

CUTICULAR FEATURES AND EPIDERMAL PATTERNS IN THE GENUS ARAUCARIA DE JUSSIEU

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The cuticular organization and epidermal features of leaves from the four sections of the genus *Araucaria*, growing under similar environmental conditions, were studied by scanning electron microscopy. Cuticles from these extant species and the Jurassic fossil *Araucarites santaecrucis* were compared by rubber replicas and examination of the fossil leaf surfaces. Two distinct groups of araucarian leaves are distinguished by cuticular features. The *Columbea-Bunya* species have regular stomatal rows with polar cells always oriented in the same direction, four to five subsidiary cells, and a granular inner cuticle surface on both epidermal and subsidiary cells. The *Eutacta-Intermedia* species have four to seven subsidiary cells with thin cuticular flanges between guard cells and subsidiary cells, a smooth inner cuticular surface on both epidermal and subsidiary cells, and thinner intercellular flanges on epidermal cell walls. Epidermal features of araucarian leaves appear to be taxonomically useful at the section level.

Introduction

The family Araucariaceae has been regarded as one of the most primitive of the Coniferales with a long geologic history in both the Northern and Southern Hemispheres. It contains only two genera, *Araucaria* de Jussieu and *Agathis* Salisbury. The genus *Araucaria* is a group of Southern Hemisphere conifers with a very restricted distribution. DE LAUBENFELS (1972) recognizes 14 of the 21 species endemic to the island of New Caledonia; two species are restricted to South America, three to New Guinea, and one to Australia (WILDE and EAMES 1952). The genus is divided into the sections *Columbea*, *Eutacta*, *Intermedia*, and *Bunya*, each with a distinctive leaf form (WILDE and EAMES 1952). Leaves of living species were studied with the light microscope by FLORIN (1931) and COOKSON and DUGAN (1951). Fossil araucarians were investigated mainly by KENDALL (1949), COOKSON and DUGAN (1951), MENENDEZ and CACCAVARI (1966), PANT and SRIVASTAVA (1968), and BOSE (1975).

This investigation characterizes the cuticular features and epidermal patterns of leaves from each of the four sections of the genus with scanning electron microscopy. Features of these leaves are compared with those of the Jurassic fossil *Araucarites santaecrucis* Calder, the foliage type associated with the ovulate cone *Araucaria mirabilis* (Speg.) Calder at the Cerro Cuadrado Petrified Forest in Patagonia.

Material and methods

Fresh leaves from four sections of the genus including one of the two *Columbea* species, *Araucaria angustifolia* (Bertolini) O. Kuntze; one of the three *Intermedia* species, *A. klinkii* Lauterbach; the only extant *Bunya* species, *A. bidwillii* Hooker (WILDE and EAMES 1952); and one of the 15 *Eutacta* species

(DE LAUBENFELS 1972), *A. cunninghamii* Aiton ex Lambert, were prepared for study. Leaves were collected at the Imbil Forestry Research Station in Southern Queensland, Australia, in January 1977 from trees growing under similar environmental conditions. Cuticles were prepared by cutting the leaves longitudinally to expose the mesophyll and immersing them in 20% chromium trioxide solution for 6, 18, and 24 h (ALVIN and BOUTLER 1974). The 24-h treatment produced the cleanest cuticle preparations since some leaves were rather thick and contained many fibers. Cuticles were washed in water, air-dried, and mounted on stubs with silver conductive paint. Both surfaces were examined by scanning electron microscopy. Some cuticles were prepared according to standard schedules for examination by transmitted light. Fresh leaves from these four species were also dehydrated and embedded in glycol methacrylate (FEDER and O'BRIEN 1968; ROBISON and MILLER 1975) for sectioning and light microscope examination.

Rubber replicas were made of the surfaces of *Araucarites santaecrucis* leaves with KERR Perm-lastic dental rubber (KERR Sybron Corp., Romulus, Michigan 48174), similar to a technique by WATSON and ALVIN (1976). The light-bodied base and catalyst mixture were applied first to infiltrate the small pores, using a dissecting needle to puncture and eliminate bubbles from the final cast. After drying, the heavy-bodied base and catalyst were used as a second coat to hold the mold in shape. Replicas were dried thoroughly for 24 h before coating to avoid out-gassing of the catalyst mixture in the coater. The inner surfaces of these replicas were examined and their structure compared to the inner cuticular surface of living araucarian species. Since there are no cuticular remains on the fossils, the replicas represent the actual cuticle in places where epidermal cells are preserved. The outer surfaces of

the specimens were sputter coated with gold and examined with a Hitachi S-500 Scanning Electron Microscope at 20 kV.

Results

ARAUCARIA ANGUSTIFOLIA, SECTION COLUMBEA.—The mature leaves are broad, leathery, and imbricate with acute tips. The cuticle is thick over the entire leaf surface, especially surrounding the subsidiary cells (fig. 1). Stomata occur in regular rows on both the abaxial and adaxial surfaces and are usually covered by a waxy cuticular plug (fig. 3). When this plug is mechanically removed (fig. 6), the sunken nature of stomata becomes visible with three levels of cuticular thickening. The cuticle covering the subsidiary cells is slightly more sunken than that of the surrounding epidermis; cuticle surrounding the guard cells is further depressed (fig. 6).

The inner cuticle surface reveals the most information regarding stomatal apparatus and epidermal patterns (figs. 1, 2, 4, 5). Stomata are arranged in regular rows with the polar cells always oriented in the same direction (fig. 2). Subsidiary cell number is commonly four, rarely five. The fifth cell usually results from the division of one of the polar cells (fig. 1), but some lateral subsidiary cells occasionally appear to have undergone division. Intercellular flanges (BOULTER 1971) on epidermal cells (extensions of the inner surface of the cuticle produced at the boundary of juxtaposed epidermal cells) are steep in this species when compared to those of other conifers. Flanges are thick and become pitted after 24 h in chromium trioxide (figs. 1, 5). Six- and 18-h treatments generally failed to remove the thick bands of hypodermal fibers. Epidermal cell walls appear straight to slightly sinuous in outline (fig. 2). The cuticle on the surfaces of the epidermal cells is granular in texture (fig. 5), similar to that reported in the Taxodiaceae (ALVIN and BOULTER 1974) but unlike that of other conifers.

