage (figs. 101, 110, 113), but these are lacking in adult foliage. Grooves in this cuticle surface are not as deep as in many other *Agathis* species.

The cuticular flange between guard cells is thick and slightly granular (figs. 101, 107). Bilobed polar extensions are present (fig. 107), but usually the two delicate lobes are broken off or are not visible when the extension overlies a subsidiary cell wall flange (figs. 101, 110, 113). The cuticle on guard cell surfaces is rugose, especially near the stoma (figs. 101, 107). There is also a crease in the guard cell cuticle near the subsidiary cell wall flange that may be inrolled (figs. 101, 107, 113).

Epidermal cells on adaxial leaf surfaces are rectangular to nearly square (fig. 106), with those in juvenile foliage being slightly more elongate and sinuous (fig. 111) than those on adult leaves (fig. 106). Cells are more elongate between stomatal rows on both leaf types and broader than long within a row (figs. 102, 103). Cuticle on epidermal cell surfaces varies depending on the leaf surface and maturity. Adaxial epidermis on juvenile leaves shows cuticle with a smooth surface (fig. 104), while abaxial cuticle shows large, often lens-shaped pits (fig. 112). On adult leaves the cuticle on both epidermal cell surfaces is pitted and rugose (fig. 108).

AGATHIS LENTICULA (FIGS. 114–126)

Adult leaves were collected from the south slope of Mount Kinabalu, Sabah, Malaysia, at 1,372 m (table 1). Leaves are lens-shaped, more or less acute, 5–7 cm long and 0.9–1.0 cm wide, tapering to a 3–7-mm petiole (de Laubenfels 1988). Stomata have only been observed on abaxial surfaces.

The external cuticle surface is undulating, with outlines of underlying epidermal cells sometimes visible (fig. 116). Distinct Florin rings occur (fig. 116) that are sometimes plugged with what looks like cuticular material (fig. 123). Stomatal plugs are present (fig. 117) and composed of short rods (fig. 119).

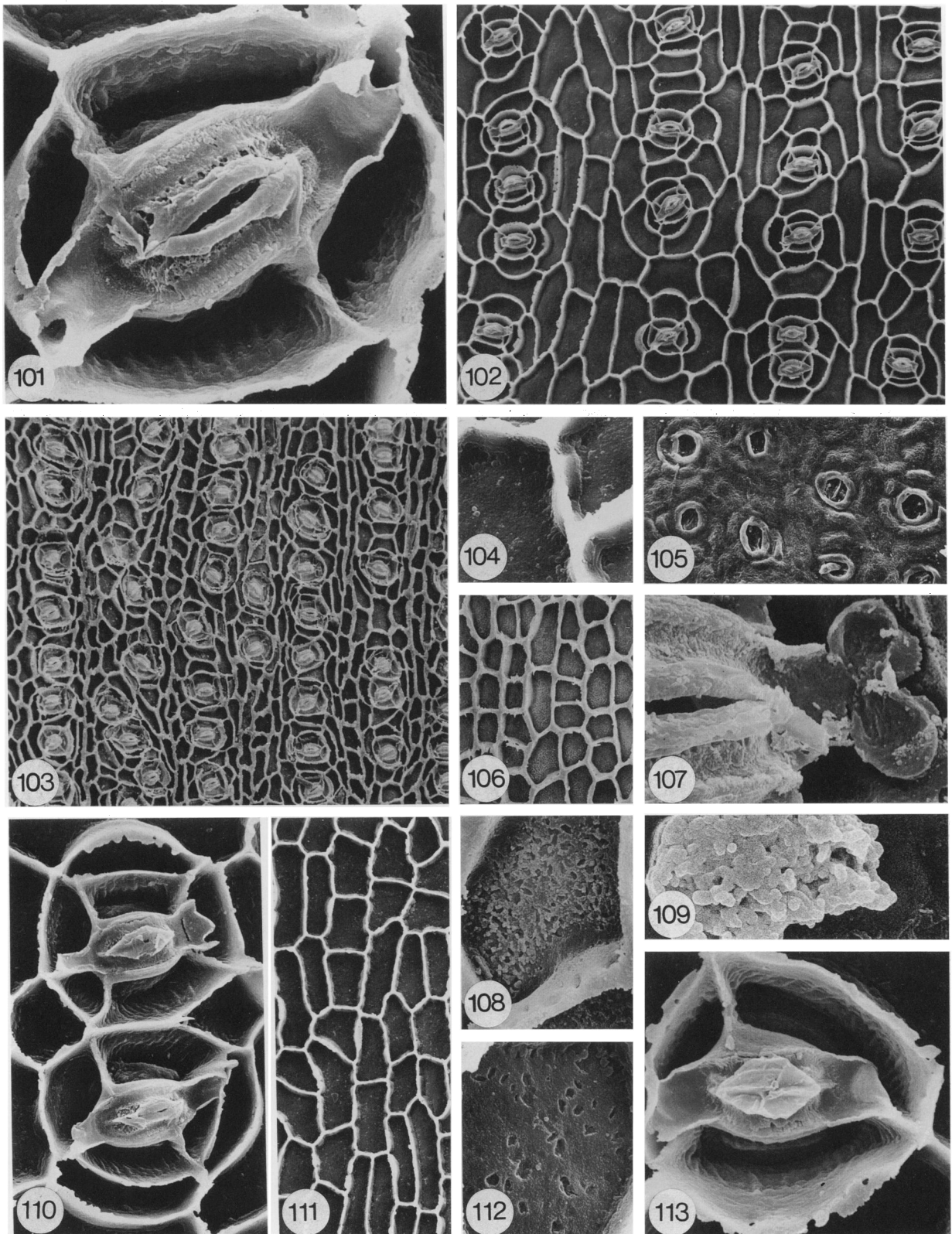
Inner cuticle surfaces show stomata in discontinuous rows of varying orientation, with perpendicular and oblique being the most common (figs. 115, 118). Shape of the stomatal apparatus varies widely depending on the number of subsidiary cells and their proximity to adjacent stomata (figs. 114, 118, 120, 121, 124, 126). Four is the most common number; however, three to six subsidiary cells occur (figs. 114, 120, 121, 124, 126). Occasionally polar subsidiary cells are lacking (fig. 121).

Cuticle on the outer subsidiary cell wall flange is thick and somewhat irregular when it extends to the hypodermal level (figs. 114, 124). Occasional stomata on a leaf, however, may show a thin outer subsidiary wall flange (fig. 126). The surface of subsidiary cell cuticle is granular to rugose and often pitted (fig. 114). Some indications of both longitudinal and horizontal striations occur, but these are not usually pronounced (figs. 114, 120, 121, 124). A deep groove in this cuticle is also present but is not as pronounced as in many other species (fig. 114).

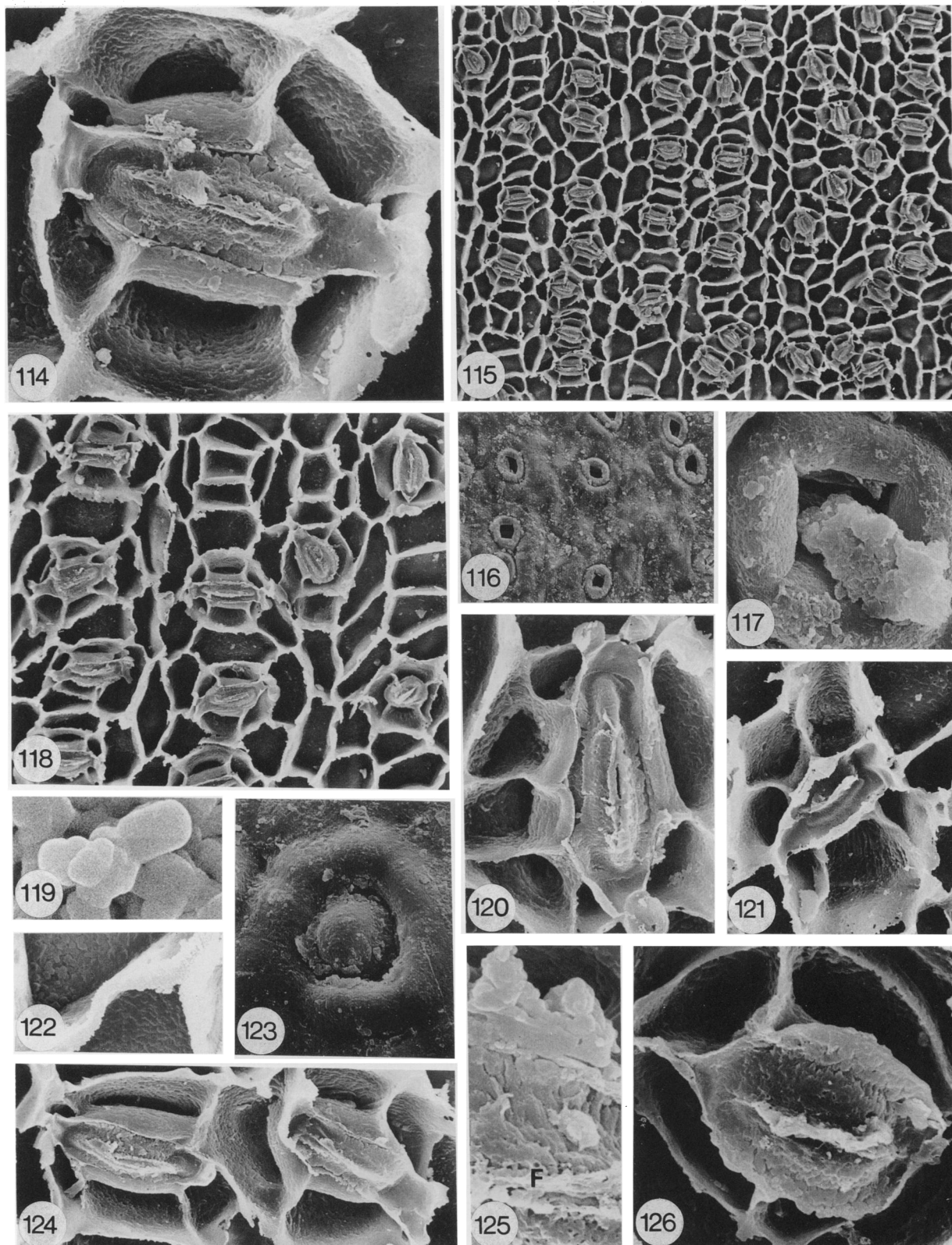
The cuticular flange between guard cells is thin and rugose (figs. 114, 125). Bilobed polar extensions occur; however, these are often broken or lack lobes when situated over a subsidiary cell wall flange (figs. 114, 120, 126). Cuticle on guard cell surfaces is very rugose (figs. 114, 125, 126). Both a ridge (near the stoma) and a crease (near the subsidiary cell wall flange) occur on this cuticle surface (figs. 114, 125). The flange of cuticle between subsidiary cells and the guard cells is rugose and inrolled (figs. 114, 120, 121, 125, 126).

Epidermal cells are rectangular to square on adaxial surfaces. On abaxial surfaces they are more elongate between stomatal rows and broader than long within a row (figs. 115, 118). Epidermal cell flanges are straight to slightly curving and on abaxial surfaces show an irregular edge where they extend to the hypodermal level (fig. 118). Cuticle on epidermal cell surfaces is smooth to slightly rugose on adaxial surfaces (fig. 122) and smooth with a few pits on abaxial surfaces.

