Int. J. Plant Sci. 156(5):723–730. 1995.

1058-5893/95/5605-0015$02.00

CUTICLE MICROMORPHOLOGY OF PARASITAXUS DE LAUBENFELS (PODOCARPACEAE)

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Cuticle micromorphology of three collections of the parasitic conifer *Parasitaxus ustus* (Vieillard) de Laubenfels (Podocarpaceae) was studied with scanning electron microscopy. External and internal cuticle features of abaxial and adaxial leaf surfaces of both vegetative and epimatium-bearing branches are characterized. Leaves are amphistomatic with an abaxial tip lacking stomata and a small marginal frill. Cuticle is thin and external surfaces exhibit sunken Florin rings and highly undulating epidermal cell surfaces. Stomata have a scattered orientation on the leaf and have three to six subsidiary cells. Cuticle on the subsidiary cells, guard cells, and epidermal cells is smooth to slightly granular. Stomata lack polar extensions. Epidermal cells have variable shapes but are more elongate and rectangular near the abaxial leaf tip and between stomatal groups. Micromorphological characters are compared to those of the host plant, *Falcatifolium taxoides* (Brongniart et Gris.) de Laubenfels, and Florin's *Dacrydium* group C species that are considered by some workers to represent three separate genera: *Halocarpus* Quinn, *Lepidothamnus* Philippi, and *Lagarostrobos* Quinn. Micromorphologically cuticles are most similar to those of the genus *Lepidothamnus,* in particular *L. fonkii* Philippi, but those of *Parasitaxus* have less granular epidermal cell surfaces and a more irregular outline to the stomatal apparatus.

Introduction

Leaf structure and cuticle micromorphology of the family Podocarpaceae have received increased attention in the past several years. These studies, however, are far from complete because of the large size of the family, with over 170 species (Silba 1986), and because of the rarity of some taxa (Stockey and Ko 1988). Leaves at the light microscope level were studied by Florin (1931, 1940*a,* 1940*b,* 1958), Orr (1944), Buchholz and Gray (1948*a,* 1948*b,* 1948*c*), Gray and Buchholz (1948, 1951), Townrow (1965, 1967*a,* 1967*b,* 1969), Dilcher (1969), Schoonraad and Van Der Schijff (1974), Ferré et al. (1977), Woltz (1986), and Greenwood (1987). Scanning electron microscopy (SEM) of epicuticular waxes (Morvan 1982, 1987) and leaf micromorphology of some taxa have been examined (Stockey and Ko 1988, 1990; Stockey et al. 1992; Cantrill 1989; Hill 1989; Wells and Hill 1989*a,* 1989*b;* Hill and Carpenter 1991). However, only some micromorphological observations of the cuticle of *Parasitaxus ustus* (Vieillard) de Laubenfels (1972) have been made by Wells and Hill (1989*a*) in a survey of several imbricate-leaved podocarps.

Parasitaxus ustus is the only species in the monotypic genus *Parasitaxus.* These conifers, endemic to New Caledonia, are found only as parasites on roots of *Falcatifolium taxoides* (Brongniart et Gris.) de Laubenfels (1972). The species was first described as a taxon of *Dacrydium* Solander ex Forster, then a species of *Podocarpus* L'Heritier ex Persoon, and later recognized as a unique monotypic genus and the only parasitic gymnosperm (de Laubenfels 1972; Cherrier 1981; Cherrier et al. 1990, 1992; Woltz et al. 1994). Plants are small trees or shrubs, 1.0–1.8 m tall, that usually grow at high elevations (de Laubenfels 1972).

We have examined three collections of *P. ustus* in this article to characterize fully its cuticle micromorphology. These characters are compared to those of *Falcatifolium* de Laubenfels, its host plant; *Dacrydium,* from which the genus has been segregated; and three recently segregated taxa, *Halocarpus* Quinn, *Lepidothamnus* Philippi, and *Lagarostrobos* Quinn. The usefulness of cuticular features in distinguishing these taxa is evaluated, and comparisons are made among these podocarps.

Material and methods

Adult leaves from three different localities in New Caledonia were investigated in this study (table 1). Several branches were mounted without treatment on SEM stubs using double-sided tape. All leaves prepared for cuticular study were removed intact, leaving both abaxial and adaxial epidermis attached. Preparations were immersed in 20% chromium trioxide solution for 96 h (Alvin and Boulter 1974; Stockey and Ko 1986). Because of the delicate nature of this cuticle, abaxial and adaxial epidermis always separated from one another using this treatment.