The cuticle in the region of the stomatal apparatus is usually regarded as one of the most important parts taxonomically. Features present here are not distinct under the light microscope due to overlap of cuticular material and the complex pattern that it forms. The guard cells are situated at the hypodermal level, unlike those in *Tsuga heterophylla* (Rafinesque) Sargent in which the guard cells lie just below the surface, but they are similar in position to those in the Miocene fossil *Cryptomeria rhenana* Kilpper and *Sequoiadendron giganteum* (Lindley) Buchholz (BOULTER 1971). The cuticle on the subsidiary cells is depressed and shaped like an open umbrella (fig. 1), as in *S. giganteum* (BOULTER 1971). The surface of the cuticle on subsidiary cells is granular. The flanges of cuticle between the guard cells and subsidiary cells are thick and irregular in outline (figs. 1, 4). A ridge of cuticular tissue occurs in the aperture between the guard cells in *A. angusti-*

folia which has slight polar extensions. The surface ornamentation on the guard cell walls has several rounded pits represented by small rounded bumps of cuticular material (fig. 4). There are no striations or folds similar to those that have been described in other conifer taxa such as *Pinus peuce* Grisebach or *Sequoiadendron* (BOULTER 1971).

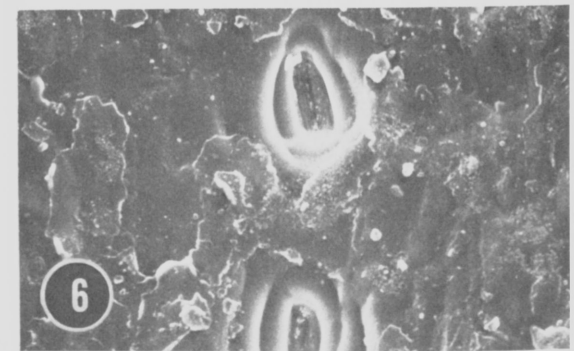
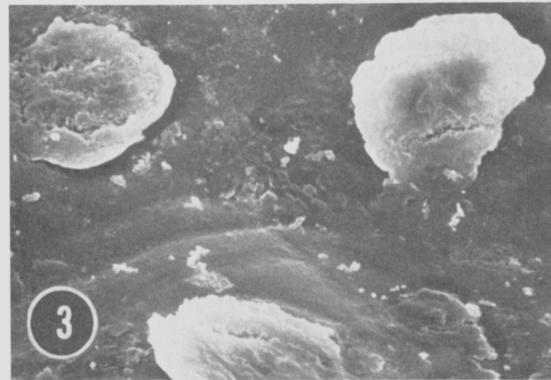
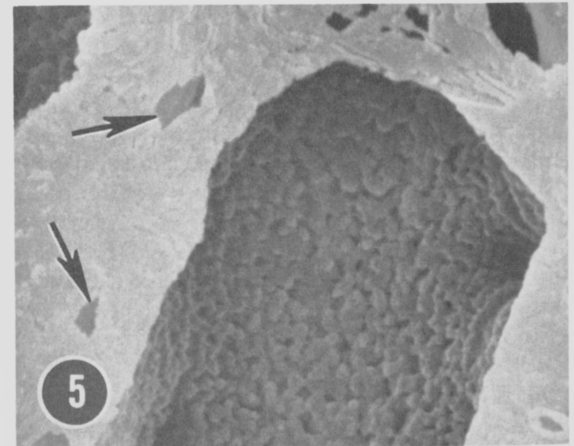
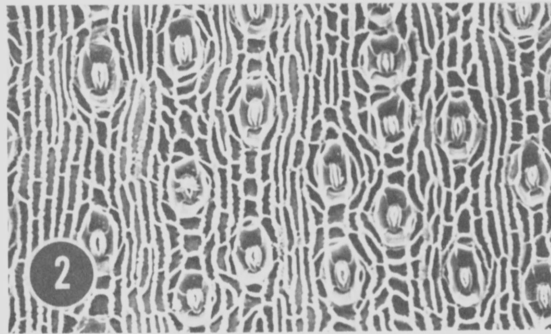
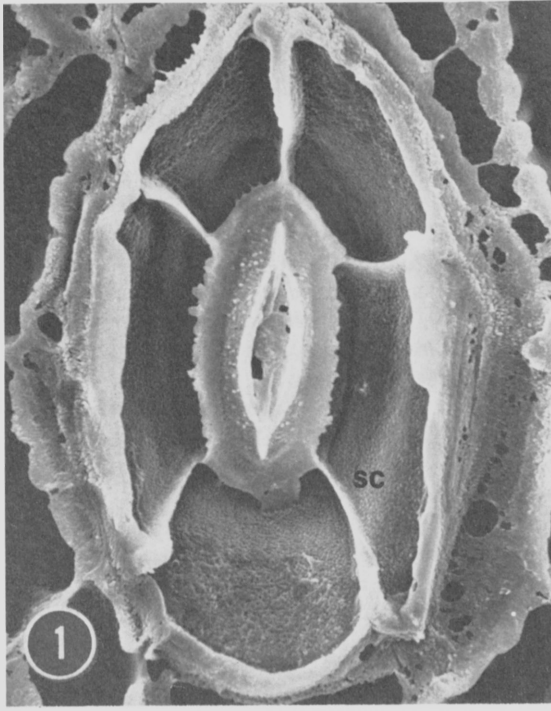
ARAUCARIA KLINKII, SECTION INTERMEDIA.—These leaves are the largest known for the genus. Mature leaves reach 12 cm long and are thin, flat, and often imbricate. Cuticle from this species is thick, and stomata occur in regular rows on both surfaces. Externally, stomata have cuticular plugs similar to other araucarian species (fig. 9). Removal of these plugs reveals three levels of cuticular thickening similar to those of *A. angustifolia* (fig. 6). No raised areas or Florin rings have been observed.

