

MICROMORPHOLOGICAL STUDIES OF THE LEAF CUTICLE
IN SELECTED LAURALES

BY

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2. DEDICATION

To my Mum
and my fiancé
Ron.

3. PREFACE WITH ACKNOWLEDGEMENTS

The ease with which the cuticle may be obtained from leaves by maceration has been known for many years. Light microscopic studies of such isolated membranes have indicated that the cuticle is an important source of characters for diagnostic and taxonomic work. Recently, scanning electron microscopy has permitted separate investigation of both surfaces of a cuticle. In gymnosperms, the inner side has been shown to be of particular interest and significance. It reflects not only the epidermal structure often in great detail but also exhibits a considerable wealth of fine sculptural patterns. These features appear to be remarkably constant within species thereby rendering them of value in taxonomy. However, the range of inner surface micro-morphology, its constancy and, therefore, its taxonomic importance is not well known in angiosperms, although its probable usefulness has been suggested.

The aim of the following study is to add to our knowledge of these aspects in selected members of a closely related flowering plant group, the Laurales [i.e. Lauraceae, Austrobaileyaceae, Gomortegaceae, Hernandiaceae and Trimeniaceae] by 1, describing the variation in internal microrelief; 2, establishing its relationship with the outer surface and 3, determining the nature of any intra-specific differences, from light- and scanning electron-microscopic observations as well as 4, assessing its potential for indicating taxonomic affinities by numerical methods.

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4. ABSTRACT

The range of cuticle micromorphology in leaves of Lauraceae and the related families Austrobaileyaceae, Gomortegaceae, Hernandiaceae and Trimeniaceae has been studied in detail using light- and scanning electron-microscopy. Results indicate that there is a great deal of variation in aspects of the outer and most particularly, the inner surface of isolated membranes. The features observed are described and illustrated diagrammatically or in micrographs.

The microrelief of the stem cuticle in the leafless parasitic genus Cassytha of the Lauraceae has also been examined. Stomata are similar to those of other members of the family and stem cell morphology is closely allied to that of costal cells in leaves.

The structural organisation of the complex appearance of the abaxial epidermis of Caryodaphnopsis tonkinensis has been investigated. Paradermal sections clearly reveal it to consist of densely packed, coronulate, striate papillae which often fuse at the apices, interspersed by deeply sunken stomata. Its development has also been followed in a preliminary way from young leaves.

A study of intraspecific variation of cuticular characters in five morphologically distinct species [Beilschmiedia madang, Caryodaphnopsis tonkinensis, Dehaasia cuneata, Cinnamomum oliverii and Laurus canariensis] has been undertaken. Specimens of each species are basically very similar. Nevertheless, some dissimilarity may be recognised. An attempt has been made to relate differences found with environment.

Numerical analyses of subsets of 381 cuticular and epidermal features derived from aspects described in the main part of the study within 88 Operational Taxonomic Units [OTUs] has been carried out. Principal co-ordinates analysis results show that families considered to be related to Lauraceae are distinct from it but closely allied

amongst themselves. The Lauraceae itself appears to be a very close group. Cluster analysis gives a taxonomic structure which is comparable in some respects with classifications of these families.

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6. LITERATURE REVIEW

In seed plants, the outer wall of all epidermal cells of mature foliage leaves is covered by a continuous layer or sheet of mainly lipid, wax and cutin components known as the cuticle or cuticular membrane. Fundamentally, this comprises the epicuticular wax overlying the cuticle proper, beneath which a cuticular layer may be present. The cuticle was first demonstrated clearly by Brongniart [1834] in leaves of Brassica oleracea [Cruciferae], although its existence on exposed parts of the plant had been recognised previously in the mid-eighteenth century [Ludwig, 1757; de Saussure, 1762; Hedwig, 1793] according to Barthelemy [1868]. Many workers have given accounts of the history of the study of this layer, covering most especially aspects of structure, including Edwards [1935], Roelofsen [1952], Stace [1965a], Martin & Juniper [1970], Napp-Zinn [1973], Sargent [1976b], Wilkinson [1979], Oladele [1981] and Holloway [1982]. Therefore, it will not be dealt with here.

Whilst they may be visible in thin transverse sections, cuticular features, particularly those of the inner surface [abutting the epidermal cellulose cell wall in situ], may most successfully be detected using light- and scanning electron-microscopy from isolated cuticles prepared either by chemical maceration or by enzyme degradation. These techniques have been well described by Stace [1965a], Martin & Juniper [1970], Alvin & Boulter [1974] and Juniper & Jeffree [1983].

It has been established by Barthlott & Ehler [1977] and Barthlott [1981] that sculptural characters of the cuticle may be classified according to whether they are basic features [primary], such as cell shape, course of anticlinal walls, relief of cell boundary and curvature of outer periclinal wall, or are superimposed on others, e.g. surface ornamentation [folding, granularity, micro-papillation resulting from subcuticular or cuticular crystal inclusions: secondary] and epicuticular secretions [tertiary]. Inner surface characters may also

be arranged on the basis of these criteria, although Barthlott & Ehler [1977] and Barthlott [1981] considered them all to be secondary microrelief.

6.1 PRIMARY SCULPTURE

6.1.1 FLANGES: TERMINOLOGY

At the boundary of adjacent epidermal cells, the cuticular layer often penetrates between the cellulose anticlinal walls forming a three-dimensional system of projections which have been variously named in the literature. They have been called 'lamellae or pegs' [Solereeder, 1908], 'cuticular pegs' [Eames & Macdaniels, 1947; Skoss, 1955; Sargent, 1976a & b; Holloway, 1982], 'cutinised pegs' [Ihlenfeldt & Hartmann, 1982], 'ribs' [Fritz, 1935; Oztig, 1940; Lange, 1965] 'anticlinal ribs' [Norris & Bukovac, 1968], 'internal cuticular ribs' [Priestley, 1943], 'ridges' [Stace, 1966, Baker, 1970, 1971], 'anticlinal extensions' [Dilcher, 1974], 'spandrels' [Frey-Wyssling, 1976] and 'wedges' [Napp-Zinn, 1973; Barthlott & Ehler, 1977; Ehler, 1977]. Currently, the most favoured terms are 'anticlinal' or 'intercellular flanges' or simply 'flanges' [Skoss, 1955; C.I.M.P., 1964; Stace, 1965a & b; Boulter, 1971; Wilkinson, 1971, 1979, 1983; Bongers, 1973; Van Staveren & Baas, 1973; Alvin & Boulter, 1974; Stockey & Taylor, 1978a & b; Miranda & Chaphekar, 1980; Barthlott, 1981; Gibbon, 1981; Oladele, 1981; Alvin, Dalby & Oladele, 1982], first used by Haberlandt [1910, 1914].

This variety of terminology may lead to a misconception of the cuticular membrane micromorphology, especially where similar terms have been employed for other cuticle features, such as ridges [outer surface sculpture] and pegs [corner projections]. Here, the term 'flange' has been used throughout. 'Peg' is reserved for flange corner extensions.

6.1.2a FLANGES: PROMINENCE

The degree to which flanges project between the epidermal anticlinal walls varies [Brongniart, 1834; Von Mohl, 1842; Skoss, 1955; Stace, 1965a; Lange, 1969; Baker, 1970, 1971; Bongers, 1973; Napp-Zinn, 1973; Wilkinson 1979 ; Miranda & Chaphekar, 1980; Oladele, 1981]. Recently, Holloway [1982] gave a diagrammatic representation of this variability. In it, he recognised three basic states: 1, absence of flanges; 2, flanges just extending into the uppermost portion of the anticlinal wall and 3, flanges penetrating deeply between the abutting cells. Previously, Lange [1969] used the terms 'rudimentary' [e.g. in Pittosporum undulatum: Pittosporaceae] and 'complex, honey-comb' [as in Dissilaria tricomis: Euphorbiaceae] for the two main types of flange prominence. He also noted the existence of many intermediates.

The depth to which the flanges project determines the extent of definition of epidermal cells on isolated cuticles. Skoss [1955] noticed this after examination of membranes of Citrus limon [Rutaceae] which showed only slight flange extension and vague delimitation of cells and Clivia nobilis [Amaryllidaceae] where there were deep flanges and therefore strong cellular 'impressions'. It has been confirmed in a range of different seed plants by a number of authors [Norris & Bukovac, 1968; Boulter, 1971; Bongers, 1973; Miranda & Chaphekar, 1980].

The conspicuousness of epidermal outlines is thought to be connected with the thickness of the cuticle as a whole [Stace, 1980]. The earlier results of Baker [1970, 1971] support this since thin, delicate membranes were shown to have fine flanges [e.g. in Bryonia dioica: Cucurbitaceae] and robust cuticles, deeper flanges, producing more distinct relief on the inner surface [as in Sansevieria trifasciata: Liliaceae].

Flange prominence and cuticle thickness as well as other aspects of cuticular structure are known to reflect plant type and growth habit [Stace, 1965a, Baker 1970,

1971; Barthlott & Ehler, 1977; Wilkinson, 1979). Herbaceous plants tend to have very fine relief whereas evergreens and xerophytes have more conspicuous flanges. Baker (1971) suggested that the chemical composition of the cuticle is also related to plant habit since he discovered that thin, fragile membranes of some herbs had a high proportion of fatty acids in the cutin matrix and certain xerophytes and evergreens with thick, complex cuticles had a high hydroxy-fatty acid content.

Flanges may sometimes be entirely absent. Various examples have been reported (Von Mohl, 1842; Skoss, 1955; Baker, 1970). Stace (1965a) stated 'there is some evidence that the cuticular membrane is more or less completely lacking in cell outline in many, though by no means all, herbaceous dicotyledons'. Wilkinson (1979) also found this to be sometimes so in water plants as well as in herbs with membranous leaves. According to Stace (1965a), the absence of flanges is rare in woody plants.

Differences in flange prominence between plants of various habits, however, were not noted by Orgell (1955) from her observations on, for example, Cinnamomum camphora (Lauraceae), Convolvulus arvensis (Convolvulaceae), Ficus elastica (Moraceae), Lactuca scariola (Compositae), Magnolia grandiflora (Magnoliaceae) and Zea mays (Graminae), in all of which flanges were said to be 'quite prominent'.

The extent to which flanges project in different parts of one leaf may not be the same, as shown by Pant & Verma (1974) in their studies of Ephedra (Ephedraceae). Cells were normally clearly marked on the abaxial cuticle surface but on the adaxial, from the basal part of the lamina, cell outlines were obscure in certain species of the genus.

6. 1.2b EXTENSIVE CUTINISATION: PERICLINAL AND ANTICLINAL

The inner limit of cutinisation varies greatly, as recognised by Stace (1965a). The leaf epidermis in some

seed plants may sometimes be very extensively cutinised so that the outer periclinal walls of the cells are completely impregnated with cutin, as seen in transverse sections of Gasteria sp. (Liliaceae) and Yucca sp. (Agavaceae) [Meyer, 1938]. As Eames & Macdaniels [1947] point out, the entire radial walls of the epidermis and even the inner periclinal walls may become cutinised. Partial cutinisation of the inner periclinal walls has been illustrated in Abies recurvata and some Pinus species by Miranda & Chaphekar [1980].

Holloway [1982] in his diagrammatic portrayal of states of flange prominence, showed a stage [4] where the whole of epidermal cell may be cutinised. Eames & Macdaniels [1947] mentioned that such cells may die but commonly 'remain alive with normal pits and plasmodesmata'.

The walls of subepidermal cells are known to be partially cutinised in a range of seed plants. Skoss [1955] found it impossible to isolate certain cuticles by enzyme 'retting' e.g. of species of Ceratonia (Leguminosae), Diospyros (Ebenaceae), Eucalyptus (Myrtaceae), Feijoa (Myrtaceae), Ficus (Moraceae), Hedera [helix] (Araliaceae) and Hypericum (Guttiferae) due to extensive cutinisation or 'suberization of interior cell walls', as he called it. Lange [1969] produced scanning electron micrographs of Dysoxylon fascernum (Meliaceae) and Stenocarpus sinuatus (Proteaceae) internal sculpture, showing 'fine' and 'mesh of polygons' respectively which exemplified extensively cutinised epidermis and included flanges penetrating the hypodermis. Later, Sitholey [1971] described and illustrated cutinised hypodermal cells in Magnolia grandiflora (Magnoliaceae), Mimusops elengi (Sapotaceae) and Psidium guajava (Myrtaceae). Even deeper cutinisation i.e. of palisade and spongy mesophyll cells, was recorded by the same author in other species, such as Piper betle (Piperaceae). The various cell types could be distinguished at different levels of focus in the light microscope; the flanges of the epidermis appearing as dark outlines and those of the hypodermis as light. In Limonia acidissima (Rutaceae)

and Mangifera indica [Anacardiaceae] cutinised sub-epidermal cells frequently formed particularly refractive aggregations.

Cutinisation of cell layers beneath the epidermis may be characteristic of certain plant types: xeromorphs or xerophytes [Stace, 1965a; Wilkinson, 1979] and those with coriaceous leaves, although this is by no means always so.

6.1.3 FLANGES: SHAPE IN PROFILE AND SURFACE VIEW

When flanges are present, their profiles are a particularly characteristic feature seen in thin transverse sections with the light microscope, especially when the cuticle is stained. This was shown by Von Mohl [1842]. 'V'- or 'wedge'-shaped flanges have been illustrated or described in numerous angiosperms [Von Mohl, 1842; Fritz, 1935; Meyer, 1938; Watson, 1942; Scott, Schroeder & Turrell, 1948; Scott, Hamner, Baker & Bowler, 1958; Brachet & Mirsky, 1961; Lange, 1969; Baker, 1970, 1971; Napp-Zinn, 1973; Holloway, 1982; Ihlenfeldt & Hartmann, 1982] for example, in the monocotyledons Aloë acinacifolia [Liliaceae: Haberlandt, 1914], Eria barbarosa [Orchidaceae: Barthlott & Ehler, 1977] and Libertia elegans [Iridaceae: Sargent, 1976b] as well as in the dicotyledons Citrus aurantifolia [Rutaceae: Baker, 1970], Hartleya inopinata [Icacinaceae: Van Staveren & Baas, 1973] and Pyrus communis [Rosaceae: Norris & Bukovac, 1968]. The same configuration has also been found to occur commonly in gymnosperms [Florin, 1931], such as Callitris endlicheri [Cupressaceae: Oladele, 1981] Picea engelmannii [Pinaceae: Miranda & Chaphekar, 1980] and Welwitschia mirabilis [Welwitschiaceae: Barthlott & Ehler, 1977].

However, other profile forms are known: 'spinning-top', 'rod' or 'spindle'-shaped in certain Aizoaceae, notably Lithops spp. [Oztig, 1940], 'peg-shaped' in Musa spp. [Musaceae: Eames & Macdaniels, 1947], 'hemicylindrical' in Dysoxylon fuscum [Meliaceae] or 'U-sectioned' in Aloë succotrina [Liliaceae] [Lange, 1969] and 'hook-like' [Haberlandt, 1910].

Thus, the literature indicates that the 'V'- or 'wedge' type is the most common flange profile. Baker [1970] also found this to be so from his observations whereas earlier Lange [1969] asserted rarity of 'keeled' or 'V-shaped' outlines. Barthlott & Ehler [1977] even based flange nomenclature on the assumption that the cuticle penetrating between the anticlinal walls normally formed a wedge shape. The C.I.M.P. [1964] mentioned only triangular (V-shaped) outlines for flanges in section in their scheme of terminology, presumably for the same reason.

The shape of the flange seen in T.S. by light microscopy corresponds to the configuration revealed with the S.E.M., i.e. U-sectioned flanges tend to be blunt or rounded ridges, V-sectioned tapering and pointed.

In most plants, flanges are essentially single, undivided projections. Nevertheless, certain taxa appear to have double flanges due to the presence of a more or less conspicuous median longitudinal groove, e.g. Apollonias barbujana [Lauraceae: Ferguson, 1974b], Belliolum crassifolium and some Pseudowintera spp. [Winteraceae: Bongers, 1973] as well as Pinus rigida [Pinaceae: C.I.M.P., 1964]. Here, according to Boulter [1971] the middle lamella is not replaced by cutin although the wall on either side is cutinised. Sometimes the groove is less deep, such as in Athrotaxis selaginoides [Alvin & Boulter, 1974], Sequoia sempervirens [Taxodiaceae: Oladele, 1981], Juniperus communis and var. siberica [Cupressaceae: Oladele, 1981; Alvin, Dalby & Oladele, 1982] where it has been considered 'shallow', presumably owing to some cutinisation at the middle lamella. The groove may also vary in width. Miranda & Chaphekar [1980] found this amongst Pinaceae showing double flanges: those between rows of stomata in Pinus peuce had a broad furrow whilst flanges between adjacent epidermal cells in for example, Abies concolor, Pseudotsuga japonica and certain Tsuga spp. had a narrow groove in comparison. Such grooved flanges have a characteristic profile in T.S. bearing a well-defined median indentation, as illustrated by the same

workers in Tsuga caroliniana. Plants may exhibit this type of flange on cuticles of both leaf surfaces or only on one side, e.g. in Aucuba japonica [Cornaceae: Gibbon, 1981], Belliolum crassifolium and Pseudowintera traversii [Winteraceae: Bongers, 1973]. It has been suggested that grooved flanges may be connected with the occurrence of lignification of the anticlinal cell walls [Miranda & Chaphekar, 1980].

6.1.4 FLANGES: CELL FORM AND UNDULATION

In a cuticle, flanges [if present] appear as a network of lines marking the middle region between abutting epidermal anticlinal walls and, therefore, reflect cell shape. Cells are very variable in outline, differing in different areas on one leaf surface, for example in intercostal, costal [p. 43] and marginal [p. 45] regions and on the adaxial side to the abaxial, as recognised by many workers including Dilcher [1974], Cutler [1978] and Metcalfe [1979]. Outlines have been shown to be isodiametric [length to width approximately equal] or elongated in one direction, with four or more sides. Commonly, cells are tetra- to hexagonal although the existence of between 3- and 30-gonal has been reported by Barthlott [1981]. Plants with narrow leaves, such as members of the dicotyledonous families Caryophyllaceae, Epacridaceae, Fabaceae and Polemoniaceae [Metcalfe, 1979], conifers [Florin, 1931] and many monocotyledons e.g. Clintonia uniflora [Liliaceae] and Kniphofia macowanii [Liliaceae] [Cutler, 1978] have been found to have cells which are elongated in the same direction as the organ. In Graminae, e.g. Festuca ovina [Haberlandt, 1914], Anudo donax and Phalaris canariensis [Cutler, 1978] these 'long' cells are known to be interspersed by 'short' cells. Some plants, however, have cells elongated perpendicularly to the long axis of the leaf, as reported by Haberlandt [1914] in Bromeliaceae, Crassula [Crassulaceae], Cycadaceae, Silene fruticosa [Caryophyllaceae] and Tradescantia [Commeliniaceae]. Most dicotyledons and many monocotyledons without the strap-like type of leaf often have more isodiametric [Haberlandt, 1914] or irregular shaped cells [Cutler, 1978]. According to the latter author, cells of

dicotyledonous taxa, e.g. Acacia alata [Leguminosae] and Plumbago zeylanicum [Plumbaginaceae], are rarely organised in distinct rows since their leaves typically grow in area by a marginal rather than a basal meristem. Various schemes have been suggested in the literature to describe cell shape [C.I.M.P., 1964; Barthlott & Ehler, 1977], size [length:width ratio] and arrangement [Dilcher, 1974].

The basic form of the cells in a cuticle preparation may be modified by the shape of the individual flanges constituting the cell outlines, as noted by Barthlott & Ehler [1977]. Their course, which is variable, has been described simply as 'straight' or 'undulate' by some workers, for example Boulter [1971], and Miranda & Chaphekar [1980]. Others have attempted to distinguish a number of distinct categories, generally three of increasing sinuosity termed 'straight', 'slightly undulate (or sinuate)' and 'strongly undulate (or sinuate)' [Thomas & Bancroft, 1913; Bandulska, 1926, 1928, 1931; Odell, 1932; Stace, 1965a, 1980; Ramayya & Rajagopal, 1968; Wilkinson, 1971, 1978; Bongers, 1973; Ferguson, 1974b; Barthlott, 1981]. Some, however, have used four [C.I.M.P., 1964; Van Staveren & Baas, 1973; Ahmad, 1974a & b; Baas, 1975].

Attempts have been made to express undulation in terms of vibratory wave characters. For example, Watson [1942] utilised height of waves [amplitude] and number of undulations per cell and Stace [1965a] suggested the usefulness of three variables: frequency [wavelength per wall; half wavelengths or peaks per cell], amplitude and wavelength. This treatment has been recommended more recently by Barthlott & Ehler [1977], Wilkinson [1979] and Barthlott [1981].

Sinus shape has also been shown to vary. U-, V- and Ω -forms have been detected in a range of plants by Stace [1965a] and Wilkinson [1971] and these, together with S-type by Barthlott & Ehler [1977] and Barthlott [1981].

Stace [1965a] was first to employ wave features, sinus details and the degree of undulation in a scheme for the description of flange shape. In it he recognised 7 types. This system was later modified by other workers [Barthlott & Ehler, 1977; Wilkinson, 1979]. Numbers [increasing from 1 to n with increasing sinuosity] have been assigned to each type to simplify application.

Flange undulation is a widespread phenomenon among seed plants and has often been used as a character in systematic studies.

Different families may exhibit a similar range or type of patterns. This has been found to be so in Araliaceae and Myristicaceae [Odell, 1932] as well as in Avicenniaceae and Rhizophoraceae [Stace, 1965a & b]. Constituent genera may show variation in the degree of undulation, as demonstrated by Bandulska [1926, 1928] and Ferguson [1974b] [Lauraceae], Stace [1966, 1980] [Combretaceae], Ramayya & Rajagopal [1968] [Portulacaceae], Van Staveren & Baas [1973] [Icacinaceae] and Miranda & Chaphekar [1980] [Pinaceae]. Differences are also known to occur between species of a genus. Such variability has been reported in a range of seed plants, e.g. Cinnamomum [Lauraceae: Odell, 1932]; Belliolum, Bubbia and Pseudo-wintera [Winteraceae: Bongers, 1973]; Lophopetalum [Celastraceae: Jansen & Baas, 1973]; a number of Icacinaceae [Van Staveren & Baas, 1973], Aquifoliaceae [Baas, 1975], Pycnarrhena [Menispermaceae: Cutler, 1975], Araucaria [Araucariaceae: Stockey & Taylor, 1978a & b], Abies and Pinus [Pinaceae: Miranda & Chaphekar, 1980] and various other conifers [Florin, 1931].

Flanges may display similar undulation patterns on cuticles of both leaf surfaces, as in the case of many of the examples mentioned above although in other plants, flange shape may differ on the two sides. This has been recognised by a number of workers [Solereeder, 1908; Bandulska, 1926; Odell, 1932; Stace, 1965a]. According to Bandulska [1926], 'sinuation of epidermal walls [= flanges] is.... even more frequent on the upper than

on the lower surface' in Lauraceae. The results of Baas [1975] also indicated such a trend, especially in Nemopanthus, Phelline and Sphenostemon [Aquifoliaceae]. In contrast, Solereder [1908] made the general statement that cell outlines were rarely undulate on the adaxial [upper] side. Odell [1932], likewise, concluded that straight 'walls' were characteristic of the upper cuticle and wavy 'walls' of the lower. Whilst a greater degree of undulation is common in abaxial than adaxial flanges [Stace, 1965a, 1966, 1980; Ferguson, 1974b] nevertheless the reverse configuration may occur, occasionally, such as in Acer pseudoplatanus [Aceraceae: Odell, 1932], Terminalia microcarpa and T. plagata [Combretaceae: Stace, 1965a], or more regularly, e.g. in Acanthaceae [Ahmad, 1974a & b], Celastraceae [Jansen & Baas, 1973], Icacinaceae [Van Staveren & Baas, 1973] and Winteraceae [Bongers, 1973].

The degree of flange undulation may be influenced by plant habit. Stace [1965a] noticed that straight 'walled' cells seemed to be more frequent in xeromorphic species than in mesomorphic. The reason for this was not understood. Flange shape also appears to be correlated with habitat, according to observations made by Baas [1975] for Ilex spp. [Aquifoliaceae]. In the tropics this author reported that the percentage of species with undulate outlines increased with decreasing altitude. About 17% exhibited this flange configuration in high mountain habitats, approximately 45% in mountain habitats at 1000-2500 m, whilst about 60% of species had undulate outlines in tropical lowland areas and a similar percentage in both temperate and sub-tropical regions. The relative advantages and disadvantages of situation are unknown [Stace, 1965a].

Flanges may show different degrees of undulation at different levels of focus in the light microscope. Watson [1942] described this phenomenon in Hedera helix [Araliaceae]. Undulations tend to be more pronounced or sometimes even confined to the base of the flange [where it joins the periclinal cuticle], as in Afrostryax

lepidophyllus and Hua gabonii [Styraceae: Baas, 1972], Ilex spp., e.g. I. ovalifolia [Aquifoliaceae: Baas, 1975], Gymnacranthera, Horsfieldia, Knema and Myristica spp. [Myristicaceae: Koster & Baas, 1981] and one group of Zygogynum species [Winteraceae: Bongers, 1973]. In contrast to this usual situation, Stace [1965a] reported that in some straight 'walled' species, for example, Conocarpus erectus [Combretaceae], flange tips were irregularly undulate and suggested this might be an artifact due to the effect of displacement of cellular material from the cuticle during maceration of the leaf.

Some plants have sinuous flanges which appear to be of uneven width in the light microscope. Ferguson [1974a] found that 'cells' seemed to be thickened at the crests of the undulations in Cocculus laurifolius [Menispermaceae]. He also recognised the significance of the angle made by the flange with the periclinal surface and realised that the characteristic appearance was due to variation in this angle. Ferguson [1974b] recorded a similar case in Laurus azorica [= L. canariensis] [Lauraceae]. Scanning electron microscopic examination of the inner surface of such isolated membranes e.g. those of Parishia maingayi [Anacardiaceae] carried out by Wilkinson [1979], has provided further evidence for Ferguson's [1974a] interpretation. Similar investigations in certain conifers [Boulter, 1971; Stockey & Taylor, 1978a & b; Miranda & Chaphekar, 1980] have indicated that undulation arises due to the existence of alternating buttresses and cavities [cellulose filled before isolation] throughout the length of the flange between adjacent cells. Florin [1931] was first to illustrate these buttressed flanges in certain Picea spp. [Pinaceae] and Podocarpus spp. [Podocarpaceae]. Much later Boulter [1971] observed this type of flange in Metasequoia glyptostroboides [Taxodiaceae] and Pinus peuce [Pinaceae] and Barthlott & Ehler [1977] reported such regularly arched and perforated flanges in all the Pinaceae they examined as well as in Ginkgo [Ginkgoaceae] and Gnetum spp. [Gnetaceae]. However, Barthlott [1981] mentioned the presence of a more irregular configuration in Gnetum gnemon. Miranda & Chaphekar [1980] recognised

four cavity types amongst the Pinaceae: rounded-oval [e.g. in Abies koreana], elliptical [as in A. homolepis], semicircular [e.g. in Pinus contorta or P. echinata] and flask-shaped.

Therefore, buttressed or according to Barthlott [1981] 'perforated' flanges, appear to be characteristic of all the major groups of gymnosperms. Barthlott also noted the absence of this flange form in angiosperms with the exception of a few specialised taxa, for example, in the family Bromeliaceae although earlier, Ehler [1977] described such flanges in Tillandsia hildae.

6.1.5 FLANGES: WIDTH OR THICKNESS

Another important feature contributing to the form of cells outlined on a cuticle is the thickness or width of the flanges. Wilkinson [1971] determined wall width at the top of the flange where it abutts onto the cuticle proper. Oladele [1981] recorded the width of the flange base at the level of the interface between the periclinal cuticle and the cell wall.

Various states of flange thickness have been reported. These have usually been defined qualitatively in categories ranging from thin to very thick [Thomas & Bancroft, 1913; Bandulska, 1926; Jansen & Baas, 1973]. However, Oladele [1981] recognised three states of thickness in his studies of Cupressaceae and Taxodiaceae, based on quantitative data. Most commonly, workers have only noted the presence of especially thick flanges, for example Alvin & Boulter [1974], Stockey & Taylor [1978a & b] and Gibbon [1981].

Flange width may be similar in cuticles of both leaf surfaces or different [see Oladele, 1981]. Adaxial flanges are thicker than abaxial in some plants, such as all species of Aniba, Lindera and Litsea [Lauraceae] examined by Bandulska [1926]. Generally those of the adaxial were thick and the abaxial thin in comparison. Notable exceptions were A. robusta, where flanges were intensely thick on the upper cuticle and thick on the lower and Lindera rufa with thick adaxial outlines and moderately thick abaxial

flanges. Wider adaxial flanges have also been found in some Cupressaceae, e.g. Callitris spp. and many Chamaecyparis spp. [Oladele, 1981]. However, the reverse situation is also known. Baas [1975] recorded the remarkable occurrence of this in a few species and varieties of Ilex [Aquifoliaceae] particularly in I. paraguayensis var. sincorensis. Oladele [1981] likewise, showed it to exist in a range of coniferous taxa, such as Cryptomeria japonica, Sequoiadendron spp. [Taxodiaceae] and Thujopsis dolabrata [Cupressaceae].

6.1.6 FLANGES: CONTINUITY

Flanges may be completely continuous, i.e. uninterrupted along their length [Bandulska, 1926; Dewar & Wallis, 1935; Wilkinson, 1971, 1978; Bongers, 1973; Van Staveren & Baas, 1973; Baas, 1975; Oladele, 1981] in angiosperms, e.g. Agave americana [Agavaceae: Baker, 1971], Dianthus caryophyllus cv. White [Caryophyllaceae: Reed, 1982; Reed & Tukey Jnr., 1982], Eria barbarosa [Orchidaceae: Barthlott & Ehler, 1977] and Kokoona spp. [Celastraceae: Jansen & Baas, 1973] as well as in gymnosperms, such as Cedrus, Larix, Pseudolarix and Pseudotsuga spp. [Miranda & Chaphekar, 1980].

Sometimes, however, flanges have a distinctly beaded appearance especially in the light microscope. Haberlandt [1910] made one of the first references to this feature in a diagram of Prunus laurocerasus [Rosaceae]. A number of cuticular studies, for example, those of C.I.M.P. [1964], Wilkinson [1971, 1979], Bongers [1973], Ferguson [1974a & b], Pant & Verma [1974] and Oladele [1981] have revealed that beading results from the presence of non-cutinised areas in the anticlinal walls. The minute striae detected across flanges by Skoss [1955] were thought to indicate that epidermal cell plasmodesmata penetrate them. Oladele [1981], more recently, considered interruptions to represent pits in the anticlinal walls because they were easily observed in leaf surface sections and pit frequency corresponded to the number of gaps in the flanges of cuticular preparations. Nevertheless, Bongers [1973] was unable to decide whether flange pits in Winteraceae

members were continuous with those in the cellulose walls.

The presence of beaded or pitted flanges has been detected in a range of seed plants [Bandulska, 1926; Dewar & Wallis, 1935; Skoss, 1955; Lange, 1969; Bongers, 1973; Jansen & Baas, 1973; Van Staveren & Baas, 1973; Ferguson, 1974a; Baas, 1975; Gibbon, 1981; Koster & Baas, 1981; Holloway, 1982], such as Amentotaxus argotaenia and A. formosana [Taxaceae: Ferguson, Jähnichen & Alvin, 1978], many Ephedra spp. [Ephedraceae: Pant & Verma, 1974], Lumnitzera racemosa [Combretaceae: Stace, 1966], Robinia pseudacacia [Leguminosae: C.I.M.P. 1964] and Schizachyrium sanguineum [Graminae: Barthlott & Martens, 1979].

Most workers have failed to give any further details regarding this feature. However, Wilkinson [1971] from her studies of Anacardiaceae, recognised six types based on differences in size, frequency and density of wall pitting seen in the light microscope and represented them in a series of diagrams designated a-f. Later, Wilkinson [1979], in a review of cuticular features in angiosperms, simply reported that beading may vary from fine to coarse and that flanges are either completely or only partially interrupted. Oladele [1981] distinguished three states of interruption founded on the number of interrupted flanges in a cell and the number of gaps per flange. Cupressus macrocarpa, most Chamaecyparis species and Thujaopsis dolabrata exemplified low, moderate and high frequencies of interruption respectively.

Aspects of flange beading or pitting are known to differ between cuticles of the adaxial and abaxial surfaces: presence of the feature [Bandulska, 1926; Bongers, 1973; Van Staveren & Baas, 1973; Alvin & Boulter, 1974; Wilkinson, 1978], prominence [Pant & Verma, 1974], size [Wilkinson, 1978] and frequency [Oladele, 1981]. Differences have also been found depending on the tissue type. Sitholey [1971] noticed that in certain species with extensive cutinisation such as Psidium guajava [Myrtaceae],

flanges of the epidermal layer were beaded whilst those of the hypodermal layer were continuous. In Stemonurus grandiflorus [Icacaceae], Van Staveren & Baas [1973] discovered that unspecialised cells had pitted flanges whereas those adjacent to the 'arms' of astereosclereids had unpitted outlines.

Pore-like discontinuities or holes may perforate the flanges of some taxa e.g. Allium cepa [Liliaceae: Bancher *et al.*, 1960; Franke, 1961; Wilson *et al.*, 1972] and Araucaria angustifolia, A. cunninghamii and A. klinkii [Araucariaceae: Stockey & Taylor, 1978a & b]. Such pores may be located either at the flange edge [partially bounded by cutin] or in the main flange body, according to the micrographs of Lange [1969]. They vary in form: small, rounded in Amentotaxus argotaenia [Taxaceae: Ferguson, 1978], minute to window-like in Dissilaria tricomis [Euphorbiaceae: Lange, 1969], indistinctly developed and irregular in Gunnera tinctoria [Malvaceae] and Paulownia tomentosa [Scrophulariaceae] [Barthlott & Ehler, 1977], as well as in frequency. They may be particularly associated with extensive cutinisation, e.g. in Pinus ponderosa [Pinaceae: Miranda & Chaphekar, 1980] between the epidermis and the hypodermis. It seems likely that perforations in flanges are non-cutinised regions associated with plasmodesmata, although there is no evidence to support this. Barthlott & Ehler [1977] suggested that such perforated flanges result from inter-cellular spaces being packed towards the outside between the anticlinal epidermal walls. However, the situation is difficult to visualise.

6.1.7 FLANGES: MARGIN FORM AND CORNER EXTENSIONS

Flanges may have an even [i.e. regular] or non-jagged margin, such as in Agave americana [Agavaceae: Baker, 1971], Eria barbarosa [Orchidaceae: Barthlott & Ehler, 1977], certain Abies, Cedrus and Larix species [Pinaceae: Miranda & Chaphekar, 1980] and Thuja orientalis [Cupressaceae: Oladele, 1981] or an uneven or 'irregular' marginal configuration, for example in Clivia nobilis [Liliaceae: Skoss, 1955], Callitris endlicheri and

Fitzroya cupressoides [Cupressaceae: Alvin, Dalby & Oladele, 1982]. These probably arise due to the depth of cutinisation being either similar or different respectively along the flange length. When uneven, the margin may show various degrees of irregularity. Most workers have failed to determine this. However, Oladele [1981] recognised a number of states of what he termed 'jaggedness' in Cupressaceae and Taxodiaceae based on the number of 'teeth' or irregularities per flange seen in oblique side view with S.E.M: 1, Low [less than 5 teeth/flange], as in Calocedrus macrolepis, 2, moderate [5-10 teeth/flange], e.g. in Callitris endlicheri and high state [more than 10/flange], such as in Widdringtonia juniperoides. Irregularity shape may differ. Blunt irregularities have been illustrated in Euonymus europaeus [Celastraceae] by Baker [1971] and described in Araucaria spp. by Stockey & Taylor [1978a & b]. Sharply projecting or pointed forms are known in for example Amentotaxus argotaenia [Taxaceae: Ferguson, 1978; Ferguson, Jähnichen & Alvin, 1978], Clivia miniata [Liliaceae: Holloway, 1982] and Welwitschia mirabilis [Welwitschiaceae: Barthlott & Ehler, 1977].

In many plants, the depth of cutinisation at the cell corners is similar to elsewhere. In some, however, it is conspicuously deeper where flanges of several cells meet, due to the presence of a cutin extension [C.I.M.P., 1964]. This may be of various forms as seen in the scanning electron microscope: blunt [peg-like], as illustrated by Baker [1971] in Ilex aquifolium [Aquifoliaceae], Bongers [1973] in Bubbia viellardii [Winteraceae] and Barthlott & Ehler [1977] in Eria barbarosa [Orchidaceae], tapering, e.g. in Bubbia pachyantha [Winteraceae: Bongers, 1973] and Clivia miniata [Amaryllidaceae: Holloway, 1982] or long and whip-like, such as in Buchanania arborescens [Anacardiaceae: Wilkinson, 1979]. Occasionally, they are restricted to flanges of either the adaxial or the abaxial cuticle, according to the results of Bongers [1973]. These extensions appear as thickened cell corners when viewed with light microscopy [Wilkinson, 1979]. Nevertheless, C.I.M.P. [1964] showed the possibility of flat corner

thickenings i.e. without any cutin extension.

6.1.8 FLANGES: BASE FORM

In certain gymnosperm cuticles, the base of the flanges may be swollen giving a tiered or terraced appearance in surface view in the S.E.M. Oladele [1981] found this to be particularly characteristic of those of the adaxial side in a number of Cupressaceae. The author described and illustrated a range of prominence of this feature from moderate, for example in Cupressocyparis leylandii and Pilgerodendron uviferum to prominent, as in Chamaecyparis nootkatensis. He called these swollen bases buttresses, a term which may be confused with the buttresses involved in flange undulation. Oladele [1981] also recognised that their development was related to the prominence or bulging of the cells, as seen from the outer surface but not to other external characters such as papillae.

6.1.9 PERICLINAL SURFACE: SCROBICULI AND THIN AREAS

Cells are known to be flat, concave or convex. The cuticle overlying the cell reflects these shapes on its inner surface, for example, where there are papillae on the outside, the inside may show round or oval cavities [corresponding to the lumina]. Baker [1970] found these concave depressions in Gasteria planifolia [Liliaceae]. Miranda & Chaphekar [1980] included this pattern as type I, in their scheme of cuticular microsculpture noted in the Pinaceae and termed the concavities 'scrobiculi'. The configuration was shown to be characteristic of Larix potanini and Pseudotsuga flahaultii. 'Crater-like deepenings' or 'thin places' may occur in the middle of the periclinal surface in certain membranes, e.g. in Welwitschia mirabilis [Welwitschiaceae: Barthlott & Ehler, 1977].

6.2 SECONDARY SCULPTURE

6.2.1 ORNAMENTATION: PERICLINAL SURFACE

The surface of contact between the cuticle and the underlying epidermal cellulose cell wall, in the periclinal region, may be readily observed in the light microscope from thin transverse sections stained with Sudan IV. This was recognised by various early workers e.g. Von Mohl [1842] and Haberlandt [1910, 1914]. The latter, in his [1914] paper, noted that the boundary could either be even or uneven as a result of the way the two zones interlocked [the latter pattern being brought about by the projection of minute cutinised teeth or ridges of various shapes into the cellulosic region at a number of points]. Intrusion of the cuticle by cellulose was also shown to be possible [Haberlandt, 1910]. These observations have been supported by the more recent work of Alvin & Boulter [1974] and Juniper & Jeffrey [1983] who, in their discussion of cuticle structure gave a generalised diagram depicting the interface as irregular with a reticulum of channels, often cellulose filled, permeating the cuticular layer.

When an isolated cuticle is examined with light- or scanning electron-microscopy the surface micromorphology of the inner side of the membrane in the periclinal region, corresponds to the cuticle/cellulose wall boundary configuration as seen in leaf sections and, therefore, may or may not be ornamented.

Smooth cuticles [i.e. with an even interface in T.S. and no surface sculpture] are found in a variety of seed plants [Barthlott & Ehler, 1977]. They are known to be characteristic of a wide range of angiosperms [Kurer, 1917; Skoss, 1955; Brachet & Mirsky, 1961; Bongers, 1973; Jansen & Baas, 1973; Van Staveren & Baas, 1973; Reed & Tukey, Jr., 1982; Holloway, 1982], for example in Stenocarpus sinuatus [Proteaceae: Lange, 1969], Sansevieria trifasciata [Liliaceae: Baker, 1971], Oncotheca [Aquifoliaceae: Baas, 1975], Schinus longifolia and

Lithraea caustica [Anacardiaceae: Wilkinson, 1979]. Priestly [1943] stated that 'the cuticular layer lies smoothly over the whole intricate pattern of epidermal tissue' implying this was generally the case in flowering plants. Smooth periclinal surfaces have been detected in a few conifers: Araucaria cunninghamii and A. klinkii [Araucariaceae: Stockey & Taylor, 1978a & b], Larix spp., such as L. gmelini [Pinaceae], Metasequoia and Taxodium [Taxodiaceae] [Miranda & Chaphekar, 1980]. This unornamented configuration has been designated as the first category or type of surface in the classification of periclinal sculpture [Wilkinson, 1979; Miranda & Chaphekar, 1980].

A variety of patterns have been described in the literature where the inner periclinal region of the cuticle is ornamented. Granular cuticular membranes occur in both angiosperms and gymnosperms [Barthlott & Ehler, 1977]. The sculptural components, granules or protrusions, are thought to be cutin elements of regular or irregular shape and size, which protrude from the solid mass of the cutinised layer [Alvin & Boulter, 1974; Miranda & Chaphekar, 1980]. Results of transmission electron microscopic studies of certain Cupressaceae cuticles by Oladele [1981], has confirmed this hypothesis in gymnosperms. Granules are probably similar in angiosperms, according to the work of Bancher, Hölzl & Klima [1960] on Allium cepa [Liliaceae], although Bringmann & Kühn [1955a], in a study of the morphology of leaf cuticles of garden and agricultural crop plants, stated that granulose sculpture was a preparation artifact [due to residual cell debris adhering to the membrane on isolation]. As Skoss [1955] pointed out, a wax 'bloom' on the outer surface may sometimes be responsible for the granular appearance of the cuticle seen in the light microscope, e.g. in Nicotiana glauca [Convolvulaceae]. Such wax may be confused with a granular inner surface.

Granulation has been found to be characteristic of a wide range of seed plants [Von Mohl, 1842; Haberlandt, 1910; Kurer, 1917; Florin, 1931; Orgell, 1935; Skoss, 1955;

Baker, 1970; Sitholey, 1971; Dilcher, 1974; Ferguson, 1974b; Stockey & Taylor, 1978a & b; Gibbon, 1981; Oladele, 1981; Wilkinson, 1983] such as in Aloe succotrina [Liliaceae: Lange, 1969], Amentotaxus argotaenia [Taxaceae: Ferguson, 1974a], Schizachyrium sanguineum [Graminae: Barthlott & Martens, 1979] and Sequoia sempervirens [Taxodiaceae: Dilcher, 1974]. According to Boulter [1971], granular cuticles are typical of Taxodiaceae members [Dilcher, 1974]. However, although Alvin & Boulter [1974] detected this pattern in some members of the family, they also recorded other configurations so that this type of sculpture cannot be considered as representative of all Taxodiaceae.

Many studies, particularly those using light microscopy have omitted to make evident the location of the granulation, that is, whether it is on the inside or on the outside of the membrane [Wilkinson, 1979]. Stace [1965a] was convinced that authors who described granular cuticles in the light microscope, were referring to the ornamentation of the outer cuticle surface, presumably by wax. This, however, is not always the case.

Some workers have described membranes with protrusions as granular regardless of the size or definition of the cutin elements, e.g. C.I.M.P. [1964]. Others have attempted to indicate individual dimensions by dividing such forms into several categories based on these criteria [Wilkinson, 1971, 1978, 1979; Bongers, 1973; Van Staveren & Baas, 1973; Oladele, 1981, 1983; Koster & Baas, 1981]. The arrangement of protrusions on the periclinal surface has also been neglected except in a few studies. Wilkinson [1979] illustrated three patterns observed in Anacardiaceae, which resulted in different cuticle texture: rounded granules [in Lansea stuhlmannii], flocculent [aggregated] granules [in Buchanania arborescens] and a crustose surface [in B. obovata]. Miranda & Chaphekar [1980] discovered that periclinal protrusions are variously arranged in Pinaceae and that the organisation could be described according to protrusion shape and distribution. The authors provided a system of surface view diagrams which represented the range of configurations found. These

included B, granules of uniform size and shape, not more than 1 μm in diameter e.g. in Abies bracteata; E, protrusions of irregular size or joined in clusters, as in Cedrus atlantica and F, protrusions tending to form a network or reticulum, for example in Tsuga caroliniana.

Wart-like protrusions, about 1 μm in diameter may occur in certain gymnosperms, such as Abies alba [Pinaceae] according to Boulter [1971]. This author noticed these 'verrucae' to be distributed singly per cell, or in groups of two or three. He also detected the presence of more papillate protruberances, 'cuticular pegs' in other taxa, for example in Metasequoia glyptostroboides [Taxodiaceae] near stomata. Alvin & Boulter [1974] described small grana [3 μm in diameter] in another Taxodiaceae member, Cunninghamia lanceolata. In some Cupressaceae, Oladele [1981] discovered structures similar to the grana of Alvin & Boulter [1974] and showed them to be associated with the inclusion of calcium oxalate crystals during cuticle development. Oladele [1981] recognised different degrees of 'crystal tubercle' prominence: moderate, as in Callitris rhomboidea and highly prominent, e.g. in Chamaecyparis lawsoniana.

Pits or depressions, sometimes termed 'scorbiculae' [Alvin & Boulter, 1974], arising from removal of intruding cellulosic 'fibres' in isolation [Oladele, 1981], have also been detected on the inner periclinal surface in some seed plants. Haberlandt [1910] was one of the first to note the existence of this sculpture type in transverse sections. In such views, pits are represented by fine lines or tiny indentations extending into the cutin matrix from the periclinal surface. Peg-like structures or ectodesmata are known to resemble these structures in T.E.M. preparations when stained with Gilson fixative [Lambertz, 1954; Franke, 1961, 1964]. However, it has been conclusively established by Schönherr & Bukovac [1970] that ectodesmata are merely artifacts of this specialised fixation technique [Hallam, 1982].

There is some evidence to suggest that true pits may

sometimes occur through the membrane in certain plants e.g. Abies alba [Pinaceae: Boulter, 1971] and Euonymus pendulus [Celastraceae: Pant & Kidwai, 1966]. However, such a pitted condition is at best extremely rare. Baker [1970] using S.E.M. was unable to discern the true situation in the taxa he examined which appeared pitted. In a later [1971] paper, he proposed that periclinal pits may be connected with cuticular absorption. This hypothesis was discussed and supported by Barthlott & Ehler [1977].

Blindly ending pits or depressions are common on the inner surface of isolated cuticles in many plants. They are variable in morphology and occurrence [Alvin & Boulter, 1974]. In surface view, they may give rise to a dotted appearance [C.I.M.P., 1964] or to a surface resembling a 'porous sponge', when extensively developed, e.g. in Citrus aurantifolia [Rutaceae: Baker, 1970]. Sometimes, there are only a few per cell, as in Abies alba [Pinaceae] studied by Boulter [1971]. 3-6 pits, called 'pores' were found in this species, each no greater than 0.1 μm in diameter. Depressions, in the form of cracks have been reported in Pistacia lentiscus [Anacardiaceae: Wilkinson, 1971]. Two patterns of depressions are known to occur in Pinaceae, according to Miranda & Chaphekar [1980]. The authors represented these diagrammatically in their scheme for description of periclinal ornamentation: type C, consisted of a series of regular and irregular [shape and size] depressions [in Picea montigena] rather like the dots of C.I.M.P. [1964] or the pores of Baker [1970] and G, showed channels running together, tending to form a reticulum [in Pinus aristata], similar to the 'cracks' of Wilkinson [1971].

The cuticle of some plants may possess periclinal ornamentation consisting of both protrusions and depressions. Oladele [1981] revealed that a great number of Cupressaceae had periclinal microrelief consisting of these two element types, which he termed 'cuticular protruberances' and 'cavities'. He also found a virtually continuous variation amongst the taxa investigated so that

it was impossible to describe the constituents separately in terms of size or form. The author, therefore, designated three grades of sculpture for numerical analytical purposes, based on the size of both elements: 1, fine, as in Callitris endlicheri; moderate e.g. in Chamaecyparis lawsoniana and 3, coarse, such as in Juniperus sabina. Miranda & Chaphekar (1980) distinguished protrusions and depressions in certain Pinaceae and showed them to be organised into two sculptural patterns which they represented by diagrams. Type D, depicted the components as regular or irregular [shape and size] granules and dot-like pits [in Abies concolor and Picea brachytyla] and H, as granules separated by channels running together, tending to form a reticulum [in Pinus peuce]. A somewhat more complex configuration has been detected in Aucuba japonica [Cornaceae] by Gibbon (1981) consisting of reticulate protrusions and several randomly distributed depressions resembling fissures or cracks.

Cuticular folding of striae, ridges or wrinkles may occur on one [inside or outside] or both surfaces of an isolated cuticle. Most workers have assumed it to be an outer surface feature, although in the light microscope its location cannot be discerned. However, Van Staveren & Baas (1973) positively identified a striate cuticular layer in Hartelya inopinata [Icacinaceae] from transverse sections. Wilkinson (1979) noted that granules on the inner side of the cuticle may be distributed in rows producing a granular striate pattern of ornamentation, e.g. in Schinus terebinthifolius [Anacardiaceae].

The periclinal sculpture adjacent to flanges may differ in appearance from that elsewhere in some plants. Oladele (1981) found this to be the case in certain genera of the Cupressaceae, for example, Chamaecyparis and Widdringtonia, due to the presence of wider cavities [depressions]. He also recorded a range of prominence of the feature from moderate [in Juniperus recurva] to prominent [in Widdringtonia whytei].

Small dissimilarities in the size of sculptural elements may occur in the various cell types within a species, such as in different epidermal cells of Picea orientalis or P. smithiana [Pinaceae] according to Miranda & Chaphekar [1980].

The fine microrelief of inner crystal tubercles of Cupressaceae studied by Oladele [1981] was smoother than areas free of crystals in only a few southern hemisphere members, e.g. of the genera Callitris, Fitzroya, Neocallitropsis and Pilgerodendron. Usually the grade of sculpture was similar.

Consistent differences in periclinal ornamentation [aspects such as presence, size and form of components] are known to exist between adaxial and abaxial cuticles [Miranda & Chaphekar, 1980; Oladele, 1981]. They have been described in angiosperms, including certain Icacinaceae [Van Staveren & Baas, 1973], Cocculus hirsutus [Menispermaceae: Ferguson, 1974a] and all species in the tribe Coccineae [Menispermaceae: Wilkinson, 1978], as well as in gymnosperms, for example, Sequoia sempervirens [Taxodiaceae: Alvin & Boulter, 1974] and a range of Pinaceae, such as Abies veitchii, Pseudotsuga flahaultii and Tsuga dumosa [Miranda & Chaphekar, 1980].

Periclinal microrelief may be related to plant habit. From results of detailed studies of cuticles of angiosperms, particularly Anacardiaceae, Wilkinson [1979] reported that coarser granulation occurred on membranes of the more xeromorphic leaves. Miranda & Chaphekar [1980] proposed that 'thinness and smoothness could be related to the deciduous habit' in conifers, after discovering the deciduous genera of Pinaceae, such as Larix [except L. potanini] and Pseudolarix to have the smoothest cuticles. This agreed with observations made by Alvin & Boulter [1974] for the deciduous Taxodiaceae Metasequoia and Taxodium. In the remaining evergreen Pinaceae, Miranda & Chaphekar [1980] found a range of increasing complexity of periclinal ornamentation from simple patterns involving individual protrusions or depressions

to those brought about by intricate fusion of the constituent elements into clusters or reticula.

6.2.2 ORNAMENTATION: FLANGES

The form of the cuticle/cellulose wall interface at the flanges seen in T.S. corresponds to their surface configuration when viewed from above. Thus, flanges, just as the periclinal region, may or may not be ornamented. Commonly, their surface is similar to that of periclinal areas, as recognised in Pinaceae by Miranda & Chaphekar [1980] as well as in various Cupressaceae and Taxodiaceae by Oladele [1981], although differences are known to occur in a few taxa, e.g. Pinus peuce and Pseudotsuga japonica [Pinaceae: Miranda & Chaphekar, 1980]. Most workers have not treated flange and periclinal ornamentation separately.

Where details of the flange surface have been described, it is clear that a range of configurations is possible. Flanges may be smooth i.e. 'without sculpture' [C.I.M.P., 1964] in gymnosperms, including Amentotaxus argotaenia [Taxaceae: Ferguson, 1978; Ferguson, Jahnichen & Alvin, 1978], certain Araucaria spp. [Araucariaceae: Stockey & Taylor, 1978a & b] and Larix species [Pinaceae: Miranda & Chaphekar, 1980] and most particularly, in angiosperms [Von Mohl, 1842, 1852; Haberlandt, 1914; Eames & Macdaniels, 1947; Scott, Schroeder & Turrell, 1948; Skoss, 1955; Brachet & Mirsky, 1961; Lange, 1969; Baker, 1971; Van Staveren & Baas, 1973; Barthlott & Ehler, 1977; Holloway, 1982] such as, Dianthus caryophyllus cv. White [Caryophyllaceae: Reed & Tukey Jnr, 1982], Lithraea caustica [Anacardiaceae: Wilkinson, 1979] and Pyrus communis [Rosaceae: Norris & Bukovac, 1968].

Granular or rough flanges are characteristic of a wide range of seed plants [Von Mohl, 1842; Lange, 1969; Bongers, 1973; Van Staveren & Baas, 1973; Alvin & Boulter, 1974; Baas, 1975; Barthlott & Ehler, 1977] e.g. Iris foetidissima [Iridaceae: Baker, 1970], Sequoia sempervirens [Taxodiaceae: Dilcher, 1974], Schizachyrium sanguineum [Graminae: Barthlott & Martens, 1979], Abies

bracteata and Cedrus atlantica [Pinaceae: Miranda & Chaphekar, 1980]. As in the case of the periclinal sculpture, most workers have not attempted to give any other details of individual granules, for example, their size or form. There are a few exceptions, however. Van Staveren & Baas [1973] recognised four states of granulation in Icacinaceae: 1, very finely granular, as in Nothopodytes pittosporoides, 2, finely granular, e.g. in some Miquelia spp., 3, granular, such as in various Rhyticaryum spp., and 4, coarsely granular, for example in Platea spp. In contrast, Bongers [1973] only made special mention of densely and coarsely granular flanges exemplified by certain Zyggogynum species and Belliolum haplopus [Winteraceae] respectively.

Miranda & Chaphekar [1980] showed many of the patterns of sculpture observed in periclinal regions to exist on flanges and implied that the scheme devised for categorising the type and form of elements was applicable to both the periclinal and flange surfaces.

Sculptural differences may be distinguished between adaxial and abaxial flanges [Bongers, 1973; Van Staveren & Bass, 1973]. In addition, flanges may display different configurations at their base and apex. A progressive increase in granularity towards the flange base has been demonstrated by various workers, including Wilkinson [1971] and [1979] in respectively Pistachia lentiscus and Parishia maingayi [Anacardiaceae], Alvin & Boulter [1974] in Sequoiadendron giganteum [Taxodiaceae] and Barthlott [1981] in Gnetum gnemon [Gnetaceae].

Oladele [1981], due to the possibility of this sculptural difference, treated base and apex relief as separate characters in his numerical studies. He recognised three states in each; fine, moderate and coarse and most of his results were in agreement with the trend described above. However, a few exceptions were detected i.e. with finer sculpture at the base than at the apex, e.g. in X Cupressocyparis leylandii [Cupressaceae].

6.3 FEATURES OF PARTICULAR REGIONS OR SPECIALISED CELL TYPES

6.3.1 VEINS

The extent to which veins are marked in the cuticle varies [from absent to prominent] and there may also be differences between the two sides of the leaf [Bandulska, 1926, 1928; Stace, 1965a, 1980; Bongers, 1973, Koster & Baas, 1981]. Stace [1965a] found that vein prominence is related to cuticle thickness and also the more xeromorphic the leaf the less conspicuous the veins are. In addition, he noticed that where veins are more or less well defined, the cell shape over the midrib, laterals and secondaries is usually considerably modified and the degree of modification determines vein prominence, being greater on the abaxial than on the adaxial. Furthermore, cells in the centre of a vein are the most modified and at the edges, a gradual or sudden merger occurs into the intercostal region. Overlying lower order veins and venules [smallest 1-2 cells wide], modification is essentially similar in type to that seen over major veins although it is less well developed.

Generally, cells are rectangular and elongated parallel to the direction of the veins, e.g. in most cycads [Thomas & Bancroft, 1913], some Lauraceae [Bandulska, 1926], Acanthaceae [Ahmad, 1974b], Aquifoliaceae [Baas, 1975] and many species of Ephedra [Ephedraceae: Pant & Verma, 1974]. However, sometimes vein cells are much shorter. They have been described as square to rectangular or slightly elongated in a range of seed plants including Zamia linderi [Cycadaceae: Thomas & Bancroft, 1913], certain Rhizophoraceae [Stace, 1965a], Huaceae [Baas, 1972] and Ephedra spp. [Ephedraceae: Pant & Verma, 1974] or even broader than long, as in most Gluta spp. [Anacardiaceae: Wilkinson, 1983]. Occasionally, vein cells are isodiametric or polygonal for example, in Aniba hostmanniana, species of Litsea [Lauraceae: Bandulska, 1926] and Ephedra [Ephedraceae: Pant & Verma, 1974], or 'bead-like' or 'moniliform', such as Litsea

stocksii var. glabrata [Lauraceae: Bandulska, 1926]. Stace [1965a] recognised that in some cases, at least, these shorter cell shapes may be produced by secondary transverse divisions occurring during development. Such divisions are rare or absent over minor veins.

Vein cells are commonly arranged end to end in parallel rows or may be less regularly placed [Stace, 1965a; Ahmad, 1974b]. According to Stace [1965a] end walls are 'truncate, oblique or almost pointed, interlocking'. Such walls have been illustrated by Ahmad [1974b]. Stace [1965a] also noticed the tendency for flanges of the majority of elongate vein cells to be straight even when the outlines in areolae are sinuate, so that undulation decreases towards the veins. The results of many of the workers quoted above support this finding, although exceptions have been described e.g. some cycads [Thomas & Bancroft, 1913], Lauraceae [Bandulska, 1926, 1928] and certain Gluta spp. [Anacardiaceae: Wilkinson, 1983].

Flange thickness is known to vary in vein areas. A number of states have been found to occur [see Thomas & Bancroft, 1913; Bandulska, 1926]. Usually flanges are thick, sometimes considerably so, or they may be intermediate or fairly thin to thin. In some cases, both thick [primary] and thin [secondary] flanges exist together, as in several Macrozamia and Zamia spp. [Cycadaceae] examined by Thomas & Bancroft [1913]. Where primary and secondary cell divisions are indistinguishable the flanges are equally thick, e.g. in Combretum demeusei, Strephonema spp. and Terminalia spp. [Combretaceae: Stace, 1965a].

Only a few authors have provided information regarding the vein micromorphological features of isolated cuticles. Wilkinson [1978] recognised that when pits are present in vein flanges of certain Menispermaceae, they may be indistinct [inconspicuous] or obvious [conspicuous] and the extent of pitting may differ on the adaxial cuticle from that on the abaxial. Generic and specific differences

have also been indicated by the observations of Koster & Baas [1981] and Wilkinson [1983] respectively.

Vein cells may be unornamented [smooth], such as in Coscinium fenestratum [Menispermaceae: Wilkinson, 1978] and Gluta velutina [Anacardiaceae: Wilkinson, 1983] or variously ornamented. A range of patterns have been recorded including granular, e.g. in Laurus nobilis [Lauraceae: Gibbon, 1981 unpublished], finely to coarsely granular, as in most Gluta spp., for instance G. laxiflora [Anacardiaceae: Wilkinson, 1983], reticulate with randomly dispersed depressions, for example, Aucuba japonica [Cornaceae: Gibbon, 1981] and striate such as in Gluta aptera [Anacardiaceae: Wilkinson, 1983]. Wilkinson's [1978] work on certain Menispermaceae taxa showed that periclinal ornamentation may or may not be similar over veins on adaxial and abaxial cuticles.

Very little has been written about structures associated with veins in cuticles, e.g. trichomes. Bandulska [1926] noticed that in some Lauraceae, for example, Lindera rubronervia, hair bases are present on veins of both leaf surfaces whilst in others, such as Aniba desertorum var. glabrata and Lindera oldhamii, they are confined to those of the abaxial. In addition, she found that hair bases are especially abundant on veins of A. firmula, A. hostmanniana, L. pulcherrima and Litsea fuscata, particularly small in A. laevigata, sclerenchymatous in Lindera strychnifolia and thick-walled, tubular in Litsea sebifera var. tomentosa.

6.3.2 LEAF MARGINS

Cuticular details of marginal regions of leaves are somewhat lacking in the literature. However, it has been established that in general, an abrupt or gradual change in size [Pant & Verma, 1974] and shape [Kakkar & Paliwal, 1973] of cell outlines as well as in flange thickness occurs towards the lamina margin. Thus, the area bounded by flanges decreases, cells become more isodiametric or elongate, flange thickness increases and undulation becomes less pronounced. This has been reported, for

example, in certain cycads [Thomas & Bancroft, 1913], members of the Avicenniaceae, Combretaceae and Rhizophoraceae [Stace, 1965a] and Thunbergia spp. [Acanthaceae: Ahmad, 1974b].

6.3.3 TRICHOMES, SECRETORY CELLS AND CORK WARTS

Leaf cuticles of many seed plants (not conifers) may exhibit evidence of trichomes (non-glandular or glandular) on their inner surface. The extent to which these are represented has been found by Stace [1965a] to depend on the 'degree of cuticularisation'. This may be easily established from observations of transverse sections made either with T.E.M., such as those carried out by Hallam & Juniper [1971] on simple hairs of Phaseolus [Leguminosae], or using light microscopy, e.g. the studies of Cutter [1976] on salt glands of Limonium latifolium [Plumbaginaceae] and Tamarix aphylla [Tamaricaceae].

