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CUTICLE MICROMORPHOLOGY OF *PODOCARPUS*, SUBGENUS *PODOCARPUS*, SECTION *SCYTOPODIUM* (PODOCARPACEAE) OF MADAGASCAR AND SOUTH AFRICA

Ruth A. Stockey,[1,]* Brenda J. Frevel,* and Philippe Woltz†

*Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada; and †Laboratoire de Morphogenèse Végétale, I.M.E.P. CNRS-URA 1152, Université d'Aix, Marseille III, Centre St. Jérôme, France

Cuticle micromorphology of leaves from seven species and three varieties of the conifer genus *Podocarpus* subgenus *Podocarpus* section *Scytopodium* from South Africa and Madagascar was studied with scanning electron microscopy. External and internal features of abaxial and adaxial cuticles are characterized for all taxa and are compared with other known *Podocarpus* species. External cuticles exhibit Florin rings and stomatal plugs with underlying epidermal cell outlines usually visible. Leaves are hypostomatic and stomata occur in discontinuous but fairly regular rows in most species. Stomata are oriented parallel to the long axis of the leaf and usually lack polar subsidiary cells. From two to six subsidiary cells occur, with two or three being the most common. Internal cuticle on subsidiary cell surfaces is granular to rugose, usually with a deep groove corresponding to the external Florin ring. Cuticle on guard cell surfaces is granular or rugose to pitted, and prominent polar extensions are present in all species. Epidermal cell outlines are undulating and cuticle on epidermal cell surfaces is granular to rugose and pitted. The most useful characters to distinguish species of this section are the micromorphology of cuticle on the guard cell and subsidiary cell surfaces, epidermal cell shapes, and sometimes the length of polar extensions.

Introduction

The genus *Podocarpus* L'Heritier ex Persoon, today containing 99 recognized species, is the largest in the family Podocarpaceae (Silba 1984, 1986, 1990; de Laubenfels 1985, 1992; de Laubenfels and Silba 1988*a*, 1988*b*). The taxonomy of this genus of mostly Southern Hemisphere conifers has undergone extensive revisions (Pilger 1926; Wasscher 1941; Buchholz and Gray 1948*a*, 1948*b*, 1948*c*; Gray and Buchholz 1948, 1951*a*, 1951*b*; Gray 1953*a*, 1953*b*, 1955, 1956, 1958, 1960, 1962, 1969; de Laubenfels 1969, 1971, 1972*a*, 1972*b*, 1978, 1985, 1988, 1992; Quinn 1982; Page 1988). The need for revision of the genus prompted both the deletion and the addition of several taxa (de Laubenfels 1985). De Laubenfels (1985) currently divides the genus into two subgenera and 18 sections. Subgenera *Podocarpus* and *Foliolatus* contain nearly equal numbers of species in this classification scheme.

The section *Scytopodium* of subgenus *Podocarpus* contains species from the highlands of Madagascar and Tanganyika and eastern South Africa (de Laubenfels 1985). These taxa have been studied since the early 1900s (Laurent 1915; Lecomte 1922; Perrier de la Bathie 1927; Humbert 1955; Humbert and Cours-Darne 1965). De Laubenfels (1985) recognizes only five species in this section of the genus, in disagreement with the assessment of several authors (Woltz 1969*a*, 1969*b*, 1971, 1973, 1986; Gaussen 1974; Gaussen and Woltz 1975; Marguerier and Woltz 1977; Page 1988). Several taxa have been examined using light microscopy (Townrow 1965; Woltz 1973, 1986; Schoonraad and Van Der Schijff 1974; Greenwood 1987), but cuticle micromorphology has not been examined. We have examined cuticle micromorphology of seven species and three varieties within this section, several of which are unrecognized or listed as synonyms by de Laubenfels (1985).

The utility of cuticle micromorphological characters in conifer taxonomy has been shown in several families including the Taxodiaceae (Alvin and Boulter 1974), Cupressaceae (Alvin et al. 1982), Araucariaceae (Stockey and Ko 1986; Stockey and Atkinson 1993), and several taxa of the Podocarpaceae (Stockey and Ko 1988, 1990; Wells and Hill 1989; Hill and Carpenter 1991; Hill and Pole 1992; Pole 1992*a*, 1992*b*, 1993; Stockey et al. 1992, 1995; Stockey and Frevel 1997). In this article we examine the cuticle micromorphology of section *Scytopodium* to characterize this section of genus *Podocarpus* and to determine whether cuticle micromorphology can provide useful characters in distinguishing the species within this section. We compare these results with those described in studies of fossil *Podocarpus*.

Material and Methods

Adult leaves from all species were taken from herbarium material (table 1). All leaves were rehydrated and cut into sections with the leaf margin intact, leaving both abaxial and adaxial epidermis attached for cuticle examination. All preparations were immersed in 20% chromium trioxide solution for 96 h (Alvin and Boulter 1974; Stockey and Ko 1986).

Cuticles were washed in distilled water, air-dried, and mounted on stubs with silver conductive paint. Both inner and outer surfaces of adaxial and abaxial cuticles were examined by SEM. Specimens were sputter-coated with 150 Å Au on a

[1] Author for correspondence and reprints. E-mail ruth.stockey@ualberta.ca.

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Table 1

***Podocarpus* L'Heritier ex Persoon Section *Scytopodium* de Laubenfels—Material Examined in This Study**

Species	Herbarium	Voucher	Source
P. capuronii de Laubenfels	P	11566 Capuron	Antanimena
P. henkelii Stapf ex Dallimore et Jackson	MARSJ	1968 Woltz	Kirstenboch Newlands, S. Afr.
P. humbertii de Laubenfels	P	24741 Humbert	Anjanaharibe
P. madagascariensis var. *madagascariensis* Baker	P	5891 Decary	Ambatolaona
P. madagascariensis var. *procerus* de Laubenfels	P	11774 Capuron	Bemangidy
P. madagascariensis var. *rotundus* Laurent	P	15359 Perrier de la Bathie	Tsaratanana
P. perrieri Woltz	P	17109 Perrier de la Bathie	Andringitra
P. rostratus Laurent	P	2303 Morat	Tsaratanana
P. woltzii Gaussen	TAN	27065 Service Forestier	Tsaratanana

Note. All material collected in Madagascar unless otherwise indicated.

Nanotek sputter-coater and examined with a Cambridge Stereoscan 250 at 20 kV.

From two to 10 leaves of each species were examined with SEM depending on availability (table 1). All stubs are deposited in the University of Alberta Paleobotanical Collections (UAPC-ALTA). Stomatal distribution was determined by the examination of several leaves. The descriptions disregard obvious debris on cuticle surfaces. All 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

Podocarpus capuronii (*Fig. 1*)

Adult leaves were obtained from a shrub in central Madagascar in the Antanimena forest, Ambatomenaloha Mountains, west of Itremo. These were part of the holotype specimen (table 1). Leaves of this species are linear, with acute tips and decurrent bases, 2.5–5 cm long, 2.5–3.5 mm wide, with prominent midribs and revolute margins (de Laubenfels 1971). Stomata have been observed only on abaxial surfaces (Woltz 1973).

The external cuticle surface is undulating, with outlines of underlying epidermal cells visible on both leaf surfaces (figs. 1.4, 1.5). Distinct Florin rings (Buchholz and Gray 1948*a*) are visible surrounding the stomatal apparatus (fig. 1.4) These rings may be slightly sunken into the surrounding cuticle that covers epidermal cells (fig. 1.4). Stomatal plugs occur and have small globular or rodlike components (fig. 1.6).

Inner cuticle surfaces show stomata in fairly regular but discontinuous rows (fig. 1.3). Stomata are oriented parallel to the long axis of the leaf (figs. 1.2, 1.3). The shape of the stomatal apparatus varies depending on its proximity to others, with most stomata being elliptical in outline (fig. 1.2). Two lateral subsidiary cells are most common, with three or four being the result of the division of these lateral subsidiary cells (figs. 1.2, 1.10). Polar subsidiary cells are usually absent with cells in the polar region that have ornamentation similar to the surrounding epidermal cells (figs. 1.1, 1.2). Unusual shapes of stomata occur when subsidiary cells are in contact with one another (figs. 1.2, 1.10).

Cuticle on the outer cell wall flange of subsidiary cells is thin and irregular (figs. 1.1, 1.2, 1.8, 1.10). That on the surface of subsidiary cells is rugose and has a central, pitted groove where the subsidiary cell extends toward the leaf surface (figs. 1.1, 1.8, 1.10). Vertical striations sometimes occur on the subsidiary cell wall flanges (figs. 1.2, 1.10).

The cuticular flange between guard cells is thick and rugose (figs. 1.1, 1.8). Polar extensions are very long in this species, extending out over the polar epidermal cells, and show a central flange corresponding to the line of guard cell separation (figs. 1.1, 1.8, 1.9). Cuticle on the guard cell surface is rugose and may show some deeper pits (figs. 1.1, 1.8). The flange of cuticle between guard and subsidiary cells is thick and usually appears rolled and slightly rugose (figs. 1.1, 1.8).

Epidermal cells usually are rectangular in shape, often longer than broad on adaxial surfaces (fig. 1.11). On abaxial surfaces they are more elongate between stomatal rows (fig. 1.3). On adaxial leaf surfaces epidermal cells are slightly undulating, with prominent buttresses (fig. 1.11). Buttressing is not as pronounced on abaxial surfaces, and cell wall flanges show a more irregular edge (fig. 1.2). Cuticle on the epidermal cell surfaces is rugose (fig. 1.7), with abaxial cuticles showing slightly more rugose surfaces with creases (fig. 1.2, bottom center).

Podocarpus henkelii (*Fig. 2*)

Adult leaves were obtained from the National Botanic Gardens of South Africa, Kirstenboch, Newlands, near Capetown (table 1). Leaves are opposite to subopposite, falcate, with a prominent midrib, attenuate apex, and short petiole, 7–16 cm long and 8–13 mm wide (Schoonraad and Van Der Schijff 1974; Silba 1986; and R. A. Stockey, personal observation). Stomata were observed only on abaxial surfaces (Schoonraad and Van Der Schijff 1974).

The external cuticle surfaces are only slightly undulating and, unlike *P. capuronii*, do not show distinct underlying epidermal cell outlines (fig. 2.14). Florin rings are present but have a low relief (fig. 2.14). Stomatal plugs are present, fairly solid, and show globular components (fig. 2.17).

