CUTICLE MICROMORPHOLOGY OF FALCATIFOLIUM DE LAUBENFELS (PODOCARPACEAE)

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Cuticle micromorphology of leaves from all five species of the Southern Hemisphere conifer genus *Falcatifolium* de Laubenfels (Podocarpaceae) was studied with scanning electron microscopy. Both herbarium and preserved specimens were examined and showed no differences in micromorphology. External and internal features of abaxial and adaxial cuticles are characterized for the five species and compared to other known podocarps. External cuticle surfaces exhibit undulating surfaces that may reflect underlying epidermal cell outlines, stomatal plugs composed of irregular blocks, and fairly regular stomatal rows. Stomata are separated by one to three epidermal cells. Two lateral subsidiary cells are present with polar subsidiary cells usually lacking. There is a deep crease in subsidiary cell cuticle, smooth to slightly undulating cuticle on guard cell surfaces near the stoma, a ridge on guard cell cuticle, thin cuticular flanges between guard and subsidiary cells, polar extensions, nonsinuous epidermal cell outlines with cuticle extending to the hypodermis, more elongate epidermal cells between stomatal rows than within rows, and usually granular epidermal cell surfaces.

Introduction

The genus *Falcatifolium* de Laubenfels (Podocarpaceae) contains five species that range from Malaysia to the Philippines and New Caledonia (de Laubenfels 1969, 1972; Silba 1986). These are reportedly dioecious shrubs or trees that are distinguished from the other podocarps by their sickle-like or falcate, laterally flattened, spirally arranged leaves with twisted bases that spread out distichously from the branch (de Laubenfels 1969; Silba 1986). The name *Falcatifolium* refers to the basal falcate curvature of leaves away from the branch (de Laubenfels 1969). The genus *Falcatifolium* was split from *Dacrydium* Solander ex Lambert, Florin's (1931) "Gruppe A," by de Laubenfels (1969), based on its fertile structures, which are produced on specialized axillary shoots; a pronounced "hump" on the epimatium that projects laterally from the mature cone; pollen morphology; and lack of vascular fibers in leaves (Tengner 1965), as well as on general leaf morphology.

Cuticular studies of the Podocarpaceae, while numerous, have neglected some of the less accessible species. The family is a large one with over 170 species (Silba 1986). Leaf structure and cuticle morphology at the light microscope (LM) level of some species were studied by Florin (1931, 1940a, 1940b, 1958), Orr (1944), Buchholz and Gray (1948a, 1948b, 1948c), Gray and Buchholz (1948, 1951), Townrow (1965, 1967a, 1967b, 1969), Dilcher (1969), Schoonraad and Van Der Schijff (1974), Ferré et al. (1977), and Greenwood (1987). Scanning electron microscopy (SEM) of epicuticular waxes (Morvan 1982, 1987) and leaf morphology of some taxa have been examined recently (Stockey and Ko 1988, 1990; Cantrill

1989; Wells and Hill 1989a, 1989b). Leaves of *Falcatifolium taxoides* (= *Dacrydium taxoides*) from New Caledonia have been examined using LM by Greenwood (1987) and by SEM by Stockey and Ko (1988), while the four other taxa in this genus have not so far been examined micromorphologically. Greenwood (1987) also studied *F. falciforme* (Parlatore) de Laubenfels and *F. papuanum* de Laubenfels with LM but did not include detailed descriptions or any illustrations of the cuticle of these taxa. He distinguished leaves of *Falcatifolium* from those of other podocarps; however, several cuticular characters overlap with those of *Dacrycarpus* (Endl.) de Laub. and *Nageia* Gaertner (= *Decussocarpus* de Laub.). The usefulness of SEM and its importance in taxonomy have been emphasized in recent years (Wells and Hill 1989a). Because of the complex relief of many gymnosperm cuticles, SEM has been shown to provide more detail than is possible with the light microscope (e.g., Stockey and Ko 1986; Wells and Hill 1989a).

In this paper we examine micromorphological features of all five currently recognized species of *Falcatifolium* using SEM. The micromorphological similarities are assessed to determine which characters can be used most consistently for taxonomic purposes. The usefulness of micromorphological cuticular features in distinguishing these taxa is examined and comparisons are made between these and other known podocarps.

Material and methods

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

All leaves were sectioned with the leaf margins

Table 1

FALCATIFOLIUM DE LAUBENFELS

| Species | Material examined | | | Source |
	Type[a]	Herbarium	Voucher	
F. angustum de Laubenfels	H	K	E. F. Brunig 5963	Sarawak
	H	K	J. A. R. Anderson 2448	Sarawak
F. falciforme (Parlatore) de Laubenfels........................	H	MO 2728237	P. J. Martin S.37583	Gunong Santubong 1st division, Sarawak
F. gruezoi de Laubenfels...............	H	CAHUP	Gruezo and Hernaz 27033	Oriental Mindoro, Phillippines
F. papuanum de Laubenfels............	H	MO 3058387	K. Kerenga 3	Menyamya, Morobe, New Guinea
F. taxoides (Brongniart et Grisebach) de Laubenfels	H, P	UAPC-ALTA	McPherson and Stockey 3960D	Road to Mt. Dzumac, Dumbea Valley New Caledonia

[a] H = herbarium specimen, P = preserved specimen.

intact, leaving both abaxial and adaxial epidermis attached for cuticle examination. All preparations were rehydrated in distilled water for 24 h and then immersed in 20% CrO_3 (chromium trioxide) solution for 96 h (Alvin and Boulter 1974; Stockey and Ko 1986). Approximately 10 leaves of each species were examined with SEM. Stomatal distribution was determined by examining leaves on several branches when specimens were available.

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

All stubs are deposited in the University of Alberta Paleobotanical Collection (UAPC-ALTA). Stomatal distribution was determined by the examination of leaves from several branches. Descriptions disregard what is obvious 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.

Results

FALCATIFOLIUM ANGUSTUM (FIGS. 1–8)

Adult leaves of this species from Sarawak (table 1), are 18–35 mm long by 1–2.5 mm wide (table 2). The external cuticle surface is undulating with outlines of underlying epidermal cells clearly vis-

Table 2

EXTERNAL CUTICULAR FEATURES ON LEAVES OF FALCATIFOLIUM

Species	Leaf dimensions (length × width in mm)[a]	Florin ring	Stomatal plug	Stomatal distribution	Stomatal orientation to long axis of leaf
F. angustum ...	18–35 × 1–2.5	Present	Irregular blocks, perforate	Discontinuous rows, both surfaces except on midrib	Parallel
F. falciforme ...	20–65 × 5–7	Present/absent on same leaf	Solid, irregular blocks or sheets	Discontinuous but extensive rows, both surfaces, except on midrib	Parallel
F. gruezoi	3.5–20 × 3.5–7	Present/absent on same leaf	Irregular blocks, or entire stoma blocked	Discontinuous rows, both surfaces, except on midrib	Parallel
F. papuanum ..	12–17 × 2–3.5	Present/absent on same leaf	Irregular blocks, granular to solid	Discontinuous rows, both surfaces, except on midrib	Parallel
F. taxoides	10–31 × 3–6	Absent/present sunken	Solid, irregular blocks	Discontinuous but extensive rows, both surfaces, except on midrib	Parallel