Details of trichome basal parts given in the literature have been obtained mainly through light microscopic examination of membranes in surface view. Particularly notable is the work of Stace [1965a] who showed, after extensive study of cuticles of members of the Avicenniaceae, Combretaceae and Rhizophoraceae, that the cells constituting trichome bases are usually elongated radially to the pore and have straight or straighter flanges than those of normal cells. He found that a range of numbers of basal cells is characteristic of a species; 5-8 being the most common. Such bases have been recorded previously by Bandulska [1926, 1931] in certain Lauraceae and Myrtaceae. Stace [1965] also noticed the frequent occurrence, especially in xeromorphic species, of bases with rings of tangentially divided cells, the innermost tending to be longer in the tangential plane than in the radial and usually possessing thick, straight flanges.

In addition, Stace noted that the 'poral rim' thickness may vary towards the centre of the trichome pore, such as in Thiloa glaucocarpa [Combretaceae]

as well as towards the middle of the leaf. Bases with thick rims often have extensively cutinised radial walls resulting in a stellate pattern of thickening. This star-like appearance has been described and illustrated by Bandulska [1926, 1931].

Sometimes, only the poral rim is thickened. Thomas & Bancroft [1913] showed this configuration in Stangeria paradoxa [Cycadaceae] and Bandulska [1926] in Neolitsea apoensis and N. zeylanica [Lauraceae]. Small, rounded thick-rimmed openings were also noted in many Aniba and Lindera species [Lauraceae: Bandulska, 1926].

Where there is more than one type of trichome present, each type will have a different base form, for example, in Combretum spp. [Combretaceae], according to Stace [1965a]. He described two forms of trichome base in Conocarpus erectus with radially- and tangentially-elongated basal cells respectively and illustrated three types with differently thickened poral rims in Quisqualis hensii. Furthermore, this author recognised the possibility of deepening of the rim to the inner epidermal wall by cutinisation of the trichome foot. Workers have not made special mention of the inner surface micro-sculpture of basal cell flanges or periclinal areas.

A few details of secretory [oil or mucilage] cells are known. Bongers [1973] noticed that flanges overlying subepidermal cells were either more strongly developed or less so, than those of unspecialised cells in Winteraceae. Recently, Wilkinson [1979] showed that hydropoten of Nymphaea capensis var. zanzibarensis [Nymphaeaceae] were striate and lacked boundary flanges on the inner cuticle surface.

The nature of cork warts and related structures in cuticle preparations has been described from light microscopic observations by Stace [1965a]. According to the author, cork warts are marked by a circular or more irregular hole, surrounded by strict radiating rows of modified epidermal cells (meristematic in function) which

are often considerably smaller than ordinary cells, with thicker flanges. One such group was illustrated in Rhizophora mucronata [Rhizophoraceae]. Three types of wound were found to have a similar appearance: 1, scars due to mechanical damage, commonly with a thin amorphous or cell marked cuticle covering the wound; 2, insect punctures, like small cork warts but with a circular outline, and 3, fungal wounds, such as in Buchenavia kleinii [Combretaceae]. The fine sculpture of these groups has not been reported or illustrated in the literature.

6.3.4 STOMATA

It is well known from transverse sections of leaves that not only is the outer wall of the epidermal cells covered by cuticle but, in addition, at each stoma, the membrane extends over the guard cells forming a continuous lining through the outer cavity and the pore to the inner cavity [Artz, 1933; Eames & MacDaniels, 1947; Esau, 1965; Stace, 1965a; Norris & Bukovac, 1968; Sitholey, 1971; Barthlott & Ehler, 1977; Wilkinson, 1979].

Stomata tend to be well preserved in cuticular preparations and represent a valuable source of characters, as suggested by Stace [1965a]. In fact, certain workers e.g. Boulter [1971] consider a stoma to be one of the most informative parts of the cuticle for morphological and taxonomic [p. 78] purposes, especially when viewed by scanning electron microscopy. Recently, Stockey & Taylor [1978a & b], in their studies of members of the gymnosperm family Araucariaceae using this technique, found that the inside of the cuticle revealed the greatest amount of information regarding the stomatal apparatus. Similar investigations of angiosperm cuticular membranes [Lange, 1969; Dilcher, 1974; Barthlott & Ehler, 1977; Barthlott, 1981; Wilkinson, 1983] have given clear indications of the usefulness of S.E.M. examination of this surface in flowering plants, as recognised by Wilkinson [1979]. In the light microscope, many stomatal characters are barely resolved because of their size and ambiguous, due to much variation being confined to the third dimension i.e. depth [Stace, 1965a]. However, light micro-

scopic observations, particularly those of transverse sections, are known to be of value as an aid to interpretation of the organisation of a stoma, for example, according to Stace [1965a], in ascertaining the exact relative position of the guard cells and neighbouring cells and determining the precise structure beneath the outer stomatal ledge.

Many of the most conspicuous aspects of stomata such as their distribution, frequency, orientation, size, shape and arrangement of constituent cells, have been regularly described by anatomists from light microscopic observations of cuticular preparations. Whilst it is recognised that these characters are visible and sometimes more evident on the inner surface [e.g. stomatal arrangement: Boulter, 1971; Stockey & Taylor, 1978a & b; Wilkinson, 1979], excellent reviews dealing with such aspects have already been prepared [Solereeder, 1908; Florin, 1931; Metcalfe & Chalk, 1950; Stace, 1965a; Wilkinson, 1979] and therefore, they will not be discussed here.

Features of ordinary epidermal cells described previously under primary and secondary sculpture may also be distinguishable in the region of the stomatal complex. These include definition of cell outlines [Skoss, 1955], flange width [Thomas & Bancroft, 1913; Bandulska, 1928], flange shape in T.S. [Scott, Schroeder & Turrell, 1948; Norris & Bukovac, 1968] and surface view, i.e. degree of undulation [Baas, 1970; Ferguson, 1947b], flange margin form [Lange, 1969; Ferguson, 1978], striae [Wilkinson, 1983] and periclinal ornamentation [Van Staveren & Baas, 1973; Koster & Baas, 1981; Reed & Tukey, Jnr., 1981]. Some workers have given details of several such stomatal characters, for example, Bandulska [1931], Florin [1931], Baker [1971], Boulter [1971], Jansen & Baas [1973], Alvin & Boulter [1974], Ferguson, Jahnichen & Alvin [1978], Stockey & Taylor [1978a & b], Miranda & Chaphekar [1980], Gibbon [1981], Oladele [1981] and Wilkinson [1983].

Guard cells and subsidiary cells may be similar in a

number of respects, for example, flange height, such as in many Cupressaceae and Taxodiaceae [Oladele, 1981], flange width, e.g. in Hoya carnosa [Asclepidaceae: Skoss, 1955] and Euonymus europaeus [Celastraceae: Baker, 1970], flange shape, in Tristania suaveolens [Myrtaceae: Bandulska, 1931], presence of pegs, as in certain Taxodiaceae, for instance Cunninghamia lanceolata [Alvin & Boulter, 1974; Oladele, 1981] and Sequoiadendron giganteum [Boulter, 1971; Oladele, 1981] and periclinal microrelief, e.g. in some Cupressaceae & Taxodiaceae [Oladele, 1981].

Commonly, however, the cells constituting the stomatal complex exhibit various differences. Where flange height differs, some workers have found the guard cell/subsidiary cell flange to be deepest, such as Norris & Bukovac [1968] in Pyrus communis [Rosaceae], Oladele [1981] in Callitris and Juniperus species [Cupressaceae] and Wilkinson [1983] in certain Gluta spp. [G. laxiflora and G. oba: Anacardiaceae]. The reverse situation may occur in other taxa, for example, in Athrotaxis spp. [Taxodiaceae], according to observations made by Oladele [1981].

Flanges bounding guard cells are usually straight in surface view, as in Pinaceae [Miranda & Chaphekar, 1980]. Subsidiary cell flanges tend to show some degree of undulation: straight to curved in Apollonias barbujana [Lauraceae: Ferguson, 1974b], curved to sinuous in Cratoxylum and Eliaea [Guttiferae: Baas, 1970], sinuous in Rhodomyrtus macrocarpa [Myrtaceae: Bandulska, 1931] and Ω -undulate in Laurus spp. [Lauraceae: Ferguson, 1974b; Gibbon, 1981].

They may also vary in shape depending on their location. In Cinnamomum zeylanicum [Lauraceae], Bandulska [1928] noticed that near to the aperture, subsidiary cell flanges were straight whilst at the boundary between the stoma and ordinary cells, they were sinuous. Such flanges may sometimes be of a different form at the base to elsewhere. This is so in Amentotaxus argotaenia [Taxaceae]

studied by Ferguson, Jähnichen & Alvin [1978] where subsidiary cell/encircling cell flanges were shown to be straight with small cavities [due to undulation] in the basal region.

Guard cells often have a smoother or more finely sculptured periclinal surface than subsidiary cells [Boulter, 1971; Alvin & Boulter, 1974; Oladele, 1981; Reed & Tukey, Jnr., 1982], although this is not always the case. Van Staveren & Baas [1973] and Oladele [1981] detected less smooth guard cell ornamentation in Rhyticarium spp. [Icacinaceae] and certain Cupressaceae [Austrocedrus chilensis, Callitris spp., Chamaecyparis lawsoniana] respectively. In a few gymnosperms, lateral subsidiary cells exhibit a different pattern of sculpture to polar subsidiary cells. This has been recorded in Cedrus atlantica, Pseudotsuga flahaultii and Tsuga mertensiana by Miranda & Chaphekar [1980].

The dissimilarity between the cells of the stomatal complex and those of unspecialised regions is due to a number of features. Oladele [1981] noticed that flanges of the stoma, particularly those of the subsidiary cells, may be of different height to ordinary flanges in some Cupressaceae and Taxodiaceae. In Pinaceae, however, the guard cell/subsidiary cell flanges are always well developed irrespective of the degree of development of the non-specialised flanges [Miranda & Chaphekar, 1980].

Stomatal flanges often tend to be narrower than ordinary flanges, as in Zamia spp. [Cycadaceae: Thomas & Bancroft, 1913]. This is also so in guard cells of, for example, Clivia nobilis [Amaryllidaceae: Skoss, 1955] and many of the angiosperms examined by Baker [1970]. Lateral subsidiary cells have especially thin flanges in Araucaria klinkii [Araucariaceae: Stockey & Taylor, 1978].

In taxa with undulate unspecialised flanges, there may be a noticeable gradation in the degree of undulation from the stoma to the ordinary epidermal cells, as

recognised in Pinaceae by Miranda & Chaphekar [1980] and shown in certain cycads e.g. Stangeria paraxoda and S. paradoxa var. schizodon by Thomas & Bancroft [1913].

The guard cell/subsidiary cell flange crest (margin), according to Oladele [1981] commonly differs from the crest of other anticlinal flanges, tending to be less uneven than the non-specialised cell margins, such as in Athrotaxis spp. [Taxodiaceae], Thujopsis dolabrata and Widdringtonia spp. [Cupressaceae]. A similar trend may be detected between guard cell and ordinary cell flanges in Ilex aquifolium [Aquifoliaceae: Baker, 1971] and Gluta obo [Anacardiaceae: Wilkinson, 1983]. Occasionally, guard cell/subsidiary cell flange crests are more jagged than unspecialised cell margins, for example in Chamaecyparis obtusa and Thuja occidentalis [Cupressaceae: Oladele, 1981].

The periclinal sculpture of the stomatal complex is known often to differ in size and element composition from that of ordinary cells. Jansen & Baas [1973] found finer microrelief in the region of the stoma than elsewhere in Lophopetalum micranthum [Celastraceae] and Oladele [1981] likewise recorded this tendency between guard cells and non-specialised cells in various Cupressaceae, such as Actinostrobus pyramidalis, Pilgerodendron uviferum and certain Thuja spp. Subsidiary cell ornamentation may be smooth e.g. in Apollonias barbujana and Laurus azorica [Lauraceae: Ferguson, 1974b]; finer, as in Austrocedrus chilensis [Cupressaceae: Oladele, 1981] and Horsfieldia [Myristicaceae: Koster & Baas, 1981] when striae are absent, or coarser, for example in Juniperus communis [Cupressaceae: Oladele, 1981] when compared with ordinary cell sculpture. The pattern observed on the periclinal surface of the subsidiary cells may contrast greatly with that of unspecialised cells, according to observations made by Van Staveren & Baas [1973] and most particularly by Miranda & Chaphekar [1980]. The latter authors showed that in certain Pinaceae, such as Abies firma, Pseudotsuga flahaultii and Tsuga dumosa, only the lateral subsidiary cell differs in microrelief from elsewhere.

The appearance of stomata on the inner surface of the cuticle viewed by scanning electron microscopy, is known to be affected by the depth of the guard cells within the leaf tissue [Boulter, 1971] and by the position and arrangement of any accompanying surrounding [subsidiary or encircling] cells. According to Stace [1965a], guard cells are usually level or very slightly sunken [depressed] below or raised above the ordinary epidermal cells in transverse sections, but in some xeromorphic plants they are distinctly sunken sometimes considerably so, as in many conifers. This means that, on the inside of an isolated membrane, the cutinised parts of the guard cell will be variously positioned with respect to the surrounding cells, e.g. if sunken, the cuticle will appear raised. The differences observed due to this variation in stomatal organisation and arrangement have been especially well demonstrated by Boulter [1971] in the coniferous families Pinaceae and Taxodiaceae. For example, in Tsuga heterophylla [Pinaceae], the guard cell periclinal and anticlinal cuticle is raised above both the subsidiary and ordinary cells which are in the same plane. Adjacent subsidiary cells are often shared and specialised encircling cells are absent. In contrast, in Sequoiadendron giganteum [Taxodiaceae], the entire stomatal cuticle is raised, that of the subsidiary cells being shaped like an opened umbrella, bearing the cutinised portion of the guard cells at its centre and positioned above the encircling cells. The umbrella-like cuticle of the subsidiary cells may vary in morphology, as noticed and described by Stockey & Taylor [1978a & b] in species of Araucaria [Araucariaceae].

Where guard cells are deeply sunken to the level of the hypodermis, e.g. in some members of the genera Abies, Picea and Pinus [Pinaceae], Boulter [1971] discovered that hypodermal cells may not always be completely removed by maceration or else the depressed [raised on inner surface] parts of the cuticle may become distorted and collapse. However, later work on the same family, by Miranda & Chaphekar [1980] showed no evidence of adhering cells in the stomatal region. These authors illustrated a variety of inner surface configurations of stomata which could be

interpreted using transverse sections presented by Florin (1931) and Boulter (1971) and made special mention of conspicuous wing-like subsidiary cell flanges in Abies recurvata.

Similar structures seem to occur in Lauraceae, according to the results of Bandulska's (1926) investigation of species of four genera: Aniba, Lindera, Litsea and Neolitsea. These so-called 'scales' were found to vary in persistence, when cuticles were isolated, as well as in shape. The author illustrated a range of forms, each differing in presence or absence of a thickened scale edge or rim, shape of the polar tips and length of the pore compared with that of the scale.

Other aspects of guard cells contribute to the morphological diversity of stomata, particularly the structure of the lamellae or thickenings which may be located at the stomatal poles in the region of the common wall between adjacent guard cells. These have been routinely recorded by anatomists studying cuticular preparations, especially those of angiosperms (Bandulska, 1931; Bailey & Nast, 1948; Brown & Johnson, 1962; Singh & Kundu, 1962; Stace, 1965a & b; Baker, 1970; Baas, 1972; Baranova, 1972; Jansen & Baas, 1973; Van Staveren & Baas, 1973; Baas, 1975; Wilkinson, 1979, 1983; Gibbon, 1981; Koster & Baas, 1981) but also those of gymnosperms (Thomas & Bancroft, 1913; Florin, 1931, 1951; Boulter, 1971; Pant & Verma, 1974; Ferguson, Jähnichen & Alvin, 1978; Stockey & Taylor, 1978a & b). These lamellae are known to be lignified in some plants, for example, Cycads (Thomas & Bancroft, 1913) and in Ephedra spp. (Ephedraceae) they may be dissolved away by maceration, leaving behind transparent areas in place of the thickening (Pant & Verma, 1974). It has been suggested from work on Pinaceae and Taxodiaceae cuticles by Boulter (1971) that such thickenings may provide support for the moveable parts of the lateral guard cell wall since they are firmly fixed between neighbouring encircling or subsidiary cells and the subepidermal (hypodermal) cells.

A variety of lamellae types occur. The pattern most frequently found is a T-shaped thickening often termed a 'T-piece' formed from an upright or rod orientated along the common wall and a cross-piece or bar arranged perpendicularly to the upright across the pole. This has been described and often also illustrated in members of a range of families by a number of workers including Thomas & Bancroft [1913], Bandulska [1931], Baker [1970], Baas [1972], Ferguson [1978], Wilkinson [1979, 1983] and Gibbon [1981]. T-pieces vary in form. A pear-shaped T is characteristic of Bowenia spp. e.g. B. spectabilis var. serrulata [Cycadaceae: Thomas & Bancroft, 1913], a 'three-pronged' shape [forked with rounded end] of Tristania suaveolens [Myrtaceae: Bandulska, 1931] and a T formed like a 'head with a broad-rimmed hat', of Illicium philippensis [Illiciaceae: Baranova, 1972; Wilkinson, 1979].

Sometimes, only a rod or a bar may be found at the stomatal poles. Wilkinson [1979] mentioned the possibility of this but stated that T-pieces may be reduced to these other types of thickening, implying that rods and bars are modified or derived forms. This is probably not the case, however. T-thickenings are likely to result from more extensive cutinisation of the wall between adjacent guard cells and the rods or bars from less. Rods or uprights have been found in diverse families, according to the literature. They tend to vary in shape and size [length and width].

Incomplete rods, extending along only part of the common wall from the aperture are characteristic of for example, species in all four sections of the genus Araucaria [Araucariaceae: Stockey & Taylor, 1978a & b], Mangifera indica [Anacardiaceae: Wilkinson, 1979] and Aucuba japonica [Cornaceae: Gibbon, 1981]. Boulter [1971] noted that in taxa with such rods, e.g. Pinus peuce, P. sylvestris [Pinaceae] and Sciadopitys verticillata [Taxodiaceae], the guard cell cuticles appeared united at the polar ends. Brown & Johnson [1962] from their T.E.M. studies on grass stomata, suggested that the actual guard cells might have confluent protoplasts. A

similar investigation to ascertain whether the situation is the same in conifers was called for by Boulter [1971].

Complete rods, extending from the aperture to the outermost point of the guard cell poles have been shown to exist in angiosperms, such as Tristania spp. [Myrtaceae: Bandulska, 1931] and Lannea gosweileri var. gossweiler [Anacardiaceae: Wilkinson, 1979] as well as in gymnosperms e.g. Abies alba [Pinaceae: Boulter, 1971]. In the latter example, there is prominent separation of the end walls so that each lamella appears to lie in a groove.

Reports of cross-pieces or bars, without rods or uprights are rare in the literature. Baas [1975] discovered this type only in certain Sphenostemon spp.

Polar thickening may show variable development [based on the degree to which the T-piece is formed]. This has been demonstrated by a number of workers studying flowering plant cuticles [Jansen & Baas, 1973; Van Staveren & Baas, 1973].

Lamellae are not universally present, however. There are many taxa in which the common wall is clearly unthickened, e.g. in all species examined in the genera Anogeissus, Bucida, Calopyxis, Conocarpus, Guiera and Thiloa [Combretaceae: Stace, 1965b], those in Nemopanthus, Oncotheca and Phelline as well as some members of Ilex and Sphenostemon [Aquifoliaceae: Baas, 1975] and in certain Gymnacranthera and Horsfieldia spp. [Myristicaceae: Koster & Baas, 1981].

Thin-walled areas of oval outline at the ends of the guard cells so characteristic of Graminae may occasionally be found in dicotyledons, such as in Eriandra fragrans [Polygalaceae: Wilkinson, 1979]. Similar circular, elliptical or comma shaped thin regions are also present in other flowering plants according to the studies of Avicenniaceae, Combretaceae and Rhizophoraceae by Stace [1965a].

The extreme poles of the guard cells where they meet, may be variously shaped: obtuse, e.g. in Iris foetidissima [Iridaceae: Baker, 1971], truncate, rounded, as in Aucuba japonica [Cornaceae: Gibbon, 1981], or retuse. The latter form appears to be a feature of many xeromorphic plants [Stace, 1965a], for example Ilex aquifolium [Aquifoliaceae: Baker, 1971]. It is also the commonest polar pattern illustrated in the literature [see Aniba amazonica and A. desertorum var. glabra [Lauraceae: Bandulska, 1926], Laurus nobilis [Lauraceae: Gibbon, 1981] and Cyrilla racemosa [Cyrillaceae: Wilkinson, 1979].

Sometimes, in cuticles of gymnosperms, the periclinal surface of the guard cell is obscured by what has been shown to be lignified wall thickenings. This is the case in certain Pinaceae e.g. Abies alba, Picea abies and Pinus peuce and Taxodiaceae, such as Sequoiadendron giganteum according to the results of Boulter [1971]. These thickenings appear to be affected during cuticle maceration [Pant & Srivastava, 1968; Boulter, 1971] and disintegrate as maceration progresses. Boulter [1971] illustrated 3 stages in the procedure in Sequoiadendron giganteum: 1, an initial stage where both upper and lower thickenings are present; 2, a stage where only the upper remains and finally 3, where all thickening is removed to reveal details of flange shape and periclinal ornamentation in the region of the stoma. It is these thickenings that exhibit a striate pattern which Boulter [1971] has suggested could be involved in opening and closing the stomatal aperture.

Internally, except in conifers, where the cuticle meets the poral wall of the guard cell, the cuticle may project to form an inner ledge which appears as a pair of processes in T.S. In many xeromorphic flowering plants, these projections meet when the stoma is closed [Stace, 1965a]. The inner ledge varies in its degree of development or prominence when viewed in section, as described by Jansen & Baas [1973] in Lophopetalum spp. [Celastraceae], Van Staveren & Baas [1973] in certain Icacinaceae and Baas [1975] in Aquifoliaceae and illustrated by Brandham &

Cutler [1981] in Haworthia spp. [Liliaceae].

In cuticular preparations, according to Van Staveren & Baas [1973], the inner ledge tends to be clearly visible only if the stomatal flap, the cutinised part of the stomatal chamber [Stace, 1965a; Wilkinson, 1979], remains attached to it. They recognised the possibility that this ledge could be present in some species where it is inconspicuous due to the absence of adhering cuticular material.

The presence of a lining or envelope [Skoss, 1955] of cuticle following the contours of the subsidiary and even the mesophyll cell walls bounding the stomatal chamber, has been known for many years. Some of the first to record it were Brenner [1900] in certain Crassulaceae and Hausen [1900] in Aloe obscura [Liliaceae]. Since that time various workers have demonstrated its existence in a range of plants, including Agave yuccifolia and Yucca aloifolia [Agavaceae: McClendon, 1908]. Clivia nobilis [Liliaceae], Hoya carnosa [Asclepidaceae] [Skoss, 1955], Pyrus communis [Rosaceae: Norris & Bukovac, 1968], Cedrus and Pinus spp. [Pinaceae: Miranda & Chaphekar, 1980]. Baker [1970] found that such linings ruptured during isolation of cuticles by maceration. Recently, Reed & Tukey, Jnr. [1982] showed these to remain as delicate strands linking adjacent stomata in preparations of Dianthus caryophyllus cv. White [Caryophyllaceae].

Structural complexity of the stoma seems to depend somewhat on the thickness of the cuticle and the habit of the plant [Baker, 1970]. Fragile membranes, such as those of the herbs Beta vulgaris [Chenopodiaceae] and Bryonia dioica [Cucurbitaceae] have very simple stomata according to observations made by Baker [1970]. Thick cuticles, characteristic of many evergreens and xerophytes e.g. Araucaria [Araucariaceae], Pinus [Pinaceae] [Barthlott & Ehler, 1977], Gasteria planifolia [Liliaceae] and Iris foetidissima [Iridaceae] [Baker, 1970] tend to have rather complex, protruding heavily cutinised stomata. The formation of such complicated structures is likely to be

the result of increasing interesterification of the constituent cutin acids [Baker, 1970].

The amount of cuticular ornamentation on the guard cells has been found frequently to be proportional to the thickening of the cell walls and hence to the degree of xeromorphism, by Stace [1965a].

6.4 DEVELOPMENT

Whilst it is well known that the cuticle shows considerable diversity in structure and composition [see review of Holloway, 1982], details of its development, particularly those of the flanges, the periclinal surface and any associated microrelief, are relatively few. Oladele [1981, 1982] studying Chamaecyparis lawsoniana [Cupressaceae] with transmission and scanning electron microscopy, has made the greatest contribution to our knowledge of these aspects. In his work, he described cuticle development with reference to the four main phases of leaf growth. He found no indication of flanges at the primordial stage. During the apical growth phase, however, a triangular shaped ridge of electron dense material, becomes visible above the anticlinal walls in Ruthenium red-stained preparations, its summit directed towards or continuing vaguely into the middle lamella whilst its base is continuous with the subcuticular lamella, the pectic layer underlying the young cuticle proper [see Sargent, 1976a & b]. The cuticular layer is also initiated in this growth phase, in the subcuticular lamella by the appearance of small, round or elliptical [electron-lucent] bodies, believed to represent cutin particles, either linked with the cuticle proper or located away from it. The developing cuticular layer in the anticlinal zone becomes considerably thicker than that in the periclinal by accumulation of these cutin bodies particularly in the region of the ridge axis. It exhibits a characteristic electron-lucent/electron-dense ultrastructure due to the presence of a network or reticulum of non-cutinised material between the cutin bodies.

In the apical differentiation to early maturation phase, development of the cuticular layer follows the outline of the round crested ridge, which increases to 4-5 times its original size. The crest becomes pointed when the ridge is more or less completely invaded by cutin bodies and reticulum. During further flange development after cessation of cell expansion, the cuticular layer extends beyond the cutinised ridge into adjacent wall layers. However, the ridge remains more or less distinct from the later formed portions by different patterning of the reticulum and cutin bodies.

In the final phase of leaf growth, as the tissues of the apex approach maturity and those at the base undergo differentiation, ornamentation of the periclinal and anticlinal surfaces is initiated. The almost smooth cuticle/wall interface develops an interlocking system of cuticular and wall protruberances. On the inner surface of isolated cuticles, this pattern is seen to consist of granules, 0.5-1.5 μm in diameter interspersed by cavities of similar size representing regions once occupied by wall material. Granules tend to be characteristically coarser at the flange base. As maturity is approached, the flange crest becomes rounded through being covered by continuing wall cutinisation.

In addition to describing the general development of anticlinal and periclinal cuticle, Oladele [1981, 1982] made a special study of the formation of inner crystal tubercles in Chamaecyparis lawsoniana. He noted that these commence as flat, membranous structures in the inner part of the periclinal wall during the apical growth phase. Small calcium oxalate crystals develop first at the edges of each structure and then grow periclinally within it merging with later formed crystals at its centre until eventually it is entirely filled by a single parallelogram-shaped crystal. The edge of the developing cuticular layer migrates towards the crystal and eventually embeds it. The crystal meanwhile grows anticlinally and assumes a more rectangular shape. At apical differentiation to early maturation, Oladele found tri-

angular electron-opaque areas to develop at each end of the crystal which later become cutinised but separated from the cuticular layer by a narrow electron-opaque strip, the crystal ramp. Small, later-formed crystals in deeper layers of the wall lack ramps. The wall beneath each crystal distends inwards due to anticlinal crystal growth. Examination of the inner cuticle surface at this stage shows the cuticular layer to have developed over and obliterated polygonal crystal impressions leaving only irregular openings or none. At maturity, the large early formed crystals are seen to be associated with especially prominent tubercles or convexities on the inside of the cuticle, resulting in the characteristic sculptural type of the crystalliferous periclinal surface.

Earlier, Sargent [1976a & b], using similar techniques to Oladele [1981], examined cuticle development in Libertia elegans [Iridaceae]. This author, although recognising two phases based on growth of the epidermal cells, made little reference to aspects of flanges or the periclinal surface. She mentioned that during primary growth, cell expansion is accommodated in costal regions by rupture of the cuticle followed by reformation. Sargent also thought the fibrillate structure of the cuticular layer developing in secondary growth to be non-cellulosic, in contrast to Oladele's [1981] findings, and suggested that fibrillae might be concerned with movement of solutes [cutin and wax] towards the outside of the plant.

The cause of flange waviness has been discussed for many years. Its origin has been correlated with the structure of the mesophyll [Treviranus, 1821; Arechoug, 1897; Linsbauer, 1930; Winkler, 1934], differential growth rates in this and epidermal cells setting up tensions [Linsbauer, 1930; Avery, 1933]. Winkler [1934] in contrast, believed that a secretion produced by subepidermal cells influences the growth of epidermal cell walls. Zimmermann [1893] however, showed that the cuticle is involved in the formation of waviness but failed to determine whether it has an active or a passive role. Watson's [1942]

investigation of the development of adaxial intercostal flange undulation in Hedera helix [Araliaceae] indicated that this layer is indeed most likely to be capable of causing sinuosity. Using differential staining and light microscopy he demonstrated that flange cuticle varies in plasticity, consisting of alternating inextensible [darkened] and extensible [light] regions. There is also some difference in plasticity between the cuticle of the flange base and apex. Watson [1942] found different light regimes [sun and shade] to influence the rate at which the cuticle hardens and therefore, the degree of waviness as leaves reach maturity. In dark shade, the author noted that cuticle hardening is slow in comparison with that in strong sunlight so waviness is pronounced along the entire flange length. In light shade, hardening is more rapid, resulting in less undulation at the apex than the base. In full sunlight cell walls become thick and hardened very quickly, giving some undulation at the base and distinctly straight outlines at the apex. Contrary to this, Haberlandt [1926, 1930, 1934, 1935] attributed straightness in sun leaves to inhibition of the genes for waviness by sunlight. No recent confirmation of this genetic explanation has been given.

6.5 INTRASPECIFIC VARIATION

Although little or no variation in cuticle features [including those of the inner surface] may be encountered between entities or specimens of some species [Edwards, 1935], according to Stace [1965a], a considerable degree is possible in others. Such variability may be genotypic, arising from some kind of genetic variation or phenotypic, due to differences in developmental [seasonal], positional or, more particularly, environmental factors, though these may be closely interrelated. Intraspecific variation has been recorded in both macro- and micro-morphological characters of the cuticle.

Results produced by Koster & Baas [1981] for total cuticle thickness in specimens of members of four Myristicaceae genera demonstrate differences which may be

related to flange prominence i.e. degree of cutinisation of the anticlinal walls. Dissimilarities were detected in the thickness of cuticles from either one or both surfaces of the leaf.

Aspects of cell form may also vary intraspecifically. Ferguson, Jähnichen & Alvin [1978] reported variation in both size and shape of cells in two specimens of Amentotaxus formosana [Taxaceae]. In addition, they noticed that flange thickness varied. Earlier, Jansen & Baas [1973], working on certain Celastraceae, recorded a series of anticlinal wall thicknesses ranging from very thin to extremely thick amongst eleven Kokoona littoralis entities, suggesting continuous variation of the character. Similarly, flanges may exhibit a variety of undulation states [straight to sinuous] within a single species [Van Staveren & Baas, 1973; Ferguson, 1974b; Baas, 1975; Ferguson, Jähnichen & Alvin, 1978; Wilkinson, 1983]. Such variable situation may sometimes be shown by flanges on either one or both cuticles, as in the six specimens of Iodes cirrhosa [Icacinaceae] studied by Van Staveren & Baas [1973].

The frequency of hairs or, as is usually the case with cuticles, their remaining basal parts and the number of basal cells per hair, may be variable e.g. in certain Myristicaceae investigated by Koster & Baas, [1981]. Again, variation may be detected in one or both cuticles of a leaf, as with cuticle thickness and flange undulation.

Intraspecific differences may sometimes be found in inner surface ornamentation, such as the presence or absence or form of flange pitting [Bongers, 1973; Van Staveren & Baas, 1973; Baas, 1975], periclinal sculpture [Bongers, 1973; Jansen & Baas, 1973; Van Staveren & Baas, 1973; Baas, 1975] and papillae [scrobiculi] [Solereeder, 1908; Goris, 1910; Baas, 1970; Wilkinson, 1971].

Seasonal changes may influence certain inner cuticle characters. Eames & Macdaniels [1947] noticed that cuticle thickness varies from season to season and Norris & Bukovac

[1968] discovered membranes of greenhouse grown Pyrus communis, Bartlett Pear (Rosaceae) were too thin to be successfully isolated in winter. Both groups of workers recorded a correlation of seasonal effects with those of the surroundings, that is, with weather conditions and the 'unnatural environment of the glasshouse' respectively.

Yapp [1912] produced evidence of variation in leaves of Filipendula ulmaria (Rosaceae) unfolding during March, May and June. A progressive reduction in cell dimensions and sinuation [undulate to more or less straight] was noted.

Flowering and fruiting may affect the degree of flange undulation in certain plants, such as Buchenavia capitata (Combretaceae: Stace, 1965a). At flowering time, flanges are less undulate than at fruiting indicating that the amplitude of undulation increases independently of any increase in cell area, especially on the upper leaf surface. In a later paper, Stace [1980] recorded that Combretum hensii, in the same family, also exhibits seasonal sinuation differences on the adaxial cuticle, with flanges becoming undulate only at fruiting time. It was not made clear, however, whether this referred to leaves spatially associated with the fruiting organs or to leaves produced anywhere on the plant during the fruiting season. The occurrence of striae is said to be similarly affected by season, being present at flowering and absent at fruiting.

Abundance of hairs and therefore, the corresponding bases, may show 'marked periodicity, on both flowering and non-flowering shoots in adult plants' [Yapp, 1912]. In the flowering shoots of Filipendula ulmaria (Rosaceae), for example, leaves unfolding in March are glabrous, those at the end of April or early May are partly hairy and at flowering [May-June] leaves are completely pubescent abaxially. Leaves of non-flowering shoots commence without hairs on the cuticle, then become more hairy and at midsummer pubescence decreases. Finally, in the autumn, hairs are not observed.

Stace [1965a] concluded that it was possible for a densely pubescent leaf to develop into a sparsely pubescent mature leaf and for the proportion of hairs to cells to vary considerably. He also asserted that the number of hair bases may decrease at senescence in certain taxa [in Buchenavia, Combretum and Conocarpus: Combretaceae]. In some cases, they were said to become occluded so that the majority were not perceptible, such as in Buchenavia capitata and B. kleinii.

The structure of any leaf depends, in part, on the position of that leaf on the shoot so that two leaves from opposite ends of an axis may be similar in size but may display dissimilar morphology [Yapp, 1912] as well as surface and cuticular features. These differences may be determined by changes in the environment during the seasonal growth of the shoot.

Cuticular characters, such as thickness [Eames & Macdaniels, 1947] and therefore, prominence of flanges on the inner surface, may reflect differences in leaf insertion. Yapp [1912] reported a thicker cuticle on upper stem leaves of Filipendula ulmaria [Rosaceae] than on lower stem or radical leaves, but Stober [1917] discovered the reverse situation in certain other herbs. Cell size tends to decrease with increasing height of insertion in various angiosperms [Stober, 1917; Odell, 1932; Turrell, 1942; Ashby & Wangermann, 1950; Stace, 1965a], although Yapp [1912] found that cells become longer in Filipendula ulmaria [Rosaceae]. Cells may also vary in size within a single leaf, as in Kalanchoë fedschenkoi [Crassulaceae] described by Sharma & Dunn [1968]. Cuticles isolated from near the leaf tip had the smallest cells, the next smallest occurred at the base and the largest cells were in the mid-lamina region.

The position of the leaf on the stem appears also to affect the degree of flange undulation observed in cuticle preparations. Maximov [1929] quoted Zalenski's results showing that waviness decreases the higher the point of insertion and Stober [1917] reported a decrease in

sinuosity from cauline to radical leaves in a variety of herbs. However, Stace [1965a] described opposite trends in Avicenniaceae, Combretaceae and Rhizophoraceae. Within a leaf, there may be a decrease in flange undulation towards the leaf tip, as noted by Neese [1916] and Rippel [1919: Sinapis alba [Cruciferae]] or the 'wall pattern' may be more tabular at the base for example, in Kalanchoë fedschenkoi [Crassulaceae: Sharma & Dunn, 1968].

Positional differences may influence pubescence but, as already suggested, these may only reflect environmental changes during shoot growth. In some plants, hairiness decreases downwards from the top of the shoot [Yapp, 1912; Stober, 1917]. Stace [1965a] recorded more hairs on inner radical leaves than on outer ones in certain angiosperms and stated that 'in many plants, radical leaves are almost smooth and upper cauline are conspicuously pubescent'. Ascherson & Graebner [1900-05] likewise, discovered radical leaves to be less hairy than cauline.

The length and width of guard cells represented on the cuticle may also vary depending on the position of the leaf on the shoot, as in Salix [Pataky, 1969].

The inner surface features of a cuticle may be influenced by the general nature of the habitat [Yapp, 1912], that is, the environment in which the plant is situated. A variety of characters may show significant responses, although Barthlott [1981] concluded that environmental effects were slight.

According to Stace [1965a] on angiosperms and Boulter [1971] on gymnosperms, cuticle thickness and flange height or prominence are known to be affected by the environment. Hallam & Juniper [1971] proposed that dense cutinisation occurred only in cells which were extensively exposed. Differences in levels of wind exposure [Odell, 1932], light, temperature, soil and atmospheric moisture, altitude and certain other unknown factors [Wilkinson, 1979] may be involved in causing variable reactions. Where

plants are more exposed to the wind [Odell, 1932] or to more sunlight [Dufour, 1886; Kny, 1909; Maximov, 1929; Skoss, 1955; Wilkinson, 1979] thicker cuticles may be developed. Also, higher altitudes have been correlated with greater cuticle thickness [Schroeter, 1923; Odell, 1932; Wilkinson, 1979]. Leaves in dry air often produce thicker cuticles, in humid air thinner [Eberhardt, 1903; Kunze, 1926; Odell, 1932; Wilkinson, 1979] and plants of arid soils, where they are under water stress, may have strongly cutinised leaves, [Linsbauer, 1930; Odell, 1932; Skoss, 1955; Pyykkö, 1966; Wilkinson, 1979].

Cell size may be influenced by light, soil and atmospheric moisture, quantity of atmospheric carbon dioxide and altitude. Generally, plants growing in shade i.e. 1% full summer daylight [Watson, 1942], have the largest cells [Yapp, 1912], although some, such as Kalanchoë fedschenkoi [Crassulaceae] appear to respond rather differently, with the smallest cells occurring in shade specimens [Sharma & Dunn, 1968]. The size of cells tends to decrease with increasing altitude [Odell, 1932; Stace, 1965a], excess carbon dioxide [Odell, 1932] soil moisture [Odell, 1932; Stace, 1965a; Sharma & Dunn, 1968] and atmospheric moisture [Yapp, 1912; Salisbury, 1927; Odell, 1932; Watson, 1942; Stace, 1965a]. In contrast, some plants produce the same size cells in wet and dry conditions [Ashby, 1948]. Bongers [1973] showed that in Drimys piperata, the ratio of the size of unspecialised cells to guard cells was smaller in specimens growing in open situations than in those from forests. He also noted that specimens of open conditions possessed broader than long midrib cells whilst those of the forest had longer than wide cells in the same area.

Wall or flange undulation may again vary considerably depending on environmental differences in both angiosperms [Watson, 1942; Stace, 1965a] and gymnosperms [Boulter, 1971]. Light and moisture are known to cause variation in undulation, although pollution seems to have no significant effect, according to Sharma [1981] in Liriodendron tulipifera [Magnoliaceae] and Polygonum pensylvanicum

[Polygonaceae]. Generally sinuation is more strongly marked in cuticles of shade plants, the amplitude of undulation increasing with decreasing illumination levels [Areschoug, 1897; Anheisser, 1900; Stober, 1917; Odell, 1932; Watson, 1942; Stace, 1965a; Dilcher & Zeck, 1968, Wilkinson, 1979]. Cuticles of sun specimens of Hedera helix [Araliaceae] show undulation only at the upper part of the flanges, when it is present, whereas those of shade are wavy throughout [Watson, 1942]. In some angiosperms, however, e.g. Laurus nobilis [Lauraceae] the degree of sinuation, represented by 'angle of tangent to slope of undulation' is greater in primary and secondary flanges of sun specimens than in those of shade conditions [Gibbon, 1981]. Flange waviness in other plants, such as certain succulents [Crassulaceae], is apparently not affected by illumination [Brenner, 1900]. Amplitude of undulation appears to increase with increasing humidity, although a decrease in sinuosity has been detected in some species and waviness is much reduced in xeric [dry] environments [Brenner, 1900; Odell, 1932; Stace, 1965a]. Emergent leaves of some water plants, e.g. Ranunculus aquatilis [Ranunculaceae], tend to show wavy flanges whereas those of submerged leaves are straight [Askenasy, 1870].

Leaf pubescence and, therefore, hair base frequency on the cuticle, depends in some plants on size and vigour of the shoot so that if the latter is large and vigorous most leaves will be almost or completely hairy or if small and weak the majority of leaves will be glabrous [Yapp, 1912]. Again, this may be due to environmental factors which are known to be closely linked to plant growth. Differences in light, soil and atmospheric moisture as well as altitude produce variation in trichome frequency. According to Odell [1932] and Stace [1965a], trichomes tend to be more abundant in plants growing in strong illumination, high altitude, dry air or soil than in low illumination, low altitude or moister air or soil conditions. However, McDougall [1927] reported that in Lactuca biennis [Compositae], more trichomes were produced in shade than in brighter light.

It has been recognised by various authors such as Sharma & Dunn [1968] that stomatal frequency and absolute stomatal number may be easily modified by environmental conditions. Light particularly seems to affect the number of stomata per unit area, resulting in more in sun than in shade [Gibbon, 1981]. In some plants, the size of stomata observed on a cuticle may not be influenced by external factors, i.e. dimensions are constant, whilst in others light, altitude and atmospheric moisture may lead to size modification. Full sunlight may induce larger stomata than shade [Wilkinson, 1979] and at high altitudes a slight decrease in size has been detected [Tarnavschi & Paucă-Comănescu, 1972]. A humid atmosphere is correlated with smaller stomata and dry air with larger stomata [Wilkinson, 1979]. Stomatal shape may change according to the vegetation type of the plant. Thus, in Drimys piperata [Winteraceae] constituents of open communities show circular guard cell pairs and those of the forest slender, elongate stomata [Bongers, 1973].

Little has been recorded in the literature regarding the effect of the environment on micromorphological features of the inner cuticle surface. Double or furrowed flanges may be influenced by level of illumination. In sun specimens of Aucuba japonica [Cornaceae], the furrow is wider than in shade, on the adaxial [Gibbon, 1981]. Light may also promote differences in periclinal sculpture, including striae and papillae [scrobiculi]. Cuticles of shade leaves in Aucuba exhibit depressions which are slightly deeper [in the case of the adaxial side] or more frequent [in the case of the abaxial] than those of plants growing in bright sunlight; there also tend to be more striae. However, in Pistacia spp. [Pistaciaceae], the striate appearance is more marked in high illumination [Bergen, 1904]. Although many authors have described differences in striae caused by the environment [e.g. Lee & Priestley, 1924; Martens, 1934, 1937, 1938 & 1940; Ahmad, 1962], it is unclear whether the markings are on the inside of the cuticle or on the outside and thus, their conclusions will not be discussed here. Stace [1965a] noticed a considerable variation in the degree of striation

between specimens of some species, particularly in the genus Combretum [Combretaceae], such as C. molle, which seemed to be correlated with geographical distribution and climate. Conspicuously striated entities originated from a relatively dry environment.

Papillae, which may act as lenses to concentrate low levels of light for photosynthesis, are known to be affected by environmental conditions [Wilkinson, 1971], especially climate and distribution of the species. These factors may influence both presence and prominence [Goris, 1910; Wilkinson, 1979]. Cuticles may vary from being strongly papillose in particularly shaded or damp situations to flat under more normal conditions of growth.

6.6 TAXONOMIC IMPORTANCE

It has been well established that cuticular features in seed plants are 'of undoubted importance as further pieces of the jigsaw of complete systematic evidence and at times are, in fact, of greater value in identification and taxonomy than any other characters of which we know' [Stace, 1965a]. Furthermore, they may assist the comprehension of evolutionary processes [Boulter, 1971; Stockey & Taylor, 1978b]. This is in accordance with the belief that features with little or no obvious differential survival value are of most phylogenetic significance [Stace, 1965a].

The usefulness of inner surface micromorphology in taxonomy [i.e. identification, description, classification and phylogeny], has only been realised in recent years [Oladele, 1983b]. Boulter [1971] was first to recognise the potential of these characters in gymnosperms [Pinaceae and Taxodiaceae] pointing out that by extending the range of taxonomically useful features, the value of the cuticle may be greatly enhanced. However, he was unable to evaluate particular characters in terms of their taxonomic significance.

In fact, the inner surface may provide more information of taxonomic importance than the outer cuticle surface, especially concerning the stomatal apparatus, cell patterns and details of flanges between the epidermal cells [Stockey & Taylor, 1978a]. Such characters may have considerable value in taxonomy. The high degree of constancy in internal features within a given species and the relation between sculptural details and the accepted taxonomic structure of a group suggests that this is so in conifers [Miranda & Chaphekar, 1980; Oladele, 1981, 1983b; Alvin, Dalby & Oladele, 1982]. This is also likely to be the case in angiosperms, since Barthlott [1981] detected great structural diversity in seed plants generally, which he considered would provide most valuable criteria for classification. Below species level, inner surface micromorphology may be of limited use in demarcating taxa, according to Oladele [1983a] in his studies of Cupressaceae.

Stace [1965a] doubted whether differences in a single feature of any organ [such as the cuticle], would discriminate between taxa above species level. However, differentiation between taxa may be more effective when an assemblage of characters is considered collectively [Oladele, 1983a], especially since it has been demonstrated that the degree of constancy of internal features commonly decreases towards higher taxonomic ranks [Oladele, 1981]. Koster & Baas [1981] stressed the importance of ascertaining which characters are constant for a variety, species or genus and which are not, in order to identify the features of diagnostic value and determine the nature of any relationships at these levels. If, as in the Winteraceae [Bongers, 1973], the characters are very variable they may have different significance in the various genera, sections and species corresponding to the variational range within each taxon and thus, it may not be possible to estimate the usefulness of an individual feature within the family as a whole.

According to Stace [1965a], no single character exceeds all others in value and 'in different groups any

character can be a family, generic or specific criterion or of no systematic importance at all' irrespective of the significance of the other features. Trends found in one taxon, he said, should not be applied to others even if the plants are closely related.

The usefulness of inner surface characters in taxonomy has been dealt with by a number of authors. Some literature describes the importance of features in particular families whilst other work incorporates information about useage in general. Many aspects have been discussed.

Cuticle thickness, related to the extent of cutinisation, is considered of some importance in certain plants [Thomas & Bancroft, 1913; Stace, 1965a; Wilkinson, 1979; Oladele, 1981; Alvin, Dalby & Oladele, 1982]. However, Baas [1981] found that the taxonomic and diagnostic value of this character is not very strong in Myristicaceae since it may be influenced by the environment as well as various other factors and thus may exhibit considerable phenotypic variation [Stace, 1965a; Wilkinson, 1979]. Sometimes cuticle thickness may be of significance for discriminating between species or varieties [Koster & Baas, 1981] but in angiosperms, according to Wilkinson [1979], it is often more important as an indicator of climate or habitat. Another feature reflecting the degree of cutinisation, flange prominence, is thought to be of value [C.I.M.P. 1964; Barthlott & Ehler, 1977; Wilkinson, 1979; Oladele, 1981; Alvin, Dalby & Oladele, 1982]. Nevertheless, it is known to be correlated with leaf shape i.e. adult and juvenile forms in Cupressaceae [Oladele, 1981] and the exposure range of the plant [Barthlott & Ehler, 1977].

A number of characters concerned with cell form have been found to be useful, e.g. cell size or frequency per mm^2 , for the taxonomy and separation of angiosperm and gymnosperm species [Stace, 1965a; Sharma & Dunn, 1968; Ahmad, 1974a; Ferguson, 1974a; Oladele, 1981; Alvin, Dalby & Oladele, 1982; Wilkinson, 1983]. Details of cell size may be of taxonomic and diagnostic value at genus

level in some cases, such as in Myristicaceae [Koster & Baas, 1981]. However, variability with age, environment, minor genetic variation, position of leaf on the shoot and cells in the leaf may pose serious taxonomic difficulties [Stace, 1965a]. Cell size expressed in terms of median length or area may also show correlation with leaf shape in certain families, for example, Cupressaceae according to the work of Oladele [1981] and Alvin, Dalby & Oladele [1982]. Cell shape has systematic and diagnostic significance in seed plants [Thomas & Bancroft, 1913; C.I.M.P., 1964; Stace, 1965a; Ferguson, 1974a]. Although it may be consistent in a number of different leaves from different specimens of certain taxa [Alvin & Boulter, 1974: Taxodiaceae] and may be diagnostically useful at species or genus level [Ahmad, 1974a & b: Acanthaceae], cell shape may vary intraspecifically, as in some Taxaceae [Ferguson, Jähnichen & Alvin, 1978] thereby reducing its value in taxonomy. Cell arrangement also appears to be valuable. It is known to be of minor taxonomic importance and sometimes of use in the determination of taxa between species and genus levels in certain families [Barthlott, 1981]. The character is consistent in a number of different leaves of different plants in some species [Alvin & Boulter, 1974: Taxodiaceae].

Many aspects of flanges are known to be of use in taxonomy, for example, outline in T.S. [C.I.M.P., 1964], buttresses [Ehler, 1977; Oladele, 1981; Alvin, Dalby & Oladele, 1982], furrowing [Miranda & Chaphekar, 1980; Oladele, 1981, 1983b; Alvin, Dalby & Oladele, 1982], margin irregularity [Oladele, 1981; Alvin, Dalby & Oladele, 1982] and corner extensions or pegs [C.I.M.P., 1964; Wilkinson, 1979]. Wall thickness or width of flange base has been shown to sometimes be of value for comparing various taxa, cycads [Thomas & Bancroft, 1913] and conifers [Oladele, 1981; Alvin, Dalby & Oladele, 1982]. According to C.I.M.P. [1964], flanges of average width greater than 1 μm are likely to be most significant diagnostically in seed plants. Indeed, certain angiosperm species may be characterised by especially thick flanges, such as Combretum obanense [Combretaceae: Stace, 1965a]. In other

families, e.g. Celastraceae, this feature is of no importance at all at species level [Jansen & Baas, 1973].

Anticlinal wall pitting or beading, reflecting flange continuity is useful for discrimination and comparison [Thomas & Bancroft, 1913; Dewar & Wallis, 1935; C.I.M.P. 1964; Wilkinson, 1971, 1979; Baas, 1972; Jansen & Baas, 1973; Alvin & Boulter, 1974; Barthlott, 1981; Oladele, 1981; Alvin, Dalby & Oladele, 1982]. Dewar & Wallis [1935] noted that the presence of distinct beading is diagnostic at species level in Digitalis [Scrophulariaceae]. In other angiosperms, such as members of the Icacinaceae, pitting is very variable [Van Staveren & Bass, 1973] and may not be constant for a species, e.g. in Winteraceae [Bongers, 1973], Ilex [Aquifoliaceae: Bass, 1975] and Myristicaceae [Koster & Baas, 1981] suggesting little or no importance in taxonomy. In coniferous taxa, such as those of the Taxodiaceae, Alvin & Boulter [1974] failed to detect any intraspecific variation of this character.

Presence or absence of thin areas and/or pit-like structures in cell corners and presence or absence of pit-like cavities in the outer walls between anticlinal wall undulations have been found to be significant diagnostically at genus level in some flowering plant families, such as Celastraceae [Jansen & Baas, 1973] and Huaceae [Baas, 1972] respectively.

Flange undulation [as seen in surface view] is undoubtedly of use in some instances [Stace, 1965a]. Undulation type is generally important at levels of secondary systematic rank i.e. species, subgenus, genus according to Barthlott & Ehler [1977] and may occasionally be of significance for subtribe and tribe [Barthlott, 1981]. Presence or absence of wavy walls may even be valuable above family level, particularly in angiosperms [Linsbauer, 1930]. In spite of the fact that the degree of sinuation or undulation is known to vary within some species [see p. 63-68], this character has nevertheless been found to be one of the few features of great

taxonomic value in certain flowering plant genera such as Combretum [Combretaceae: Stace, 1965a; 1980] and Cocculus [Menispermaceae: Ferguson, 1974a]. In Lemna [Lemnaceae: Stace, 1965a] it is known to be the major character for classification. Discrimination between subfamilies or genera may be achieved by differences in sinuosity of intercostal walls, e.g. in the Acanthaceae [Ahmad, 1974b], and Portulacaceae [Ramayya & Rajogopal, 1968] respectively. The degree of undulation of flanges on the cuticle from one leaf surface only may assist separation of some genera, such as those of the adaxial in Litsea and Neolitsea [Lauraceae: Bandulska, 1926]. Together with other features, undulation may distinguish individual species, e.g. Cinnamomum [Lauraceae: Bandulska, 1928], Pycnarrhena [Menispermaceae: Cutler, 1975] and Gluta [Anacardiaceae: Wilkinson, 1983]. Especially well-developed patterns [zig-zag] are known to be the only types of use for diagnostic purposes in Ilex [Aquifoliaceae, Baas, 1975].

The fine sculpture of flanges has considerable taxonomic significance and may be important diagnostically [C.I.M.P. 1964; Boulter, 1971; Barthlott & Ehler, 1977; Stockey & Taylor, 1978a; Wilkinson, 1979; Gibbon, 1981 unpublished; Oladele, 1981, 1983b; Alvin, Dalby & Oladele, 1982]. Stockey & Taylor [1978a] found it to be of value for distinguishing species and subdividing genera in Araucariaceae. Patterns at the base and apex of flanges are known to be characteristic of certain genera in some gymnosperm families, e.g. Cupressaceae [Oladele, 1983b]. However, the value of microrelief at the flange base may be somewhat reduced in such families due to meaningful correlation with leaf shape.

The ornamentation of the periclinal surface is also known to be taxonomically and most particularly, diagnostically useful [C.I.M.P. 1964; Wilkinson, 1971, 1979; Alvin & Boulter, 1974; Barthlott & Ehler, 1977; Miranda & Chaphekar, 1980; Gibbon, 1981; Oladele, 1981, 1983a]. The high degree of constancy within a given species e.g. in Pinaceae [Miranda & Chaphekar, 1980] and

Taxodiaceae [Alvin & Boulter, 1974] together with its repeated occurrence in different plant groups, shows that it acts as a taxon-specific distinction of the cuticle [Barthlott & Ehler, 1977]. Sculptural type is valuable generally below family level [Boulter, 1971] for discrimination of genera, species or varieties, such as in Gymnacranthera and Horsfieldia [Myristicaceae: Koster & Baas, 1981] and in subdividing genera, e.g. Araucaria [Araucariaceae: Stockey & Taylor, 1978a]. Granulation, especially, has been found to be significant at species level in some plants, for example, genera of the Ericaceae, Scrophulariaceae and Solanaceae studied by Kurer [1917]. However, evidence of intraspecific variation has been recorded [Baas, 1975; Koster & Baas, 1981]. In the Icacinaceae examined by Van Staveren & Baas [1973], the type of granulation was rather constant in some genera whilst the character was confined to only certain species, in others. Bongers [1973], after detecting variability within entities of Drimys piperata [Winteraceae], concluded that granulation may be a feature of somewhat minor taxonomic importance. Stace [1965a] asserted that smooth or minutely granular surfaces are of no general use in angiosperms. According to the work of Oladele [1981, 1983b], the grade of periclinal sculpture may sometimes be useful for separating certain genera since it is 'reasonably constant', although there may be some variation in granule size and to a greater extent, cavity size in comparable cells of a single example.

Ornamentation of the marginal strip adjacent to the flange base has taxonomic and diagnostic significance at genus level in some conifer families, such as Cupressaceae and the degree of development of the sculpture may vary between species [Oladele, 1981, 1983b].

The microrelief of crystal tubercles is also of value for distinguishing genera. In the Cupressaceae, Oladele [1981; 1983b] showed that this sculpture is an important difference between those with different geographical distributions i.e. Northern and Southern.

Thin areas in the periclinal cuticle are characteristic of a few seed plants and are, therefore, valuable for identification of such taxa, e.g. Combretum obanense [Combretaceae: Stace, 1965a] and Welwitschia mirabilis [Welwitschiaceae: Barthlott & Ehler, 1977].

Papillae, often represented by scrobiculi on the inner surface, are also of some importance taxonomically such as in Cocculus [Menispermaceae: Ferguson, 1974a] and diagnostically for distinguishing between genera, for example Afrostryax and Hua [Huaceae: Baas, 1972] or separating taxa similar in other cuticle characters e.g. Cinnamomum zeylanicum and the papillate Lindera megaphylla [Lauraceae: Bandulska, 1928]. In Cupressaceae, Oladele [1983a] discovered papillae to be good taxonomic features since they were not correlated with leaf shape. Nevertheless, in certain genera, for instance Cratoxylum [Guttiferae], papillae are not of constant occurrence in the species and thus, are considered unreliable and of no value in taxonomy. Any significance may also be reduced as environmental conditions are known to promote differences in the extent of papillation [see p. 63, 69, 70].

Cuticular striations may have taxonomic and diagnostic importance at species level [Kurer, 1917; Stace, 1965a]. Above species their usefulness is limited, according to Barthlott [1981] and Koster & Baas [1981]. The type of striation may be very variable, as in some Icacinaceae studied by Van Staveren & Baas [1973] and the degree exhibited is not always constant [Stace, 1965a], variation being brought about by environmental factors [see p. 69, 70].

The significance of inner surface features in certain regions of the cuticle has been dealt with briefly: those of veins, for example, prominence [Stace, 1965a, 1980; Bongers, 1973], cell shape [Thomas & Bancroft, 1913], flange shape, presence and type of pitting [Thomas & Bancroft, 1913; Wilkinson, 1978] as well as nature of periclinal sculpture [Wilkinson, 1978], and margin areas, e.g. degree of modification expressed as cell size, arrangement,

wall thickness and lumen shape [Stace, 1965a]. Although there has been some indication of their importance at genus level in some angiosperms [Stace, 1965a, 1980], cautious use of certain of these characters is to be recommended: vein prominence since it may be variable within entities, as in Winteraceae [Bongers, 1973] and is subject to phenotypic variation, partly environmental and partly positional in origin in a number of tropical species [Stace, 1965a], as well as general margin features, due to high correlation with leaf shape in certain families, e.g. Cupressaceae and Taxodiaceae [Oladele, 1981].

The cuticle in the region of the stomatal apparatus is a particularly valuable source of characters for use in taxonomy [see p. 48]. The importance of many aspects has been critically examined [see Florin, 1931; Dilcher, 1974; Wilkinson, 1979]. Individual features have a range of uses and vary in value.

According to Barthlott [1981] the distribution of idioblastic elements such as stomata is of minor taxonomic interest but may be systematically significant in some families for determination of taxa at species to genus levels. The presence of stomata on the adaxial leaf surface is recognised as a character of limited taxonomic importance in some angiosperms, such as members of the Combretaceae with the mangrove habit [Stace, 1965a] and Gymnacranthera [Myristicaceae: Koster & Baas, 1981]. In others, the character is known to be unreliable at species level [Koster & Baas, 1981], varying from species to species and often even intraspecifically [Stace, 1965a].

The systematic usefulness of stomatal frequency is liable to vary, being of value sometimes for families, genera or species [Edwards, 1935; Ahmad, 1974a] or not at all [Edwards, 1935; Ferguson, 1974a]. Stace [1965a] recognised that this feature is one which is 'regularly expected to show sufficient environmental and developmental variation to pose serious taxonomic difficulties' since it often varies considerably in the mature leaf, on

different parts of the same leaf and on different leaves of the plant. It may, in addition, be regulated by environmental conditions, especially light [see p. 69].

Stomatal index may be important taxonomically where it has been shown to be consistent, e.g. in Kalanchoe fedschenkoi [Crassulaceae: Sharma & Dunn, 1968]. In Cocculus [Menispermaceae], however, Ferguson [1974a] was unable to use it to discriminate between species.

Stomatal size may be of some significance in taxonomy. It may, in association with other characters, distinguish taxa in a subfamily, for example the Nelsonioideae [Acanthaceae: Ahmad, 1974a]. Where consistent, Sharma & Dunn [1968] showed that the largest and smallest stomata could be valuable for taxonomic purposes in certain plants, such as Kalanchoe fedschenkoi [Crassulaceae]. Stomatal size is known to vary often with environment and position on the plant although it appears to be less subject to phenotypic variation than some features e.g. epidermal cell size [Stace, 1965a]. Koster & Baas [1981] found that the size of guard cell pairs was not constant for most species and varieties in Myristicaceae and concluded, therefore, that it may have very little value in this family.

The outline or shape of the stoma [seen in surface view] may be useful in the taxonomy of some genera, for example Cocculus [Menispermaceae] particularly if expressed as a length : breadth ratio [Ferguson, 1974a] and for discrimination of species and genera, for instance, in Cupressaceae [Oladele, 1981, 1983a: Alvin, Dalby & Oladele, 1982] and Anacardiaceae [Wilkinson, 1983].

Stomatal type, reflecting the arrangement of guard cells and any accompanying subsidiary or bordering cells in the complex in surface view, has long been considered of great importance especially in conifers, for taxonomic and diagnostic work [see Thomas & Bancroft, 1913; Florin, 1931; Wilkinson, 1979; Oladele, 1981; Alvin, Dalby & Oladele, 1982] at genus [Bandulska, 1931; Koster & Baas,

1981] and species [Sharma & Dunn, 1968] levels. Sometimes, however, its significance for comparing high ranking taxa, as in certain Huaceae, is uncertain according to Baas [1972].

The presence of giant or water stomata may be taxonomically and diagnostically valuable at genus level in some angiosperms e.g. Gymnacranthera [Myristicaceae] although not useful for species or varieties [Koster & Baas, 1981].

The inner ledge is of variable value in seed plants. Sometimes, when in association with the stomatal flap, it may be of taxonomic importance at genus level, such as in the Icacinaceae studied by Van Staveren & Baas [1973]. However, in other families, for instance the Myristicaceae, the inner ledge varies intraspecifically and is, therefore, of no use diagnostically or taxonomically [Koster & Baas, 1981].