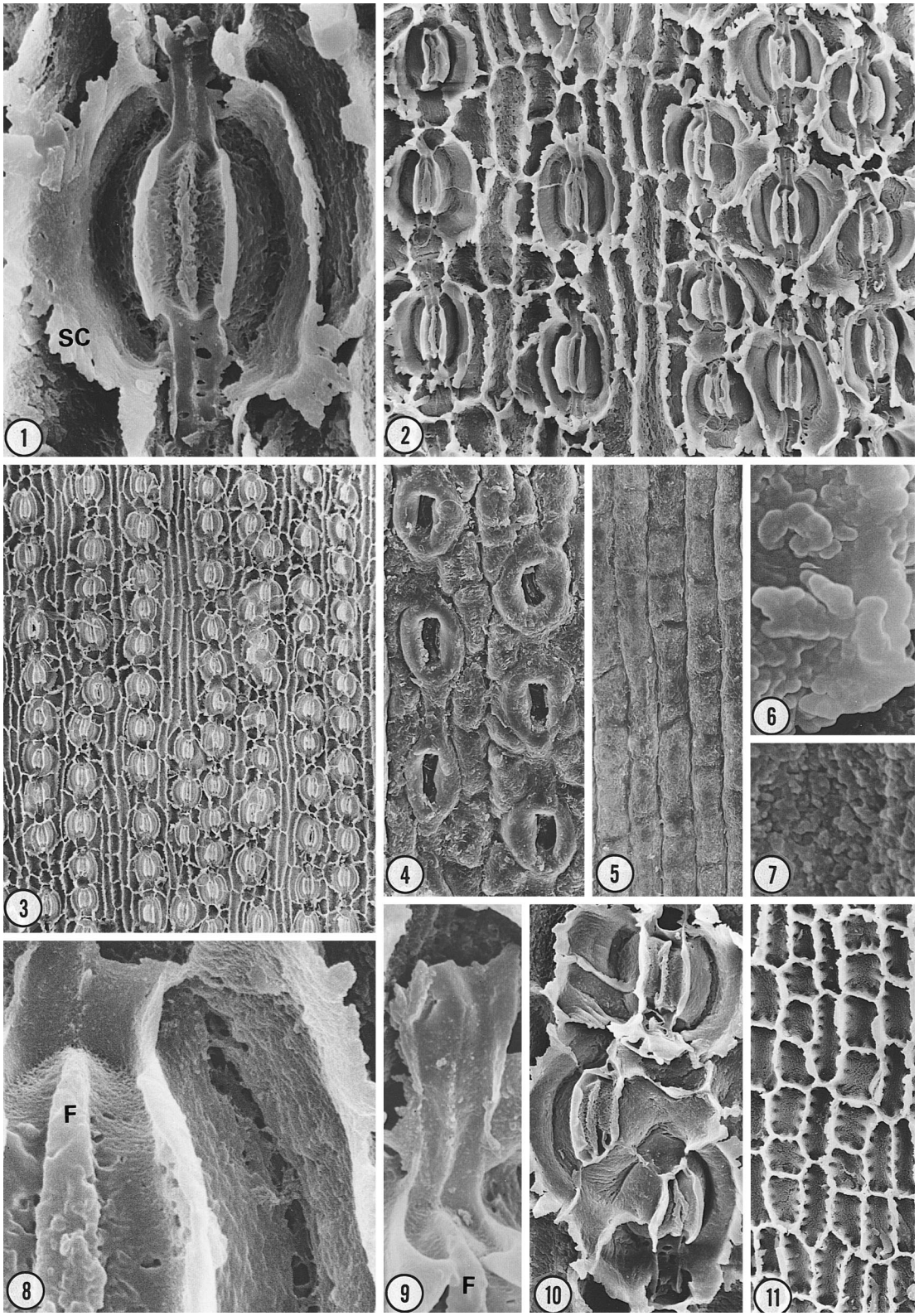

Fig. 1 *Podocarpus capuronii*. Fig. 1.1, Inner view, abaxial cuticle on stomatal apparatus; × 1565. Fig. 1.2, Inner view, abaxial surface, showing variable subsidiary cell numbers; × 460. Fig. 1.3, Inner view, abaxial surface, showing stomatal rows; × 150. Fig. 1.4, Outer view, abaxial surface, showing Florin rings and underlying epidermal cell outlines; × 390. Fig. 1.5, Outer view, adaxial surface, showing underlying epidermal cell outlines; × 390. Fig. 1.6, Outer view, abaxial surface, showing stomatal plug components; × 3680. Fig. 1.7, Inner view, adaxial cuticle on epidermal cell surface; × 5060. Fig. 1.8, Inner view, abaxial cuticle on stomatal apparatus; × 4140. Fig. 1.9, Inner view, abaxial surface, showing elongate polar extensions; × 2530. Fig. 1.10, Inner view, abaxial surface, showing closely spaced stomata sharing subsidiary cells and the resulting unusual subsidiary cell shapes; × 690. Fig. 1.11, Inner view, adaxial surface, showing sinuous epidermal cell outlines; × 345. *F*, flange of cuticle between guard cells; *SC*, subsidiary cell.

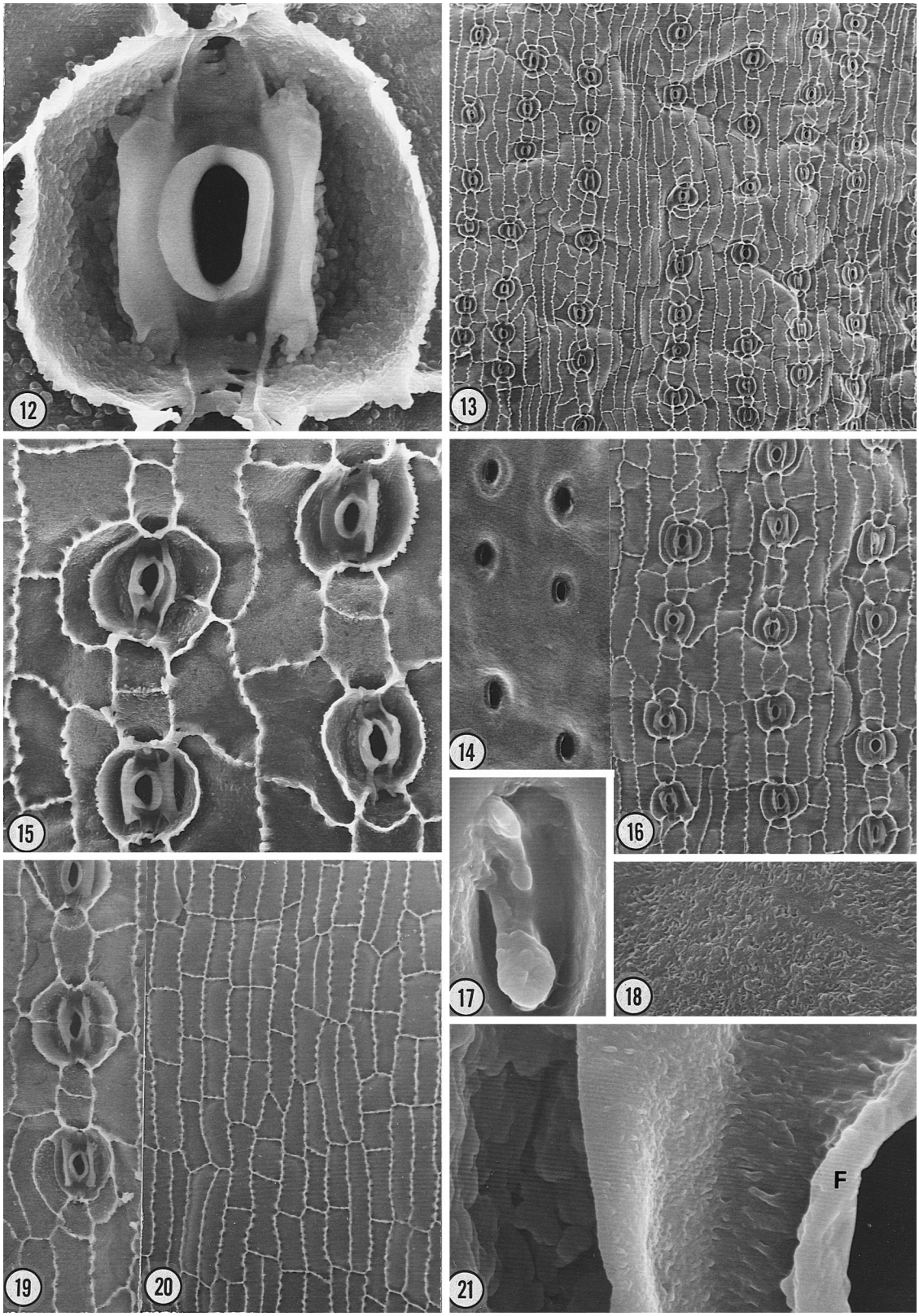

Fig. 2 *Podocarpus henkelii*. Fig. 2.12, Inner view, abaxial cuticle on stomatal apparatus; ×1770. Fig. 2.13, Inner view, abaxial surface, showing stomatal rows; ×95. Fig. 2.14, Outer view, abaxial surface, showing Florin rings with little relief and relatively smooth cuticle surface; ×190. Fig. 2.15, Inner view, abaxial surface, showing variation in subsidiary cell number and arrangement of epidermal cells near stomata; ×465. Fig. 2.16, Inner view, abaxial surface, showing stomatal rows and sinuous epidermal cell outlines; ×170. Fig. 2.17, Outer view, abaxial surface, showing stomatal plug; ×1770. Fig. 2.18, Inner view, adaxial cuticle on epidermal cell surface; ×3720. Fig. 2.19, Inner view, abaxial surface, showing the presence of encircling cells around some stomata; ×310. Fig. 2.20, Inner view, adaxial surface, showing sinuous epidermal cell outlines; ×190. Fig. 2.21, Inner view, abaxial cuticle on subsidiary and guard cell surfaces; ×310. *F*, flange of cuticle between guard cells.

Inner cuticle surfaces show widely spaced stomatal rows with sometimes three to four epidermal cells between stomata of a row (figs. 2.13, 2.16). We have not observed stomatal crowding or the sharing of subsidiary cells in this species. Stomata are oriented parallel to the long axis of the leaf. The stomatal apparatus is circular to elliptical in shape, with its widest dimensions laterally (figs. 2.12, 2.13, 2.15, 2.16, 2.19). Two subsidiary cells are most common, with three and four being the result of the divisions of lateral subsidiary cells (figs. 2.12, 2.15, 2.16, 2.19). Polar subsidiary cells usually are absent, and lateral subsidiary cells extend toward the polar regions (fig. 2.15). Frequently there are crescent-shaped encircling cells surrounding the stomatal apparatus (figs. 2.15, 2.16, 2.19).

Cuticle on the outer cell wall flange of subsidiary cells is thick and irregular (figs. 2.12, 2.15) but not as extensive as in *P. capuronii*. The surface of subsidiary cells is very rugose, with globular cuticle in the central crease or groove where the subsidiary cell extends toward the leaf surface (figs. 2.12, 2.21).