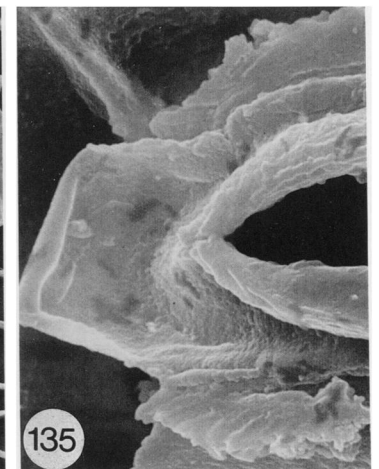
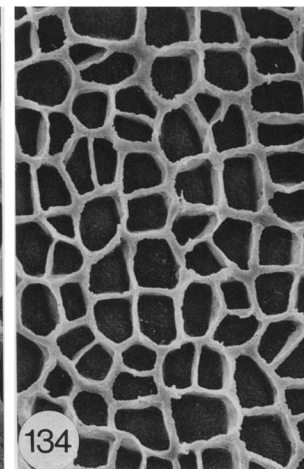
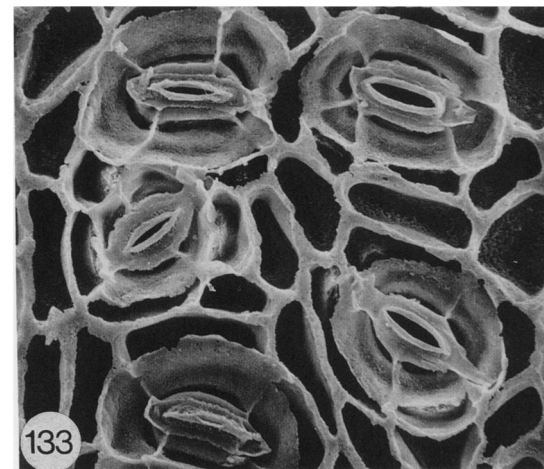
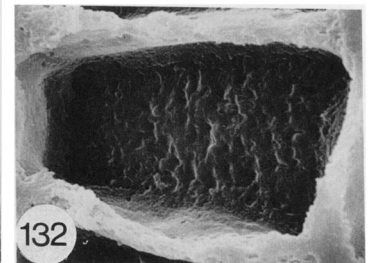
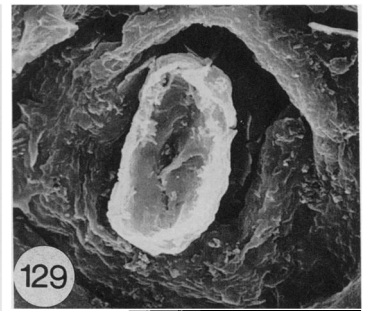
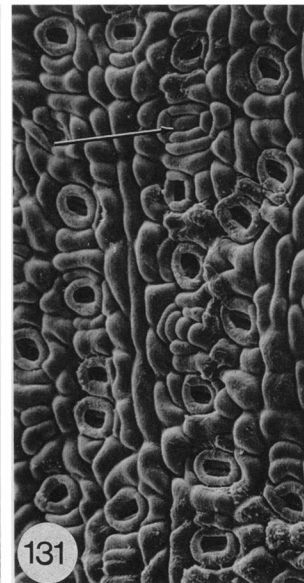
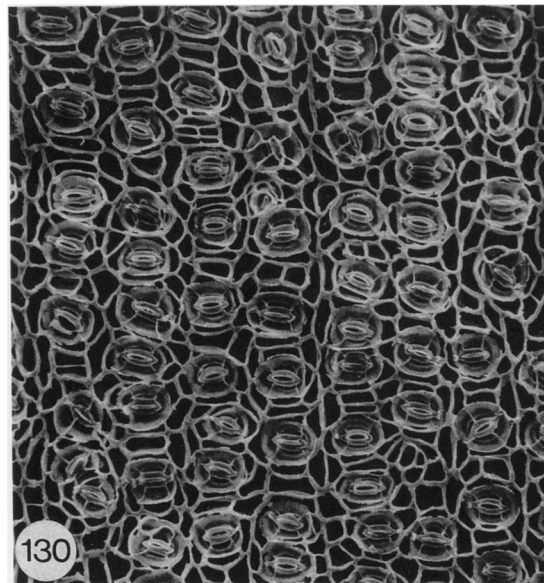
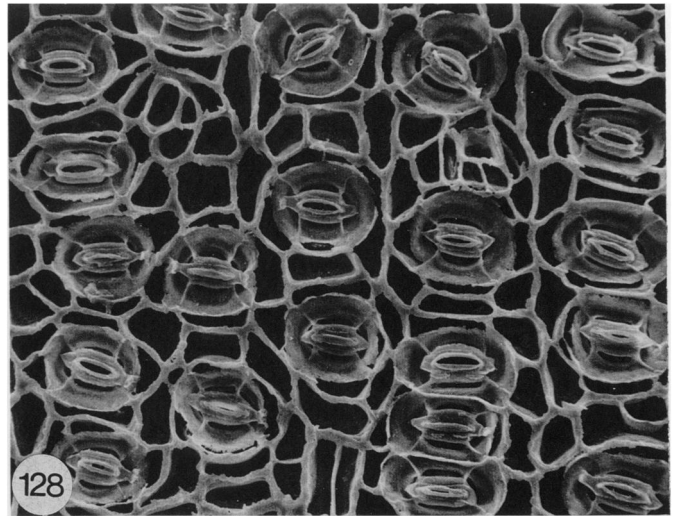
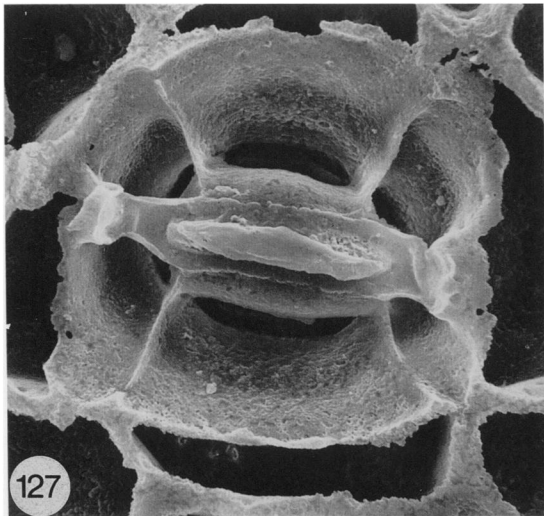
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Inner view, adaxial cuticle, adult foliage, showing epidermal cell outlines and sparse stomata; $\times 120$. Fig. 95, Outer view, abaxial cuticle, adult foliage, showing Florin ring and stomatal plug; $\times 1,600$. Fig. 96, Inner view, adaxial cuticle on epidermal cell surfaces, juvenile foliage; $\times 3,600$. Fig. 97, Inner view, abaxial cuticle, juvenile foliage, showing abnormal subsidiary cell; $\times 1,300$. Fig. 98, Inner view, abaxial cuticle on guard cell surfaces of juvenile foliage; $\times 3,200$. Fig. 99, Inner view, abaxial cuticle on epidermal cell surfaces, adult foliage; $\times 2,300$. Fig. 100, Inner view, adult foliage, region of the stomatal apparatus; $\times 1,300$.



Figs. 101–113 *Agathis lanceolata*. Fig. 101, Inner view, abaxial cuticle, region of the stomatal apparatus, showing four subsidiary cells; $\times 1,900$. Fig. 102, Inner view, abaxial cuticle, juvenile foliage, stomatal rows; $\times 150$. Fig. 103, Inner view, adaxial cuticle on epidermal cell surface, juvenile foliage; $\times 750$. Fig. 104, Inner view, adaxial cuticle on epidermal cell surfaces; $\times 160$. Fig. 105, Outer view, abaxial cuticle, Florin rings and undulating epidermal cell surfaces; $\times 150$. Fig. 106, Inner view, abaxial cuticle, adult foliage, stomatal rows; $\times 95$. Fig. 107, Inner view, abaxial cuticle on guard cell surfaces and bilobed polar extension; $\times 1,900$. Fig. 108, Inner view, adaxial cuticle on epidermal cell surface of adult foliage; $\times 800$. Fig. 109, Outer view, abaxial cuticle, stomatal plug morphology; $\times 2,400$. Fig. 110, Inner view, abaxial cuticle of juvenile foliage, two stomata with four subsidiary cells and encircling cells; $\times 650$. Fig. 111, Inner view, adaxial cuticle, juvenile foliage, epidermal cell outlines; $\times 150$. Fig. 112, Inner view, abaxial cuticle on epidermal cell surface, juvenile foliage; $\times 950$. Fig. 113, Inner view, abaxial cuticle, region of the stomatal apparatus with three subsidiary cells; $\times 1,350$.



Figs. 114–126 *Agathis lenticula*. Fig. 114, Inner view, abaxial cuticle, region of the stomatal apparatus, showing four subsidiary cells; $\times 1,400$. Fig. 115, Inner view, abaxial cuticle, stomatal rows; $\times 155$. Fig. 116, Outer view, abaxial cuticle, showing Florin rings and undulating epidermal cell surfaces; $\times 160$. Fig. 117, Outer view, abaxial cuticle, Florin ring and stomatal plug; $\times 1,600$. Fig. 118, Inner view, abaxial cuticle, showing varying stomatal orientation; $\times 330$. Fig. 119, Outer view, abaxial cuticle, stomatal plug morphology; $\times 8,500$. Fig. 120, Inner view, abaxial cuticle, region of the stomatal apparatus, showing six or seven subsidiary cells and bilobed polar extensions; $\times 1,200$. Fig. 121, Inner view, abaxial cuticle, region of the stomatal apparatus, showing six lateral subsidiary cells; $\times 725$. Fig. 122, Inner view, adaxial cuticle on epidermal cell surface; $\times 1,300$. Fig. 123, Outer view, abaxial surface, showing plugged stoma; $\times 800$. Fig. 124, Inner view, abaxial cuticle, two stomata sharing a subsidiary cell; $\times 775$. Fig. 125, Inner view, abaxial cuticle on guard cell surfaces; $\times 3,200$. Fig. 126, Inner view, abaxial cuticle, stomatal apparatus with three or four subsidiary cells and small subsidiary cell wall flanges; $\times 1,650$; *F* = flange of cuticle between guard cells.



Figs. 127–135 *Agathis macrophylla*. Fig. 127, Inner view, abaxial cuticle, region of the stomatal apparatus, showing four subsidiary cells and bilobed polar extensions; $\times 1,000$. Fig. 128, Inner view, abaxial cuticle, stomata, showing broad subsidiary cell wall flanges; $\times 210$. Fig. 129, Outer view, abaxial cuticle, stomatal plug; $\times 1,150$. Fig. 130, Inner view, abaxial cuticle, stomatal rows; $\times 105$. Fig. 131, Outer view, abaxial cuticle, showing Florin rings and epidermal cell outlines; arrow indicates plugged stoma; $\times 160$. Fig. 132, Inner view, adaxial cuticle on epidermal cell surface; $\times 1,250$. Fig. 133, Inner view, abaxial cuticle, showing variable stomatal orientation and size of stomatal apparatus; $\times 400$. Fig. 134, Inner view, adaxial cuticle, showing epidermal cell outlines; $\times 250$. Fig. 135, Inner view, abaxial cuticle on guard cell surfaces; $\times 2,900$.

AGATHIS MACROPHYLLA (FIGS. 127–135)

Adult leaves were obtained from Fiji on the island of Viti Levu and on Aneityum Island in the New Hebrides (table 1). Leaves are lanceolate, 9–18 cm long and 1.8–5.0 cm wide, with a short petiole (Silba 1986). Stomata have only been observed on abaxial surfaces.

External cuticle surfaces are very undulating, with outlines of underlying epidermal cells clearly visible (fig. 131). Stomata are sunken and prominent Florin rings occur (fig. 131). Occasionally a ring will be plugged with cuticular material (fig. 131, arrow). Stomatal plugs are present and appear to be solid blocks of material (fig. 129).

Inner cuticle surfaces show stomata in fairly regular rows, most of which are oriented perpendicularly (figs. 128, 130). Oblique orientations are also common. The stomatal apparatus is usually elliptical (figs. 127, 128, 130, 133), but occasionally this shape is altered when subsidiary cell wall flanges come in contact with one another (figs. 128, 130). Four subsidiary cells are most common (fig. 127), with five also occurring (fig. 133), making this one of the most conservative species with respect to subsidiary cell number.

Cuticle on the outer subsidiary cell wall flange is thick and irregular (figs. 127, 133). The surface of subsidiary cell cuticle is granular to pitted with no obvious striations (fig. 127). A deep groove occurs in this cuticle surface (figs. 127, 133).

The cuticular flange between guard cells is thick and rugose (fig. 135). Polar extensions are bilobed (fig. 127), but are often broken or lack lobes when situated over a subsidiary cell wall flange (figs. 133, 135). Cuticle on guard cell surfaces is rugose (figs. 127, 135). This cuticle often appears to lack distinct pitting due to the large cuticular flange between guard cells that obscures pitting near the stoma (fig. 133). A distinct ridge occurs on the guard cell cuticle surface (fig. 135), but the usual crease seen in most *Agathis* species is not obvious in *A. macrophylla*. The flange between guard and subsidiary cells is not pronounced.

Epidermal cells on adaxial surfaces are rectangular to square to triangular (fig. 134). On abaxial surfaces, cells are more elongate between stomatal rows (figs. 128, 130). Epidermal cell flanges are nearly straight with the tops of flanges occasionally irregular when they extend to the hypodermal level. Cuticle on epidermal cell surfaces is slightly rugose to pitted on adaxial surfaces (fig. 132) and rugose on abaxial surfaces.

AGATHIS MICROSTACHYA (FIGS. 136–146)

Adult leaves were obtained from the Cook District of northern Queensland (table 1). Leaves are linear to elliptical, 2–9 cm long and 0.5–2.5 cm wide, with short, 1–2-mm-long petioles (Hyland

1977). Leaves of this species are very coriaceous, so clean preparations were difficult to obtain, and debris is present on most cuticle. Stomata were observed on both leaf surfaces but are more prevalent on the abaxial surface.