The inner cuticle surface has regularly arranged stomata, most with the polar cells oriented in one direction. A few stomata have slightly skewed guard cells with the ridge of cuticle separating them aligned with one of the ridges dividing subsidiary cells (fig. 8). Four is the most common number of subsidiary cells. Five subsidiary cells do, however, occur with higher frequency in this taxon than any other araucarians examined; six to seven subsidiary cells occur in lesser frequencies. Divisions of these subsidiary cells appear not to be the result of the polar cell division, but rather lateral cell division.

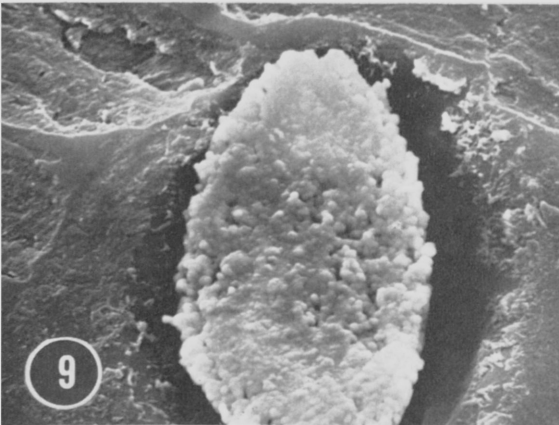
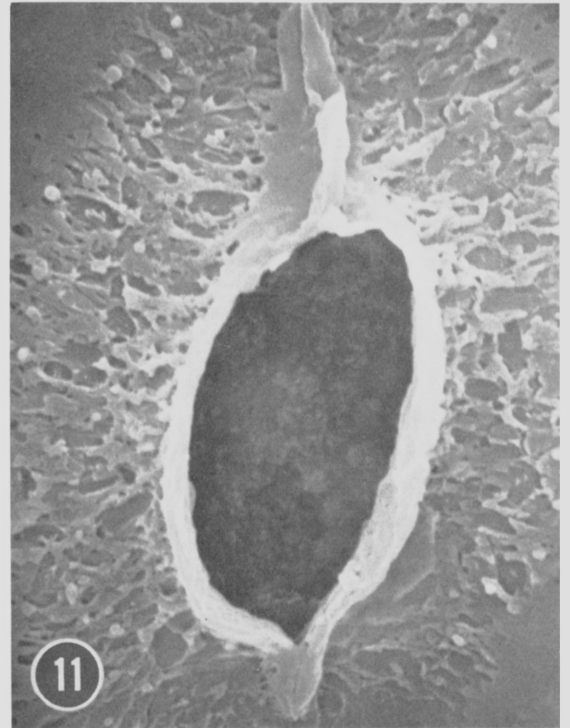
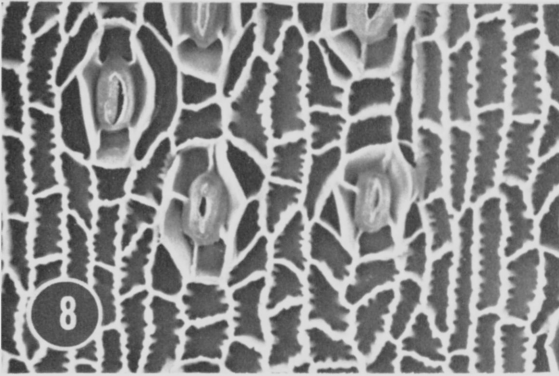
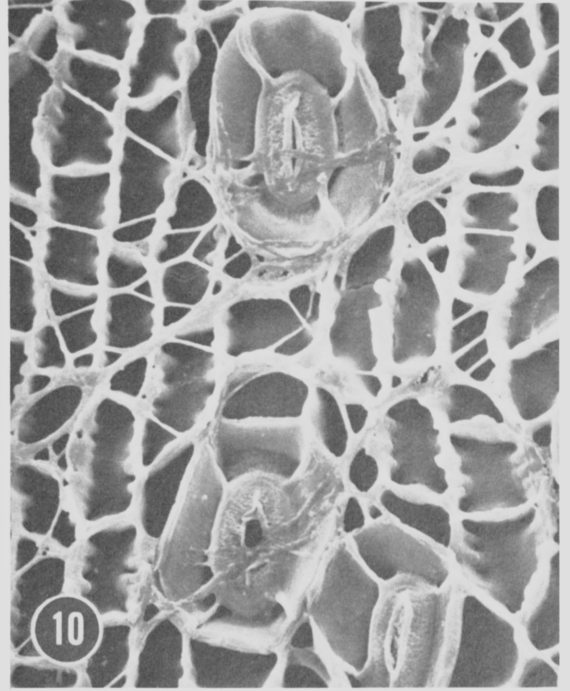
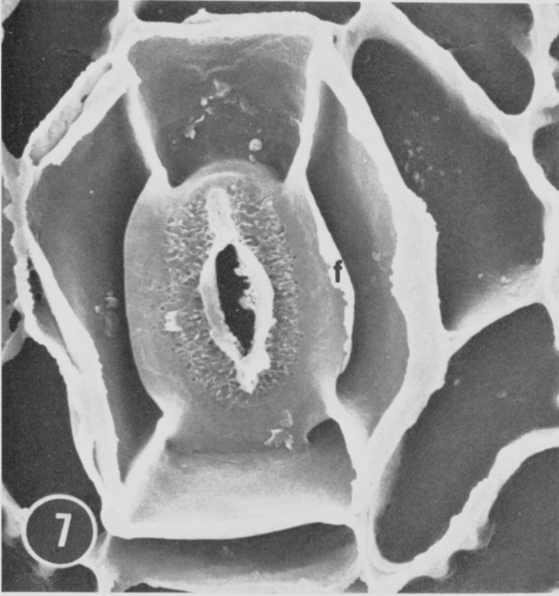
An 18-h chromium trioxide treatment of the leaves reveals cellular debris which has not been removed (fig. 10). The leaves of *A. klinkii* have scattered sclereids and lack the massive bundles of fibers that occur in Sections *Bunya* and *Columbea* (fig. 18). Flanges on epidermal cells are very steep and usually unpitted. Epidermal cell walls appear slightly wavy or undulating with very steep buttresses. At the bases of these buttresses are prominent ridges or striations similar to those in some of the Taxodiaceae (BOULTER 1971). Cell surfaces are entirely smooth and lack a granular texture (fig. 7).