The usefulness of polar thickening i.e. T-pieces etc., is also known to vary. In some genera e.g. Rhodomyrtus [Myrtaceae], such structures may be diagnostic at species level [Bandulska, 1931]. Boulter [1971] recognised this thickening to be 'the most important character of the lignified guard cells' in Taxodiaceae. There may, nevertheless, be intraspecific differences in the feature in other plants, such as the Myristicaceae and thus, in these examples, polar thickening is of no value for taxonomy [Koster & Baas, 1981].

Consistent variation in height [depth] or prominence [Boulter, 1971] and thickness [Bandulska, 1931; Boulter, 1971] of stomatal flanges is shown by many genera, particularly in gymnosperm families, providing a means of identification at genus level. However, evidence from numerical analysis given by Oladele [1981] suggests that there is a high correlation between height of guard cell/subsidiary cell flanges and leaf shape in some families [Cupressaceae] and indicates, therefore, that this aspect is of less significance in certain cases. The morphology of

flanges between guard and subsidiary cells has been found to be useful for distinguishing species, especially where they are extremely well-developed, for example the wing-like type of Abies recurvata [Pinaceae: Miranda & Chaphekar, 1980] and for subdividing genera, such as Araucaria [Araucariaceae: Stockey & Taylor, 1978a]. The shape of the cutinised parts of the guard cells, e.g. the 'scales' referred to by Bandulska [1926] in Lauraceae, may be diagnostic at genus or family levels. The presence or absence of grooved [double] flanges in the stomatal region is recognised as diagnostically important for species in some families, for instance, the Pinaceae [Miranda & Chaphekar, 1980].

The surface ornamentation of the cells constituting the stoma appears to be significant for all aspects of taxonomy. Details of its importance have mainly been provided for gymnosperms, although the usefulness of striae for distinguishing species [Wilkinson, 1983] and the presence of scrobiculi [papillae] in the taxonomy of certain genera [Ferguson, 1974a] as well as the reduction of value of such characters by environmental conditions and differences in geographical distribution [see p. has been mentioned, in angiosperms.

The periclinal sculpture of the guard cells is taxonomically [Alvin & Boulter, 1974] and diagnostically important at species level in some genera [e.g. Araucaria: Araucariaceae: Stockey & Taylor, 1978b] and families [such as Pinaceae: Miranda & Chaphekar, 1980]. Certain types of guard cell microrelief where they are distinct, may characterise particular genera, for example the pock-marked sculpture [left behind after removal of calcium oxalate inclusions] of Callitris and Neocallitropsis [Cupressaceae] described by Oladele [1981, 1983a].

The periclinal sculpture of the polar subsidiary cells is known to be consistent in a number of different leaves from different plants of a species, e.g. Sequoia sempervirens [Taxodiaceae; Alvin & Boulter, 1974] suggesting potential taxonomic usefulness. The type of subsidiary

cell surface may be diagnostic at genus level, for instance in Callitris [Oladele, 1981, 1983b]. Alternatively, the sculpture of these cells [polar and lateral] can be indicative of a species, as in Pinaceae especially where the pattern is particularly distinctive, e.g. protrusions in a concentric arrangement [some species of Abies, Picea and Pseudotsuga] [Miranda & Chaphekar, 1980].

Sculptural differences between cells of the stomatal complex and non-specialised epidermal cells have been recognised as important for separating certain species, for example, in the genus Thuja [Cupressaceae: Oladele, 1981, 1983b] and the family Pinaceae [Miranda & Chaphekar, 1980].

Trichomes [glandular and non-glandular] are of considerable importance in comparative systematic investigations of angiosperms [Theobald, Krahulik & Rollins, 1979] and cycads [Thomas & Bancroft, 1913]. The usefulness of various individual features has been discussed in the literature [Dilcher, 1974] including presence [Thomas & Bancroft, 1913; C.I.M.P., 1964; Bongers, 1973], number of base types [Stace, 1965a], base distribution [Ahmad, 1974a; Ferguson, 1974a; Koster & Baas, 1981, Barthlott, 1981], frequency [Bandulska, 1928; Stace, 1965a; Ferguson, 1974a; Koster & Baas, 1981], size and elevation of basal parts [Koster & Baas, 1981], basal cell diameter [Ferguson, 1974a], cell arrangement [Koster & Baas, 1981], cell number and pore size [Stace, 1965a]. Most of these characters have some taxonomic or diagnostic significance at species level. Certain aspects are known to be important at other ranks. According to Barthlott [1981], trichome distribution is of value in some families for determination of taxa at species to genus level. Where hair covering is particularly marked [sparse or dense] this may be used diagnostically at a range of taxonomic levels i.e. species, subspecies and variety as well as for separating phenotypic modifications [Stace, 1965a]. Observations made by Koster & Baas [1981] have shown that in Myristicaceae this feature, together with the arrangement, size and elevation of basal parts, may be useful for classification and discrimination

of genera.

Trichome characters, such as the number of base types [Stace, 1965a] or base distribution [Koster & Baas, 1981] are not always of equal significance in a closely related assemblage and indeed, may be of little or no value in some cases due to the influence of ecological factors [Koster & Baas, 1981]. Trichome frequency, for example, is one of those features considered by Stace [1965a] to show 'sufficient environmental and developmental variation to pose serious taxonomic difficulties' due to variability with age, individual leaf, position on the shoot and different environments. He recommends therefore, that its use should be preceded by an exhaustive investigation to determine the changes accompanying growth and senescence as well as the degree of phenotypic variation.

The importance of a few miscellaneous characters has also been mentioned. Small groups of cells with especially long, straight anticlinal walls and thick periclinal walls in contrast to surrounding cells have been found to be useful for identification of some flowering plants [Wilkinson, 1979].

The presence or absence of anticlinal or periclinal secondary divisions of non-venous areas is known to be of significance in angiosperms generally, for aiding discrimination between families [Stace, 1966] and taxonomic application at genus level [Stace, 1965a]. Where present, this feature is usually constant and well-developed [Stace, 1965a] although below species there may be strong variability in the extent of adaxial subdivision, as in the Aquifoliaceae [Baas, 1975].

Another character with some value taxonomically and diagnostically is the presence of cork warts. These are often constant in occurrence and may be of use for identifying genera [Stace, 1965a]. In certain families, however, e.g. the Myristicaceae, the significance is known to be low at this level [Koster & Baas, 1981].

If these structures are regular in shape and frequency, they may be of use for diagnosing species [Stace, 1965a] and together with other features, may be used in discussions of infrageneric affinities, such as in the Aquifoliaceae [Bass, 1975].

7. MATERIALS [See Table I]

7.1 SOURCES

Specimens of 1-4 species of each genus within the Lauraceae and the related families Austrobaileyaceae, Gomortegaceae, Hernandiaceae and Trimeniaceae represented in the Herbarium, Royal Botanic Gardens, Kew, were chosen for sampling. The few Lauraceae growing in Chelsea Physic Gardens, London were used for a preliminary study.

7.2 SELECTION OF TAXA

Preference was shown in the selection of species for those with the most herbarium sheets. Special care was taken in this procedure due to the possibility of incorrect identification where specimens were sterile or female, in the case of Lauraceae. Gross morphology, venation and features of the chosen specimen seen with a x 10 hand lens were checked against similar characters of the Type specimen.

7.3 SELECTION OF SAMPLE LEAF

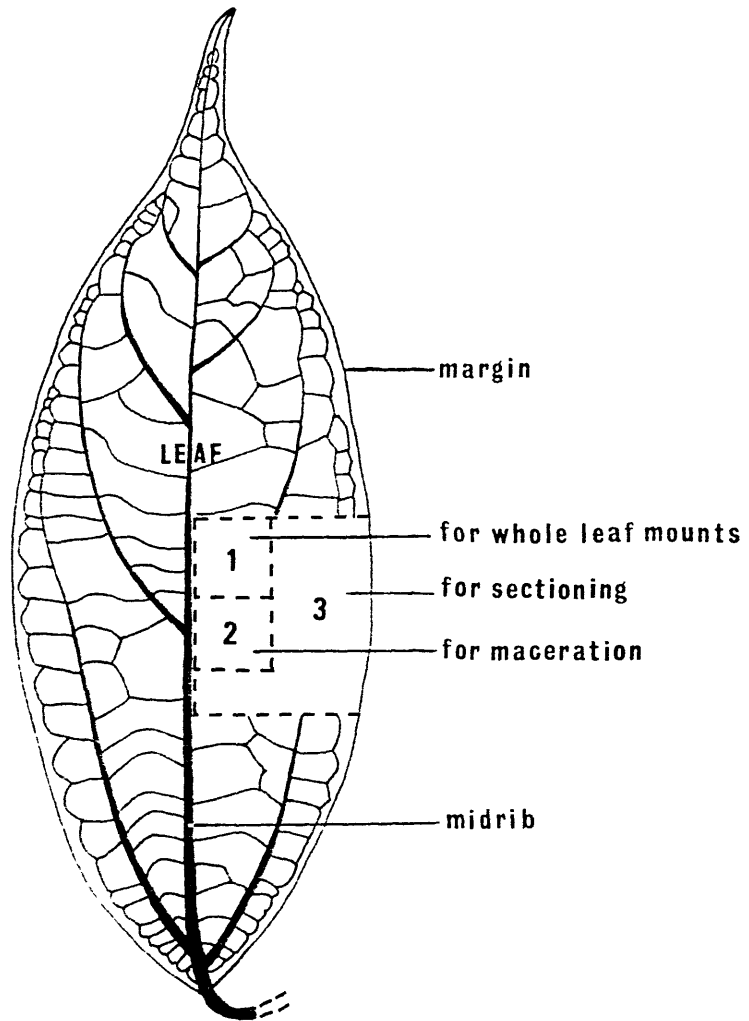
A mature leaf, about half-way down the twig axis was selected for sampling. Damaged leaves, where the apex or part of one side was absent, were used rather than whole ones to conserve, as far as possible, the visual and scientific value of the herbarium specimen. When the number of available specimens of a particular species was low and the quality was poor, capsule material was utilised provided that good evidence of prior leaf attachment [i.e. a scar] could be detected on the twig axis.

7.4 SELECTION OF SAMPLE AREA

A portion of one side of the leaf about 2.5 cm wide including all areas from the midrib to the margin [Text-Fig. 1], was removed from the middle lamina region, where anatomical features are generally considered to be most representative. This method of sampling was adopted for all species except Caryodaphnopsis tonkinensis, where young leaves were collected from the twig apices of three specimens so that a brief study of the development of the abaxial epidermis could be attempted.

Stem samples of two species of Cassytha, a genus of leafless parasites, were taken from half-way down an axis for comparison of characters, particularly stomatal, with those of other Lauraceae.

TEXT-FIGURE 1. Diagram showing sampling of leaf specimen and location of portions for use in preparation of whole leaf mounts, cuticles (maceration) and sections.



8. METHODS

8.1 CUTICLE ISOLATION

A 1 cm² portion [2 in Text-Fig. 1] was cut from each sample adjacent to the midrib. In the case of Cassytha, 2 x 1 cm lengths were taken from the stem samples.

8.1.1 DEWAXING

Wax often forms a dense covering particularly in those species with thicker leaves, which may obstruct the fine details of the cuticle especially in the light microscope. Since also wax type can alter in the drying of specimens for the herbarium as well as in maceration, it was considered desirable to de-wax.

The sample for investigation was de-waxed with cold chloroform for 15 minutes in an open glass vial fitted with a wire stirrer designed to hold down the material and agitate the organic solvent, to promote action all over the surface. Dewaxing was continued with cyclohexane for 5 minutes in the same way. Finally, the sample was washed thoroughly [3 times] with double distilled water.

8.1.2 MACERATION - Removal of cuticle from underlying cells

The chemical method of isolation [maceration] using chromium trioxide described by Alvin & Boulter [1974] for conifers, was slightly modified. Oladele [1981] showed this method to be the most satisfactory of a number of methods he tried for light-and scanning electron-microscopic studies since few artifacts are created in preparation of the cuticle.

The de-waxed portion of leaf of each sample was cut into 4 pieces. These were then placed in 2-3 mls of 20% [w:v] chromium trioxide solution in a covered glass embryo cup for 12-48 hours at room temperature. At regular intervals the progress of maceration was monitored with the light microscope, placing a leaf piece or cuticle in a 'well' of distilled water with a Blu-tack surround on a slide. In this way, over-maceration was avoided. When cellular material was not completely removed after 48 hours

in chromium trioxide, further treatment of 2-8 hours in 10% chromium trioxide and concentrated nitric acid [1:1] was given.

The isolated cuticles [abaxial and adaxial] were transferred to double distilled water in a covered embryo cup and soaked overnight to remove the chromium trioxide. Finally, the cuticles were rinsed 2 times with double distilled water.

Cassytha stems were divided in two [to give 4 pieces] and split along their length to allow good penetration of the macerating solution. Isolation and washing of the cuticles were carried out as described for the leaves.

8.1.3 MOUNTING

8.1.3a FOR LIGHT MICROSCOPY

For each sample, 2 adaxial and 2 abaxial [2 stems in Cassytha] cuticles were stained overnight with Sudan IV [2% solution in 70% alcohol] in a covered embryo cup. Excess stain was removed by quickly rinsing in 70% alcohol. Adaxial and abaxial [stem only in Cassytha] cuticles were placed on separate slides, warmed by a Photax dishwarmer 2A, in a drop of 50% glycerol and arranged so that one cuticle piece had its outer surface uppermost and the second its inner surface. The 50% glycerol was withdrawn by pipette and the cuticles were mounted in glycerol jelly. On cooling, surplus mountant was scraped off the slides, then the preparations were cleaned with 70% alcohol and ringed with clear nail varnish.

8.1.3b FOR SCANNING ELECTRON MICROSCOPY

Each cuticle [adaxial, abaxial and stem in Cassytha] was cut in half in a 'well' of distilled water with a Blu-tack surround on a slide. The pieces were transferred to a drop of double-distilled water on an aluminium stub covered by double-sided Sellotape. Under a dissecting microscope, one cuticle piece was unfolded with blunt or curved-ended mounted needles until it was flat. Gentle pressure was applied to the cuticle at selected points to

effect adhesion to the Sellotape. Rubbing down over the entire surface was to be avoided as it causes severe damage to the delicate structure. The second cuticle piece was inverted and mounted in the same way as the first. The drop of double-distilled water was withdrawn with a pipette and the cuticle pieces were air-dried in a dessicator containing silica-gel.

8.2 WHOLE MOUNTS

A 1 cm² portion [1 in Text-Fig. 1] was routinely removed from each leaf sample adjacent to the midrib and cut in half. Selected portions [from the mid-zone, margin, base and apex] of the young Caryodaphnopsis tonkinensis leaves were also used.

The bodies of trichomes often become detached during dewaxing and maceration, and papillae or domed cells may collapse when cuticles are air dried. Therefore, it was considered useful to examine the unmacerated leaf surface.

The pieces for investigation were mounted on an aluminium stub with 'Durofix' adhesive so that one leaf piece showed its adaxial surface and the other exhibited its abaxial side. Silver conductive paint ['Dag'] was spotted at the corners of each piece of leaf to increase conductivity between the specimen and the stub. The adhesive and 'Dag' were allowed to dry thoroughly in a dessicator.

Whole stem mounts of Cassytha species were made by cutting a 1 cm length of stem into two and mounting the pieces on a stub with the long axis in the horizontal position. Conductive paint was applied at intervals.

8.3 SECTIONING

The remainder of each sample [3 in Text-Fig. 1] was used for sections.

8.3.1 T.S.

Transverse sections were essential for the proper interpretation of the stomatal complex, which tends to be ambiguous in structure in the isolated cuticle. Both

the extent of cutinisation and the relationship between the inner and outer surface features may also be better understood with the aid of a section.

The leaf portion was boiled in a water bath until the material felt pliable [usually for 5-10 minutes]. Transverse sections, 10-20 μm thick, were cut on a Reichert 'sledge' microtome fitted with a 'Frigister' freezing stage. The sections were partially decolourised to a pale yellow or straw colour with household bleach ['Parazone'] so that the dark-brown or green-brown colouration produced by drying did not obscure the epidermal and cuticle structure. The sections were then thoroughly washed [3 times] with double distilled water.

About 5-10 transverse sections were stained in Sudan IV and mounted as described above [8.1.3a]. Sections were also tested for presence of lignin [Jensen, 1962] by placing in one drop of phloroglucinol solution followed by one drop of concentrated hydrochloric acid on a slide. They were then mounted in 50% glycerol and observed by light microscopy. An intense red colouration indicated a positive reaction.

In an attempt to elucidate the epidermal organisation on the abaxial surface of Caryodaphnopsis tonkinensis thick [60-80 μm] transverse sections were cut as described above, mounted on a stub and air-dried before being examined by scanning-electron microscopy.

8.3.2 L.S.

Cassytha spp. have stomata arranged in rows along the stem. Longitudinal sections of the axis were necessary to obtain transverse sections of the stomata. A 1.5 cm length of stem was boiled for about 1 minute. 10-20 μm thick sections were cut on the Reichert freezing microtome and stained for the light microscope according to method 8.3.1.

8.3.3 PARADERMAL SECTIONS

To further assist interpretation of the abaxial epidermis structure in Caryodaphnopsis tonkinensis 10 μm thick paradermal sections were cut with the Reichert

freezing microtome. The sections were prepared for scanning-electron microscopy in the same way as cuticles [Method 8.1.3b].

8.4 MISCELLANEOUS

Two other methods were utilised in the study of abaxial C. tonkinensis, prior to examination in the S.E.M.

8.4.1 SELLOTAPE PULL

A 1 cm² piece of double-sided sellotape was rubbed over the lower side of a standard portion of C. tonkinensis leaf. It was then gently removed by pulling away with fine forceps and mounted on a stub with the surface that had been adjacent to the specimen facing uppermost. Conductive paint was applied at the edges.

The portion of leaf from which the Sellotape had been pulled was also mounted, to show the abaxial side, as described in 8.2.

8.4.2 SURFACE SCRAPES

The abaxial surface of a softened portion of the leaf, prepared by boiling in a water bath for 5-10 minutes, was carefully scraped several times with a razor blade held horizontally. The piece of leaf was then arranged on a stub so that the treated side was uppermost [Method 8.2].

8.5 EXAMINATION OF PREPARATIONS

8.5.1 BY LIGHT MICROSCOPY

Observations were made using a Gillett and Sibert M I 5553 microscope fitted with an eyepiece graticule. Drawings were produced at standard magnifications with the aid of a Reichert microscope and camera lucida attachment.

8.5.2 BY SCANNING ELECTRON MICROSCOPY

Whole leaf, stem and paradermal mounts and isolated cuticles as well as the sellotape pull, surface scrapes and thick sections were coated with about 300Å gold using a Polaron E 5000 Sputter coater. All surfaces were observed with a Philips S.E.M.500 at 25 KV, 0° tilt and spot size

320Å. A short working distance was utilised to permit good resolution at high magnifications. Features were recorded on Ilford Pan F or 35 mm fine-grain film at standard magnifications. Photographs were mounted in a series of albums, arranged in alphabetical order of species so as not to infer taxonomic relationships and according to aspect of the leaf, stem or cuticle.

9. ABBREVIATIONS AND SYMBOLS

A	Aperture
AB	Anticlinal border
ABX/abx.	Abaxial
ADX/adx.	Adaxial
AP	Apex
av.	Average
B	Polar bar
ba	Base
bc	Basal cell [hair]
ca.	Approximately
c./c	Costal region
CP	Corner peg
D/d.	Depression
EC	Epidermal cell
EP	Epidermal papilla
F/OF	Flange
G	Gland
GC	Guard cell
GS	Giant stoma
GSF	Guard cell/Subsidiary cell flange
H	Hair [body]
HB	Hair base
HF	Hypodermal flange
HP	Hair pore
I	Interruption
ic./IC	Intercostal region
IL	Inner ledge
IP	Inner periclinal cutinisation
is	Internal striae
I.S.	Inner surface
L	Lumen
LE	Lateral extension
LL	Lateral line
M	Mesophyll
MI	Margin irregularity
o	Perforation
OL	Outer ledge
O.S.	Outer surface
P/p.	Protrusion

PA	Papilla apex
PB	Papilla base
PF	Poral flange
PL	Length of stomatal pit
PP	Polar papilla
PS	Periclinal surface
PW	Width of stomatal pit
R	Polar rod
S	Stoma
SC	Subsidiary cell
SF	Secondary flange
SOF	Subsidiary cell/surrounding cell flange
SP	Stomatal pit
T	Terrace
TF	Triple flange
W	Wing [guard cell]
WF	Wax flake
WN	Wax needle
WP	Wing peg
X	Secretory cell periclinal cuticle
VS	Vein stoma
ZI	Zone of inhibition
&	And
*	Column/buttress
◁	Cavity
◀	Groove/furrow
☆	Scrobiculus [= papilla]

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12. RESULTS

12.1 CHARACTERS OF NON-SPECIALISED CELLS: GENERAL

[For abbreviations see p. 94, 95].

12.1.1 SHAPE AND ARRANGEMENT OF CELLS

In surface view, the outline of a cell represented by flanges may vary from isodiametric [length approximately the same as width] or short [length up to twice width] to conspicuously elongate [length up to ten times width]. When a cell is surrounded by four others, as is often the case over veins, a four-cornered or tetragonal shape results; when five or more cells are adjacent, a many-cornered or polygonal outline is produced. Any cuticle generally shows both isodiametric and variously elongate cells, with between four and seven sides.

Cells may occasionally be the same shape in all regions of cuticles from the adaxial [adx.] and abaxial [abx.] leaf surfaces, e.g. in Cinnadenia paniculata, Gomortega keule [isodiametric-short], Gyrocarpus americanus ssp. africanus and Persea americana [isodiametric-elongate], or just on the membrane of one side, as in certain Cinnamomum spp. [C. iners & C. oliverii: adx. isodiametric-short] Illigera spp. [adx. isodiametric-elongate] and Umbellularia californica [abx. isodiametric-elongate]. Commonly, there are differences between the two cuticles. Generally, abaxial cells are more elongate than adaxial, for example in Cryptocarya weinlandii [adx. isodiametric-short; abx. i.c. short-elongate, c. elongate], Ocotea spp. [adx. isodiametric; abx. isodiametric-elongate] and Potameia spp. [adx. isodiametric, P. crassifolia: abx. isodiametric-elongate, P. thouarsii: abx. i.c. isodiametric-short, c. short-elongate].

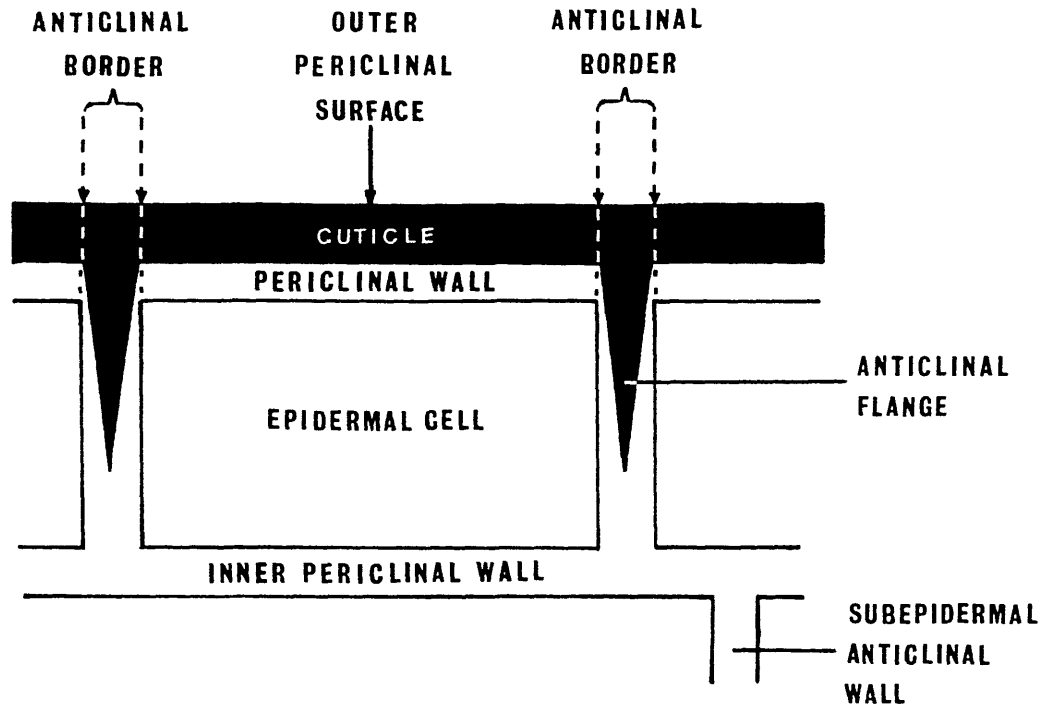
Intercostal cells [i.c.] are frequently dissimilar in outline from costal [c.], the latter often being more elongate than the former, for example in Dicypellium caryophyllum [i.c. isodiametric, c. isodiametric-elongate], Laurus spp. [i.c. isodiametric-short, c.

TEXT-FIGURE 2. Diagrams of non-specialised epidermal cells in T.S.

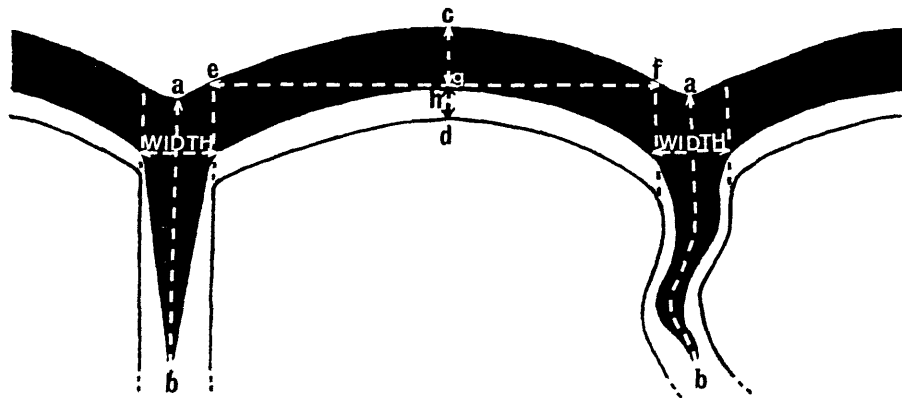
- A. Whole cell showing terminology used throughout the study.

- B. Portion of a cell demonstrating how measurements of anticlinal and periclinal cuticle thickness as well as periclinal curvature have been made.

A



B



- a-b cuticle thickness at flange
- c-d periclinal thickness (median)
- c-h periclinal cuticle thickness
- $\frac{c-g}{e-f}$ periclinal curvature

short-elongate], Litsea monopetala [i.c. isodiametric, c. elongate] and Trimenia papuana [i.c. isodiametric-short, c. elongate]. This trend may sometimes be confined to the cuticle of one leaf surface only, as in Aniba megaphylla [abx. i.c. isodiametric-short, c. short-elongate], Hypodaphnis zenkeri [abx. i.c. isodiametric, c. short-elongate], Neocinnamomum delavayi [adx. i.c. isodiametric, c. short-elongate] and Systemonodaphne mezii [adx. i.c. isodiametric, c. isodiametric-elongate]. A few taxa exhibit the reverse situation, with slightly more elongate cells in intercostal areas, e.g. Caryodaphnopsis spp. [adx.] Eusideroxylon spp. [abx.] Hernandia olivacea [abx.] and Micropora curtisii [adx.] [i.c. isodiametric-short, c. isodiametric].

Intercostal cells are orientated randomly and occasionally show evidence of having divided secondarily during development, as in Illigera pentaphylla [adx.] [Fig. 70]. Costal cells are generally arranged end to end in approximately parallel rows, usually with their long axes following the direction of the vein. The degree to which the veins are marked on the cuticle inner surface is determined by a number of features, including the difference in cell shape between costal and intercostal regions [also flange shape and prominence], and the order of veins present. Modification of outlines tends to be greatest over high order veins [secondaries and laterals] particularly in the centre of the vein [i.e. cells are most elongate] and becomes less over lower order veins and venules. Cells of the abaxial costal regions are commonly more modified than those of the adaxial and veins also tend to be most conspicuous abaxially. On the adaxial side, costal outlines may sometimes be very similar in shape and prominence to those of the intercostal [the cells being mainly isodiametric to short polygonal], resulting in an inconspicuous costal system, e.g. in Eusideroxylon spp. and Gomortega keule.

The shape of cells observed in vein regions may be further modified by the presence of secondary anticlinal divisions, producing isodiametric or short tetragonal

[square] outlines and sometimes even in cells with greater width than length. Secondary flanges are a regular feature of most taxa in costal regions, especially on the abaxial cuticle.

12.1.2 SIZE OF CELLS

In any cuticle cell size varies considerably. Length and width are often not easy to measure since many cells are irregularly polygonal and the outline may be further complicated by the flange course, especially where it is undulate. The average number of cells found per unit area gives an indication of this feature.

The size of cells only in intercostal regions has been used to compare taxa. Costal cell size tends to vary depending on the vein order, making strict interspecific comparison difficult.

In the adaxial cuticle, almost always, cells are largest [less than $10/\text{mm}^2$] in members of the Trimeniaceae, e.g. Piptocalyx moorei, certain Hernandiaceae, such as Illigera pulchra and Austrobaileya scandens of the Austrobaileyaceae. Only one Lauraceae taxon, Endlicheria piriformis possesses cells of this size; in all others, cells are of smaller area. The average number ranges from about $11/\text{mm}^2$, as in some species of Persea [P. americana & P. chinensis] to a maximum of $84/\text{mm}^2$, in Potameia crassifolia. Various intermediates occur including $22/\text{mm}^2$ in Beilschmiedia madang, $34/\text{mm}^2$ in certain Cryptocarya spp. [C. alleniana & C. weinlandii] and $44/\text{mm}^2$ in Alseodaphne semecarpifolia. Most Lauraceae taxa have less than 49 cells/ mm^2 . In a few, however, such as Caryodaphnopsis spp. cells are smaller [average about $55-58/\text{mm}^2$].

In abaxial cuticles, stomata vary in number and size and these influence the amount of surface occupied by non-specialised cells. It is, therefore, not possible to compare abaxial cell size in the same way as adaxial. However, distinct differences in the size of cells between the intercostal region of the abaxial cuticle and that of

the adaxial may be recognised from camera lucida drawings and from scanning electron micrographs. Occasionally, the difference in size between adaxial and abaxial cells is not very apparent, e.g. in Gomortega keule, but most commonly cells of the adaxial region are larger than those on the abaxial.

All members of the Hernandiaceae show this tendency, particularly Illigera pulchra, although it is less marked in Hernandia olivacea ; so also do all Trimeniaceae and many Lauraceae, such as Persea spp., Ravensara spp., Sassafras albidum var. molle and Umbellularia californica. Some Lauraceae exhibit the reverse situation, with bigger abaxial cells, e.g. Phyllostemonodaphne geminiflorum, Potameia crassifolia and Urbanodendron verrucosum.

12.2 THE PERICLINAL WALL REGION

12.2.1 EXTENT OF PERICLINAL CUTINISATION

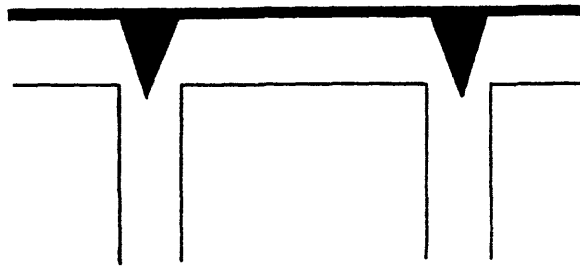
12.2.1a THICKNESS OF PERICLINAL CUTICLE IN T.S.

Examination of leaves in transverse section with light microscopy reveals that periclinal cuticle thickness may vary considerably, especially in the Lauraceae. Average median values [recorded at the centre of the cell], range from 0.6 μm , in Beilschmiedia micrantha to 10.1 μm , in Ravensara elliptica on the adaxial surface and from 0.5 μm , in Sassafras albidum var. molle to 9.5 μm , in Ravensara elliptica on the abaxial. Thickness may occasionally be similar in all periclinal regions of the cuticle on both leaf surfaces, e.g. in Nothaphoebe umbelliflora [adx. i.c. 3.8 μm , c. 4.0 μm ; abx. i.c. 3.9 μm , c. 4.2 μm] or only on one side, as in Austrobaileya scandens [adx. 4.0 μm], Gyrocarpus americanus ssp. africanus [abx. 0.7 μm], Ravensara aromatica [adx. 5.8 μm] and Trimenia weinmanniaefolia [abx. 3.4 μm], or just in certain areas, for example, the costal in Cinnamomum camphora [5.8 μm] and the intercostal in Piptocalyx moorei [0.9 μm]. Generally, however, there are some differences in thickness. Usually, average values are greatest for the adaxial side of the leaf, although the reverse situation exists in some taxa, such as Austrobaileya scandens [adx. 4.0 μm ; abx. 4.5 μm] and Pleurothyrium nobile [adx. 1.1 μm ; abx. 2.1 μm]. Commonly, vein cuticle is thicker than non-vein cuticle, as in Caryodaphnopsis baviensis [abx. i.c. 0.7 μm , c. 2.1 μm], Gomortega keule [adx. i.c. 7.2 μm , c. 9.0 μm ; abx. i.c. 4.9 μm , c. 7.0 μm] and Sparattanthelium tupini-quinorum [adx. i.c. 2.9 μm , c. 4.3 μm]. However, costal cuticle may be thinner than that of intercostal areas in a number of taxa, particularly on the adaxial.

Examples exhibiting this trend include Beilschmiedia madang [adx. i.c. 6.7 μm , c. 5.0 μm ; abx. i.c. 8.2 μm , c. 6.2 μm], Hernandia spp. [H. olivacea : adx. i.c. 6.2 μm , c. 5.3 μm ; H. nymphiifolia: abx. i.c. 2.8 μm , c. 1.2 μm] and Laurus nobilis [adx. i.c. 6.4 μm , c. 4.6 μm].

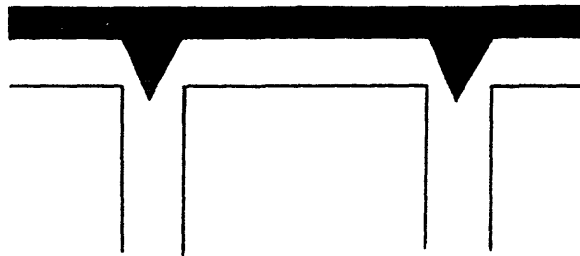
TEXT-FIGURE 3. Diagrams showing different degrees of cutinisation of the outer periclinal wall of the epidermis, as seen in T.S.

A



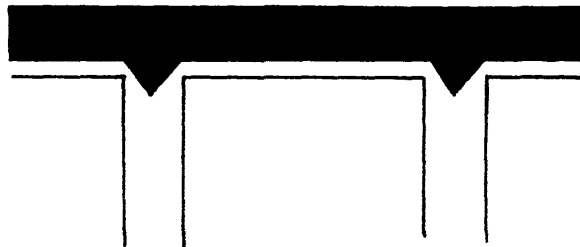
10% wall cutinised

B



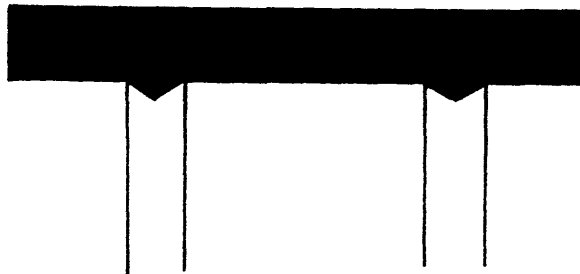
40% wall cutinised

C



70% wall cutinised

D



100% wall cutinised

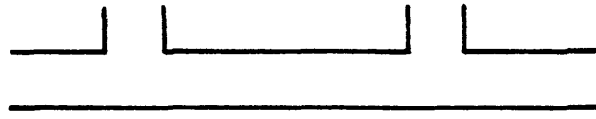
From leaf transverse sections, it is also clear that different proportions of the outer epidermal cell wall may be cutinised [Text-Fig. 3]. On the adaxial surface, averages range between 10%, in Illigera pulchra and 100%, in Beilschmiedia madang and on the abaxial from 10% to 92% [in the same species]. The average amount of wall cutinised may sometimes be similar in both intercostal and costal regions of one leaf surface, e.g. in Aiouea saligna [adx. 80%], Gyrocarpus americanus ssp. africanus [adx. 65%], Ocotea guianensis [abx. 72%] and Piptocalyx moorei [abx. 25%]. Frequently, a different proportion of the outer wall is cutinised over the veins to between the veins: more in costal areas, of cuticle, from one side of the leaf, as in Beilschmiedia micrantha [adx. i.c. 33%, c. 69%] and Micropora curtisii [abx. i.c. 12%, c. 80%] or rarely, from both sides, such as in Gomortega keule [adx. i.c. 73%, c. 81%; abx. i.c. 58%, c. 76%] and Nectandra pichurim [adx. i.c. 42%, c. 55%; abx. i.c. 63%, c. 89%]. The reverse situation, in which a greater proportion of the outer wall is impregnated with cutin in intercostal regions than in costal is observed in other species, e.g. in Aiouea guianensis [adx. i.c. 81%, c. 67%], Gyrocarpus americanus ssp. africanus [abx. i.c. 54%, c. 29%] and Illigera pentaphylla [adx. i.c. 33%, c. 19%; abx. i.c. 53%, c. 35%]. The cell walls, themselves, of veins are often thicker than those between veins. Therefore, if the cuticle has not also become proportionally or more greatly thickened costally during development, the percentage of cuticle to wall at maturity will be less than that of intercostal regions, as in the examples described above.

12.2.1b EXTENT OF INNER PERICLINAL CUTINISATION

Generally, cutin impregnates only the region above the anticlinal wall or the wall itself; it is this, of course, that forms the typical flange [see Section.3]. However, in some taxa cutinisation may occur to various extents in the inner periclinal wall [Text-Fig. 4]. This phenomenon is very rarely found everywhere in a leaf, e.g. in Beilschmiedia madang, Eusideroxylon melagangai and Ravensara elliptica. It may, however, sometimes

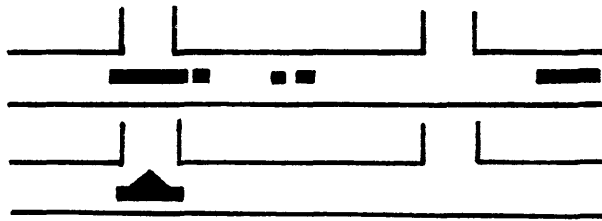
TEXT-FIGURE 4. Diagrams showing different degrees and patterns of cutinisation of the inner periclinal wall of the epidermis, as seen in T.S.

A



NONE

B



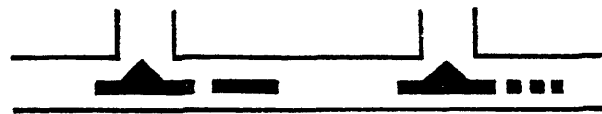
INTERMITTENT

C



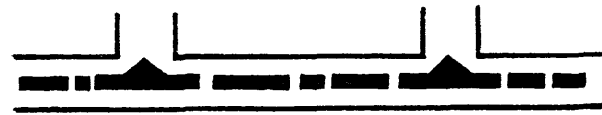
CORNERS

D



CORNERS & INTERMITTENT

E



CORNERS & DISCONTINUOUS
ACROSS INNER PERICLINAL
WALL

F



CORNERS & ENTIRE INNER
PERICLINAL WALL

occur in all but one region, such as in Eusideroxylon zwageri, Licaria guianensis and Nectandra pichurim. Inner periclinal cutinisation is more commonly characteristic of just one side, usually the adaxial, as in Dicypellium caryophyllum, Illigera pentaphylla and Litsea meissneri, or certain regions of the surface, generally costal, such as in Cryptocarya weinlandii [abx.], Gomortega keule [adx. & abx.], Hernandia olivacea [adx. & abx.] and Litsea monopetala [adx.] but also the intercostal, e.g. in Cinnadenia paniculata [abx.].

In the simplest type, inner periclinal cutinisation takes the form of intermittent irregular patches in T.S. These may be horizontally elongated and deeply staining in Sudan IV, in Nectandra salicifolia [abx. i.c.], faintly staining aggregates of rather dotted/granular appearance, in Licaria triandra [c.] which are sometimes found near a flange apex, as in Ravensara elliptica [abx. c.] or deeply staining triangular shaped regions located at the point where the lower part of the anticlinal and periclinal walls of two adjacent cells meet ['corners' in T.S.]. This rather triangular cutinisation may [in Cinnamomum pachyphyllum: abx. c.] or may not [in Cinnadenia paniculata] be associated with a flange apex, depending on the flange prominence.

Where such cutinised 'corners' occur more regularly, they are always continuous with a flange [resulting in the 'I' configuration] and this more complex pattern is shown by a number of taxa, e.g. Dicypellium caryophyllum. It is not usual for the 'corner' and sporadic irregular types of cutinisation seen in T.S. to be observed on the inner surface of isolated cuticles. However, there may be exceptions, as in Pleurothyrium cuneifolium [adx. i.c.] where cuticle may stretch from one flange apex to an adjacent flange of the same cell, or may simply extend laterally at the apex and flop over the periclinal surface. This depends on the degree of continuity between the periclinal and anticlinal cutinisation.

Sometimes, both cutinised 'corners' and intermittent

patches are present in transverse section, for example in Mezilaurus lindaviana (adx. & abx. c.). Immediately above subepidermal anticlinal walls in sections of this and a few other taxa, cutinised areas resembling the epidermal inner periclinal 'corners' may occur, which are somewhat triangular or rhombic in outline. 'Corners' and intermittent patches are usually seen in the S.E.M. at the cell edges, as in Ravensara elliptica (adx. c., abx. i.c.) but may also cover the inner periclinal surface more continuously, e.g. in Mezilaurus lindaviana. Occasionally, however, taxa showing this kind of cutinisation in section reveal no evidence of it in the S.E.M., for example, Cryptocarya alleniana (adx. c.), possibly due either to its extreme thinness or to the small amount of cutin present.

Other taxa may be cutinised more extensively across all of the inner periclinal wall in addition to possessing 'corners', as in Eusideroxylon spp. (abx. c. & adx.). In T.S., this cutinisation is composed of horizontally elongated areas of variable size interspersed with non-cutinised regions or spaces and is seen clearly in the S.E.M., usually extending over the entire inner periclinal wall but may also be confined to cell borders.

The most extreme and extensive pattern consists of 'corners' and all or almost all of the inner periclinal wall cutinised and is observed only in Beilschmiedia spp. (B. madang: abx. c. & adx; B. micrantha: adx.). On the inner cuticle surface in these taxa and others with cutinised patches or whole areas across the wall, perforations of various shapes and sizes occur. These are reminiscent of those through flanges (round to oval) but tend to be more irregular in outline. They range from tiny holes, about 0.1 μm in diameter to large, window-like openings, approximately 10 μm in diameter. They may be separated only by threads of cutin when located very closely together [see Beilschmiedia micrantha Fig. 53]. Perforations probably arise due to uneven cutinisation of the wall and may be associated with plasmodesmata between the epidermis and subepidermis. Even when many

epidermal cells appear totally cutinised on all sides, as in Beilschmiedia madang, there are always some cells with a single small round hole in the periclinal cutinisation [see Fig. 54].

The inner periclinal wall is never cutinised to the same degree on both leaf surfaces. However, the adaxial side may show a similar configuration in vein and non-vein areas: 'corners' only in Dicypellium caryophyllum, with patches across the wall in Potameia crassifolia or with almost all parts cutinised in Beilschmiedia spp. Commonly, there are differences in the degree of cutinisation: costal more than intercostal, as in Endiandra rubescens [adx. i.c. corners, c. corners & intermittent], Eusideroxylon malagangai [abx. i.c. corners & intermittent, c. corners & most of inner periclinal wall] and Nectandra salicifolia [abx. i.c. intermittent, c. corners], although the reverse situation may exist, for example in Nectandra pichurim [adx. i.c. corners & intermittent, c. corners] and Ravensara elliptica [abx. i.c. corners & intermittent; c. intermittent].

12.2.1c PERICLINAL SUBDIVISION OF THE EPIDERMIS

This is indicated by the presence of horizontal or oblique cross walls in T.S. and is rare or absent in most taxa. Occasionally, some adaxial epidermal cells [up to 50% amongst an otherwise undivided layer] show this feature, as in certain Litsea spp. [L. meissneri and L. monopetala] and Sparattanthelium guianense [i.c. only]. Such subdivisions, producing a multiple epidermis, are characteristic of members of one Lauraceae genus, Eusideroxylon, occurring frequently in all regions of both leaf surfaces in E. melagangai and the adaxial only of E. zwageri. The secondary walls often become variously cutinised [best seen in sections], giving rise to a very complex three-dimensional appearance on the inner side of the isolated cuticle, with periclinal surfaces [both primary and secondary] at different levels and orientations throughout the preparation [Figs. 51, 52], perforated with assorted pores and window-like openings similar to the types present in flanges.

In Eusideroxylon spp., adaxial periclinal subdivisions are particularly associated with lignified sclereids, always occurring in epidermal cells immediately above and adjacent to them [see Text-Fig. 9]. Portions of these cells, nearest to the sclereids, are also usually impregnated with lignin. In addition, the epidermis is more deeply cutinised and has a greater number of anti-clinal walls in the region of the sclereids resulting in T.S. in smaller, longer and narrower cells than in the other non-specialised areas. Surface views of the inner side of adaxial isolated cuticles in Eusideroxylon spp., therefore, reveal groups (ca. 63-100 μm in diameter) of cells with particularly deep anticlinal flanges radiating out from a central thickly cutinised area which had been associated with a sclereid 'head' or end in the unmacerated leaf [see E. melagangai: Fig. 51].

12.2.1d STAINING OF PERICLINAL CUTICLE IN T.S.

Transverse sections of leaves stained with Sudan IV show that the cuticle may be either homogeneous, i.e. distinguishable as a single red layer, equally well-cutinised throughout, as in most taxa, or heterogeneous, comprising of two chemically distinct zones: an outermost red area extending into the centre of the flanges and an inner pink region presumably cutinised to a lesser degree abutting the periclinal and anticlinal cell walls. Examples with heterogeneous cuticles are confined to the families Hernandiaceae [Hernandia spp.] and Lauraceae, such as Beilschmiedia madang, Endiandra spp. [see Text-Fig. 8] and Phoebe sheareri. Generally, the configuration is rare and is inherent in cuticle of all regions and surfaces of only two taxa, Endiandra rubescens and Hernandia nymphiifolia. In others, the pattern may be observed on particular sides of the leaf, usually the adaxial, e.g. in Beilschmiedia madang, Endiandra kingsiana (adx.) and Hernandia olivacea (abx.) or only in certain areas, especially the costal, such as in Cinnadenia paniculata (adx. c.), H. olivacea (adx. i.c.), P. thunbergii (adx. c.) and Sassafridium macrophyllum (abx. c.).

The boundary between the zones in the periclinal

region of the heterogeneous cuticle form tends to be more or less even, except in Endiandra spp. [abx.] where it is irregularly and coarsely undulate in sections.

12.2.2 CURVATURE OF THE OUTER PERICLINAL WALL

The region between one anticlinal wall and another, the outer periclinal wall, may show varying degrees of curvature in transverse section. This may be described using a ratio of the median height (h) of concavity or convexity [taken at the centre of the cell from the level adjacent to the cell anticlinal borders] to the width of the cell between the borders [w] [see Text-Fig. 2]. Three main patterns may be recognised from the results based on average values. The outer periclinal wall may sometimes be slightly concave, corresponding to cells which are sunken most conspicuously in the central field region in surface view [S.E.M.], with a negative h:w value never greater than -0.08:1 [Caryodaphnopsis tonkinensis: adx. i.c.], such as in certain regions of the leaf in Alseodaphne oblanceolata (Fig. 1), Cryptocarya alleniana and Nothaphoebe spp. Alternatively, the wall may be flat, the h:w approximately 0, e.g. in some areas in Aiouea guianensis, Eusideroxylon melagangai and Pleurothyrium nobile (Fig. 4) or, most commonly, convex, the cells bulging to varying extents in the S.E.M. and always with positive h:w values, up to a maximum of 1.01:1 [Dehaasia cuneata: abx. i.c. Figs. 271-276], as in regions of Caryodaphnopsis baviensis [Text-Fig. 11A], Litsea monopetala and Persea spp. All these configurations contribute greatly to and affect the outward appearance of cell surfaces in the S.E.M. along with the anticlinal border shape [see p.141].

Periclinal curvature is never the same in all regions of both sides of the leaf. However, cells may show a similar degree of periclinal curvature on one surface only, such as in Cinnamomum iners [adx. 0.01], Dodecadenia grandiflora [abx. 0.11], Eusideroxylon melagangai [adx. 0.00] and Neocinnamomum caudatum [abx. i.c. 0.16, c. 0.17]. Most commonly there are differences. These may be minimal, for example in

Adaxial: morphology

Outer surface.

1. Alseodaphne ob lanceolata. Cells with undulate raised borders and slightly concave periclinal surface. ca. x 565.

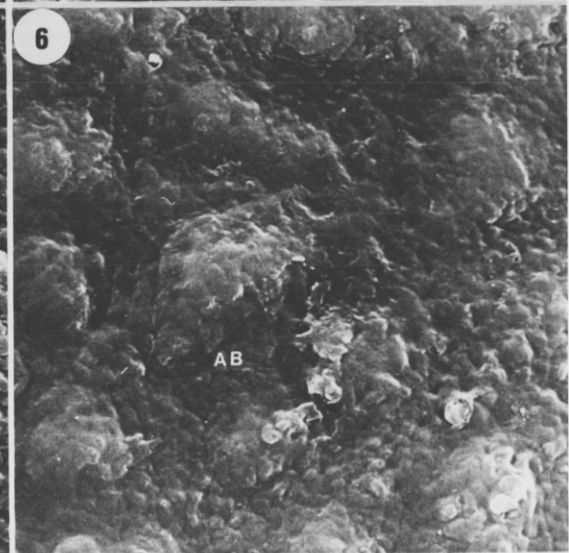
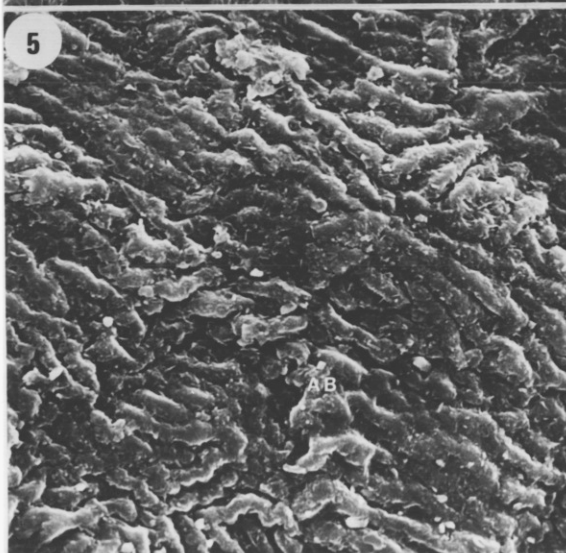
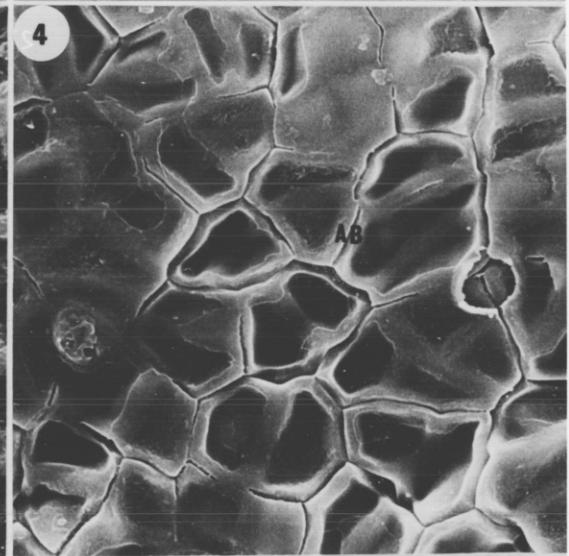
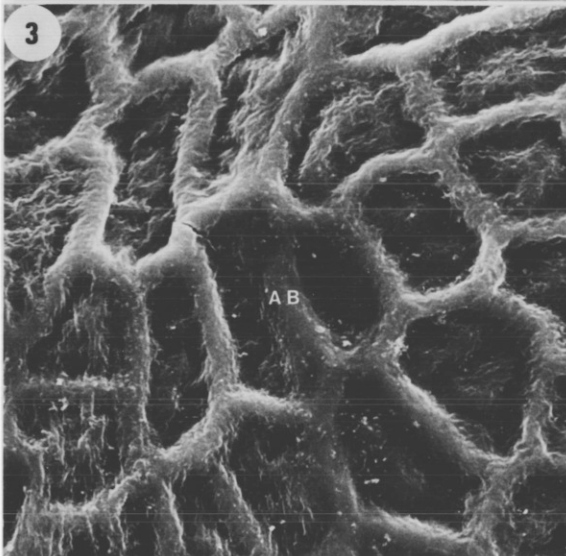
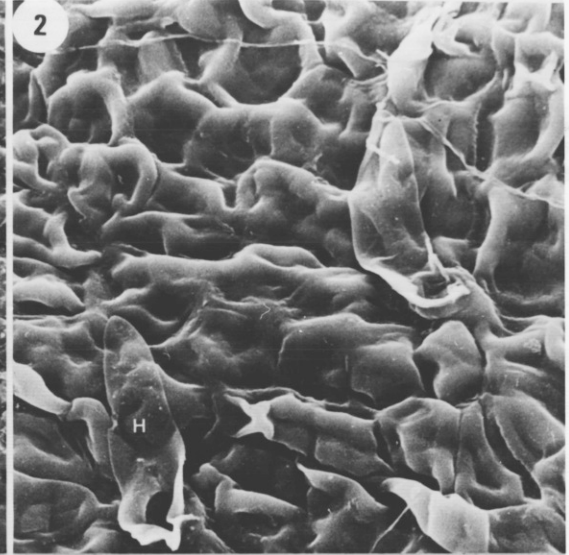
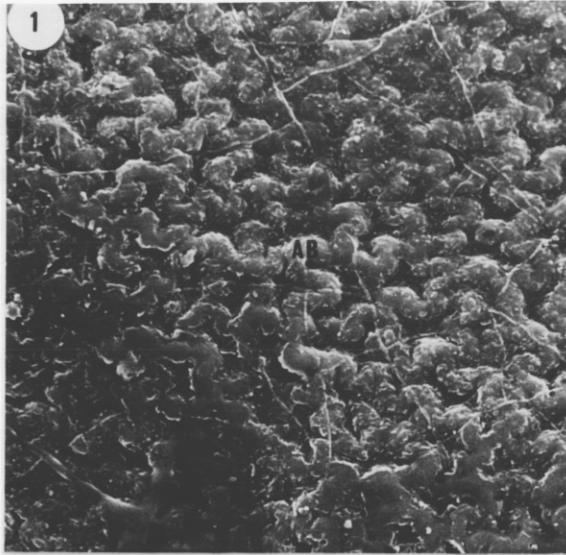
2. Pleurothyrium cuneifolium. Cells with sunken borders and convex periclinal surface. ca. x 540.

3. Persea chinensis. Cells with straight to curved raised borders (AB) and flat periclinal surface. ca. x 525.

4. Pleurothyrium nobile. Cells with straight sunken borders and flat periclinal surface. ca. x 560.

5. Persea thunbergii. Cells with flat borders and slightly convex periclinal surface. Conspicuously striate. ca. x 1040.

6. Actinodaphne stenophylla. Cells with sunken borders and slightly convex periclinal surface. ca. x 1055.



Adaxial morphology

Outer surface.

7. Cinnamomum iners. Costal areas conspicuous.
ca. x 265.

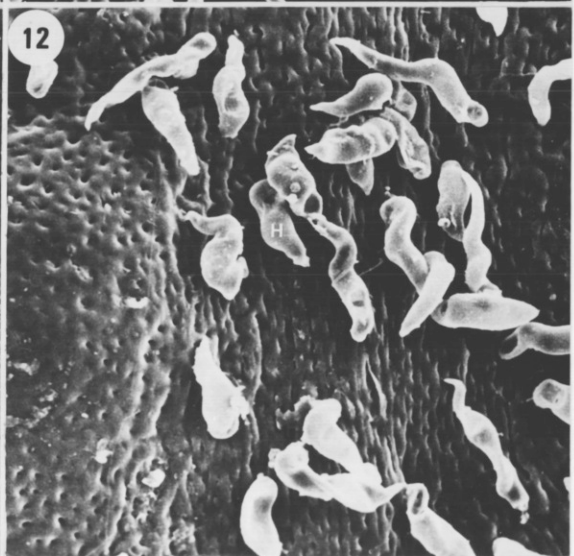
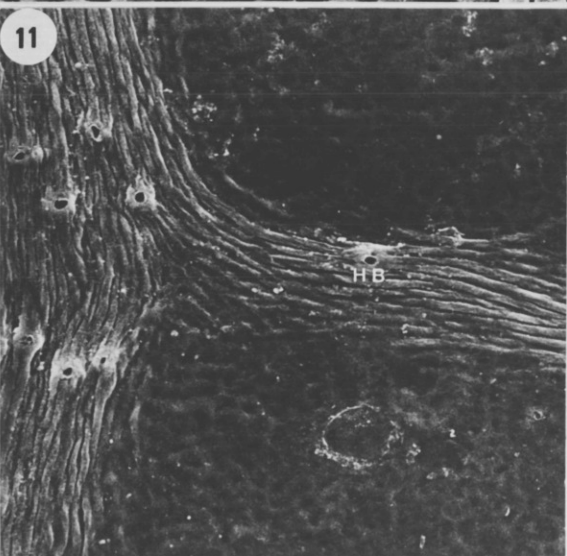
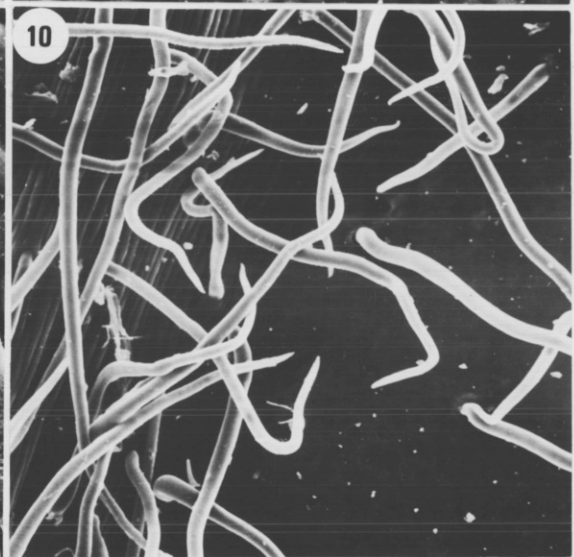
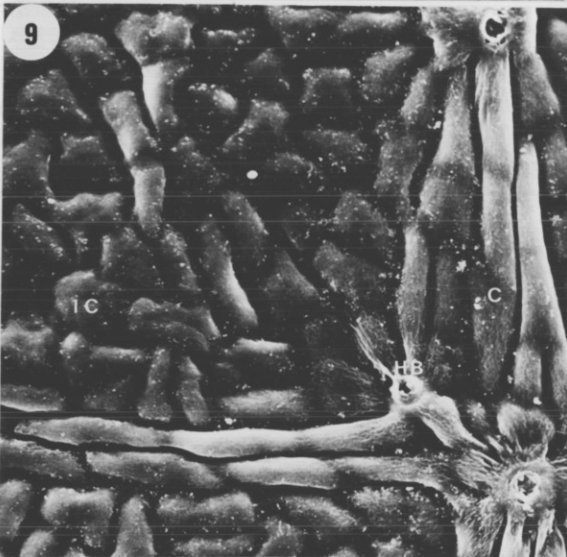
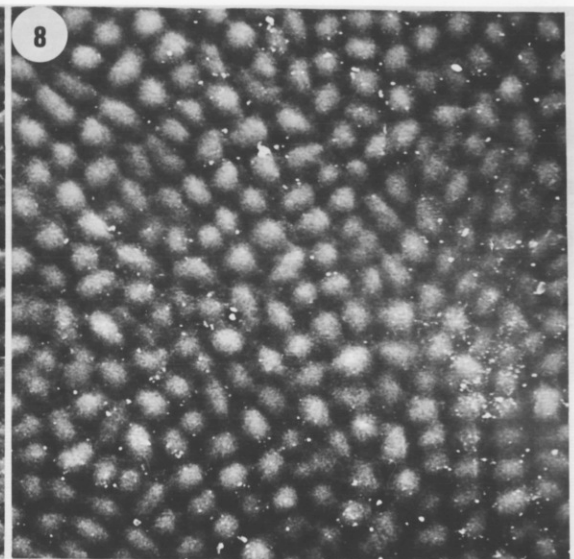
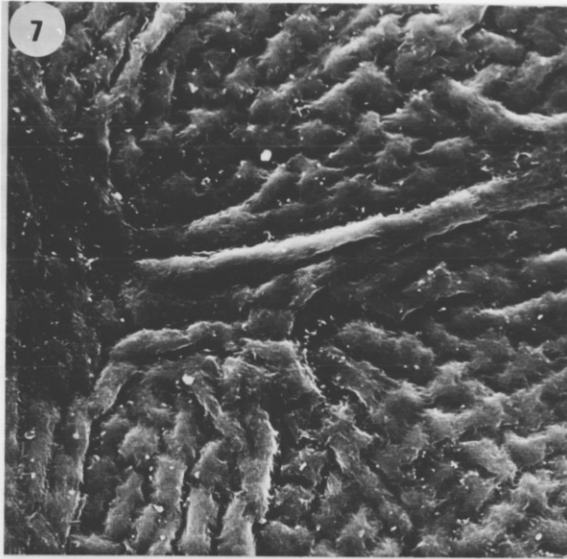
8. Endiandra kingsiana. Costal areas inconspicuous.
ca. x 305.