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. All 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-

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Manuscript received February 1995; revised manuscript received April 1995.

Table 1

PARASITAXUS USTUS (Vieillard) DE LAUBENFELS

Herbarium	Voucher	Source
MO 3011044 ...	McPherson 4172	Rivière Bleue Reserve, forested slopes 400 m; tree 1.8 m tall; young glaucous cones
MO 3130558 ...	McPherson 5232	Massif de Boulinda, forest, 900 m; young glaucous, blue cones; older purple cones
MO 3220467 ...	McPherson 6606	Mount Dzumac, north of Nouméa, forested slopes, 900 m; tree 1.5 m tall; blue, glaucous pollen cones

ALTA). Stomatal distribution was determined by examining leaves from several branches. Descriptions disregard was is obvious debris on cuticle surfaces. All photographs (except fig. 1) 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

Parasitaxus bears helically arranged, small, triangular, imbricate, scalelike leaves (figs. 1, 6, 7). Leaves are red or purple, 1–2 mm long, with acute incurved apices (figs. 1, 5, 6; de Laubenfels 1972; Silba 1986). The longest leaves occur just below an ovule-bearing structure (fig. 1), as in several other podocarpaceous taxa (Tomlinson et al. 1991). Ovules are borne singly, embedded in an epimatium and subtended by a bract (figs. 2, 3). At maturity, seeds are glaucous, globular and 3–4 mm in diameter, becoming wrinkled on drying (fig. 5; de Laubenfels 1972). Surfaces of the epimatium are covered with rodlets of epicuticular waxes that are easily removed on handling the cuticles (fig. 4).

Wells and Hill (1989*a*) reported that leaves are amphistomatic with a slight marginal frill, randomly oriented stomata, and epidermal cells. We observed the very delicate nature of the adaxial epidermis. This cuticle is extremely thin. In some leaves there are no stomata on the abaxial surface in a rhomboidal area near the tip of the leaf (figs. 6, 7). The marginal frill is more elongated and irregular on the widely separated leaves near the epimatium (figs. 5, 6, arrows), than on the more closely spaced, imbricate leaves on sterile branches (fig. 7, arrow).

The external cuticle surface is uneven and epidermal cell outlines are clearly visible. Epidermal cells near the leaf tip are oriented in more regular rows than those near the leaf base (figs. 6, 7, 16). Prominent Florin rings are usually sunken beneath the level of the epidermal cells (figs. 9, 11). Stomatal plugs have not been observed on any of the leaves examined.

Inner cuticle surfaces show scattered stomata of varying orientations on adaxial cuticles (fig. 10). The stomatal apparatus is elliptical and has an irregular outline in most cases (figs. 10, 14, 17). As few as three and as many as six subsidiary cells have been observed, with four and five being the most common numbers (figs. 10, 14, 17).

Cuticle on the outer subsidiary cell wall flange is thin and slightly irregular (figs. 8, 14, 17). No polar extensions have been observed. Cuticle on subsidiary cell surfaces is smooth to slightly granular and almost identical to that on the surrounding epidermal cell surfaces (figs. 10, 14, 15, 17). The flange of cuticle between guard and subsidiary cells is slightly rugose and inrolled (figs. 10, 12, 17). Cuticle on guard cell surfaces is relatively smooth, may be slightly rugose (figs. 12, 17), and is also similar in appearance to the cuticle on subsidiary cell surfaces. The flange of cuticle between the guard cells is thin and slightly granular (fig. 12).

Epidermal cells have variable shapes, with those near the frill and the leaf tip elongated and nearly rectangular (figs. 15, 16) and those near the stomata (encircling cells) shorter with irregular shapes (fig. 10). Between stomata, epidermal cells are also more elongated (fig. 10). Epidermal cell wall flanges are straight to slightly curving and very short, lacking buttresses (figs. 13, 15). Cuticle on epidermal cell surfaces is smooth to slightly rugose and concave (figs. 13, 15).