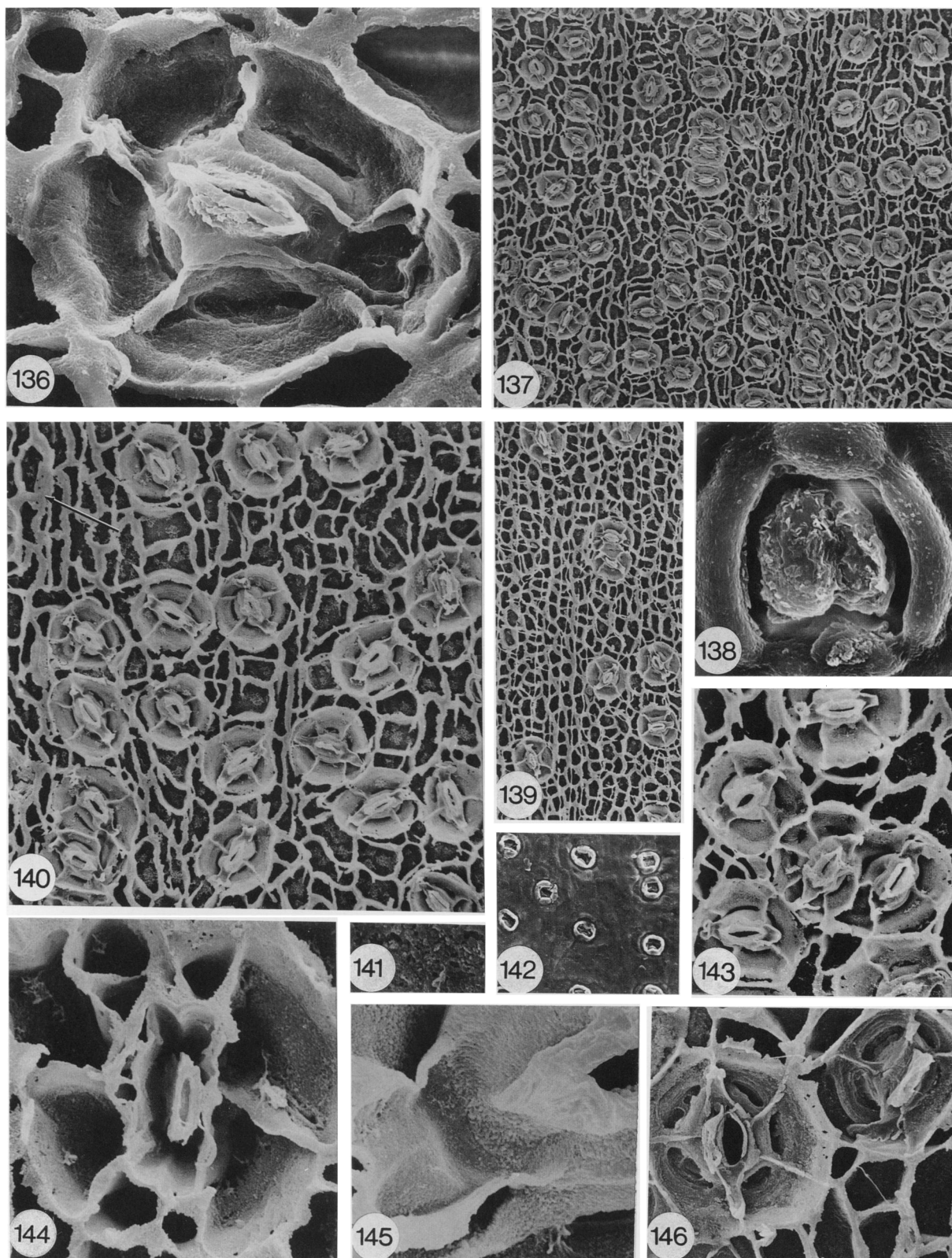
The external cuticle surface is slightly undulating, with outlines of underlying epidermal cells often visible (fig. 142). Stomata are sunken and surrounded by Florin rings (fig. 142) that are often broken up to reveal the underlying subsidiary cells (fig. 138). Stomatal plugs are present and appear to be composed of irregular blocks, with a longitudinal plug slit or a thin area coinciding with the stoma (fig. 138).

Inner cuticle surfaces show stomata in discontinuous rows with varying orientations, with oblique being the most common (figs. 137, 140). The stomatal apparatus is usually elliptical to nearly circular, with variable shapes resulting when subsidiary cell wall flanges meet (figs. 136, 137, 140, 143). Four subsidiary cells are most common, with four to eight observed (figs. 136, 137, 140, 143, 144, 146). In one stomatal apparatus, an unusual number of subsidiary cells occur as a result of very irregular cell divisions (fig. 144).

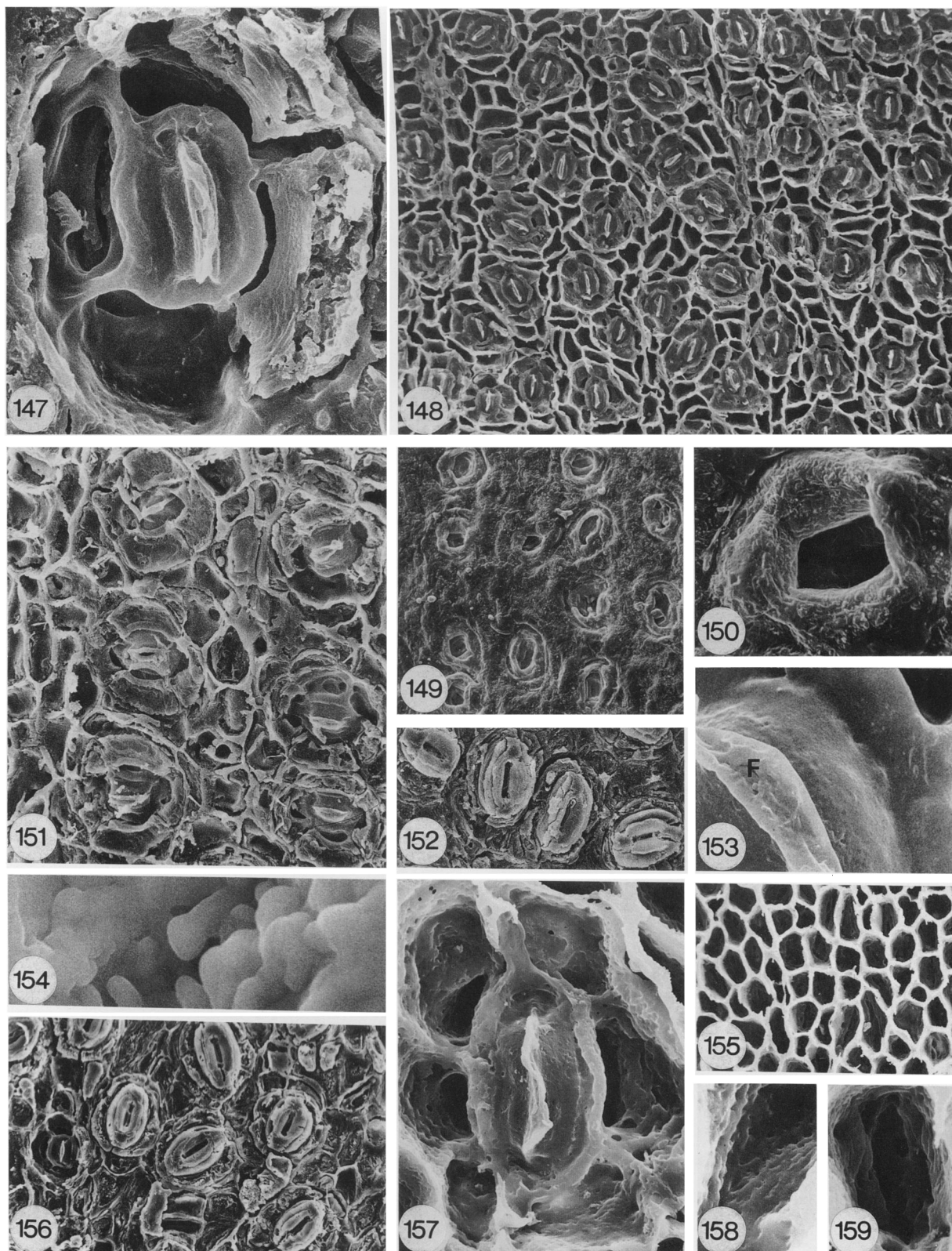
Cuticle on the outer subsidiary cell wall flange is thick and irregular and sometimes pitted when extending to the hypodermal level (figs. 136, 144, 146). The surface of subsidiary cell cuticle is slightly rugose with occasional pits (figs. 136, 144). Horizontal striations have been observed on some subsidiary cell cuticles (fig. 146). A deep groove occurs in the subsidiary cell cuticle that varies in depth on the leaf (figs. 136, 143, 144, 146).

The cuticular flange between guard cells is usually thick and rugose (fig. 145). Bilobed polar extensions occur but are usually broken or incomplete when over a subsidiary cell wall flange (figs. 136, 143–146). Cuticle on guard cell surfaces is slightly rugose and lacks extensive pitting (fig. 145). A longitudinal crease occurs on this cuticle surface toward the subsidiary cell wall flange, but in most cases it is not pronounced (figs. 136, 145). The flange of cuticle between guard and subsidiary cells is not very pronounced (fig. 136).

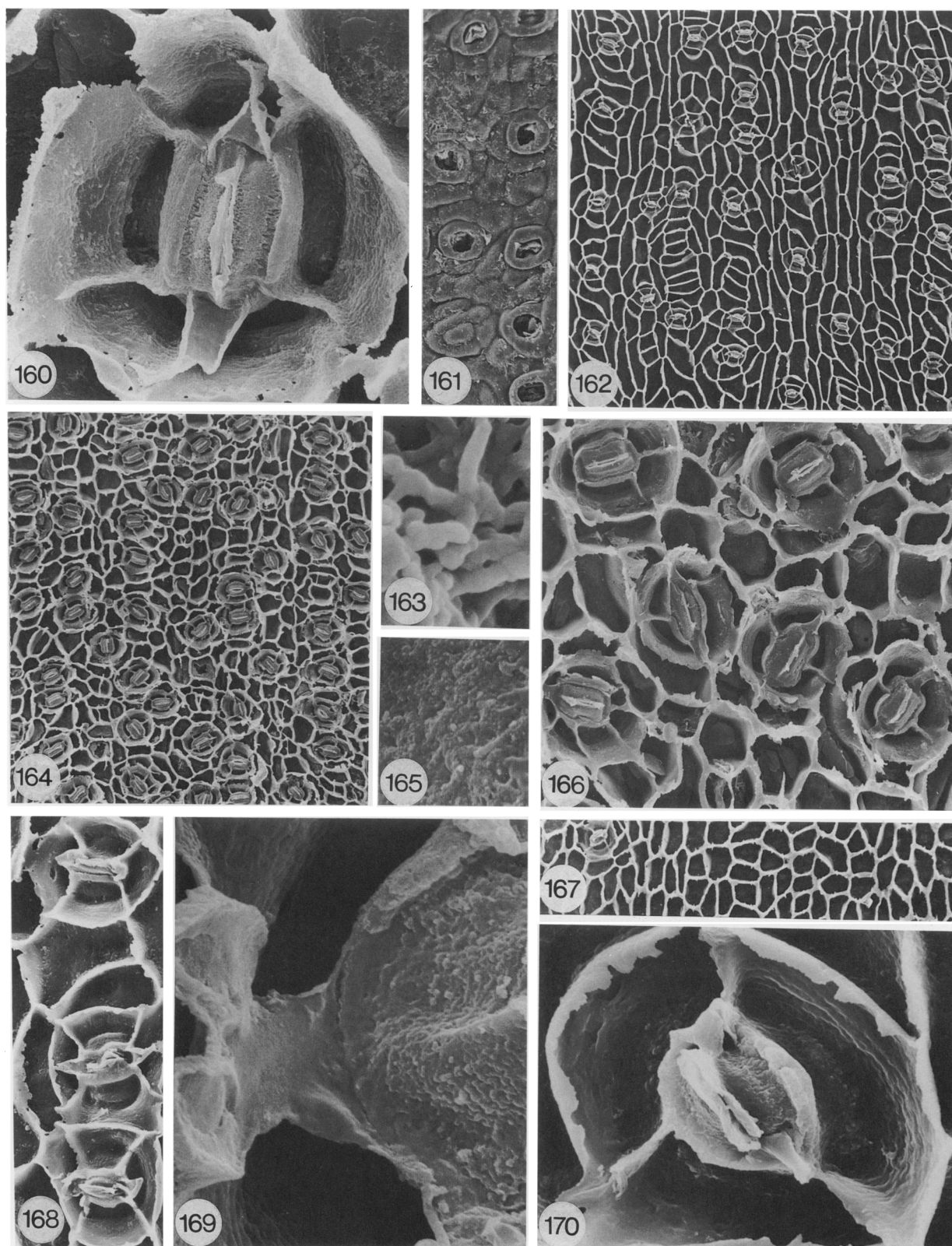
Epidermal cells are usually square to rectangular on adaxial leaf surfaces, with irregular shapes occurring (fig. 139). On abaxial surfaces cells are more elongate between stomatal rows than within a row (fig. 137). Epidermal cell wall flanges are relatively straight on adaxial surfaces (fig. 139) and only slightly sinuous on abaxial surfaces (fig. 140). Edges of the epidermal cell wall flange extend to the hypodermal level and sometimes almost completely surround epidermal cells on abaxial surfaces (fig. 140, arrow), making clean preparations even more difficult to make. Cuticle on epidermal cell surfaces is rugose and pitted (fig. 141).



Figs. 136–146 *Agathis microstachya*. Fig. 136, Inner view, abaxial cuticle, region of the stomatal apparatus, showing four subsidiary cells and a bilobed polar extension; $\times 950$. Fig. 137, Inner view, abaxial cuticle, stomatal rows; $\times 90$. Fig. 138, Outer view, abaxial cuticle, dissected Florin ring and stomatal plug; $\times 1,200$. Fig. 139, Inner view, adaxial cuticle, showing epidermal cell outlines and scattered stomata; $\times 95$. Fig. 140, Inner view, abaxial cuticle, stomata, showing varying orientation and subsidiary cell number; arrow indicates cuticle extending to the hypodermal level; $\times 190$. Fig. 141, Inner view, abaxial cuticle on epidermal cell surface; $\times 1,775$. Fig. 142, Outer view, abaxial cuticle, showing Florin rings and undulating epidermal cell surfaces; $\times 95$. Fig. 143, Inner view, abaxial cuticle, showing stomata with shared and adjacent subsidiary cells; $\times 300$. Fig. 144, Inner view, abaxial cuticle, showing abnormal stomatal apparatus with at least nine subsidiary cells; $\times 900$. Fig. 145, Inner view, abaxial cuticle on guard cell surfaces and bilobed polar extension; $\times 2,600$. Fig. 146, Inner view, abaxial cuticle, showing different sizes of stomatal apparatus; $\times 400$.