[a] From Silba (1986), and personal observation.
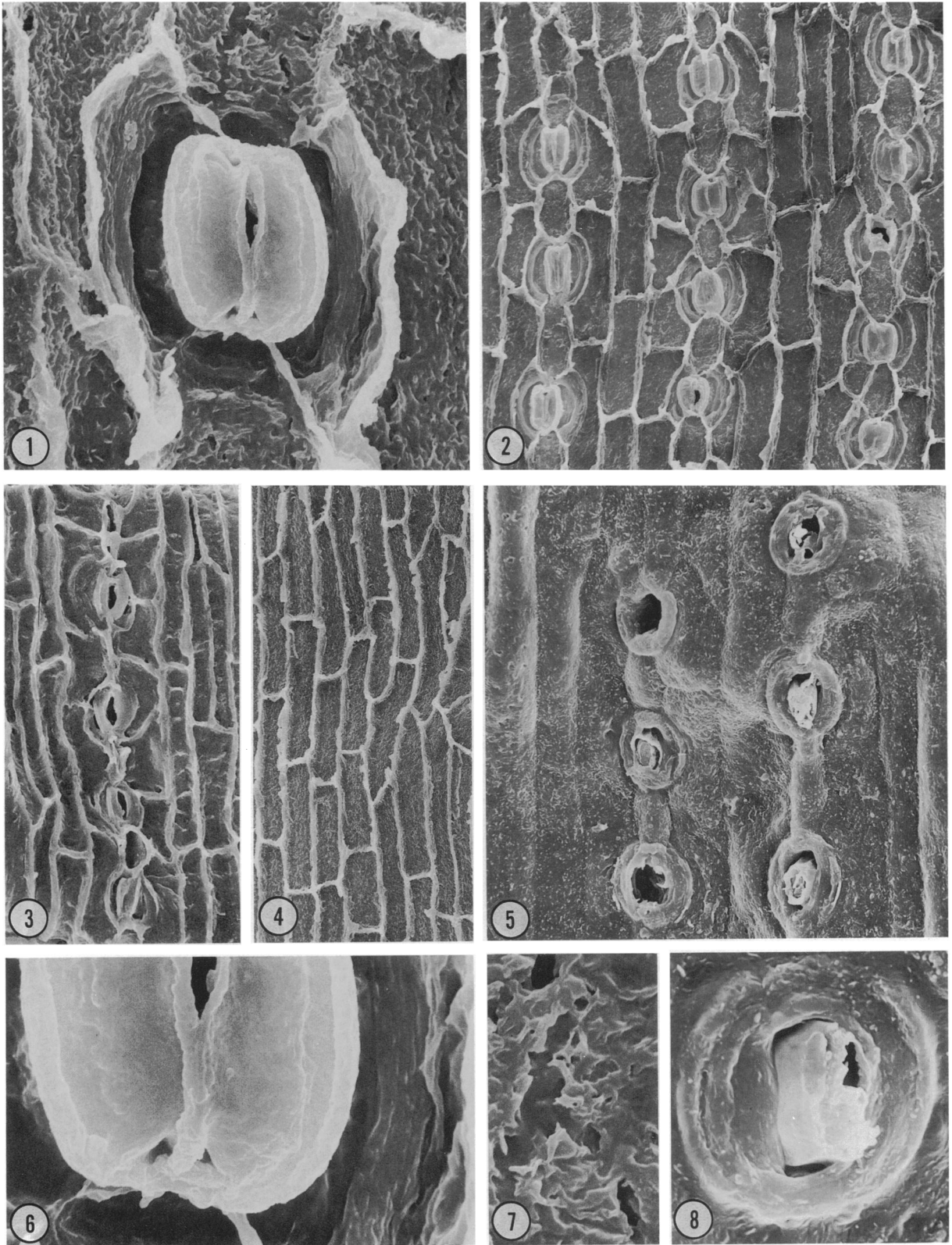
Figs. 1-8 *Falcatifolium angustum*. Fig. 1, Inner surface, region of stomatal apparatus with two subsidiary cells; × 1,500. Fig. 2, Inner surface, stomatal rows, showing two and three subsidiary cells per stomatal apparatus; × 310. Fig. 3, Inner surface, stomatal row; × 280. Fig. 4, Inner surface, epidermal cell outlines; × 280. Fig. 5, Outer surface, showing undulating epidermal cell outlines and Florin rings. Several stomata show plugs; × 488. Fig. 6, Inner view, cuticle on guard and subsidiary cell surfaces; × 3,100. Fig. 7, Inner surface, epidermal cell surface cuticle; × 3,100. Fig. 8, Outer surface, Florin ring surrounding stoma with plug; × 1,600.

Table 3

INTERNAL CUTICULAR FEATURES (μM) ON LEAVES OF FALCATIFOLIUM

Species	Stomatal dimensions (polar × lateral)	No. subsidiary cells	Epidermal cell dimensions (length × width)		Epidermal cell surface
			Between stomatal bands	Within stomatal bands	
F. angustum . . .	42 × 38	2 common, 3 occur	91 × 16	37 × 17	Rugose, enlarged pits
F. falciforme. . .	39 × 36	2 common, 3 occur	67 × 21	12 × 6	Rugose and pitted
F. gruezoi	52 × 41	2 common, 3 occur	40 × 13	9 × 8	Pitted usually, to smooth
F. papuanum . .	37 × 39	2 common, 3 occur	38 × 13	16 × 10	Smooth to slightly pitted
F. taxoides	41 × 45	2 common, 3 rare, 4 rare	87 × 14	46 × 17	Rugose and pitted

ible (fig. 5). Stomatal plugs are irregular, composed of block-like components (table 2) and are often perforated by channels or free near the edge (figs. 5, 8). Prominent upraised Florin rings (Buchholz and Gray 1948a) surround the stomata. Rings may be complete or interrupted (fig. 5) and reflect the underlying pattern of the stomatal apparatus.

Stomata in discontinuous but fairly regular rows are oriented parallel to the leaf axis (figs. 2, 3; table 2). Polar subsidiary cells are often missing (table 3; fig. 1). Stomata are situated close to one another usually with one elongate, epidermal cell between them (fig. 2). The presence of this cell is also noticeable on external cuticle surfaces (fig. 5). Two subsidiary cells are most common with three occasionally arising from the division of a lateral subsidiary cell (fig. 2, top). Cuticle on the subsidiary cells is often rugose and longitudinally striated (figs. 1, 6). A deep crease or groove is often seen in this cuticle surface corresponding on the external surface to the Florin ring (fig. 1).

The flange of cuticle between guard cells is relatively thin and slightly rugose (fig. 6). Cuticle on guard cell surfaces is smoother toward the stoma to more rugose toward the lateral, subsidiary cells (fig. 6). A distinct rugose ridge occurs near the lateral edge of the guard cell cuticle. The flange between guard and subsidiary cells is slightly rugose, often with an inrolled edge that partially surrounds the guard cells (figs. 1, 6). Small ribbon-like polar extensions are found but are often broken or curled in preparations revealing their delicate nature (fig. 2).