Discussion

The genus *Dacrydium* was commonly divided into three sections (groups A, B, and C of Florin 1931) prior to the late 1960s when de Laubenfels

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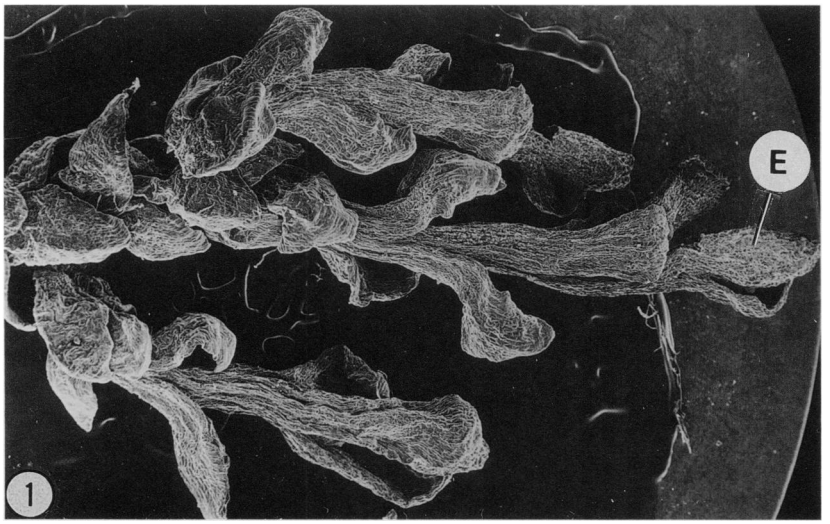
Figs. 1–7 *Parasitaxus ustus* external morphology. Fig. 1, Leafy branches with a terminal epimatium; × 14. Fig. 2, Terminal epimatium with subtending bract in face view showing elongate rectangular cells; × 48. Fig. 3, Terminal epimatium with subtending bract in side view; × 55. Fig. 4, Epicuticular waxes on epimatium; × 1600. Fig. 5, Mature ovule-bearing epimatium with wrinkled surface; arrow shows marginal frill on leaf; × 10. Fig. 6, Abaxial view of leaves on epimatium-bearing branch showing stomatal free zone near the leaf apex with rectangular epidermal cells and a distinct marginal frill (arrow); × 48. Fig. 7, Abaxial view of imbricate leaves showing small marginal frill (arrow), area lacking stomata near apex, and two stomatal bands; × 80. *B*, bract; *E*, epimatium.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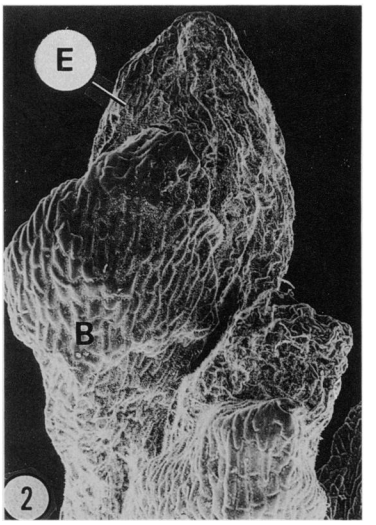