Figs. 147-159 *Agathis montana*. Fig. 147, Inner view, abaxial cuticle, region of the stomatal apparatus, showing four subsidiary cells and extensive cuticular thickening; $\times 1,500$. Fig. 148, Inner view, abaxial cuticle, discontinuous stomatal rows and crowded stomata; $\times 115$. Fig. 149, Outer view, abaxial cuticle, Florin rings and undulating epidermal cell surfaces; $\times 160$. Fig. 150, Outer view, abaxial cuticle, dissected Florin ring; $\times 800$. Fig. 151, Inner view, abaxial cuticle, stomatal rows and extensive epidermal thickening; $\times 280$. Fig. 152, Inner view, abaxial cuticle enclosing guard cells, showing prominent polar extensions; $\times 210$. Fig. 153, Inner view, abaxial cuticle on guard cell surfaces; $\times 2,000$. Fig. 154, Outer view, abaxial cuticle, stomatal plug morphology; $\times 7,000$. Fig. 155, Inner view, adaxial cuticle, showing epidermal cell outlines; $\times 190$. Fig. 156, Inner view, abaxial cuticle enclosing guard cells; exposed stomatal surface at left; $\times 170$. Fig. 157, Inner view, abaxial cuticle, stomatal apparatus with six subsidiary cells; $\times 800$. Fig. 158, Inner view, abaxial cuticle on epidermal cell surface; $\times 1,450$. Fig. 159, Inner view, adaxial cuticle on epidermal cell surface; $\times 950$; *F* = flange of cuticle between guard cells.



Figs. 160–170 *Agathis moorei*. Fig. 160, Inner view, abaxial cuticle, adult foliage, region of the stomatal apparatus, with four subsidiary cells and polar extensions; $\times 1,050$. Fig. 161, Outer view, abaxial cuticle, adult foliage, showing Florin rings, stomatal plugs, undulating epidermal cell surfaces, and a closed stoma (lower left); $\times 200$. Fig. 162, Inner view, abaxial cuticle, juvenile foliage, showing stomatal rows; $\times 95$. Fig. 163, Outer view, abaxial cuticle, stomatal plug morphology; $\times 9,250$. Fig. 164, Inner view, abaxial cuticle, adult foliage, showing stomatal rows; $\times 105$. Fig. 165, Inner view, adaxial cuticle on epidermal cell surface of adult foliage; $\times 4,000$. Fig. 166, Inner view, abaxial cuticle, adult foliage, showing variable stomatal orientation

AGATHIS MONTANA (FIGS. 147–159)

Adult leaves of this species were obtained from Mount Panié, New Caledonia, from an altitude of 1,450 m (table 1). Leaves are oval-lanceolate, 6–8 cm long and 1.5–2.0 cm wide, with bluntly acute apices and bases that taper to a short petiole (de Laubenfels 1972; Silba 1986). Stomata have only been observed on abaxial surfaces.

The external cuticle surface is undulating, but underlying epidermal cell outlines are not readily visible (fig. 149). Stomata are sunken and surrounded by Florin rings that are sometimes almost sunken into the surrounding cuticle (fig. 149). Often these rings are broken up, revealing the underlying subsidiary cell structure of the stomatal apparatus (fig. 150). Stomatal plugs are present and are composed of short rods (fig. 154).

Inner cuticle surfaces show stomata in very crowded discontinuous rows (fig. 148). All stomatal orientations are present, but parallel orientations are more common in this taxon than in any other *Agathis* species (fig. 148). Due to the thick nature of the cuticle that often completely reaches the hypodermal layer, clean preparations were extremely difficult to obtain. Cuticle often completely covers the stomatal apparatus, and descriptions here are based on clean sections of otherwise debris-covered cuticles (figs. 147, 151, 152, 156). The stomatal apparatus is usually elliptical in shape but varies when subsidiary cell wall flanges of adjacent stomata come in contact with one another (fig. 148). Four subsidiary cells are the most common number, with three to seven occurring (figs. 147, 148, 157).

Cuticle on the outer subsidiary cell wall flange is thick and irregular when extending to the hypodermal level (fig. 157) or completely surrounds the subsidiary cell (fig. 147). The surface of the cuticle on subsidiary cells is often pitted and shows some evidence of horizontal striations (fig. 157). When preparations are not completely clean, this surface appears smooth (fig. 147). A groove occurs in this cuticle surface where the subsidiary cell reaches the leaf surface (figs. 147, 157).

The cuticular flange between guard cells is relatively thin and just slightly rugose (fig. 153). Polar extensions are probably bilobed (fig. 152); however, most of the preparations that would show this feature still have cuticle covering the entire guard cell region (fig. 156). When polar extensions coincide with a subsidiary cell wall flange, the bilobed nature is not apparent (fig.

157). The cuticle on the guard cell surfaces is smooth to slightly pitted (figs. 153, 157). A longitudinal ridge occurs on this surface (figs. 147, 153, 157). The flange between guard and subsidiary cells is smooth to slightly rugose, often with an inrolled edge (figs. 153, 157).

Epidermal cells are irregular in shape on adaxial leaf surfaces, but most approach a rectangular to square shape (fig. 155). On abaxial surfaces they are even more irregular and somewhat more elongate between stomatal rows (fig. 151, left); however, due to the crowded nature of the stomata, stomatal rows are not always distinguishable (fig. 148). Epidermal cell wall flanges are straight to curving on adaxial surfaces (fig. 155) and slightly sinuous on abaxial surfaces (fig. 148). Cuticle on epidermal cell surfaces of adaxial cuticles shows longitudinal grooves and pits (fig. 159). Cuticle on abaxial leaf surfaces shows large numbers of pits (fig. 158).

AGATHIS MOOREI (FIGS. 160–170)

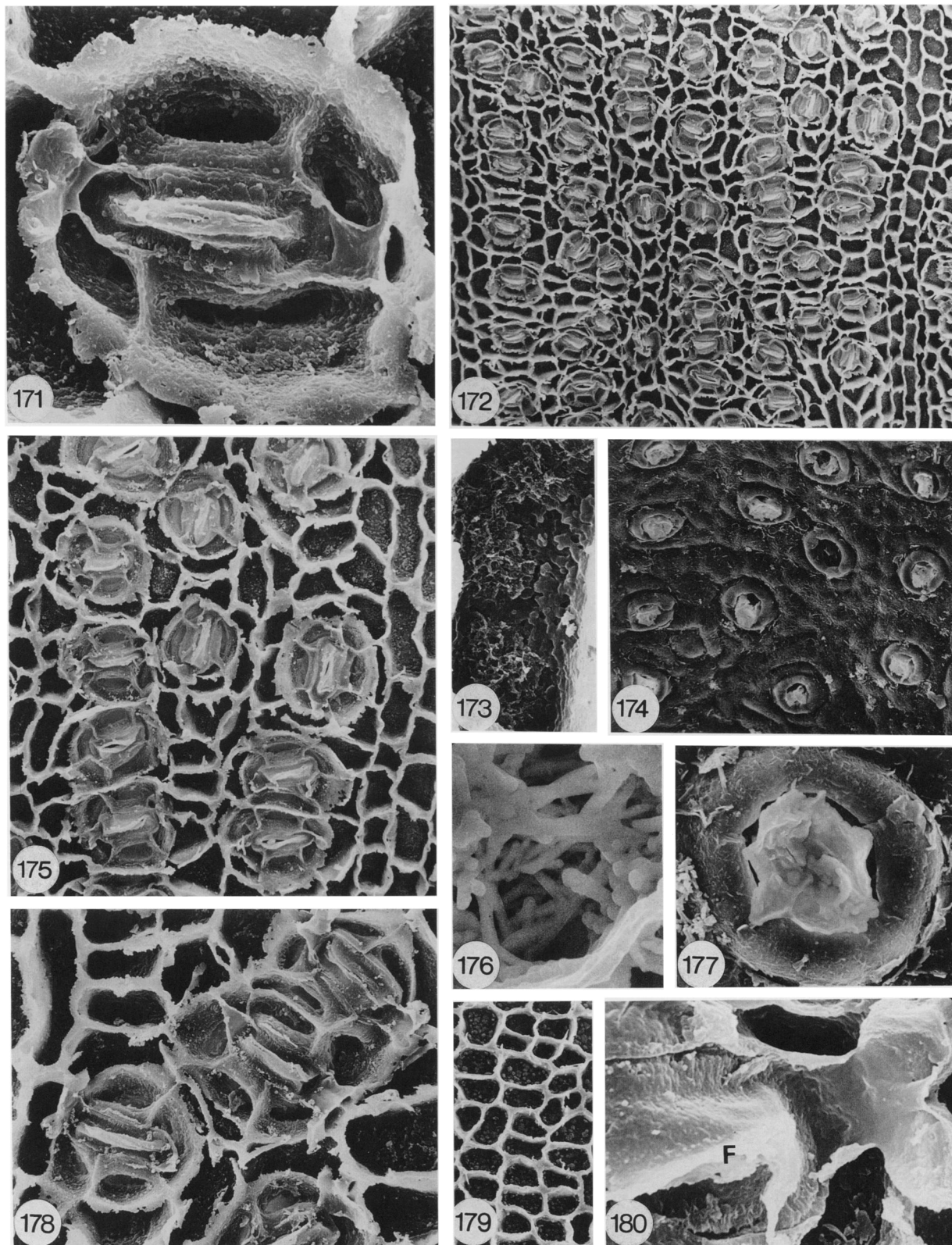
Both adult and juvenile foliage of this species was examined from herbarium sheets, leaves preserved in FPA, and greenhouse plants (table 1). Adult leaves were obtained from Tao, New Caledonia, and greenhouse and preserved leaves came from plants grown from seed collected in 1977 near Nouméa, New Caledonia (table 1). Juvenile leaves are lanceolate, 20 cm long and 3.3 cm wide, on short broad petioles, and grade gradually into the adult form (de Laubenfels 1972). Adult leaves are oval-lanceolate, 5–7 cm long and 0.8–1.2 cm wide, with bluntly acute apices, and taper to a very short petiole (de Laubenfels 1972). Most stomata are situated on the abaxial leaf surface; however, scattered stomata occur on adaxial leaf surfaces (fig. 167).

The external cuticle surface is very undulating, with outlines of underlying epidermal cells clearly visible (fig. 161). Stomata are sunken, and prominent Florin rings occur that are sometimes plugged with what appears to be cuticular material (fig. 161, lower left). Stomatal plugs also occur (fig. 161) and are composed of rod-shaped components (fig. 163).

Inner cuticle surfaces show discontinuous stomatal rows, with stomata being more widely spaced in juvenile foliage (figs. 162, 164). Most stomata are perpendicularly or obliquely oriented to the long axis of the leaf (figs. 162, 164, 166). The stomatal apparatus is usually elliptical in

←

and subsidiary cell number; $\times 325$. Fig. 167, Inner view, adaxial cuticle, juvenile foliage, showing epidermal cell outlines and one stomatal apparatus; $\times 110$. Fig. 168, Inner view, abaxial cuticle, juvenile foliage, stomatal row, showing contact of subsidiary cell wall flanges; $\times 480$. Fig. 169, Inner view, adult foliage, abaxial cuticle on guard cell surfaces and bilobed polar extension; $\times 4,500$. Fig. 170, Inner view, abaxial cuticle, juvenile foliage, region of the stomatal apparatus, with three subsidiary cells; $\times 1,650$.



Figs. 171–180 *Agathis orbicula*. Fig. 171, Inner view, abaxial cuticle, region of the stomatal apparatus, with four subsidiary cells and polar extensions; $\times 1,250$. Fig. 172, Inner view, abaxial cuticle, stomatal rows; $\times 130$. Fig. 173, Inner view, abaxial cuticle on epidermal cell surface; $\times 1,600$. Fig. 174, Outer view, abaxial cuticle, showing Florin rings, stomatal plugs, and undulating epidermal cell surfaces; $\times 260$. Fig. 175, Inner view, abaxial cuticle, showing variable stomatal orientation and subsidiary cell number; $\times 210$. Fig. 176, Outer view, abaxial cuticle, stomatal plug morphology; $\times 3,250$. Fig. 177, Outer view, abaxial cuticle, showing Florin ring and stomatal plug; $\times 1,150$. Fig. 178, Inner view, abaxial cuticle, showing shared subsidiary cells; $\times 500$. Fig. 179, Inner view, adaxial cuticle, showing epidermal cell outlines; $\times 190$. Fig. 180, Inner view, abaxial cuticle on guard cell surfaces and bilobed polar extension; $\times 2,100$; F = flange of cuticle between guard cells.

outline to almost circular in some cases on adult foliage (figs. 160, 164). In juvenile leaves the outline of the apparatus is usually elliptical, but it can be angular in some instances (figs. 162, 168). The shape of the stomatal apparatus is also variable when subsidiary cell wall flanges from adjacent stomata are in contact with one another (fig. 168).

Cuticle on the outer subsidiary cell wall flange is thick and irregular in both leaf types when cuticle extends to the hypodermal level (figs. 160, 170). In general, this flange is thinner in juvenile greenhouse specimens than in plants collected in the field. The cuticle on subsidiary cell surfaces is granular to pitted in adult foliage (fig. 160), and slightly less so in juvenile leaves (fig. 170). Both leaf types show indications of horizontal striations on the cuticle of subsidiary cell surfaces (figs. 160, 170). A deep groove occurs in this surface on adult foliage (fig. 160) that is not as deep as in many other *Agathis* species and not as pronounced in juvenile leaves as in adult foliage (figs. 168, 170).