Epidermal cells surrounding the subsidiary cells are shorter and often broader than those between

stomatal rows (figs. 2, 3). There are usually one or two lateral epidermal cells opposite each lateral subsidiary cell (fig. 2). Cuticular flanges on epidermal cells are not sinuous (fig. 4), and irregular flanges often extend to the hypodermal level (fig. 2, upper left). Cuticle on epidermal surfaces is rugose and pitted (fig. 1; table 3) with extensive channels into the cuticle sometimes visible (fig. 7).

FALCATIFOLIUM FALCIFORME (FIGS. 9–22)

Adult leaves of this species were collected from a coastal area in Sarawak (table 1) from a tree 4 m tall. The external cuticle surface is undulating with epidermal cell outlines clearly visible (fig. 11). Cuticle on epidermal cell surfaces between stomatal bands often shows a large number of small undulations on the surface (figs. 11, 16), while surrounding epidermal cells have relatively smooth cuticular surfaces (figs. 11, 12, 15). Stomatal plugs are fairly solid and appear to be composed of irregular blocks or sheets (figs. 15, 17; table 2). Prominent upraised Florin rings are usually seen surrounding the stoma (figs. 11, 12, 15–17). Rings may be complete or interrupted (fig. 12) and reflect the underlying pattern of the stomatal apparatus. Occasional double rings have been observed (fig. 16). On some areas of a leaf, Florin rings may be lacking (fig. 13), while they are present on other areas of the same leaf.

Stomata are in discontinuous but fairly regular rows that are oriented parallel to the leaf axis (figs. 10, 14; table 2). Polar subsidiary cells are lacking (figs. 10, 14, 19, 20), and cell flanges of lateral subsidiary cells can be found in contact with one another (fig. 9). Stomata are situated close to one

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Figs. 9–22   *Falcatifolium falciforme.* Fig. 9, Inner surface, region of stomatal apparatus with two subsidiary cells and ribbon-like polar extensions (*PE*); × 1,800. Fig. 10, Inner surface, stomatal rows; × 150. Fig. 11, Outer surface, showing Florin rings, epidermal cell outlines and rugose texture of epidermal cells not in stomatal band; × 165. Fig. 12, Outer surface, Florin ring with modified polar regions reflecting the underlying cell structure; × 400. Fig. 13, Outer surface of same leaf as in fig. 12, showing lack of Florin rings or slightly depressed rings; × 135. Fig. 14, Inner surface; stomatal bands showing two and three subsidiary cells per stomatal apparatus; × 270. Fig. 15, Outer surface, Florin rings, stomatal plugs, and smooth cuticle texture on epidermal cell between stomata; × 650. Fig. 16, Outer surface, showing double Florin ring and rugose epidermal cell cuticle outside the stomatal band; × 230. Fig. 17, Outer surface, Florin ring and sheetlike stomatal plug; × 1,350. Fig. 18, Inner view,
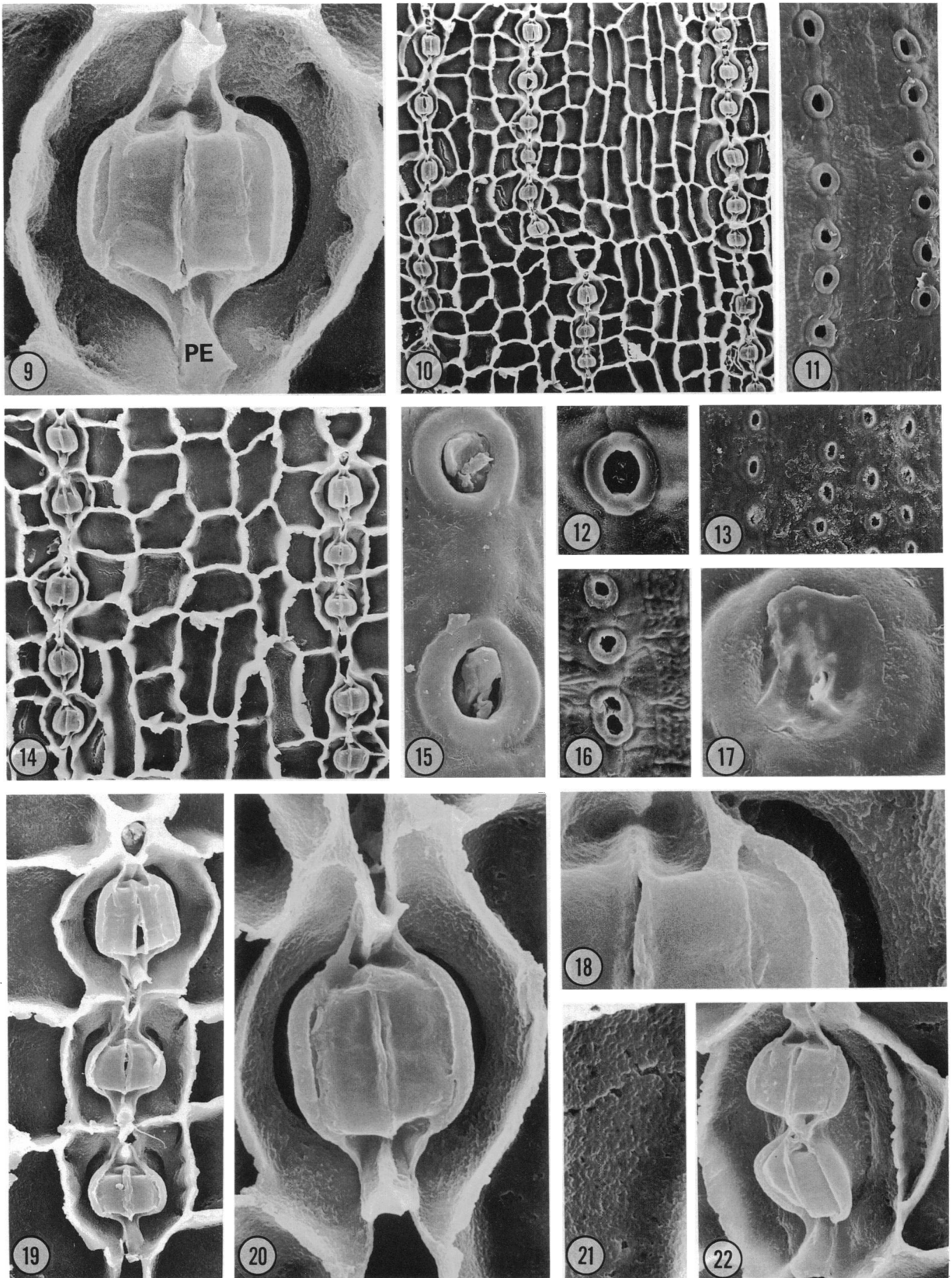
cuticle on guard cell surface; × 3,600. Fig. 19, Inner surface, stomatal row with subsidiary cell wall flanges in contact; × 650. Fig. 20, Inner surface, region of stomatal apparatus; × 1,700. Fig. 21, Inner view, cuticle on epidermal cell surface; × 1,650. Fig. 22, Inner surface, two stomata sharing two subsidiary cells. Note encircling cell at right with cuticle micromorphology similar to its adjacent subsidiary cell; × 875.

another with one to three intervening epidermal cells (figs. 10, 14). Occasionally closely spaced chains of stomata are seen without intervening epidermal cells (fig. 19). Two subsidiary cells are most common with three occasionally arising from the division of a lateral subsidiary cell (fig. 14). One double stomatal apparatus was observed with four guard cells sharing two subsidiary cells (fig. 22). Furthermore, one of these lateral subsidiary cells probably divided longitudinally to produce a third cell with cuticular micromorphology identical to that on lateral subsidiary cells (fig. 22). Cuticle on subsidiary cells is rugose, usually with a thick outer wall flange with lateral undulations (fig. 9). Striations are not common as in *F. angustum,* but a deep crease or groove is often seen in this cuticle surface (figs. 9, 18, 20, 22) corresponding to the external Florin ring.