The cuticular flange between guard cells is thick and smooth to slightly rugose (figs. 2.12, 2.21). Polar extensions are smooth, broad, and thin (fig. 2.12). The cuticle on the guard cell surfaces is slightly rugose, but the large pits present in *P. capuronii* have not been observed in this species (fig. 2.21). The flange of cuticle between guard and subsidiary cells is thick, fairly smooth, and rolled as in *P. capuronii* (figs. 2.12, 2.21). Often these flanges stand out laterally, giving the inner portion of the cuticle on the stomatal apparatus a rectangular shape (figs. 2.12, 2.19).

Epidermal cells are rectangular in shape and more elongate than those in *P. capuronii* (figs. 2.13, 2.16, 2.20). Cells are more elongate between stomatal rows on abaxial surfaces (fig. 2.13). Epidermal cell outlines are undulating on both leaf surfaces (figs. 2.13, 2.15, 2.16, 2.20). Cuticle on epidermal cell surfaces is slightly rugose and is similar on both leaf surfaces (fig. 2.18).

Podocarpus humbertii (*Fig. 3*)

Adult leaves were obtained from a small tree from the basin of the Lokoho River, northwest of Andapa, Massif de l'Anjanaharibe, in northern Madagascar (table 1). Leaves are oval, with bluntly acute apices and short petioles, with revolute margins and prominent midveins, 8–12 mm long, 2.5–5.5 mm wide (de Laubenfels 1971). Stomata were observed only on abaxial surfaces.

The external cuticle surface is distinctly undulating, with the outlines of underlying epidermal cells visible (fig. 3.24). Stomata are surrounded by sunken, prominent Florin rings as in *P. capuronii* (fig. 3.24). Stomatal plugs occur and appear as solid sheets or globular components (fig. 3.27).

Inner cuticle surfaces show discontinuous stomatal rows (figs. 3.23, 3.26). These are not as widely spaced as those reported for *P. henkellii*. Stomata are oriented parallel to the long axis of the leaf (fig. 3.23). The stomatal apparatus is circular to elliptical in outline and, like that found in *P. henkelii*, is broader than tall (figs. 3.22, 3.26, 3.30). Two and three subsidiary cells are most common, with three and four being the result of the division of lateral subsidiary cells (figs. 3.22, 3.26, 3.30). Occasionally, polar subsidiary cells are observed (fig. 3.30, upper right). Not much stomatal crowding has been observed, but subsidiary cells of adjacent rows sometimes border one another (fig. 3.23).

Cuticle on the outer cell wall flange of subsidiary cells is thick, very irregular, and frilled on most stomata (figs. 3.22, 3.26, 3.30). The surface of subsidiary cells is rugose and pitted with occasional horizontal creases (figs. 3.22, 3.29, 3.30). A deep groove occurs in this cuticle surface where each subsidiary cell extends toward the leaf surface (figs. 3.22, 3.29).

The cuticular flange between guard cells is thick and rugose (figs. 3.22, 3.29). Polar extensions are elongate and often flare outward from the center of the stomatal apparatus (figs. 3.22, 3.30). The cuticle on guard cell surfaces is rugose and pitted (fig. 3.29) and sometimes shows an oval-shaped ridge (fig. 3.22). The flange of cuticle between guard and subsidiary cells is thick and inrolled and sometimes is very broad (figs. 3.22, 3.29, 3.30).

Epidermal cells can be irregular in shape but usually are rectangular in outline, especially between stomatal rows (figs. 3.23, 3.25, 3.26). On both abaxial and adaxial surfaces, epidermal cells can be broader than they are long (figs. 3.25, 3.26). In general, more elongate epidermal cells are seen between stomatal rows on abaxial surfaces (fig. 3.23), but this feature is distinctly different from epidermal cell shapes in *P. capuronii* and *P. henkelii*. On adaxial leaf surfaces, epidermal cells can be broader than long, and often pairs of epidermal cells are oriented parallel to the long axis of the leaf and perpendicular to the long axis of other epidermal cells (fig. 3.25). Epidermal cell wall flanges are undulating on both leaf surfaces, with prominent buttresses present (figs. 3.25, 3.30). Cuticle on epidermal cell surfaces is rugose and pitted on both sides of the leaf (fig. 3.28).

Podocarpus madagascariensis *var.* madagascariensis (*Fig. 4*)

Adult leaves were obtained from the east side of the high plateaus near Ambatolaona in central Madagascar (table 1). Leaves are helically arranged, narrow, linear, reflexed with prominent midribs, channeled on the upper surface with revolute margins, have bluntly acute apices and narrow petioles, and are 9–12 cm long and 11–12 mm wide (Silba 1986). Stomata have been observed only on abaxial surfaces (Woltz 1973).

The external cuticle surface is slightly undulating, and epidermal cell outlines are only slightly visible (fig. 4.35). Florin rings usually have distinct outlines and are slightly sunken into the epidermal cell cuticle (fig. 4.35). Occasionally a double stoma has been observed (fig. 4.33). These correspond to closely spaced pairs of guard cells (fig. 4.37). Stomatal plugs are porous, showing delicate rodlike components (fig. 4.36).

Inner cuticle surfaces show fairly regular stomatal rows with a lack of crowding, generally, between rows (fig. 4.32). Stomata are oriented parallel to the long axis of the leaf (fig. 4.32). The stomatal apparatus usually is elliptical in outline and more elongate than broad. Two subsidiary cells are common, with three and four being the result of the divisions of the lateral subsidiary cells (figs. 4.31, 4.32, 4.34, 4.37). Occasionally two pairs of closely spaced guard cells share four subsidiary cells

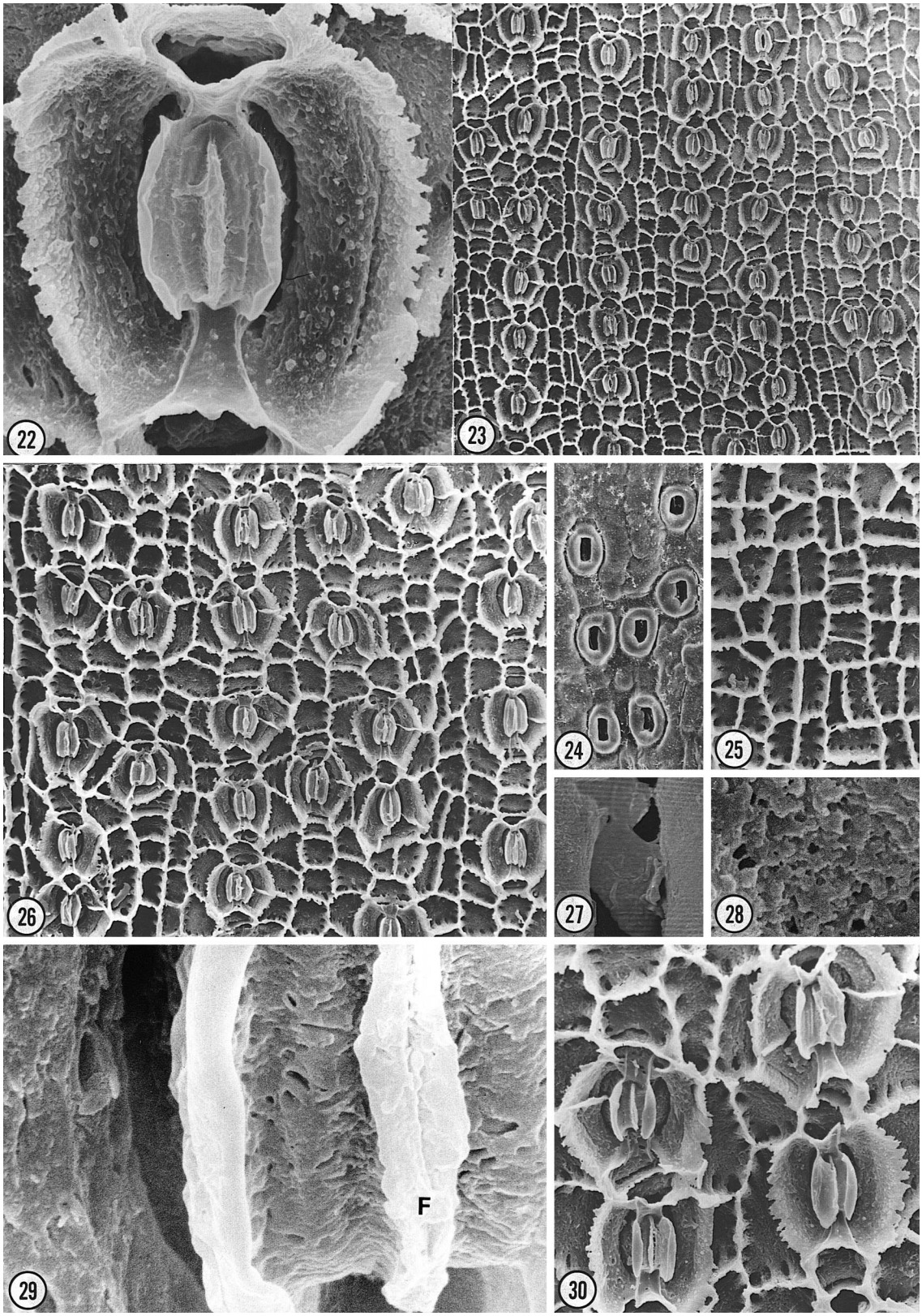

Fig. 3 *Podocarpus humbertii*. Fig. 3.22, Inner view, abaxial cuticle on stomatal apparatus; × 1790. Fig. 3.23, Inner view, abaxial surface, showing stomatal rows; × 190. Fig. 3.24, Outer view, abaxial surface, showing Florin rings and underlying epidermal cell outlines; × 205. Fig. 3.25, Inner view, adaxial surface, showing sinuous epidermal cell outlines with steep flanges; × 350. Fig. 3.26, Inner view, abaxial surface, showing a lack of elongate epidermal cells between stomatal rows and variable subsidiary cell numbers; × 310. Fig. 3.27, Outer view, abaxial surface, showing stomatal plug; × 2070. Fig. 3.28, Inner view, abaxial cuticle on epidermal cell surface; × 5875. Fig. 3.29, Inner view, abaxial cuticle on guard and subsidiary cell surfaces; × 6110. Fig. 3.30, Inner view, abaxial surface, showing variability in subsidiary cell number; × 635. *F*, flange of cuticle between guard cells.