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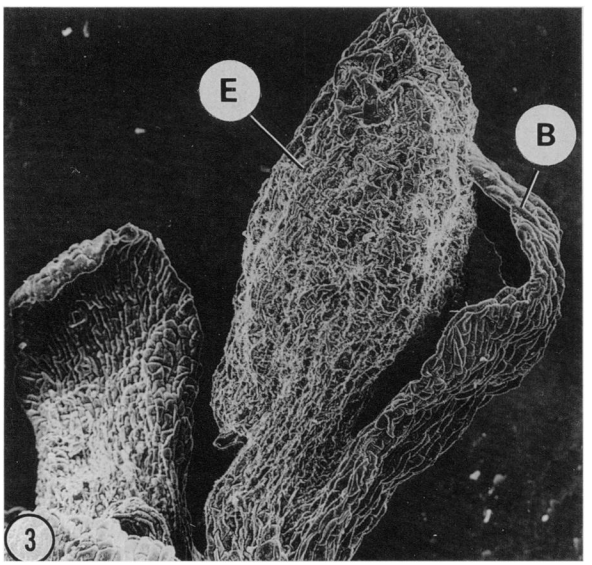
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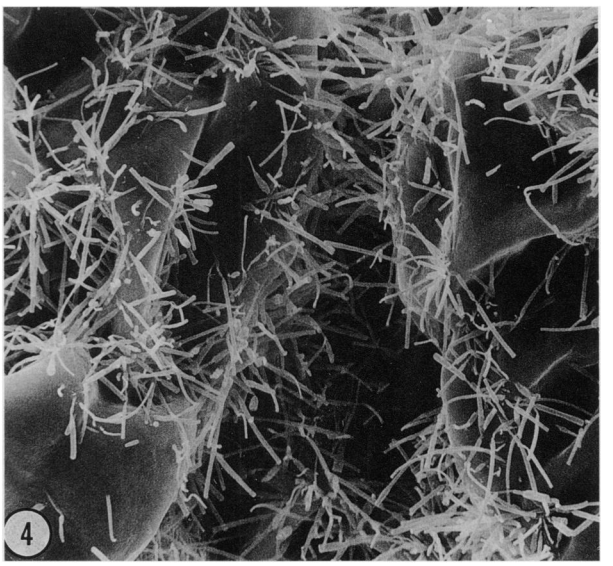
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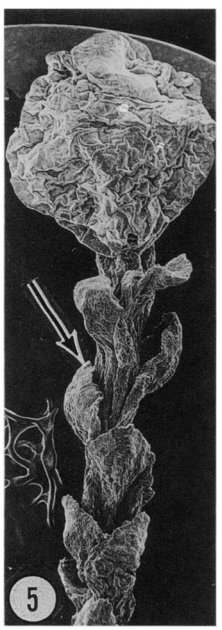
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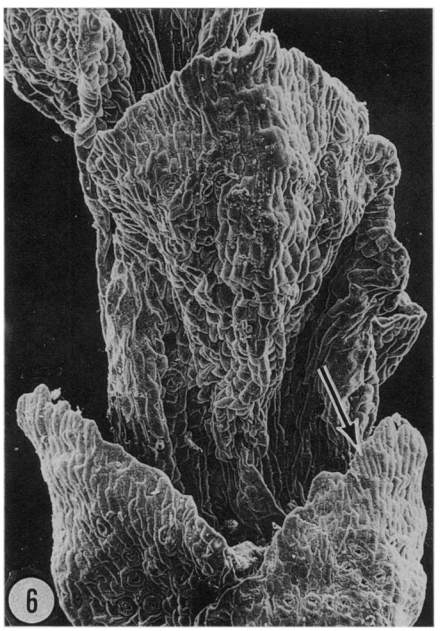
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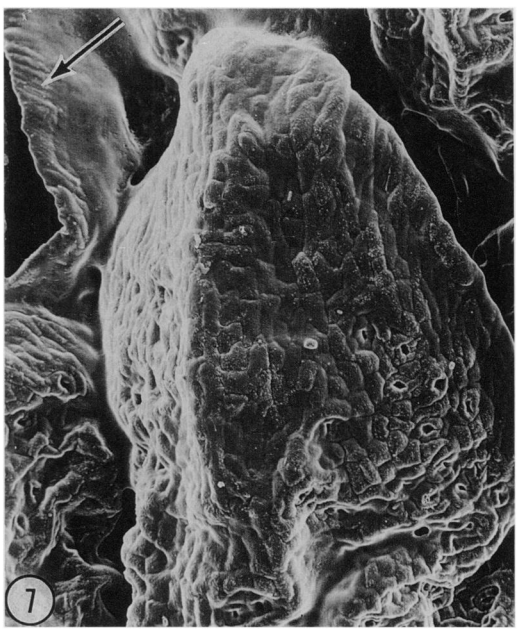
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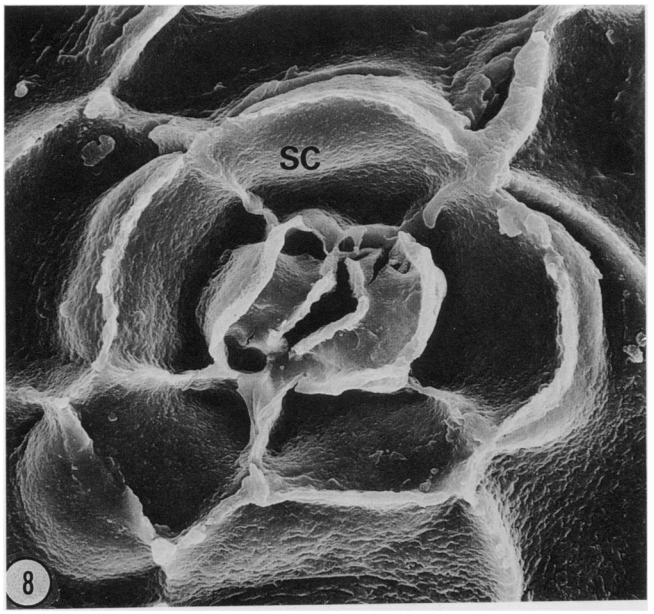
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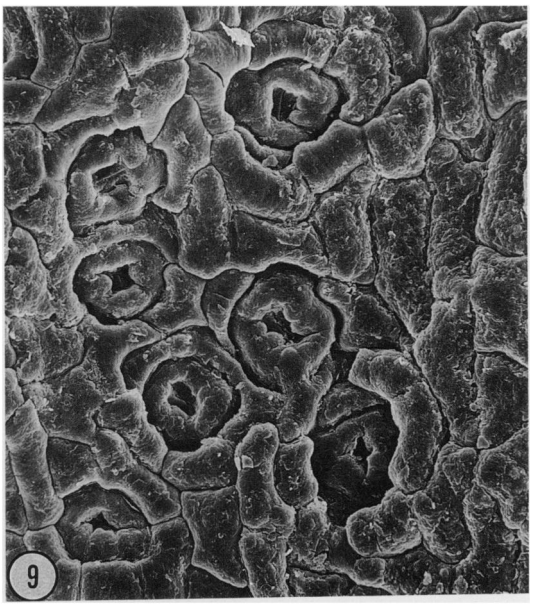
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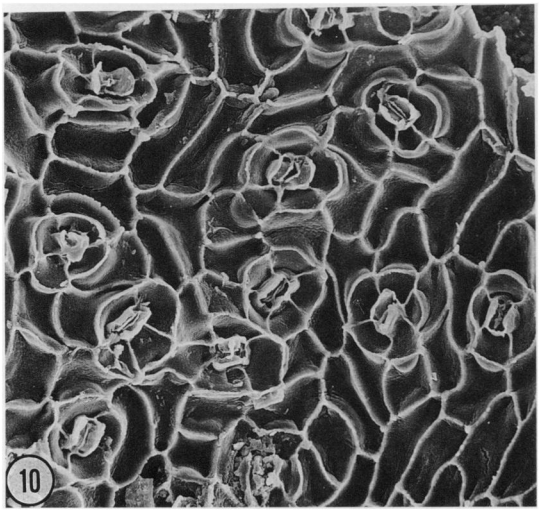
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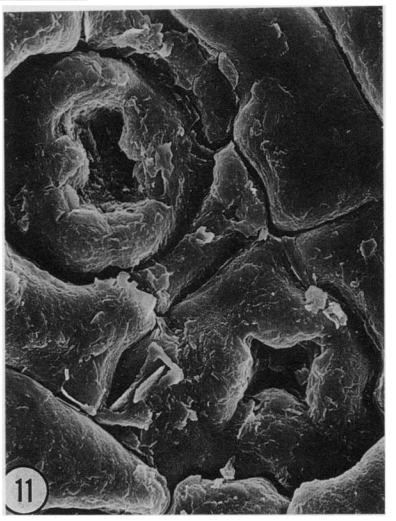
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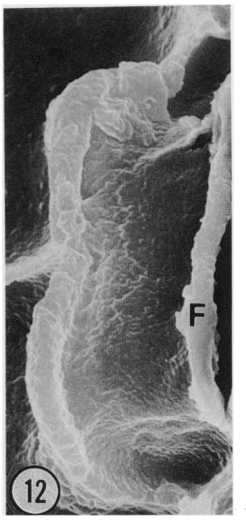
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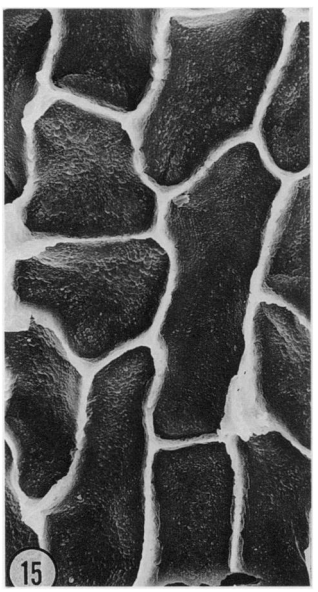
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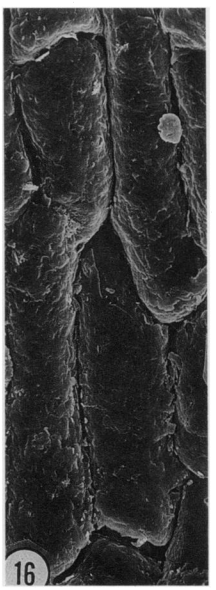