The flange of cuticle between guard cells is thin and relatively smooth (figs. 18, 20). Cuticle on guard cell surfaces is smooth toward the stoma and slightly more rugose near the subsidiary cell wall flange (fig. 18). A distinct ridge is present on the guard cell cuticle with a prominent, inrolled edge on the flange between guard and subsidiary cells (figs. 9, 18, 20). Polar extensions are pronounced, fairly thick, and often exhibit a central ridge (figs. 9, 18–20).

Epidermal cells surrounding the subsidiary cells are shorter, broader, and more irregular in shape than those between stomatal rows (fig. 10; table 3). If stomatal rows are closely spaced, the intervening epidermal cells are broader and shorter than those between widely spaced rows (fig. 10). Cuticular flanges on epidermal cells are not sinuous (figs. 10, 14), and irregular flanges may extend to the hypodermal level (fig. 14). Cuticle on epidermal cell surfaces is rugose and pitted (fig. 21) but lacks the extensive channeling as in *F. angustum* (fig. 7).

FALCATIFOLIUM GRUEZOI (FIGS. 23–33)

Adult leaves of this species were obtained from an isotype specimen from Oriental Mindoro in the Philippines (table 1). External cuticle surfaces are undulating with epidermal cell outlines partially visible (fig. 28). Cuticle on epidermal cell surfaces between stomatal bands on some leaves shows a number of small undulations (fig. 28) like those in *F. falciforme.* These, however, are not as pronounced as in *F. falciforme* and do not occur on all leaves examined (fig. 30). Stomatal plugs are composed of irregular blocks (fig. 26); or stomata are also completely blocked with cuticle (figs. 28, 30). Prominent Florin rings are often seen around stomata and may be complete or interrupted (figs. 28, 30). They may, however, be lacking especially around plugged stomata (figs. 28, 30).

Stomata are in closely spaced discontinuous

rows that are oriented parallel to the long axis of the leaf (figs. 25, 27; table 2). Polar subsidiary cells are lacking (figs. 23, 27, 29, 32), and the two lateral subsidiary cells may be in contact as in *F. falciforme.* Stomata in a row are usually separated by one to three intervening epidermal cells (figs. 25, 27, 29, 32). Two subsidiary cells are most common, with three occasionally arising from a division of a lateral subsidiary cell (figs. 29, 33). One double stomatal apparatus was observed with four guard cells sharing three subsidiary cells (fig. 33).
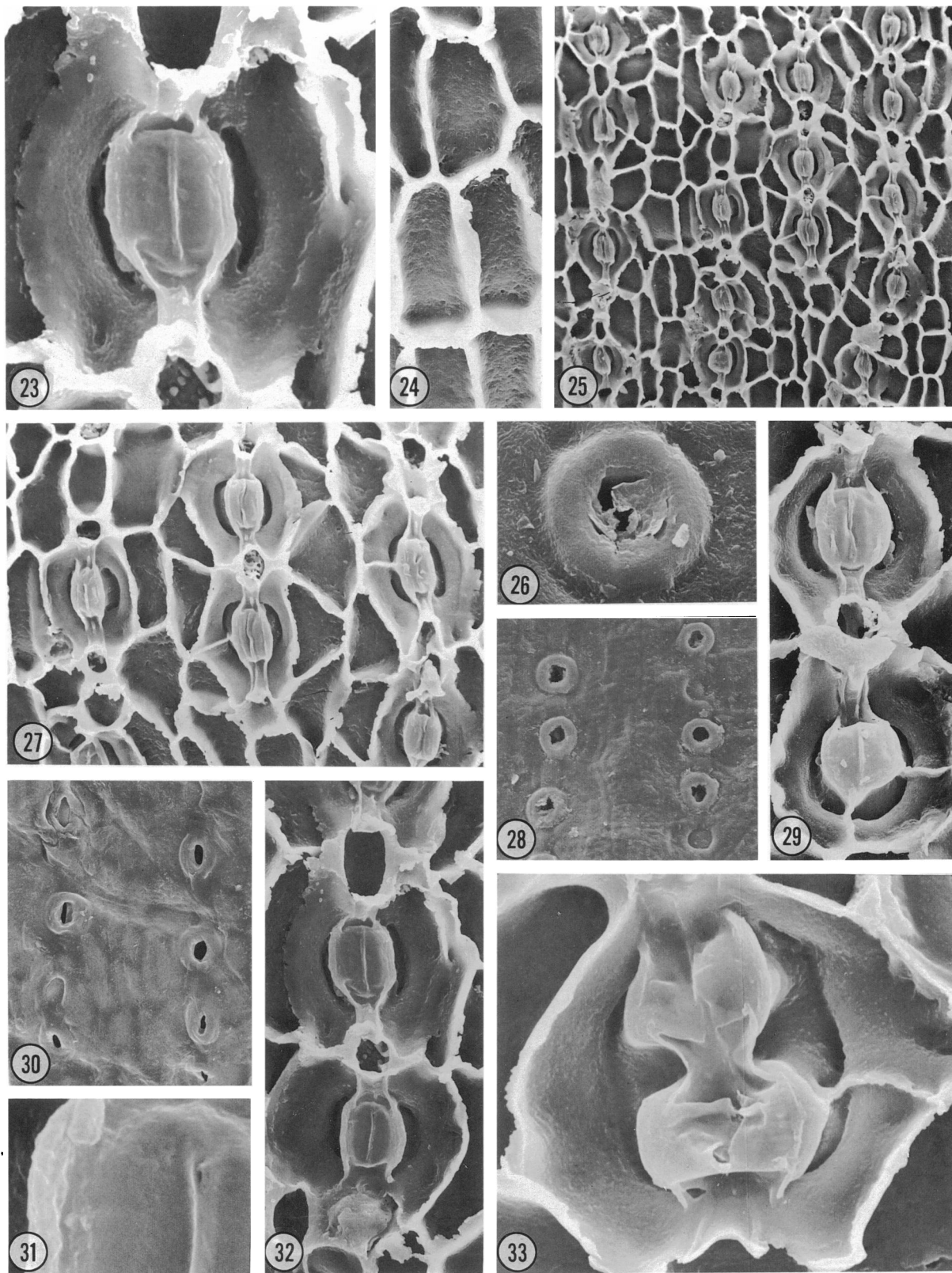
Cuticle on subsidiary cell surfaces usually appears as two broad winglike flanges that often show a thin irregular outer flange (figs. 23, 32). This cuticular flange can also be thicker when it coincides with an epidermal cell wall flange (figs. 27, 29, 33). Occasionally, lateral undulations of this outer flange are seen as in *F. falciforme* (fig. 29). In general, cuticle on subsidiary cell surfaces is smooth to slightly rugose (figs. 23, 33). Striations have not been observed as in *F. angustum,* but a deep crease or groove is present in this cuticle surface (figs. 23, 27, 29, 32, 33) as in other *Falcatifolium* species.