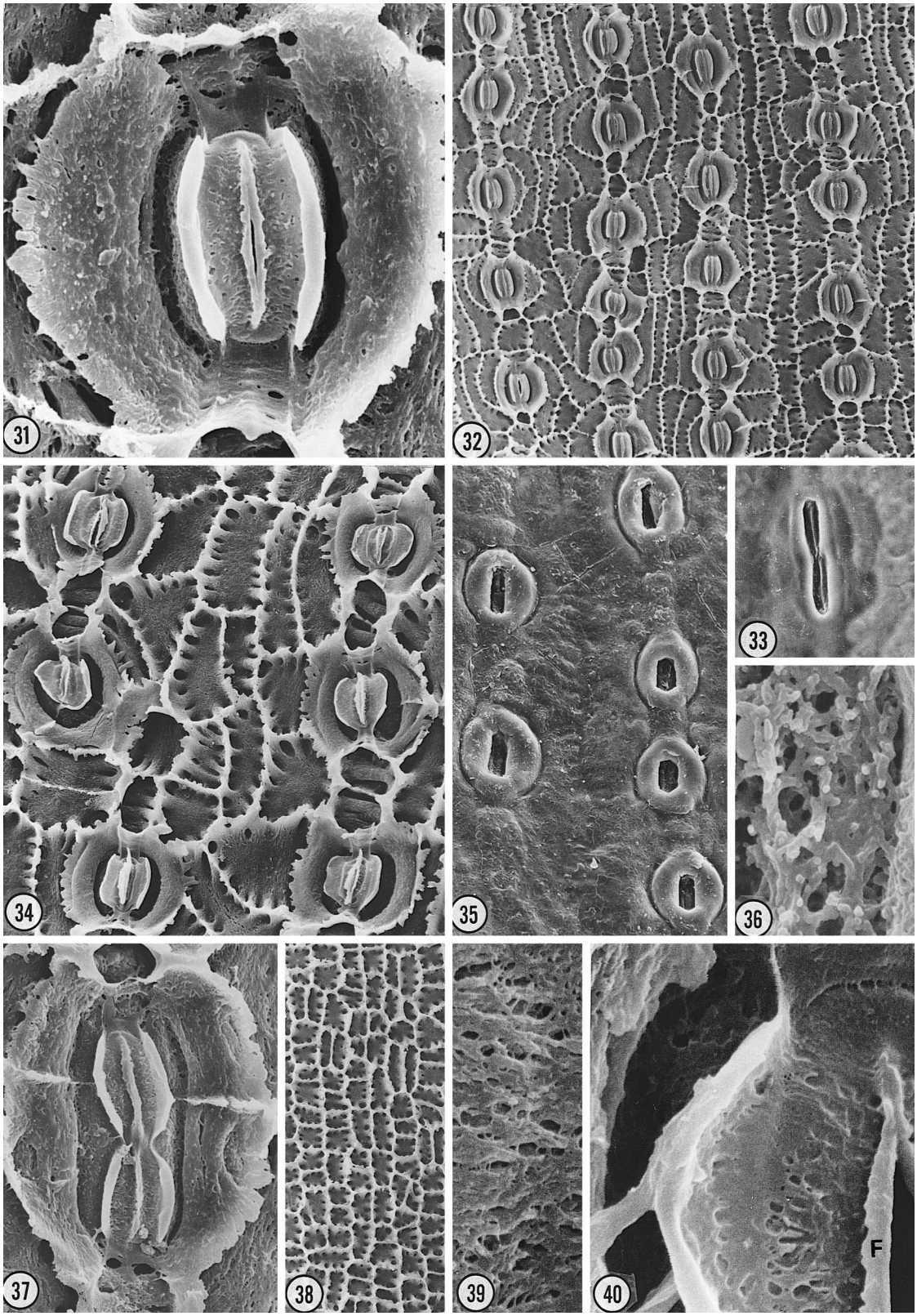

Fig. 4 *Podocarpus madagascariensis* var. *madagascariensis*. Fig. 4.31, Inner view, abaxial cuticle on stomatal apparatus; ×2050. Fig. 4.32, Inner view, abaxial surface, showing stomatal rows; ×255. Fig. 4.33, Outer view, abaxial view, showing two closely spaced sunken stomata lacking a pronounced Florin ring; ×440. Fig. 4.34, Inner view, abaxial surface, showing broad cuticular flanges on guard cell surfaces and sinuous epidermal cell outlines; ×510. Fig. 4.35, Outer view, abaxial surface, showing Florin rings; ×440. Fig. 4.36, Outer view, abaxial surface, showing stomatal plug components; ×4650. Fig. 4.37, Inner view, abaxial cuticle on two pairs of guard cells that share four subsidiary cells; ×1115. Fig. 4.38, Inner view, adaxial surface, showing sinuous epidermal cell outlines; ×255. Fig. 4.39, Inner view, abaxial cuticle on epidermal cell surface; ×5115. Fig. 4.40, Inner view, abaxial cuticle on guard cell surface; ×5580. *F*, flange of cuticle between guard cells.

(fig. 4.37). Polar subsidiary cells usually are absent, and cells with epidermal cell micromorphology occur in the polar region (figs. 4.32, 4.34).

Cuticle on the outer cell wall flange of subsidiary cells is thick, thinning toward the outer edge, which is frilled (figs. 4.31, 4.34, 4.37), as in *P. humbertii*. The surface of subsidiary cells is granular to pitted, with a deep groove where each subsidiary cell extends toward the leaf surface (figs. 4.31, 4.37, 4.40).

The cuticular flange between guard cells is relatively thick and slightly rugose (figs. 4.31, 4.40). Polar extensions are broad and thin, sometimes showing a central ridge, and flaring slightly in the polar region (figs. 4.31, 4.34). The cuticle on guard cell surfaces is rugose and distinctly pitted (figs. 4.31, 4.40). A slight ridge occurs in the polar region at the base of the polar extension (figs. 4.31, 4.40). The flange of cuticle between guard and subsidiary cells is broad, thick, slightly rugose, and usually inrolled (figs. 4.31, 4.34, 4.37, 4.40).

Epidermal cells usually are rectangular in shape and more elongate between stomatal rows than within a row (figs. 4.32, 4.38). On adaxial leaf surfaces epidermal cells can be broader than long, and often pairs of epidermal cells are oriented parallel to the long axis of the leaf and perpendicular to the long axis of other epidermal cells (fig. 4.38), as in *P. humbertii*. Epidermal cell wall flanges are undulating, and buttresses are prominent (figs. 4.32, 4.34, 4.38). Cuticle on epidermal cell surfaces is rugose and pitted (fig. 4.39).

Podocarpus madagascariensis *var.* procerus (*Fig. 5*)

Adult leaves were obtained from north of Fort-Dauphin and Mahatalaky, in the forest of Bemangidy, on coastal dunes that are exposed to fog in southeastern Madagascar, and come from the holotype (table 1). Leaves are narrow, linear, reflexed, and pendulous, on upright shoots with acute apices, 5–13 cm long and 4–6 mm wide (de Laubenfels 1971). Stomata were observed only on abaxial surfaces (Woltz 1973).

The external cuticle surface, like that of *P. madagascariensis* var. *madagascariensis*, is slightly undulating, with epidermal cell outlines that are only slightly visible (fig. 5.44). Florin rings usually have less distinct outlines and are more flush with the cuticle on epidermal cell surfaces or slightly sunken into the epidermal cell cuticle (fig. 5.44). Stomatal plugs are present and less porous but still show rodlike components (fig. 5.45).

Inner cuticle surfaces show fairly regular stomatal rows with generally a lack of crowding between rows (fig. 5.42) as in *P. madagascariensis* var. *madagascariensis*. Stomata are oriented parallel to the long axis of the leaf with occasional slight deflections (fig. 5.42). The stomatal apparatus usually is elliptical in outline and more elongate than broad, but occasionally subsidiary cells have very broad flanges (fig. 5.43). Two subsidiary cells are common, with three and four being the result of the divisions of the lateral subsidiary cells (figs. 5.41–5.43, 5.49). Occasionally two pairs of closely spaced guard cells share three or four subsidiary cells (figs. 5.42, 5.49). Polar subsidiary cells usually are absent, and cells with epidermal cell micromorphology occur in the polar region (figs. 5.43, 5.49).

Cuticle on the outer cell wall flange of subsidiary cells is thick and is frilled toward the outer edge (figs. 5.41, 5.43, 5.49), as in *P. humbertii* and *P. madagascariensis* var. *madagascariensis*. The surface of subsidiary cells is granular to pitted, with a deep groove where each subsidiary cell extends toward the leaf surface (figs. 5.41, 5.46), but the groove is farther from the guard cell cuticle and shallower than that seen in *P. madagascariensis* var. *madagascariensis*. This feature is reflected on the outer surface by the Florin ring that has less relief.

The cuticular flange between guard cells is thick and rugose (figs. 5.46). Polar extensions are broad and thin, sometimes showing a central ridge, and flaring in the polar region (figs. 5.41, 5.46). The cuticle on guard cell surfaces is rugose (fig. 5.46). A slight ridge occurs in the polar region at the base of the polar extension (fig. 5.46). The flange of cuticle between guard and subsidiary cells is broad, thick, slightly rugose, and usually extensively inrolled or covering the abaxial guard cell cuticle, making observation of the surface difficult (figs. 5.41, 5.46, 5.49).

Epidermal cells usually are rectangular in shape, more elongate between stomatal rows than within a row (fig. 5.42). On adaxial leaf surfaces epidermal cells can be broader than long (fig. 5.47). Epidermal cell wall flanges are undulating and buttresses are prominent (figs. 5.42, 5.43, 5.47). Cuticle on epidermal cell surfaces is rugose and often has large pits (fig. 5.48).

Podocarpus madagascariensis *var.* rotundus (*Fig. 6*)

Adult leaves were obtained from a small tree on the Massif du Tsaratanana in northern Madagascar (table 1). Leaves are lanceolate; erect, not pendant; with bluntly acute apices; 4–7 cm long and 5.5 mm wide (Silba 1986). Stomata were observed only on abaxial surfaces (Woltz 1973).

The external cuticle surface, like that of *P. madagascariensis* var. *madagascariensis* and *P. madagascariensis* var. *procerus*, is slightly undulating, with epidermal cell outlines that are only slightly visible (fig. 6.54). Florin rings usually have distinct outlines and are slightly sunken into the epidermal cell cuticle (fig. 6.54), as in *P. madagascariensis* var. *madagascariensis*. Stomatal plugs are porous and show short, rodlike components (fig. 6.52).

Inner cuticle surfaces show fairly regular stomatal rows and a general lack of crowding between rows (fig. 6.51), as in *P. madagascariensis* var. *madagascariensis* and *P. madagascariensis* var. *procerus*. Stomata are oriented parallel to the long axis of the leaf (figs. 6.51, 6.53). The stomatal apparatus is elliptical to circular in outline and usually more elongate than broad, but occasionally subsidiary cells have very broad flanges (fig. 6.50, 6.53, 6.58). Two subsidiary cells are common, with three and four being the result of the divisions of the lateral subsidiary cells (figs. 6.50, 6.51, 6.53). Occasionally two pairs of closely spaced guard cells share a pair of subsidiary cells (fig. 6.58). Usually these closely spaced guard cell pairs are in the same stomatal row as in the other two varieties of this species. We also observed two adjacent guard cell pairs sharing what appear to be five subsidiary cells (fig. 6.59). Polar subsidiary cells usually are absent, and cells with epidermal cell micromorphology occur in the polar region (figs. 6.53, 6.58).