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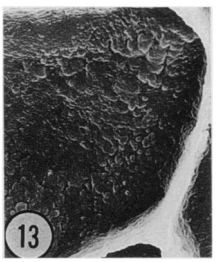
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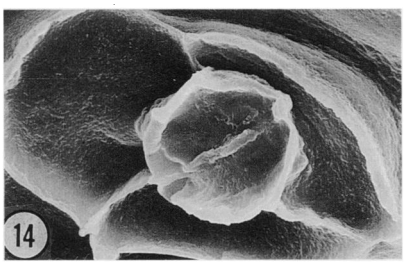
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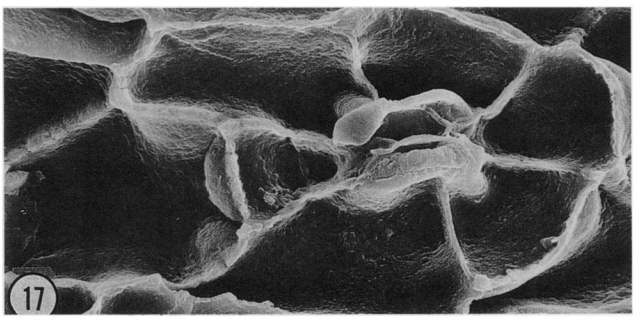
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(1969) treated some of these taxa as separate genera. Florin's group A was recognized by de Laubenfels (1969) as the genus *Falcatifolium.* Even earlier, Guillaumin (1957) recognized the unique nature of *Parasitaxus ustus.* Its parasitic nature was the subject of discussion in the late 1950s (de Laubenfels 1959), and later the genus was removed from Florin's (1931) *Dacrydium* group C taxa (de Laubenfels 1972). Quinn (1982) further subdivided Florin's group C into three separate genera: *Halocarpus, Lepidothamnus,* and *Lagarostrobos,* thus leaving Florin's group B as the only group included in the genus *Dacrydium* at the present time. While this classification has been accepted by other workers (Wells and Hill 1989*a,* 1989*b*), de Laubenfels (1984) has rejected the genera *Lagarostrobos* and *Lepidothamnus.*