9. Sassafras albidum var. molle. ca. x 285.

10. Mezilaurus lindaviana. ca. x 130.

11. Dodecadenia grandiflora. ca. x 140.

12. Beilschmiedia madang [3] ca. x 145.
Costal areas conspicuous, particularly associated with
simple hairs (H) in unmacerated preparations or hair
bases (HB) in isolated cuticles.
Note variable morphology of hairs: long, filiform in
Fig. 10; short, wide in Fig. 12.



Hypodaphnis zenkeri [i.c. 0.00, adx. c. 0.03; abx. c. 0.02] and Micropora curtisii [adx. i.c. 0.00, c. 0.01; abx. i.c. 0.01, c. 0.04], but usually they are more considerable. Values for adaxial periclinal curvature tend to be less than abaxial, as in Dehaasia cuneata [adx. 0.04; abx. i.c. 1.01, c. 0.32], Nectandra pichurim [adx. i.c. -0.01, c. -0.02; abx. i.c. 0.12, c. 0.24] and Phoebe opaca [adx. i.c. -0.05, c. 0.00; abx. i.c. 0.64, c. 0.23], although this is not always so, e.g. in Beilschmiedia madang [adx. i.c. 0.13, c. 0.11; abx. i.c. 0.09, c. 0.05].

Slightly sunken and flat cells are particularly characteristic of the adaxial surface, such as in Cryptocarya alleniana [i.c. -0.04, c. -0.02], Mezilaurus itauba, Pleurothyrium nobile and Trimenia weinmanniaefolia [i.c. -0.04, c. -0.06].

In contrast, convex cells are most frequently found on the abaxial, producing a dull or white appearance externally when strongly developed.

Costal periclinal curvature is often greater than intercostal, for example in Alseodaphne semecarpifolia [adx. i.c. -0.04, c. 0.10; abx. i.c. 0.06, c. 0.20], Dodecadenia grandiflora [adx. i.c. 0.00, c. 0.15] and Sassafras albidum var. molle [i.c. 0.08, adx. c. 0.18; abx. c. 0.25]. There are exceptions, however, in which the most convex cells occur in areas between veins rather than over them, as in Caryodaphnopsis spp. [C. baviensis: i.c. 0.57, c. 0.12, C. tonkinensis: i.c. 0.58, c. 0.17], Dehaasia cuneata [abx.], Phoebe opaca [abx.] and Sassafridium macrophyllum [adx. i.c. 0.15, c. -0.06].

Sometimes, especially in Lauraceae, on the abaxial leaf surface and the outer side of the cuticle, each cell may be observed to project distinctly outwards producing a relatively tall dome or papilla which is often wax covered. These cells generally possess a comparatively high value for periclinal curvature ($h:w > 0.23$) and usually belong

Papillae: morphology

Outer surface. Abaxial.

13. Persea americana. ca. x 520.

15. Persea chinensis. ca. x 565.

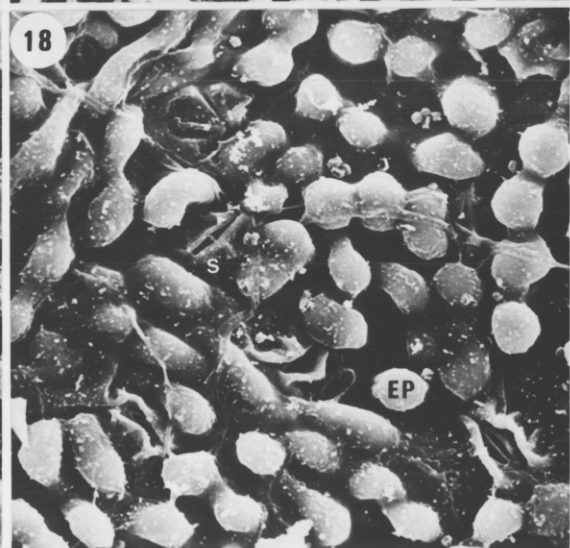
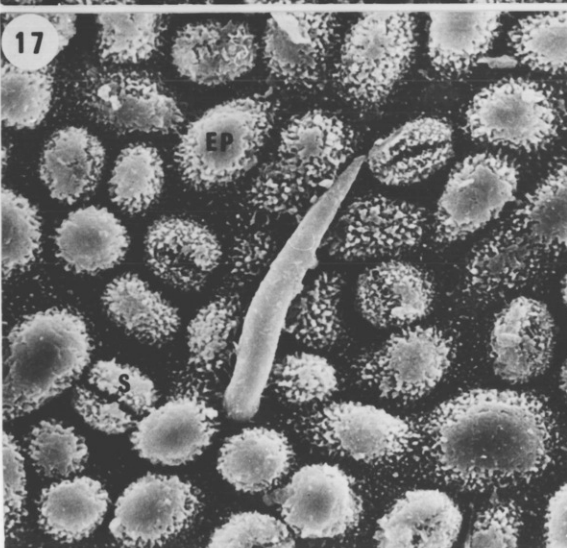
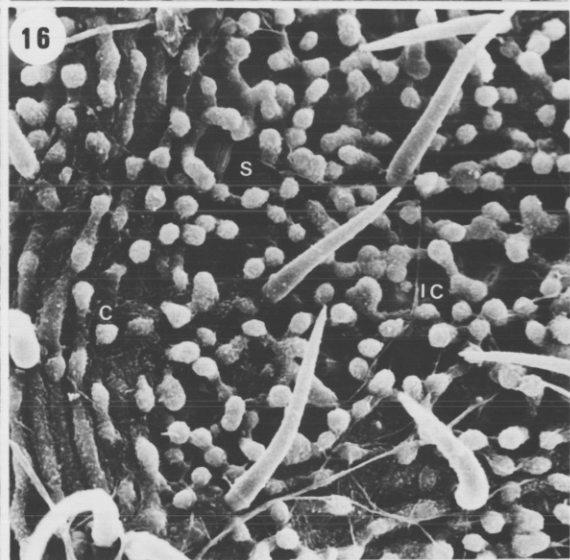
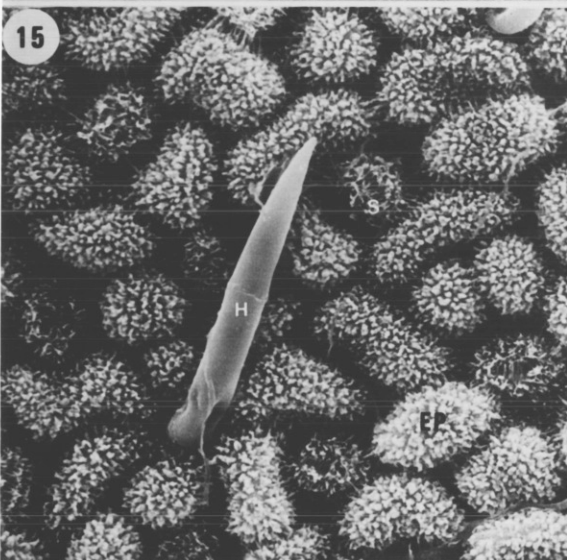
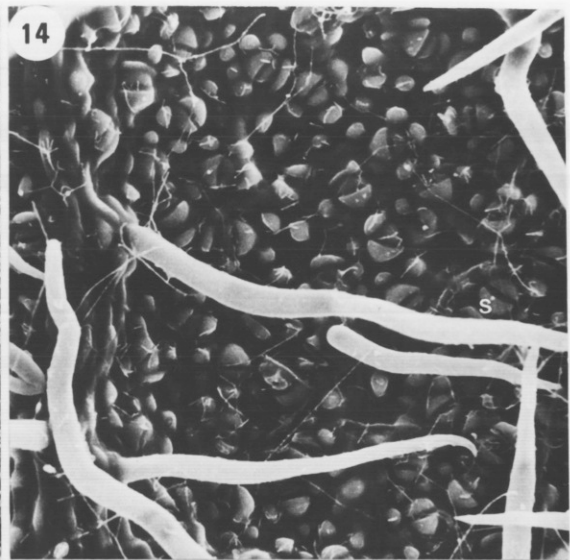
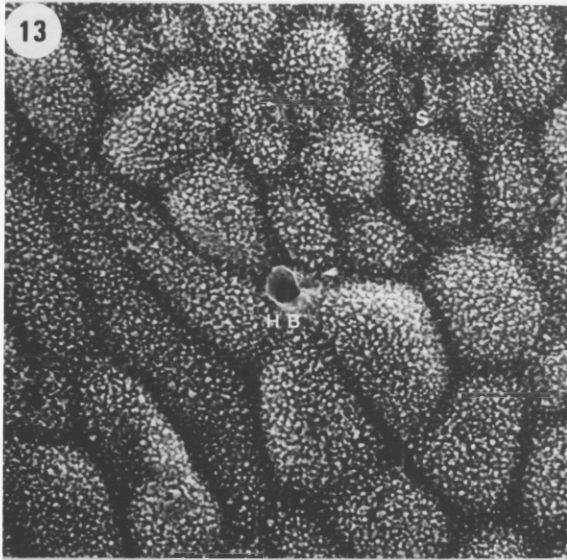
17. Persea thunbergii. ca. x 555.

Whole of outer periclinal wall forming low papillae [1 per cell] on ordinary epidermal cells, surrounding stomata [s] and associated with cells of hair base [HB].

14. Phoebe sheareri. Globular papillae consisting of most of outer periclinal wall of cell. Over and between minor veins, at base of hairs and around stomata [s].
ca. x 285.

16. Phoebe opaca. Distinctly globular epidermal papillae formed from central circumscribed area of outer periclinal wall, associated with intercostal [ic] and minor costal [c] cells, hair bases and cells surrounding stomata [s]. ca. x 275.

18. Litsea monopetala. Globular papillae [EP] similar to those shown in Fig. 16. ca. x 555.



to the group in which non-vein cells have a greater degree of convexity than vein cells [see examples for slightly concave and flat above, Beilschmiedia micrantha [i.c. 0.31, c. 0.13] and Persea spp. [P. americana: i.c. 0.23, c. 0.14; P. thunbergii: i.c. 0.33, c. 0.17][Figs. 13, 15, 17]. Papillosity clearly also decreases with increasing vein order, in such taxa.

Commonly, the papilla apex is hemispherical [blunt], for example, in Dehaasia cuneata [Fig. 271], Litsea monopetala [Fig. 18] and Phoebe spp. [Figs. 14, 16: Text-Fig. 11.B) and may be described as globular. Members of one Lauraceae genus Caryodaphnopsis, however, show a particularly elaborate apical form [Text-Fig. 11 A, see also p. 342-349].

Transverse sections reveal that various proportions of the epidermal cell are involved in the formation of a papilla. They fall into two main groups: occasionally where only part of the outer periclinal wall produces the papilla [a central circumscribed area], as in Caryodaphnopsis spp. [Fig. 30], Dehaasia cuneata [Fig. 28] and Phoebe opaca, or more frequently, where all of the wall is involved, e.g. in Beilschmiedia micrantha and Litsea monopetala. The latter is often a feature of the papillae of lower convexity, except in Pleurothyrium cuneifolium.

On the inside of a cuticle, the outer surface curvature is represented by the degree of concavity or sunkenness observed in the periclinal region of the cell. Most taxa appear more or less flat or slightly sunken but hollows of various depths [due to height [h] differences] are produced as a result of strongly domed or papillate surfaces. These concavities, scrobiculi, are rounded and correspond to the cutinised lumen region of the cell projections. The proportion of cell occupied on the inner surface, therefore, depends on the amount of outer wall [and cuticle] originally forming the papilla in the leaf. The degree of inward-sloping of the concavity sides observed in the cuticle, reflects the way in which the epidermal wall curves outward to produce the main papilla

FOLDING means RIDGING or STRIATION

body, a steep-sided scrobiculus resulting from the sudden projection of a papilla from a cell [see Text-Fig. 11 B].

12.2.3 PATTERN OF FOLDING [STRIAE]

Sometimes, the outer surface of the unmacerated leaf or isolated cuticle shows no form of ornamentation in the S.E.M. e.g. in species of Aiouea, Aniba, Endiandra and Pleurothyrium (Figs. 2, 4). Commonly, where there is evidence of external sculpture, it is confined to the vein regions, frequently on both sides, such as in Alseodaphne spp., Litsea spp., Micropora curtisii and Sparattanthelium spp. but sometimes only on one surface, for example in Cinnamomum spp. [adx.], Dehaasia caesia [abx.], Endlicheria spp. [abx.] and Ocotea guianensis [adx.]. Occasionally, this sculpture occurs in non-vein areas, as in Austrobaileya scandens [adx. & abx.], Gomortega keule [abx.], Persea spp. [adx.] and Trimenia spp. [adx. & abx.].

The ornamentation observed, of folds or striae in the cuticle, is of two main forms. The first, common over the costal surface in many Lauraceae and a few Hernandiaceae, consists of fine [ca. less than 0.7 μm in diameter], solitary, more or less continuous [across more than one cell] parallel, straight lines or 'microstriae', running in the direction of the vein. Similar striae are found in intercostal regions of a few taxa, Nothaphoebe heterophylla [adx.], for example.

In others, whilst the form observed is the same, the approximate fold diameter is always greater; 0.7 μm , such as in Illigera pentaphylla [abx.] and Persea chinensis [adx.] [Fig. 3], between 0.7 and 1.3 μm , e.g. in Hernandia olivacea [adx. & abx.] and Piptocalyx moorei [abx. c.], or between 1.3 and 2.0 μm , as in Caryodaphnopsis spp. [abx. c.], Persea americana [adx.] and Trimenia spp. [adx. & abx.].

The second main type of folding appears as a network of randomly orientated, undulate striae which are discontinuous across the surface of individual cells. The constituent folds or 'macrostriae' are variable in diameter

and usually distinguishable in T.S. with light microscopy: about 0.7-1.3 μm , e.g. in Caryodaphnopsis spp. [abx. i.c.] [Fig. 245], between 1.3 and 2.0 μm , such as in Austrobaileya scandens [abx.] [Fig. 83] and Persea thunbergii [adx. i.c.] [Fig. 5], 2.7-3.3 μm , as in Austrobaileya scandens [adx.] and 4.0-5.3 μm , in Gomortega keule [abx.]. [The latter very irregular striae are more suitably termed 'ridges' due to their extreme coarseness] [see Fig. 84].

Generally, a taxon only exhibits one form of striae [with the exception of Caryodaphnopsis spp. and Persea thunbergii] although there may be differences in fold diameter in surface view, for example in Austrobaileya scandens [adx. striae wider than abx.], Caryodaphnopsis spp. and Nothaphoebe heterophylla [c. striae wider than i.c.].

Folding may also be observed on the inner periclinal surface of cells in isolated cuticular preparations. In general, striae are far less common on the inside of the cuticle than on the outside [the ridges on one side corresponding to furrows on the other]. The finest type is occasionally represented, generally only in costal regions, such as those of Dodecadenia grandiflora [adx.], Endlicheria reflectens [adx. & abx.], Phoebe spp. [P. opaca: adx. & abx., P. sheareri: abx.] and Ravensara aromatica [adx.]. The wider striae of this form are also found in a few taxa, e.g. in Caryodaphnopsis spp. [abx. c.] [Fig. 36], Illigera pentaphylla [adx. c. & abx.], Hernandia olivacea [abx.] and Persea americana [adx. c.]. The second type of folding never occurs on the inside of the cuticle in the adaxial intercostal regions, unlike on the outer side. In Gomortega keule, internal striae are of similar distribution to those found externally. However, in Austrobaileya scandens and Trimenia spp. this is not so, the folding being confined to the inner periclinal surface of the abaxial costal and, to the adaxial costal and abaxial respectively.

12.2.4 PERICLINAL SURFACE SCULPTURE

12.2.4a CUTICLE/CELLULOSE WALL INTERFACE IN T.S.

Under the light microscope, the surface of contact between the cuticle and the underlying epidermal cellulose wall in transverse sections stained with Sudan IV, appears to be of various shapes due to the way the two zones interrelate. Three basic patterns may be identified: the interface may be even, a more or less smooth line at high power ($\times 1000$), the interdigitation of the cutinised layer and cell wall being visible only over the anticlinal wall in the form of flanges, e.g. in many Lauraceae, such as species of Eusideroxylon, Licaria, Nectandra, Pleurothyrium and Potameia, and most Hernandiaceae [not Hernandia spp.], or it may be seen to be uneven, with minute cutinised teeth or variously shaped ridges projecting into the cellulosic region of the periclinal wall at a number of points (in addition to the flanges), producing a jagged line, either of low amplitude [slightly uneven], a relatively common pattern, for example, in Austrobaileya scandens, Endiandra spp., Hernandia olivacea and Persea americana [Text-Fig. 7A] or of high amplitude [very uneven], occurring more rarely, as in, Aiouea spp. [Text-Fig. 7B] and Cinnamomum spp.

Although the boundary between the cutinised layer and the cellulose cell wall is often similar in configuration in the periclinal area of the intercostal and costal regions of both leaf surfaces [see taxa mentioned above], sometimes the patterns observed in different parts are dissimilar.

Generally, no more than two of the main interface forms may be recognised in a taxon, usually even and slightly uneven, but there are a few exceptions with slightly and very uneven interfaces, e.g. Cinnamomum camphora and Gomortega keule. One taxon, Micropora curtisii shows all three forms. One region of a leaf surface may often exhibit a different configuration to other areas: the costal, such as in Dodecadenia grandiflora [adx.] and Lindera spp. [L. pulcherrima: abx., L. strychnifolia: adx.]

[slightly uneven, others even], or in Hernandia nymphii-folia [even, others slightly uneven] or the intercostal, for example, in Gomortega keule [abx. slightly uneven, others, very uneven], Litsea umbellata [abx.] and Neocinnamomum delavayi [adx.] [even, others slightly uneven]. Alternatively, in a few taxa the type of interface on the whole of the adaxial surface may differ from that on the abaxial e.g. in Alseodaphne semecarpifolia and Mezilaurus itauba [adx. slightly uneven; abx. even], Dehaasia cuneata and Trimenia spp. [adx. even, abx. slightly uneven], and in Neolitsea dealbata [adx. i.c. & abx. c. slightly uneven; adx. c. & abx. i.c. even].

12.2.4b PERICLINAL SURFACE IN S.E.M.

The periclinal region of the cuticle may, in some taxa, be non-ornamented or smooth in the S.E.M., such as in Caryodaphnopsis baviensis [abx.] [Fig. 30], Licaria spp. [adx. & abx.], Nectandra spp. [abx.], Ravensara pervillei [adx.] and Systemonodaphne mezii [adx. & abx.] [Fig. 19]. This is represented by an even cuticle/cellulose wall boundary in sections.

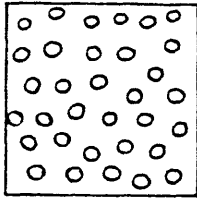
More usually, periclinal surfaces are ornamented in some way. Details cannot be realised with the light microscope due often to the extreme fineness of the constituent elements and so the interface appears even in sections. It is only when the cuticle/cellulose wall boundary is composed of more complex or coarser elements that the pattern may be observed to form an uneven line and any indication of the presence of periclinal ornamentation is, therefore, given.

A wide range of microrelief, however, may be detected with scanning electron microscopy. The following account is based on a scheme, suggested by Miranda & Chaphekar [1980] for gymnosperm cuticles, that has been modified for use with angiosperms. Two main types of element may be recognised [see Text-Fig. 5]: protrusions or cutin particles which protrude from the solid mass of the cutinised layer and depressions, arising from the removal of the intruding cellulosic inpushings in cuticle isolation. These are not

TEXT-FIGURE 5. Diagrams giving a schematic representation of the basic patterns of protrusions and depressions which may, individually or in some combination, comprise the ornamentation of the inner periclinal surface and anticlinal flanges of the isolated cuticle.

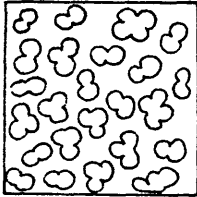
Note that cutin particles are depicted as white areas outlined by black and channels in the cutin matrix as solid black regions.

A



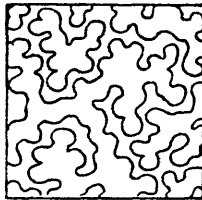
PROTRUSIONS - GRANULES

B



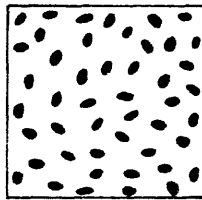
- CLUMPS

C



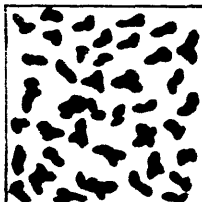
- RETICULA

D



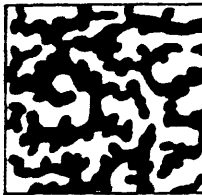
DEPRESSIONS - PITS

E



- CLUMPS

F



- RETICULA

the areas between adjacent protrusions, but are distinct [darkened] cavities, distributed in these [lighter] gaps, which penetrate the cutinised layer. The definition between depressions [cavities] and gaps between protrusions is not always clear, particularly when the cutin particles are separated by narrow gaps of some depth.

All ornamented surfaces show patterns of sculpture involving protrusions or a combination of both element types. Examples with periclinal microrelief composed entirely of protrusions include Aniba megaphylla, Dehaasia caesia (Fig. 22), Gomortega keule, Hernandia nymphiifolia (Fig. 21), Piptocalyx moorei (Fig. 41), Trimenia spp. and Urbanodendron verrucosum [see also Figs. 20, 23, 24]. Taxa with sculpture composed of protrusions and depressions, occasionally show a predominance of depressions as in some surfaces of Alseodaphne semecarpifolia (Fig. 27), Cinnamomum pachyphyllum (Fig. 25) and Mezilaurus itauba (Fig. 26), but generally both types of element are distinguishable and prominent, e.g. in Aiouea saligna (Fig. 35), Austrobaileya scandens (Fig. 33), Hernandia olivacea, Illigera pulchra (Figs. 31, 32) and certain regions of Micropora curtisii (Fig. 34).

Four factors have a profound influence on the appearance of the microrelief in the S.E.M., contributing to differences observed within and between cuticles of every taxon. These are as follows: [i] size, [ii] density, [iii] arrangement and form, and [iv] prominence of individual elements.

12.2.4b(i) SIZE OF ELEMENTS

Protrusions. These vary from very fine [with a minimum of ca. 0.04 μm in diameter] which are barely visible [flecks] even at high power [x 2500-5000] in the S.E.M., for example, in certain regions of Gyrocarpus americanus (Fig. 44), Mezilaurus lindaviana (Fig. 71), Phyllostemonodaphne geminiflorum and Ravensara pervillei to coarse [with a maximum of approximately 1.5 μm], which are always clearly distinguishable, as in Hernandia

nymphiifolia (Fig. 21). Within any cuticle, a range of individual protrusion size may usually be detected.

Commonly, particles are approximately 0.2 μm or less, up to 0.4 μm or between 0.2 μm and 0.5 μm . Protrusions are larger in a few taxa, e.g. in Gomortega keule (ca. 0.7-0.9 μm) and Trimenia weinmanniaefolia (ca. 0.5-0.7 μm) and are always visible projecting into the cellulose wall in sections viewed with the light microscope.

Cutin particles may be of similar size in all regions of the membranes from both leaf surfaces, for example, in Aiouea saligna (ca. 0.4-0.7 μm), Micropora curtisii (ca. 0.2-0.4 μm) and, Ocotea guianensis and Urbanodendrum verrucosum (ca. 0.2 μm or less), or, only in the vein and non-vein areas of one cuticle, as in Hernandia olivacea (adx. ca. 0.2-0.5 μm), Illigera spp. (abx. less than 0.2 μm) and Neocinnamomum spp. (abx. N. caudatum: ca. 0.2-0.4 μm ; N. delavayi: ca. 0.4-0.5 μm). More usually there is some size variation.

Differences may occur between protrusions on the adaxial and abaxial cuticles. Frequently, the former exhibits at least some coarser particles, such as, in Endlicheria reflectens (adx. ca. 0.2-0.4 μm ; abx. ca. 0.2 μm or less), Hernandia spp. (H. nymphiifolia: adx. ca. 0.5-1.5 μm ; abx. ca. 0.4-0.7 μm ; H. olivacea: adx. ca. 0.2-0.5 μm ; abx. ca. 0.2-0.4 μm), Illigera spp. (I. pentaphylla: adx. ca. 0.2 μm or less; abx. less than 0.2 μm ; I. pulchra: adx. ca. 0.2 μm ; abx. less than 0.2 μm] [see Figs. 31, 32] and Neocinnamomum delavayi (adx. ca. 0.7-0.9 μm ; abx. ca. 0.4-0.5 μm). However, this is not the case in other taxa, e.g. Laurus nobilis (adx. ca. 0.2-0.5 μm ; abx. ca. 0.5-0.7 μm) and Potameia crassifolia (adx. ca. 0.2 μm or less; abx. ca. less than 0.2 μm -0.4 μm), which show greater protrusion size on the abaxial.

Generally, the overall value for particle size is greater, i.e. coarser, in costal regions than in inter-costal, particularly on the abaxial. Examples showing

this tendency include Lindera strychnifolia [abx. i.c. ca. 0.2 μm or less, c. ca. 0.5-0.7 μm], Litsea umbellata [abx. i.c. ca. 0.2 μm , c. ca. 0.4-0.5 μm], Neolitsea dealbata [adx. i.c. ca. less than 0.2 μm - 0.4 μm , c. ca. 0.4-0.5 μm] and Sassafridium macrophyllum [adx. i.c. ca. 0.2 μm or less, c. ca. 0.4 μm].

A few exceptions exist with larger protrusion elements in non-vein regions than over veins, e.g. Sparattanthelium tupiniquinorum [adx. i.c. ca. 0.4-0.5 μm , c. ca. 0.2-0.4 μm] and Trimeria weinmanniaefolia [abx. i.c. ca. 0.7-0.9 μm , c. ca. 0.5-0.7 μm].

Sometimes protrusions in one area of a cuticle, the adaxial or the abaxial, may be of a different size to those of the periclinal surface elsewhere in a taxon. When this occurs, the particles involved may be finer than in all other regions, often in intercostal areas, such as those of Cinnadenia paniculata [abx. ca. 0.2 μm or less, others ca. 0.4-0.5 μm] and Hypodaphnis zenkeri [abx. ca. 0.2 μm or less, others ca. 0.5-0.7 μm] or coarser than elsewhere, usually in costal areas, for example, in Aniba megaphylla [abx. ca. 0.2 μm , others ca. less than 0.2 μm] and Piptocalyx moorei [adx. ca. 0.4-0.5 μm , others ca. 0.2 μm or less].

Depressions. These also vary individually in diameter [approximate width across the cavity] and like protrusions, range from very fine, [minimum ca. 0.04 μm] as seen in certain regions of cuticles in Illigera spp. [Fig. 32], Nothaphoebe heterophylla and Neocinnamomum delavayi, but only to moderate with a maximum of about 0.7 μm , found in Aiouea guianensis, considerably less than the greatest value for protrusions. A number of cavity diameters may be detected in a preparation, when depressions are present, in the same way as for protrusions. Most values fall between very fine and approximately 0.2 μm , or vary from about 0.2 μm to 0.5 μm .

Depressions tend to follow some of the trends shown by cutin particles. A few taxa possess depressions of

similar diameter in all regions of cuticles from both surfaces of the leaf, such as Endiandra spp. (ca. less than 0.2 μm - 0.4 μm), Litsea monopetala (ca. 0.2 μm or less) and Ravensara aromatica (less than 0.2 μm). Others exhibit cavities of similar width over and between the veins on just one surface, usually the adaxial, for example in Endlicheria piriformis (less than 0.2 μm) and Litsea umbellata (ca. 0.2-0.5 μm), or occasionally, on the abaxial, such as, in Nothaphoebe umbelliflora (ca. less than 0.2 μm - 0.4 μm) and Phoebe sheareri (ca. 0.2 μm or less).

More frequently, there are differences in cavity size, sometimes only very little between the various areas or membrane surfaces. Depressions may be widest on the adaxial cuticle, e.g. in Aiouea spp. [A. guianensis: adx. ca. 0.2-0.7 μm ; abx. ca. 0.2 μm or less; A. saligna: adx. ca. 0.2-0.5 μm ; abx. ca. less than 0.2 μm -0.4 μm], Eusideroxylon melagangai (adx. ca. less than 0.2 μm - 0.4 μm ; abx. ca. 0.2 μm or less) and Illigera spp. (adx. ca. 0.2 μm or less; abx. ca. less than 0.2 μm) [see Figs. 31, 32] or on the abaxial, as in Austrobaileya scandens (adx. ca. 0.2 μm or less; abx. ca. 0.2-0.5 μm). However, generally cavities of the greatest dimensions are found in vein regions, for example, in Actinodaphne stenophylla (adx. i.c. ca. 0.2-0.4 μm , c. ca. 0.2-0.7 μm ; abx. i.c. ca. 0.2 μm or less, c. ca. 0.2-0.5 μm), Dodecadenia grandiflora (adx. & abx. i.c. ca. 0.2 μm or less, c. ca. less than 0.2 μm - 0.4 μm) and Hernandia olivacea (adx. & abx. i.c. ca. less than 0.2-0.4 μm ; adx. c. ca. 0.2 μm or less; abx. c. ca. less than 0.2-0.5 μm).

In some taxa, depression width is different only in one region of one cuticle, commonly the non-vein area of the abaxial, cavity size being similar elsewhere on the inside of the periclinal surface, e.g. in Cinnamomum spp., with the exception of C. camphora, (ca. 0.2 μm or less, other areas ca. 0.2-0.4 μm), Hypodaphnis zenkeri (ca. less than 0.2 μm , others ca. less than 0.2 μm - 0.4 μm) and Lindera spp. (ca. 0.2 μm or less, L. pulcherrima: others ca. 0.2-0.4 μm , L. strychnifolia: ca. less than 0.2 μm - 0.4 μm).

Where both element types are present in a preparation, the size range of the individual protrusions (p) and depressions (d.) is sometimes similar, such as in, Alseodaphne oblongata [abx. i.c. ca. less than 0.2 μm , c. ca. 0.2 μm or less], Illigera pulchra [abx. ca. less than 0.2 μm], Litsea monopetala and Ravensara elliptica [adx. ca. 0.2 μm or less]. Most frequently protrusions are coarser than depressions, e.g. in Aiouea saligna [adx. p. ca. 0.4-0.7 μm , d. ca. 0.2-0.5 μm ; abx. p. ca. 0.4-0.7 μm , d. ca. less than 0.2 μm - 0.4 μm] and Hypodaphnis zenkeri [adx. p. ca. 0.5-0.7 μm , d. ca. less than 0.2 μm - 0.4 μm ; abx. i.c. p. ca. 0.2 μm or less, c. ca. 0.5-0.7 μm , i.c. d. ca. less than 0.2 μm , c. ca. less than 0.2 μm - 0.4 μm]. A number of taxa exhibit the reverse situation with coarser depressions than protrusions, such as Alseodaphne semecarpifolia [adx. p. ca. 0.2 μm or less, d. ca. 0.2-0.5 μm], Austrobaileya scandens [abx. p. ca. 0.2-0.4 μm , d. ca. 0.2-0.5 μm] and Micropora curtisii [abx. c. & adx. p. ca. 0.2-0.4 μm , d. ca. less than 0.2 μm - 0.5 μm]. This phenomenon is particularly evident in costal regions, e.g. in Actinodaphne stenophylla [adx. p. ca. 0.2-0.5 μm , d. ca. 0.2-0.7 μm] and Nothaphoebe heterophylla [abx. c. p. ca. 0.2 μm or less, d. ca. 0.2-0.4 μm], although it is not always so, as in Litsea monopetala [abx. i.c. p. ca. less than 0.2 μm , d. ca. 0.2 μm or less] and L. umbellata [adx. i.c. p. ca. 0.2-0.4 μm , d. ca. 0.2-0.5 μm].

12.2.4b(ii) DENSITY OF ELEMENTS. The second factor influencing the appearance of the periclinal microrelief is the density of separation of the sculptural components. This contributes to the complexity of the pattern observed in the S.E.M. and is closely linked with element size and arrangement in determining the texture seen.

It is difficult to measure quantitatively [i.e. the distance that the elements are apart] due to complications arising through grouping of components and only distinct differences can be described adequately. Elements may be termed 'dense' when the constituents of the pattern, whether individuals or groups, are distributed almost or

immediately adjacent to one another with little or no visible separation, such as, in Dehaasia caesia [adx.], Dicypellium caryophyllum [Figs 55, 57], Hernandia olivacea [Fig. 61], Illigera pulchra [Figs 31, 32] [adx. & abx.], Ocotea guianensis and Persea chinensis [Fig. 58] [adx.].

Other taxa may have a less dense pattern of sculpture, e.g. Alseodaphne semecarpifolia, Caryodaphnopsis tonkinensis [Fig. 24], Cinnamomum pachyphyllum [Fig. 25] [adx.], Dehaasia caesia [abx.] [Fig. 22] and Litsea meissneri [adx. & abx.].

12.2.4b(iii) ARRANGEMENT AND FORM OF ELEMENTS. This is the third factor of importance, which together with size, is mainly responsible for the texture or roughness of the surface observed in the light microscope and more particularly, in the S.E.M.

Protrusions. Three main types exist: granules, more or less rounded cutin particles protruding individually from the main body of the matrix, e.g. in regions of Endlicheria piriformis [Fig. 20], Hernandia nymphiifolia [Fig. 21], Laurus nobilis [Fig. 42], Phyllostemonodaphne geminiflorum and Urbanodendron verrucosum, the outline of which is barely perceptible when very fine [at the limit of resolution even in the S.E.M. at high power], as in Litsea meissneri [abx.], Mezilaurus lindaviana [abx.] [Fig. 71] and Nectandra spp.; clumps or clusters of granules [usually of different shapes and sizes according to number and arrangement of the constituent protrusions] for example, in Dehaasia caesia [abx.] [Fig. 22], Dicypellium caryophyllum [Fig. 57], Piptocalyx moorei [Fig. 41], Ravensara aromatica [Fig. 47] and Trimenia papuana, and reticula [irregular aggregates of cutin particles tending to form elongated masses which interlock to various degrees with protrusions of adjacent groups producing a network] as in Aiouea spp. [Figs 35, 40], Endiandra spp. [Fig. 39], Illigera spp. [Figs 31, 32], Litsea umbellata, Neocinnamomum caudatum [not abx. i.c.] and Micropora curtisii [not abx. i.c.] [Figs 34, 78].

Periclinal sculpture: smooth and protrusions

Inner surface of isolated cuticles.

19. Systemonodaphne mezii. Smooth. Abx. ca. x 2450.

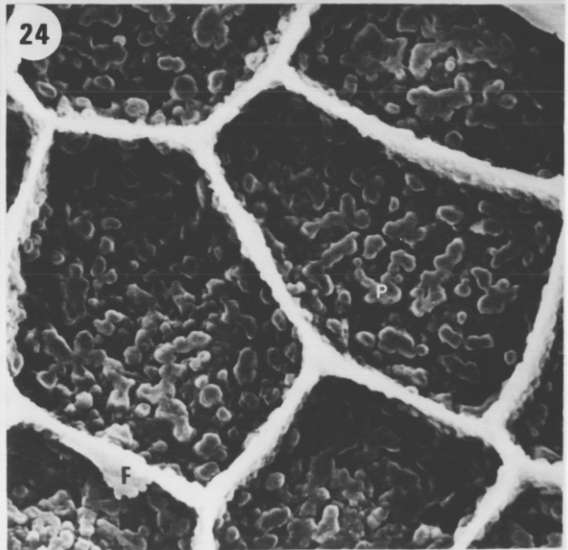
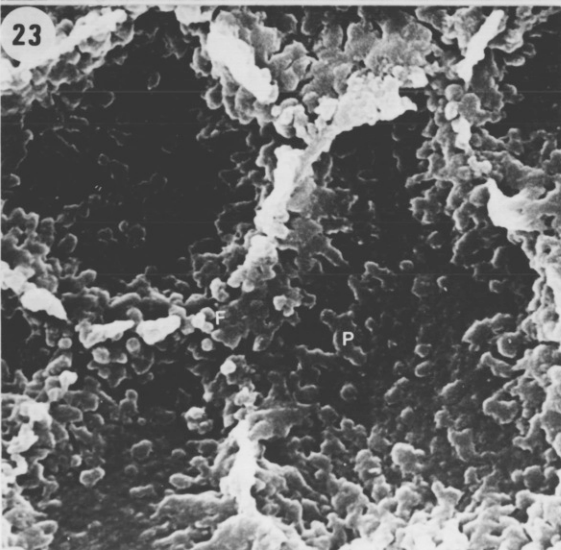
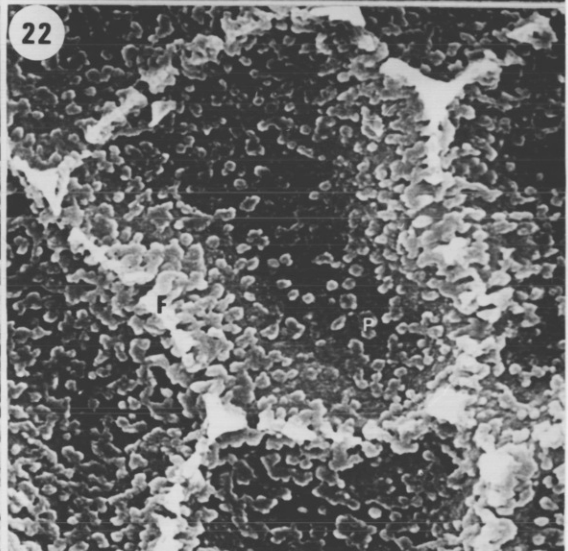
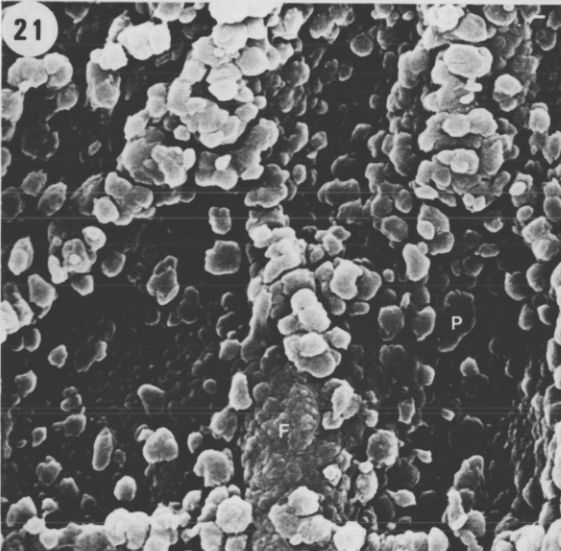
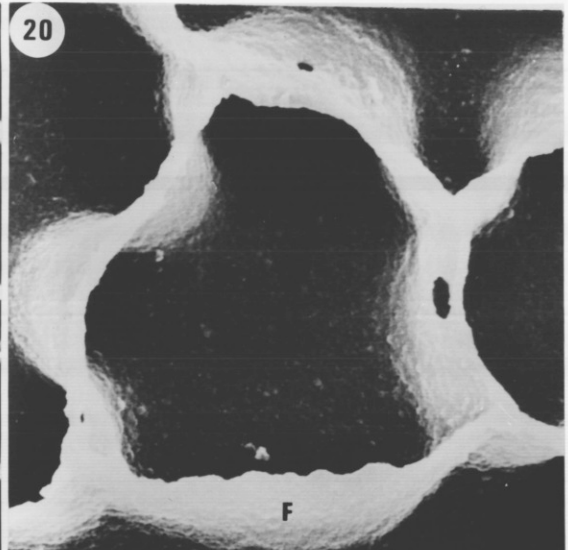
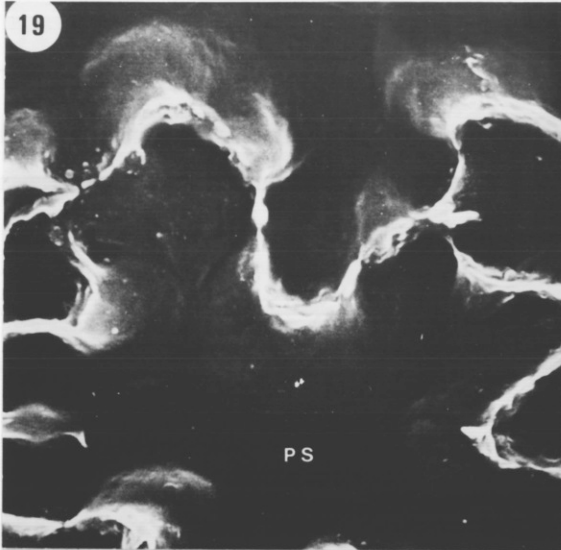
20. Endlicheria piriformis. With finely granular protrusions. Adx. ca. x 2350.

21. Hernandia nymphiifolia. With moderately to coarsely granular or clumped protrusions. Note periclinal surface predominantly ornamented with granules; conspicuously larger clumps distributed at intervals. Adx. ca. x 2160.

22. Dehaasia caesia. With finely to moderately coarse granular, clumped and reticulate protrusions [P]. Abx. ca. x 2365.

23. Neocinnamomum delavayi. With moderately coarse granular, clumped and reticulate protrusions [P]. Note occurrence of reticula particularly adjacent to flange base. Adx. ca. x 2215.

24. Caryodaphnopsis tonkinensis. Predominantly with moderately coarse reticulate protrusions [P]. Adx. ca. x 2115.



Granules may be regarded as the simplest form of protrusion organisation and reticula the most complex.

Although, only one type of protrusion form may be identified in any cuticle preparation of some taxa: granules in Cryptocarya alleniana and Ocotea spp. or reticula in Austrobaileya scandens (Figs 33, 76) and Hypodaphnis zenkeri, it is quite common for a second pattern (clusters) to be exhibited, resulting in various intermediates: granules and clusters in Dicypellium caryophyllatum and Ravensara spp. (R. aromatica and R. elliptica) and clusters with reticula in certain regions of Gomortega keule (abx.), Laurus spp. (adx.) and Sassafridium macrophyllum (c.) (Fig. 60). Occasionally all three protrusion types may be observed, e.g. in some areas of Dehaasia caesia (abx. i.c.) (Fig. 22), Sassafras albidum var. molle (abx. c.) and Trimenia weinmanniaefolia (adx.). Clusters never occur in isolation; they are always associated with granules, reticula or both of these element forms.

In a taxon, the cuticular periclinal protrusion ornamentation may be similar everywhere, regardless of region or surface. However, commonly there are substantial differences in protrusion organisation. These may sometimes be between the adaxial and abaxial cuticle, often more complex on the latter, such as in Alseodaphne semecarpifolia and Sparattanthelium guianense (adx. granules; abx. reticula), Hernandia nymphiifolia (adx. granules; abx. granules - clumps) and Gomortega keule (adx. granules - clumps; abx. clumps - reticula), although this is not always so, as in Laurus nobilis (adx. clumps - reticula; abx. granules) and Mezilaurus itauba (adx. reticula; abx. granules). Differences may also exist between the intercostal and costal regions of both surfaces, the vein pattern being more complicated than that of non-vein areas, e.g. in Sassafridium macrophyllum (i.c. granules - clumps, c. clumps - reticula) and Sparattanthelium guianense (i.c. granules, c. reticula). Alternatively, the arrangement in the intercostal or costal region of one surface may differ from that detected elsewhere, rarely on the adaxial,

as in Nothaphoebe heterophylla [i.c. granules, rest granules - clumps] and Piptocalyx moorei [c. all three types, rest granules - clumps], more usually on the abaxial, especially in the intercostal which tends to be simpler in type, for example, in Micropora curtisii [granules, others reticula] (Fig. 43), Lindera strychnifolia and Persea spp. [P. chinensis & P. thunbergii: granules - clumps, others reticula] or sometimes in the costal, where the pattern is usually more complex, such as in Aniba megaphylla, Gyrocarpus americanus ssp. americanus [granules - clumps, others granules] and Litsea monopetala [all 3 forms, others granules].

The protrusion form may be even more variable in a number of taxa. Three areas out of four may possess different patterns; generally, with a similar type only on the adaxial, e.g. in Dehaasia caesia [adx. reticula; abx. i.c. all 3, abx. c. clumps - reticula], Laurus canariensis [adx. clumps - reticula; abx. i.c. granules, abx. c. clumps - granules] and Persea americana [adx. reticula; abx. i.c. granules, abx. c. all 3 types], or very rarely similar in intercostal areas, as in Neolitsea cassia [i.c. granules, adx. c. clumps - reticula; abx. granules - clumps] or the intercostal of one surface and the costal of another, in Neocinnamomum delavayi [all 3 forms, adx. c. reticula; abx. i.c. granules - clumps].

Individual protrusion elements are usually basically rounded in form, but sometimes, as in Austrobaileya scandens [adx. & abx.] (Figs 33, 76), Hernandia olivacea [abx.], Illigera spp. [adx. & abx.] (Figs 31, 32), Litsea umbellata [i.c.] and Micropora curtisii [all except abx. i.c.] (Figs 34, 78), they are particularly elongated [threadlike] and may be considered as filamentous. Various intermediates between the rounded and distinctly filamentous types exist, as might be expected, for example, in Hernandia olivacea [adx.], Neocinnamomum caudatum [i.c.] (Fig. 77) and Nothaphoebe heterophylla [adx.]. This feature of the protrusions is, thus, also likely to affect the appearance of the sculpture, when observed

with scanning electron microscopy.

Depressions. These also exist in a range of forms: simple, round or irregular pits, for example, in Alseodaphne oblanceolata [abx.], Cryptocarya weinlandii, Illigera spp. [Figs 31, 32] and Neocinnamomum delavayi [abx.]; clumps [small groups of pits clustered together resulting in irregular shaped cavities], such as in Aiouea spp. [Figs 35, 40], Endiandra spp., Sparattanthelium guianense [c.] and Umbellularia californica and reticula, [networks of elongate, irregularly interlocking channels sunken into the main cutin matrix] e.g. in certain areas of Apollonias arnottii [c.], Cinnamomum oliverii, Eusideroxylon melagangai [adx.] and Sassafridium macrophyllum [c.] [Fig. 60]. As in the case of protrusions pits may be considered as the simplest, reticula the most complex, and clumps never occur on their own. Most taxa with depressions on the periclinal surface possess at least some pit-like cavities; exceptions, lacking this form, are Caryodaphnopsis spp. and Nothaphoebe umbelliflora [in certain regions]. Many have, in addition, either clusters of pits [see examples above] and some even show reticulate depressions as well, e.g. certain areas of Actinodaphne stenophylla [c.], Mezilaurus itauba [adx.] and Persea spp. [all except abx. i.c.]. Depression form is often similar throughout cuticles of a taxon, where the element occurs, such as in Aiouea spp. [pits - clumps] [Figs 35, 40], Cinnamomum pachyphyllum [pits - reticula] [Fig. 25] and Illigera spp. [pits only] [Figs 31, 32]. However, sometimes differences are exhibited, as in the case of protrusions, between depressions on the adaxial and the abaxial cuticle, e.g. in Austrobaileya scandens [adx. pits; abx. pits - clumps], Eusideroxylon melagangai [adx. reticula; abx. pits] and Umbellularia californica [adx. pits - clumps; abx. pits - reticula], or between those of intercostal and costal regions, on the cuticle of both leaf surfaces, the pattern being more complex over the veins, as in Cinnamomum camphora [i.c. pits, c. pits - reticula] and Dehaasia cuneata [i.c. pits, c. pits - clumps]. Depressions of one area, generally the intercostal, of the adaxial and abaxial cuticles may differ in organisation from those

Periclinal sculpture: depressions

Inner surface of isolated cuticles.

25. Cinnamomum pachyphyllum. Adx. ca. x 4630.

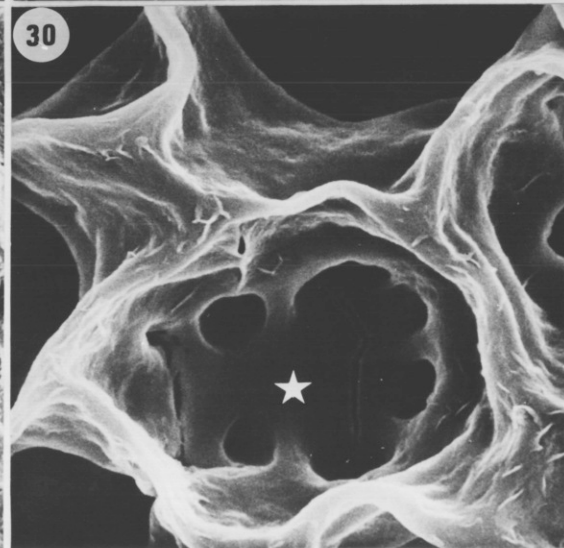
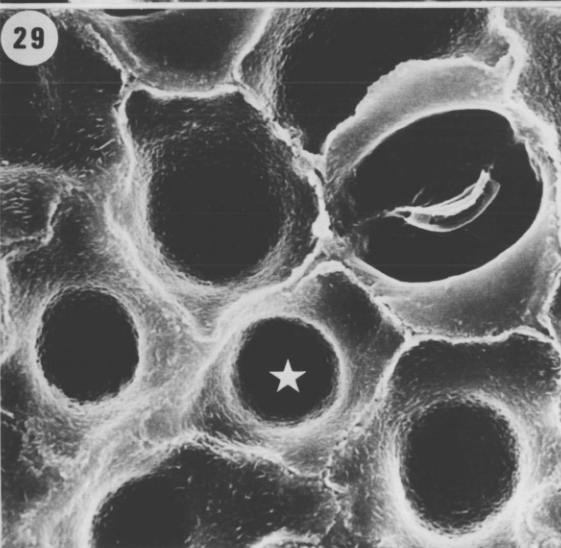
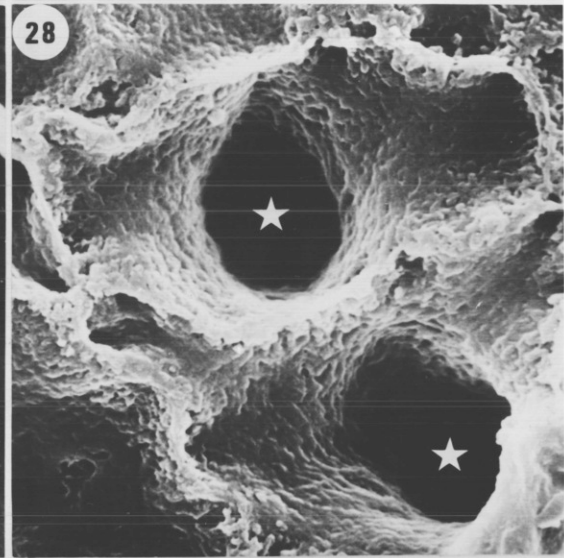
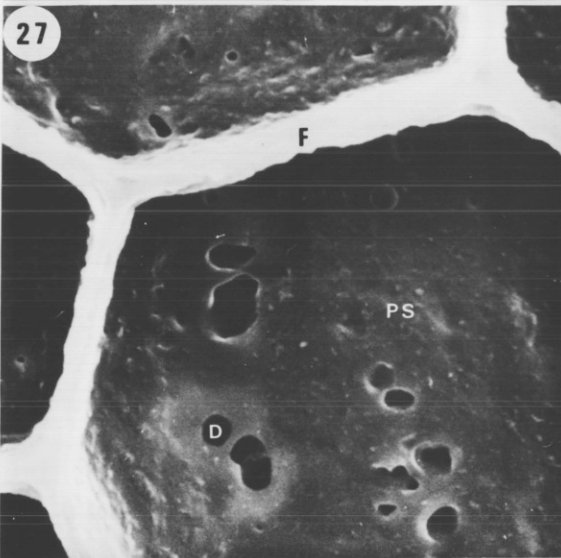
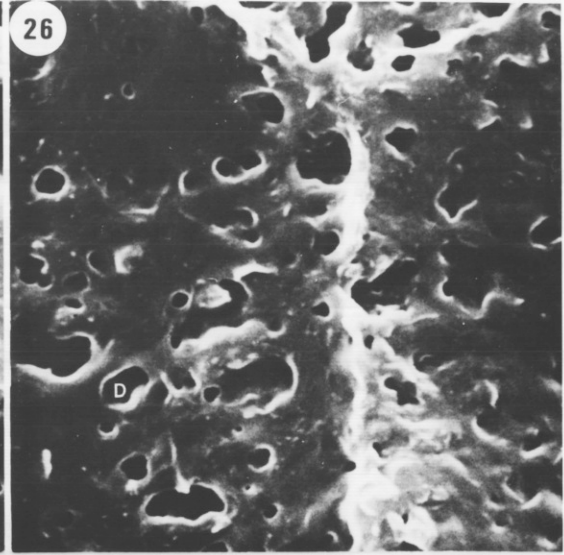
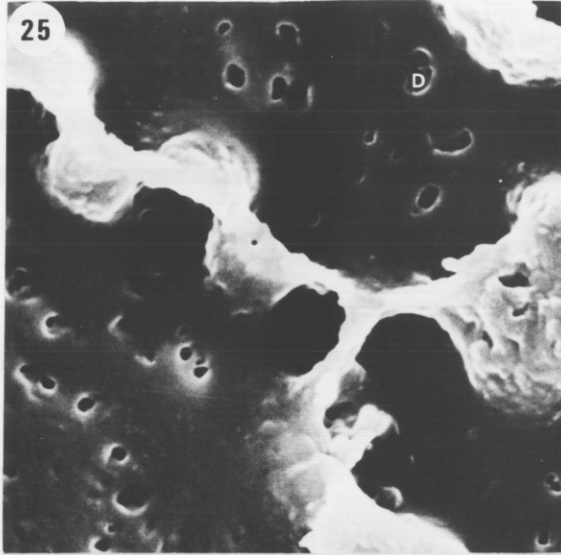
26. Mezilaurus itauba. Abx. ca. x 4885.

27. Alseodaphne semecarpifolia.
With pit-like or irregular, clumped depressions (D)
Adx. ca. x 4285.

28. Dehaasia cuneata. Abx. ca. x 2125.

29. Persea thunbergii. Abx. ca. x 1060.

30. Caryodaphnopsis baviensis. Abx. ca. x 2135.
Cells each with a single, large central depression on scrobiculus (starred) corresponding to lumen of external papilla. Note rounded shape of depression in Figs. 28 and 29 due to globular nature of papillae and undulate outline in Fig. 30, representing striate coronulate papilla type.



Periclinal sculpture: protrusions with depressions and striae

Inner surface of isolated cuticles.

31. Illigera pulchra. With very fine to fine filamentous reticulate protrusions [P] and pit-like depressions [D].
Adx. ca. x 4565.

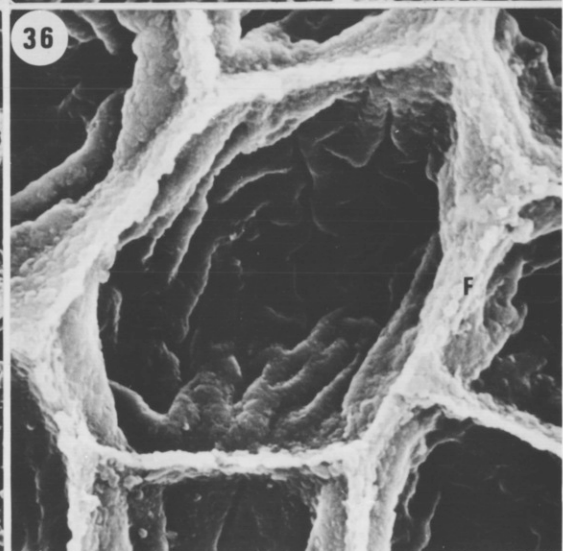
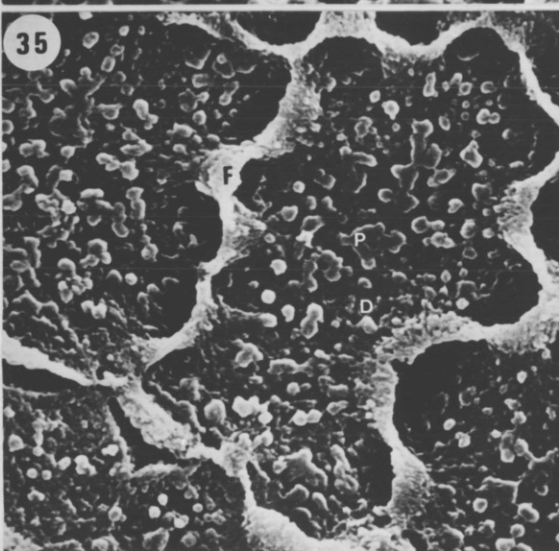
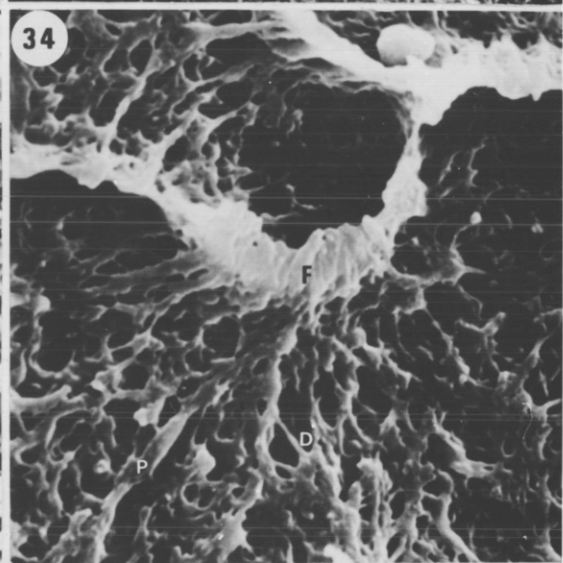
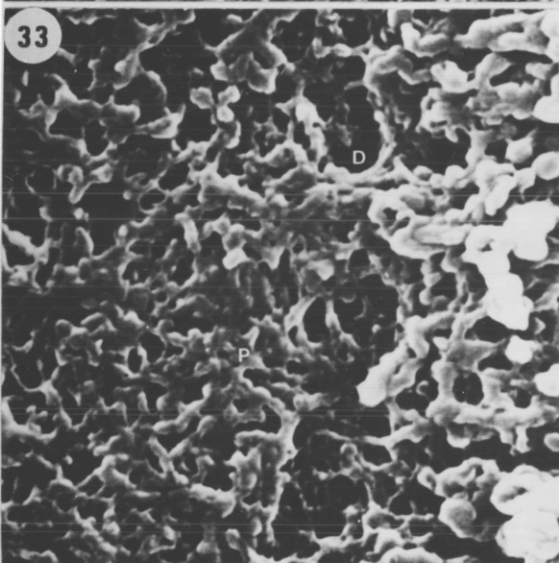
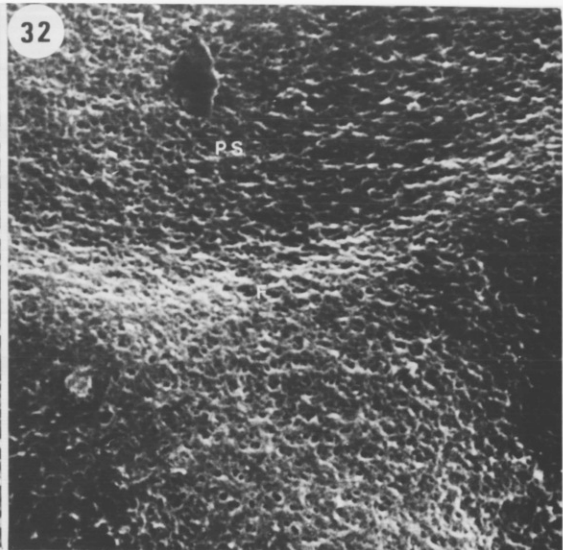
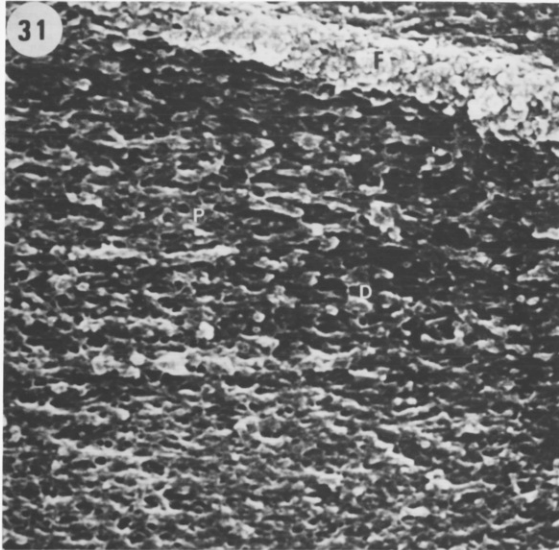
32. Illigera pulchra. With very fine filamentous reticulate protrusions and pit-like depressions.
Abx. ca. x 4655.

33. Austrobaileya scandens. With finely to moderately coarse filamentous protrusions and fine pit-like to clumped depressions. Abx. ca. x 5000.

34. Micropora curtisii. With fine filamentous protrusions and fine to moderately coarse pit-like, clumped or reticulate depressions. Note conspicuous radiation of protrusions from undulation in flange [F].
Adx. ca. x 4670.

35. Aiouea saligna. With moderately coarse, rounded reticulate protrusions and fine pit-like to clumped depressions. Abx. ca. x 2500.

36. Caryodaphnopsis tonkinensis. With undulate ridges and furrows corresponding to striate outer surface.
Abx. ca. x 2295.



elsewhere, for example, in Actinodaphne stenophylla [adx. i.c. pits - clumps, abx. pits only, others pits - reticula] and Sassafridium macrophyllum [adx. i.c. pits - clumps, others pits - reticula] or alternatively just one region of the membrane from a single surface, usually the abaxial, may show such differences in cavity form when compared with all other areas, e.g. in Persea spp. [P. chinensis & P. thunbergii: i.c. pits, others pits-reticula] and Nothaphoebe heterophylla [c. pits - reticula, others pits].

In any taxon, it is common to find one or two different ranges of depression forms, only occasionally are three observed, such as in Apollonias arnottii [pits - clumps, pits - reticula and reticula], Litsea umbellata and Ravensara elliptica [pits, pits - clumps and pits - reticula], the most complex organisation always being located on the periclinal surface of veins.