Cuticle on the outer cell wall flange of subsidiary cells is thick and is frilled toward the outer edge (figs. 6.50, 6.53,

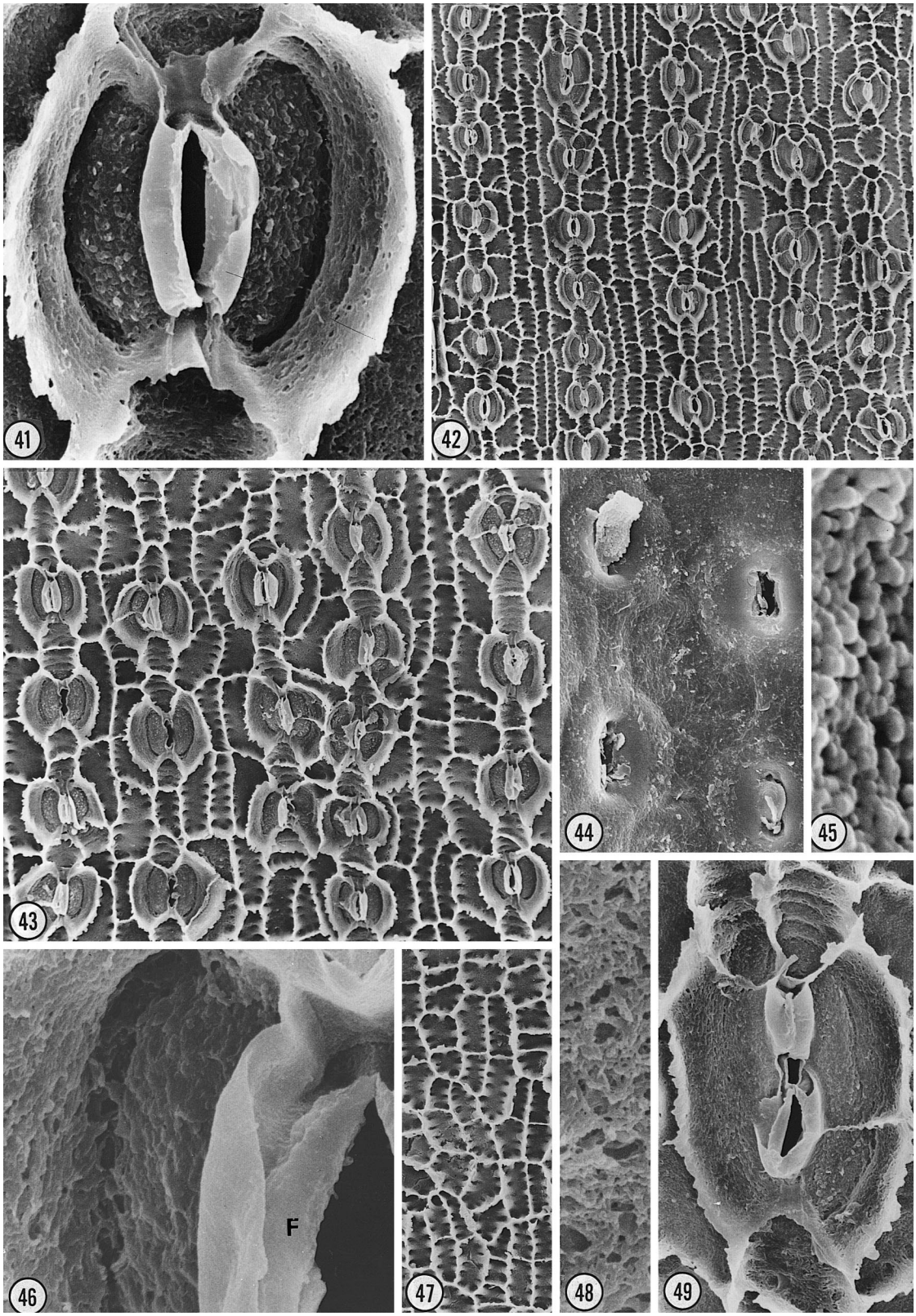

Fig. 5 *Podocarpus madagascariensis* var. *procerus*. Fig. 5.41, Inner view, abaxial cuticle on stomatal apparatus; ×1860. Fig. 5.42, Inner view, abaxial surface, showing stomatal rows; ×185. Fig. 5.43, Inner view, abaxial surface, showing stomata with variable number of subsidiary cells and an absence of polar subsidiaries; ×300. Fig. 5.44, Outer view, abaxial surface, showing stomata with Florin rings of low relief and stomatal plugs; ×675. Fig. 5.45, Outer view, abaxial surface, showing stomatal plug morphology; ×6510. Fig. 5.46, Inner view, abaxial cuticle on guard and subsidiary cell surfaces; ×4185. Fig. 5.47, Inner view, adaxial surface, showing sinuous epidermal cell outlines; ×1025. Fig. 5.48, Inner view, abaxial cuticle on epidermal cell surface; ×4880. Fig. 5.49, Inner view, abaxial cuticle on two pairs of guard cells that share subsidiary cells. Note the epidermal cell cuticle micromorphology in the plar regions; ×885. *F*, flange of cuticle between guard cells.

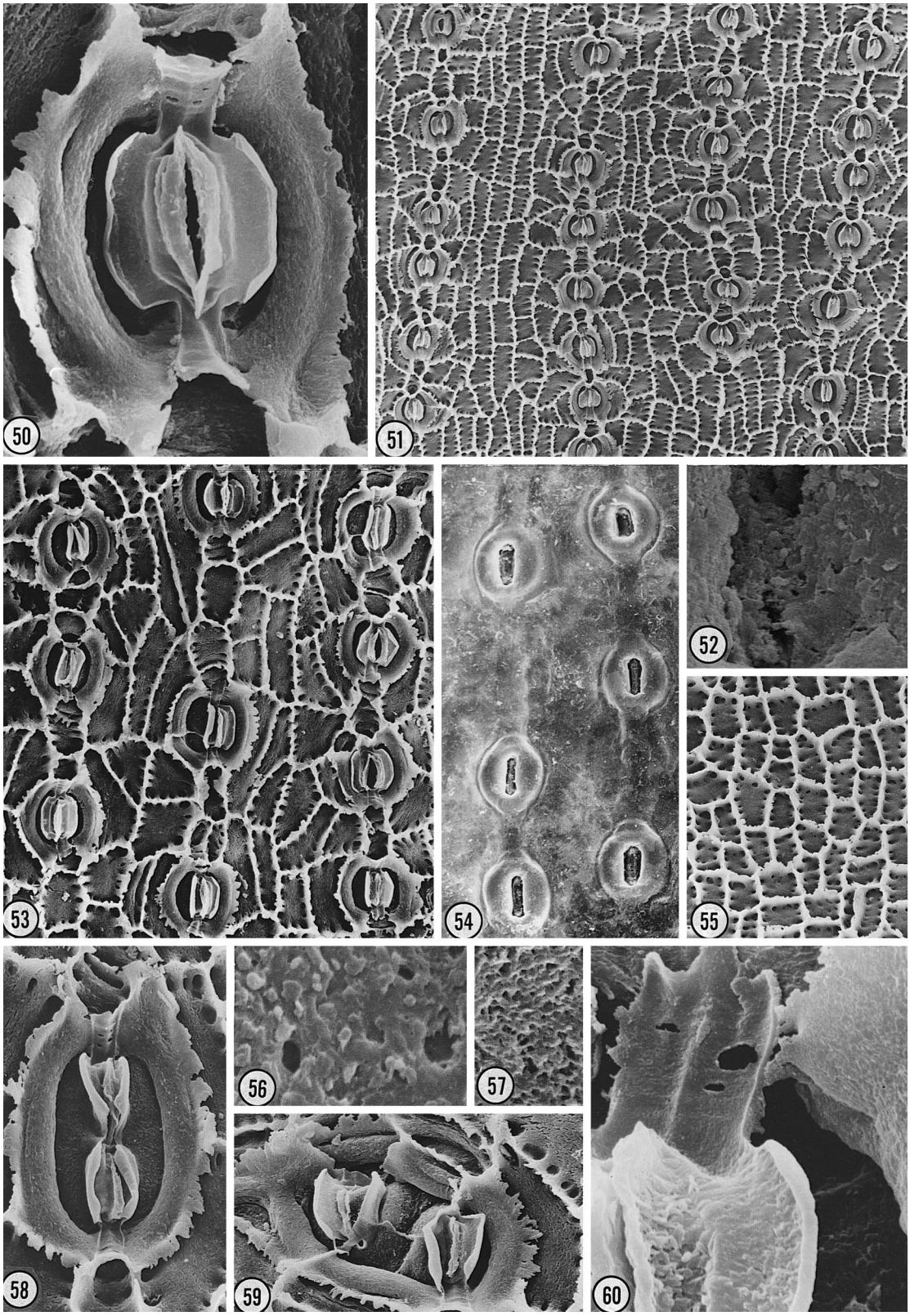

Fig. 6 *Podocarpus madagascariensis* var. *rotundus*. Fig. 6.50, Inner view abaxial cuticle on stomatal apparatus; × 1565. Fig. 6.51, Inner view, abaxial surface, showing stomatal rows; × 160. Fig. 6.52, Outer view, abaxial surface, showing stomatal plug components; × 305. Fig. 6.53, Inner view, abaxial surface, showing stomata and subsidiary cell variability; × 505. Fig. 6.54, Outer view, abaxial surface, showing Florin rings and underlying epidermal cell outlines; × 345. Fig. 6.55, Inner view, adaxial view of epidermal cell outlines; × 275. Fig. 6.56, Inner view, abaxial cuticle on subsidiary cell surface; × 8280. Fig. 6.57, Inner view, abaxial cuticle on epidermal cell surface; × 5060. Fig. 6.58, Inner view, abaxial cuticle on two pairs of guard cells that share two subsidiary cells; × 735. Fig. 6.59, Inner view, abaxial cuticle on two stomata with shared subsidiary cells; × 645. Fig. 6.60, Inner view, abaxial cuticle on guard cell surface and polar extension; × 3680.

6.58, 6.59), as in *P. humberti*, *P. madagascariensis* var. *madagascariensis* and *P. madagascariensis* var. *procerus*. The surface of subsidiary cells is granular to pitted, with a deep groove where each subsidiary cell extends toward the leaf surface (figs. 6.50, 6.53, 6.58, 6.60), similar to that seen in *P. madagascariensis* var. *madagascariensis*. This feature is reflected on the outer surface by the Florin ring, which has greater relief than that seen in *P. madagascariensis* var. *procerus*.