The genus *Falcatifolium* was separated from *Dacrydium* on the basis of fertile structures that are produced on specialized axillary shoots, a pronounced "hump" on the epimatium that projects laterally from the mature cone, pollen morphology (de Laubenfels 1969), and a lack of vascular fibers in leaves (Tengner 1965). It is easily distinguished on the basis of leaf morphology from the imbricate-leaved *Parasitaxus* by its sickle-shaped or falcate, laterally flattened leaves with twisted bases that spread out distichously from the branch (de Laubenfels 1969; Silba 1986).

Five species of *Falcatifolium* have been examined recently for cuticle micromorphology (Stockey et al. 1992). The host plant for *Parasitaxus, Falcatifolium taxoides,* was described in detail by Stockey and Ko (1988) and Stockey et al. (1992). Micromorphologically these leaves are very different from those of the parasite. *Parasitaxus* cuticles are much thinner than those of *F. taxoides,* and epidermal cell outlines are visible externally where surfaces are very undulating. The random orientation of stomata in *Parasitaxus* contrasts with the regular rows of stomata parallel to the long axis of the leaf in *F. taxoides.* Three to six subsidiary cells are common in *Parasitaxus,* with four or five being the most common number. Two subsidiary cells are the common number, with three or four rarely occurring in *Falcatifolium.* Cuticle on subsidiary cell surfaces is also rugose in the host plant, while in *Parasitaxus* the surface is relatively smooth. Cuticle on guard cell surfaces, while smooth in *Parasitaxus,* is rugose in part and delicate polar extensions are present in *F. taxoides* (Stockey et al. 1992). Cuticle on epidermal cell surfaces in *Parasitaxus* is smooth to slightly rugose while in *F. taxoides* it is rugose and pitted. Epidermal cell outlines are rectangular in *Falcatifolium,* while their irregular nature in *Parasitaxus* is very characteristic of this taxon.