The flange of cuticle between guard cells is thin and relatively smooth (figs. 23, 31) as in *F. falciforme.* Cuticle on guard cell surfaces is smooth toward the stoma and slightly more rugose near the subsidiary cell wall flange (fig. 30). A ridge also occurs on the guard cell cuticle surface as in other *Falcatifolium* species (figs. 23, 33) but is not as prominent. The flange between guard and subsidiary cells also has an inrolled edge (figs. 23, 31), which again is not as prominent as in other species. Polar extensions are pronounced with a central ridge (figs. 23, 27, 29, 33) as in *F. falciforme.*

Epidermal cells are more irregular in shape than in the previously described species but generally more elongate between stomatal rows and shorter when near the stomatal apparatus (figs. 25, 27; table 3). Cuticular flanges on epidermal cells are not sinuous, and irregular flanges may extend to the hypodermal level (figs. 25, 27). Cuticle on epidermal cell surfaces is pitted (fig. 24) but less rugose than *F. angustum* or *F. falciforme.*

FALCATIFOLIUM PAPUANUM (FIGS. 34–45)

Adult leaves of this species were obtained from a tree 8 m high from Menyamya, Morobe, New Guinea (table 1). External cuticle surfaces are undulating; however, underlying epidermal cell outlines are not as visible as in other *Falcatifolium* species (fig. 39). Stomatal plugs are irregular with block-like, granular components (figs. 34, 38, 42). Florin rings are present in some areas of the leaf (figs. 37, 43), while only slightly raised areas occur in others (fig. 39). On some leaves the whole area

Figs. 23–33 *Falcatifolium gruezoi*. Fig. 23, Inner surface, view of stomatal apparatus with two subsidiary cells, × 1,350. Fig. 24, Inner view, cuticle on epidermal cell surfaces; × 650. Fig. 25, Inner surface, stomatal rows; × 235. Fig. 26, Outer surface, Florin ring and stomatal plug; × 1,025. Fig. 27, Inner surface, stomata with two and three subsidiary cells; × 470. Fig. 28, Outer surface showing epidermal cell outlines, Florin rings, and partial rings around plugged stomata; × 225. Fig. 29, Inner surface, stomata with two and three subsidiary cells; × 725. Fig. 30, Outer surface, Florin rings, partial rings, and plugged stomata; × 230. Fig. 31, Inner surface, cuticle on guard cell surfaces; × 4,000. Fig. 32, Inner surface, stomatal row with broad subsidiary cell wall flanges; × 700. Fig. 33, Inner surface, stomatal group with four guard cells sharing three subsidiary cells; × 1,250.
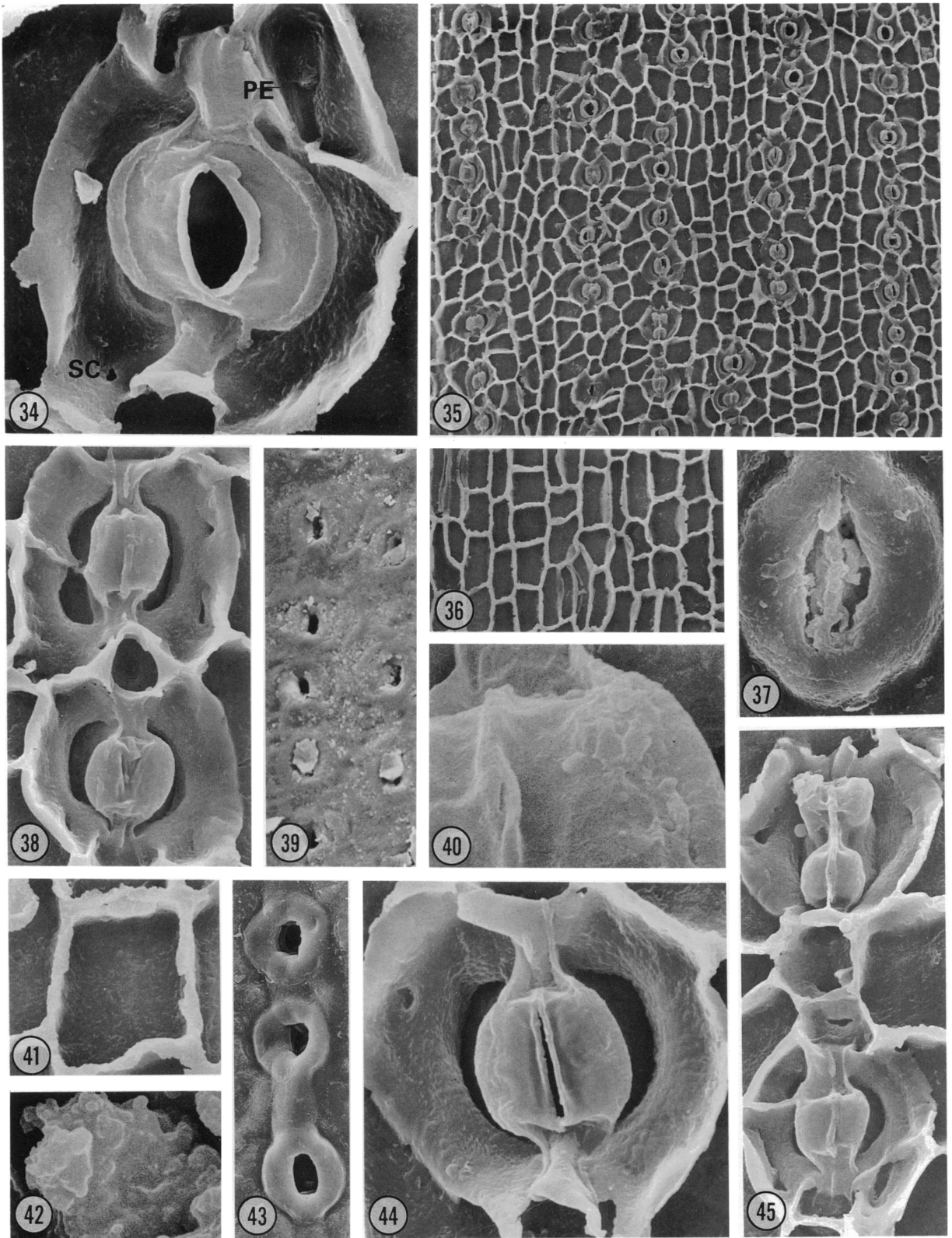
Figs. 34–45 *Falcatifolium papuanum.* Fig. 34, Inner surface, region of stomatal apparatus showing three subsidiary cells (*SC*) and ribbon-like polar extensions (*PE*); × 1,800. Fig. 35, Inner surface, stomatal rows; × 175. Fig. 36, Inner surface, epidermal cell outlines; × 230. Fig. 37, Outer surface, Florin ring and stomatal plug; × 1,400. Fig. 38, Inner surface, stomatal band with two and three subsidiary cells per stomatal apparatus; × 938. Fig. 39, Outer surface, showing stomatal plugs and lack of distinct Florin rings; × 185. Fig. 40, Inner view, cuticle on guard cell surface; × 3,750. Fig. 41, Inner view, cuticle on epidermal cell surface; × 1,000. Fig. 42, Outer surface, stomatal plug morphology; × 5,250. Fig. 43, Outer surface, stomatal row with Florin

of the stomatal row is upraised resulting in a chain of Florin rings (fig. 43).