The cuticular flange between guard cells is thick and rugose (fig. 6.50). Polar extensions are broad and thin, showing a central ridge and flaring in the polar region (figs. 6.50, 6.58, 6.60). The cuticle on guard cell surfaces is rugose and pitted near the flange of cuticle between guard cells (fig. 6.60). A ridge occurs in the polar region at the base of the polar extension and extends around the guard cell surface cuticle (figs. 6.50, 6.60). The flange of cuticle between guard and subsidiary cells is broad, thick, slightly rugose, and usually inrolled (figs. 6.50, 6.53, 6.58, 6.60). This flange is normally flared out and does not normally cover the abaxial guard cell cuticle (figs. 6.50, 6.53, 6.58, 6.60).

Epidermal cells usually are rectangular in shape and more elongate between stomatal rows than within a row (fig. 6.51). On adaxial leaf surfaces epidermal cells can be broader than long (fig. 6.55). Epidermal cell wall flanges are undulating and buttresses are prominent (figs. 6.51, 6.53, 6.55). Cuticle on epidermal cell surfaces is rugose and pitted on both sides of the leaf (figs. 6.56, 6.57), often with large pits on abaxial surfaces (fig. 6.56).

Podocarpus perrieri (*Fig. 7*)

Adult leaves were obtained from a large tree in the forest of Andasibé on the Massif d'Andringitra in south-central Madagascar and come from the holotype (table 1). Leaves are narrowly linear, bluntly acute, with prominent midribs and an apiculate apex, 8–10 mm long and 1 mm wide (Gaussen and Woltz 1975; de Laubenfels 1985; Silba 1986). Stomata were observed only on abaxial surfaces (Woltz 1986).

The external cuticle surface is undulating, with epidermal cell outlines more or less visible (fig. 7.65). Florin rings usually have distinct outlines and are slightly sunken into the epidermal cell cuticle (figs. 7.63, 7.65). Stomatal plugs are present and appear as sheets (fig. 7.63) or may have globular or very short, rodlike components (fig. 7.66).

Inner cuticle surfaces show very discontinuous stomatal rows that may be in contact with one another laterally (figs. 7.62, 7.64). Stomata are oriented parallel to the long axis of the leaf, sometimes slightly deflected from the parallel orientation (figs. 7.62, 7.64). The stomatal apparatus is elliptical to circular in outline and usually more elongate than broad (figs. 7.61, 7.62, 7.64). Two subsidiary cells are common, with three and four being the result of the divisions of the lateral subsidiary cells (figs. 7.61, 7.62, 7.64). Occasionally, polar subsidiary cells are present (figs. 7.62, 7.64), as in *P. humbertii*. As many as six subsidiary cells can sometimes be present (fig. 7.64, near center). The distinction between polar subsidiary cells and epidermal cells within the stomatal row is not as pronounced in this species as it is in others in this section of the genus (figs. 7.62, 7.64).

Cuticle on the outer cell wall flange of subsidiary cells is thick and very frilled toward the outer edge. (figs. 7.61, 7.64). The surface of subsidiary cells is granular and very pitted, with a deep groove where each subsidiary cell extends toward the leaf surface (figs. 7.61, 7.69).

The cuticular flange between guard cells is thick and rugose (figs. 7.61, 7.69). Polar extensions are broad and thin, showing a central ridge and flaring slightly in the polar region (figs. 7.61, 7.64). The cuticle on guard cell surfaces is rugose and pitted over most of its surface (fig. 7.69). A distinct ridge does not occur on the guard cell surface cuticle (figs. 7.61, 7.69), as occurs in *P. madagascariensis* var. *rotundus*. The flange of cuticle between guard and subsidiary cells is broad, thick, smooth to slightly rugose, and usually inrolled, but does not cover the abaxial guard cell cuticle (figs. 7.61, 7.64, 7.69).

Epidermal cells usually are rectangular in shape and more elongate between stomatal rows than within a row (fig. 7.62, 7.64). On adaxial leaf surfaces epidermal cells usually are longer than broad, but they can be broader than long and sometimes triangular in outline (fig. 7.67). Epidermal cell wall flanges are undulating and buttresses are prominent (figs. 7.62, 7.64, 7.67). Cuticle on adaxial surfaces is very thick between epidermal cells (fig. 7.67). Cuticle on epidermal cell surfaces is rugose and pitted on both sides of the leaf (fig. 7.68).

Podocarpus rostratus (*Fig. 8*)

Adult leaves were obtained from a large tree from the Massif du Tsarantanana, on the crest that separates the valleys of Mahavavy and Sambirano in northern Madagascar (table 1). Leaves are twisted, narrowly linear with a prominent midrib, bluntly acute with apiculate apices, and 7–25 mm long, 0.5–1.5 mm wide (de Laubenfels 1985; Silba 1986; and R. A. Stockey, personal observation). Stomata have been observed only on abaxial surfaces (Woltz 1973).

The external cuticle surface is undulating, with epidermal cell outlines visible (fig. 8.73). Florin rings have distinct outlines and are slightly sunken into the epidermal cell cuticle (fig. 8.73). Stomatal plugs are present and, like those in *P. perrieri*, are fairly solid and globular or composed of fused rods (fig. 8.76).

Inner cuticle surfaces show very discontinuous stomatal rows that often are in contact with one another laterally, forming chains of stomata perpendicular to the long axis of the leaf (figs. 8.71, 8.72). Stomatal crowding is more common than in *P. perrieri* (fig. 8.77). Stomata are oriented parallel to the long axis of the leaf, sometimes slightly deflected from the parallel orientation (figs. 8.71, 8.72). The stomatal apparatus is elliptical to circular in outline and usually more elongate than broad, but shapes often vary with stomatal crowding (figs. 8.70–8.72, 8.74, 8.77). Two subsidiary cells are common, with three and four being the result of the divisions of the lateral subsidiary cells (figs. 8.70, 8.71). Occasionally, polar subsidiary cells are present (figs. 6.62, 6.64), as in *P. humbertii* and *P. perrieri*, and five and six subsidiary cells can be present (figs. 8.71, 8.72, 8.77). As in the varieties of *P. madagascariensis*, pairs of closely spaced guard cells within a stomatal row that share subsidiary cells have been observed (fig. 8.74). The distinction between polar subsidiary cells and epidermal cells within the stomatal row, as in *P. perrieri*, is not as pro-

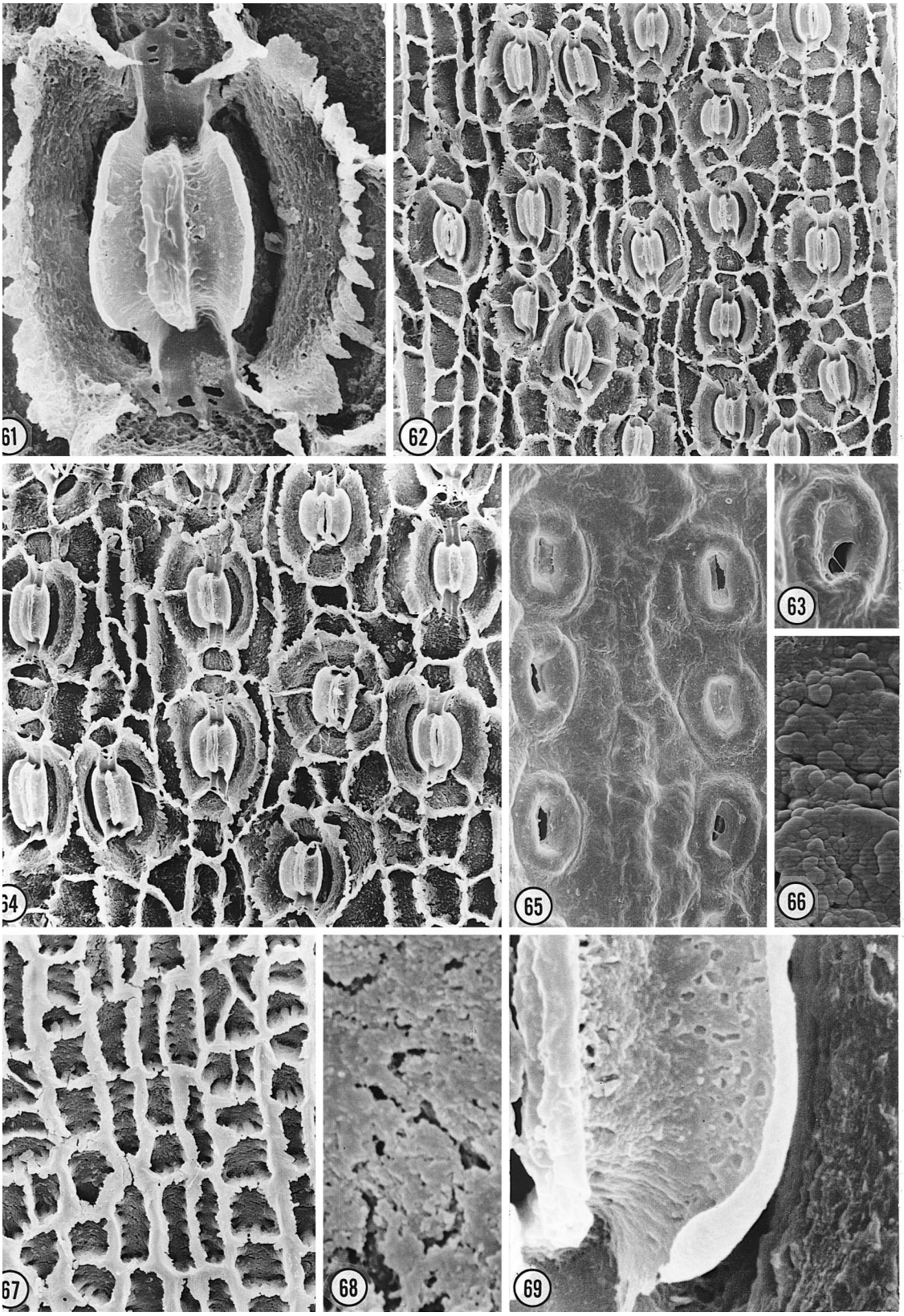

Fig. 7 *Podocarpus perrieri*. Fig. 7.61, Inner view, abaxial cuticle on stomatal apparatus; ×1900. Fig. 7.62, Inner view, abaxial surface, showing discontinuous stomatal rows; ×355. Fig. 7.63, Outer view, abaxial surface, showing one Florin ring and partially covered stoma; ×665. Fig. 7.64, Inner view, abaxial view showing stomata with variable number of subsidiary cells; ×500. Fig. 7.65, Outer view, abaxial cuticle showing Florin rings and underlying epidermal cell outlines; ×475. Fig. 7.66, Outer view, abaxial surface, showing stomatal plug components; ×2850. Fig. 7.67, Inner view, adaxial view of epidermal cell outlines; ×520. Fig. 7.68, Inner view, abaxial cuticle on epidermal cell surface; ×5225. Fig. 7.69, Inner view of cuticle on guard and subsidiary cell surfaces; ×5490.