Cuticle of *Dacrydium sensu stricto* and *Parasitaxus* show many differences. Most species of *Dacrydium* are amphistomatic, with two bands of stomata on each leaf surface (Wells and Hill 1989*a;* Stockey and Ko 1990). Florin rings are often absent; stomatal plugs are present; and stomata are mostly oriented parallel to the long axis of the leaf, unlike the haphazard arrangement of stomata in *Parasitaxus.* The number of subsidiary cells in *Dacrydium* is most often two to four or five, with six rarely occurring. Polar subsidiary cells are often absent (Stockey and Ko 1990). The stomatal apparatus is elliptical, and polar extensions are common. Epidermal cell surfaces are often smooth, and epidermal cell outlines are usually rectangular and sinuous with pronounced buttresses (Wells and Hill 1989*a;* Stockey and Ko 1990), contrasting dramatically to the smooth, rounded outlines and irregular shapes of the epidermal cells in *Parasitaxus.*

Since *Parasitaxus* seems most closely related to the former *Dacrydium* group C taxa, a closer comparison is necessary. To clarify leaf micromorphology of these taxa, Wells and Hill (1989*a*) reported that all three genera, *Halocarpus, Lepidothamnus,* and *Lagarostrobos,* are amphistomatic with randomly oriented stomata, stomatal apparati with a rounded outline, polygonal and isodiametric epidermal cells that are arranged randomly except over the midrib. Most species of the three genera have leaves with marginal frills or fringes (Wells and Hill 1989*a*).

Differences do occur between these genera and *P. ustus.* Wells and Hill (1989*a*) point out differences between the species of the genus *Lagarostrobos,* with *L. colensoi* (Hook.) Quinn having many characters in common with *Halocarpus* species. Unfortunately, these taxa are distinguished from one another along with four other podocarpaceous genera in a dichotomous key, and

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Figs. 8–17 *Parasitaxus ustus* cuticle micromorphology. Fig. 8, Inner view, abaxial surface showing one stomatal apparatus with an irregular outline and five subsidiary cells (*SC*); × 850. Fig. 9, Outer view, abaxial cuticle showing sunken Florin rings and distinct epidermal cell outlines; × 180. Fig. 10, Inner view, abaxial cuticle showing scattered stomatal arrangement, irregular outline of stomatal apparatus, and elongate, rectangular epidermal cells between stomata; × 170. Fig. 11, Outer view, abaxial cuticle showing sunken Florin rings and surrounding epidermal cells; × 350. Fig. 12, Inner view, abaxial cuticle on guard cell surface showing inrolled edge and flange (*F*) of cuticle between guard cells; × 2400. Fig. 13, Inner view showing granular cuticle on epidermal cell surface; × 900. Fig. 14, Inner view, abaxial cuticle showing stomatal apparatus with three subsidiary cells; × 800. Fig. 15, Inner view showing slightly granular cuticle on epidermal cell surfaces; × 375. Fig. 16, Outer view of abaxial cuticle near leaf apex showing distinct outlines of nearly rectangular epidermal cells; × 350. Fig. 17, Inner view, abaxial cuticle showing one stomatal apparatus with irregular outline and six subsidiary cells; × 675.

Table 2

COMPARISON OF TAXA SEGREGATED FROM DACRYDIUM GROUP C BASED ON CUTICLE MICROMORPHOLOGY

Taxon	No. subsidiary cells	Florin ring	Polar extensions	Epidermal cell outlines	Marginal frill	Epidermal cell surface	Outline of stomatal apparatus
Parasitaxus de Laubenfels:							
P. ustus (Vieillard) de Laubenfels	3–6	Present	Absent	Smooth, thin, curved	Small	Smooth to slightly granular, concave	Elliptical, uneven
Halocarpus Quinn:							
H. bidwillii (Hook. f. ex T. Kirk) Quinn	4–6	Present	Present/rare	Small buttresses	Large	Smooth to slightly granular	Circular to elliptical
H. biformis (Hook.) Quinn	4–6	Present	Present/rare	Small buttresses	Large	Smooth to slightly granular	Circular to elliptical
H. kirkii (F. Muell. ex Parl.) Quinn	4–6	Present	Present/rare	Smooth	Large	Smooth to slightly granular	Circular to elliptical
Lagarostrobos Quinn:							
L. colensoi (Hook.) Quinn	4–6	Present	Present	Smooth	Small	Very granular to pitted, creases or striations	Circular to elliptical
L. franklinii (Hook. f.) Quinn	4–6	Absent	Present/rare	Smooth	Small	Granular to pitted, creases or striations	Circular to elliptical
Lepidothamnus Phil.:							
L. fonkii Phil.	4–6	Present	?Absent	Smooth, thin, curved	Small	Granular, concave	Circular to elliptical, uneven
L. intermedius (T. Kirk) Quinn	4–6	Present	Present	Smooth	Small	Granular, concave	Circular to elliptical
L. laxifolius (Hook. f.) Quinn	4–6	Present	Present	Smooth, thin	Absent	Granular, concave	Circular to elliptical