The cuticular flange between guard cells is relatively thin and rugose (fig. 160). Bilobed polar extensions occur (fig. 169) but are often broken or lack lobes when situated over a subsidiary cell wall flange (figs. 160, 166, 168). Cuticle on guard cell surfaces is rugose, with pits present in two zones, close to the stoma and toward the subsidiary cell wall flange in adult foliage (fig. 170). The flange of cuticle between guard and subsidiary cells is slightly granular and inrolled in both leaf types (figs. 160, 169, 170).

Epidermal cells are irregular in shape, varying from square to triangular to rectangular on adaxial leaf surfaces (fig. 167). Abaxial epidermal cells are more elongate in juvenile leaves than in adult foliage (figs. 162, 164). Epidermal cells are more elongate between stomatal rows than within a row. Cuticle on epidermal cell surfaces is rugose and slightly pitted on adult leaves (fig. 165). It is smooth on adaxial surfaces of juvenile foliage to slightly pitted on abaxial surfaces (Stockey and Taylor 1981). Epidermal cell wall flanges are nearly straight, with an irregular outline when they extend to the hypodermal level (figs. 166, 168).

AGATHIS ORBICULA (FIGS. 171–180)

Adult leaves were obtained from Bumbong Ruma, Sarawak, at 915 m (table 1). Leaves are ovate to orbicular, broadly rounded to slightly angled at the apex, 2.4–4.0 cm long and 1.2–2.4 cm wide, tapering sharply at the base to a 3–7-mm petiole (de Laubenfels 1988). Stomata have only been observed on abaxial surfaces.

The external cuticle surface is undulating, with outlines of underlying epidermal cells often visible (fig. 174). Stomata are sunken and prominent

Florin rings are present (figs. 174, 177). Stomatal plugs also occur (figs. 174, 177) and are made up of rod-shaped components (fig. 176).

Inner cuticle surfaces show discontinuous rows of often closely spaced stomata, frequently having subsidiary cells in contact (figs. 172, 175, 178). The stomatal apparatus is elliptical to nearly circular in outline in isolated stomata (figs. 171, 172, 175) but varies when subsidiary cell wall flanges come into contact with one another (figs. 175, 178). Stomata are oriented in all directions, with perpendicular and oblique orientations being the most common (figs. 172, 175). Four subsidiary cells are most common, with three to six occurring (figs. 171, 175, 178).

Cuticle on the outer subsidiary cell wall flange is thick and irregular where it extends to the hypodermal level (fig. 171). The surface of the subsidiary cell cuticle is very granular to rugose and somewhat pitted (fig. 171). A deep groove occurs in this cuticle surface (fig. 171) but is not as pronounced as in some *Agathis* species, and varies on one leaf (fig. 175, 178).

The cuticular flange between guard cells is thin and rugose (figs. 171, 180). Bilobed polar extensions occur (figs. 171, 180) but are often broken or lack lobes when situated over a subsidiary cell wall flange (fig. 178). The cuticle on guard cell surfaces is rugose, especially toward the subsidiary cell wall flange (figs. 171, 180). A crease occurs on this cuticle surface, and the flange between subsidiary cells and guard cells is slightly inrolled and connects to the polar extension (figs. 171, 180).

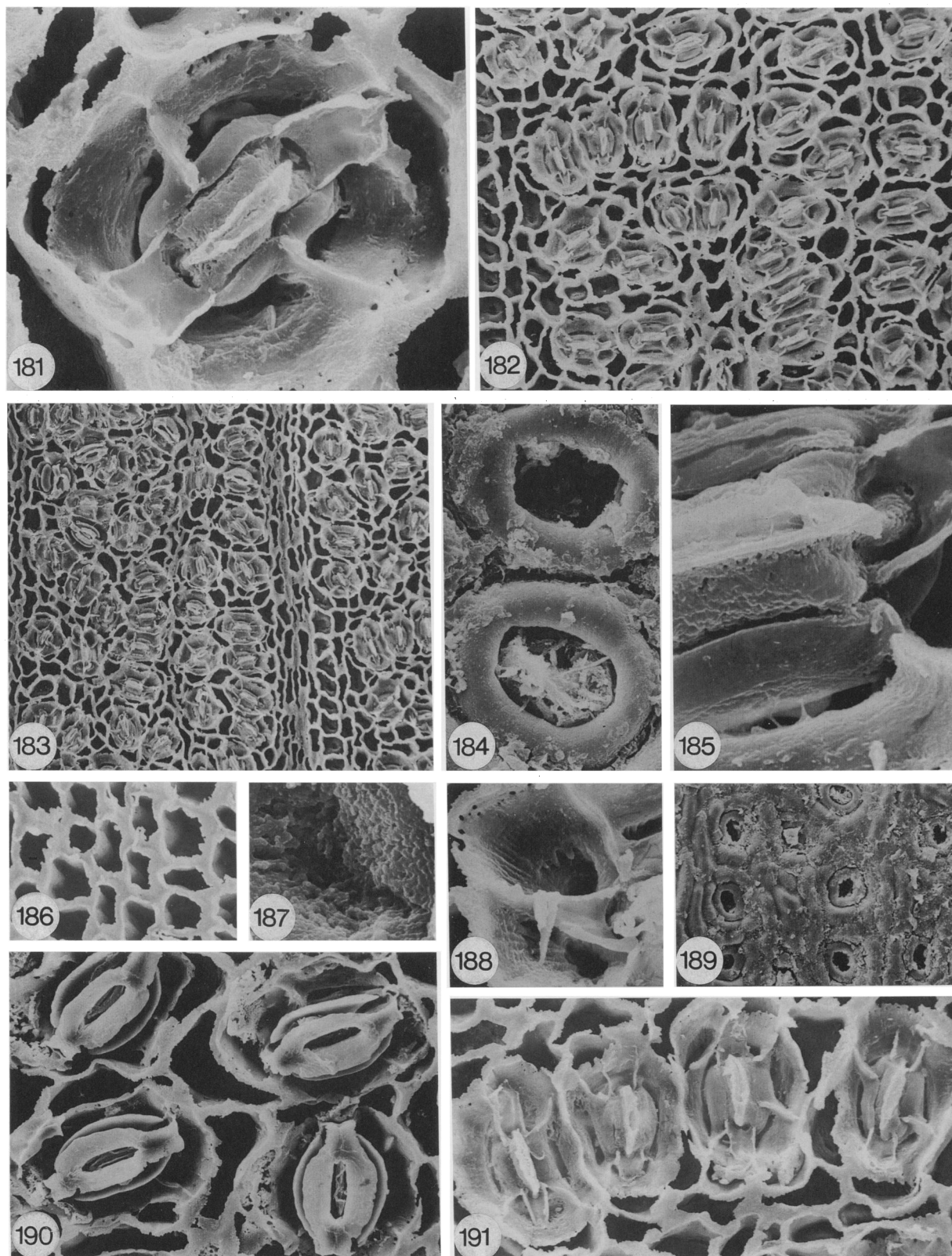
Epidermal cells on adaxial leaf surfaces are sometimes broader than long and vary in shape from rectangular to triangular to square (fig. 179). On abaxial surfaces they are longer between stomatal rows than within a row (fig. 172). Epidermal cell wall flanges are straight to curving, and cell surfaces are rugose to pitted (fig. 173).

AGATHIS OVATA (FIGS. 181–191)

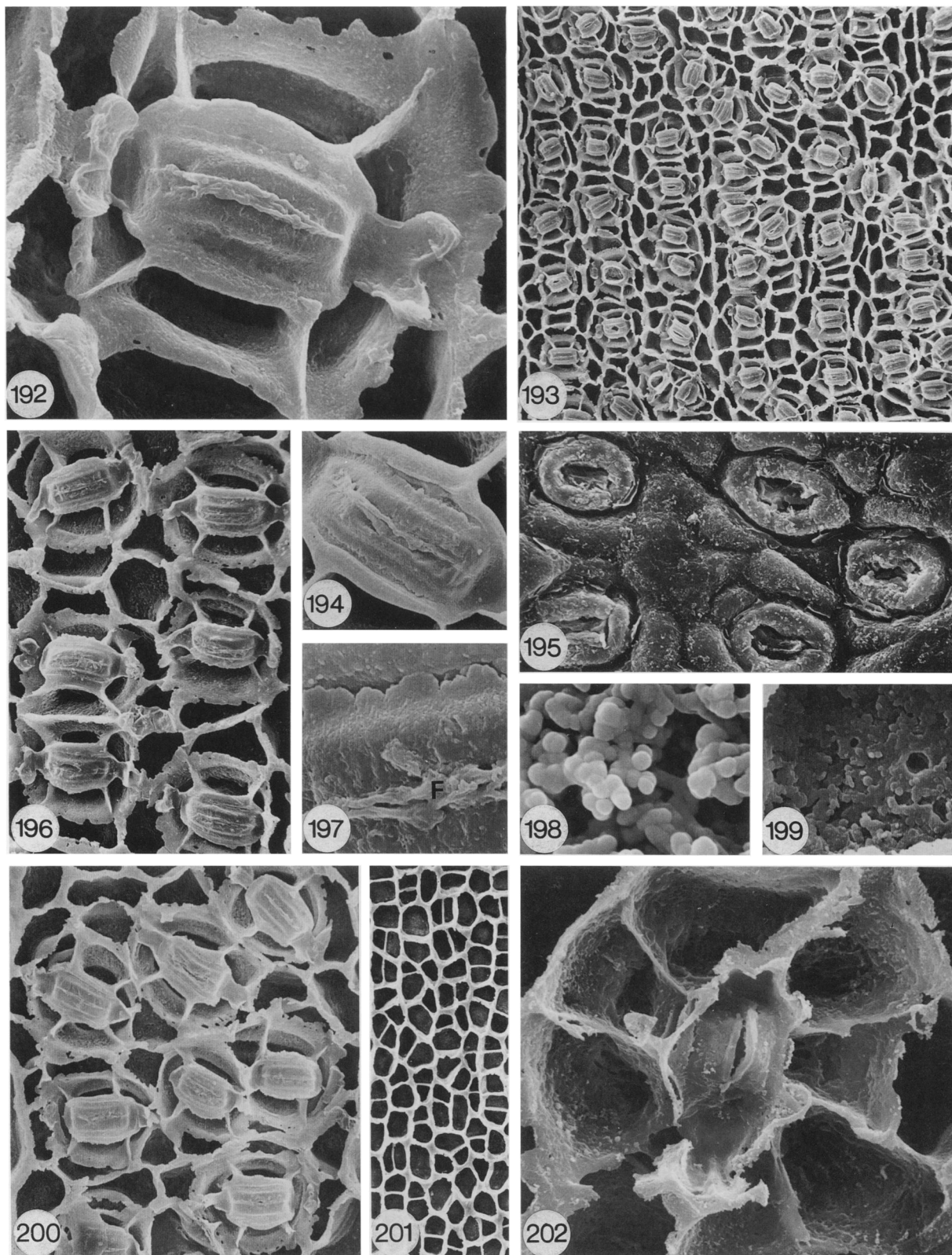
Adult foliage of both preserved and herbarium specimens was obtained from the road to Mount Dzumac from the Dumbéa Valley in New Caledonia (table 1). Leaves are oval with blunt tips, 4–6 cm long and 1–1.3 cm wide (de Laubenfels 1972). Stomata have only been observed on abaxial surfaces.

The external cuticle surfaces are very undulating, with underlying epidermal cell outlines clearly visible (fig. 189). Leaf surfaces are often covered with irregular platelets (fig. 189). Cuticle in this species is very thick, and clean preparations were hard to obtain. Stomata are sunken and prominent Florin rings are present (figs. 184, 189). Stomatal plugs are composed of rods (fig. 184).

Inner cuticle surfaces show stomata in discontinuous rows (figs. 182, 183). In some areas sto-



Figs. 181-191 *Agathis ovata*. Fig. 181, Inner view, abaxial cuticle, region of the stomatal apparatus, with four subsidiary cells and polar extensions; $\times 975$. Fig. 182, Inner view, abaxial cuticle, stomatal rows; $\times 155$. Fig. 183, Inner view, abaxial cuticle, stomatal bands and elongate epidermal cells between rows; $\times 100$. Fig. 184, Outer view, abaxial cuticle, Florin rings and stomatal plug; $\times 775$. Fig. 185, Inner view, abaxial cuticle on guard cell surfaces; $\times 1,900$. Fig. 186, Inner view, adaxial thick cuticle on epidermal cells; $\times 290$. Fig. 187, Inner view, abaxial cuticle on epidermal cell surface; $\times 1,550$. Fig. 188, Inner view, abaxial cuticle on subsidiary cell surfaces; $\times 975$. Fig. 189, Outer view, abaxial cuticle, Florin rings and undulating epidermal cell surfaces; $\times 155$. Fig. 190, Inner view, abaxial cuticle enclosing guard cells; $\times 400$. Fig. 191, Inner view, abaxial cuticle, horizontal stomatal row with subsidiary cell wall flanges in contact; $\times 390$.