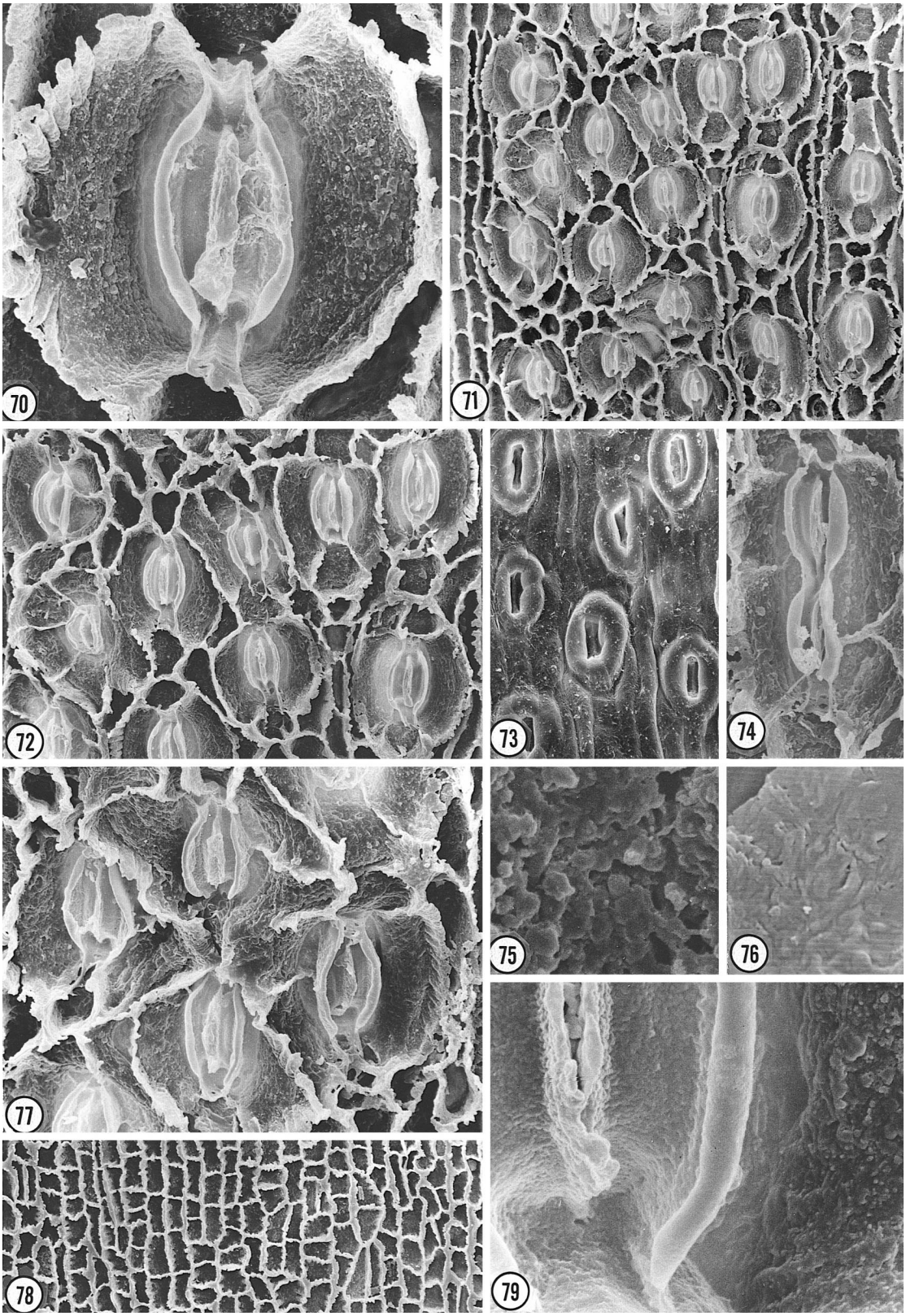

Fig. 8 *Podocarpus rostratus*. Fig. 8.70, Inner view, abaxial cuticle on stomatal apparatus; ×1675. Fig. 8.71, Inner view, abaxial surface, showing crowded stomatal rows; ×440. Fig. 8.72, Inner view, abaxial surface, showing stomata with variable subsidiary cell numbers; ×490. Fig. 8.73, Outer view, abaxial surface, showing Florin rings and very undulating cuticle on epidermal cell surfaces; ×395. Fig. 8.74, Inner view, abaxial cuticle on two pairs of guard cells that share subsidiary cells; ×835. Fig. 8.75, Inner view, adaxial cuticle on epidermal cell surface; ×5580. Fig. 8.76, Outer view, abaxial surface, showing stomatal plug components; ×5580. Fig. 8.77, Inner view, abaxial surface, showing crowded stomata with variable numbers of subsidiary cells that border on each other; ×1300. Fig. 8.78, Inner view, adaxial surface, showing epidermal cell outlines; ×260. Fig. 8.79, Inner view, abaxial cuticle on guard and subsidiary cell surfaces; ×3950.

nounced as it is in others in this section of the genus (figs. 8.70–8.72).

Cuticle on the outer cell wall flange of subsidiary cells is thick and very frilled toward the outer edge (figs. 8.70–8.72, 8.77). The surface of subsidiary cells is very granular and pitted (figs. 8.70, 8.79). The deep groove where each subsidiary cell extends toward the leaf surface, common to other species, is shallow in this taxon (figs. 8.70–8.72, 8.77, 8.79). This zone appears near the flange between guard and subsidiary cells as a smooth region, and the subsidiary cell wall flanges show a gradual slope (figs. 8.70, 8.79). Florin rings are still distinct externally, unlike those in *P. madagascariensis* var. *procerus*.

The cuticular flange between guard cells is thick and rugose (fig. 8.70). Polar extensions are broad and thin, showing a central ridge and flaring slightly in the polar region (figs. 8.70, 8.72). The cuticle on guard cell surfaces is rugose but not pitted as in *P. perrieri* (fig. 8.79). A slight ridge occurs on the guard cell surface cuticle in some stomata, but this is not pronounced (figs. 8.70, 8.72, 8.79). The flange of cuticle between guard and subsidiary cells is broad, very thick, smooth to slightly rugose, and usually inrolled, but does not cover the abaxial guard cell cuticle (figs. 8.70, 8.77, 8.79).

Epidermal cells usually are rectangular in shape and more elongate between stomatal rows than within a row (fig. 8.71, 8.78). On adaxial leaf surfaces epidermal cells usually are longer than broad and sometimes are triangular in outline (fig. 8.78), as in *P. perrieri*. Epidermal cell wall flanges are undulating and buttresses are prominent (figs. 8.78). Cuticle on adaxial surfaces is very thick between epidermal cells (fig. 8.78), as in *P. perrieri*. Cuticle on epidermal cell surfaces is rugose and pitted on both leaf surfaces (fig. 8.75).

Podocarpus woltzii (*Fig. 9*)

Adult leaves were obtained from a tree on the Massif du Tsaratanana on the crest that separates the Sambirano and Mahavavy basins in northern Madagascar (table 1). Leaves are narrowly linear, with acute apices and revolute margins, sessile with a prominent midrib, 2.5–5.3 cm long and 2.5–5.5 cm wide (Gaussen 1974; R. A. Stockey, personal observation). Stomata have been observed only on abaxial surfaces.

The external cuticle surface is undulating, with outlines of underlying epidermal cells clearly visible (fig. 9.82), as in *P. capuronii*. Distinct Florin rings are sunken into the surrounding cuticle that covers epidermal cells (fig. 9.82). One double Florin ring has been observed surrounding two closely placed pairs of guard cells that presumably shared subsidiary cells (fig. 9.83), as occurs in the three varieties of *P. madagascariensis* and *P. rostratus*. Stomatal plugs occur and have globular components (fig. 9.86).

Inner cuticle surfaces show stomata in fairly regular but discontinuous rows (fig. 9.81). Stomata are oriented parallel to the long axis of the leaf (figs. 9.81, 9.84, 9.87). The shape of the stomatal apparatus is elliptical in outline and usually is broader than tall due to the wide subsidiary cell wall flanges (figs. 9.81, 9.82). Two lateral subsidiary cells are most common, with three or four being the result of the division of these lateral subsidiary cells (figs. 9.84, 9.87). Polar subsidiary cells usually are absent, with cells in the polar region that have ornamentation similar to the surrounding epidermal cells (fig. 9.84).

Cuticle on the outer cell wall flange of subsidiary cells is thin and very frilled (figs. 9.80, 9.84, 9.87). That on the surface of subsidiary cells is rugose and has a central, pitted groove where the subsidiary cell extends toward the leaf surface (figs. 9.80, 9.89). Vertical striations sometimes occur on the subsidiary cell wall flanges (fig. 9.84).

The cuticular flange between guard cells is thick and rugose (figs. 9.80, 9.89). Polar extensions are thin and flare out in the polar region, sometimes showing a central flange corresponding to the line of guard cell separation (figs. 9.80, 9.84, 9.87, 9.89). Rarely, they extend out over polar epidermal cells (fig. 9.84, left center), as in *P. capuronii*. Cuticle on the guard cell surface is rugose (figs. 9.80, 9.89) but lacks the deeper pits seen in *P. capuronii*. The flange of cuticle between guard and subsidiary cells is thick and usually appears rolled and slightly rugose (figs. 9.80, 9.84, 9.87, 9.89).

Epidermal cells are square to rectangular in outline, often broader than long on adaxial surfaces (fig. 9.88). On abaxial leaf surfaces they are only slightly more elongate between stomatal rows (fig. 9.81). Epidermal cells are undulating, with prominent buttresses on both leaf surfaces (figs. 9.81, 9.84, 9.88). Cuticle on the epidermal cell surfaces is rugose and pitted (fig. 9.85).

Discussion

External cuticle micromorphology of leaves of *Podocarpus* subgenus *Podocarpus* section *Scytopodium* is characterized by slightly sunken Florin rings and stomatal plugs, with underlying epidermal cell outlines usually visible. Leaves are hypostomatic and stomata occur in discontinuous but fairly regular rows in most species. Stomata are oriented parallel to the long axis of the leaf or may be slightly oblique and usually lack polar subsidiary cells. From two to six subsidiary cells occur, with two or three being the most common. Internal cuticle on subsidiary cell surfaces is granular to rugose, usually with a deep groove corresponding to the external Florin ring. Cuticle on guard cell surfaces is granular or rugose to pitted, and prominent polar extensions are present in all species. Epidermal cell outlines are undulating, and cuticle on epidermal cell surfaces is granular to rugose and pitted. The most useful characters to distinguish species of this section are the micromorphology of cuticle on the guard cell and subsidiary cell surfaces, epidermal cell shapes, and sometimes the length of polar extensions.