Sources. Florin 1931; other data modified from Wells and Hill 1989*a*.

complete information on all taxa is not retrievable in this format. We have attempted to compare these taxa in table form (table 2) on the basis of the information presented in Wells and Hill (1989*a*) and our observations.

The number of subsidiary cells (four to six) is standard for the group. The rare occurrence of three subsidiary cells in *Parasitaxus* reported in this article may be a factor of larger sample size. In other conifer cuticle micromorphology studies, when large samples of leaves are examined (e.g., the genus *Agathis,* Araucariaceae), three subsidiary cells appear infrequently in most species (Stockey and Atkinson 1993). In other genera, however (e.g., *Araucaria*), three subsidiary cells have been reported only in some species despite large sample sizes (Stockey and Ko 1986). Therefore, it may be that differences in subsidiary cell number between *Parasitaxus* and the three recent *Dacrydium* segregates (table 2) are unimportant taxonomically and simply reflect a larger sample size.

The presence or absence of a Florin ring in this group, or at least within the genus *Lagarostrobos,* may have limited taxonomic value. In *Lagarostrobos franklinii* (Hook. f.) Quinn the rings may be indistinct or absent. Perhaps a larger sample size might reveal even more variability. A similar situation is reported in *Falcatifolium,* where several of the species show the presence and absence of Florin rings on parts of the same leaf (Stockey et al. 1992). In some conifer genera (e.g., *Agathis*), the presence of a Florin ring is taxonomically significant (Stockey and Atkinson 1993), while in others (e.g., *Dacrydium sensu stricto*) its significance is doubtful (Wells and Hill 1989*a*).

The absence of polar extensions in *Parasitaxus* probably reflects the thickness of the cuticle in general. Furthermore, this delicate piece of cuticle is often lost in preparations for SEM depending on cuticle thickness and handling. Large enough samples, however, usually reveal the presence of a polar extension when it does occur in a species. The presence or absence of a polar extension in *Lepidothamnus fonkii* Phil. is not clear at the present time. Extensions are absent in all of the *Parasitaxus* leaves examined so far.

Epidermal cell characters and those of the leaf marginal frill appear to be the most important taxonomically, based on the findings of Wells and Hill (1989*a*). Cuticle on the epidermal cell surfaces (periclinal walls of Wells and Hill 1989*a*) is smooth to slightly granular in *Parasitaxus* and *Halocarpus* species while that on epidermal cell surfaces of *Lepidothamnus* is granular. Wells and Hill (1989*a*) report great differences in the cuticle on epidermal cell surfaces among the *Lagarostrobos* species. They appear to us to be granular to pitted with irregular creases or striations, and thus very distinct from those of *Parasitaxus* and the other two group C genera.

Of all of the taxa in the former *Dacrydium* group C, the cuticle of *Parasitaxus* is most similar to that of *Lepidothamnus fonkii* (table 2). Cuticle on the epidermal cell surfaces is smoother in *Parasitaxus* and epidermal cell outlines more irregular. The outline of the stomatal apparatus is irregular in *Parasitaxus.* While it is not particularly noted to be irregular in *L. fonkii,* Wells and Hill (1989*a,* fig. 30) show an irregular outline in their material. It is not clear just how common this character is in the species at the present time.

Acknowledgments

We wish to thank Drs. Peter Raven and Gordon McPherson, Missouri Botanical Garden, for help in obtaining specimens; Dr. Gar W. Rothwell, Ohio University, for the use of laboratory facilities; and George Braybrook, University of Alberta, for technical assistance. Supported in part by Natural Sciences and Engineering Research Council of Canada grant A-6908 and Central Research Fund Grant, University of Alberta, to Ruth A. Stockey.

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