Figs. 192–202 *Agathis philippinensis*. Fig. 192, Inner view, abaxial cuticle, region of the stomatal apparatus, with four subsidiary cells and bilobed polar extensions; $\times 1,600$. Fig. 193, Inner view, abaxial cuticle, stomatal rows; $\times 170$. Fig. 194, Inner view, abaxial cuticle on guard cell surfaces; $\times 1,250$. Fig. 195, Outer view, abaxial cuticle showing Florin rings and undulating epidermal surfaces; $\times 450$. Fig. 196, Inner view, abaxial cuticle, stomatal rows, showing polar extensions; $\times 450$. Fig. 197, Inner view, abaxial cuticle on guard cell surface; $\times 3,000$. Fig. 198, Outer view, abaxial cuticle, stomatal plug morphology; $\times 3,800$. Fig. 199, Inner view, abaxial cuticle on epidermal cell surface; $\times 1,900$. Fig. 200, Inner view, abaxial cuticle, stomatal cluster; $\times 420$. Fig. 201, Inner view, adaxial cuticle, showing epidermal cell outlines; $\times 190$. Fig. 202, Inner view, abaxial cuticle region of the stomatal apparatus, with eight subsidiary cells; $\times 975$.

mata are very crowded, and often perpendicular rows (figs. 182, 191) or clusters lacking a parallel alignment occur (fig. 183). Stomata are oriented in all directions on the leaf (fig. 182). The shape of the stomatal apparatus is usually elliptical (figs. 181–183) but can vary depending on the proximity of subsidiary cells to one another (fig. 191). Four subsidiary cells are most common (fig. 181), with five and six occurring (figs. 182, 191).

Cuticle on the outer subsidiary wall flange is thick and irregular where it extends to the hypodermal level (figs. 181, 191). The surface of subsidiary cell cuticle is slightly rugose and pitted, with horizontal and vertical striations sometimes visible (figs. 181, 188). A deep groove occurs in this cuticle where the cells extend toward the leaf surface (fig. 181).

The cuticular flange between guard cells is thick and rugose (figs. 181, 185). Bilobed polar extensions occur (fig. 181), but the bilobed nature may be obscured by breakage or when the extension coincides with a subsidiary cell wall flange. Often cuticle completely covers the guard cells (fig. 190), making polar extensions difficult to observe. The cuticle on guard cell surfaces is rugose (fig. 185). A very distinct groove occurs in this surface near the subsidiary cell wall flanges. The flanges are nearly smooth and slightly inrolled (figs. 181, 185).

Epidermal cells on adaxial leaf surfaces are square to rectangular, and the cuticular flanges are very thick (fig. 186). On abaxial surfaces, cells are more elongate between stomatal rows (fig. 183) and show irregular shapes within a row. Epidermal cell wall flanges are straight to curving. Cuticle on epidermal cell surfaces is granular to pitted, often with a deep central pit on abaxial leaf surfaces (figs. 182, 187), and it is smooth to rugose on adaxial surfaces.

AGATHIS PHILIPPINENSIS (FIGS. 192–202)

Adult leaves were obtained from the Lamao River, Mount Mariveles, province of Bataan, Luzon, the Philippines (table 1). Leaves are ovate, slightly to distinctly acute, 4–6 cm long and 1.5–2.0 cm wide, tapering at the base to a 5–8-mm petiole (de Laubenfels 1988). Stomata have only been observed on abaxial leaf surfaces.

External cuticle surfaces are very undulating, with outlines of underlying epidermal cells visible (fig. 195). Stomata are sunken and prominent Florin rings are present (fig. 195). Stomatal plugs are present and composed of short rods (fig. 198).

Inner cuticle surfaces show stomata in discontinuous rows with various orientations, but perpendicular and oblique orientations are most common (figs. 193, 196, 200). As in *A. ovata*, clusters of crowded stomata also occur (fig. 200). The stomatal apparatus is elliptical to nearly circular in outline (figs. 192, 193, 196) but varies depending on the proximity of subsidiary cell wall

flanges (fig. 200). Four subsidiary cells are most common (fig. 192); however, from three to eight occur (figs. 200, 202), making this one of the more variable species with respect to subsidiary cell number.

Cuticle on the outer subsidiary cell wall flange is thick and irregular where it extends to the hypodermal level (fig. 192). Subsidiary cell surfaces are granular with occasional pits (fig. 192). Some indication of vertical striations has been observed on these surfaces (fig. 202). A deep groove occurs in this cuticle surface (fig. 192).

The cuticular flange between guard cells is relatively thin and rugose (figs. 192, 194, 197). Polar extensions are bilobed (figs. 192, 196) but are often broken, or the bilobed nature is not obvious when they coincide with a subsidiary cell wall flange (fig. 200). Cuticle on guard cell surfaces is rugose, especially near the subsidiary cell wall flange (fig. 197). A crease also occurs in this cuticle surface near the subsidiary cell wall flange (fig. 194). The flange of cuticle between subsidiary cells and guard cells is smooth (fig. 192) as in *A. ovata*.

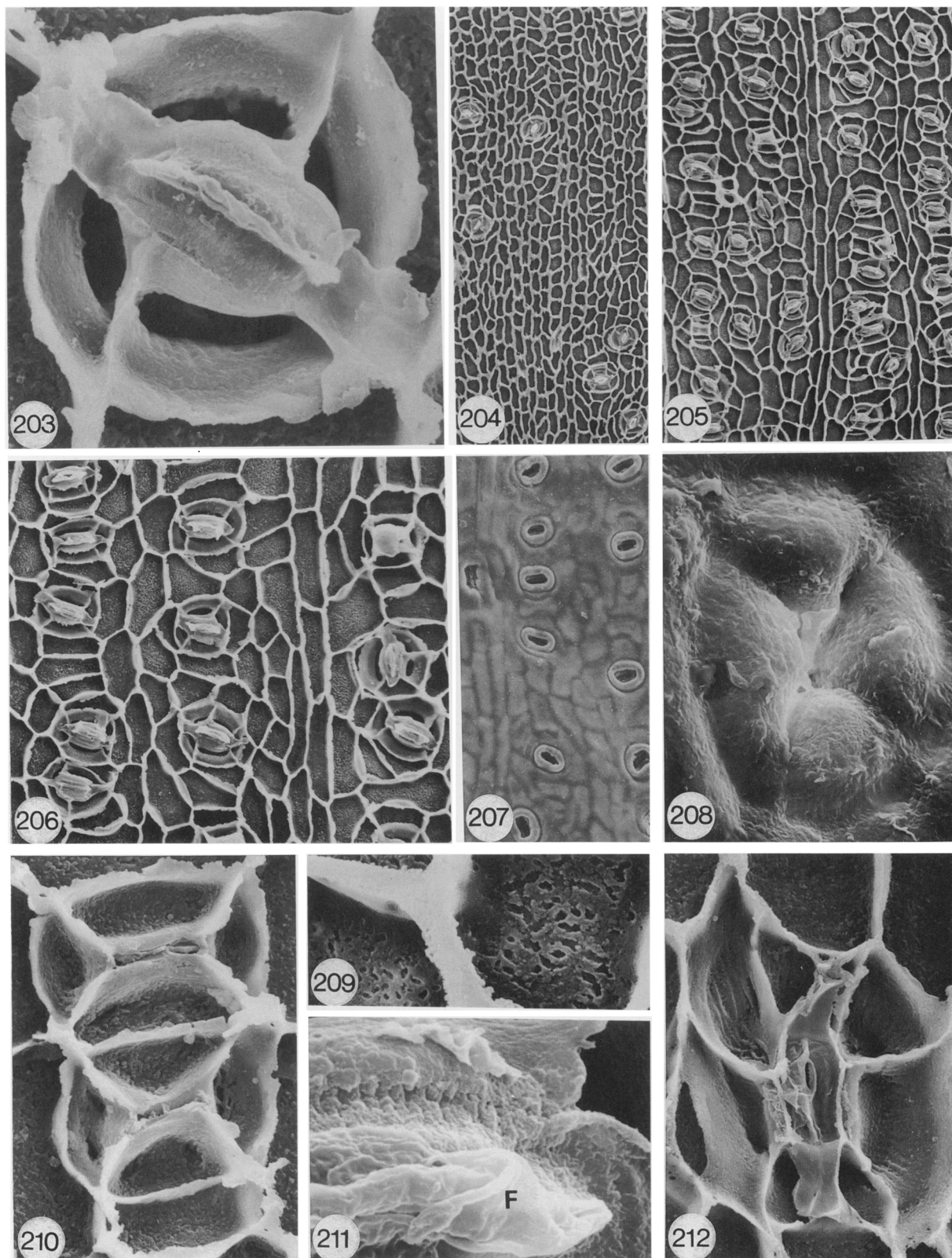
Epidermal cells on adaxial surfaces are square to rectangular to triangular (fig. 201). On abaxial surfaces the cells are more elongate between stomatal rows than within a row (fig. 193). Epidermal cell flanges are straight to curving and the tops of the flanges are irregular on abaxial leaf surfaces where cuticle extends to the hypodermal level (figs. 193, 196, 200). The cuticle on epidermal cell surfaces is rugose and pitted (fig. 199).

AGATHIS ROBUSTA (FIGS. 203–212)

Adult leaves were taken from trees in southern Queensland (table 1). Leaves are lanceolate to elliptical, 5–15 cm long and 2–5 cm wide, with acuminate apices and broad, flattened petioles (Silba 1986). Stomata have been observed on both surfaces but are more common on abaxial leaf surfaces (figs. 204, 205).

The external cuticle surface is slightly undulating, with underlying epidermal cell outlines visible (fig. 207). Stomata are sunken and distinct Florin rings are usually visible (fig. 207). In some instances the Florin ring may be broken up to reveal distinct underlying subsidiary cells (fig. 208). Some stomata have been observed in which the ring nearly completely occludes the stoma (fig. 208). Stomatal plugs have not been observed in this species.

Inner cuticle surfaces show scattered stomata on adaxial leaf surfaces (fig. 204). On abaxial surfaces, stomata are in discontinuous rows and not as crowded as in other *Agathis* species (figs. 205, 206). Stomatal orientation varies, with oblique being the most common (fig. 205). The stomatal apparatus is usually elliptical to circular in outline (figs. 203, 206). Shape varies somewhat when



Figs. 203–212 *Agathis robusta*. Fig. 203, Inner view, abaxial cuticle, region of the stomatal apparatus, with four subsidiary cells and bilobed polar extensions; $\times 1,700$. Fig. 204, Inner view, adaxial cuticle, showing widely scattered stomata and epidermal cell outlines; $\times 80$. Fig. 205, Inner view, abaxial cuticle, stomatal rows; $\times 115$. Fig. 206, Inner view, abaxial cuticle, stomatal rows and variable stomatal orientation; $\times 230$. Fig. 207, Outer view, abaxial cuticle, showing Florin rings and undulating epidermal cell surfaces; $\times 160$. Fig. 208, Outer view, abaxial cuticle, with dissected Florin ring and plugged stoma; $\times 1,600$. Fig. 209, Inner view, adaxial cuticle on epidermal cell surfaces; $\times 1,150$. Fig. 210, Inner view, abaxial cuticle, epidermal cells in stomatal configuration; $\times 925$. Fig. 211, Inner view, abaxial cuticle on guard cell surface and polar extension at right; $\times 4,250$. Fig. 212, Inner view, abaxial cuticle, region of the stomatal apparatus showing six subsidiary cells with striated surfaces; $\times 825$; *F* = flange of cuticle between guard cells.

subsidiary cell wall flanges of adjacent stomata are in contact with one another (fig. 206). What we interpret as aborted stomata have been found scattered on the abaxial leaf surfaces. They show cells arranged as in a stomatal apparatus (fig. 210); but guard cell surface cuticle is not present, and the cells corresponding in shape and size to subsidiary cells show epidermal cell ornamentation rather than the type typically seen on subsidiary cells (fig. 203). Perhaps these aborted stomata correspond to the closed rings (e.g., fig. 208) observed on the exterior of the cuticle. Four subsidiary cells are most common (fig. 203), with from three to six occurring (fig. 212).

Cuticle on the outer subsidiary cell wall flange is thick and somewhat irregular where it extends to the hypodermal level (figs. 203, 212). Subsidiary cell surfaces are smooth to slightly rugose, with longitudinal striations (figs. 203, 212). A deep groove usually occurs in this cuticle surface (figs. 203, 206).

The cuticular flange between guard cells is relatively thick and rugose and extends out in the polar region (fig. 211). Bilobed polar extensions occur (fig. 203). Cuticle on guard cell surfaces is rugose (fig. 211) and a distinct crease is usually visible near the subsidiary cell wall flange (fig. 203). The flange of cuticle between guard and subsidiary cells is relatively smooth, as in the two previously described species (fig. 203).

Epidermal cells are square to rectangular to triangular in shape on adaxial leaf surfaces (fig. 204). On abaxial surfaces the cells are more elongate between stomatal rows than within a row (figs. 205, 206). Epidermal cell wall flanges are straight to curving and may be slightly irregular when they extend to the hypodermal level (fig. 206). Cuticle on epidermal cell surfaces is rugose and pitted, often with elongated pits on adaxial leaf surfaces (fig. 209).

AGATHIS SILBAI (FIGS. 213–223)

Adult leaves were obtained from Espiritu Santo, on the path to Santo Peak at 800–1,000 m in the New Hebrides (table 1). Leaves are 6–11.8 cm long and 2.1–3.7 cm wide, lanceolate, with a 1.5–3-mm petiole (de Laubenfels and Silba 1987). Stomata have only been observed on abaxial surfaces.

The external cuticle surface is slightly undulating, with underlying epidermal cell outlines somewhat visible (fig. 215). Stomata are sunken and prominent Florin rings are present (figs. 215, 220). Stomatal plugs are present and are solid blocks (fig. 220).

Inner cuticle surfaces show stomata in fairly regular but discontinuous rows (figs. 214, 217). Stomatal orientation is variable; however, perpendicular and oblique orientations are the most common (figs. 214, 217, 221, 223). Cuticle often

covers the complete stomatal apparatus to the hypodermal level (fig. 222). The stomatal apparatus is usually elliptical in shape (fig. 213), but varies when two subsidiary cell wall flanges are in contact (figs. 221, 223). Four subsidiary cells are most common (fig. 213), but five also occur, making this one of the more conservative species with respect to subsidiary cell number.