Stomata in discontinuous but fairly regular rows are oriented parallel to the long axis of the leaf (fig. 35; table 2). As in other *Falcatifolium* species polar subsidiary cells are lacking, and as in *F. falciforme* lateral subsidiary cell wall flanges may be in contact or connected to the polar extension (figs. 34, 38, 44). Stomata are usually separated from one another by one to three intervening epidermal cells. Two subsidiary cells are most common, with three rarely being the result of the division of a lateral subsidiary cell (figs. 34, 38, 45). One stomatal apparatus was observed with four guard cells sharing two subsidiary cells (fig. 45).

Cuticle on subsidiary cell surfaces usually appears as two broad flanges, the outer edges of which may be thin and, as in *F. gruezoi,* thicken when coinciding with an epidermal cell wall flange (figs. 34, 38, 44, 45). Cuticle on subsidiary cells is rugose (figs. 34, 44), sometimes showing lateral undulations (fig. 38) and horizontal striations (fig. 44). A deep crease or groove is usually seen in this cuticle surface (figs. 38, 44) as in other *Falcatifolium* species.

The flange of cuticle between guard cells is usually thin and relatively smooth (figs. 40, 44). Cuticle on guard cell surfaces is smooth to undulating near the stoma and more rugose toward subsidiary wall flanges (figs. 34, 40, 44). A distinct ridge can occur on this cuticle surface (fig. 44) and a prominent inrolled edge of the flange between guard and subsidiary cells (fig. 34). Polar extensions are pronounced, fairly thick, and often exhibit a central ridge (figs. 34, 38, 44, 45).

Epidermal cells surrounding the stomatal apparatus are shorter and often broader than those between stomatal rows (fig. 35; table 3). Cuticular flanges on epidermal cells are not sinuous (fig. 36). Cuticle on epidermal cell surfaces is smooth to slightly rugose (fig. 41); however, pitting or channels have not been observed as in other *Falcatifolium* species.

FALCATIFOLIUM TAXOIDES (FIGS. 46–53)

The external cuticle shows slight undulations (fig. 52). Stomatal plugs are composed of block-like components, and upraised Florin rings have not been observed (fig. 52). The stomata show three levels of cuticular thickening around the stomatal apparatus. The stoma is surrounded by a ring that is in turn surrounded by a higher level ring that may be interrupted at the poles (fig. 52).

The inner sunken ringlike zone corresponds to the position of the Florin ring in other *Falcatifolium* species and the deep crease in subsidiary cell cuticle internally. The outer ring corresponds to the outer edge of the subsidiary cell wall cuticle internally (e.g., fig. 46). The leaves observed in this study show deep creases in the subsidiary cell wall cuticle and, therefore, what might be interpreted as a partially sunken Florin ring externally (fig. 52).

Stomatal rows are discontinuous, fairly regular, with stomata oriented parallel to the long axis of the leaf (figs. 47, 49; table 2). Polar subsidiary cells are usually lacking, with two subsidiary cells being the most common condition (figs. 47, 49). However, during the present study we found a few stomata with three or four subsidiary cells (fig. 51). Stomata are usually separated by one to three intervening epidermal cells (figs. 47, 49). On some parts of a leaf an epidermal cell in the terminal position may have the appearance of a polar subsidiary cell, but an intermediate morphology of the cuticle is present (fig. 53). In one leaf a pair of stomata are separated by an epidermal cell but have adjoining subsidiary cells (fig. 51). One of the stomatal apparati is larger than the other, and the two lateral subsidiary cells have divided to produce four, resulting in an unusual morphology for the pair (fig. 51).

Cuticle on subsidiary cell surfaces is rugose and may show longitudinal striations (figs. 46, 53), as in *F. angustum.* The outer subsidiary cell wall flange is usually very irregular (figs. 46, 51, 53). A deep crease or groove occurs in this cuticle (Stockey and Ko 1988) as in other *Falcatifolium* species (figs. 46, 53). When these grooves are shallow, a rugose ornamentation can be seen on the subsidiary cell surface (figs. 48, 51). Irregular peaks of cuticle also occur in this region (fig. 51).

The flange of cuticle between guard cells is thin and relatively smooth to slightly rugose (fig. 48). Cuticle on guard cell surfaces is smooth near the stoma with slight undulations grading to rugose approaching subsidiary cells (figs. 46, 48). A ridge is present on the guard cell cuticle as in other *Falcatifolium* species (figs. 46, 48, 51, 53). The cuticular flange between guard and subsidiary cells has an inrolled edge (fig. 48). Polar extensions are delicate, sometimes elongate (fig. 51), with a central ridge (figs. 46, 53).

Epidermal cells are distinctly shorter and broader when in contact with a stomatal row and more elongate between rows (figs. 47, 49; table 3). Cuticular flanges on epidermal cells are not