Three species groups occur in the nine taxa described in this study. De Laubenfels (1985) recognizes five species in section *Scytopodium* (table 2). He lists *Podocarpus ensiculus* as a synonym of *Podocarpus henkelii*, *Podocarpus woltzii* as a synonym of *Podocarpus capuronii*, and *Podocarpus perrieri* as a synonym of *Podocarpus rostratus*. In this study we also examined the three recognized varieties of *Podocarpus madagascariensis* (table 1). We have compared the taxa in these species groups to determine whether they can be distinguished on the basis of leaf micromorphology. The rarity of some of these species has probably resulted in their being lumped into a single taxon.

Podocarpus capuronii and *P. woltzii* show a very similar

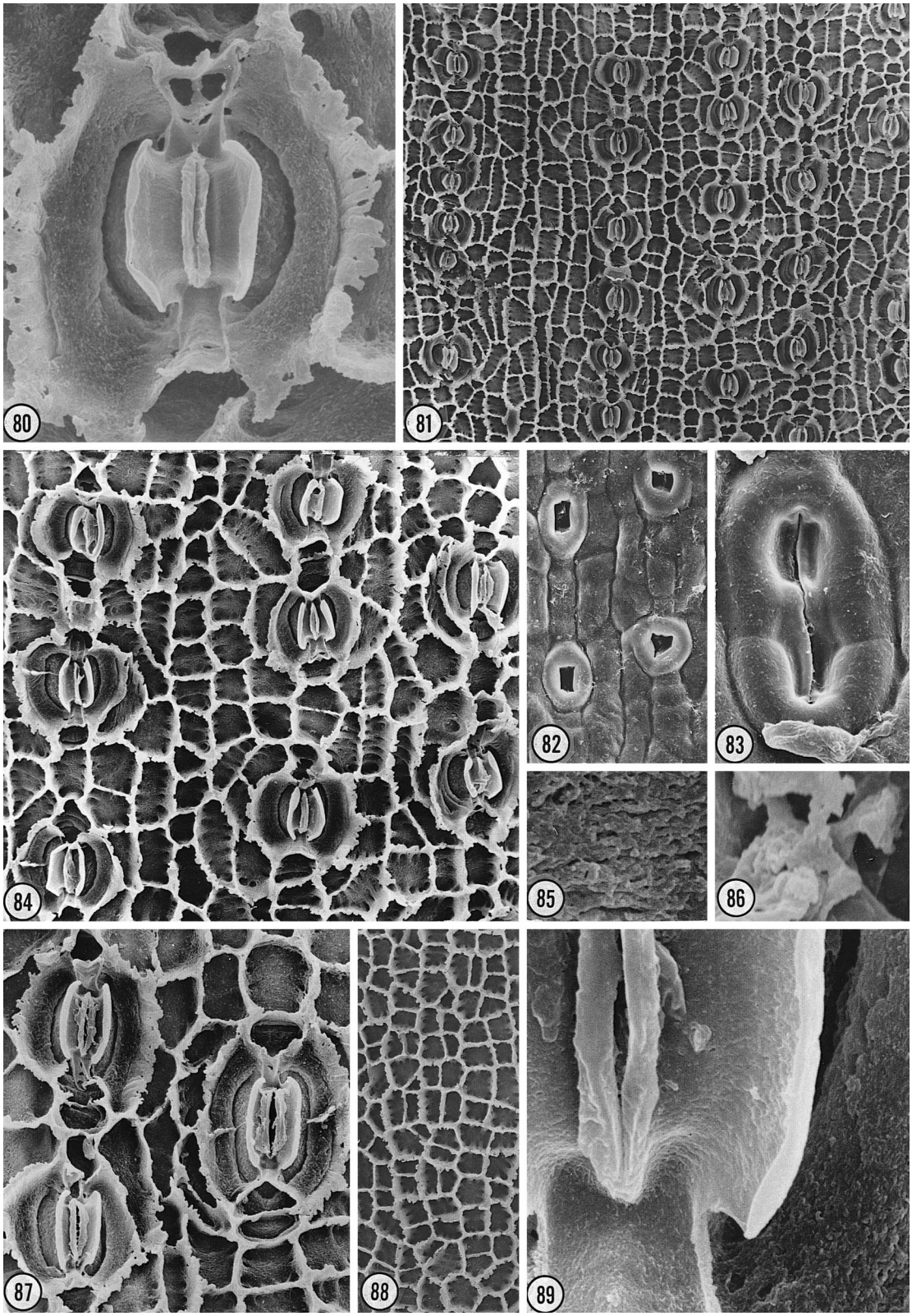

Fig. 9 *Podocarpus woltzii*. Fig. 9.80, Inner view, abaxial cuticle on stomatal apparatus; × 1675. Fig. 9.81, Inner view, abaxial surface, showing stomatal rows; × 205. Fig. 9.82, Outer view, abaxial surface, showing Florin rings and distinct underlying epidermal cell outlines; × 350. Fig. 9.83, Outer view, abaxial surface, showing double Florin ring around two pairs of closely spaced guard cells; × 930. Fig. 9.84, Inner view, abaxial surface, showing stomata with variable numbers of subsidiary cells; × 440. Fig. 9.85, Inner view, abaxial surface, showing cuticle on epidermal cell surface; × 5580. Fig. 9.86, Outer view, abaxial surface, showing stomatal plug components; × 6045. Fig. 9.87, Inner view, abaxial surface, showing stomata with four to six subsidiary cells; × 650. Fig. 9.88, Inner view, adaxial surface, showing epidermal cell outlines; × 280. Fig. 9.89, Inner view, abaxial cuticle on guard and subsidiary cell surfaces; × 4650.

Table 2

Classification of *Podocarpus* Section *Scytopodium* De Laubenfels (1985)

Section *Scytopodium* de Laubenfels:
Podocarpus madagascariensis Baker
Podocarpus henkelii Stapf ex Dallimore et Jackson (=*P. ensiculus* Melville)
Podocarpus capuronii de Laubenfels (=*P. woltzii* Gaussen)
Podocarpus humbertii de Laubenfels
Podocarpus rostratus Laurent (=*P. perrieri* Gaussen et Woltz)

cuticle micromorphology. These two taxa have been segregated on the basis of leaf and juvenile stem anatomy (Gaussen 1974; Marguerier and Woltz 1977; Woltz 1986). *Podocarpus woltzii* leaves have peripheral resin canals in the leaf, while those of *P. capuronii* lack these lateral resin canals (de Laubenfels 1985). In cuticle micromorphology these two species look very similar to one another. External cuticular surfaces are essentially identical. The differences in stomatal plug components may not be significant. Studies of epicuticular waxes on leaves of other species of *Podocarpus* (Morvan 1982, 1987) indicate that the configuration of surface waxes can change depending on how long the leaves have been removed from the tree. Internal cuticle micromorphology, however, shows some differences between the two species. In *P. capuronii* polar extensions are longer than those of *P. woltzii* or any other species in the section. Epidermal cell shapes in *P. woltzii* are generally shorter, and those on abaxial surfaces have slightly more sinuous outlines than those of *P. capuronii*. Cuticle on the guard cell surface is more pitted in *P. capuronii*. The groove in subsidiary cell cuticles in *P. woltzii* is more pronounced and smoother than in *P. capuronii*. While these two species show many similarities in micromorphology, they can still be distinguished by a number of features, indicating that they may indeed be separate taxa.

The second species group includes *P. perrieri* and *P. rostratus*. Leaves of these two species have been distinguished by the numerous peripheral resin canals in the leaf of *P. rostratus* (Gray 1953*b*; Gaussen and Woltz 1975; de Laubenfels 1985). The two taxa are similar in cuticle micromorphology. Externally they appear identical. Internally both show stomatal apparati that are in lateral contact with one another. This is more pronounced in *P. rostratus* than in *P. perrieri*. Both have thick adaxial epidermal cell cuticle, very frilled subsidiary cell cuticle, and epidermal cell surfaces with the same type of pitting. However, the crease in subsidiary cell cuticle of *P. rostratus* is smooth and not as pronounced as in *P. perrieri* and the other species of Section *Scytopodium*. Cuticle on the guard cell surface of *P. perrieri* is granular and pitted, while that in *P. rostratus* lacks these pits. Pairs of guard cells sharing subsidiary cells, as have been observed in *P. rostratus*, so far have not been seen in *P. perrieri*.

The three varieties of *P. madagascariensis* all show a very similar cuticle micromorphology. Externally *P. madagascariensis* var. *madagascariensis* and *P. madagascariensis* var. *rotundus* are identical. *Podocarpus madagascariensis* var. *procerus*, however, shows Florin rings with less relief. This is reflected internally in the subsidiary cell surface cuticle, which has very wide flanges and a groove that is well separated from the guard cell cuticle, unlike that seen in the other varieties. Internally all three varieties show similar sinuous epidermal cell shapes. *Podocarpus madagascariensis* var. *rotundus* does not show the distinct patterns of epidermal cell orientation on adaxial leaf surfaces to the extent seen in the other two varieties (see figs. 4.38, 5.47, and 6.55). All three varieties show pairs of guard cells that share subsidiary cells, similar cuticle on epidermal cell surfaces, and similar stomatal plug components. Cuticle on guard cell surfaces is the most distinctive difference among the varieties. In *P. madagascariensis* var. *madagascariensis* cuticle on guard cell surfaces is very pitted. In *P. madagascariensis* var. *rotundus* pitting is smaller and this cuticle surface appears granular. In addition, there is a distinct ridge present on the guard cell cuticle that does not occur in the other two varieties. In *P. madagascariensis* var. *procerus* the surface is even smoother and this face usually is enclosed by a cuticular envelope that almost completely covers the guard cells. Cuticular micromorphology for this group shows differences that may be used in combination with other characters to separate these podocarps into separate taxa.

The most distinctive species is *P. henkelii*, in which the cuticle surface is nearly smooth, Florin rings are indistinct, cuticle is thin, epidermal cells are more elongate and less pitted, and the two lateral subsidiary cells join to form nearly circular stomata. The flange between guard cells and subsidiary cells when unrolled has a rectangular shape.

Greenwood (1987) surveyed about half of the then known species of *Podocarpus* with light microscopy. Several fossil species in the genus and new genera in this family have been described recently using SEM, especially from Australia and New Zealand (Greenwood 1987; Hill and Carpenter 1991; Hill and Pole 1992; Pole 1992*a*, 1992*b*, 1993). Many of these taxa have been described as new species of *Podocarpus*; however, the total basis for comparison of these fossils was lacking. Hill and Carpenter (1991) had a survey of about 30% of the species with which to compare *Podocarpus witherdenensis*. Pole (1992*b*, 1993) had about half of the known species when *Podocarpus alwyniae* and *Podocarpus travisiae* were described. None of these taxa appear to be similar to *Podocarpus* section *Scytopodium*. It is hoped that, with further systematic surveys of the genus *Podocarpus* and related genera, identification of fossil material will be simplified and these taxa will be completely characterized on the basis of cuticle micromorphology.

Acknowledgments

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