Cuticle on the outer subsidiary cell wall flange is thick and relatively smooth (fig. 213) but can be slightly irregular when it extends to the hypodermal level (fig. 222). Cuticle on subsidiary cell surfaces is slightly rugose and pitted (fig. 213). Some slight indications of both horizontal and vertical striations occur on this surface (figs. 213, 221, 223); there is no deep groove in this surface as in most of the other *Agathis* species.

The cuticular flange between guard cells is relatively thick and slightly rugose (figs. 213, 216). Polar extensions are present and show a distinct ridge down the center. They were possibly bilobed (fig. 221, top left), but most of these appear to be broken (fig. 217). Cuticle on guard cell surfaces is rugose and pitted (fig. 216). The edge of this cuticle slopes toward the subsidiary cell wall flange, and no distinct flange occurs here (figs. 214, 216, 221).

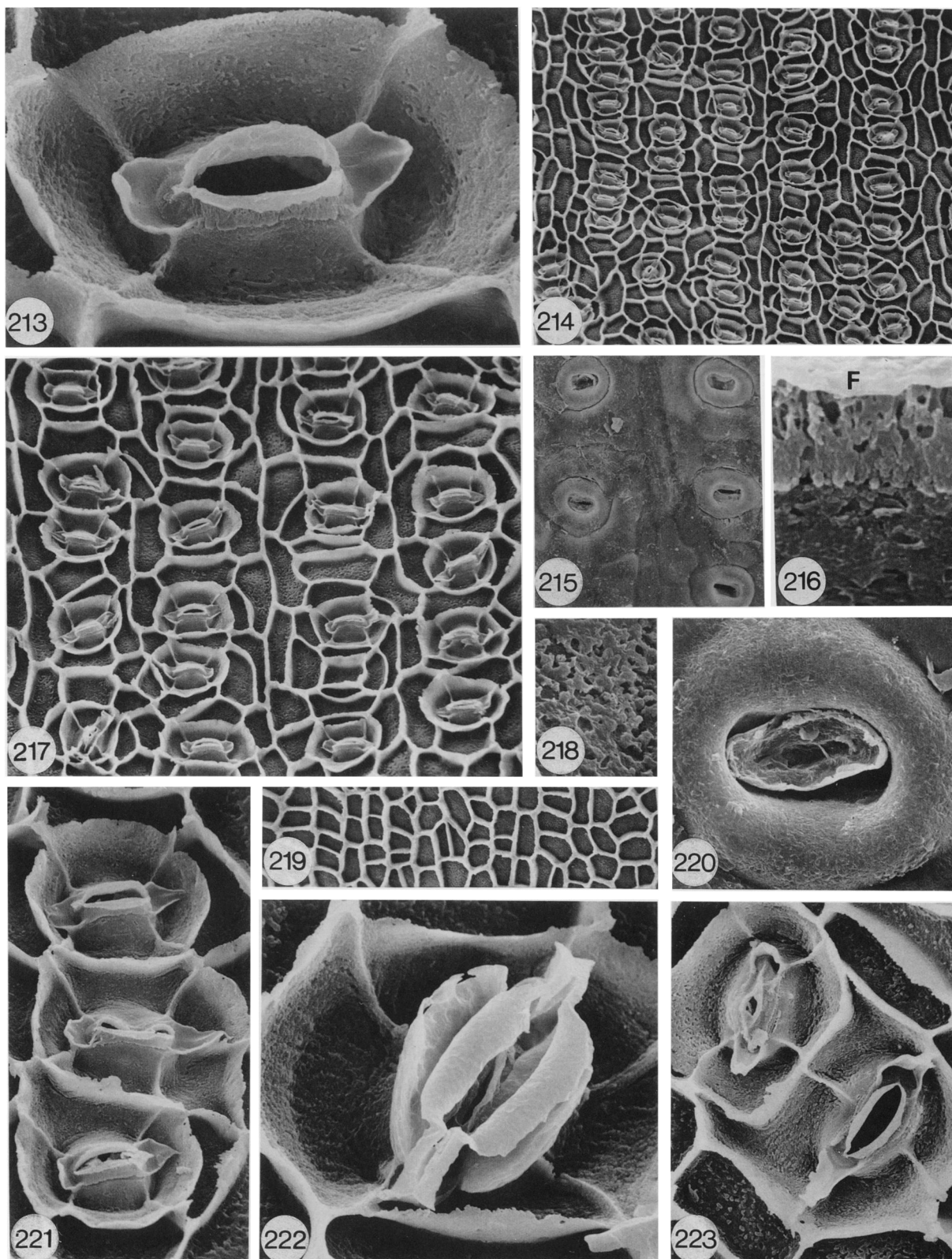
Epidermal cells are usually square to rectangular in shape on adaxial leaf surfaces (fig. 219). On abaxial leaf surfaces the cells are irregular and elongate between stomatal rows and broader than long within a row (figs. 214, 217). Epidermal cell wall flanges are nearly straight on both leaf surfaces (figs. 214, 219). Epidermal cell surfaces are rugose and very pitted (fig. 218).

AGATHIS SPATHULATA (FIGS. 224–232)

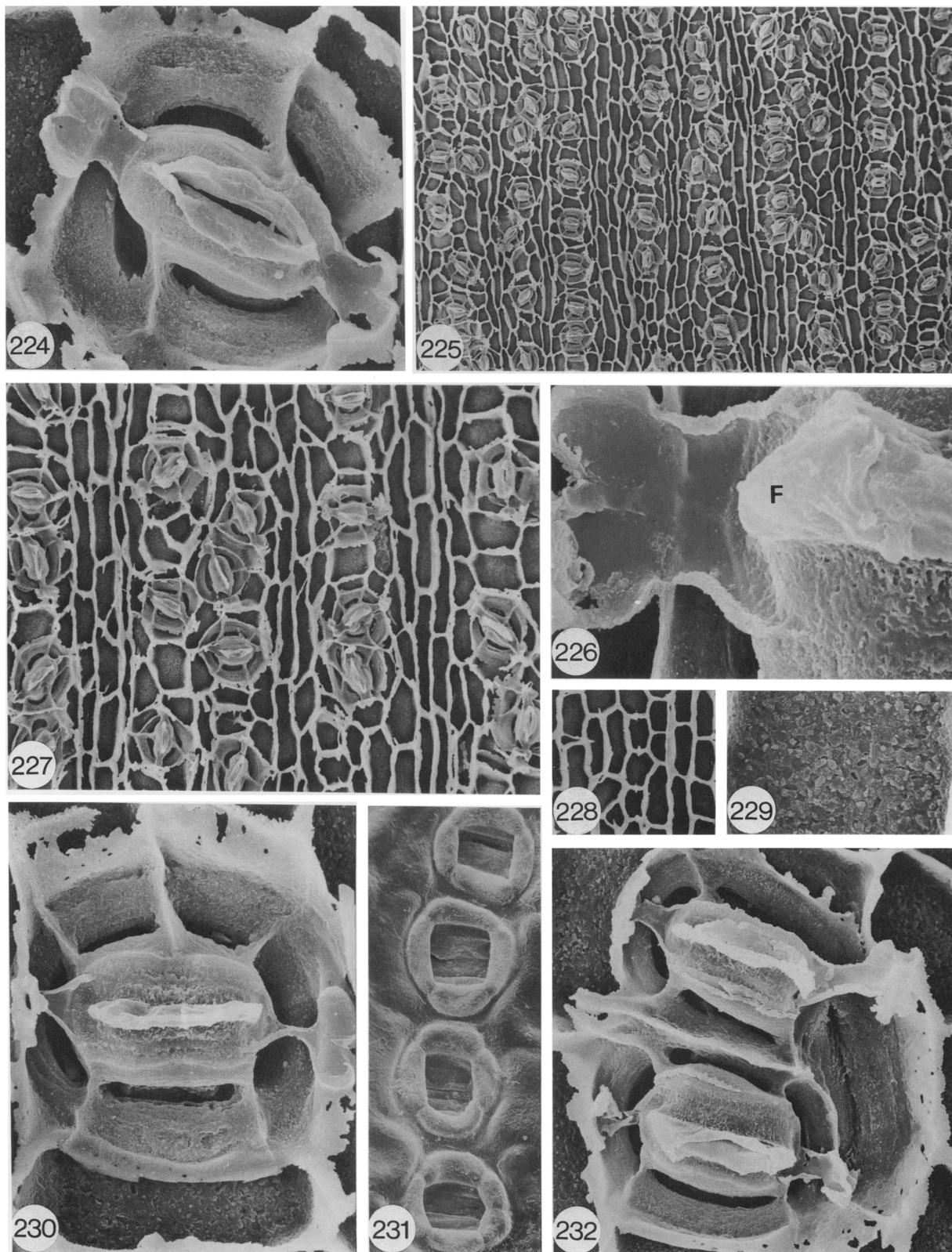
Adult leaves were collected in Bulolo, New Guinea, at about 915 m from a rain forest tree (table 1). Leaves are bluntly acute, 9–10 cm long and 2–3 cm wide to bluntly rounded and 7–9 cm long and 1.8–2.0 cm wide, tapering at the base to a 5–10-mm petiole (de Laubenfels 1988). Stomata have only been observed on abaxial leaf surfaces.

The external cuticle surface is slightly undulating, with underlying epidermal cell outlines sometimes visible (fig. 231). Stomata are sunken and prominent Florin rings are present. These are often broken up so that the underlying subsidiary cells are visible (fig. 231). Stomatal plugs have not been observed in this species.

Inner cuticle surfaces show discontinuous rows of stomata with variable orientations (figs. 225, 227). Perpendicular and oblique orientations are the most common. The stomatal apparatus is usually elliptical in outline (fig. 224). This shape varies, however, when two or more subsidiary cells from adjacent stomata are in contact with one another. Sometimes, unusual shapes occur



Figs. 213–223 *Agathis silbai*. Fig. 213, Inner view, abaxial cuticle, region of the stomatal apparatus, showing four subsidiary cells and polar extensions; $\times 1,550$. Fig. 214, Inner view, abaxial cuticle, stomatal rows; $\times 120$. Fig. 215, Outer view, abaxial cuticle, Florin rings and undulating epidermal cell surfaces; $\times 240$. Fig. 216, Inner view, abaxial cuticle on guard cell surface; $\times 5,000$. Fig. 217, Inner view, abaxial cuticle, showing stomatal orientation; $\times 240$. Fig. 218, Inner view, adaxial cuticle on epidermal cell surface; $\times 1,450$. Fig. 219, Inner view, adaxial cuticle, showing epidermal cell outlines; $\times 150$. Fig. 220, Outer view, abaxial cuticle, Florin ring and stomatal plug; $\times 1,250$. Fig. 221, Inner view, abaxial cuticle, stomatal row with subsidiary cells in contact and variable subsidiary cell number; $\times 600$. Fig. 222, Inner view, abaxial cuticle, showing cuticle enclosing guard cells and striated cuticle on subsidiary cell surfaces; $\times 1,450$. Fig. 223, Inner view, abaxial cuticle, showing adjacent stomata with modified subsidiary cell shapes; $\times 675$; *F* = flange of cuticle between guard cells.



Figs. 224–232 *Agathis spathulata*. Fig. 224, Inner view, abaxial cuticle, region of the stomatal apparatus, showing four subsidiary cells and bilobed polar extensions; $\times 1,000$. Fig. 225, Inner view, abaxial cuticle, stomatal rows; $\times 80$. Fig. 226, Inner view, abaxial cuticle on guard cell surface and bilobed polar extension; $\times 2,600$. Fig. 227, Inner view, abaxial cuticle, stomatal orientation and variable subsidiary cell number; $\times 180$. Fig. 228, Inner view, adaxial cuticle, showing epidermal cell outlines; $\times 160$. Fig. 229, Inner view, abaxial cuticle on epidermal cell surface; $\times 1,450$. Fig. 230, Inner view, abaxial cuticle, region of the stomatal apparatus, with five subsidiary cells and bilobed polar extension; $\times 1,000$. Fig. 231, Outer view, abaxial cuticle, showing Florin rings and undulating epidermal cell surfaces; $\times 425$. Fig. 232, Inner view, abaxial cuticle, showing two stomata with one large shared subsidiary cell; $\times 800$.

when one shared subsidiary cell acts as an encircling epidermal cell for an adjacent apparatus (fig. 232).

Cuticle on the outer subsidiary cell wall flange is thick and usually very irregular when this flange extends to the hypodermal level (figs. 224, 230, 232). The subsidiary cell cuticle surface is slightly granular and may have a few scattered pits (figs. 224, 230). Some indications of horizontal striations also occur on this surface (figs. 224, 230). A deep groove is found in this cuticle surface (figs. 224, 230, 232).

The cuticular flange between guard cells is relatively thick and rugose (figs. 224, 226). Bilobed polar extensions occur (figs. 224, 226, 230). These are often broken due to their delicate nature. Cuticle on guard cell surfaces is rugose, with small pits (fig. 226). A ridge occurs on this cuticle surface (figs. 224, 230), and in some cases a groove can also be seen near the subsidiary cell wall flange (fig. 232). The flange of cuticle between guard and subsidiary cells is not usually visible, but in some stomata it appears thin and irregular when present (fig. 232).

Epidermal cells are usually square to rectangular in shape on adaxial leaf surfaces (fig. 228). On abaxial surfaces epidermal cells are pronouncedly elongate between stomatal rows and shorter within a row (figs. 225, 227). Epidermal cell wall flanges are nearly straight (figs. 227, 228). Cuticle on epidermal cell surfaces is rugose and slightly pitted on both leaf surfaces (figs. 229).