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rings and raised cuticle on polar epidermal cells; × 525. Fig. 44, Inner surface, region of stomatal apparatus showing two lateral subsidiary cells; × 150. Fig. 45, Inner surface, stomatal row with four guard cells sharing two subsidiary cells and abnormal subsidiary cell divisions on lower stomatal apparatus; × 725.
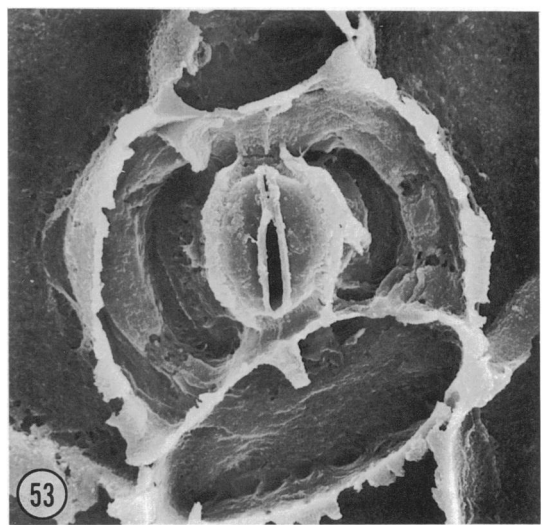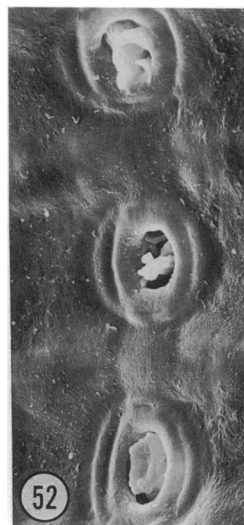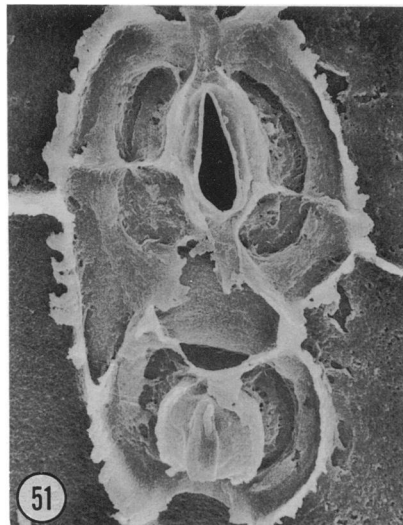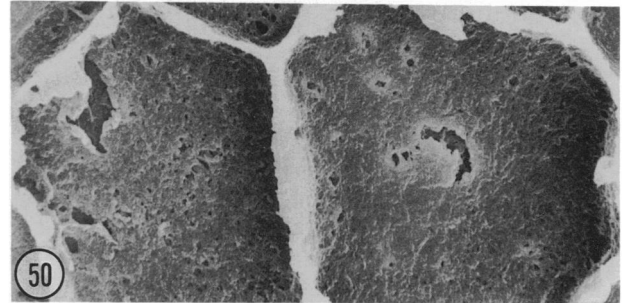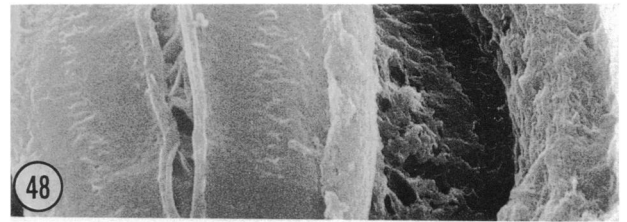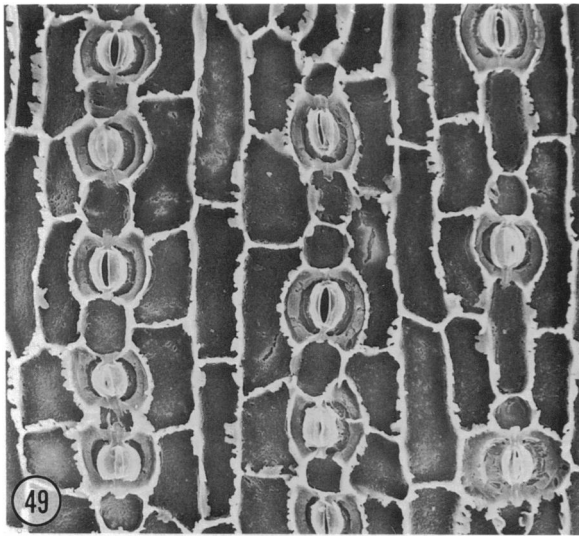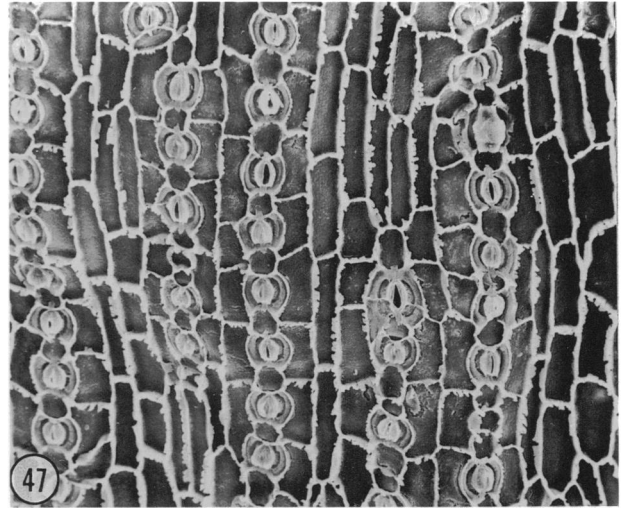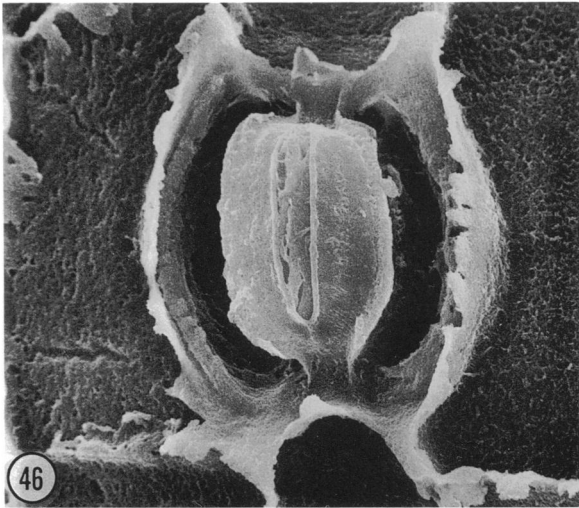
Figs. 46-53 *Falcatifolium taxoides.* Fig. 46, Inner surface, region of the stomatal apparatus showing two subsidiary cells; × 1,400. Fig. 47, Inner surface, stomatal rows; × 150. Fig. 48, Inner view, cuticle on guard and subsidiary cell surfaces; × 3,000. Fig. 49, Inner surface, stomata with two and three subsidiary cells; × 270. Fig. 50, Inner view, cuticle on epidermal cell surfaces; × 1,500. Fig. 51, Inner surface, stomatal pair sharing seven subsidiary cells; × 750. Fig. 52, Outer surface, showing sunken Florin rings and stomatal plugs; × 550. Fig. 53, Inner surface, stomatal apparatus with three subsidiary cells and one polar epidermal cell; × 1,750.

sinuous, and irregular flanges may extend to the hypodermal level (figs. 47, 49, 50). Cuticle on epidermal cell surfaces is rugose, pitted (fig. 50), and may be channeled as in *F. angustum.*

Discussion

With the present study of *Falcatifolium* we are now able to characterize the cuticle micromorphology of all five species within the genus. The genus itself is characterized micromorphologically by undulating outer cuticle surfaces that may reflect the underlying epidermal cell outlines; stomatal plugs composed of irregular blocks; fairly regular stomatal rows; stomata separated by one to three epidermal cells; two lateral subsidiary cells present, with polar subsidiary cells usually lacking; a deep crease in subsidiary cell cuticle; smooth to slightly undulating cuticle on guard cell surfaces near the stoma; a ridge on guard cell cuticle; thin cuticular flanges between guard cells; rolled cuticular flanges between guard and subsidiary cells; polar extensions; nonsinuous epidermal cell outlines with cuticle extending to the hypodermis; more elongate epidermal cells between stomatal rows than within rows; and usually granular epidermal cell surfaces.