Where both protrusions and depressions occur together in a cuticle preparation, protrusions are usually arranged into more complex patterns than depressions, for example in Endiandra spp. [p. reticula, d. pits - clumps], Illigera spp. [p. reticula, d. pits] [Figs 31, 32] and Micropora curtisii [where present p. reticula, d. pits - reticula] [Fig. 34]. However, the reverse situation may occur, the depressions forming more complicated groupings: in all regions of a cuticle, as in Eusideroxylon melagangai [adx. p. granules - clumps, d. reticula] and Nothaphoebe umbelliflora [abx. p. granules - clumps, d. clumps - reticula] or in only one area, occasionally in the intercostal, for example in Actinodaphne stenophylla and Neolitsea cassia [adx. p. granules, d. pits - clumps] or, more frequently, in the costal, such as in Nothaphoebe heterophylla [abx. p. granules, d. pits - reticula] and Ravensara elliptica [abx. p. granules - clumps, d. pits - reticula].

In a number of taxa, protrusions and depressions are organised to a similar degree, e.g. in certain areas of the cuticle of Alseodaphne oblanceolata [abx. p. granules, d.

pits) and Phoebe opaca [adx. p. granules - clumps, d. pits - clumps; abx. i.c. p. granules, d. pits].

12.2.4b(iv) PROMINENCE OF ELEMENTS. Although it cannot be measured quantitatively, due to lack of adequate tilt at high magnifications in the S.E.M., the prominence of the elements, i.e. how much the individual protrusions project and the degree of extension of the depressions into the cutin matrix, is undoubtedly an important factor contributing towards the distinctiveness of periclinal microrelief on the inner cutin surface. Where cuticle particles or groups of protrusions appear rather smooth topped, then prominence is low. This is evident particularly on the adaxial surface, for example in Alseodaphne semecarpifolia [Fig. 27], certain Cinnamomum spp. [C. iners & C. pachyphyllum], Cryptocarya weinlandii and Endiandra spp. [Fig. 39]. Protrusions of greater prominence give rise to a more uneven or lumpy appearance, such as those in Dehaasia caesia [abx.] [Fig. 22], Hernandia nymphiifolia [adx. & abx.] [Fig. 21] and Laurus spp. [abx.] [Fig. 42]. These may be located in a certain region of the periclinal surface e.g. near to the flange base in Neocinnamomum delavayi [adx.] [Fig. 23].

Variation in prominence of protrusions, especially within and between clumps and reticula, is usually detectable in any isolated membrane of a taxon so that the general overall picture must be considered when comparing cuticles.

As in the case of protrusions, depression depth probably varies, but in the S.E.M. they appear simply as darkened hollows of indeterminable dimensions [apart from surface diameter]. It may be, at least in some cases, that this depth depends on the degree to which the cuticle is macerated when observed. The diameter of the depressions may thus determine the effectiveness of exposure of these elements, those of narrow width tending to limit the rate of penetration of the chromium trioxide and maceration.

12.3 THE ANTICLINAL WALL REGION

12.3.1 DEVELOPMENT OF ANTICLINAL BORDERS

The region overlying the anticlinal wall on the outer surface of the leaf, the anticlinal border [see Text-Fig.2A], may be of various shapes in transverse section which contribute to their prominence and distinctiveness in surface view. They may be sunken, decreasing to a point over the centre of the wall [giving a V-configuration], as in Beilschmiedia madang [Text-Fig. 8A], Litsea monopetala and Sytemonodaphne mezii; flat, at the same level across the entire anticlinal wall [appearing as a more or less horizontal line], for example, in Endiandra rubescens, Eusideroxylon zwageri and Hypodaphnis zenkeri or raised, producing a dome [an inverse U-shape] in the region of the wall, such as in certain areas of the leaf in Dicypellium caryophyllatum, Sassafridium macrophyllum [Text-Fig.10B] and Trimenia spp.

Anticlinal borders may be of similar shape in all regions of both leaf surfaces. This is so only in the case of taxa with the sunken or flat border configuration [see examples above]. More usually there are differences. The adaxial borders sometimes differ in shape from the abaxial, the latter always tending to be sunken or most so, as in Austrobaileya scandens [adx. raised; abx. sunken], Cinnamomum iners [adx. flat; abx. sunken], and Phoebe spp. [P. opaca: adx. raised; abx. sunken, P. sheareri: adx. flat; abx. sunken]. Commonly, anticlinal borders are dissimilar in costal and intercostal areas: occasionally, on both sides of the leaf, e.g. in certain Cryptocarya spp. [C. ainikini and C. weinlandii] [i.c. flat, c. sunken], Gomortega keule [adx. i.c. flat, abx. raised; abx. & adx. c. sunken] and Urbanodendron verrucosum [adx. i.c. raised, c. flat; abx. i.c. flat, c. sunken] or more frequently, on one side, as in Dehaasia caesia [adx. i.c. raised, c. flat], Illigera pentaphylla [abx. i.c. raised, c. sunken] and Piptocalyx moorei [adx. ic. flat, c. sunken]. When such differences occur, it is usual for anticlinal borders over veins to be most sunken. However, there are exceptions

in which the reverse situation may be found, e.g. in Actinodaphne stenophylla [adx. i.c. sunken, c. flat] and Alseodaphne oblanceolata [adx. i.c. flat, c. raised].

The degree of curvature of the outer periclinal wall of the epidermal cell influences the shape of the anticlinal border observed on the outside of unmacerated leaf portions and isolated cuticles with the S.E.M. [see Figs 1-6]. Where the borders are raised and the cell surface is more or less flat, the cells appear sunken. When cells possess sunken borders and the outer periclinal wall is flat to convex, they look more domed, i.e. convexity is accentuated.

12.3.2 FLANGE FORM

12.3.2a FLANGE SHAPE

In transverse section, at the boundary of abutting epidermal cells, the cuticle normally forms an anticlinal projection or flange. This may be one of two basic shapes: the common V-type, which tapers from its base, at the junction with the periclinal surface, to its apex and may appear flap-like in the S.E.M. particularly those of deeper prominence, sometimes collapsing onto the periclinal region, e.g. in Dicypellium caryophyllatum (Fig. 57), Lindera pulcherrima (Fig. 65) and Nothaphoebe heterophylla (Fig. 38) or the more rare U-type, rounded at its apex, frequently found when flanges are of low or very low prominence, such as in Gyrocarpus americanus ssp. africanus (Fig. 44), Illigera pulchra (Figs 31, 32) and Sassafras albidum var. molle. Occasionally U-sectioned flanges have a flattened apex, for example in Neocinnamomum caudatum (Text-Fig. 10A) and are considerably deeper, as in Endiandra kingsiana [adx.]

Where anticlinal cutinisation continues into part of the inner periclinal wall of the epidermis, flange shape may be modified. Cutin may extend laterally from the apex producing an 'I'-configuration in T.S., e.g. in Beilschmiedia micrantha.

Flanges are usually of similar shape on the adaxial and abaxial cuticles; V-type in many Lauraceae, Gomortega keule and Trimenia spp., U-type in Hypodaphnis zenkeri, a number of Hernandiaceae and Piptocalyx moorei. There may, however, be differences in some taxa. These may be between flange shape in all areas of both surfaces, as in Endiandra spp. [adx. U; abx. V], and Gyrocarpus americanus ssp. americanus [adx. V; abx. U], or between that in the vein [V] and non-vein [U] regions, particularly on the abaxial, e.g. in Dodecadenia grandiflora, Micropora curtisii, Phoebe sheareri and Sparattanthelium tupiniquinorum although, occasionally, this dissimilarity may be detected on the adaxial and the abaxial cuticles, as in Austrobaileya scandens and Litsea umbellata, or the adaxial, for example in Sassafras albidum var. molle.

12.3.2.b VARIATION IN THE COURSE OF FLANGES

Flanges representing cell outlines in a cuticle may be straight, as in Dodecadenia grandiflora [Fig. 37], Eusideroxylon spp. and Gomortega keule or may exhibit varying degrees of waviness, when observed in surface view with light- or scanning electron-microscopy.

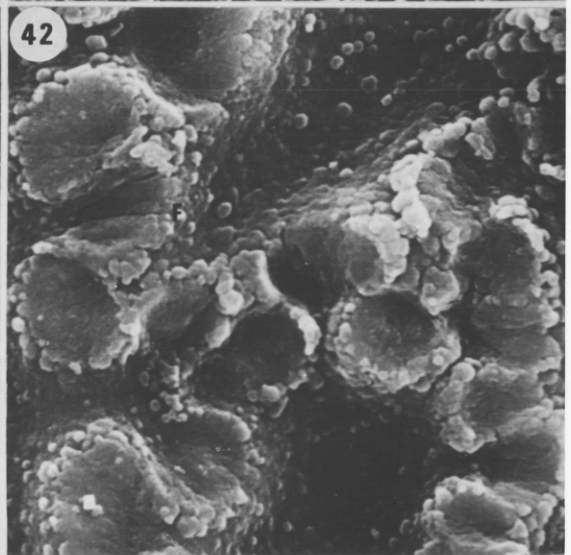
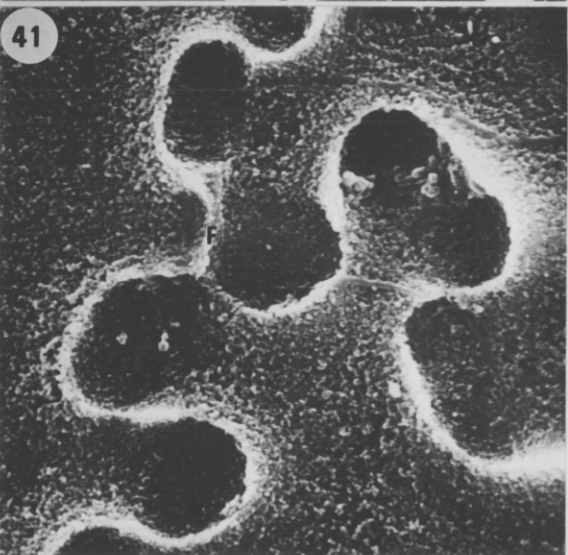
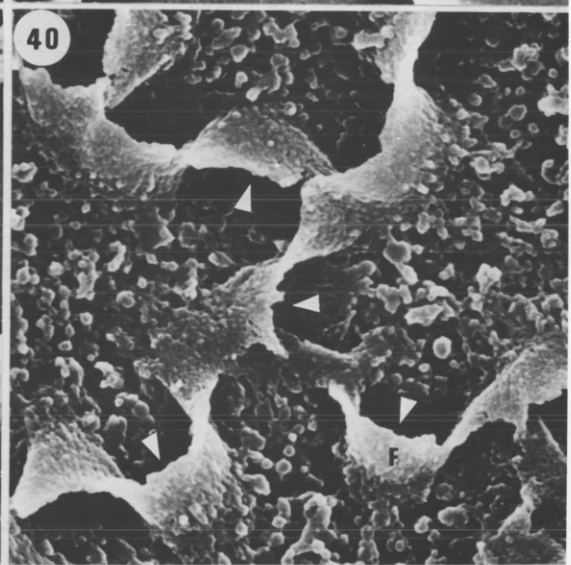
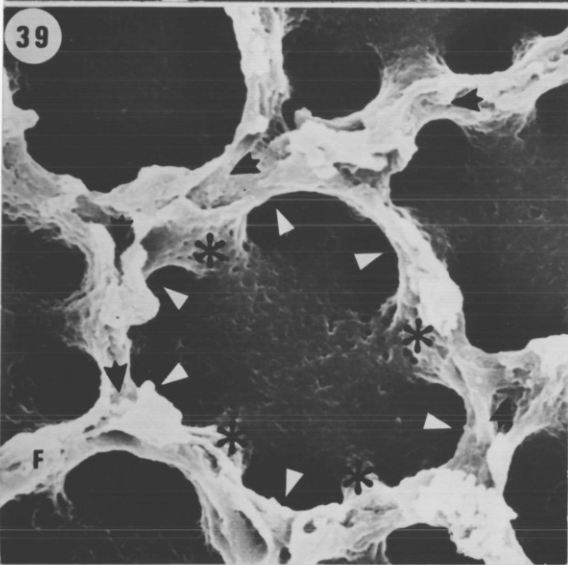
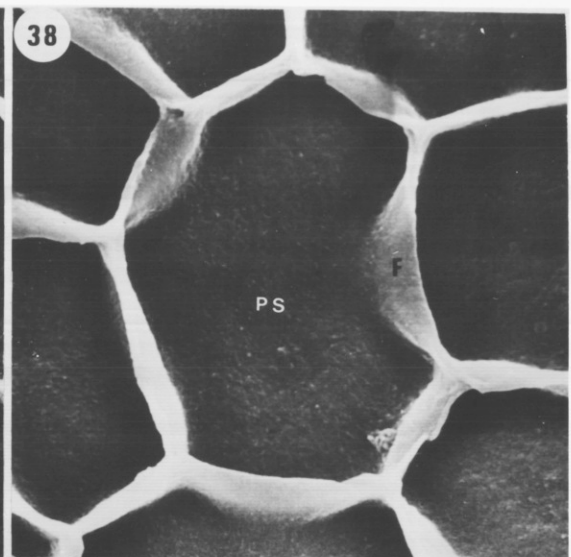
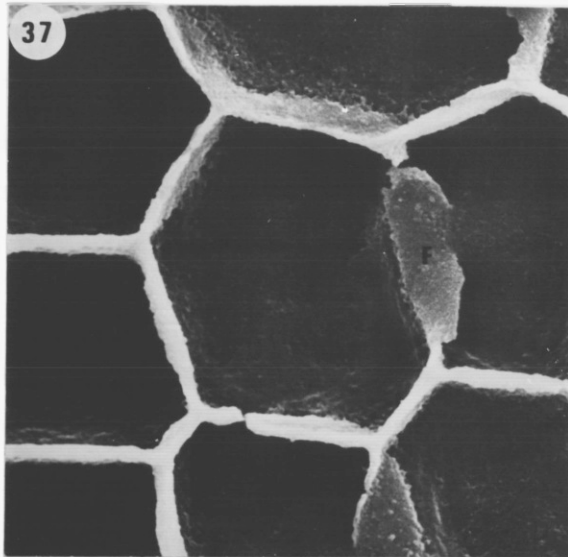
The flange may display only a single loop in its course between two adjacent epidermal cells, equivalent to half a wavelength if described in terms of vibratory waves as recommended by Stace [1965a] e.g. in Nectandra salicifolia [adx.] and Nothaphoebe heterophylla [adx. i.c.] [Fig. 38] and may be termed 'curved'. Flanges showing more lobes of sinuation are 'undulate'. Two main shapes of sinus exist: the common U-form, such as in Aiouea saligna [Fig. 40], Austrobaileya scandens, Systemonodaphne mezii [Fig. 19] and Umbellularia californica and, the more rare and complex Ω -form, e.g. in Laurus nobilis [Fig. 42], Micropora curtisii [c.] [Fig. 43] and Piptocalyx moorei [Fig. 41].

Undulate flanges regularly form cavities in each sinus which often appear to be darkened hollows in the S.E.M. These may be accentuated both by increasing flange depth and more particularly, by thinning of the periclinal cuticle towards the base of the flange [Fig. 40]. Cavity shape is

Flange shape

Inner surface of isolated cuticles.

37. Dodecadenia grandiflora. Straight. Adx. ca. x 2160.
38. Nothaphoebe heterophylla. Curved. Adx. ca. x 2135.
39. Endiandra kingsiana. Undulate, sinuses U-form. Flanges consisting of cavities [white arrowed] and buttresses [starred]. Note flange apex grooved [black arrowed]. Adx. ca. x 2500.
40. Aiouea saligna. Undulate, sinuses U-form. Flanges with conspicuous cavities [white arrowed], appearing alternately thick and thin. Adx. ca. x 2500.
41. Piptocalyx moorei. Undulate, sinuses Ω -form. Flanges with shallow cavities. Abx. ca. x 2500.
42. Laurus nobilis. Undulate, sinuses Ω -form with smooth periclinal sculpture. Abx. ca. x 2500.



also determined, to some extent, by the frequency and amplitude of undulation: wide hemispherical cavities may be the result of a low number of shallow lobes [up to $2/\text{flange}$] and narrower cavities may arise when the amplitude and frequency of sinuosity is increased.

Light microscopic examination of many taxa with curved to undulate outlines reveals that, at different levels of focus, the flanges differ in shape i.e. they may exhibit different degrees of undulation. In all cases where this phenomenon is observed, the flange becomes straight or less wavy towards the apex, as in Alseodaphne oblanceolata [Fig. 73]. This feature is commonly associated with moderate to deep flanges. In those of low prominence, straightening is not perceptible in either the light microscope or in the S.E.M. [see Figs. 41, 42].

Occasionally, when flanges are deep, conspicuously U-undulate at the base and straight to curved at the apex, as in Endiandra kingsiana [Fig. 39], the flange may form a system of alternating columnar or almost parallel-sided buttresses arching over cavities. The amplitude of undulation appears to decrease very sharply at the flange base, then remain constant for most of the buttress and finally change again at the apex.

Sometimes, under the light microscope, flanges appear to be of uneven width, i.e. thickened at the lobes of the undulation. This may be interpreted with the aid of the scanning electron microscope, to be the result of alteration in the angle made by the anticlinal flange with the periclinal surface at each lobe and is, therefore, not connected with flange width in any way. Where the angles are especially acute and obtuse the apparent 'thickening' seen with light microscopy is particularly great, e.g. in Aiozea saligna [Fig. 40]. Cavities are often partially obscured in the S.E.M. by the overhanging apex of the flange at each lobe in taxa showing this form of sinuation.

It is most usual for a cuticle to exhibit flanges of a range of shapes. Straight, curved and U-undulate types

may be present in any field of view depending somewhat on the length of individual flanges. Generally, there is a predominance of one or sometimes two configurations. Where secondary anticlinal divisions have formed during development, comparatively straight flanges occur, as in Illigera pentaphylla [Fig. 70]. Flange shape may sometimes be similar in all regions of cuticles from both leaf surfaces, for example, in Austrobaileya scandens [U-undulate], Eusideroxylon spp. [straight] and Laurus spp. [Ω -undulate] or more commonly, everywhere on one membrane only, such as in Alseodaphne semecarpifolia [adx. straight], Hernandia olivacea [adx. straight-curved], Piptocalyx moorei [abx. Ω -undulate] and Urbanodendron verrucosum [abx. U-undulate]. Alternatively, differences may occur. Flanges tend to be more undulate on the abaxial than the adaxial, e.g. in Dehaasia caesia [adx. straight; abx. curved], Micropora curtisii [adx. i.c. U-undulate, c. curved-U-undulate; abx. Ω -undulate] and Phyllostemonodaphne geminiflorum [adx. curved; abx. i.c. U-undulate, c. curved-U-undulate]. However, this is not always the case, as in Cryptocarya ainikini [adx. U-undulate; abx. i.c. curved-U-undulate, c. straight-curved] and Sassafras albidum var. molle [adx. U-undulate; abx. i.c. curved, c. straight], where the reverse situation exists. When dissimilarities are found between the degree of flange undulation detected in costal and intercostal regions, the former usually shows straighter flanges than the latter, for example, in Aioouea spp. [adx. i.c. U- Ω undulate, c. U-undulate], Cinnamomum camphora [adx. & abx. i.c. straight-curved, c. straight], Neocinnamomum caudatum [abx. i.c. U-undulate, c. straight] and Piptocalyx moorei [adx. i.c. Ω -undulate c. U-undulate]. Again, there are exceptions, such as in Cinnamomum pachyphyllum [abx. i.c. U-undulate, c. Ω -undulate] and Licaria guianensis [adx. i.c. straight, c. straight-curved]. The differences in waviness observed between flanges of the two regions are likely to depend on vein order and the degree of modification of cells in the costal areas.

Where the anticlinal cutinisation continues into part of the inner periclinal wall, it may not be possible to

observe the degree of undulation shown by the flanges in the S.E.M. This can then only be determined by light microscopy by focussing at different levels.

12.3.2c FLANGE WIDTH

Examination of leaves in transverse section with the light microscope reveals that, in the anticlinal wall region, flanges either gradually or more abruptly project from the periclinal surface. Although it is possible to obtain some measurement of the width of the flange at its base from a T.S., it is more difficult when progression from periclinal to anticlinal cutinisation is gradual, particularly when the outer periclinal wall of the cell is domed as it may frequently be in costal regions. Flange width, in association with flange course and prominence, and cell shape contribute much to the overall appearance of a cuticle observed either with light- or scanning electron-microscopy.

Epidermal flanges range in average width [see Text-Fig. 2B] from thin [0.8 μm] in Micropora curtisii [abx. c.] to very thick [7.1 μm] in Sassafras albidum var. molle [adx. i.c.]. Commonly, average values fall between 1.1 and 2.3 μm . The wider flanges are often U-sectioned although this is not always so.

Occasionally, flanges are of similar width in all regions, as in Apollonias arnottii [abx. 2.0 μm], Beilschmiedia madang [adx. 4.6 μm] and Piptocalyx moorei [adx. & abx. 1.4 μm]. Commonly, flange width differs. Sometimes, it is greater on the adaxial, e.g. in Eusideroxylon zwageri [adx. 2.3 μm , abx. 1.4 μm] although in others, such as Austrobaileya scandens [adx. 2.3 μm ; abx. i.c. 5.7 μm , c. 4.3 μm] and Cinnamomum camphora [adx. 2.8 μm ; abx. 5.1 μm] flanges are wider on the abaxial.

More usually, flanges are of different widths over and between the veins. Generally, they are of greater average width in costal regions than intercostal, most often on both surfaces, but sometimes just on the abaxial,

as in Caryodaphnopsis baviensis [i.c. 1.1 μm ; c. 3.4 μm]. Some taxa, however, have wider flanges in intercostal regions rather than in costal: occasionally on both adaxial and abaxial cuticles e.g. in Sassafras albidum var. molle [adx. i.c. 7.1 μm , c. 4.6 μm ; abx. i.c. 4.3 μm , c. 3.4 μm] or more frequently on the abaxial only, as in Austrobaileya scandens.

12.3.3 EXTENT OF ANTICLINAL CUTINISATION

The cuticle at the flanges of ordinary cells varies in thickness.

Values for anticlinal cuticle thickness [see Text-Fig. 2B] range from approximately 1.3 μm , in Piptocalyx moorei to 31.7 μm , in Ravensara elliptica for the adaxial and from about 0.6 μm , in Illigera pulchra to 19.7 μm in Gomortega keule for the abaxial. Taxa never possess the same cuticle thickness at flanges in all regions of membranes of both leaf surfaces. Sometimes, however, averages are more or less the same for cuticle in vein and non-vein areas on one side only, for example in Aniba megaphylla [abx. 3.6 μm], Cryptocarya alleniana [abx. 10.1 μm], Lindera strychnifolia [adx. 9.6 μm] and Piptocalyx moorei [adx. i.c. 1.4 μm , c. 1.3 μm]. Generally, the cuticle is thickest at the flanges on the adaxial surface, e.g. in Eusideroxylon zwageri [adx. i.c. 29.9 μm , c. 27.1 μm ; abx. i.c. 15.0 μm , c. 13.7 μm], Litsea meissneri [adx. i.c. 30.7 μm , c. 31.3 μm ; abx. i.c. 2.2 μm , c. 11.3 μm], and Pleurothyrium cuneifolium [adx. i.c. 13.4 μm , c. 12.4 μm ; abx. i.c. 3.7 μm , c. 5.5 μm]. Occasionally, the reverse situation occurs, as in Gomortega keule [adx. i.c. 14.6 μm , c. 15.4 μm , abx. i.c. 19.7 μm , c. 18.0 μm].

There are often distinct differences between the average anticlinal cuticle thickness over and between veins. Commonly, the cuticle is thickest at the costal flanges on both surfaces of the leaf, e.g. in Endiandra kingsiana [adx. i.c. 9.9 μm , c. 22.0 μm ; abx. i.c. 4.3 μm , c. 7.2 μm], Nothaphoebe umbelliflora [adx. i.c. 17.7 μm , c. 22.5 μm ; abx. i.c. 5.7 μm , c. 13.4 μm] and Phoebe shearerii [adx. i.c. 7.7 μm , c. 11.6 μm ; abx. i.c. 1.6 μm ,

c. 4.3 μm). This is not always so, however. The cuticle may be thicker at the intercostal flanges: particularly those of the adaxial side. Examples demonstrating this trend include Alseodaphne oblanceolata [abx. i.c. 5.8 μm , c. 4.5 μm], Illigera pentaphylla [adx. i.c. 16.6 μm , c. 14.0 μm], Pleurothyrium nobile [adx. i.c. 11.1 μm , c. 10.7 μm ; abx. i.c. 7.0 μm , c. 5.5 μm] and Trimenia papuana [adx. i.c. 10.7 μm , c. 7.9 μm].

The total anticlinal thickness of cuticle at a flange is the sum of two parts: the periclinal thickness and the flange height or depth [see Text-Fig. 2B]. The latter is a useful dimension for it shows interspecific differences. Within any preparation a number of values for flange height may be observed. Thus, an average has been used for comparison of taxa. In most cases the cuticle in the anticlinal wall region is thicker than in the centre of the periclinal, in T.S., resulting in a positive value. However, this is not so in Cinnamomum camphora [abx. i.c. -1.3 μm], Illigera pulchra [adx. c. -0.4 μm] and Laurus canariensis [abx. i.c. -0.8 μm , c. -0.5 μm]. Positive averages range from approximately 0.1 μm , in Gyrocarpus americanus ssp. africanus to 27.7 μm , in Eusideroxylon zwageri for the adaxial, and from about 0.1 μm , in Illigera pulchra to 14.8 μm , in Gomortega keule, for the abaxial.

Flanges are hardly ever the same depth everywhere in a taxon. One exception is Neocinnamomum caudatum where flanges are between 1.0 and 1.2 μm deep. Occasionally, all but one area have similar depth flanges, as in Micropora curtisii [adx. i.c. 5.1 μm , adx. & abx. c. 5.4 μm ; abx. i.c. 0.4 μm]. More often, they tend to be about the same height in vein and non-vein regions of a single surface, e.g. in Illigera pulchra [abx. 0.1 μm], Licaria guianensis [abx. i.c. 2.9 μm , c. 2.8 μm], Piptocalyx moorei [adx. 0.5 μm] and Sassafras albidum var. molle [adx. 1.3 μm].

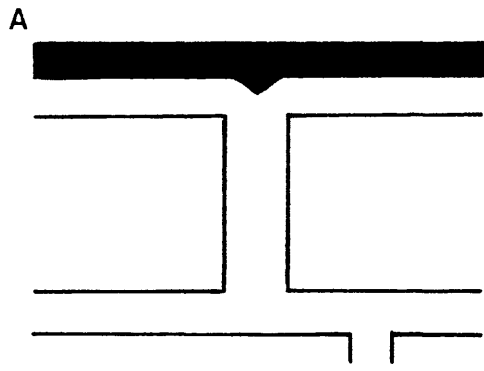
Generally, flanges are deeper on the adaxial side of the leaf than on the abaxial, for example in Beilschmiedia micrantha [adx. i.c. 12.7 μm , c. 14.2 μm ;

SHALLOW is preferable to LOW to correspond with DEEP
(see n. 154, also Text-Figure 6).

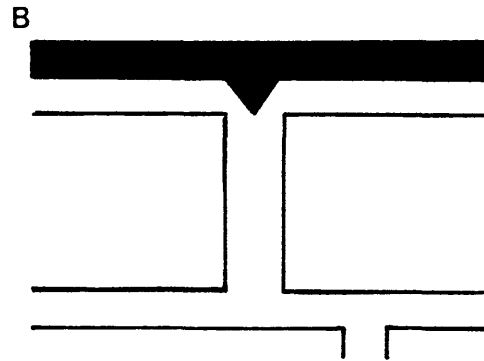
abx. i.c. 4.1 μm , c. 5.7 μm], Litsea meissneri [adx. i.c. 25.0 μm , c. 27.1 μm ; abx. i.c. 1.1 μm , c. 9.7 μm] and Sparattanthelium guianense [adx. i.c. 15.7 μm , c. 15.4 μm , abx. i.c. 1.3 μm , c. 3.7 μm]. The reverse situation does exist in a few taxa, such as Gomortega keule [adx. i.c. 7.4 μm , c. 6.4 μm ; abx. i.c. 14.8 μm , c. 11.0 μm]. Vein flanges tend to be the deepest in many taxa and non-vein, the shallowest, on both surfaces, e.g. in Hernandia nymphiifolia [adx. i.c. 1.8 μm , c. 7.6 μm ; abx. i.c. 1.6 μm , c. 3.1 μm] Mezilaurus lindaviana [adx. & abx. i.c. 8.5 μm , adx. c. 10.1 μm , abx. c. 10.4 μm] and Ravensara pervillei [adx. i.c. 8.8 μm , c. 14.0 μm ; abx. i.c. 2.0 μm , c. 5.4 μm]. Exceptions may be found with the tallest flanges occurring in intercostal areas, such as in Alseodaphne semecarpifolia [adx. i.c. 7.9 μm , c. 7.0 μm ; abx. i.c. 3.0 μm , c. 2.2 μm], Dehaasia caesia [abx. i.c. 3.0 μm , c. 1.5 μm], Ocotea guianensis [adx. i.c. 11.8 μm , c. 6.0 μm] and Potameia crassifolia [adx. i.c. 22.1 μm , c. 19.9 μm ; abx. i.c. 10.0 μm , c. 8.5 μm].

Flange height is a major factor in determining the conspicuousness of epidermal outlines on an isolated cuticle (along with width and shape). The depth to which this cutinisation, arising from the periclinal surface, protrudes into the cellulose in the region of the anticlinal wall, varies when compared with wall depth (Text-Fig. 6) and is another way to express how well-marked cells are in a preparation. Sometimes flanges hardly project at all in transverse section and never extend to the top of the anticlinal wall. This type of flange may be termed very low or very shallow and results in vague delimitation of cells on cuticles. It is characteristic of a range of taxa including Gyrocarpus americanus ssp. africanus [Fig. 44] and Illigera pulchra [Figs 31, 32, 75]. Where flanges reach the topmost portion of the anticlinal wall [the level where it meets the periclinal surface in section], they are low in prominence and are more distinctive in cuticular preparations, such as in Umbellularia californica and Hernandia olivacea [Text-Fig. 9B].

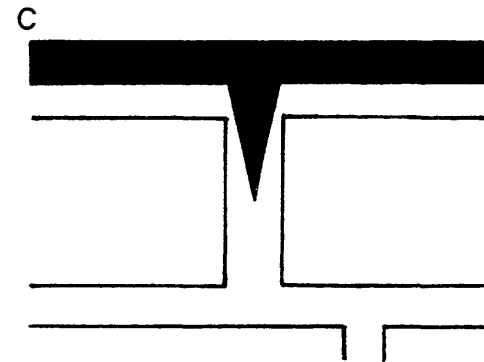
TEXT-FIGURE 6. A-E. Diagrams showing different degrees of flange prominence, as seen in T.S.



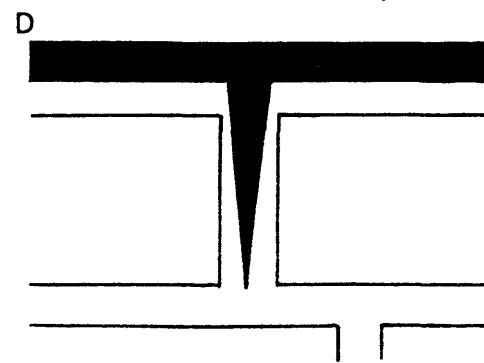
VERY LOW – not reaching top of anticlinal wall



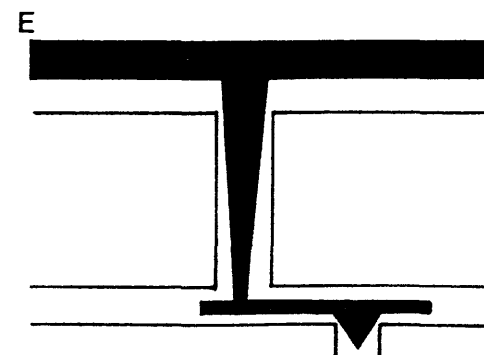
LOW – to top of anticlinal wall



MODERATE – extending half way down anticlinal wall



DEEP – to inner periclinal wall

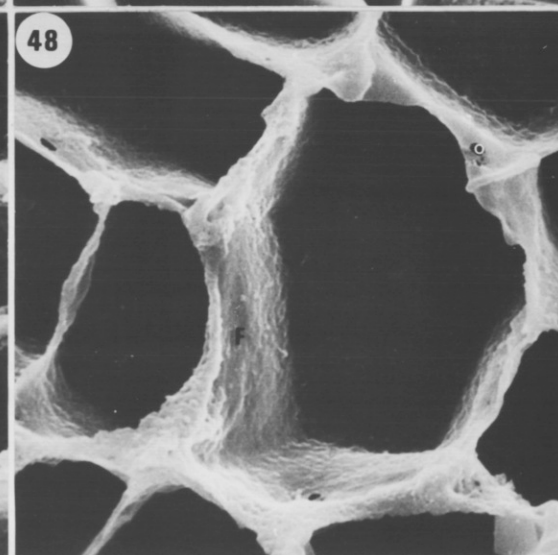
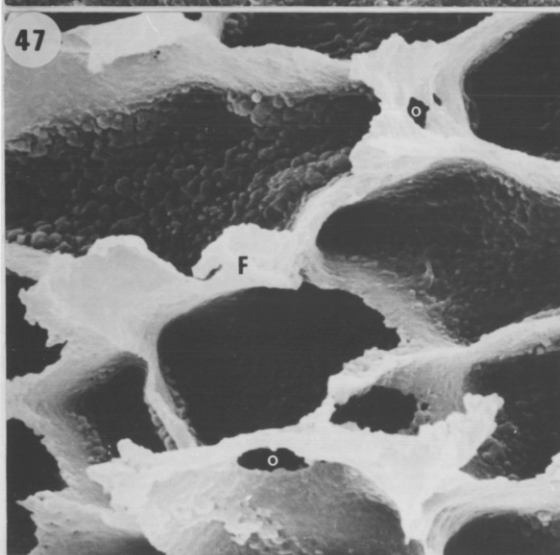
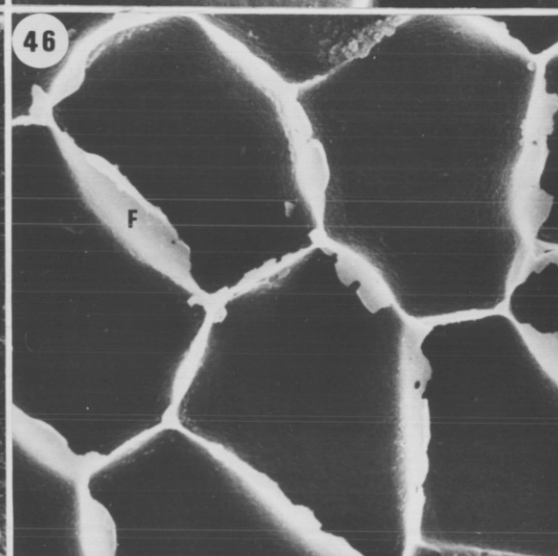
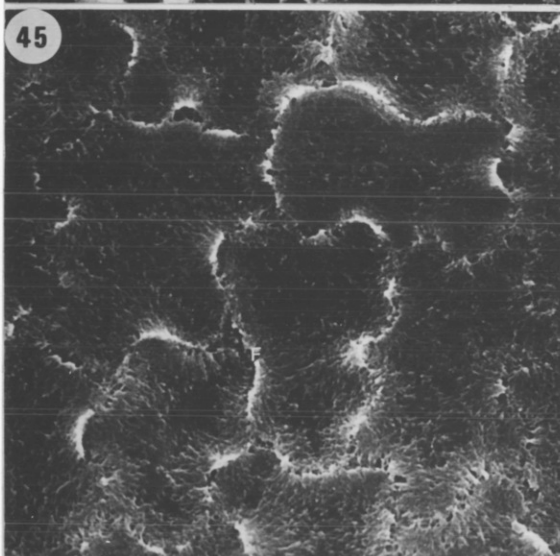
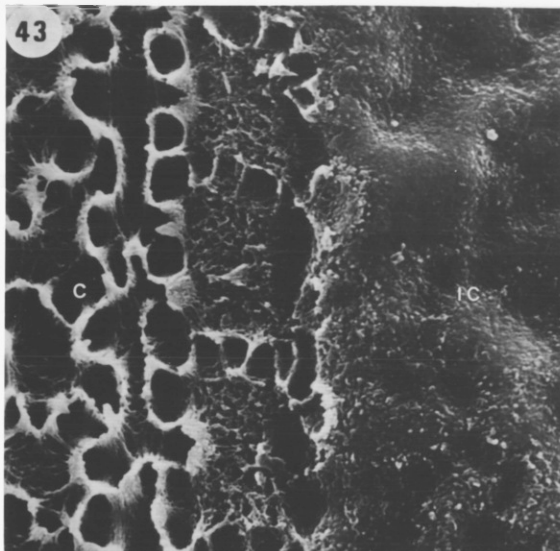


EXTENSIVE – to subepidermal layer

Flange prominence

Inner surface of isolated cuticles.

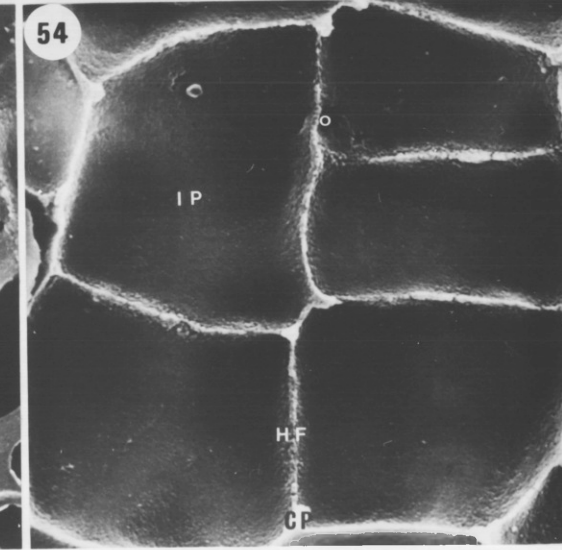
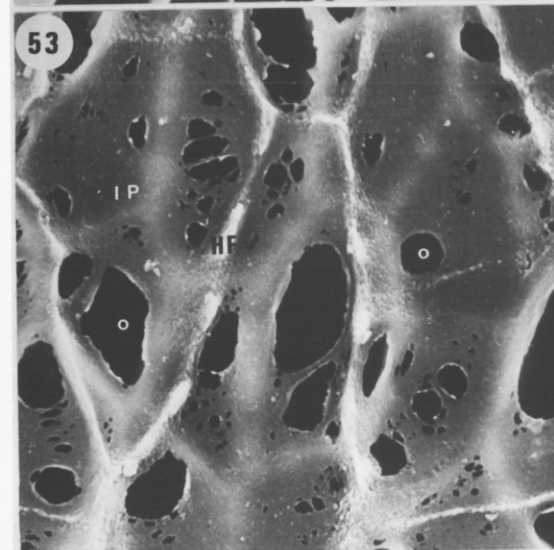
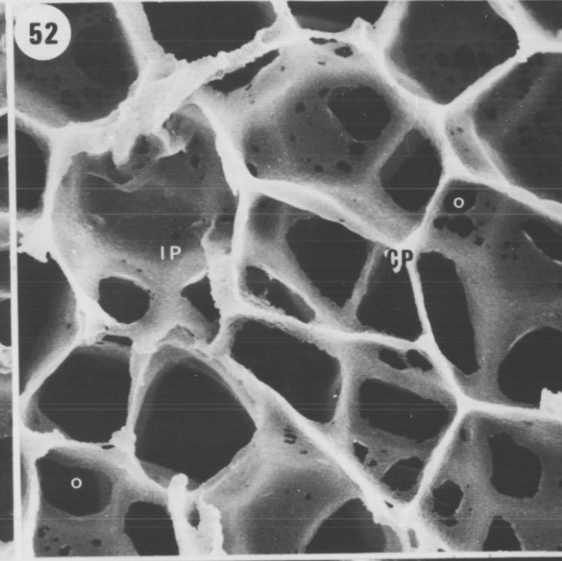
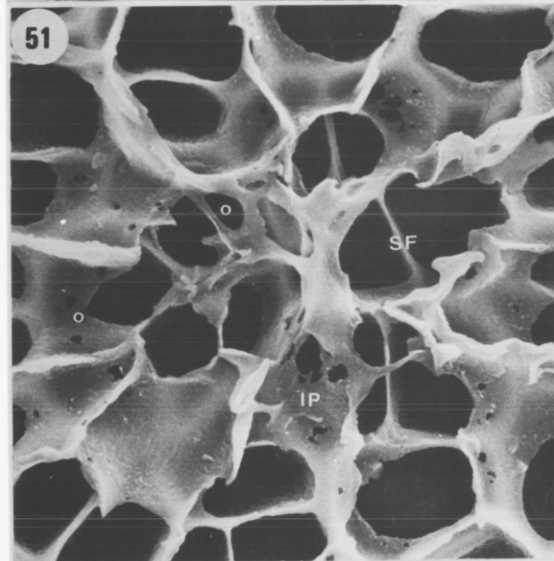
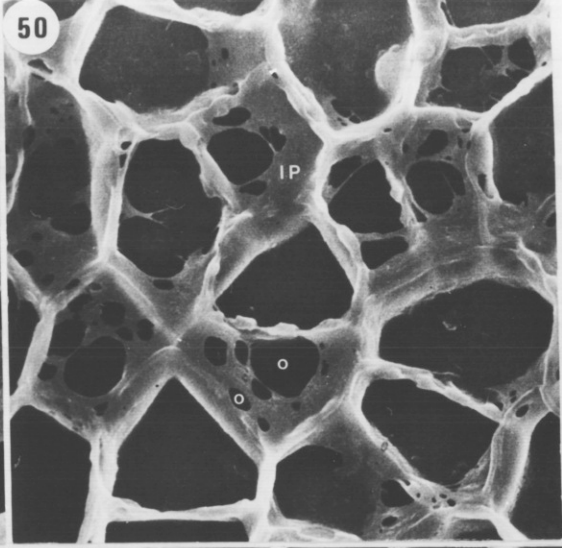
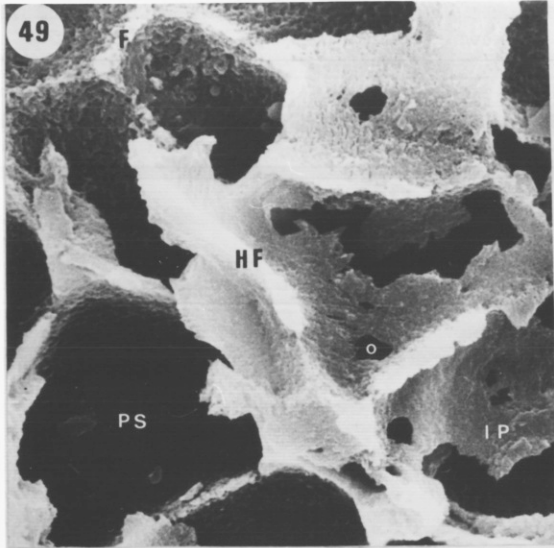
43. Micropora curtisii. Difference in flange prominence in costal [very low] and intercostal [low] regions. Note also difference in sculpture. Abx. ca. x 1195.
44. Gyrocarpus americanus ssp. africanus. Very low. Abx. ca. x 2280.
45. Neocinnamomum caudatum. Low. Adx. Ca. x 1070.
46. Sparattanthelium guianense. Moderate. Adx. ca X 1070.
47. Ravensara aromatica. Deep. Adx. ca. x 2025.
48. Eusideroxylon zwageri. Deep. Abx. ca. x 2100.



Flange prominence: extensive cutinisation

Inner surface of isolated cuticles.

49. Hernandia olivacea. Sporadic extensive cutinisation; flanges normally of low prominence. Adx. ca. x 1250.
50. Pleurothyrium nobile. Some cells with extensive cutinisation; inner periclinal wall (IP) cutinised to varying extents. Tiny rounded or oval perforations (O) present where cutinisation absent. Not detected in T.S. of leaf. Adx. ca. x 1070.
51. Eusideroxylon melagangai. Extensive cutinisation associated with sclereids, with perforations (O) and secondary anticlinal flanges (SF). Adx. ca. x 1090.
52. Eusideroxylon zwageri. Corners cutinised as well as some parts across the entire inner periclinal wall. Complex three-dimensional appearance resulting from cutinisation of secondary anticlinal and periclinal divisions. Adx. ca. x 1065.
53. Beilschmiedia micrantha. Much of the inner periclinal wall is cutinised; where there is no cutinisation, tiny irregular perforations to window-like openings (O) result, giving a holey appearance. Adx. ca. x 1250.
54. Beilschmiedia madang (2). The entire inner periclinal wall (IP) is cutinised except for small rounded perforations (O), up to two per cell. Adx. ca. x 2115.



In some taxa, e.g. Alseodaphne ob lanceolata (Fig.73) and Sparattanthelium guianense (Fig. 46) flanges may be considered as moderate. Thin T.S.'s of this type show flange penetration well down into the mid-zone of the anticlinal epidermal cell wall and isolated cuticles exhibit well-marked outlines.

Deep flanges, which project even further, to the lower regions of the anticlinal wall in section may be observed in others, for example in Cryptocarya ainikini and Ravensara elliptica.

In some taxa, cutinisation may extend beyond the epidermis to the subepidermal layer, generally the hypodermis, and may form a second system of flanges above or in the subepidermal anticlinal wall region. These are always of low or very low prominence and in the light microscope are found at a different level of focus to the epidermal outlines. Subepidermal cutinisation may be recognised by the rather small isodiametric polygonal shape of the cells and the extreme thinness (0.6 μm) of the flanges in surface view. In the S.E.M., subepidermal flanges are often distinctly marked, the epidermal flanges being obscured usually by cutinisation of the inner periclinal wall [see Figs 49, 53, 54]. However, sometimes, air-drying of the cuticle during preparation permits collapse of this periclinal wall (downwards towards the stub) so that it becomes sunken leaving a clear indication of the position and thickness of the underlying epidermal flanges. Where subepidermal cutinisation exists, flanges may be described as extensive in transverse section and in isolated cuticles may produce a complex 3-dimensional appearance [in association with varying degrees of cutin impregnation of the inner periclinal wall and sometimes also with secondary periclinal cell divisions], as in Eusideroxylon spp. (Figs 51, 52).

Whilst flange prominence may be similar in intercostal and costal regions of both leaf surfaces: e.g. very low, in Sassafras albidum var. molle; low, in Aiouea guianensis; moderate, in Ocotea guianensis; deep in Cryptocarya

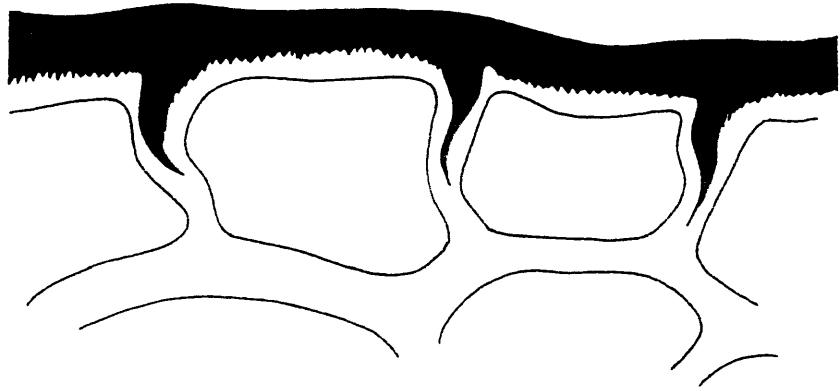
TEXT-FIGURE 7. Cuticle of epidermal cells in T.S.

- A. Persea americana [adx. c.]. Showing slightly uneven cuticle/cellulose wall interface in periclinal region, more even at flanges.

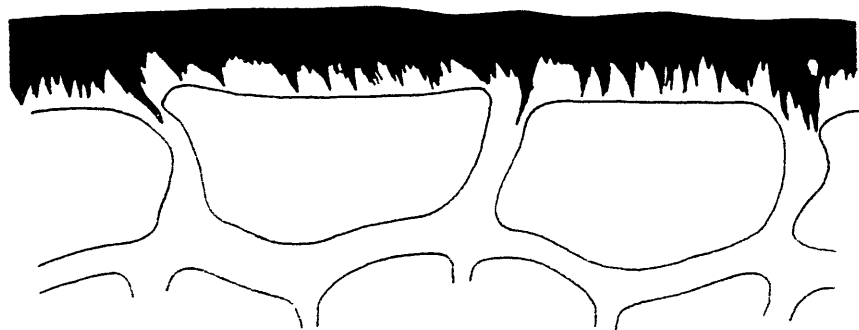
- B. Aiouea guianensis [adx. i.c.]. Showing very uneven cuticle/cellulose wall interface in all regions.

Note perforation in flange on far right. Outer periclinal surface tabular [flat].

A



B



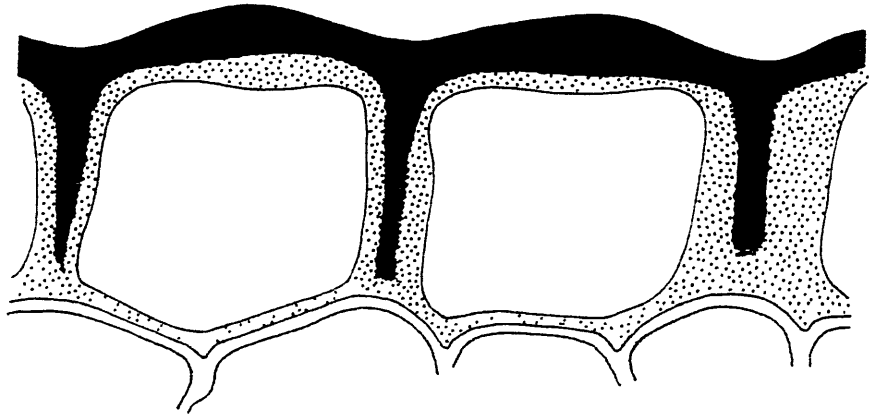
20 μ m

TEXT-FIGURE 8. Cuticle of epidermal cells in T.S.

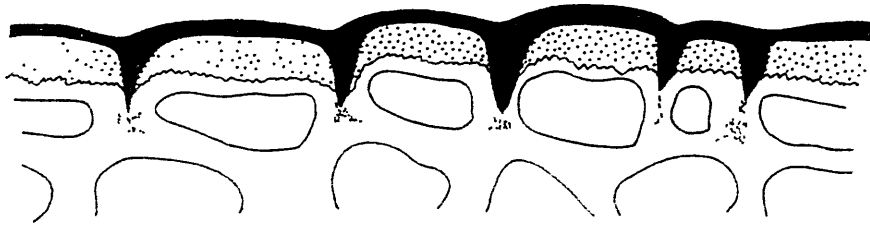
- A. Beilschmiedia madang [adx. i.c.] showing two-layered cuticle. Entire epidermis and small part of hypodermal anticlinal wall cutinised [see Fig. 54]. Anticlinal borders sunken. Outer periclinal surface convex.
- B. Endiandra kingsiana [abx. c.]. Also showing two-layered cuticle flanges of deep prominence with faint cutinised 'corners'. Anticlinal borders sunken. Outer periclinal surface convex.

Note black regions correspond to an intense red staining reaction with Sudan IV, stippled areas represent a less intense or pink reaction.

A



B



20 μm

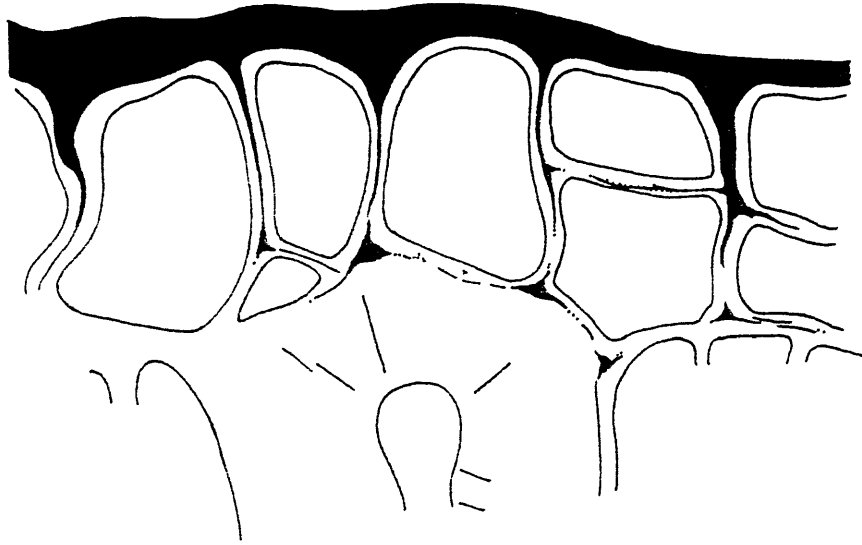
TEXT-FIGURE 9. Cuticle of epidermal cells in T.S.

- A. Eusideroxylon melagangai [adx. i.c.]. Showing extensive cutinisation associated with subepidermal sclereid [see also Fig. 51].

Note that epidermal cells may be divided periclinally.

- B. Hernandia olivacea [abx. c.] showing flanges of low prominence. Inner periclinal wall cutinised, 'corners' especially distinct.

A



B



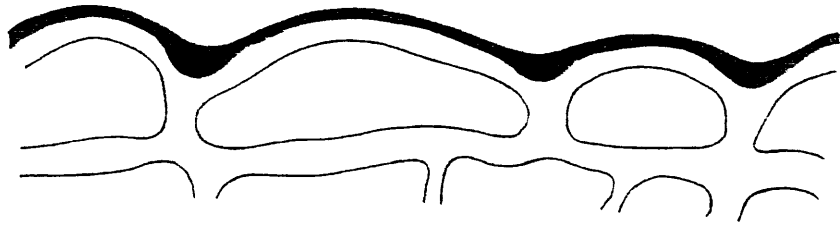
20 μm

TEXT-FIGURE 10. Cuticle of epidermal cells in T.S.

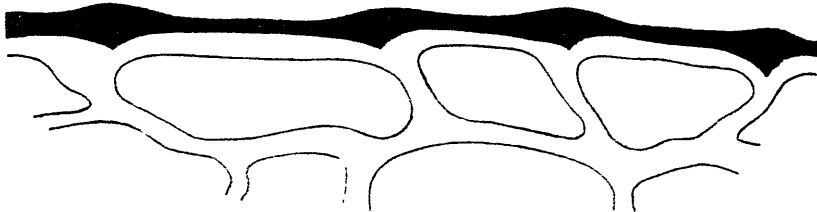
- A. Neocinnamomum caudatum [abx. i.c.]. Flanges U-shaped, of very low prominence. Anticlinal borders sunken. Outer periclinal surface convex.

- B. Sassafridium macrophyllum [abx. i.c.]. Flanges V-shaped, of very low prominence. Anticlinal borders raised. Outer periclinal surface concave.

A



B



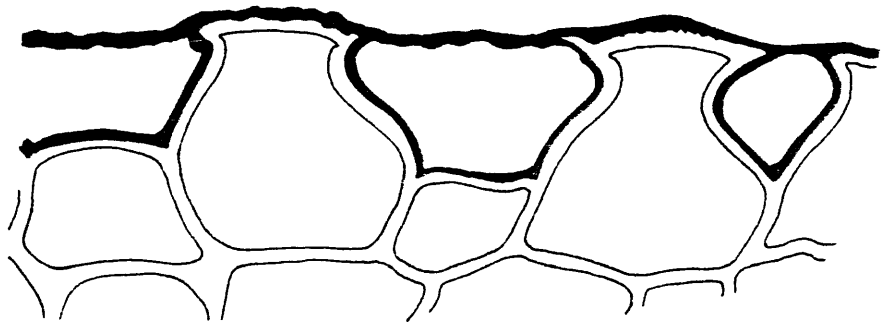
20 μm

TEXT-FIGURE 11. Cuticle of epidermal cells in T.S.

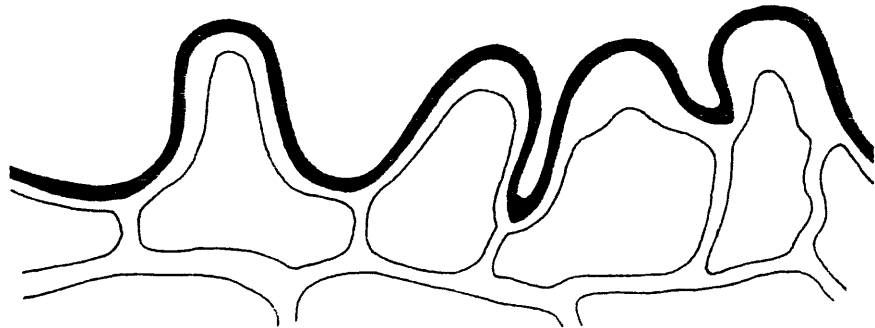
- A. Caryodaphnopsis baviensis [abx. i.c.]. Showing coronulate papillae with completely cutinised lateral extensions [see also Fig. 246].

- B. Phoebe opaca [abx. i.c.]. Showing discrete globular papillae [see also Figs. 16, 18].

A



B



20 μ m

ainikini and extensive in Eusideroxylon melagangai, generally there are differences.

Flange prominence tends to be greater on the adaxial surface than on the abaxial, with the most common patterns being moderate, deep and extensive. On the abaxial, flanges often project to a very low, low or moderate degree. A typical example is Illigera pentaphylla [adx. deep; abx. low]. In a few taxa, flanges project deeper into the epidermis on the abaxial surface, such as Cryptocarya weinlandii and Gomortega keule [adx. moderate; abx. deep].

Often flanges project deeper in costal areas than intercostal: such as in Nothaphoebe spp. [i.c. moderate, c. deep] on the adaxial, or in Neocinnamomum delavayi [i.c. very low, c. moderate] on the abaxial, or in Trimenia weinmanniaefolia [i.c. low, c. moderate] on both surfaces. Only rarely are flanges of greater prominence in intercostal regions, for example, in abaxial Endlicheria piriformis [i.c. moderate, c. low]. Here, flanges over and between the veins are of similar height but the costal epidermal cells are taller than those of the intercostal resulting in less prominence over the veins.

Commonly, either cutinisation is confined to part of the anticlinal wall, or it is absent (where flanges are low or very low). In one taxon only, Beilschmiedia madang [Text-Fig. 8A], the entire width of the wall is cutinised on both surfaces of the leaf.

12.3.4 CONTINUITY OF FLANGES

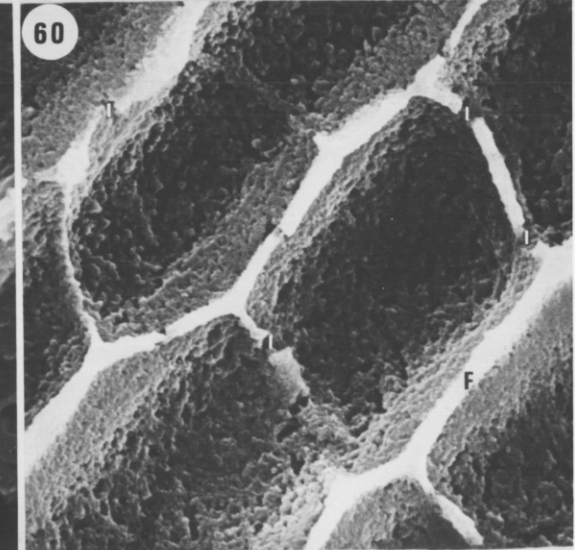
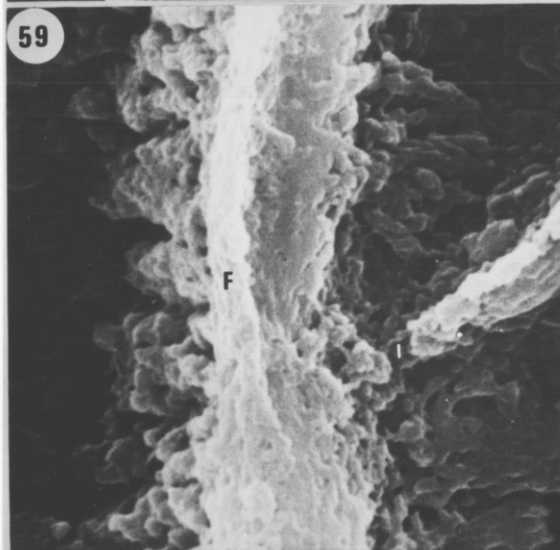
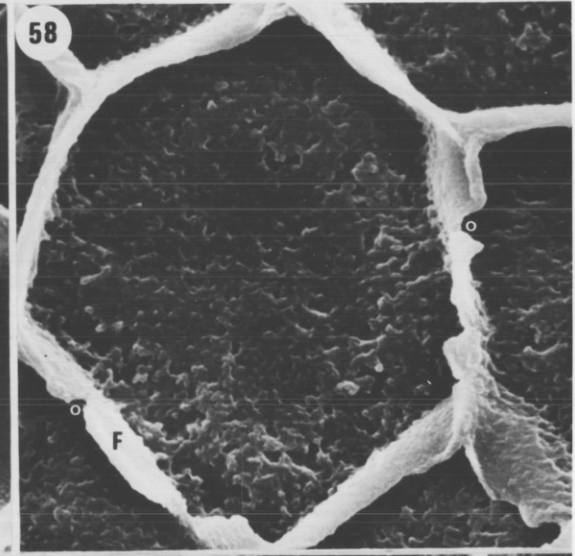
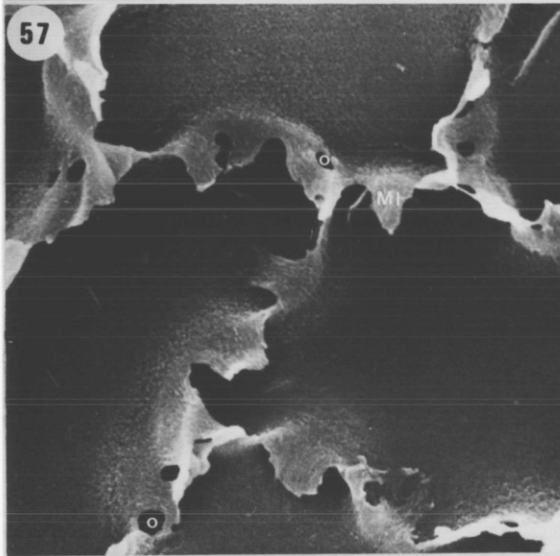
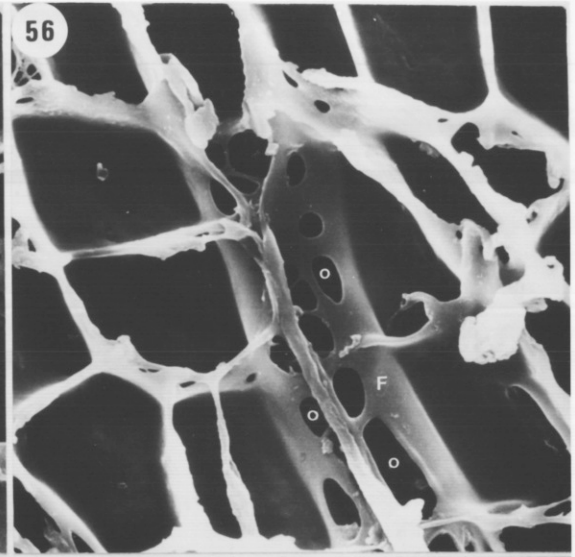
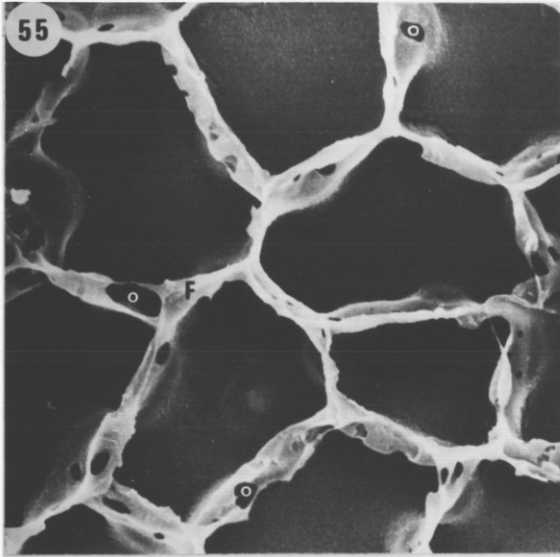
12.3.4a INTERRUPTIONS

Scanning electron microscopic observations show that flanges may sometimes be of the continuous, uninterrupted type, in all regions of the cuticles from both leaf surfaces, such as in species of Aniba, Beilschmiedia, Endiandra and Potameia or confined to just one, particularly the adaxial, e.g. in Alseodaphne oblanceolata,

Flange form: perforations and interruptions

Inner surface of isolated cuticles.