The guard cells are deeply sunken to the hypodermal level. The umbrella-shaped cuticle covering subsidiary cells is unusually thick in this species (fig. 7), especially between subsidiary and epidermal cells. The surface of the subsidiary cell cuticle is smooth, as on the epidermal cells of this species. Flanges of cuticle between guard and subsidiary cells are thin when compared to other araucarian species, especially on the lateral subsidiary cells (fig. 7). Surface ornamentation on guard cell walls is reticulate with some scattered, rounded bumps of material as in *A. angustifolia* (fig. 11). The ridge of cuticle between guard cells is similar to that in *A. angustifolia* (figs. 7, 11).

ARAUCARIA BIDWILLII, SECTION BUNYA.—Leaves from mature trees exhibit two distinct morphological types and vary from small, broadly based, imbricate forms in a tight helix to larger, broad, and flattened



FIGS. 1-6.—*Araucaria angustifolia*. Fig. 1, Lower cuticle, inner surface region of the stomatal apparatus, after 24-h treatment; *sc* = subsidiary cell; $\times 1,000$. Fig. 2, Upper cuticle, inner surface after 24-h treatment, $\times 100$. Fig. 3, Upper cuticle, outer surface showing cuticular plugs after 6-h treatment, $\times 500$. Fig. 4, Lower cuticle, inner surface showing cuticle on guard cell surfaces after 24-h treatment; *f* = flange between guard and subsidiary cells; $\times 4,000$. Fig. 5, Lower cuticle, inner surface after 24-h treatment; arrows indicate pits; $\times 5,500$. Fig. 6, Upper cuticle, outer surface after 6-h treatment, showing three layers of cuticular thickening, $\times 450$.



FIGS. 7-11.—*Araucaria klinkii*. Fig. 7, Upper cuticle, inner surface, region of stomatal apparatus, after 24-h treatment; *f* = flange between guard and subsidiary cells; $\times 1,000$. Fig. 8, Lower cuticle, inner surface after 24-h treatment, $\times 250$. Fig. 9, Cuticular plug on upper cuticle, outer surface after 24-h treatment, $\times 1,500$. Fig. 10, Lower cuticle, inner surface after 18-h treatment, $\times 500$. Fig. 11, Upper cuticle, inner surface after 24-h treatment, cuticle on guard cell surfaces, $\times 4,000$.

types with a narrower attachment and nearly distichous arrangement on the branches. Both types of leaves were examined. The cuticle of *A. bidwillii* is thinner than that of *A. angustifolia*, but thick compared to other conifer genera. Externally, stomata occur in regular rows on both adaxial and abaxial surfaces of the smaller more imbricate leaves (fig. 16). There are few to no stomata on the adaxial surfaces of the larger leaves (fig. 17), while the lower surfaces have abundant regular rows of stomata. Externally, stomata have cuticular plugs. When the plug is removed (fig. 12), a raised area of cuticle becomes visible. This area is similar to but not as pronounced as the Florin rings described by BOULTER (1971) in *Pinus sylvestris* L. or *Podocarpus* (BUCHHOLZ and GRAY 1948). Outlines of the epidermal cell walls are visible on the surface as slight depressions (figs. 12, 15).

The inner cuticle surface reveals rows of stomata with similarly oriented polar subsidiary cells. Subsidiary cell number, as in *A. angustifolia*, is four, rarely five, formed by both polar and nonpolar divisions. Intercellular flanges on epidermal cells are less steep than those of *A. angustifolia* and pitted (fig. 14). A 24-h treatment in chromium trioxide was necessary for *A. bidwillii* since leaves also have a system of hypodermal fibers (fig. 18). Epidermal cell walls are relatively straight, and the cuticle on these cell surfaces has a granular texture (fig. 13).

The guard cells of *A. bidwillii* are situated at the hypodermal level. Cuticle on the subsidiary cells is also umbrella shaped, as in *A. angustifolia*, but not as extensive between subsidiaries and epidermal cells (fig. 14). The surface of the cuticle on subsidiary cells is granular.

Flanges between guard and subsidiary cells have a smooth outline, unlike those of *A. angustifolia* (fig. 14). The surface of the ornamentation on guard cell walls has a reticulate-type pattern, as in *A. klinkii*, and the ridge of cuticular material between guard cells is similar to that in *A. angustifolia* with slight polar extensions (fig. 14).

ARAUCARIA CUNNINGHAMII, SECTION EUTACTA.—Leaves, as in all species of Section *Eutacta*, are small, needlelike, and imbricate. Cuticle was studied for both mature and juvenile foliage. Mature leaves are more imbricate, broader based, and shorter, reaching about 1 cm long; immature leaves are more narrowly attached and may be over 2 cm long. Stomata on both leaf types occur in widely spaced rows on both adaxial and abaxial surfaces and possess cuticular plugs and levels of cuticular thickening like those of *A. angustifolia* (fig. 6).