The presence or absence of Florin rings cannot be used as a diagnostic feature within the genus *Falcatifolium* since on one leaf this character varies considerably. Upraised Florin rings do not occur in *F. taxoides,* but sunken rings do occur in some cases. In *F. falciforme, F. gruezoi,* and *F. papuanum* they are present on some areas of a leaf and absent on others, while in all leaves examined of *F. angustum* they were present. While this feature is consistently present within other genera of conifers, e.g., *Agathis* (Page 1980; Stockey and Atkinson 1988), and is diagnostic for those genera, this is not so with *Falcatifolium.*

One of the micromorphological characters that appears to be most useful for taxonomic purposes is subsidiary cell cuticle micromorphology. Vertical striations appear in *F. angustum* and *F. taxoides* and horizontal striations in *F. papuanum.* Granularity varies between the taxa, with *F. gruezoi* having the smoothest subsidiary cell wall surface flanges. Thickness and outline of this cuticle appear to be taxonomically significant in the five species. While all taxa show creases or grooves near the guard cells, only in the New Caledonian species, *F. taxoides,* are they shallow enough to reveal peaks of cuticle and a granular ornamentation in the groove. Similar cuticle in this zone was reported in the Araucariaceae in *Araucaria humboldtensis* Buchholz (Stockey and Ko 1986), also from New Caledonia.

Cuticle on epidermal cell surfaces is smoothest in *F. papuanum,* then *F. gruezoi,* slightly more granular in *F. falciforme,* and distinctly pitted and channeled in *F. taxoides* and *F. angustum.* Cuticle on guard cell surfaces, while generally similar, also varies in rugosity, with *F. gruezoi, F. falciforme,* and *F. papuanum* being generally smoother over all, while *F. angustum* and *F. taxoides* are more rugose. Externally, epidermal cell undulations may be slightly diagnostic. Many fine undulations occur on the surfaces of epidermal cells between stomatal rows in *F. falciforme* and fewer in *F. gruezoi.* These undulations are lacking in the other species.

The genus *Falcatifolium* shows many similarities in cuticle micromorphology to *Dacrydium,* from which it was originally segregated (de Laubenfels 1969). Stomata, as in most Podocarpaceae (Florin 1931; Greenwood 1987), are oriented parallel to the long axis of the leaf; polar subsidiary cells are absent. There are deep creases in subsidiary cell cuticle, and polar extensions occur (Stockey and Ko 1990). However, *Dacrydium* species so far examined have sinuous epidermal cell outlines and striations at the bases of epidermal cell buttresses (Wells and Hill 1989a; Stockey and Ko 1990). Smooth epidermal cell cuticle (Stockey and Ko 1990) as well as granular surfaces (Wells and Hill 1989a) have been recorded and Florin rings, while lacking in the New Caledonian species examined (Stockey and Ko 1990), are reported to be present but variable within the genus (Wells and Hill 1989a).

Among the broad-leaved podocarpaceous taxa that may be compared micromorphologically to *Falcatifolium,* the genus *Acmopyle* Pilger has polar subsidiary cells in greater numbers and smooth epidermal cell surface cuticle and lacks Florin rings (Stockey and Ko 1988). *Nageia* Gaertner (= *Decussocarpus* de Laubenfels) have four to six subsidiary cells, usually with two polar subsidiaries (Stockey and Ko 1988). The genus *Prumnopitys* Phil. shows some similarities to *Falcatifolium,* often lacking polar subsidiary cells, but subsidiary cell cuticle is quite distinctive with lateral striations and a very rugose texture (Stockey and Ko 1988).

Imbricate-leaved taxa were recently described micromorphologically by Wells and Hill (1989a). *Dacrycarpus* (Endl.) de Laubenfels leaves have stomata parallel to the long axis of the leaf as in *Falcatifolium;* however, these stomata are interpreted as paratetracytic, i.e., with two elongate lateral subsidiary cells parallel to the guard cells and two narrow polar cells (Dilcher 1974). While it is difficult to assess the epidermal cell surface morphology from the limited number of photographs presented by Wells and Hill (1989a), it appears that at least some of the polar subsidiary cells in *Dacrycarpus dacrydioides* (Rich.) de Laubenfels, e.g., have epidermal cell micromorphology as in *Falcatifolium* reported here. Apparently, the presence of Florin rings is also variable in

this genus (Wells and Hill 1989*a*). Polar extensions occur in *Dacrycarpus* that are very similar to those reported in *Falcatifolium* species here. From the description presented by Wells and Hill (1989*a*), we cannot distinguish this cuticle from that of *Falcatifolium*. An amplification of the information on this taxon is required for further comparison.

The genera *Halocarpus* Quinn, *Lepidothamnus* Phil., and *Lagarostrobus* Quinn have randomly oriented amphicyclic stomata (Wells and Hill 1989*b*) and are, thus, quite different than the regularly oriented stomata of *Falcatifolium* described here. *Microcachrys* Hook. f. ex Hook., the Tasmanian endemic, does have regular stomatal rows but shows irregularly shaped subsidiary cells, many of which are shared by adjacent stomata, and lacks polar extensions (Wells and Hill 1989*a*). Cuticle of *Microstrobos* Garden et Johnson is similar to that of *Microcachrys* with shared subsidiary cells present, and one of the species, *Microstrobos fitzgeraldii* (F. Muell.) Gard. et Johns. also lacks polar extensions (Wells and Hill 1989*a*). *Parasitaxus* de Laub., the New Caledonian parasitic conifer, has irregularly shaped subsidiary cells, with variable orientation to the guard cells, and shows some similarity to *Lepidothamnus* (Wells and Hill 1989*a*). Leaves of all of these taxa, however, can also be easily separated from *Falcatifolium* on the basis of their external morphology.

Fossil leaves of *Falcatifolium* have been reported from the Miocene of Antarctica (Zastawniak 1981) and the Eocene of Australia (Greenwood 1987). The Antarctic material is impression material only; thus, cuticle has not been described.

Fossil cuticles of *Falcatifolium* were described by Greenwood (1987). *Falcatifolium australis* Greenwood, unlike the extant species, has sinuous epidermal cell outlines, leaves that are generally smaller than living taxa, and stomata mostly on the abaxial surface. Greenwood (1987) compares *F. australis* to *F. papuanum* with respect to stomatal apparatus morphology and to *F. falciforme* based on vegetative morphology.

This study, however, utilized only light microscopy, and certain cuticular features remain obscure using that mode of investigation. The lack of polar subsidiary cells reported in the present study for *Falcatifolium* is based on the cuticular micromorphology of cells in the polar region. The epidermal cells in the position of polar subsidiary cells have a morphology like that on the surrounding epidermal cells. The same situation occurs in species of *Podocarpus* L. Herit. ex Pers. (personal observation) and sometimes in *Prumnopitys* (Stockey and Ko 1988) and *Dacrydium* (Stockey and Ko 1990). Thus, the small cells in the position of polar subsidiary cells are, in fact, epidermal cells based on micromorphology.

We hope that studies of extant conifer cuticles at the micromorphological level will serve as the basis for comparison in future paleobotanical work (e.g., Wells and Hill 1989*b*). Within the Podocarpaceae and Araucariaceae, cuticle micromorphology has already proven to be useful in the systematic description of several fossil Southern Hemisphere taxa (Cantrill 1989; Wells and Hill 1989*b*; Hill and Carpenter 1991). Since many extant podocarpaceous taxa have not yet been described, it is critical that they be well documented for future reference.

Acknowledgments

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