55. Dicypellium caryophyllatum. With pores [O] of varying size and shape in deep flanges. Adx. ca. x 1070.
56. Mezilaurus lindaviana. As Fig. 55. Pores [O] ranging from tiny channels [right] to large, window-like openings [bottom, right of centre]. Adx. ca. x 1050.
57. Dicypellium caryophyllatum. Pores [O] in highly irregular [MI] flanges of moderate prominence. Abx. ca. x 2260.
58. Persea chinensis. Pores [O] located at flange [F] margin, partially bounded by cutin, designated 'half' pores. Adx. ca. x 2125.
59. Cinnamomum camphora. With distinct break or interruption [I] in costal flange. Abx. ca. x 4320.
60. Sassafridium macrophyllum. Costal flanges [F] commonly interrupted by breaks [I] which may extend part way or entirely down to the periclinal surface. Abx. ca. x 2100.



Gomortega keule [adx.], Illigera pulchra and Nectandra spp. [abx.]. Occasionally, only intercostal areas have continuous flanges, for example in Dicypellium caryophyllatum [adx.], certain Ravensara spp. [R. elliptica and R. pervillei; abx.] and Sparattanthelium guianense [adx.]. Even rarer is the occurrence of uninterrupted flanges in costal regions only, observed in R. elliptica [adx.].

Alternatively, flanges may possess distinct gaps or breaks in their length, the interruptions extending down to where the periclinal and anticlinal cutinisation meet (Figs 59, 60). There may be just the occasional gap per flange with the majority of flanges being continuous, as in all regions of cuticles in Aiouea spp., Caryodaphnopsis tonkinensis and Endlicheria reflectens or more regularly just on one membrane, e.g. in Micropora curtisii, Nectandra spp. [adx.], Phyllostemonodaphne geminiflorum and Systemonodaphne mezii [abx.]. Sometimes, there may occasionally be two gaps observed per flange in addition to a few single gaps, with most flanges uninterrupted, usually on the adaxial, as in Caryodaphnopsis baviensis and Sparattanthelium tupiniquinorum or alternatively on the abaxial, for example in Nothaphoebe heterophylla and certain Persea spp. [P. chinensis & P. thunbergii]. The occasional two gaps per flange may also be detected in either the intercostal areas only, such as in Cryptocarya weinlandii [adx.], Dicypellium caryophyllatum [abx.] and Trimenia weinmanniaefolia [adx. & abx.] or just the costal, e.g. in Licaria guianensis and Sassafras albidum var. molle [abx.]

The rare occurrence of up to three gaps per flange may be observed mainly on the abaxial, as in Hernandia nymphiifolia [i.c. & c.] and Sassafras albidum var. molle [i.c.].

In other taxa, a greater percentage [about 50%, i.e. some] of flanges may be interrupted; rarely with a single gap per flange, e.g. in Alseodaphne semecarpifolia [abx. c.] and Ocotea guianensis [adx. c.], but more commonly

with up to two interruptions per flange, such as in Dehaasia caesia [adx. c.] Lindera strychnifolia [adx.] Nothaphoebe heterophylla [abx. i.c.] and Persea thunbergii [abx.]. Sometimes, up to three gaps per flange may exist in about half of the flanges in a preparation, on one surface, as in Piptocalyx moorei [adx.], or more usually, in one area of a cuticle, for example, in Cinnadenia paniculata [abx. i.c.], Hernandia nymphiifolia [adx. c.] and Micropora curtisii [abx. c.]. Up to four gaps per flange may be present in a similar percentage of flanges, such as in Gyrocarpus americanus [adx.], Neolitsea dealbata [adx. c.], Piptocalyx moorei [abx.] and Sparattanthelium tupiniquinorum [abx. c.].

Taxa with 75% or more interrupted flanges only rarely have one or two gaps per flange, e.g. in Apollonias arnottii [adx. c. 1 gap] and Ocotea guianensis [adx. i.c. up to 2 gaps]. Generally, where interruptions are this frequent in a preparation, there tends to be a maximum of between 3 and 5 gaps per flange. These may occur on the cuticle of one leaf surface, such as in Gomortega keule [abx. 1-4], Laurus spp. [adx. 1-3], Litsea umbellata [adx. 1-5] and Sassafridium macrophyllum [abx. 1-3]. Alternatively, such interrupted flanges may be confined to one area of the cuticle: e.g. in Mezilaurus itauba [adx. i.c. 1-5] and Neolitsea dealbata [abx. i.c. 1-5].

In some cases, particularly where most flanges possess interruptions, there may be flanges with more than 5 gaps per flange, as in Actinodaphne stenophylla [abx. i.c. up to 7, always 3 or more per flange], Dehaasia caesia [abx. i.c. up to 8] (Fig. 22), Hernandia olivacea [adx. up to 8; abx. up to 6] and Litsea umbellata [abx. up to 7].

Only very few taxa have flanges with more than 8 distinct gaps per flange and these are always located on the abaxial cuticle; in all regions of Laurus spp. and in the intercostal area of Micropora curtisii.

Occasionally, flanges are interrupted to the same degree in all regions of cuticle from both leaf surfaces,

such as those of Aiouea spp., Caryodaphnopsis tonkinensis, Cryptocarya ainikini and Litsea monopetala [rare 0-1]. More usually, flange interruption is similar in intercostal and costal areas of one cuticle only, e.g. Apollonias arnottii [abx. frequent 0-3], Dodecadenia grandiflora [abx. frequent 0-4], Licaria triandra [adx. rare 0-2] and Lindera strychnifolia [adx. some 0-2]. Generally, flanges are more interrupted on the abaxial cuticle than on the adaxial, as in Cinnamomum iners [adx. rare 0-1; abx. frequent 0-3], Laurus spp. [adx. frequent 0-3; abx. frequent, more than 8] and Sassafridium macrophyllum [adx. some 0-2; abx. frequent 0-3].

However, there are exceptions in which the reverse situation occurs, notably in Hernandia spp. [H. nymphiifolia: adx. i.c. frequent 2-5, c. some 0-3; abx. rare 0-3; H. olivacea: adx. frequent 2-8; abx. frequent 1-6] and Litsea umbellata [adx. i.c. frequent 0-5, c. frequent 0-7; abx. i.c. rare 0-1, c. 0-2]. Other taxa exhibit differences in the degree of interruption of vein and non-vein flanges. Commonly, it is the latter which is most interrupted in a taxon, often on cuticle of one side of the leaf, the adaxial, as in Sassafras albidum var. molle [i.c. frequent 0-5, c. rare-some 0-3] or more usually, the abaxial, e.g. in Dehaasia caesia [i.c. frequent 1-8, c. frequent 0-5], Micropora curtisii [i.c. frequent, more than 8, c. some 0-3] and Nothaphoebe umbelliflora [i.c. frequent 0-5, c. some 0-3]. Occasionally, the costal flanges have the greatest level of interruption, such as in Persea americana [i.c. some 0-2, c. some-frequent 0-4].

12.3.4b HOLES OR PORES

Unspecialised flanges of some taxa may not possess any holes at all in their main body, i.e. they are non-perforated, in a number of Lauraceae including Actinodaphne glomerata and Sassafras albidum var. molle and in many members of the related families, such as Gyrocarpus americanus, Hernandia nymphiifolia, Illigera pulchra and all Trimeniaceae. In some taxa, perforations are lacking in flanges of the cuticle of one leaf surface only: occasionally, the adaxial e.g. in Cinnamomum iners,

Gomortega keule and Ocotea guianensis, or more usually, the abaxial, as in Actinodaphne stenophylla, Hernandia olivacea and Neolitsea dealbata. Alternatively, there may be no holes detected in flanges of a single area on the abaxial, commonly between the veins, for instance, in Caryodaphnopsis tonkinensis, Micropora curtisii and Persea chinensis, or rarely, over them, as in Persea thunbergii.

Ordinary flanges, however, are perforated by pores of varying morphology in many other species [Figs 55-58]. Three main types of 'full' perforation, i.e. holes bounded on all sides by cutin, may be recognised between which are many intermediates: tiny rounded channels, approximately 0.05-0.09 μm in diameter, with lumina which are difficult to resolve even in the S.E.M. at high power ($\times 2500$ or more) [Fig. 25 centre] such as in Aiouea spp., Alseodaphne semecarpifolia, Dodecadenia grandiflora and Laurus canariensis; round to oval, moderate sized [diameter about 0.18-0.36 μm] pores, each with a distinct lumen [Fig. 20 right], for example in Alseodaphne oblanceolata, Cryptocarya alleniana, Nectandra spp. and Potameia spp. and large [approximately 0.90-2.50 μm diameter] round, oval or irregular-shaped, window-like openings, as in Aniba megaphylla, Dicypellium caryophyllatum [Fig. 55], Eusideroxylon zwageri and Mezilaurus lindaviana [Fig. 56].

In taxa of the Lauraceae and Hernandiaceae with perforate flanges tiny channels are the most common pore type. It is usual for more than one pore form to be present; often two [tiny channels and moderate pores] e.g. in Beilschmiedia spp. or more rarely, all three, as in those exemplifying the third type above.

The form of pores found in non-specialised flanges may be similar in intercostal and costal regions of cuticles from both surfaces of the leaf. Commonly, however, there are differences between the configurations shown on the two sides. Where this is so, the adaxial flanges tend to have more perforation types than the abaxial, e.g. in Illigera pentaphylla [adx. 2; abx. 1], Licaria guianensis [adx. 3; abx. i.c. 1, c. 2], Phyllostemonodaphne

geminiflorum [adx. 3; abx. 2] and certain Ravensara spp. [R. aromatica and R. pervillei: adx. 3; abx. 1]. Sometimes, flanges of one area are perforated differently to all others in a taxon, especially on the adaxial cuticle. Examples demonstrating this phenomenon include Endlicheria reflectens [abx. i.c. 3 types; others 2], Mezilaurus lindaviana [adx. i.c. 2 types, others 3], Neolitsea cassia [abx. c. 2 types, others 1] and Urbanodendron verrucosum [adx. c. 1 type, others 2].

'Half' pores, partially bounded by cutin elements distributed at the flange margin, are occasionally the only type of perforation found in certain regions of the cuticle in Licaria guianensis [abx. i.c.] and Nothaphoebe heterophylla [adx.]. Generally, however, they are present in taxa with 'full' pores, e.g. in Aniba megaphylla [Fig. 64], Dicypellium caryophyllum [Figs 55 & 57] [adx. & abx.], Persea chinensis [Fig. 58] and Sparattanthelium guianense [Fig. 46] [adx.].

The number of pores in any perforate flange may vary between 1, as in Dehaasia caesia and 14, in Beilschmiedia micrantha [adx.]. A range of values is usually found in a cuticle preparation. Most taxa have up to three holes per flange, 0-1, e.g. in Dodecadenia grandiflora [adx. & abx.], Hernandia olivacea and Phoebe spp. [adx.]; 0-2, such as, in Aiouea saligna and Cryptocarya weinlandii [adx. & abx.] and 0-3, for example, in Cinnamomum pachyphyllum, Cryptocarya alleniana and Pleurothyrium cuneifolium [adx.]. In others [Lauraceae only], some regions of the cuticle may have up to 4 pores, as in Eusideroxylon melagangai, Lindera strychnifolia and Ravensara aromatica [adx.] or 5, e.g. in Eusideroxylon zwageri [abx. i.c.], Lindera pulcherrima [adx. i.c.] and Micropora curtisii [adx.] or even 6, such as in Dehaasia cuneata [adx. i.c.], Mezilaurus lindaviana [abx. c.] and Pleurothyrium nobile [adx.]. The majority of the examples cited above possess about 50% of flanges without any perforations. There are some Lauraceae taxa in which the proportions of perforate flanges is much higher. Generally, in these, 5 or more pores may be detected per

flange, e.g. Aniba megaphylla [adx. 1-6; abx. 2-8], Beilschmiedia spp. [B. madang: adx. i.c. 3-8, c. 3-11; abx. 2-7, B. micrantha: adx. i.c. 3-14, c. 2-11; abx. i.c. 1-7, c. 1-8] and Dicypellium caryophyllatum [adx. i.c. 2-11, c. 1-5; abx. i.c. 2-8, c. 2-6]. Where there are many pores per flange of variable shape and size, i.e. with all three types, a particularly distinctive 'holey' appearance is conferred upon the flanges in a preparation when viewed with light- or scanning-electron-microscopy [e.g. Figs 55, 56].

Whilst the degree of perforation or frequency of pores per flange is similar in all regions of the cuticle from both leaf surfaces in a few taxa, such as Endiandra kingsiana and Sassafridium macrophyllum [0-2], it is more usual for differences to be displayed. Commonly, pores are more abundant in flanges of the adaxial membrane, e.g. in Beilschmiedia spp. [see above], Lindera spp. [L. pulcherrima: adx. i.c. 0-5, c. 0-4; abx. 0-3, L. strychnifolia: adx. 0-4; abx. i.c. 0-3, c. 0-2] and Phyllostemonodaphne geminiflorum [adx. i.c. 1-8, c. 1-6; abx. 0-2]. However, there are exceptions, with a greater number of pores on the abaxial, such as, in Aiouea guianensis [adx. 0-1; abx. i.c. 0-3, c. 0-2], Aniba megaphylla [see above] and Eusideroxylon zwageri [adx. 0-3; abx. i.c. 0-5, c. 0-4].

Pore number may differ in flanges of only one area of a cuticle, most often on the abaxial, for example in Alseodaphne oblanceolata [c. 0-4, others 0-1], Potameia spp. [P. crassifolia: i.c. & P. thouarsii: c. 0-1, others 0-2], Systemonodaphne mezii [i.c. 0-2, others 0-1] and Urbanodendron verrucosum [i.c. 0-2, others 0-3]. Occasionally, this difference is confined to the adaxial, generally in the intercostal area, as in Cryptocarya ainikini [0-1, others 0-2] and Sparattanthelium guianense [0-3, others 0-2]. The pore frequency may, in a restricted number of taxa, vary in the non-vein region of one cuticle surface and also over the veins on the other, as in Dehaasia cuneata [adx. i.c. 0-6; abx. c. 0-3, others 0-2], Endiandra rubescens [adx. i.c. 0-4; abx. c. 0-2, others 0-3]

and Nectandra salicifolia [adx. c. 0-1; abx. i.c. 0-3, others 0-2].

Interruptions and holes, presumably, correspond to areas of intercellular connection, i.e. plasmodesmata.

12.3.5 NATURE OF FLANGE APEX

12.3.5a FURROWING

Most flanges appear 'single' in surface view in the S.E.M., with one distinct apex, due to concurrent cutinisation in the middle lamella and adjacent regions during development, e.g. in Alseodaphne ob lanceolata (Fig. 73), Illigera spp. (Fig. 75), Mezilaurus lindaviana (Fig. 56) and Sassafridium macrophyllum (Fig. 60). In a few Lauraceae taxa, however, flanges have a longitudinally running furrow at the apex, presumably arising as a result of the middle lamella being less deeply cutinised than the walls on either side in flange formation. Such 'double' or 'grooved' flanges are found in various regions of Endiandra spp. [E. kingsiana: all areas. Fig. 39; E. rubescens: abx. c.] and Neocinnamomum caudatum [all areas except abx. c.] (Fig. 67). There appears to be no correlation between flange height or prominence and the presence of grooves [N. caudatum: double flanges; very low, 1.0-1.2 μm ; Endiandra double flanges: variable prominence low-moderate, 0.6-14.4 μm].

At the cell corners on the adaxial cuticle, in one Lauraceae taxon Persea thunbergii (Fig. 68), the flange apex possesses two furrows, possibly due to the deepest cutinisation occurring at three discrete points, the middle lamella and the outer part of the wall on either side, with two other wall regions adjacent to the middle lamella being considerably less well-cutinised.

12.3.5b IRREGULARITY/JAGGEDNESS

The margin of ordinary flanges, seen from the side with scanning electron microscopy, may be more or less even, indicating that they projected to a similar depth along their entire length in the leaf, as in Gyrocarpus

Flange form: margin irregularity

Inner surface of isolated cuticles.

61. Hernandia olivacea. Margin of flange jagged; irregularities [MI] tapering, of variable amplitude. Adx. ca. x 4260.

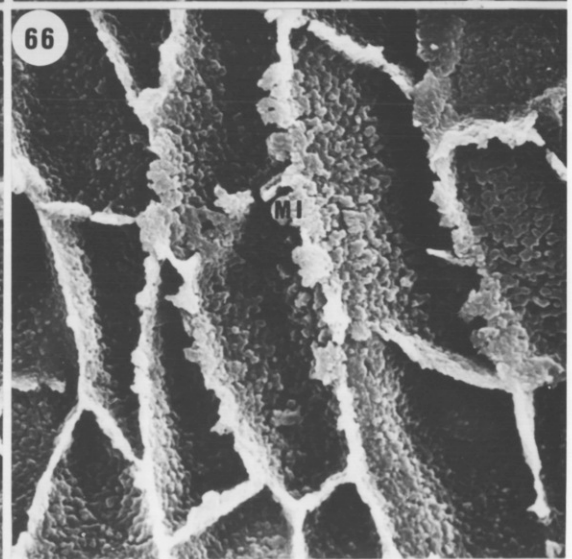
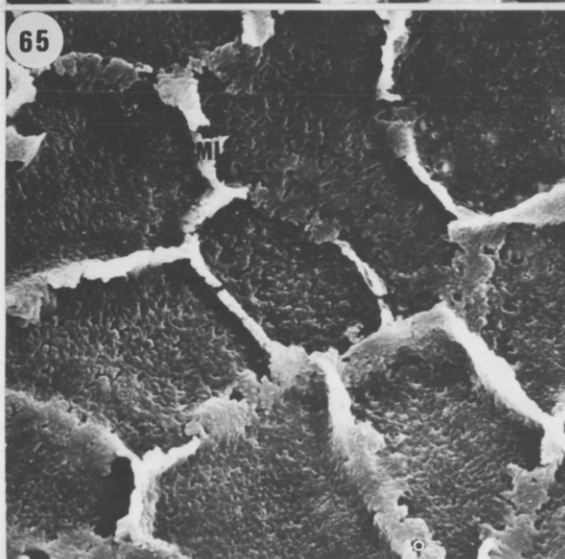
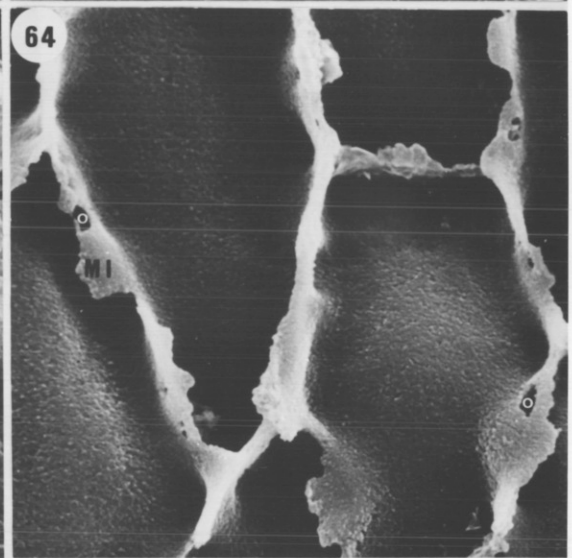
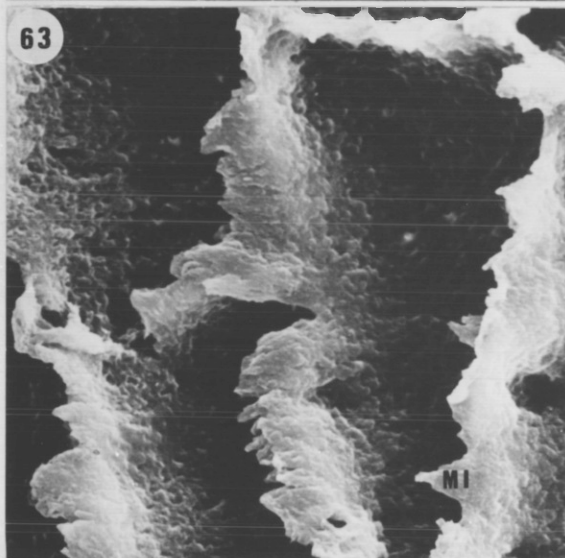
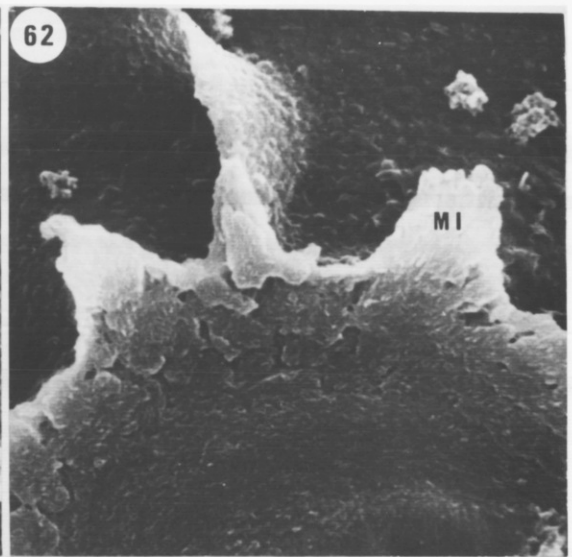
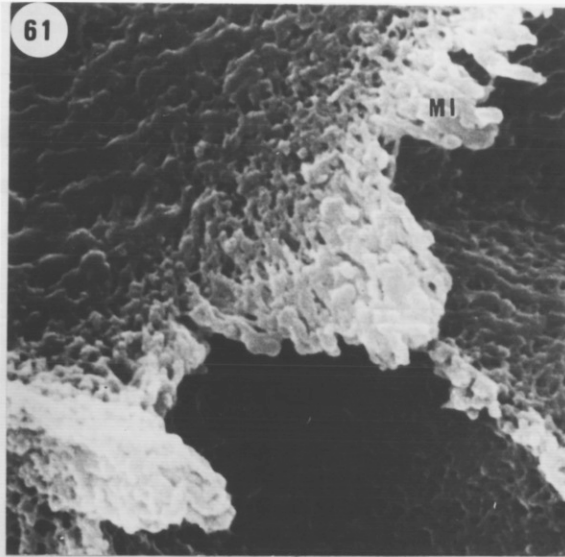
62. Cryptocarya weinlandii. Margin irregularities [MI] sharply tapering and pointed forming a frilly edge to stomatal complex. Abx. ca. x 4670.

63. Lindera strychnifolia. Margin of costal flanges irregularly jagged, showing range of irregularity amplitude. Adx. ca. x 2115.

64. Aniba megaphylla. Perforate [O] flanges with blunt irregularities [MI] of varying size. Abx. ca. x 2105.

65. Lindera pulcherrima. With distinctly jagged flanges, irregularities blunt or pointed. Flanges characteristically collapse onto periclinal surface. Adx. ca. x 1080.

66. Lindera pulcherrima. Irregularities blunt or pointed in costal region. Flanges erect [compare with Fig. 65]. Adx. ca. x 1070.



americanus ssp. africanus (Fig. 44), Hernandia nymphiifolia (Figs 21, 74), Illigera pulchra (Fig. 75) and certain areas of cuticles, mainly on the abaxial, e.g. in Austrobaileya scandens (i.c.) (Fig. 76), Gyrocarpus americanus ssp. americanus, Sassafras albidum var. molle and Sparattanthelium tupiniquinorum (i.c. & c.). Even flanges are often of either a low or very low prominence and sometimes, in addition, are rounded (U-sectioned) in profile (see examples above).

Most taxa possess flanges which exhibit some degree of irregularity, independent of variation in size of sculptural elements and may be termed uneven or jagged [see Figs 57, 61-66]. Unevenness results from the depth of cutinisation varying throughout the length of each flange.

Irregularities vary from hardly discernible deviations from the horizontal (about 0.10-0.18 μm high), as in some regions or surfaces of Aiouea saligna (abx.) (Fig. 35), Eusideroxylon spp. (adx.), Mezilaurus itauba (adx. i.c.; abx.) and Nothaphoebe heterophylla (adx. & abx.) (Fig. 38) to distinct tooth-like projections (which form a prominent irregular crest and trough pattern), with a maximum height of approximately 5.5 μm , in Phyllostemonodaphne geminiflorum (adx.). A range of irregularity amplitude is generally detected in any area of the cuticle surface within a taxon and always incorporates a minimum of less than 0.18 μm . It is rare for the maximum height of flange irregularity to be more or less the same in all regions of both the adaxial and abaxial cuticle. Examples showing such uniformity include Cinnamomum iners (max. 0.18 μm), Endiandra rubescens (2.2 μm) and Ravensara aromatica (0.5 μm). However, it is quite common for flanges over and between veins to possess irregularities with a similar amplitude range, on the membrane of one surface particularly the adaxial, as in Dehaasia spp. (D. caesia: max. 3.6 μm ; D. cuneata: 1.8 μm) Illigera pentaphylla (max. 1.1 μm), Nothaphoebe umbelliflora (max. 2.4 μm), Sparattanthelium tupiniquinorum (max. 2.5 μm) and Trimenia spp. (max. 0.4 μm), but sometimes on the abaxial, e.g. in Dodecadenia grandiflora (max. 0.5 μm), Ocotea laevis

[max. 1.8 μm], Pleurothyrium nobile [max. 2.2 μm] and Potameia crassifolia [1.3 μm].

In many taxa, the flange irregularities project to a greater height in adaxial cuticular preparations than in abaxial, such as in Dehaasia caesia [adx. max. 3.6 μm ; abx. i.c. 0.2 μm , c. 1.8 μm], Lindera spp. [L. pulcherrima: adx. max. 4.0 μm ; abx. 2.4 μm ; L. strychnifolia: adx. max. 3.6 μm ; abx. i.c. 0.9 μm , c. 1.4 μm] and Potameia thouarsii [adx. max. 2.0 μm ; abx. 0.9 μm]. There are some exceptions, of course, in which the reverse situation may be found, for example in Eusideroxylon spp. [adx. max. 0.2 μm ; abx. 0.5 μm], Hernandia olivacea [adx. i.c. max. 1.1 μm , c. 1.3 μm ; abx. i.c. 1.4 μm , c. 1.6 μm] and Nectandra pichurim [adx. i.c. max. 0.9 μm , c. 1.4 μm ; abx. 1.8 μm].

Differences in irregularity amplitude may often be exhibited by flanges of all regions of the adaxial and abaxial cuticles. When this is so, the costal irregularities usually have the highest maximum value, such as in Dicypellium caryophyllatum [adx. i.c. max. 1.1 μm , c. 3.6 μm ; abx. i.c. 3.1 μm , c. 4.4 μm], Licaria triandra [adx. i.c. max. 1.4 μm , c. 1.8 μm ; abx. i.c. 1.1 μm , c. 2.2 μm] and Mezilaurus lindaviana [adx. i.c. max. 1.8 μm , c. 2.9 μm ; abx. i.c. 0.7 μm , c. 1.4 μm]. However, occasionally the intercostal irregularities are more prominent than the costal, e.g. on the adaxial only in Phyllostemonodaphne geminiflorum [adx. i.c. max. 5.5 μm , c. 5.1 μm ; abx. i.c. 3.1 μm , c. 3.6 μm] or both the adaxial and abaxial, such as in Sparattanthelium guianense [adx. i.c. max. 2.2 μm , c. 1.3 μm ; abx. i.c. 1.1 μm , c. 0.5 μm].

Where the non-vein and vein flanges differ in the degree of irregularity and such differences are confined to the cuticle of one side of the leaf alone, the phenomenon tends to occur most often on the adaxial. In such cases the costal irregularities commonly attain a greater maximum height than the intercostal, e.g. in Gyrocarpus americanus ssp. americanus [i.c. max. 1.1 μm , c. 1.3 μm], Neocinnamomum delavayi [i.c. max. 0.2 μm , c.

1.1 μm) and Neolitsea cassia [i.c. max. 0.9 μm , c. 1.8 μm], although this is not always so, such as in Actinodaphne glomerata [i.c. max. 1.4 μm , c. 0.7 μm], Caryodaphnopsis tonkinensis [i.c. max. 1.6 μm , c. 0.9 μm] and Illigera pentaphylla [i.c. max. 0.9 μm , c. 0.4 μm]. On the abaxial, irregularities also tend to be most prominent on costal flanges, for example especially in Dehaasia caesia [see p.171] and Nothaphoebe umbelliflora [i.c. max. 0.4 μm , c. 3.1 μm]. Exceptions include Beilschmiedia micrantha [i.c. max. 5.1 μm , c. 3.3 μm] and Endlicheria piriformis [i.c. max. 1.4 μm , c. 1.1 μm], with more jagged flanges in intercostal areas.

The frequency of irregularity appears to be closely related to amplitude: when the amplitude is small, there are often more irregularities per flange than when projections are large. Since this is so, and irregularities are difficult to distinguish individually when tiny, no measure of number per flange has been made.

Individual irregularities tend to be either blunt, such as in Licaria guianensis, Mezilaurus lindaviana [adx.], Ocotea laevis [abx.] and Sparattanthelium spp. [S. guianense: adx. & abx. Fig. 46; S. tupiniquinorum: adx.], or pointed [sharply tapering], e.g. in Dicypellium caryophyllatum [adx. c., abx.] [Fig. 57], Hernandia olivacea [Fig. 61], Lindera strychnifolia [adx., abx. c.] [Fig. 63] and Micropora curtisii [adx., abx. c.]. Flanges in any cuticle preparation may show a predominance of blunt or pointed irregularities [as in the taxa mentioned above]. However, this is not always so: the pattern observed may consist of a mixture of irregularity form, for example, in Beilschmiedia micrantha [abx.], Gomortega keule [abx.], Illigera pentaphylla [adx.] and Sassafridium macrophyllum [abx.]

12.3.5c CORNER EXTENSIONS/PEGS

At cell corners, where flanges of several adjacent cells meet, cutinisation may be level in some taxa, such as in Alseodaphne spp., Gyrocarpus americanus ssp. africanus, Hernandia nymphiifolia and Neocinnamomum spp. However, in others it may be especially deep due to the presence of a

Flange form: furrowing and corner extensions [pegs]

Inner surface of isolated cuticles.

67. Neocinnamomum caudatum. Showing flange with shallow groove [starred] in apex, resulting in 'double' appearance. Adx. ca. x 4235.

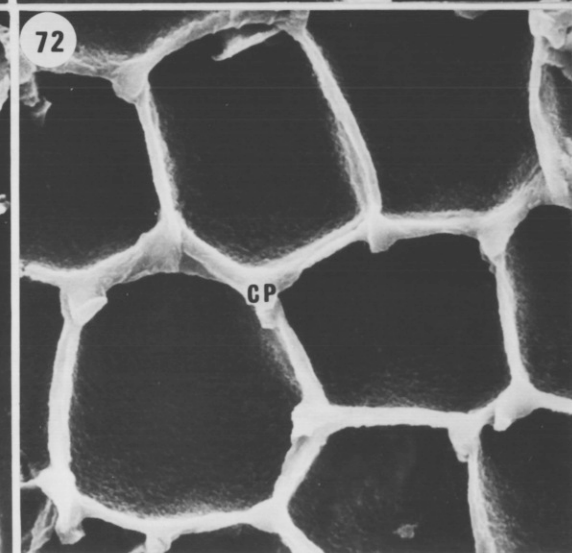
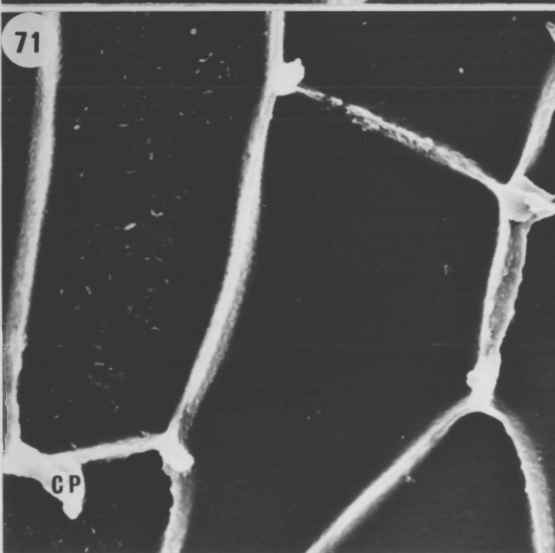
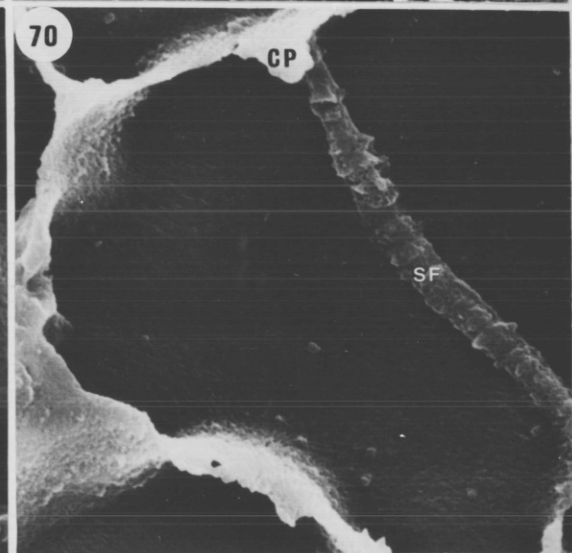
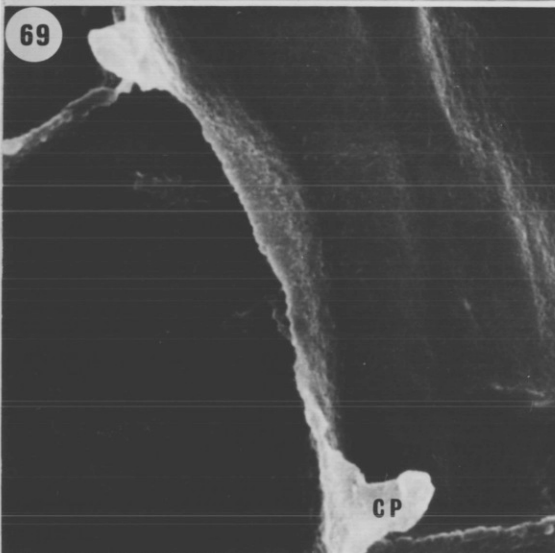
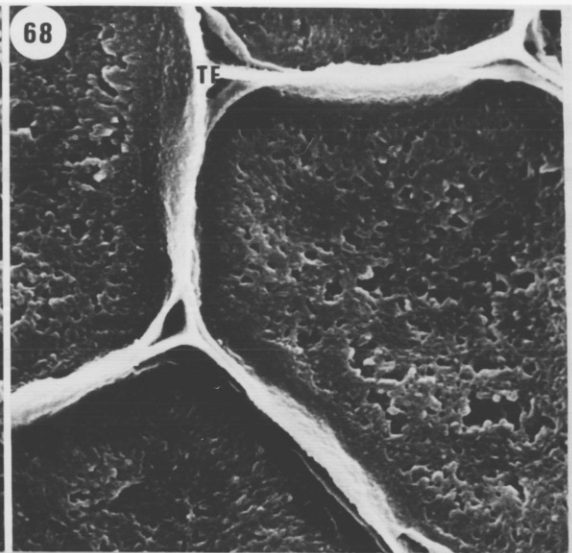
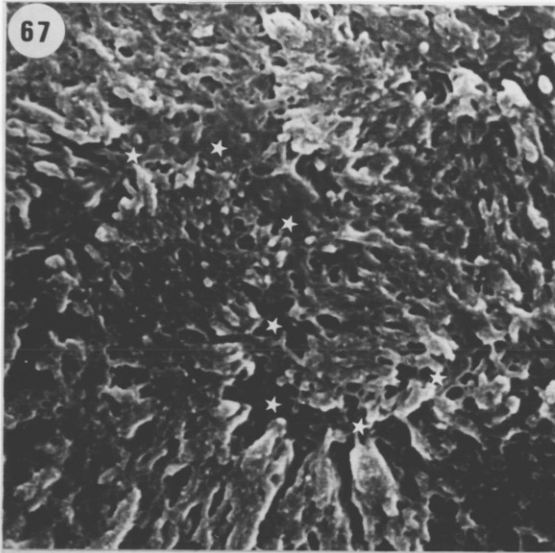
68. Persea thunbergii. Corners of cells with 'triple' flange configuration [TF]. Here, cutinisation appears to have taken place at three discrete points: in the region of the middle lamella and nearby, on either side. Adx. ca. x 2120.

69. Illigera pentaphylla. Showing deep cutinisation of cell corners forming peg-like extensions [CP] [1 per corner]. Abx. ca. x 4265.

70. Illigera pentaphylla. With peg [CP] where secondary flange [SF] meets primary flange. Adx. ca. x 2135.

71. Mezilaurus lindaviana. As Fig. 69. Pegs associated with costal cells. Abx. ca. x 2155.

72. Ocotea guianensis. As Fig. 69. Pegs associated with intercostal cells. Adx. ca. x 2130.



cutin extension or peg. Such projections are more difficult to see when the flanges have uneven margins, being inconspicuous and impossible to record particularly if the irregularity amplitude is great, e.g. in Dehaasia caesia [adx.]. Prominent pegs are shown by a variety of species, such as Cryptocarya alleniana, Gomortega keule, Hernandia olivacea [Fig. 61], Mezilaurus lindaviana [Fig. 71] and Ocotea guianensis [Fig. 72]. When present in a taxon, these pegs are generally a feature of all regions of cuticles from both leaf surfaces, e.g. in species of Aniba, Endiandra and Ravensara [also those taxa cited above] or, are exhibited by flanges of one membrane only, as in Beilschmiedia micrantha, Cryptocarya ainikini [abx.], Gyrocarpus americanus ssp. americanus and Illigera pulchra [adx.] [Fig. 69].

Sometimes, peg-like extensions are found everywhere except in one region of the abaxial cuticle; commonly the intercostal, for example, in Austrobaileya scandens, Micropora curtisii and Sparattanthelium tupiniquorum or more rarely the costal, as in Litsea monopetala.

Occasionally, pegs are conspicuous at the cell corners only in areas between veins, e.g. in Lindera pulcherrima [abx.] and Litsea umbellata [adx.] or just in vein regions, e.g. in Lindera strychnifolia [adx. & abx.] and Sassafras albidum var. molle [adx.].

Cutin extensions tend to taper towards the apex, which often appears either somewhat sharp, especially in taxa with uneven flanges [see Fig. 61] or rounded [see Fig. 70].

In the light microscope, pegs correspond to thickened corners and the degree of their thickening depends on the length of flange apex from the constituent cells involved in peg formation. The appearance of this feature is influenced by the cell shape and size when compared with peg size. Where corner thickening is particularly extensive and the cells are small, the cell lumina on the inner side of the cuticle may look rounded in the S.E.M. This gives a rather characteristic cell shape and is a

prominent feature in Ravensara elliptica on the abaxial membrane.

12.3.6 FLANGE SCULPTURE

12.3.6a CUTICLE/CELLULOSE WALL INTERFACE AT FLANGE IN T.S.

Light microscopic observations of transverse sections show that the cuticle/cellulose wall interface is often even at the flanges giving no indication of the presence of surface ornamentation. Nevertheless, the boundary may look uneven in some taxa, either in all regions of both sides of the leaf, as in Austrobaileya scandens, Cinnamomum spp. and Hernandia olivacea or just in certain areas, for example in Apollonias arnottii [abx. c.], Cinnadenia paniculata [abx.], Hernandia nymphiifolia [adx.] and Micropora curtisii [abx. c. & adx.].

12.3.6b FLANGE SURFACE IN S.E.M.

The scanning electron microscope reveals that only a restricted number of taxa lack any form of microrelief on their flanges. Usually, if the periclinal surface is unornamented then flanges are smooth also, as in Actinodaphne glomerata [adx.], Licaria spp. [adx. & abx.], Pleurothyrium cuneifolium [abx.] and Systemonodaphne mezii [adx. & abx.] [Fig. 19] although sometimes, flange sculpture is absent when the periclinal region is ornamented, e.g. in Dicypellium caryophyllatum [adx. i.c.] [Fig. 55], Gyrocarpus americanus ssp. americanus [abx. c.] Nectandra salicifolia [adx.] and Ravensara pervillei [adx. & abx.].

Flange ornamentation may be composed of either protrusions, such as in Alseodaphne oblanceolata [Fig. 73], Dehaasia caesia [Fig. 22], Hernandia nymphiifolia [Figs 21, 74] and Laurus spp. [adx. & abx.] [Fig. 42] or of protrusions and depressions, for example, in Austrobaileya scandens [Figs 33, 76], Illigera spp. [Figs 70, 75], Neocinnamomum caudatum [adx. & abx.] [Fig. 77] and Micropora curtisii [abx. c. & adx.] [Fig. 78]. Depressions are often entirely absent from flanges although present in a variety of sizes and forms in all periclinal regions, e.g. in Aiouea

guianensis, Cryptocarya weinlandii and Nothaphoebe heterophylla.

The different patterns of sculpture found on flanges may be described under four headings in the same way as the microrelief of the periclinal surface.

12.3.6b (i) SIZE OF ELEMENTS

Protrusions. These vary in diameter from very fine (less than 0.2 μm , with a minimum of approximately 0.04 μm), for example, in Alseodaphne oblanceolata [adx. & abx.] (Fig. 73), Illigera pentaphylla [abx.] and Urbanodendron verrucosum [adx. & abx.] to very large, with a maximum of 1.5 μm , in Hernandia nymphiifolia on the adaxial (Fig. 74) and large, up to about 0.9 μm , in H. nymphiifolia and Sassafras albidum var. molle, on the abaxial [c.]. Protrusions may sometimes be of similar dimensions on all flanges of both the adaxial and the abaxial cuticles, such as in Aioouea spp. [ca. less than 0.2 μm -0.4 μm] (Fig. 35), Cryptocarya spp. [C. ainikini & C. alleniana: ca. less than 0.2 μm ; C. weinlandii: ca. 0.2 μm or less], Endiandra spp. [ca. 0.2-0.4 μm] and Gomortega keule [ca. 0.2-0.5 μm] or just in all regions of one cuticle, for example, in Caryodaphnopsis spp. [adx. C. baviensis: ca. 0.2-0.5 μm ; C. tonkinensis: ca. less than 0.2 μm -0.4 μm] (Fig. 24), Hernandia nymphiifolia [adx. ca. 0.5-1.5 μm] and Laurus spp. [abx. ca. less than 0.2 μm -0.7 μm] (Fig. 42). Other taxa exhibit differences in flange protrusion size: often flange protrusions are most coarse on the abaxial membrane, as in Austrobaileya scandens [adx. ca. less than 0.2 μm -0.4 μm ; abx. ca. 0.2-0.5 μm], Cinnamomum oliverii [adx. ca. 0.4-0.5 μm ; abx. ca. 0.2-0.7 μm] and Sparattanthelium tupiniquinorum [adx. ca. 0.2 μm or less; abx. ca. 0.2-0.5 μm], although the reverse situation may exist in a few examples, e.g. Illigera spp. [I. pentaphylla: adx. ca. less than 0.2 μm -0.4 μm ; abx. ca. less than 0.2 μm ; I. pulchra: adx. ca. 0.2-0.4 μm ; abx. ca. 0.2 μm or less] (Figs 31, 32) and Neocinnamomum delavayi [adx. ca. 0.5-0.7 μm ; abx. i.c. ca. 0.2-0.5 μm , c. ca. 0.2-0.7 μm]. Where the size of these elements varies between costal and intercostal areas of a cuticle, the largest protrusions

tend to occur on flanges of veins, such as in Litsea umbellata [abx. i.c. ca. 0.2 μm , c. ca. 0.4-0.5 μm], Phoebe opaca [abx. i.c. ca. less than 0.2 μm , c. ca. 0.2-0.4 μm] and Piptocalyx moorei [adx. & abx. i.c. ca. 0.2 μm or less, c. less than 0.2 μm - 0.4 μm]. However, this is not always so, as demonstrated by Cinnadenia paniculata [abx. i.c. ca. less than 0.2 μm - 0.4 μm , c. ca. 0.2 μm or less] and Neolitsea dealbata [abx. i.c. ca. 0.2-0.5 μm , c. ca. 0.2 μm or less], in which the intercostal flanges have the coarsest protrusion elements.

Depressions. These range in size from very fine [less than 0.2 μm , with a minimum of about 0.04 μm], such as in Aiouea saligna [adx.] [Fig. 40], Illigera pentaphylla [adx. & abx.] [Fig. 70] and Micropora curtisii [abx. c. & adx.] [Figs 34, 78] to moderate with a maximum of about 0.4 μm on the adaxial, e.g. some of the cavities in Cinnamomum oliverii [Figs 297,298], Hernandia olivacea [Fig. 61] and Litsea umbellata, and approximately 0.5 μm on the abaxial, as in Austrobaileya scandens and Hernandia olivacea. Occasionally, depressions are of more or less the same size in all regions (i.c. & c.) of cuticles from both sides of the leaf, where they are present, for example in Illigera pentaphylla and Micropora curtisii [see above]. More commonly, similarities in flange depression diameter exist between vein and non-vein areas of one cuticle, either the adaxial or the abaxial, such as in Hernandia olivacea [adx. & abx. see above], Hypodaphnis zenkeri [adx. ca. less than 0.2 μm -0.4 μm], Nothaphoebe umbelliflora [abx. ca. 0.2 μm or less] and Sassafridium macrophyllum [abx. ca. less than 0.2 μm]. There may, however, be differences: sometimes the depressions observed on the adaxial flanges are greatest in size, e.g. in Endiandra spp. [adx. ca. less than 0.2 μm - 0.4 μm ; abx. ca. 0.2 μm or less] and Illigera pulchra [adx. ca. 0.2 μm or less; abx. ca. less than 0.2 μm] [Figs 31, 32]; in others the depressions are coarser on the abaxial flanges, as in Aiouea saligna [adx. ca. less than 0.2 μm ; abx. ca. 0.2 μm or less] Austrobaileya scandens [adx. ca. 0.2 μm or less; abx. ca. 0.2-0.5 μm] and Hernandia olivacea [see above]. Where the depression diameter detected on flanges in inter-

costal regions differs to that on those of costal areas, it is always the latter which possesses the largest flange cavities, for example in Apollonias annottii [adx. i.c. ca. less than 0.2 μm , c. ca. 0.2 μm or less] and Litsea umbellata [abx. i.c. ca. 0.2 μm or less, c. ca. less than 0.2 μm - 0.4 μm].

Where both protrusions and depressions comprise the flange microrelief, it is common for the latter element type to be finer than the former. Occasionally, however, the sculptural components may have similar dimensions, as in Austrobaileya scandens [abx.] (Fig. 76), Cinnadenia paniculata [abx. c.], Cinnamomum iners [abx. i.c.] and Illigera pentaphylla [abx.] or more rarely, depressions may be coarser than protrusions, e.g. in Alseodaphne semecarpifolia [abx. c.] and Phoebe sheareri [abx. i.c.].

12.3.6b (ii) DENSITY OF ELEMENTS. This may vary within and between taxa. Sculpture with little or no separation of the constituent elements [dense] is of frequent occurrence on flanges, such as those of Austrobaileya scandens (Fig. 76), Illigera pulchra (Fig. 75), Neocinnamomum caudatum (Fig. 77) and Piptocalyx moorei (Fig. 41). Widely separated components are characteristic of flanges of some species, for example, Alseodaphne oblanceolata (Fig. 73), Cinnamomum iners, Litsea meissneri and Ocotea laevis [adx.]. Various intermediates in density may be recognised between these two extremes, as on the flanges of Aniba megaphylla [adx.], Endlicheria piriformis [abx.] Laurus spp. [abx. i.c.] (Fig. 42) and Neocinnamomum delavayi [adx. i.c.] (Fig. 23).

Although sculptural density is more or less the same on flanges of both the adaxial and abaxial cuticles in many taxa, e.g. in Hernandia spp. [H. nymphiifolia: some separation, H. olivacea: dense], Mezilaurus lindaviana [widely separated] (Fig. 56) and Trimenia papuana [dense], there are a number in which differences may be detected between the two surfaces, such as Cinnamomum pachyphyllum [adx. widely separated; abx. some separation] and Ocotea laevis [adx. widely separated; abx. dense]. This feature

may also be dissimilar in intercostal and costal regions of a cuticle, particularly on the abaxial, e.g. in Cinnadenia paniculata, Dehaasia caesia and Micropora curtisii [Fig. 43] [i.c. some separation, c. dense]. In some taxa with dense flange microrelief, the costal flanges tend to have especially closely packed elements, as in Aniba megaphylla [abx.] [Fig. 64], Dicypellium caryophyllatum [adx. & abx.] and Lindera pulcherrima [abx.]. Occasionally, the intercostal flanges exhibit this tendency, for example, in Litsea umbellata [abx.] and Piptocalyx moorei [adx. & abx.].

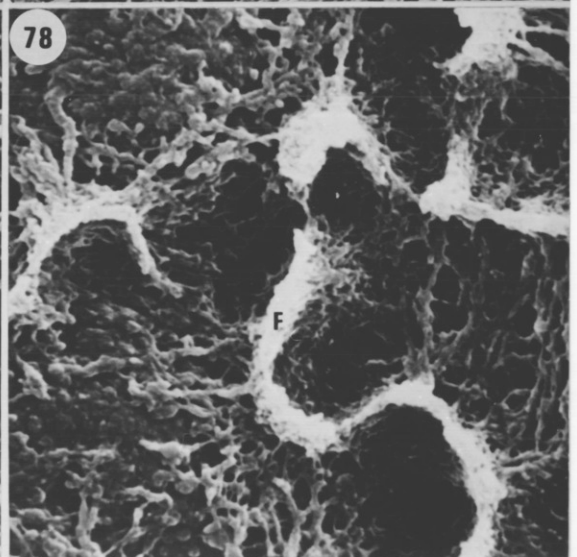
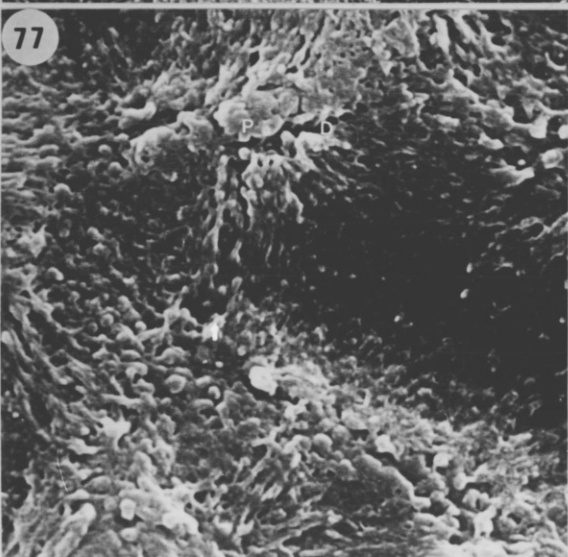
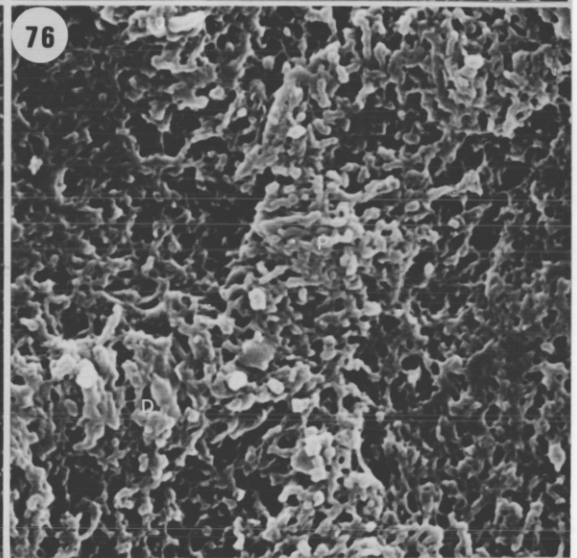
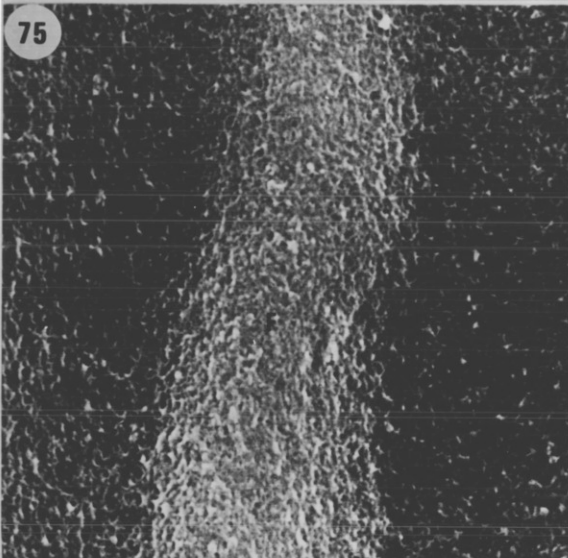
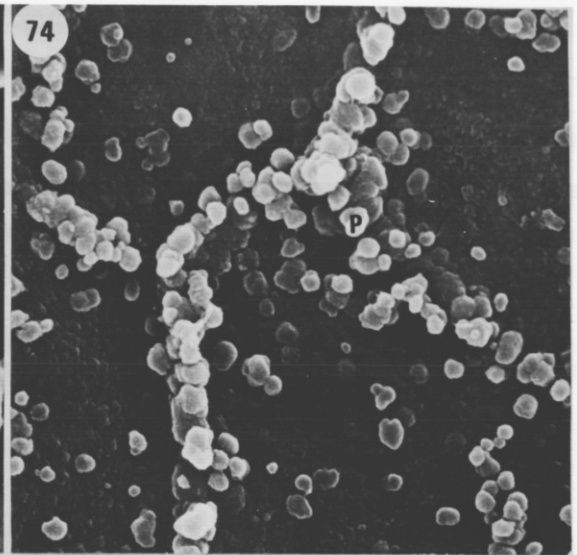
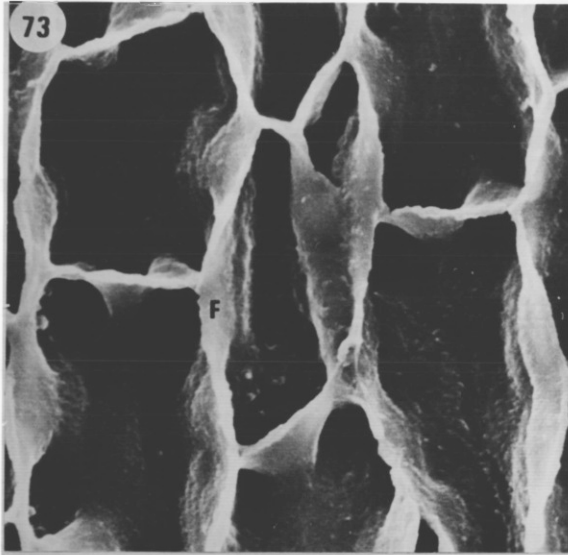
12.3.6b (iii) ARRANGEMENT AND FORM OF ELEMENTS

Protrusions. These may be found in a variety of patterns on the flanges, in the same way as on the periclinal surface of the inner side of a cuticle. Granules occur most frequently alone, as in Endlicheria piriformis [Fig. 20], Gyrocarpus americanus ssp. africanus [Fig. 44] and Urbanodendron verrucosum or less commonly, together either with clumps e.g. on certain flanges in Dicypellium caryophyllatum [abx.] [Fig. 57], Hernandia olivacea [adx. & abx.] [Figs 21, 74], Laurus spp. [adx. & abx.] [Fig. 42] and Trimenia papuana [abx. i.c. & adx.], or with both clumps and reticula, such as in some areas in Dehaasia caesia [abx. i.c.] [Fig. 22], and Trimenia weinmanniaefolia [adx.]. Occasionally, protrusion clumps and reticula may not be accompanied by granules on flanges, for example in regions of Gomortega keule [abx.], Neocinnamomum delavayi [adx.] [Fig. 23] and Trimenia weinmanniaefolia [abx.]. In a number of other taxa, flange protrusions are entirely of the reticulate form, such as those of Austrobaileya scandens [Fig. 76], Hernandia olivacea [Fig. 61], Illigera pentaphylla and Litsea umbellata [adx. & abx.]. Very often, the arrangement of protrusion elements is similar in intercostal and costal areas of cuticles from both sides of the leaf. However, sometimes there are differences. Patterns of protrusions may be more complex on the adaxial flanges than on those of the abaxial in certain taxa, e.g. in Mezilaurus itauba [adx. reticula; abx. granules], and Persea spp. [adx. reticula;

Flange sculpture

Inner surface of isolated cuticles.

73. Alseodaphne oblanceolata. Smooth to very finely granular. Adx. ca. x 2265.
74. Hernandia nymphiifolia. Coarse granules and clumps. Adx. ca. x 2135.
75. Illigera pulchra. Fine reticula and pit-like depressions. Abx. ca. x 4270.
76. Austrobaileya scandens. Coarse reticula and pit-like to clumped depressions. Abx. ca. x 2500.
77. Neocinnamomum caudatum. Filamentous reticula and pit-like depressions. Note radiation of protrusions from undulation sinuses to and over periclinal surface. Abx. ca. x 2160.
78. Micropora curtisii. Filamentous reticula and pit-like depressions. Radiation of protrusions as in Fig. 77. Abx. ca. x 4220.



P. americana: abx. granules - clumps; P. chinensis & P. thunbergii: abx. i.c. granules - clumps, c. granules - reticula) or alternatively, the reverse situation may exist, i.e. with more complicated arrangements on the abaxial flanges than on those of the adaxial, as in Gomortega keule [adx. granules - clumps; abx. clumps - reticula], Nothaphoebe heterophylla [adx. granules; abx. reticula] and Umbellularia californica [adx. granules; abx. granules - clumps]. Where a different pattern of flange protrusions may be detected over veins from that in non-vein areas, it is usual for costal flanges to show the most intricate organisation of protrusion elements, e.g. in Micropora curtisii [abx. i.c. granules - clumps, c. reticula] [Fig. 43], Piptocalyx moorei [adx. i.c. granules - clumps, c. granules - reticula] and Sassafridium macrophyllum [adx. & abx. i.c. granules - clumps, c. clumps - reticula]. There is only one exception, Dehaasia caesia [abx.] with a more complex protrusion arrangement on flanges of intercostal areas [i.c. granules - reticula, c. granules].

On the flanges, wherever protrusions exist as individuals or in aggregates, the elements appear rounded in most taxa. The filamentous form may be detected on all flanges in a few species, Endiandra spp. [Fig. 39], Illigera pentaphylla [Fig. 70] and Neocinnamomum caudatum [Fig. 77]. More usually, thread-like protrusions are confined to certain cuticles or regions of one membrane, as in Austrobaileya scandens [adx.], Illigera pulchra [abx.] [Figs. 32, 75], Litsea umbellata [abx. i.c. & adx.] and Micropora curtisii [abx. c. & adx.] [Figs 34, 78]. Protrusions of a type intermediate between round and filamentous may be observed in a restricted number of taxa, including Austrobaileya scandens [abx.] [Fig. 76], Hernandia olivacea [adx. & abx.] [Fig. 61] Mezilaurus itauba [adx.] and Phoebe opaca [abx. c.).

Depressions. Pit-like cavities are universally present whenever depressions of any sort exist on flanges. Commonly, only this form may be observed in any taxon, as in Aioouea saligna [Fig. 35], Endiandra spp. [Fig. 39],

Hernandia olivacea [Fig. 61] and Illigera spp. [Figs 31, 32, 75]. Sometimes, clumps of pits may also be detected, e.g. in Austrobaileya scandens [abx.] [Fig. 76], Cinnamomum oliverii [adx.] [Figs 297, 298] and Nothaphoebe umbelliflora [abx.]. Reticulate depressions are rarely found on flanges. They occur in association with pits and clumps in one taxon, Neocinnamomum caudatum [abx. i.c. & adx.] [Fig. 77].