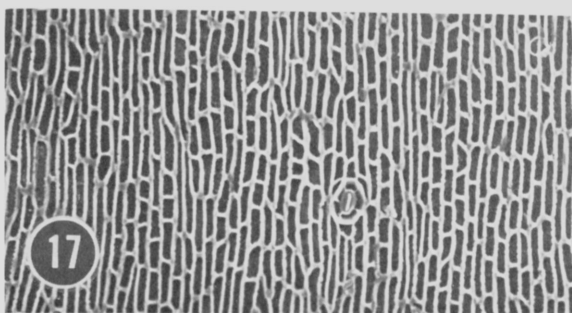
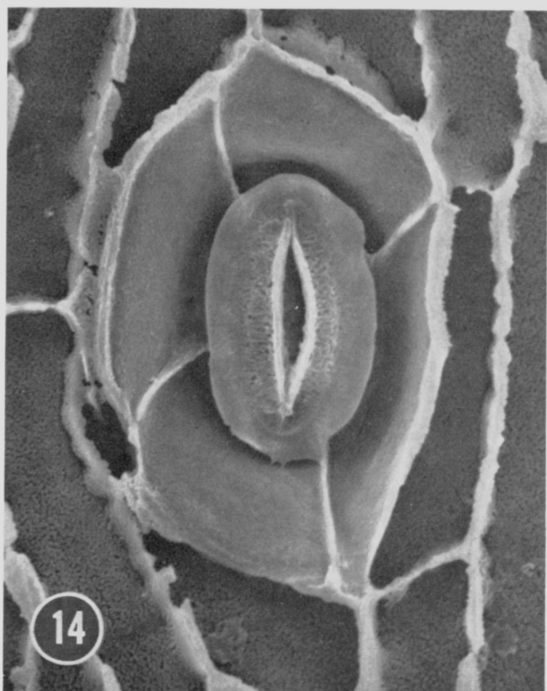
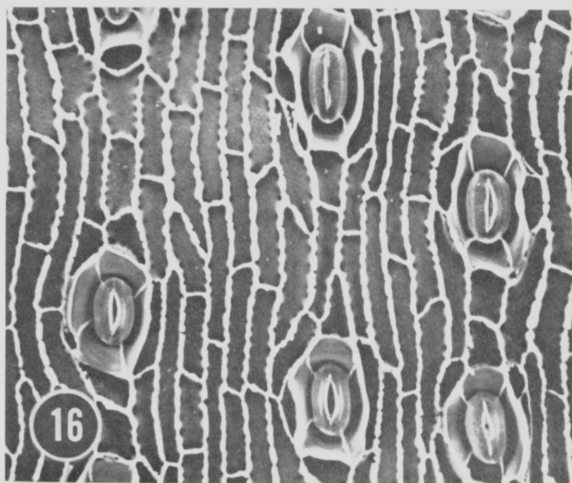
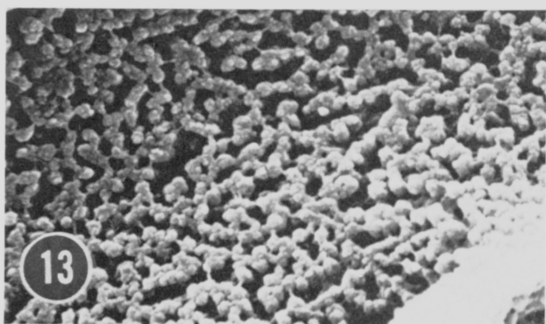
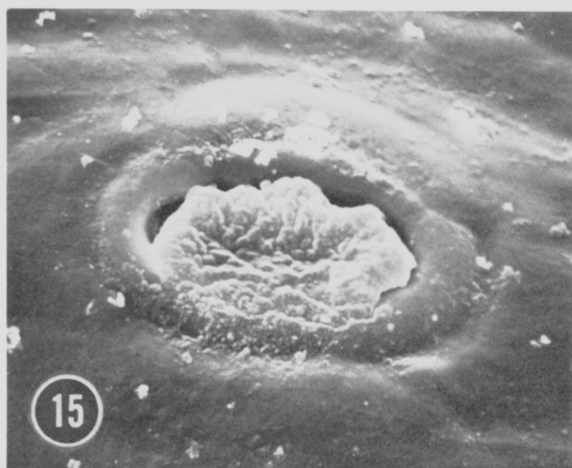
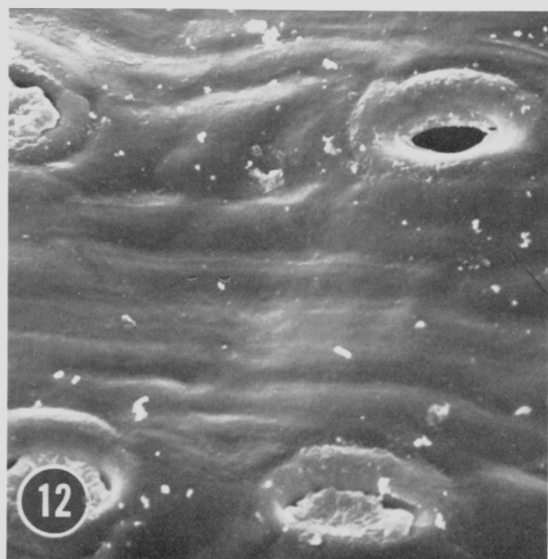
The cuticle of *A. cunninghamii* is characterized by stomata that may be arranged either in regular rows or in a haphazard fashion (figs. 19, 20). Polar cells are usually oriented in one direction, but most stomata have slightly skewed guard cells (figs. 19,

20). This feature is even more pronounced than in *A. klinkii* (fig. 8). The number of subsidiary cells ranges from four to five; four is the common number (fig. 21), and five cells are the result of both polar and lateral subsidiary cell divisions (figs. 19, 20). The intercellular flanges on epidermal cells are steep and undulating with prominent buttresses (fig. 21). Bases of buttresses, like those of *A. klinkii*, show small striated ridges. Cell surfaces are smooth or contain small lens-shaped pits (fig. 21).