Discussion

Outer surfaces of *Agathis* leaves are undulating and exhibit Florin rings and stomatal plugs. In contrast, the other genus in the family, *Araucaria*, shows relatively smooth surfaces and lacks rings, although plugs are present in both genera (Stockey and Ko 1986). Most *Agathis* species are hypostomatic, although a few (*A. australis*, *A. labillardieri*, *A. moorei*, *A. robusta*) show scattered stomata on abaxial surfaces. *Agathis microstachya* is the exception, with a larger number of adaxial stomata than any of the other species. There is a large amount of variability in the amount of undulation of cuticle surfaces. Such variability was first reported by Page (1980) in his study of sixteen species of *Agathis*; however, we do not see any distinct groupings in this continuum as Page reported. The height of the Florin ring above the cuticle surface is variable, with most species reported as having Florin rings that are slightly sunken into the cuticle surface (Page 1980). Page (1980) also reports that *A. australis* is the only species that shows Florin rings that are not set into depressions. However, we see very little difference between the position of the Florin ring in this species (fig. 13), *A. kinabaluensis* (fig.

80), and *A. microstachya* (fig. 142). In some areas of the leaf in *A. australis*, rings appear to be slightly sunken.

Stomatal plug morphology is variable, from solid to porous, with many species exhibiting rod-shaped components. Since these plugs were most probably wax (Stockey and Ko 1986), we have chosen not to use this character for taxonomic purposes. Also, Morvan (1982, 1987) has shown that the cuticular waxes in the Podocarpaceae can change shape and appearance when preserved with certain fixatives and even when untreated, depending on the length of time that the leaves have been removed from the tree.

Stomata are sunken to the level of the hypodermis and are usually in discontinuous rows, although variability from distinct rows to extreme crowding with an apparent lack of orientation can occur. Unlike the broad-leaved *Araucaria* species, stomata are usually oriented perpendicularly or obliquely to the long axis of the leaf rather than parallel. A few species show parallel orientations more commonly, but perpendicular and oblique orientations are by far the most characteristic of the genus.

Although four subsidiary cells, as in *Araucaria* (Stockey and Ko 1986), are common for the genus, five also occur very frequently. However, a greater amount of variability in subsidiary cell number occurs in *Agathis*, which shows three to nine subsidiary cells. Most *Araucaria* species are conservative, showing four or five subsidiary cells, but three to seven have been reported rarely (Stockey and Ko 1986). Most *Agathis* species show a lot of variability, with from three to seven subsidiary cells reported in several species.

Nearly all *Agathis* species show bilobed polar extensions with two small knobs of cuticle present when the extensions are complete. The exceptions to this are *A. silbai* and *A. montana*, in which the cuticle is so thick that any extensions may have been damaged by breakage when "clean" preparations of the cuticle were obtained. In addition to the possibility of breakage, wide cuticular flanges on subsidiary cells in *A. silbai* may account for the lack of polar extensions. The presence of these bilobed extensions with two circular knobs is different from anything reported in *Araucaria* or any of the podocarps studied thus far (e.g., Greenwood 1987; Stockey and Ko 1988, 1990; Wells and Hill 1989; Stockey et al. 1992a).

Cuticle on subsidiary cell surfaces is usually granular but can be relatively smooth, and in many cases shows either horizontal or vertical striations or both. Most species show a deep cleft in the subsidiary cell cuticle where the cell extended to the surface of the leaf and corresponding to the Florin ring externally. The shape of the stomatal apparatus is usually elliptical but can vary from circular to angular depending on the

species and proximity of stomata to one another. Most species have stomata of a more or less consistent size. Some species, such as *A. celebica*, show extreme variability in size and shape of stomata and their associated Florin rings (e.g., figs. 38, 44). Cuticle on guard cell surfaces is usually granular, often pitted, and rarely smooth. The flange of cuticle between guard cells is most often thin and rugose but varies with species. The flange of cuticle between subsidiary cells and guard cells is usually inrolled slightly in all species.

Epidermal cells are usually square to rectangular but can be quite variable on one leaf in almost all of the species of *Agathis* studied. In comparison, epidermal cells of *Araucaria* species are very regular (Stockey and Ko 1986). Epidermal cell wall flanges are not sinuous to any large degree in any of the *Agathis* species. This is consistent with what is seen in the broad-leaved *Araucaria* species (Stockey and Ko 1986). Epidermal cell surfaces are usually granular to pitted but can be smooth or have large lens-shaped pits in a few species.

Unlike the genus *Araucaria* (Stockey and Ko 1986), the sections of the genus *Agathis* cannot be distinguished from one another based on cuticle micromorphology. A continuum of characters exists. As Page (1980) has stated, "the genus is notoriously difficult taxonomically, offering very few diagnostic features, and this is especially true of its vegetative parts." The present study using SEM to describe cuticle micromorphology of *Agathis* certainly bears this out. However, species can be distinguished from one another by a combination of several morphological characters. Page's (1980) groupings based on external cuticle features are not distinguishable in our view, and certainly these groupings are not upheld when internal cuticle features are added to the picture. Page himself states that groups are only slightly different from one another.

There has been some controversy with respect to the delimitation of species in the genus *Agathis*. Whitmore (1977, 1980) and Bowen and Whitmore (1980) take the conservative view in recognizing thirteen species, while the latest review by de Laubenfels (1988) and earlier work (de Laubenfels 1972, 1978, 1979; Hyland 1977; de Laubenfels and Silba 1987; also see Silba [1986] for listing) account for the 21 species examined here. Since vegetative features are so conservative, the most important taxonomic characters are the shapes of the microsporophylls, cone scale tips, and seeds, according to de Laubenfels (1988). These data, in conjunction with vegetative morphology, serve to distinguish the species, with pollen cone features perhaps being the most important (Whitmore 1980; de Laubenfels, personal communication, 1991). Our study shows that all

21 *Agathis* species can be distinguished on the basis of cuticle micromorphology using a combination of several characters.

One major problem in taxonomic studies of the genus *Agathis* is that it is such a large tree, sometimes reaching heights of 65 m (Silba 1986). This makes collecting difficult. Thus, many herbaria have only juvenile foliage, which in many cases is indistinguishable between species. In our study, we examined juvenile foliage of only a few species (table 1), so the differences in cuticle micromorphology between juvenile and adult foliage for the genus are not clear at this time. Juvenile leaves, as in the araucarians and podocarps studied so far, often show more elongated epidermal cells, more widely spaced stomata, and often different pitting of cuticle on epidermal cell surfaces (Stockey and Taylor 1978a, 1978b, 1981; Stockey and Ko 1986, 1990; Stockey et al. 1992a). The full range of variability, however, is unknown at the present time.

Cookson and Duigan (1951) divided *Agathis* into two groups based mostly on the orientation of stomata on leaves. Their group A includes species in which 30% or more of the stomata are transversely placed, the number of longitudinal stomata is less than or equal to 5%, and the number of oblique stomata is less than 70%. Group B species have less than 30% of the stomata transversely placed, with the number of longitudinal stomata in this group variable but usually greater than 5% and up to 30%. Oblique stomata are more frequent in group B than in group A species and may be as high as 91%. *Agathis robusta*, *A. microstachya*, *A. celebica*, *A. flavescens*, and *A. philippinensis* are included in group A. *Agathis australis*, *A. moorei*, *A. lanceolata*, and *A. philippinensis* are included in group B. At the time Cookson and Duigan (1951) did their study, the taxonomy of *Agathis* was extremely complicated. The circumscription of several of the species has changed such that several are now placed in synonymy with other species (Hyland 1977; de Laubenfels 1978; Silba 1986). *Agathis philippinensis* and *A. microstachya* are good examples. These species were also confused in the literature at various times with *A. robusta* (Hyland 1977), making comparisons extremely difficult, especially with light microscopy. Furthermore, as Cookson and Duigan (1951) point out, the dividing line between groups A and B is arbitrary and in some cases difficult to determine. The similarity of cuticular features of all *Agathis* species, at the ultrastructural level as well, is indicated by our study.

In earlier work, Stockey and Taylor (1981) pointed out that in some species of *Agathis* included in group B, e.g., *A. lanceolata*, stomatal orientations in some cases are similar to those

species in group A. *Agathis moorei* has leaves that are borderline between groups A and B (see also Cookson and Duigan, table 4 [1951]). In addition, the leaves studied by Stockey and Taylor (1981) included juvenile forms. As stated above, the full extent of differences between juvenile and adult leaves is unknown at the present time.

The genus *Agathis*, unlike *Araucaria*, is unknown in the fossil record of the Northern Hemisphere. *Agathis* leaves with cuticle are known from the Oligocene and Miocene of New South Wales, Victoria (Cookson and Duigan 1951), New Zealand (Florin 1963), and Tasmania (Hill and Bigwood 1987). Some taxa, e.g., *A. intermedia* (Ett.) Chapman and Crespin (1934) and *A. podozamioides* (Ett.) Cookson and Duigan (1951) are incompletely known. Others such as *A. yallournensis* Cookson and Duigan (1951) and *A. parwanensis* Cookson and Duigan (1951) are known in more detail. Leaves of *A. yallournensis* can be from 3.5 cm to at least 9.5 cm long and 1–2 cm wide, and are narrow to broad-lanceolate with an obtuse apex and a 1.5-mm-wide petiole. Some stomata have been observed on adaxial surfaces. Oblique stomatal orientations are most common. Four to six subsidiary cells have been reported. Epidermal cell shapes are square, rectangular, and irregular, as in the extant species described here. Leaves of *A. parwanensis* are at least 2.8 cm long and 0.9 cm wide, but specimens are incomplete. No stomata have been observed on adaxial surfaces. Four to six subsidiary cells occur and sometimes these cells abut. At least 50% of stomata are transversely oriented. Epidermal cells are square to quadrangular to irregular. Neither of these species shows undulating cell walls.

The oldest known *Agathis* leaves based on cuticle are those of *A. dubia* from the Cretaceous Otway Formation, at Moonlight Head, Victoria (Cantrill 1989). Although preservation of the cuticle is not good, stomatal orientation and the presence of probable Florin rings are comparable to *Agathis*, and these fossils are tentatively included within the genus.

In 1985, Bigwood and Hill described fossil leaves showing araucarian cuticle from the Eocene of Tasmania, assigning them to a new genus, *Araucarioides* Bigwood and Hill. These leaves are broad and elongate, similar to *Agathis*, but they are incomplete. Stomatal orientations are transverse or oblique and there are four to six subsidiary cells, as in extant *Agathis*. The broad-leaved species of *Araucaria* (Stockey and Ko 1986) usually show almost completely parallel stomatal orientations. Two of the new species, *Araucarioides linearis* Bigwood and Hill (the generatype) and *A. sinuosa* Bigwood and Hill do not show Florin rings like *Araucaria*, whereas the third, *A. annulata* Bigwood and Hill, is reported to have

rings that are not prominent. We interpret these three species externally as most similar to *Araucaria* but similar to *Agathis* in stomatal orientation. Epidermal cell shapes are more similar to *Araucaria*.

Among the broad-leaved podocarps, i.e., *Acropyle* Pilger, *Dacrycarpus* (Endl.) de Laub., *Falcatifolium* de Laub., *Nageia* Gaertner (= *Decusocarpus* de Laub.), *Podocarpus* L. Herit. ex Pers., and *Prumnopitys* Philippi, only those of *Nageia* might be confused with *Agathis* if fairly complete branching specimens are known. Leaf arrangement in *Podocarpus* is helical; in *Acropyle*, *Falcatifolium*, and *Prumnopitys* leaves appear two-ranked but are essentially helical with a slight twist into a flattened appearance. In *Dacrycarpus* leaves are dimorphic, with adult leaves awl-shaped and helically arranged. Some leaves appear flattened and two-ranked on juvenile foliage. The falcate and bilaterally flattened leaves of *Acropyle*, *Falcatifolium*, and *Dacrycarpus* (juvenile foliage) differ considerably from the oval-shaped, flat, broad leaves of *Agathis*. In *Podocarpus* leaf shapes approach those of some *Agathis* species. However, these leaves have only one vein (de Laubenfels 1988). Therefore, if only isolated leaves are known, *Podocarpus* can still usually be distinguished from *Agathis*.

The leaves of *Nageia*, however, are more difficult to distinguish. Leaves are opposite, or mixed, with some helically arranged leaves present. Juvenile leaves in particular can be similar in appearance to those of *Agathis*. These leaves have several veins, as in *Agathis*. Florin rings are present (Stockey and Ko 1988); from four to six subsidiary cells have been reported, with four being the most common (Greenwood 1987; Stockey and Ko 1988). Stomatal orientations in this genus, however, are usually parallel to the long axis of the leaf. The narrow rectangular outline of subsidiary cells of *Nageia* has been noted (Greenwood 1987) and illustrated for two of the extant species (Stockey and Ko 1988). During this study, we also examined the cuticles of *N. nagi* (Thun.) de Laub., because of their great similarity to juvenile *Agathis* foliage, and observed similar stomatal orientations and subsidiary cell outlines. These characters can be used to distinguish the genus from *Agathis*.

Most variability in *Agathis* cuticle micromorphology and therefore the most useful characters for taxonomy, as in other araucarian leaves, are features of the guard and subsidiary cell surfaces (Stockey and Taylor 1978a, 1978b, 1981; Stockey and Ko 1986). These must be used in combination with epidermal cell surface features in taxonomic studies. Even though the sections of the genus cannot be recognized on the basis of cuticular micromorphology, the genus itself can be

distinguished from *Araucaria* and the broad-leaved podocarps.

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