It is most usual for flanges of all regions to show a similar organisation of depressions, although there may sometimes be differences. Occasionally, these elements group together to produce more intricate patterns on the flanges of the cuticle of one leaf surface, generally the abaxial, as in Austrobaileya scandens, Mezilaurus itauba and Nothaphoebe heterophylla [adx. pits; abx. pits - clumps] or rarely the adaxial, in Cinnamomum oliverii [adx. pits - clumps; abx. pits]. In other taxa, the form of depressions seen on flanges in vein regions may differ to those of the non-vein areas. Where this is so, the former often displays depressions of a more complex arrangement, for example in Apollonias arnottii [adx. i.c. pits, c. pits - clumps] and Litsea umbellata [abx. i.c. pits, c. pits - clumps]. The reverse situation may be recognised in Neocinnamomum caudatum [abx. i.c. pits-reticula, c. pits to clumps].

Commonly, when the flange sculpture consists of both protrusions and depressions, the latter are organised more simply than the former. There are a few taxa, however, in which the two types of element are arranged to a similar level of complexity, in certain areas of the leaf cuticle, such as in Alseodaphne semecarpifolia, Endlicheria piriformis [abx.] and Neolitsea cassia [abx. i.c.]. More complex organisation of depressions than protrusions is rare and may be observed in only one taxon, Mezilaurus itauba [abx.].

12.3.6b [iv] PROMINENCE OF ELEMENTS. This is variable both within and between members of the assemblage investigated. Sometimes flange protrusions are of low

prominence, barely projecting from the cutin matrix and producing microrelief with a rather flat or smooth appearance, for example, in Alseodaphne oblanceolata [Fig. 73], certain Cinnamomum spp. [C. iners & C. pachyphyllum] [Fig. 25], Lindera strychnifolia [Fig. 63] and Ocotea laevis [adx.]. More frequently, prominent protrusion elements, which distinctly project from the surface and give an uneven topography, are present on flanges, as in Hernandia spp. [particularly H. nymphiifolia] [Figs 21, 74], Laurus spp. [adx. & abx.] [Fig. 42], Neocinnamomum delavayi [adx.] [Fig. 23] and Piptocalyx moorei [adx. & abx.] [Fig. 41]. Species with flange protrusions somewhat intermediate in prominence may also be detected, e.g. Aiouea saligna [adx. & abx.] [Figs 35, 40], Cinnamomum camphora [abx.] and Mezilaurus itauba [adx.].

Protrusion prominence may often be similar on flanges of the adaxial and abaxial cuticles in all regions [i.c. & c.] as in Mezilaurus lindaviana [intermediate], Neocinnamomum caudatum [prominent], Nothaphoebe heterophylla [low] and Trimenia papuana [prominent]. There are, however, a number of examples in which protrusions project to a different degree on the flanges of each of the two membranes, including Alseodaphne semecarpifolia [adx. low; abx. prominent], Aniba megaphylla [adx. intermediate; abx. prominent] and Cinnamomum pachyphyllum [adx. low; abx. intermediate]. Protrusions tend to be of greater prominence on costal flanges than intercostal in many taxa, on both adaxial and abaxial cuticles, as in Cinnamomum camphora and Hypodaphnis zenkeri, or commonly only on one of these, e.g. in Dodecadenia grandiflora, Lindera pulcherrima [adx.] [Figs 65, 66], Litsea umbellata and Piptocalyx moorei [abx.]. Occasionally, protrusions are more prominent on flanges of intercostal rather than costal areas, particularly on the abaxial, such as in Austrobaileya scandens, Cinnadenia paniculata and Neocinnamomum caudatum.

Protrusion elements are often of similar prominence over the entire flange surface in a taxon. However, a number of species exhibit especially prominent protrusions

at the flange base. The phenomenon may be found on all flanges in only one taxon, Endlicheria piriformis (Fig. 20). Usually it is characteristic of those of either the adaxial or the abaxial membrane, for example, in Dicypellium caryophyllum (abx.) (Fig. 57), Laurus spp. (abx.), certain Persea spp. [P. americana & P. chinensis: adx.] (Fig. 58) and Sassafridium macrophyllum (abx.) or sometimes also flanges in one region of the other cuticle, as in Caryodaphnopsis tonkinensis, Dehaasia caesia and Micropora curtisii (abx. c. & adx.) (Fig. 78).

Depressions tend to look deep, whenever present. They may appear of similar depth on flanges of both membranes, in Litsea umbellata or sometimes deeper on the abaxial than the adaxial, e.g. in Austrobaileya scandens and Cinnamomum pachyphyllum. This aspect, however, is difficult to assess for reasons already described on p. 140.

The configuration observed on flanges may be similar in all respects to that seen on the periclinal surface in a range of taxa. Occasionally, this similarity is exhibited by intercostal and costal regions of the cuticle from both leaf surfaces, e.g. in Actinodaphne glomerata, Licaria spp., Litsea meissneri and Systemonodaphne mezii. More commonly, however, patterns are more or less the same on flanges and in the periclinal area on either the membrane of one side of the leaf, generally the adaxial e.g. in Aniba megaphylla, Austrobaileya scandens, Hernandia olivacea (Fig. 61) and Phoebe sheareri or only in certain regions, of one cuticle, as in Dehaasia caesia (abx. i.c.), Hernandia nymphiifolia (adx. c.) (Fig. 21), Neolitsea dealbata (adx. i.c.) and Ocotea laevis (abx. c.) or rarely, of both membranes, for example, in Eusideroxylon zwageri (abx. c. & adx.) (Fig. 48) and Piptocalyx moorei (adx. & abx. i.c.) (Fig. 41).

12.3.6c SCULPTURAL DIFFERENCES BETWEEN FLANGE AND PERICLINAL SURFACES

A wide variety of differences may be detected, mainly involving size and arrangement as well as form of the constituent elements. Dissimilarities may often only be

detected in one type of sculptural component, particularly protrusions (p.), for example in Austrobaileya scandens [abx. flange p. coarser & less filamentous] (Fig. 76), Dehaasia caesia [adx. & abx. flange p. finer; abx. c. & adx. simpler], Gyrocarpus americanus (ssp. africanus: abx. c. flange p. finer; ssp. americanus: adx. coarser), Illigera pulchra [adx. flange p. less filamentous & simpler; adx. & abx. coarser] (Figs 31, 32, 75) and Laurus nobilis [adx. c. & abx. flange p. finer; adx. i.c. coarser; adx. simpler; abx. more complex] (Fig. 42). Differences in aspects of depressions (d.) occur in Endiandra spp. [abx. flange d. finer, adx. & abx. simpler] (Fig. 39) and Litsea umbellata [adx. flange d. finer; abx. c. finer & simpler]. Sometimes, both element types show dissimilarities, such as in Endlicheria piriformis [adx. flange p. coarser; abx. d. finer & simpler], Hernandia olivacea [abx. flange p. coarser & less filamentous; abx. i.c. d. coarser, abx. c. simpler], Illigera pentaphylla [adx. flange p. coarser, d. finer] and Neocinnamomum caudatum [abx. i.c. flange p. more complex & filamentous; adx. i.c. more filamentous; abx. d. coarser; abx. i.c. & adx. more complex] (Fig. 77).

12.4 CHARACTERS OF NON-SPECIALISED CELLS: MISCELLANEOUS

12.4.1 EXTENT OF LIGNIFICATION

The non-specialised epidermis is not lignified in various Lauraceae such as species of Beilschmiedia, Dehaasia, Endiandra and Ravensara and related families, for example, Austrobaileya scandens, Gomortega keule and Piptocalyx moorei.

However, lignin is found throughout the epidermis in a few taxa, occasionally on the adaxial only, as in Licaria triandra, or more commonly, on either the abaxial only, e.g. in Aniba megaphylla, Illigera pentaphylla and Trimenia weinmanniaefolia or on both leaf surfaces, as in Mezilaurus spp. and Micropora curtisii.

It is also rather rare for lignification to be present in the outer periclinal wall area, according to results of staining transverse sections, particularly on the adaxial side, where lignin occurs in just two Lauraceae, Cryptocarya ainikini and Endlicheria piriformis. On the abaxial, the outer periclinal wall is lignified in these examples, Laurus spp. and Litsea meissneri as well as the papillae of Caryodaphnopsis spp.

More frequently, however, the epidermal inner periclinal wall exhibits evidence of lignification (mainly in Lauraceae). This may often occur on both sides of the leaf, such as in species of Actinodaphne, Cinnamomum (not C. camphora), Lindera and Nectandra.

The lower regions of the epidermal anticlinal wall may stain positively for lignin in certain Lauraceae taxa, predominantly on the adaxial surface, as in Alseodaphne oblanceolata, Laurus canariensis and Persea thunbergii, but sometimes on both sides, e.g. in Cinnamomum spp. (not C. camphora) and Persea chinensis or very rarely on the abaxial only, such as in Phoebe spp. All examples showing this pattern of lignification also have lignin in the inner periclinal wall. It may, in addition, be present in the upper part of the anticlinal wall of subepidermal

cells in some Lauraceae members when it occurs in the inner periclinal wall, e.g. in Dicypellium caryophyllum [adx.], Lindera strychnifolia [abx.] and Nectandra pichurim [adx. & abx.]. The entire hypodermis is lignified in just two taxa, Pleurothyrium nobile and Potameia crassifolia.

12.5 CHARACTERS OF SPECIALISED CELLS: STOMATA

12.5.1 GENERAL CHARACTERS

12.5.1a TYPE

In most taxa, stomata are paracytic, with a pair of subsidiary cells [one on either side] orientated parallel to the long axis of the pore and to the guard cells. Isolated cuticles of Lauraceae members show just the subsidiary cell outlines and vestiges of the guard cells [cutinised portion only] whilst in others both guard cells and subsidiary cells are more or less distinctly marked. In Austrobaileya scandens [Text-Fig. 21A], stomata may be described as anomocytic since subsidiary cells are not distinguishable in surface view [Fig. 83].

12.5.1b DISTRIBUTION

Generally, stomata are confined to areolae and occasionally veins of the abaxial leaf surface. However, in Eusideroxylon melagangai stomata are also present on the adaxial side [see Fig. 95].

12.5.1c ARRANGEMENT

Stomata are randomly distributed in all leaf specimens.

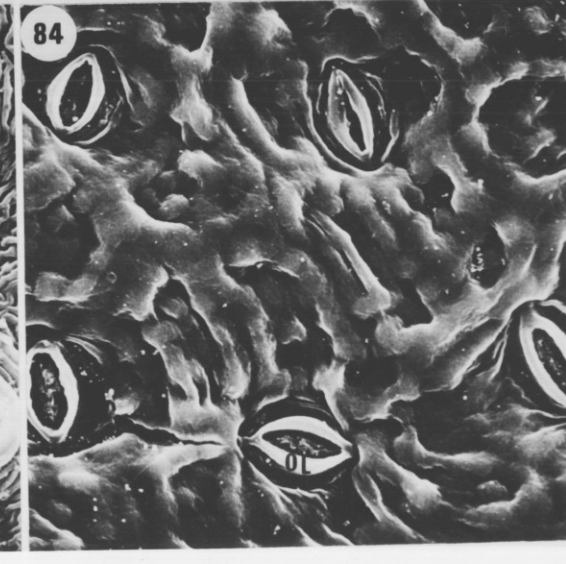
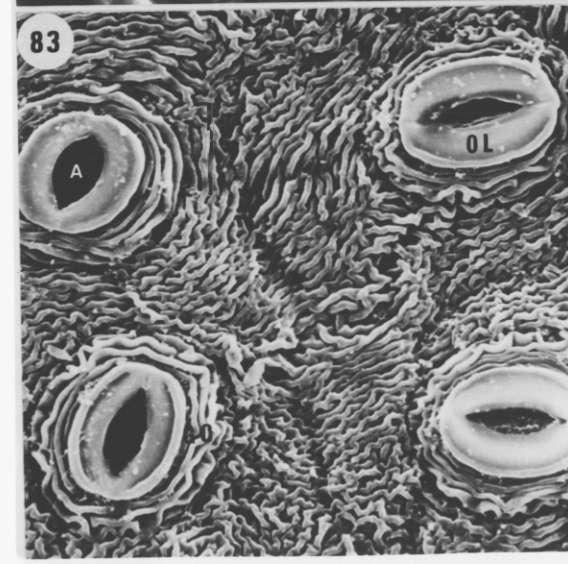
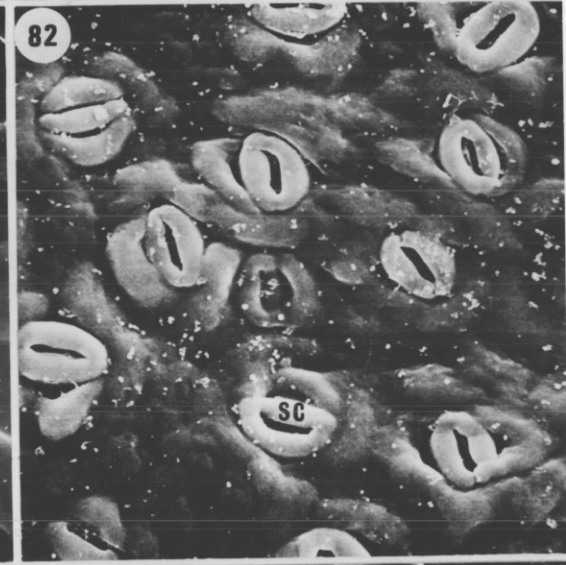
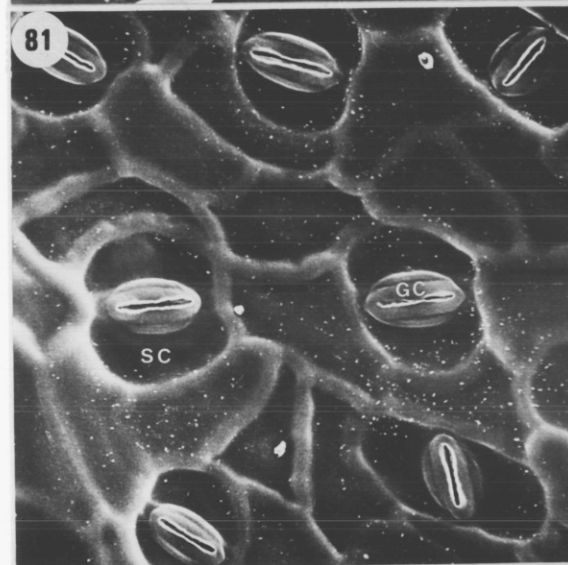
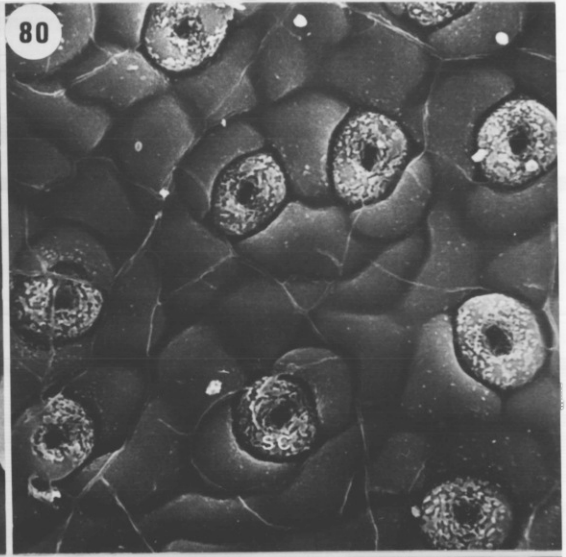
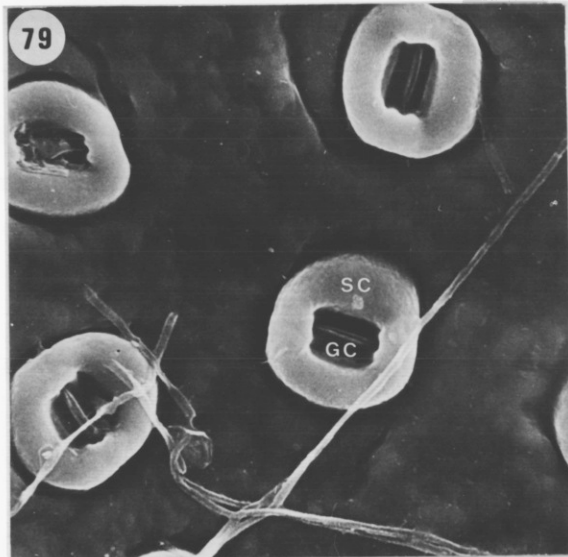
12.5.1d DENSITY/FREQUENCY

The number of stomata per unit area differs from one taxon to another. For the abaxial surface average values range from 121.8/mm², in Austrobaileya scandens to 1081.7/mm², in Cinnamomum iners. Most commonly, averages fall between 290.0 and 870.0/mm². Only a few taxa, e.g. Endiandra spp. have more frequent stomata. Those of members of the Austrobaileyaceae, Gomortegaceae, Trieniaceae and Hernandiaceae [except Hernandia spp. and Sparattanthelium spp.] have the lowest average number per unit area [less than 290/mm²]. Eusideroxylon melagangai, with stomata on both sides of the leaf, has a very low frequency [43.5/mm²] on the adaxial and considerably greater [461.1/mm²] on the abaxial. There appears to be a correlation between stomatal size, dimensions of intervening cells and stomatal frequency/density. Stomata

Stomata: Lauraceae and related families

Outer surface: Low power.

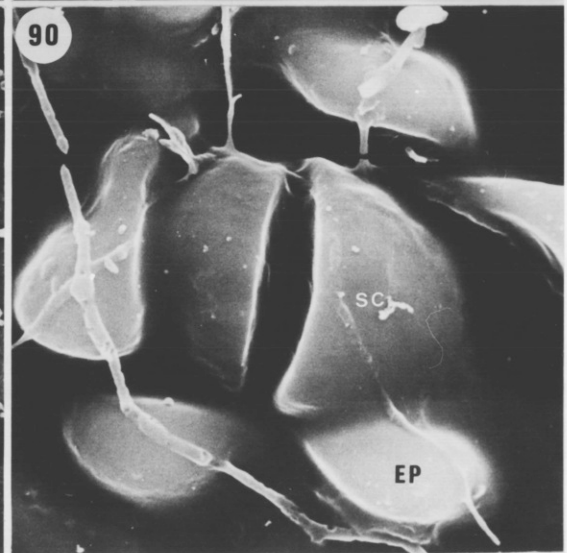
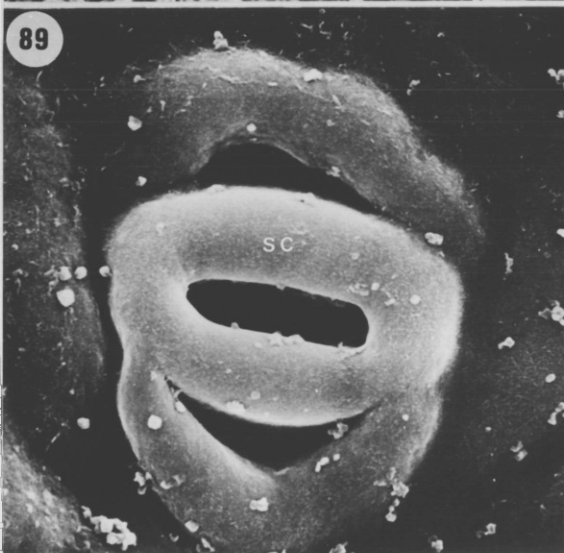
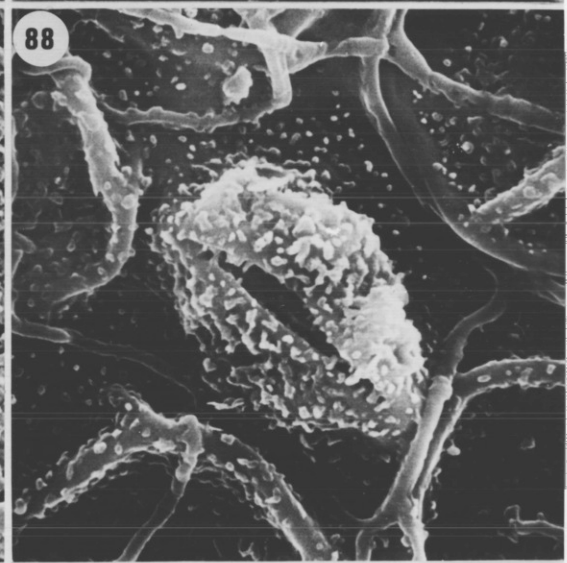
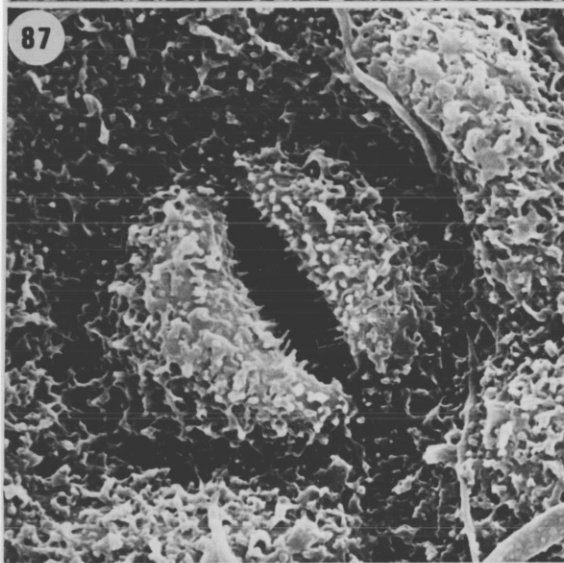
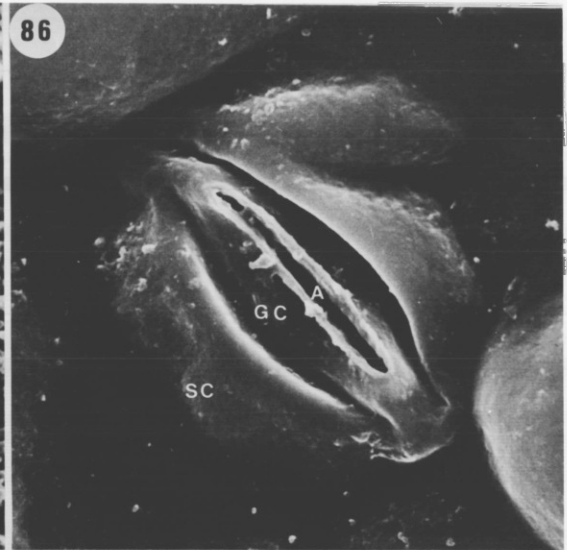
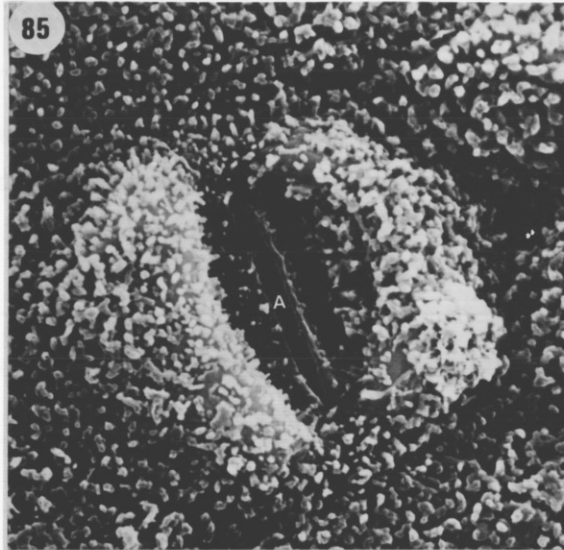
79. Endlicheria piriformis. Stomata with subsidiary cells [SC] showing apparent fusion at poles, resulting in ring configuration. Stomatal pit slightly longer than wide, with tridentate ends. Guard cell cuticle [GC] visible in pit. Stomata large compared with E. reflectens (Fig. 80) and other Lauraceae (e.g. 81, 82). ca. x 525.
80. Endlicheria reflectens. Stomata of similar arrangement to those in Fig. 79. Wax flakes concentrated on surface of subsidiary cells [SC]. Note common occurrence of reniform cells adjacent to subsidiary cells. ca. x 520.
81. Mezilaurus lindaviana. Stomata with shallow, oval stomatal pit exposing comparatively wide outer ledge and narrow periclinal cuticle of guard cell [GC]. Subsidiary cell cuticle sunken in preparation (low domed in leaf). ca. x 515.
82. Aiouea saligna. Stomata with variable degree of apparent fusion of subsidiary cell poles: none (top left), partially (centre left) and entirely (top right). Note long, narrow stomatal pit and reniform cells either side of subsidiary cells. ca. x 520.
83. Austrobaileya scandens. Stomata of the anomocytic type (guard cells only distinguishable). Smooth outer ledge [OL] prominent. Periclinal surface of guard cell [GC] with undulate concentric striae (folds). Stomata very large. ca. x 535.
84. Gomortega keule. Stomata with distinct outer ledge [OL], concentric striae on guard cell cuticle and lateral folds on subsidiary cell cuticle. ca. x 525.



Stomata: Lauraceae

Outer surface: abaxial.

85. Sassafras albidum var. molle. Stoma with apparently discrete subsidiary cells and shallow elongated oval stomatal pit. Guard cell periclinal surface, narrow outer ledge and aperture [A] visible through pit opening. Note abundant wax granules on subsidiary cells, few on guard cells. ca. x 2125.
86. Neocinnamum caudatum. Stoma with similar configuration to that of Fig. 85; stomatal pit shallower so guard cell cuticle [GC] particularly clear. Note prominent band bounding aperture [A] due to erect outcurved outer ledge. ca. x 2090.
87. Litsea umbellata. Stoma comprising apparently discrete domed subsidiary cells overhanging and obscuring guard cells in pit. Note wax rodlets projecting outward into stomatal pit. Wax abundant. ca. x 2180.
88. Beilschmiedia micrantha. Stoma similar to that illustrated in Fig. 87. Stomatal pit opening narrower but outer ledge of guard cell [upper right] just visible. Note wax covering [granules] and fungal hyphae. Compare with stoma of B. madang. [Figs. 217-222]. ca. x 2000.
89. Alouea saligna. Stoma [see also Fig. 82 low power], with ring-like subsidiary cells, elongate stomatal pit and reniform cells either side of subsidiary cells. ca. x 2090.
90. Phoebe sheareri. Stoma similar to that of Fig. 87. Surrounding cells with papillae [EP]. Note absence of wax. ca. x 2150.



96. Eusideroxylon melagangai. Abaxial stoma. With similar form to adaxial stoma (Fig. 95). Stomatal pit clearly visible including guard cell periclinal surface (GC) and outer ledge (pale narrow rim) around aperture (A). Note difference in size of stoma on two surfaces: smaller on abaxial. ca. x 2170.

Stomata: Lauraceae

Outer surface.

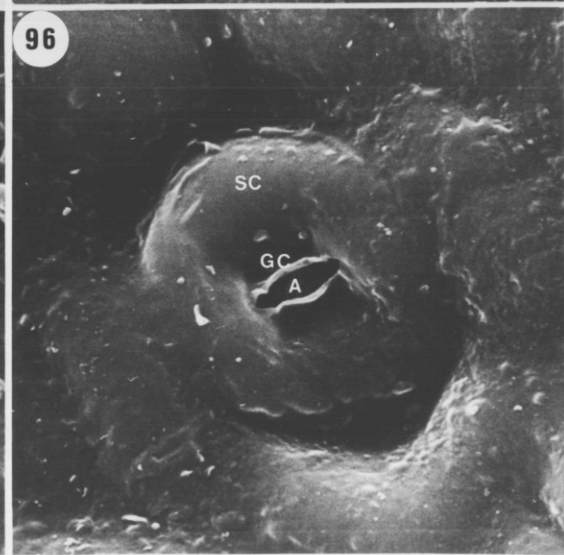
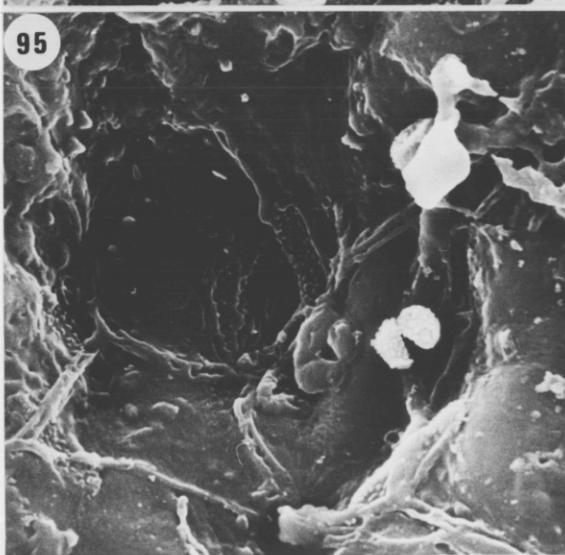
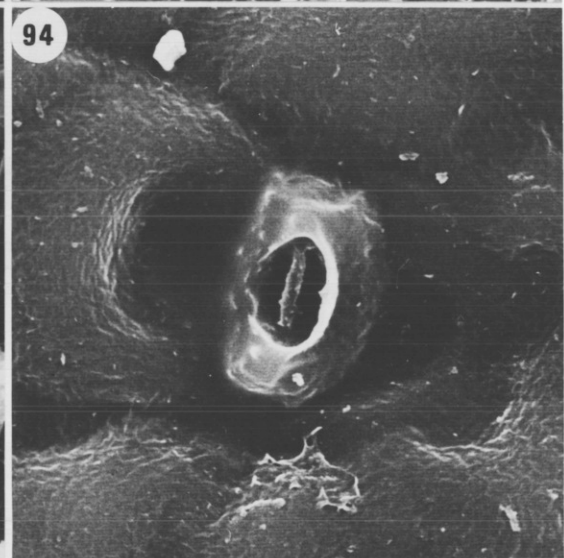
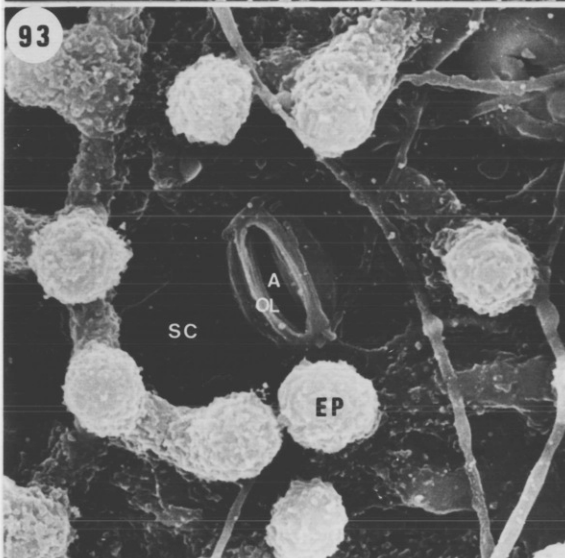
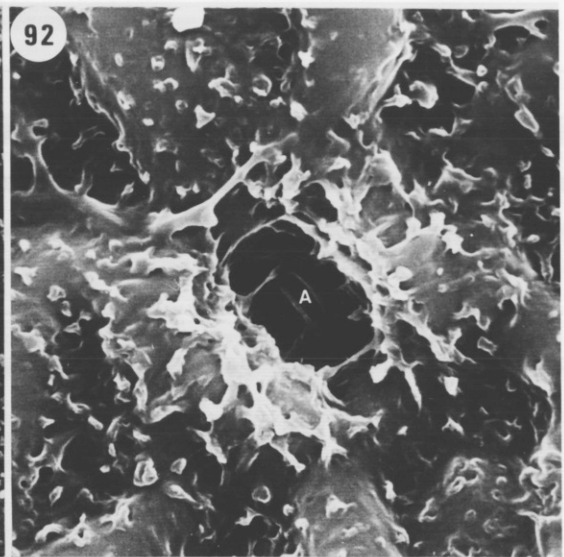
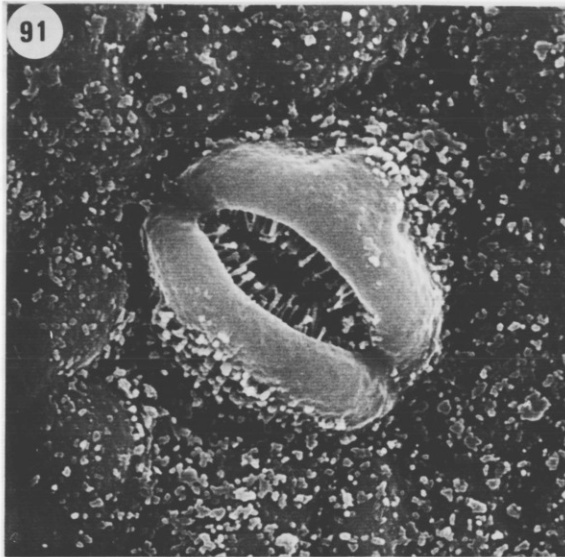
91. Dodecadenia grandiflora. Stoma with subsidiary cells apparently partially fused at poles. Guard cells hidden by overhanging subsidiary cells and wax rodlets projecting from pit walls. Note absence of wax on subsidiary cell periclinal domes; elsewhere with wax granules. ca. x 2150.

92. Alseodaphne semecarpifolia. Stoma with subsidiary cells forming a ring configuration. Stomatal pit relatively deep, but wide with only edges of guard cell periclinal cuticle obscured. Therefore, guard cells and aperture [A] visible in surface view. Note insoluble wax form after dewaxing and maceration. ca. x 2120.

93. Phoebe opaca. Stoma with subsidiary cells [SC] as in Fig. 92. Stomatal pit especially shallow. Guard cell cuticle, prominent outer ledge [OL] and aperture [A] distinct in surface view. Subsidiary cells with very low periclinal dome [not clear in this figure]. Surrounding cells papillate. Compare with Fig. 90. ca. x 2130.

94. Cryptocarya weinlandii. Stoma similar to Fig. 92, domes of subsidiary cells forming an elongate ring. Stomatal pit slightly longer than broad showing guard cell cuticle. Outer ledge narrow, appearing as single unit. Note reniform cells adjacent to subsidiary cells. ca. x 2055.

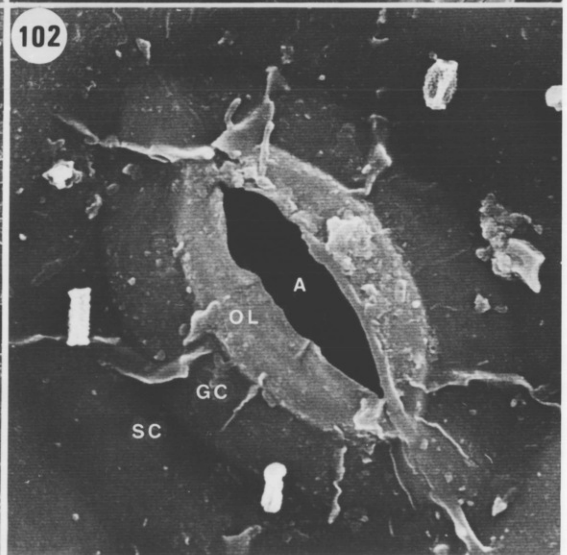
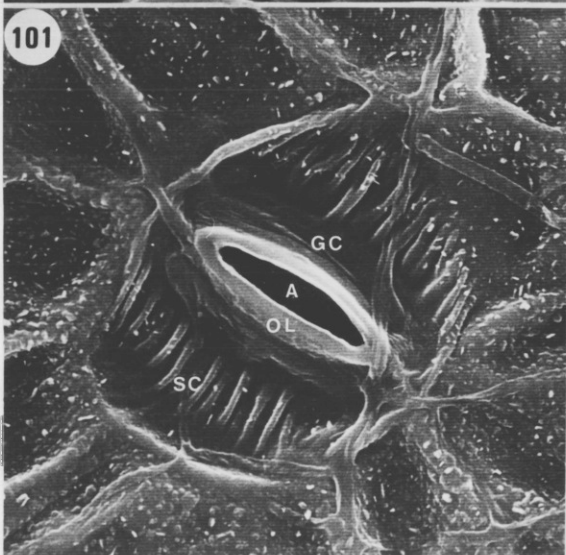
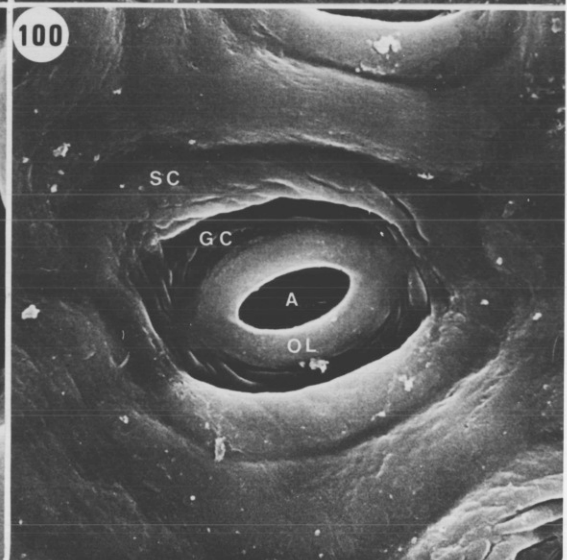
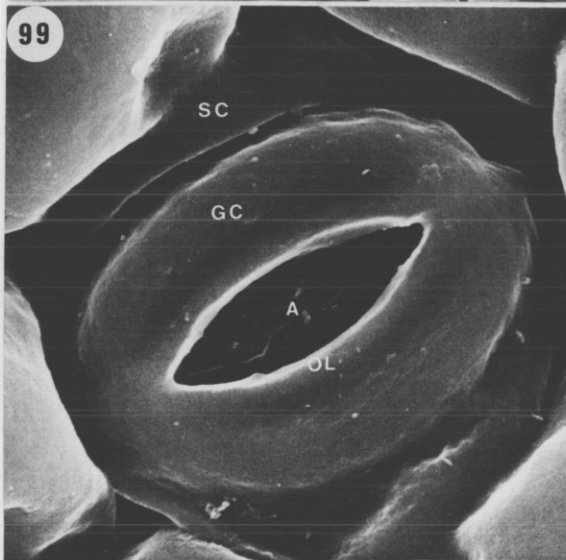
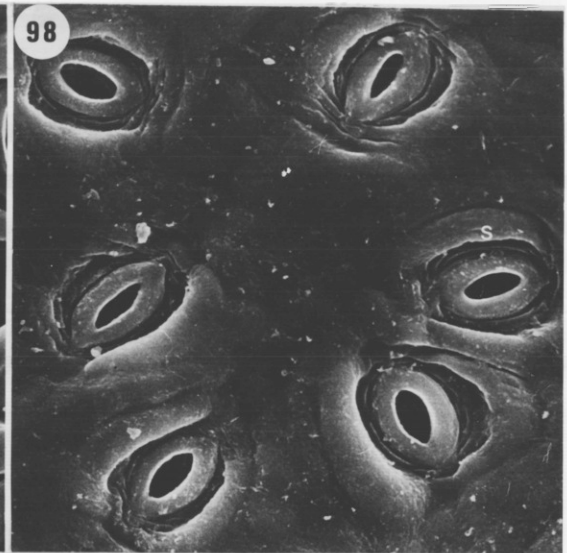
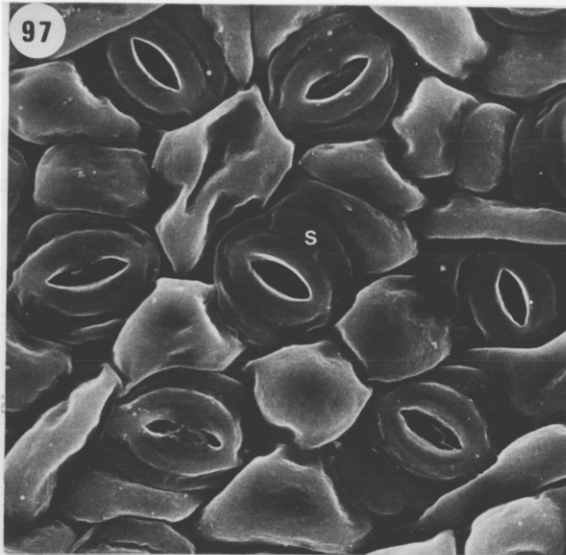
95. Eusideroxylon melagangai. Adaxial stoma. With subsidiary cells [SC] forming a ring configuration. Stomatal pit very shallow; width equal to length; tridentate at polar ends. Specimen with high level of fungal contamination resulting in occlusion of pit. ca. x 2210.



Stomata: Hernandiaceae

Outer surface.

97. Hernandia nymphiifolia. ca. x 540.
98. Hernandia olivacea.
General view. ca. x 535.
- 99-102. Fine details of stoma.
99. Hernandia nymphiifolia. Guard cells [GC] slightly sunken below subsidiary cells. Outer ledge [OL] narrow. Guard cell and subsidiary cell periclinal surface non-striate [smooth]. Note presence of poral lips through aperture opening. Subsidiary cells narrow, domed; periclinal surface sometimes collapsed. ca. x 2185.
100. Hernandia olivacea. Guard cells [GC] sunken below subsidiary cells. Outer ledge [OL] around aperture [A] wide. Guard cell and subsidiary cell periclinal surface with concentric striae. Stomatal pit oval. ca. x 1060.
101. Illigera pentaphylla. Guard cells [GC] raised above subsidiary cells. Outer ledge [OL] comparatively wide. Guard cell periclinal surface non-striate, subsidiary cells with prominent lateral striae. Stomatal cells flat. ca. x 1080.
102. Illigera pulchra. As in Fig. 101. Outer ledge [OL] wide. Guard cell and subsidiary cell surface non-striate, flat. ca. x 2140.



tend to be more frequent per unit area when they and the cells between them are small.

Within a taxon, stomatal frequency shows greater variation when there are more than 580.0 stomata/mm², for example in Phoebe shearerii [768.5-1000.5-1276.0/mm²] than when there are fewer, as in Piptocalyx moorei [87.0-130.5-159.5/mm²].

12.5.1e STOMATAL INDEX

This, $\left[\frac{S}{E+S} \times 100\%\right]$, expresses stomatal frequency independently of the size of the intervening epidermal cells [Salisbury, 1927] and also shows interspecific differences.

Average abaxial values vary from 7.8, in Ravensara aromatica to 25.8, in Hernandia nymphiifolia, with most taxa possessing stomatal indices between 10.0 and 10.9. Only a few have values less than 10.0 e.g. in Eusideroxylon spp. E. melagangai has a particularly low index for adaxial stomata [0.7], about twelve times smaller than the average for the abaxial [8.5].

The range of values of stomatal index for a taxon may be greater in some than in others. For example, 9.0-10.4-12.0 in Cryptocarya weinlandii, 14.0-17.9-21.0 in Dodecadenia grandiflora and 19.0-25.0-30.0 in Illigera pulchra. These ranges tend to overlap so that averages are most useful for comparison of taxa. In general, values for stomatal index appear to be more variable within a taxon than stomatal frequency. Taxa with a low number of stomata per unit area do not necessarily have low stomatal indices, for example, Austrobaileya scandens possesses the lowest average frequency with an average index value of 13.0 [minimum 7.8]. Sometimes those with many stomata/mm², such as Cinnamomum iners [37.3] show some of the highest stomatal indices [24.4], but they may, e.g. Pleurothyrium cuneifolium [32.3/mm²] have a value more in the middle range [14.6].

12.5.1f SIZE

Since the full extent of the guard cells is not represented in the cuticles in Lauraceae stomatal size cannot be determined in isolated membranes. However, comparison of the area bounded by the subsidiary cells in surface view, indicates that the stomatal apparatus varies in size. Approximate diameters range from small [11-20 μm], as in Phoebe sheaeri through medium [21-30 μm], e.g. Eusideroxylon spp. and large [31-40 μm] such as in Endlicheria piriformis, to very large [41-50 μm], e.g. in Trimenia spp. The size of the stoma itself is, of course, likely to be closely correlated with the overall size of the stomatal apparatus [see p.188]. Most Lauraceae members have either small or medium sized stomata, Hernandiaceae exhibit medium or large, Gomortegaceae large only and Trimenaceae very large stomata.

12.5.1g NUMBER OF STOMATA IN CONTACT

In some taxa, the subsidiary cells are always separated by one or more ordinary epidermal cells so that they never come in contact with subsidiary cells of other stomata, for example in Aiouea saligna [Fig. 82], Illigera pentaphylla [abx.] and Eusideroxylon melagangai [adx. & abx.]. Subsidiary cells, in others, abut onto those of adjacent stomata with varying frequency per unit area.

This phenomenon may be rather rare in occurrence (most to 50% areas examined lacking stomata in contact) in some taxa. In these, when subsidiary cells are adjacent, between one [Beilschmiedia micrantha, av. 0.06] and four [Hernandia olivacea: av. 0.94] stomata per unit area [1.8 mm^2] are contiguous. Where the feature occurs more regularly [greater than 50% to 75% areas examined with stomata in contact] up to three [Beilschmiedia madang: av. 1.00], four [Phoebe sheareri: av. 1.18], five [Litsea meissneri: av. 2.12] and six [Cryptocarya alleniana: av. 2.25] stomata may be found with subsidiary cells adjacent per unit area. In a number of taxa most [more than 75%] areas examined show some stomata in contact, between one and four [in 1.8 mm^2], e.g. in Ravensara

elliptica (av. 1.62) and up to five, as in Persea chinensis (av. 2.00). A few exhibit contiguous subsidiary cells in all areas, e.g. Endiandra spp. Such taxa may have one to six stomata in contact/unit area, as in Hernandia nymphiifolia (av. 3.31); two to seven, e.g. in Trimenia weinmanniaefolia (av. 3.87); up to eight, as in Potameia crassifolia (av. 4.44) and two up to as many as ten, e.g. in Endiandra kingsiana (av. 5.37).

As one might expect, this feature may depend somewhat on stomatal frequency.

12.5.1h PRESENCE OF GIANT STOMATA

Especially large stomata (1.5 to 2.5 times the size of ordinary stomata) are of common occurrence in the areolae of many taxa. They may be distinctly separated from surrounding stomata by a clear area or 'zone of inhibition' (sensu Bunning, 1956), as in Eusideroxylon melagangai (Fig. 103) and Sparattanthelium tupiniquorum (Fig. 104). Apart from their abnormally large size, these 'giant' stomata resemble the ordinary type in both internal and external structure and organisation.

12.5.1i VEIN STOMATA AND ABNORMAL STOMATA

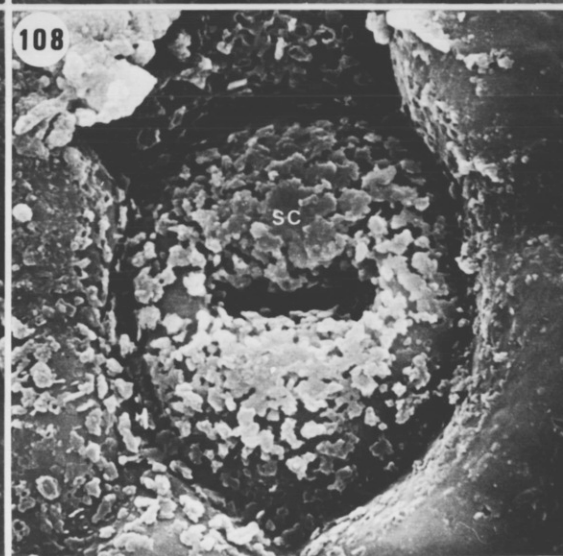
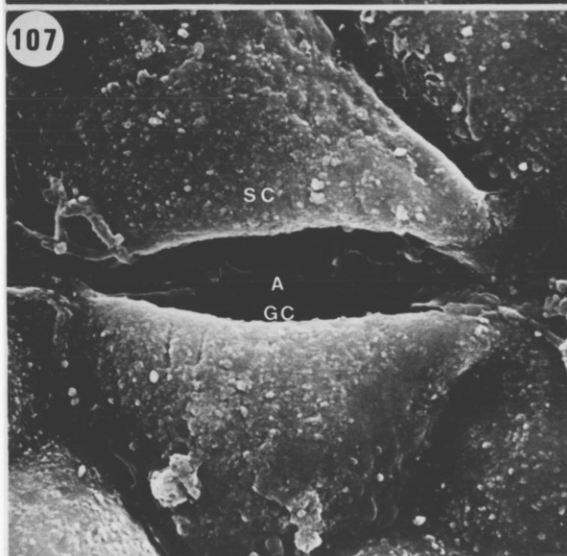
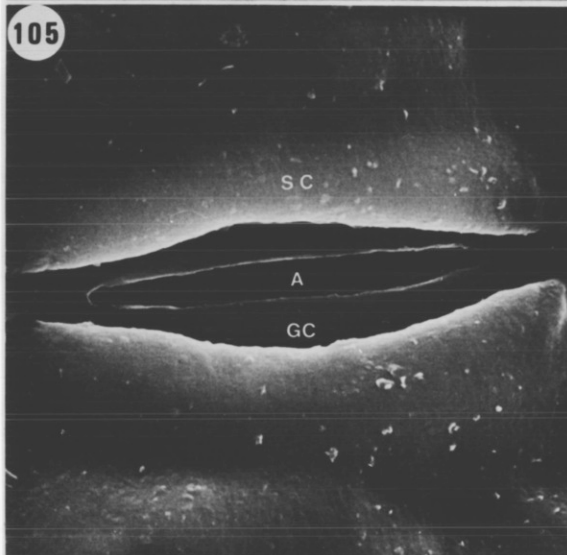
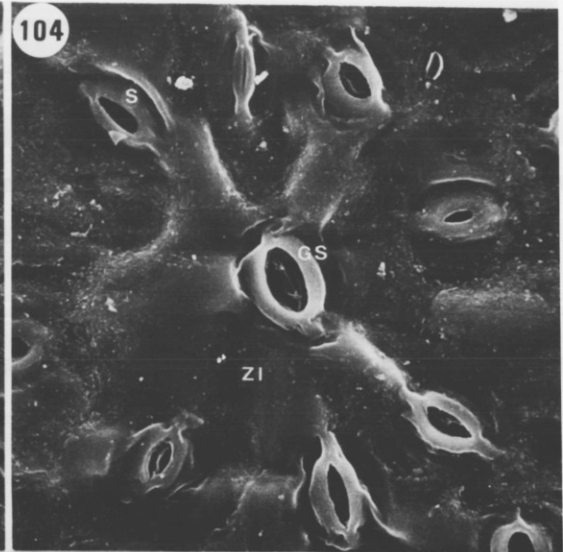
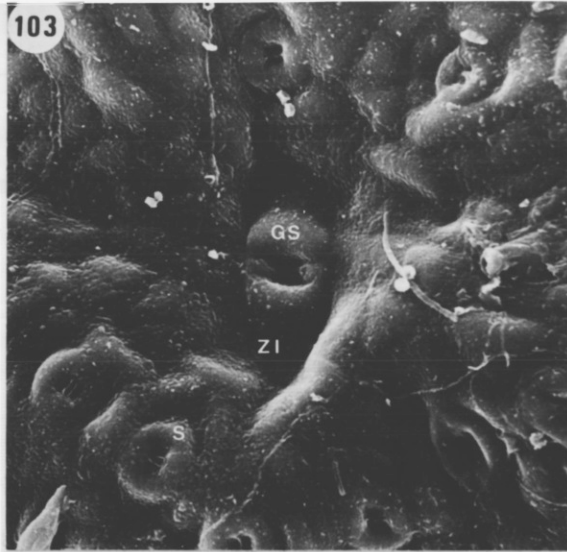
Large stomata are present in every taxon over and very close to veins, particularly minor ones. They are variable in appearance and are sometimes rather unlike ordinary stomata, for example in Ocotea laevis (Figs 107, 108) and Sassafridium macrophyllum (Figs 105, 106), where the curvature of subsidiary cells is markedly different. Distribution of such stomata in costal regions probably depends on proximity to photosynthetic tissue and absence or poor development of mechanical tissue beneath the epidermis. It is, thus, not surprising that costal stomata occur more frequently on minor veins than on major.

Abnormal stomata, which have probably resulted from incomplete development, are also commonly found. These are often represented in cuticles, as two pairs of elliptical cells (presumably two central guard cells and two lateral subsidiary cells) with no visible aperture.

Stomata: giant and vein types

Outer surface.

103. Eusideroxylon melagangai. ca. x 560.
104. Sparattanthelium tupiniquinorum. ca. x 535.
Intercostal area showing giant stoma (GS) separated from ordinary stomata (S) by clear region or 'zone of inhibition' (ZI). Note that apart from abnormally large size (1.5 to 2.0 times size of ordinary stomata), giant stoma resembles ordinary type.
105. Sassafridium macrophyllum. Vein stoma. Subsidiary cells (SC) apparently discrete at poles; periclinal surface slightly domed with scattered wax granules. Guard cells visible in elongate elliptical stomatal pit. Aperture (A) conspicuous. ca. x 2040.
106. Sassafridium macrophyllum. Ordinary stoma. Subsidiary cells (SC) apparently fused at poles giving ring configuration; periclinal domes prominent, waxy (flakes) with distinct boundary (sunken) between surrounding ordinary cells. Guard cells barely visible in elongate parallel-sided stomatal pit. Aperture inconspicuous. ca. x 2140.
107. Ocotea laevis. Vein stoma. Similar to form shown in Fig. 105. Subsidiary cell periclinal surface of greater curvature, with faint lateral striae. Anticlinal borders between subsidiary and surrounding cells more distinct. ca. x 2120.
108. Ocotea laevis. Ordinary stoma. Similar to configuration in Fig. 106. Stoma different shape to vein stoma. Wax form dissimilar, of platelets rather than granules. ca. x 2090.



TEXT-FIGURE 12. Diagrams showing the stomatal organisation in members of families related to Lauraceae and the terminology used throughout the study. [For abbreviations see p. 94, 95].

A. Transverse section of half stoma.

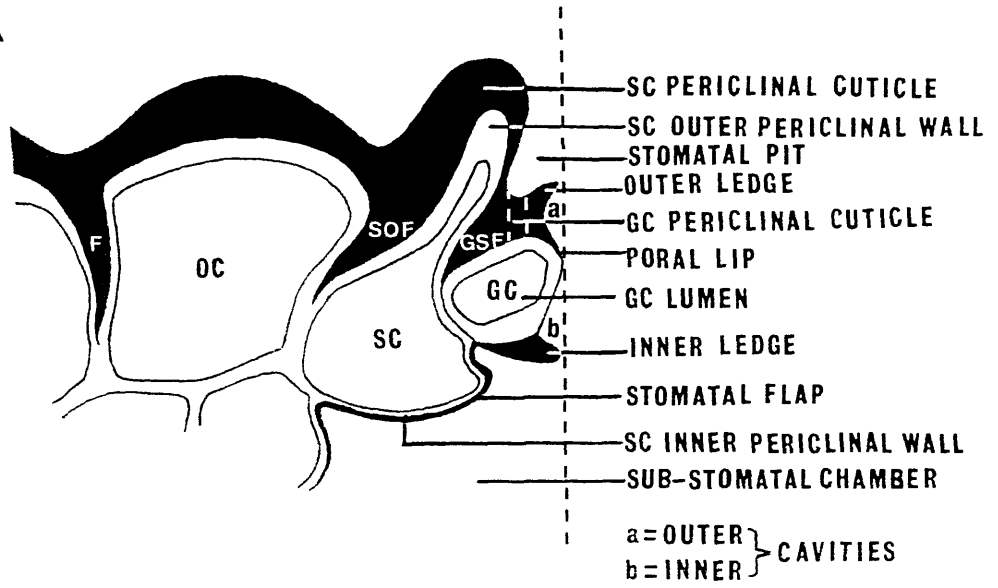
B. Inner surface view of half stoma.

TEXT-FIGURE 13. Diagrams showing the stomatal organisation in Lauraceae and the terminology used throughout the study. [For abbreviations see p. 94, 95].

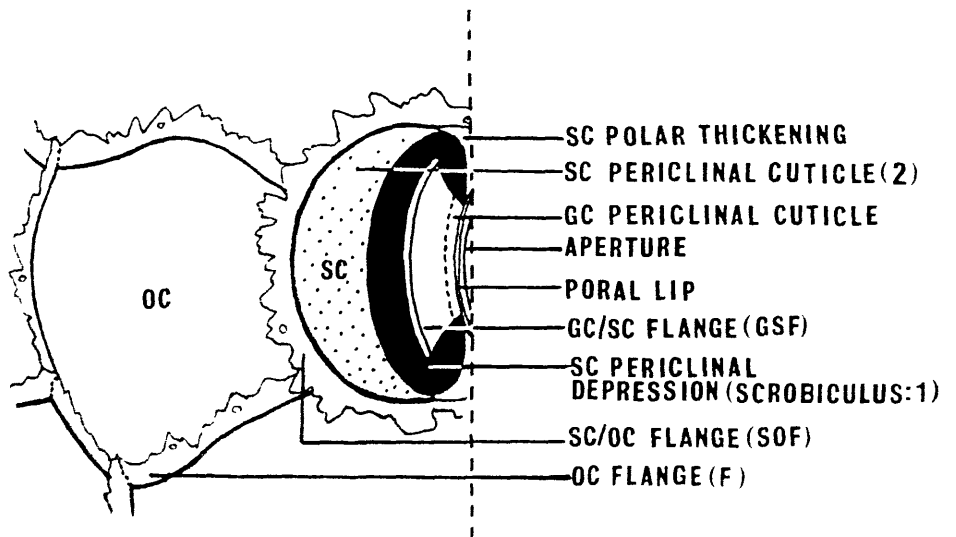
A. Transverse section of half stoma.

B. Inner surface view of half stoma.

A



B



In Lauraceae members, such stomata contrast greatly with the ordinary type composed of a pair of subsidiary cells with the cutinised portion of the guard cells located centrally on either side of a distinct pore.

12.5.2 GUARD CELL CHARACTERS

12.5.2a SIZE IN T.S.

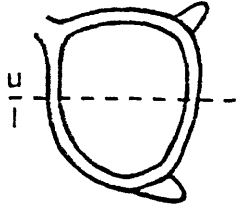
When viewed in transverse section, guard cells vary in size. They range individually in diameter from very small [3.6-4.9 μm], as in Phoebe sheareri to very large, [14.7-15.9 μm], e.g. in Austrobaileya scandens [Text-Fig. 21A]. The majority of Lauraceae have guard cells of small diameter, each between 4.9 μm and 9.8 μm [see Text-Figs 23A, 24]. A few taxa exhibit larger dimensions up to 11.0 μm , such as Mezilaurus itauba and Neocinnamomum caudatum [Text-Fig. 23B]. Guard cells of adaxial stomata in Eusideroxylon melagangai are greater in size [i.e. in the range 9.8-11.0 μm] than those of the abaxial [7.3-8.6 μm]. Most Hernandiaceae and all Trimeniaceae [see Text-Fig. 22B] have guard cells between 8.6 μm and 11.0 μm in diameter. Hernandia olivacea [Text-Fig. 22A] and Gomortega keule, exhibit even larger dimensions [diameter up to 12.2 μm].

12.5.2b EXTENT OF WALL THICKENINGS

The outer and inner walls of guard cells may be variously thickened as seen in thin median transverse sections [see Text-Fig. 14]. Three main patterns are observed: involving very little thickening, so that any wall is no greater than 1/3 guard cell radius, e.g. in Lindera spp., moderate thickening, with a wall between 1/3 and 2/3 radius, as in some Persea spp. [P. americana & P. chinensis] and massive thickening, in which the wall thickness is greater than 2/3 radius of the guard cell, e.g. in Hernandia spp. [Text-Fig. 22A]. Although both the outer and inner guard cell walls may be thickened to a similar degree [as in those examples just described], it is more usual for the amount of thickening of the two walls to differ. A wide range of combinations of two of the three main patterns may be detected. Some of the commonest

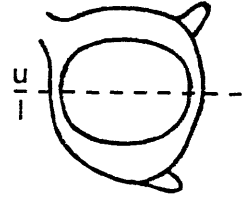
TEXT-FIGURE 14. Diagrams showing different degrees of thickening of guard cell walls (including cutinised regions) as seen in T.S.

A



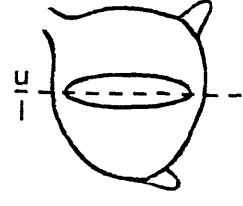
VERY LITTLE
 = $0 - \frac{1}{3}$ wall thickened

B



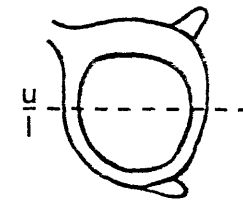
MODERATE
 = $\frac{1}{3} - \frac{2}{3}$ wall thickened

C



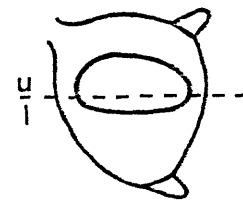
MASSIVE
 = $\frac{2}{3} - 1$ wall thickened

D



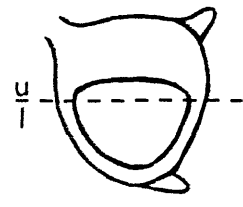
upper wall - MODERATE
 lower wall - VERY LITTLE

E



upper wall - MODERATE
 lower wall - MASSIVE

F



upper wall - MASSIVE
 lower wall - VERY LITTLE

G



upper wall - MASSIVE
 lower wall - MODERATE

types found are guard cells with very thin inner walls and either massively or moderately thickened outer walls, e.g. in Endlicheria spp. and Actinodaphne spp. respectively, or with inner walls of moderate thickness and outer walls of massive proportions, as in certain Cinnamomum spp. [C. iners & C. oliverii] (Text-Fig. 25B). In all such stomata, the lumen will be located mainly in the lower half of the guard cell and its size determined by the total thickness of the inner and outer walls. Generally, much of the thickened outer wall is deeply cutinised, e.g. in Ocotea spp. That which remains uncutinised is often approximately the same thickness as the inner wall. Notable exceptions occur in Cinnadenia paniculata and Micropora curtisii: only a very small portion of the guard cell outer wall is cutinised so that the massive uncutinised part is a particularly prominent feature in transverse sections when the cuticle is stained with Sudan IV.

Other patterns of wall thickening may be observed in guard cells. Sometimes the inner wall is thicker than the outer. Occasionally, the inner is moderately thickened whilst the outer is very thin, for example in Beilschmiedia madang (Text-Fig. 24). In this taxon almost all of the outer guard cell wall is cutinised and the lumen occupies most of the upper half of the cell. More commonly, guard cells have massively thickened inner walls and outer of moderate thickness, with lumina located rather more centrally, such as in Hypodaphnis zenkeri and Sparattanthelium guianense. Cutinisation in this type of guard cell often appears to be rather thin and is confined to the edge of the outer wall, e.g. in Laurus spp.