Guard cells are sunken to the hypodermal level, as in the other araucarian species (fig. 22). *Araucaria cunninghamii*, however, lacks the hypodermal fibers of *A. angustifolia* and *A. bidwillii* (fig. 22).

The umbrella-shaped cuticle covering the subsidiary cells is thinner than that in the other three araucarian species but is shallower and more extensive laterally. Subsidiary cells are wider than those of the other species (figs. 21, 22). The surface of the cuticle on subsidiary cells is smooth to pitted, as on the epidermal cells of this species. This portion of the cuticle sometimes has small wrinkles similar to those near the bases of epidermal cell buttresses. Flanges between guard and subsidiary cells are thin and smooth at the polar subsidiary cells and irregular in outline on lateral subsidiary cells (fig. 21). The surface ornamentation of guard cells is rough but not reticulate, as in *A. bidwillii* and *A. klinkii*, nor are there any small rounded bumps of cuticular material as in *A. angustifolia*. The ridge of cuticular tissue between the guard cells shows slight polar extensions (fig. 21) and is thicker than that found in the other three species.

ARAUCARITES SANTAECRUCIS.—The fossil leaves are preserved on some small twigs from the Cerro Cuadrado Petrified Forest. Although most of these have little internal anatomical preservation, externally there appear to be longitudinal striations on the abaxial surfaces of some specimens (STOCKEY 1977). CALDER (1953) suggested these striations might represent ribs of sclerenchyma or the position of lines of stomata. Scanning electron micrographs of the actual specimen surface indicate depressions, fairly regularly spaced and in linear rows (fig. 25). At higher magnifications (fig. 23), the outlines of cells may be seen together with depressions corresponding to the positions of sunken stomata. The positions of the stoma and guard cells can be outlined. Rubber replicas of the same surfaces show the details of epidermal cell shapes between the stomatal rows (figs. 24, 26). Buttresses on epidermal walls have been rounded by weathering and do not show the detail in living leaves (fig. 24). The stomata appear as bumps, and the outlines of the possible locations of subsidiary cells are indistinct. Cuticle of this type is typically gymnospermous and cannot be compared closely to those of living species except in gross morphology. Rows of sunken stomata are



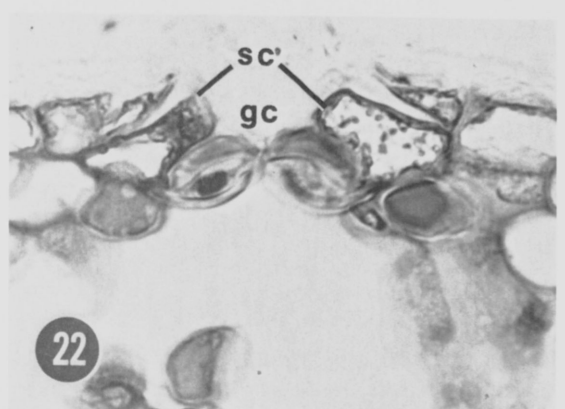
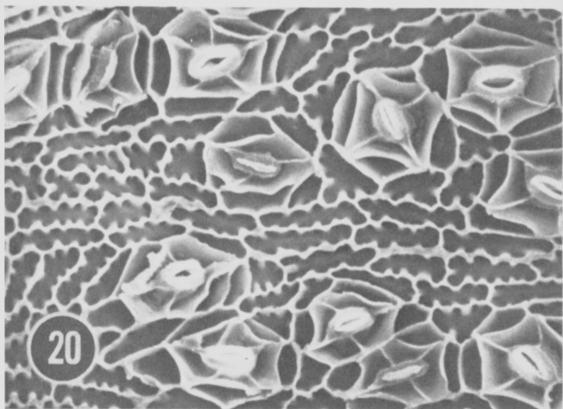
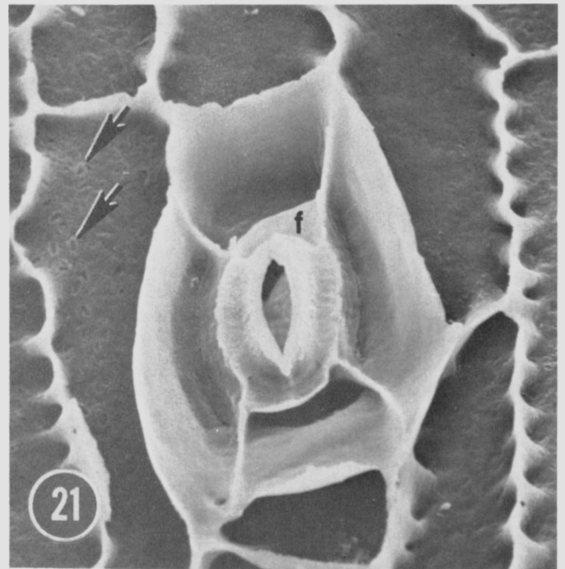
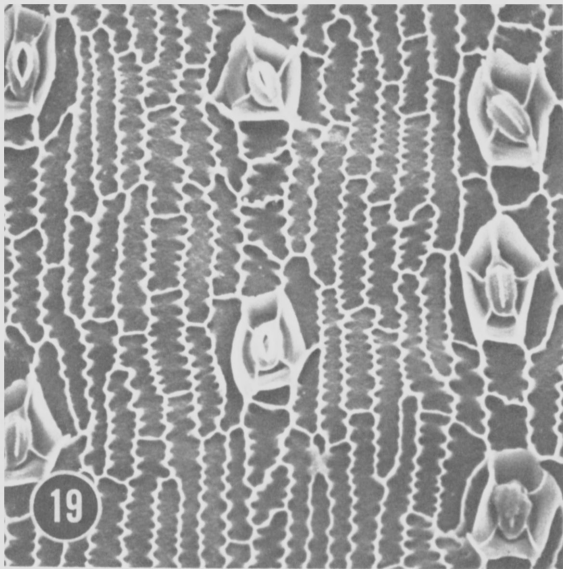
FIGS. 12-18.—*Araucaria bidwillii*. Fig. 12, Lower cuticle, outer surface after 6-h treatment, showing cuticular plugs, raised areas, and indications of epidermal cells, $\times 500$. Fig. 13, Lower cuticle, inner surface after 24-h treatment, $\times 5,500$. Fig. 14, Imbricate leaf, upper cuticle, inner surface in region of stomatal apparatus after 24-h treatment, $\times 1,000$. Fig. 15, Lower cuticle, outer surface cuticular plug after 6-h treatment, $\times 1,000$. Fig. 16, Imbricate leaf, upper cuticle, inner surface after 24-h treatment, $\times 250$. Fig. 17, Large leaf, upper cuticle, inner surface after 24-h treatment, $\times 100$. Fig. 18, Transverse section of leaf at stomatal apparatus; *fi* = fibers, *gc* = guard cells, *sc* = subsidiary cells; $\times 700$.

known to occur in the Cupressaceae, Araucariaceae, Cheirolepidaceae, Podocarpaceae, and Taxodiaceae (FLORIN 1931). The stomata are sunken singly in *A. santaecrucis* and are not situated in depressed rows. Fossil cuticular material with regular stomatal rows and singly sunken stomata includes: (Cheirolepidaceae) *Frenelopsis varians* (DAGHLIAN and PERSON 1977), *F. hoheneggeri* (WATSON and ALVIN 1976); (Araucariaceae) *Brachyphyllum mamillare* (KENDALL 1949), *Araucaria nathorstii* (MENENDEZ and CACCAVARI 1966), *Araucaria cutchensis* (PANT and SRIVASTAVA 1968), *B. macrocarpum* (HOLLICK and JEFFREY 1906); *Pagiophyllum ordinatum* (KENDALL 1948), *P. connivens* (KENDALL 1948), *P. insigne* (KENDALL 1948); (Taxodiaceae) *Cryptomeria anglica* (ALVIN and BOULTER 1974), *Sequoia langsdorfii* (ALVIN and BOULTER 1974); (Podocarpaceae) *Podocarpus strzeleckianus*, *P. gnidioides*, *P. tasmanicus*, *P. totara* (TOWNROW 1965).

Discussion

Cuticles of the four species have rows of stomata sunken to the level of the hypodermis. Intercellular flanges between epidermal cells are steep and thick. No double flanges like those reported for some fossil *Abies* specimens have been observed (BOULTER 1971). The four living species of *Araucaria* examined possess waxy plugs associated with stomata on the external cuticular surface. Internally, umbrella-shaped cuticular patterns occur over subsidiary cells. The common subsidiary cell number is four, arranged as two polar and two lateral subsidiary cells.

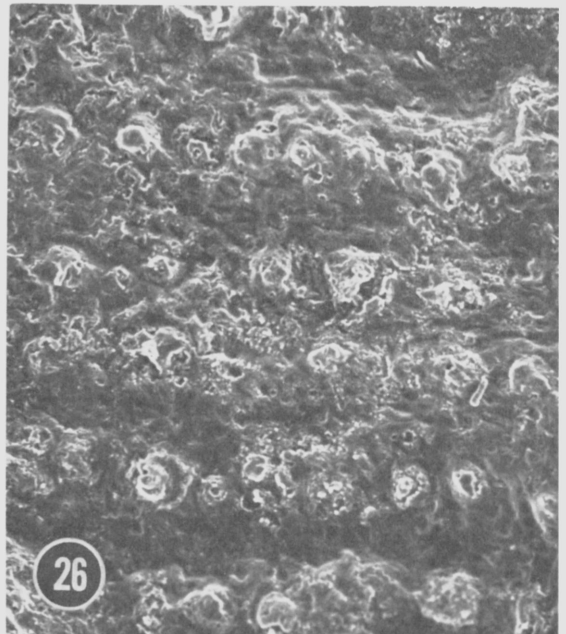
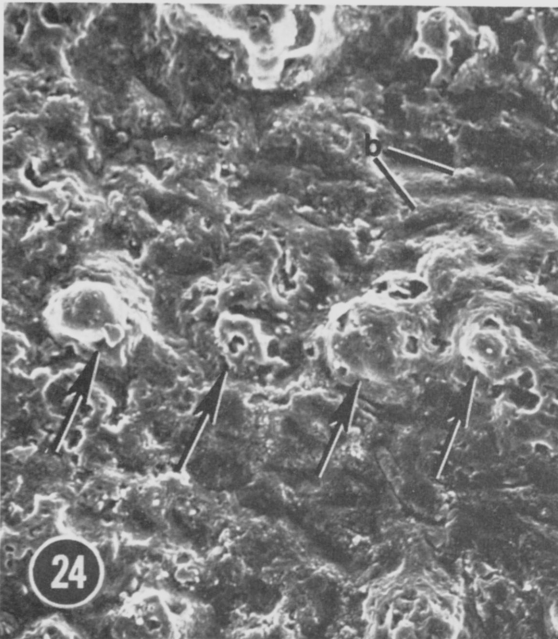
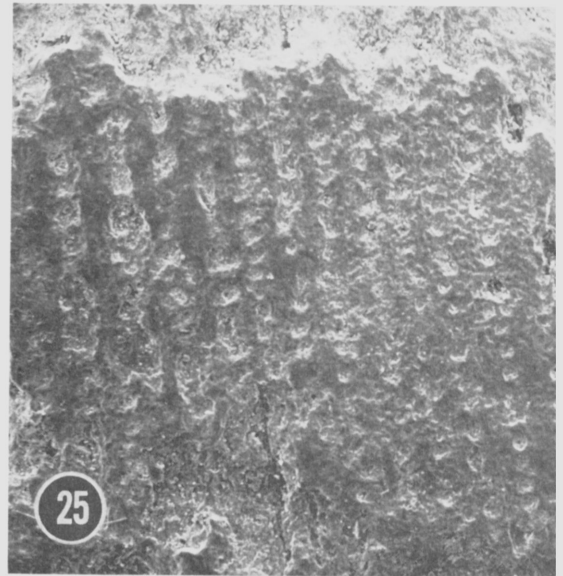
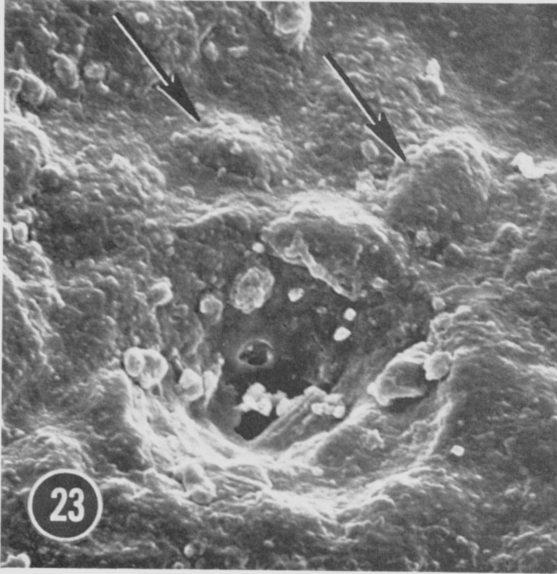
A comparison of cuticles from species of each of the four sections of the genus shows several morphological distinctions. It is possible, however, to divide the genus into two distinct sections based on these ultrastructural details. ENDLICHER (1842) divided the genus into Sections *Columbea* and *Eutacta* based mainly on cone-scale features, seedling germination,



FIGS. 19–22.—*Araucaria cunninghamii*. Fig. 19, Juvenile foliage, lower cuticle, inner surface after 24-h treatment, $\times 250$. Fig. 20, Mature foliage, upper cuticle, inner surface after 24-h treatment, $\times 250$. Fig. 21, Juvenile foliage, lower cuticle, inner surface in region of stomatal apparatus after 24-h treatment; *f* = flange between guard and subsidiary cells; arrows indicate small lens-shaped pits; $\times 1,000$. Fig. 22, Cross section of leaf in region of stomatal apparatus; *gc* = guard cells, *sc* = subsidiary cells; $\times 700$.

geographic location, and leaf morphology. WHITE (1947) described three species native to New Guinea for which he erected a new section, *Intermedia*. These species, *A. klinkii*, *A. schumanniana* Warb., and *A. hunsteinii* K. Schum., had epigeal germination and winged cone scales, like the *Eutacta* species, and broad leaves as in *Columbea*. The latest revision of the genus *Araucaria* was done by WILDE and EAMES (1952); they erected a new section *Bunya* for the Australian *A. bidwillii* that has winged cone scales resembling Section *Eutacta*, hypogeal germi-

nation like Section *Columbea*, and two foliar types unlike any other species. DE LAUBENFELS (1972) suggested there are only two sections in the genus, *Araucaria* and *Eutacta*. Within the section *Araucaria* he includes the South American species *A. angustifolia* and *A. araucana*, the Australian *A. bidwillii*, and WHITE's (1947) Section *Intermedia* (*A. klinkii*, *A. hunsteinii*, and *A. schumanniana*). The other araucarian species are included within Section *Eutacta*, based on the differences between mature and juvenile foliage in these species. Based on the limited



FIGS. 23–26.—*Araucarites santaecrucis*. Fig. 23, Outer specimen surface showing depressed stoma and position of epidermal cells (arrows), $\times 720$. Fig. 24, Rubber replica of adaxial surface showing raised areas corresponding to stomata (arrows) and depressions (epidermal cells); *b* = epidermal cell cuticular buttrusses; $\times 250$. Fig. 25, External surface of specimen showing regular rows of stomata, $\times 25$. Fig. 26, Rubber replica of five regular stomatal rows and epidermal patterns, $\times 100$.

number of species examined in this study, a division of the genus into two sections is suggested. The species assignments to these sections would differ from that of DE LAUBENFELS (1972), however.

Species of *Columbea* and *Bunya* have many cuticular features in common. The stomata are arranged in regular rows with the polar cells always oriented in the same direction. Numbers of subsidiary cells are generally constant at either four or five. The inner cuticular surface is granular on both epidermal and subsidiary cell surfaces. Holes or pits are present in the intercellular flanges.

The *Eutacta* and *Intermedia* species also share many cuticular features. The inner cuticular surface that covers subsidiary and epidermal cells is smooth with the exception of occasional lens-shaped pits in some *A. cunninghamii* leaves. Intercellular flanges are thinner in these two groups and exhibit a lower relief than the *Columbea-Bunya* species. The buttresses on epidermal cells are solid, lacking pits, and more sinuous in outline than the *Columbea-Bunya* species.

The cuticular features of the four species in this study are sufficiently distinct to permit each of them to be differentiated from the others. Study of the remaining species in the genus would, of course, be required to confirm the utility of such features in the genus as a whole. The results to date have been promising, and further study may well provide additional information of significant taxonomic value. In addition, these cuticular features may provide information of significant value in evolutionary considerations of this relict group of conifers.

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