Eusideroxylon melagangai, with stomata on both leaf surfaces, shows the same pattern of thickening (outer wall: massive, inner wall: little) in adaxial and abaxial guard cells.

Guard cell lumina, seen in section are variable in outline. This seems to depend on the orientation and shape

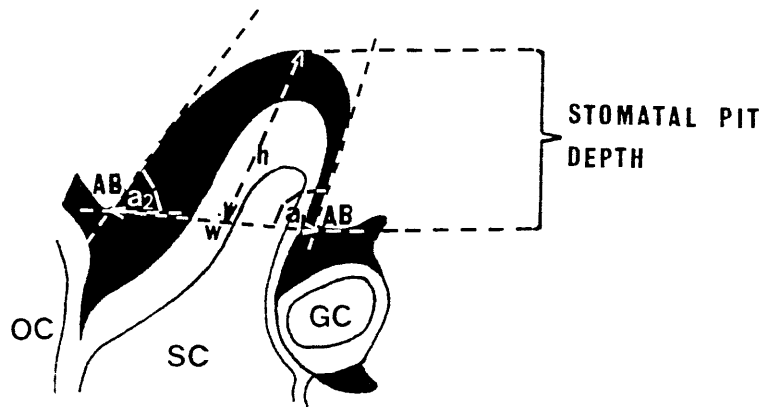
TEXT-FIGURE 15. Diagrams showing measurement of features of the stomatal complex.

- A. Stomatal pit depth; curvature of outer periclinal wall of subsidiary cell; angles between subsidiary cell periclinal wall and guard cell or surrounding cell, as seen in transverse section of half stoma.

- B,C. Cuticle thickness in periclinal region of guard cell and subsidiary cell; cuticle thickness at guard cell/subsidiary cell flanges [GSF] and subsidiary cell/surrounding cell flange [SOF] as seen in transverse section of half stoma in B) Lauraceae; C) members of related families.

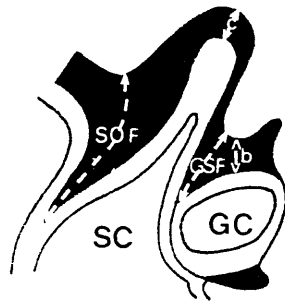
- D. Aperture length, wing length and width, subsidiary cell length as seen from the inner surface of isolated cuticles of Lauraceae.

A

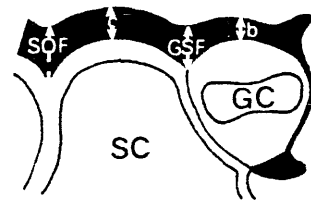


maximum height of wall above anticlinal borders (AB) = h
width from border with GC to border with OC = w
angle of SC relative to border with GC = a_1
angle of SC relative to border with OC = a_2
periclinal curvature of SC = $h = w$

B

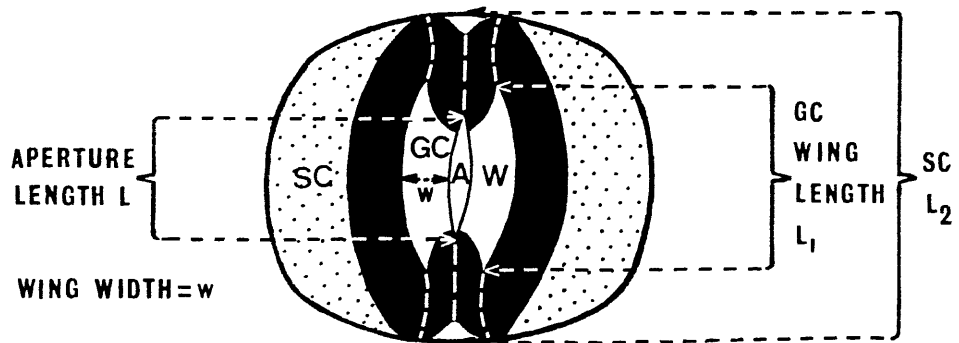


C



periclinal cuticle thickness - b = GUARD CELL (GC)
 c = SUBSIDIARY CELL (SC)
cuticle thickness - GC/SC & SC/OC FLANGES (GSF & SOF)

D



of the outer and inner wall thickenings [i.e. wall/lumen boundary] and on the amount of thickening present in the two walls. Thus, where very little of either wall is thickened, the lumen is extensive and open, tending to follow the outline of the guard cell boundary and it appears rounded or oval in T.S. e.g. in Umbellularia californica [Text-Fig. 21B]. When both or just one of the walls are greatly thickened, the lumen is usually much narrower. The wall thickening may or may not be even; commonly, it is thicker towards one lateral side of the guard cell than the other producing an oblique orientation, as in Austrobaileya scandens [downward towards inner ledge] [Text-Fig. 21A] or in Urbanodendron verrucosum [upward towards outer ledge].

Thickenings of the guard cell are often lignified to varying extents: sometimes those of the outer wall, e.g. in Aniba spp. or more regularly, the inner thickenings in addition, as in Cinnamomum spp. [not C. camphora]. The guard cell walls of some taxa, are not lignified, particularly those of the very thin type, e.g. Neocinnamomum spp. and also, interestingly, the massively thickened walls of Austrobaileya scandens and Piptocalyx moorei.

12.5.2c CUTICLE THICKNESS

Cuticle of varying thickness always covers at least some part of the outer wall of the guard cell. Generally, it lines the pore [very thinly], projects over it in the form of an outer ledge and gradually thins, then thickens towards the common wall between the guard and subsidiary cells. In Lauraceae members, there is very little distinction between cutinisation of the outer ledge, that of the outer periclinal wall and the guard cell/subsidiary cell flange. This makes measurement of the periclinal cuticle thickness in the Lauraceae and comparison with results of other families, rather difficult. However, an approximate value may be arrived at by measuring vertically downwards from where guard cell and subsidiary cell periclinal cutinisation meet in all taxa [see Text-Fig. 15].

The resulting average periclinal thickness for the

guard cell cuticle varies from very thin [0.3 μm], as in Caryodaphnopsis tonkinensis to thick [7.3 μm], e.g. in Eusideroxylon melagangai. Guard cell cuticle of adaxial stomata of the latter species is slightly thicker [7.6 μm]. Most taxa have a relatively thin guard cell cuticle, up to 3.3 μm often covering just the edges of the outer wall: many Lauraceae, such as Endiandra spp. [2.4 μm] [Text-Fig. 23A], Licaria spp. [3.0 μm], and all members of the related families, e.g. Illigera spp. [1.2 μm]. However, a number of Lauraceae have considerably thicker cuticle over the guard cells, such as Nectrandra spp. [4.3 μm], Endlicheria spp. [E. piriformis: 5.5 μm] and Phyllostemonodaphne geminiflorum [6.4 μm]. In such taxa, much of the outer wall of the guard cell is cutinised and this gradually merges into comparatively deep cutinisation associated with the wall between the guard and subsidiary cell [i.e. the guard cell/subsidiary cell flange].

12.5.2d OUTER LEDGE FORM

An elevated protruberance of the cuticle, the outer ledge projects from the guard cell, immediately above the stomatal pore. It exists in a variety of sizes and shapes, when viewed in transverse section and always extends 'protectively' over the pore and defines an outer cavity or vestibule [Text-Fig. 16A].

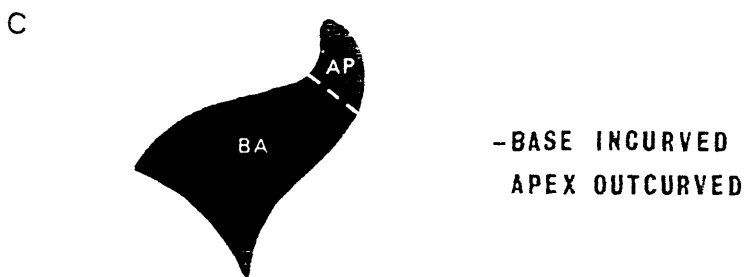
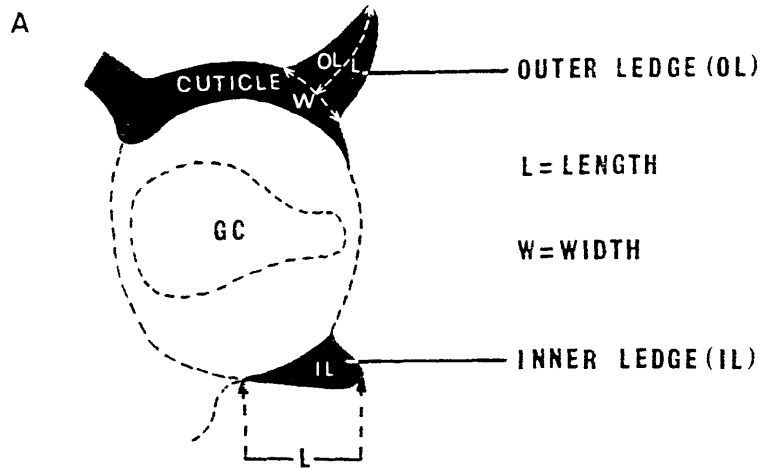
In Lauraceae, the guard cells seen from the outer surface are obscured to varying extents by the subsidiary cells, so that the form of the outer ledge is often rather inconspicuous. Therefore, sections provide the best means of determining its form. In such preparations, the outer ledge appears as two projections, one from each guard cell.

The average length of the outer ledge, taken from the basal midpoint to the tip [see Text-Fig. 16A] varies from short [0.6 μm], e.g. in Dehaasia spp. to very long [11.9 μm] in Austrobaileya scandens [Text-Fig. 21A]. Most taxa have a ledge less than 3.0 μm in length. Exceptions occur occasionally in Lauraceae, such as in Mezilaurus spp. [M. itauba: 4.9 μm , M. lindaviana: 4.0 μm] but most

TEXT-FIGURE 16. Diagrams of guard cell outer and inner ledge features as seen in T.S.

A. Showing location and measurements [length and width].

B,C,D,E. Different shapes of outer ledge.



notably in the related families, e.g. Trimenia spp. [T. papuana: 3.3 μm , T. weinmanniaefolia: 4.9 μm] and Hernandia spp. [H. nymphiifolia: 3.3 μm , H. olivacea: 5.8 μm] [Text-Fig. 22A].

At the base, the outer ledge is also variable in width, ranging from an average of 0.9 μm , as in Dehaasia spp. [very narrow] to 8.5 μm , in Austrobaileya scandens [very wide] [Text-Fig. 21A]. The majority of taxa have a narrow outer ledge of less than 3.0 μm in width. In some taxa, however, it is wider, e.g. in Mezilaurus spp. [M. itauba: 5.2 μm , M. lindaviana: 3.3 μm] and Trimenia weinmanniaefolia [5.2 μm].

Outer ledge size [length and width] seems to depend to a great extent on the size of the guard cell: where such cells are of the larger dimensions, so also is the outer ledge.

Shape of the ledge, expressed as a length:width ratio shows variation [and is not dependent on guard cell size]. Three main patterns, all basically triangular in T.S. may be recognised: length less than basal width, resulting in a rather short, wide [obtuse] shape, e.g. in Eusideroxylon zwageri [1:w 0.4:1] [Text-Fig. 25A]; length approximately or equal to width, giving an equilateral outline, as in Nothaphoebe umbelliflora [1:w 1.0:1] and length greater than width, producing a long, narrow [acute] shape, e.g. in Hernandia spp. [H. nymphiifolia 1:w 2.2:1, H. olivacea 1:w 2.1:1] [Text-Fig. 22A]. Most Lauraceae members have a guard cell outer ledge of the obtuse or equilateral type with a length:width ratio of 1.2 or less:1. Some however, show a ledge of a more elongate configuration such as, Laurus nobilis [1:w 1.5:1] and Persea thunbergii [1:w 1.7:1].

Taxa of the other families have an outer ledge with a length:width ratio between about 1.0 [Trimenia weinmanniaefolia: 0.9] and 2.2:1, that is of the equilateral or acute type. The most acute outer ledge is found in the Hernandiaceae, such as in Illigera pulchra [1:w 2.0:1].

Guard cells of adaxial stomata in Eusideroxylon melagangai have a similar shaped outer ledge to that of the abaxial [1:w 0.9:1]. The respective average ledge length and width is also alike [length: 2.1 μm , width: 2.4 μm].

The basic triangular outline observed in transverse section may be modified by different directions of curvature of the apex [top 1/3] and base [lower 2/3] of the outer ledge [see Text-Fig. 16 B-E]. Commonly, either both the basal and apical regions curve inward, forming a dome-like configuration in section corresponding to a convex rim in the S.E.M. [seen only when not obscured by subsidiary cells], for example, in Austrobaileya scandens [Text-Fig. 21A] and Alseodaphne semecarpifolia [T.S. only], or the base and apex are outward curving, as in Eusideroxylon melagangai and Nectandra spp. Sometimes, however, the basal region is clearly curved inwards and the distal region outwards. This pattern is characteristic of Trimeniaceae members, Gomortega keule, Hernandia olivacea [Text-Fig. 22A] and a few Lauraceae, e.g. Umbellularia californica [Text-Fig. 21B]. In the S.E.M., it is sometimes possible to observe that the extreme end of this upturned apex forms a prominent, rather upright, narrow edge to the outer cavity above the pore [see Hernandia olivacea] with the rest of the ledge producing a wide convex border.

Alternatively, the outer ledge may exhibit no curvature either at the base or apex, so that it appears straight, but directed outward in section, as in Beilschmiedia micrantha and, Illigera pulchra [in which the ledge, in S.E.M., forms a flat, wide, outwardly pointing rim: see Fig. 102].

The shape of the very tip of the outer ledge apical region is often rather inconspicuous when viewed in transverse section. Occasionally, it is conspicuous and distinctly blunt, e.g. in Eusideroxylon spp. [Text-Fig. 25A] and Licaria spp. or more commonly, the tip is pointed, as in Gomortega keule, Hernandia olivacea

[Text-Fig. 22A] and Pleurothyrium spp.

The guard cell outer ledge is usually non-lignified. A notable exception is that of Laurus spp. When stained with Sudan IV, the outer ledge in all taxa reacts uniformly, becoming red in colour, indicating a high degree of cutinisation.

12.5.2e INNER LEDGE FORM AND DEGREE OF CUTINISATION

At the edge of the inner wall of the guard cells, the cuticle apparently forms a second pair of projections in T.S., which extend towards each other. In fact, these are part of one unit, the inner ledge. This generally defines an inner or back cavity and beneath lies the substomatal chamber surrounded by mesophyll [Text-Fig. 16A].

Unlike the outer ledge, the inner appears to be cutinised to varying extents. Results of staining T.S.'s with Sudan IV indicate that in a few taxa, the inner ledge may possess poor cutinisation, giving an almost colourless response, e.g. in Endiandra spp. [Text-Fig. 23A] or it may sometimes be moderately cutinised, producing a pink colouration when stained, as in Micropora curtisii. More usually, the inner ledge stains deeply (red), suggesting a high level of cutinisation, for example, in Laurus spp. and Austrobaileya scandens [Text-Fig. 21A].

When the inner ledge is small (average length and width between 1.2 and 3.0 μm) its direction of curvature is virtually indistinguishable. Ledges of greater size seem to be obtuse (i.e. wider than long or equilateral if measured in the same way as the outer ledge) and curve inwards towards the inner cavity. The most noticeable difference is the prominence of the inner ledge from where it meets the lowermost portion of the guard cell inner wall to its tip. This ranges from an average of 1.2 μm , in Actinodaphne stenophylla to 13.7 μm , in Austrobaileya scandens [Text-Fig. 21A], most taxa having values less than 6.1 μm . A more prominent ledge may sometimes occur, e.g. in Aiouea spp. (A. guianensis: 7.3 μm , A. saligna: 6.4 μm) and Piptocalyx moorei (8.8 μm) [Text-Fig. 22B].

STOMATAL 'FLAP'. Note that this structure is not flap-like.

It is the cutinised lining of the substomatal chamber.

When the size of the inner ledge of the guard cells is compared with that of the outer, the inner may be smaller than the outer, as in Hernandia olivacea [Text-Fig. 22A] and Sparattanthelium spp. or is more usually of similar size, e.g. in Caryodaphnopsis spp., or larger than the outer ledge such as, in Litsea meissneri and Systemonodaphne mezii.

Commonly, the inner ledge is removed during maceration [except in Austrobaileya scandens] and is, therefore, not represented on the inside of cuticles.

The guard cell inner ledge is always non-lignified.

12.5.2f PRESENCE OF OUTER AND INNER CAVITIES

In most taxa two cavities, an outer and an inner defined by the guard cells outer and inner ledges respectively, exist above and below the pore and its 'lips'. However, in Austrobaileya scandens, only one cavity is outlined [the cuticle of the outer ledge curves downwards, meets with the cutinisation of part of the guard cell constituting the cavity lining, then curves inwards at the inner ledge with no evidence of pore 'lips'] [see Text-Fig. 21A]. The ledges in this taxon, may have been specially modified [enlarged] to maintain functional efficiency.

12.5.2g PRESENCE OF STOMATAL 'FLAP'

In transverse section, sometimes cutinisation of the stoma appears to terminate at the inner ledge, for example, in Endlicheria spp. and Trimeniaceae members [e.g. Text-Fig. 22B]. More often, a membrane [usually thin], the stomatal flap, extends back from this guard cell ledge to varying extents: over part of the inner wall of the adjacent subsidiary cells near the inner ledge, as in Austrobaileya scandens [Text-Fig. 21A] and Sparattanthelium tupiniquinorum or all of this subsidiary cell wall, e.g. in Licaria guianensis and Mezilaurus spp., or the subsidiary cell wall and beyond, either to the inner walls of other epidermal cells, as in Neolitsea dealbata or to a small part of the mesophyll surrounding the

substomatal chamber e.g. in Beilschmiedia micrantha and Cryptocarya ainikini. The stomatal flap may be variously cutinised. Usually it stains red with Sudan IV indicating the presence of a substantial amount of cutin, as in Eusideroxylon spp. [Text-Fig. 25A], although it may give only a pink coloured reaction when it is not so highly cutinised, e.g. in most Hernandiaceae [not Illigera pulchra: flap absent]. Occasionally, the portion of the flap nearest the guard cell inner ledge may stain deeply [red] and that over the inner wall of the subsidiary cell less so [pink], suggesting decreasing levels of cutinisation of the stoma with progression away from the inner ledge. This response is characteristic of Neocinnamomum spp. only [Text-Fig. 23B].

12.5.2h THICKNESS OF CUTICLE AT GUARD CELL/SUBSIDIARY CELL FLANGE

At the junction between the guard and subsidiary cells, the cuticle projects anticlinally to form a flange, in the same way as in non-specialised areas [between adjacent epidermal cells]. Measurements made from where the cells meet on the outer periclinal surface to the flange tip in T.S. [see Text-Fig. 15B,C] reveal that the average thickness of the cuticle in this region varies. It ranges from very thin (0.3 μm), in Beilschmiedia micrantha to thick (11.6 μm), in Eusideroxylon spp. for the abaxial surface. The cuticle at the guard cell/subsidiary cell flange is even thicker on the adaxial in E. melagangai (15.9 μm). Members of the families related to Lauraceae have relatively thin cuticle at this flange; the thickness never being more than 3.3 μm . Some Lauraceae also exhibit thin cuticle at the flange between the guard and subsidiary cells, such as Hypodaphnis zenkeri (1.5 μm) and Potameia spp. [P. crassifolia; 2.1 μm ; P. thouarsii: 2.4 μm]. Others have considerably thicker cuticle in this region, often between 5.5 μm and 9.8 μm , for example, Nectandra spp. [N. pichurim: 6.7 μm , N. salicifolia 7.3 μm] and Phyllostemonodaphne geminiflorum (8.8 μm) or even greater, as in Dehaasia caesia (10.7 μm).

Sometimes, cuticle thickness is similar at the guard

cell/subsidiary cell and epidermal flanges, e.g. in Gyrocarpus americanus ssp. americanus, Piptocalyx moorei and Pleurothyrium nobile. Generally, however, it is more common for the cuticle of the guard cell/subsidiary cell flange region to be either thinner than that of un-specialised flanges, predominantly in members of families related to Lauraceae, notably Gomortega keule, or thicker, as in Beilschmiedia spp. [Text-Fig. 24A].

The guard cell/subsidiary cell flange in the Lauraceae is observed in the S.E.M. to be part of the cutinised guard cell 'wing' located adjacent to the pore on the inner surface [Text-Fig. 13, see also p. 224]. The same flange, in members of related families, completely outlines distinct guard cells [Text-Fig. 12].

12.5.2i PROMINENCE OF GUARD CELL/SUBSIDIARY CELL FLANGE

The degree to which the guard cell/subsidiary cell flange extends down into the common wall towards the lowermost point of contiguity between the guard cell and the subsidiary cell [Text-Fig. 15B,C] is also variable. The flange may often be very low [penetrating from 0-¼ depth of contiguity], for example in some Lauraceae, such as Laurus spp. and Phoebe spp., and in all members of related families, or it may be low [projecting between ¼ and ½ depth of contiguity], e.g. in Actinodaphne spp. and Sassafridium macrophyllum. Sometimes the guard cell/subsidiary cell flange may be of moderate prominence [extending between ½ and ¾ depth of contiguity], as in Licaria spp. and Ravensara spp. [Text-Fig. 24B] or it may project even more, i.e. deep [up to the whole depth of contiguity], e.g. in Eusideroxylon spp. [Text-Fig. 25A] and Urbanodendron verrucosum. The guard cell/subsidiary flange is never extensive [with cutinised 'corners' etc.] as that of an ordinary epidermal cell may be.

When the prominence of the guard cell/subsidiary cell flange is compared with that of the non-specialised inter-costal flanges from transverse sections, it is observed that they may sometimes both project to a similar degree, such as in Gyrocarpus americanus, Laurus spp., Ocotea spp.,

and Piptocalyx moorei [Text-Fig. 22B] or more usually, either the guard cell/subsidiary cell flange may be less prominent than the epidermal flanges, for example, in Gomortega keule, Lindera spp., Potameia spp., and Trimenia spp. as well as a number of Hernandiaceae, or the reverse situation may exist. The latter trend may only be detected in Lauraceae, e.g. in Cinnamomum spp. [Text-Fig. 25B] and Urbanodendron verrucosum. Where the guard cell/subsidiary cell flange is very low, in T.S.'s of members of the Hernandiaceae, it is sometimes almost indistinct on the inner surface of isolated cuticles in the S.E.M., e.g. in Hernandia olivacea [Fig. 131] and Illigera pulchra [Fig. 137].

There appears to be a correlation between guard cell/subsidiary cell flange prominence and the degree of cutinisation of the guard cell outer wall in Lauraceae: as the flange becomes progressively deeper so more of the wall is correspondingly cutinised.

12.5.2j SHAPE OF GUARD CELL/SUBSIDIARY CELL FLANGE [IN T.S. AND SURFACE VIEW]

As in non-specialised regions, at the boundary between a guard cell and its adjacent subsidiary cell, the cuticular layer forms either a V- or U-shaped anticlinal flange, in sections. The V-sectioned type, as in Piptocalyx moorei [Text-Fig. 22B], occurs most commonly, although the U-sectioned form may be observed in a few Lauraceae, e.g. in Hypodaphnis zenkeri and Potameia spp. and more often in members of the related families, such as Gomortega keule, Gyrocarpus americanus and Trimenia spp. Generally, the guard cell/subsidiary cell flange [GSF] is the same shape in section as the non-specialised flanges [OF]. Sometimes, however, there are differences, for example in Beilschmiedia micrantha, Gomortega keule [GSF. U, OF. V], Litsea umbellata and Sassafras albidum var. molle [GSF. V, OF. U].

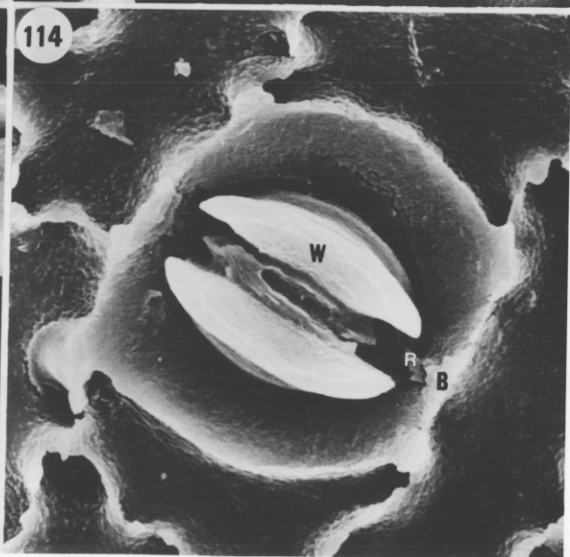
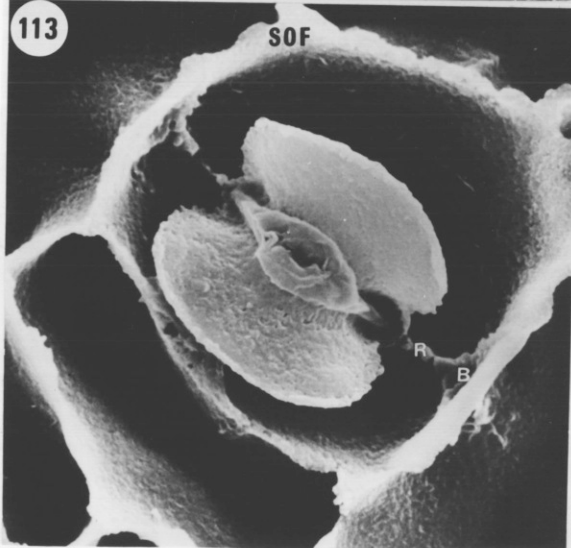
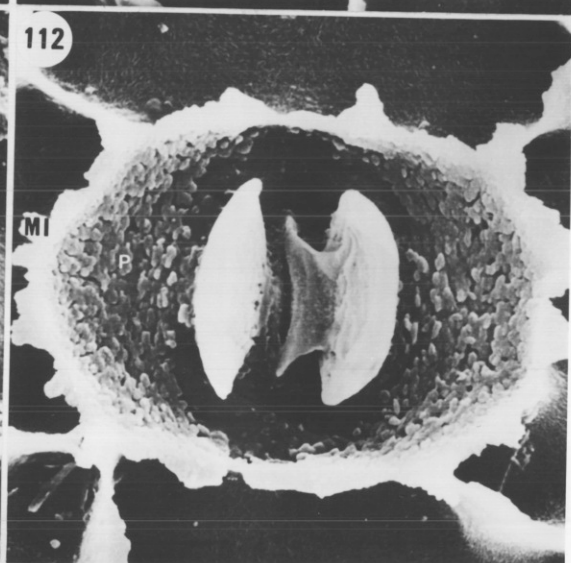
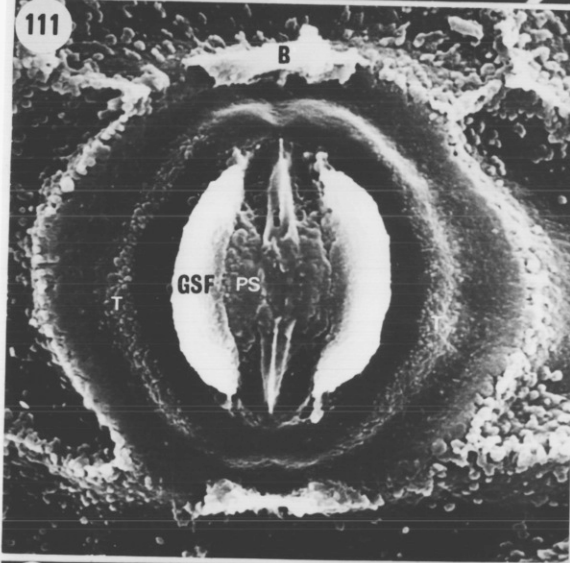
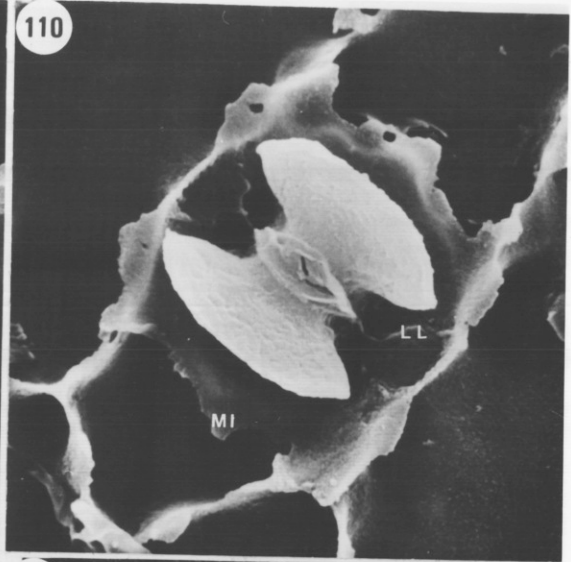
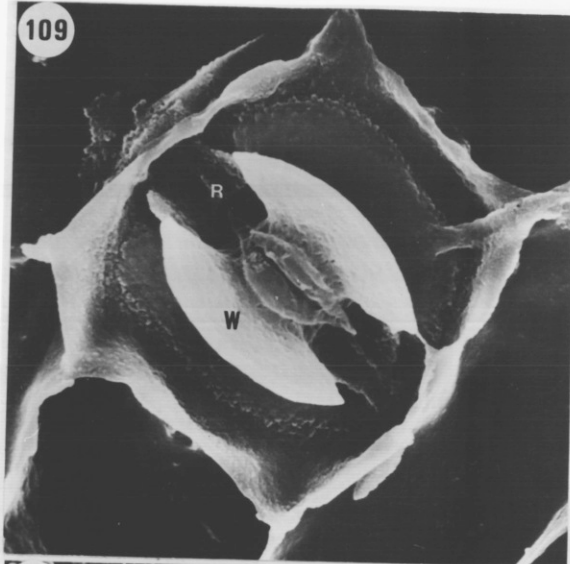
The scanning electron microscope reveals that the guard cell/subsidiary cell flange when seen in surface view is quite different in shape in Lauraceae from that

113. Ocotea laevis. Margin of subsidiary cell/surrounding cell flanges uneven, irregularities blunt. Pores present in flanges. Subsidiary cells with T-piece [of bar B and rod R]. Guard cell wings obtuse with blunt polar ends. Wings longer than polar lips, just over half polar diameter of subsidiary cells. ca. x 2155.
114. Endlicheria piriformis. Subsidiary cell/surrounding cell flanges uneven, less so than those of ordinary cells; with pegs. Subsidiary cells with T-piece [R and B]. Guard cell wings [W] located in cavity corresponding to subsidiary cell dome. ca. x 1165.

Stomata: Lauraceae

Inner surface of isolated cuticles.

109. Litsea meissneri. Subsidiary cells with cutin infilling of dome cavity. Faint polar rod and strong convex lateral lines present. Guard cell wings obtuse, appearing narrow due to almost erect orientation; periclinal surface with fine reticulate protrusions: more complex than either subsidiary cell or surrounding cell ornamentation. ca. x 2000.
110. Aniba megaphylla. Subsidiary cell/surrounding cell flanges uneven, frequently perforated. Subsidiary cells with strong convex lateral lines [LL] that fuse just above end of polar lips. Much of subsidiary cell periclinal surface obscured by wings. Guard cell periclinal surface ornamented with fine reticulate protrusions, elsewhere very finely granular. ca. x 2160.
111. Dehaasia caesia. Subsidiary cells terraced [T], with lens-shaped polar bars [B]. Guard cell poral 'lips' extending slightly beyond guard cell/subsidiary cell flange [GSF]. Wings half subsidiary cell polar diameter. Periclinal sculpture of stomatal complex finer than that of surrounding cells. ca. x 2085.
112. Urbanodendron verrucosum. Subsidiary cell/surrounding cell flanges highly uneven appearing frilly. Periclinal surface of subsidiary cell with two distinct zones of ornamentation: 1, outer with moderately coarse clumped or reticulate protrusions, 2, inner with very fine granules. Note presence of faint, straight polar lateral lines. ca. x 2025.

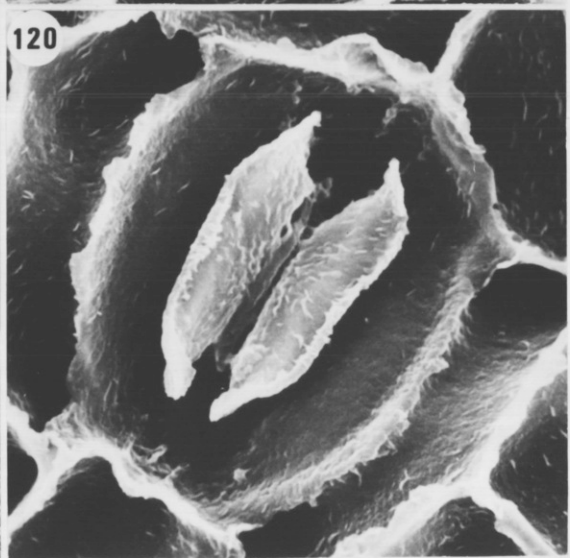
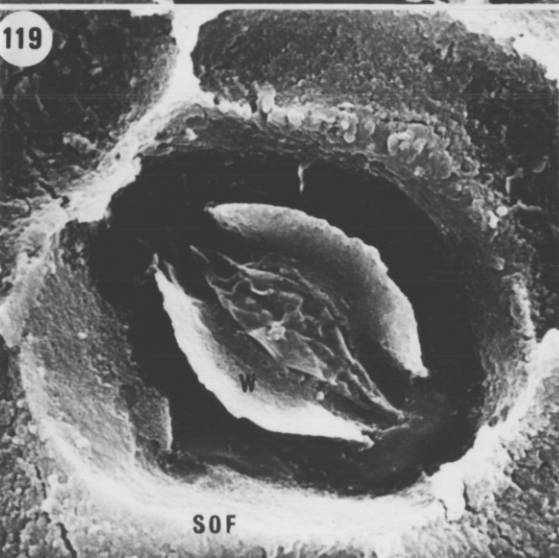
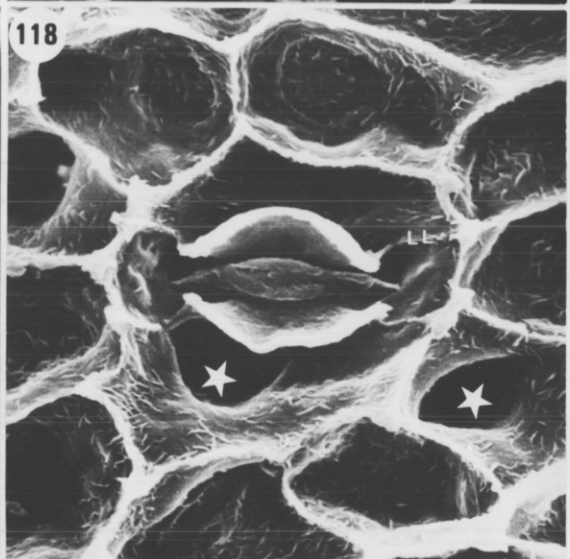
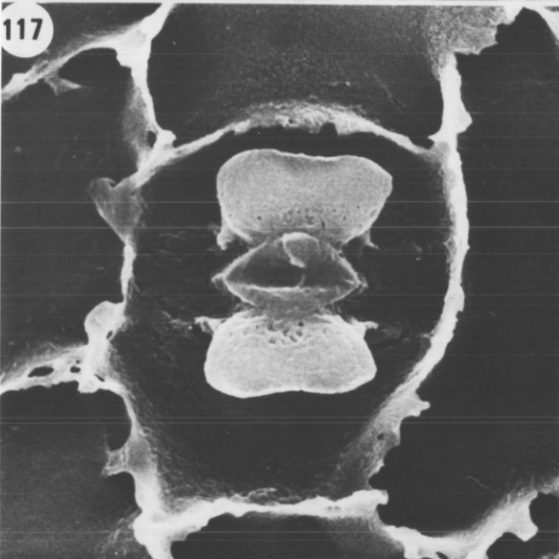
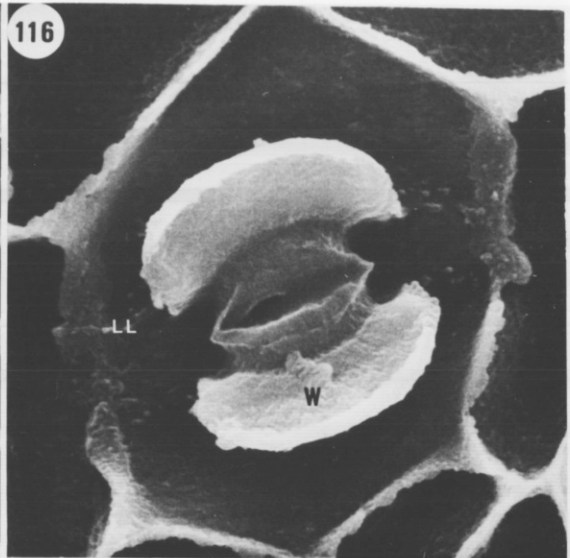
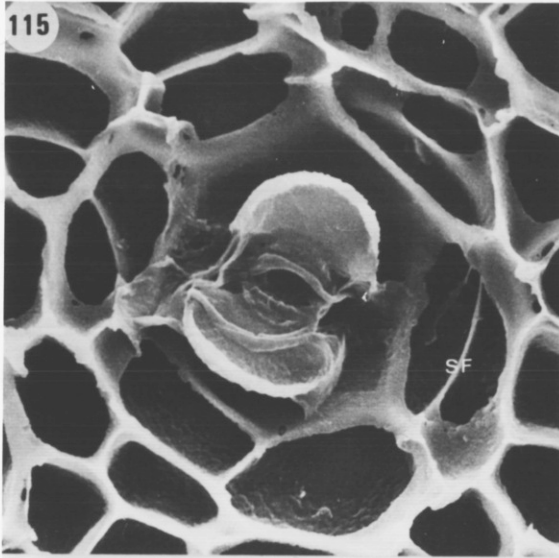


119. Nothaphoebe umbelliflora. Subsidiary cell [top right] with secondary flange, of lower prominence and more beaded than primary flanges. Conspicuous smooth area corresponding to subsidiary cell dome on O.S. Rest of subsidiary cell ornamented. Note presence of faint polar rods, straight lateral lines and lens-shaped bar. Wings (W) with surface of reticulate protrusions, tips pointed. Polar lips almost as long as wings. ca. x 2175.
120. Nectandra pichurim. Subsidiary cell/surrounding cell flange uneven at margin. Subsidiary cells with faint polar rod and strong concave lateral lines. Guard cell wings almost parallel-sided with conspicuously pointed polar tips. Polar lips about $\frac{1}{2}$ length of wings. ca. x 2140.

Stomata: Lauraceae

Inner surface of isolated cuticles.

115. Eusideroxylon melagangai. Adaxial. Subsidiary cell/surrounding cell flanges deeply to extensively cutinised, perforate. Faint lateral lines, apically thickened present at poles. Stoma encircled by six cells, often with secondary flanges (SF). Wings obtuse with distinct rim at edge and blunt polar tips. Poral lips just less than $\frac{1}{2}$ wing length. Note vestiges of stomatal flap associated with lips. ca. x 1060.
116. Eusideroxylon melagangai. Abaxial. Stoma similar in form to adaxial but less cutinised: subsidiary cell/surrounding cell flanges of moderate prominence. Cells encircling stoma not secondarily divided. Stomatal flap absent. ca. x 2150.
117. Dicypellium caryophyllatum. Subsidiary cell/surrounding cell flange frequently perforated, with uneven margin. Subsidiary cell dome not represented on I.S. Subsidiary cells with faint convex lateral lines. Poral lips slightly shorter than wings. Margin of wings with slight indentation. Note reticulate protrusions on wing surface; more complex than elsewhere (granules or clumps). ca. x 2170.
118. Pleurothyrium cuneifolium. Subsidiary cell/surrounding cell flange with tapering pegs at junction with unspecialised cell flanges. Subsidiary cell periclinal surface with deep scrobiculus (starred) representing prominent dome on O.S. Note presence of strong concave lateral lines (LL) at poles with distinct apical thickening. Poral lips approximately same length at wings. Latter with pointed tips. ca. x 2170.

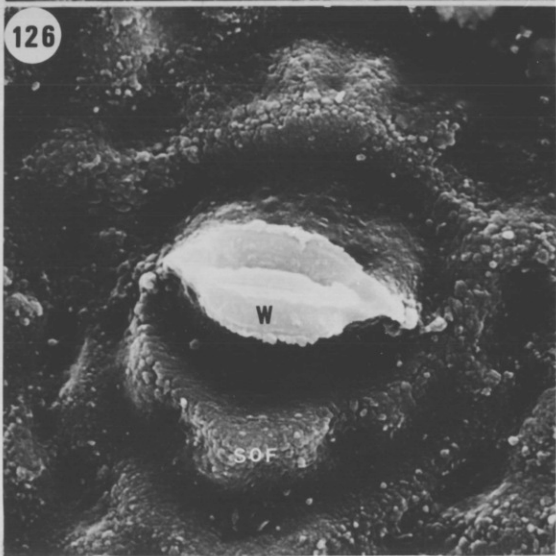
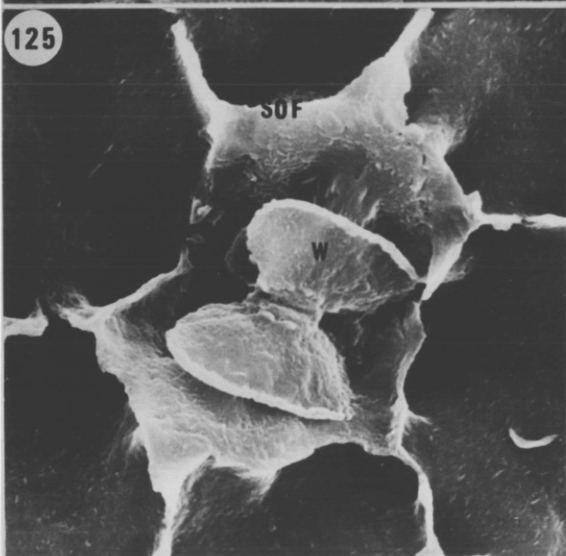
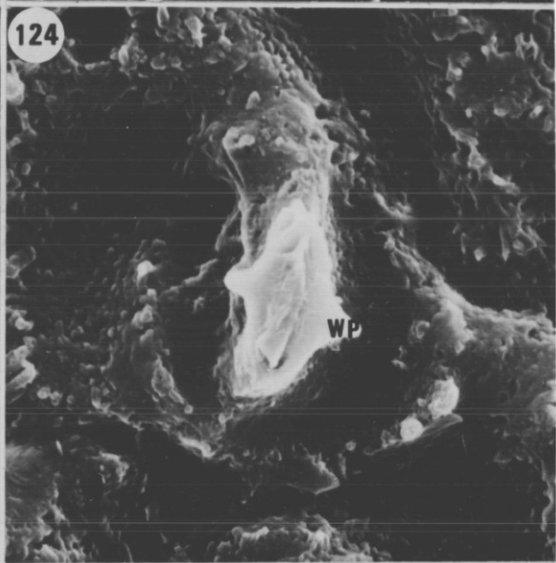
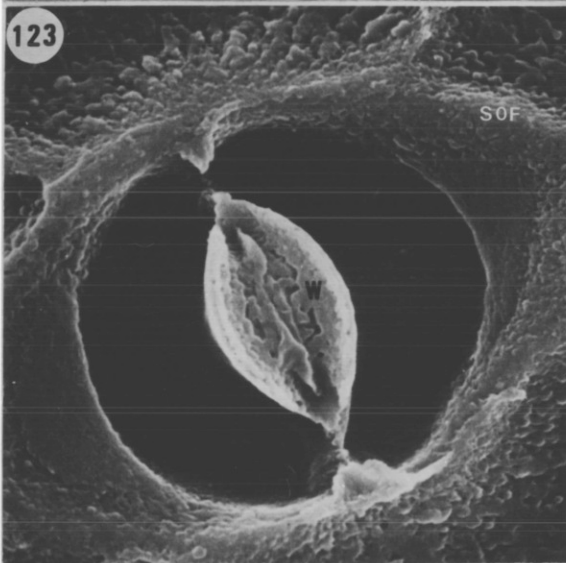
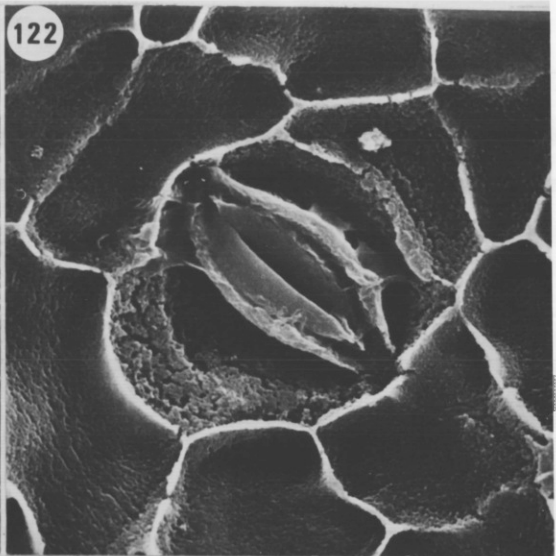
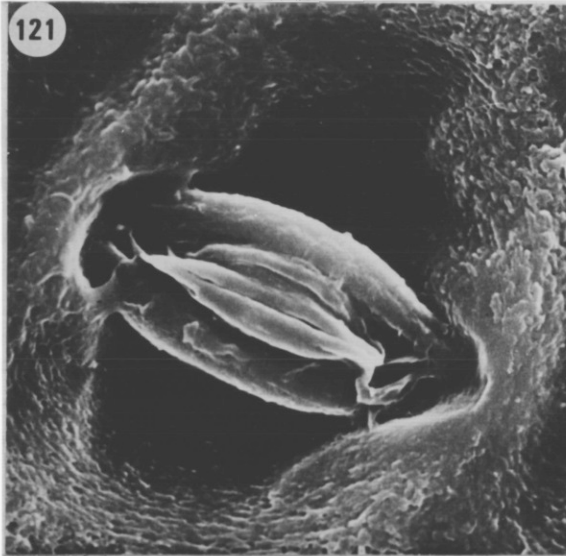


126. Micropora curtisii. Subsidiary cell/surrounding cell flanges [SOF] Ω -undulate, very low. Scrobiculus corresponding to dome on O.S. occupying most of subsidiary cell periclinal surface. Polar T-piece present. Guard cell wing cutinisation closely associated with poral lips. Periclinal surface of all cells granular. ca. x 2140.

Stomata: Lauraceae

Inner surface of isolated cuticles.

121. Neocinnamomum caudatum. Subsidiary cell/surrounding cell flanges very low with blunt apices. Scrobiculus corresponding to dome on O.S. distinct on subsidiary cell periclinal surface. Guard cell wings with blunt margin, extending across most of polar diameter of subsidiary cells. Polar lips almost as long as wings, closely appressed. ca. x 2150.
122. Sassafridium macrophyllum. Subsidiary cells both secondarily divided. Subsidiary cell periclinal surface with fine to moderate protrusions and depressions, coarser and more complex than ornamentation of unspecialised cells. Wings obtuse, obscured by very thick poral lips. ca. x 1070.
123. Cinnamomum camphora. Scrobiculus representing dome of subsidiary cells well-marked, with smoother periclinal surface than elsewhere. T-pieces also distinct. Guard cell periclinal cuticle distinguishable from guard cell/subsidiary flange in wing [W] by ornamentation of moderately coarse reticulate protrusions. Wing margin even, tips pointed. ca. x 2215.
124. Cinnamomum oliverii. Subsidiary cell/surrounding cell flanges beaded. Scrobiculus of subsidiary cell dome occupying most of the periclinal area on I.S. Subsidiary cells with narrow T-shaped polar thickening. Guard cell wings with conspicuous marginal pegs [WP]. Wings closely associated with poral lips. ca. x 2120.
125. Alseodaphne oblanceolata. Subsidiary cell/surrounding cell flanges U-undulate with cavities. Stoma outline angular. Corners with tapering pegs. Subsidiary cells without polar thickening. Scrobiculus representing O.S. dome present. Poral lips less than $\frac{1}{2}$ wing length. Wings obtuse with blunt tips. ca. x 2175.

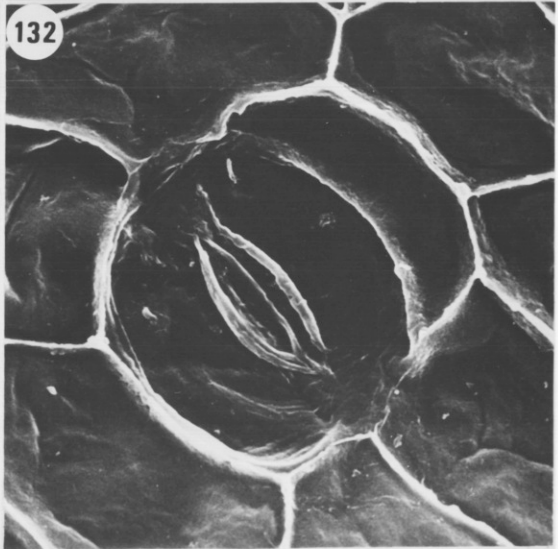
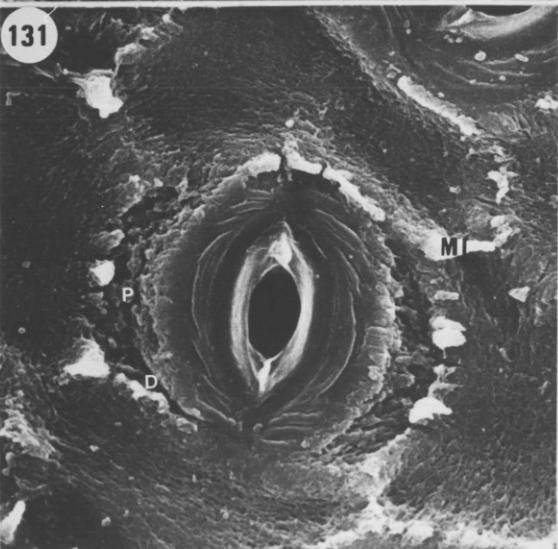
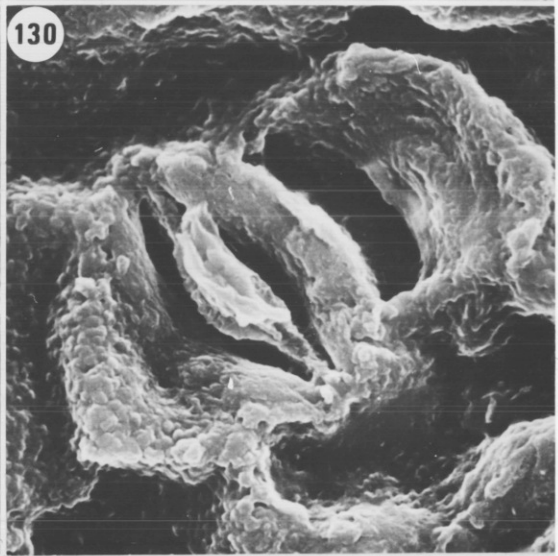
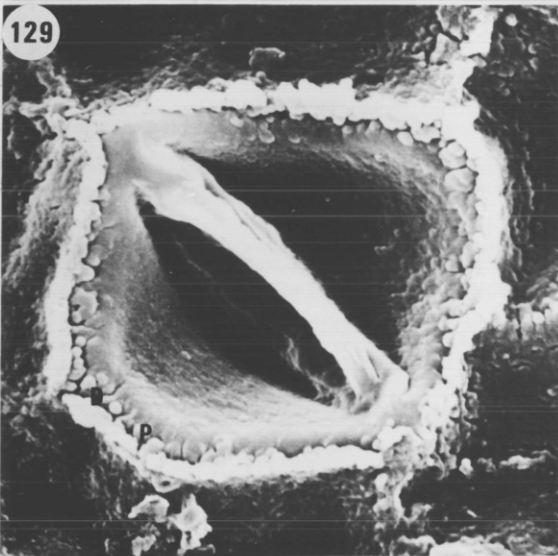
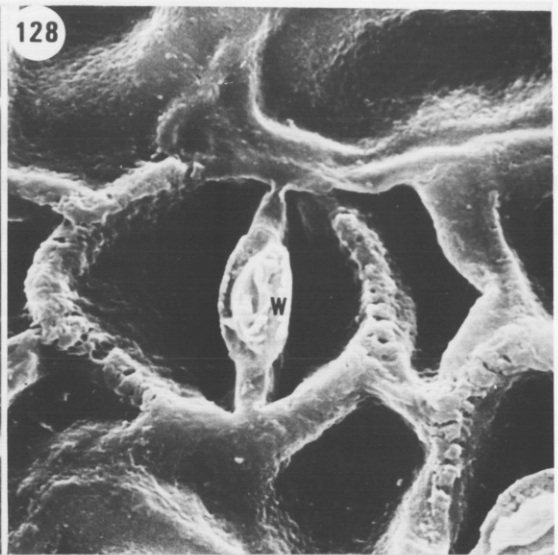
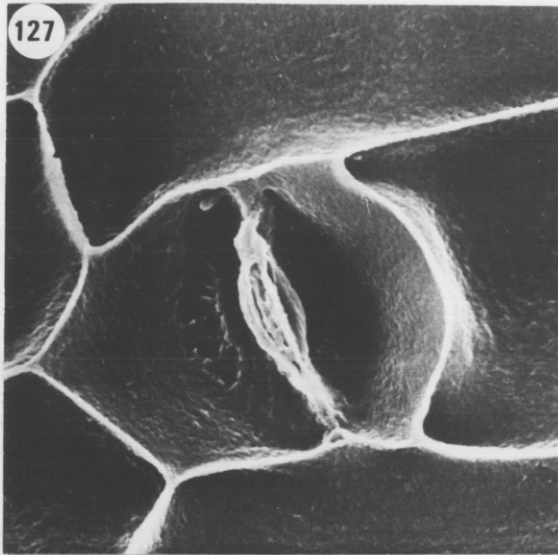


131. Hernandia olivacea. Subsidiary cell/surrounding cell flanges interrupted, highly uneven, irregularities pointed, toothlike. Subsidiary cells narrow, crescentiform with coarser sculpture (protrusions and depressions) than in unspecialised cells. Guard cell periclinal cuticle with concentric striae, very finely granular. Polar thickening consisting of short, incomplete rod. Note raised central rim representing cuticle below outer ledge. ca. x 1105.
132. Illigera pentaphylla. Subsidiary cells narrow, crescentiform, sometimes secondarily divided (right). Guard cell/subsidiary cell flanges inconspicuous. Guard cells without polar thickening; periclinal surface smooth unlike that elsewhere (extremely fine filamentous reticulate protrusions and pit-like depressions). Narrow ridge corresponding to cuticle below outer ledge prominent, also poral cutinisation (central elliptical rim). ca. x 1050.

Stomata: Lauraceae and Hernandiaceae

Inner surface of isolated cuticles.

127. Nothaphoebe heterophylla. Subsidiary cells asymmetric, with distinct cavity [scrobiculus] corresponding to dome on O.S., occupying portion of periclinal area. Thickening at poles consisting of prominent, narrow rod and bar [T-piece]. Guard cell wings acute [only one, L, illustrated] slightly longer than poral lips, with sculpture of fine reticulate protrusions, coarser than periclinal sculpture elsewhere. ca. x 2195.
128. Phoebe shearerii. Subsidiary cells sometimes secondarily divided [R]. Similar in arrangement to stoma of Fig. 127. Polar thickening of prominent, wide, rods only. Wings [W] equal in length to poral lips, with sculpture of clumped and reticulate protrusions [more complex than on other periclinal surfaces]. ca. x 2130.
129. Apollonias arnottii. Subsidiary cell/surrounding cell flange with moderate to coarsely granular protrusions [P] and fine clumped to reticulate depressions [D]. Subsidiary cell periclinal surface ornamented with fine granules. Scrobiculus representing dome, involving only a portion of subsidiary cell. Guard cell wings very narrow, rod-like [acute]. ca. x 2360.
130. Neolitsea dealbata. Subsidiary cells asymmetric, secondarily divided. Polar thickening consisting of prominent narrow rod. Scrobiculus of subsidiary cells very narrow, deep. Guard cell wings acute, closely associated with poral lips. Latter slightly longer than wings, which extend to just over half of subsidiary cell polar diameter. ca. x 2105.

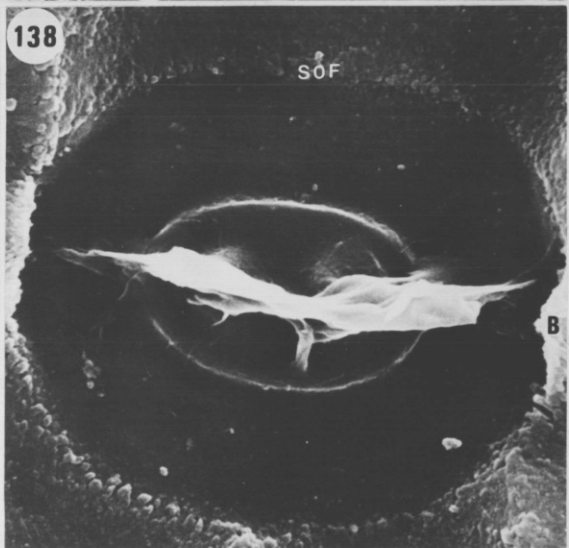
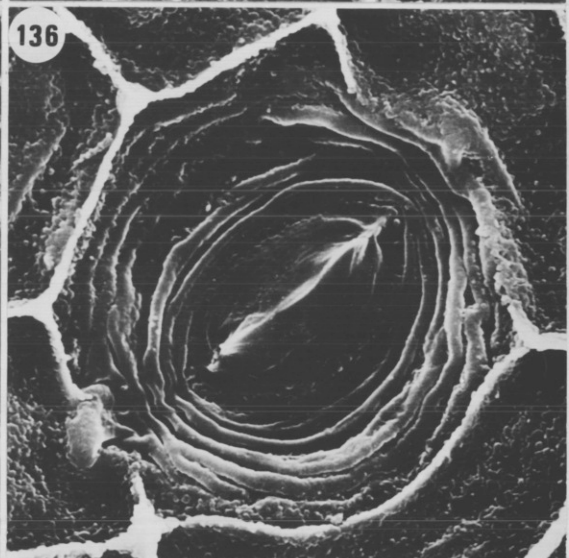
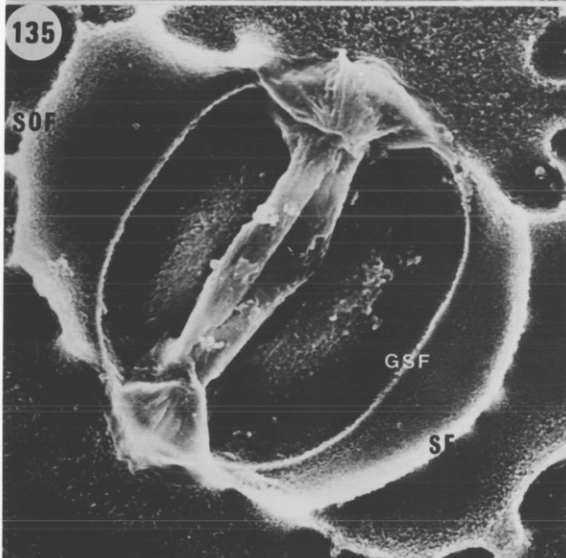
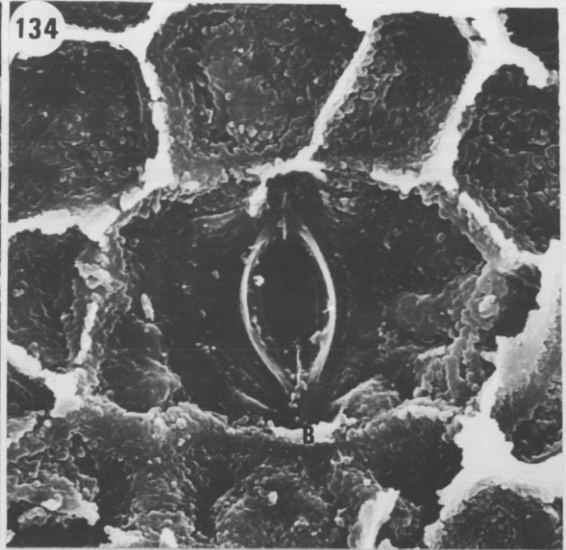
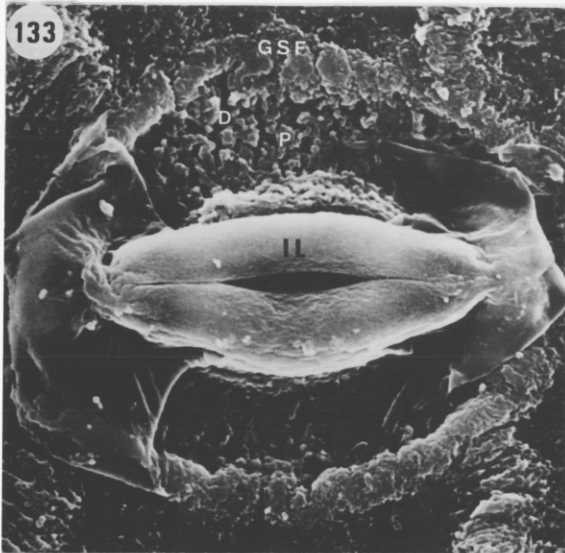


137. Illigera pulchra. Subsidiary cell/surrounding cell flanges very low of U-form [blunt] [bottom right]. Guard cell/subsidiary cell flanges similar, inconspicuous. Guard cells narrow, without polar thickening. Periclinal surface with very finely granular protrusions, less complex than elsewhere [reticula with pit-like depressions]. Narrow ridge corresponding to cuticle just below outer ledge prominent, also poral cutinisation [central ridge]. ca. x 2160.
138. Sparattanthelium tupiniquorum. Subsidiary cell/surrounding cell flanges [SOF] low, conspicuous with coarser protrusions than elsewhere. Subsidiary cells very narrow. Guard cell/subsidiary cell flanges inconspicuous. Periclinal surface of stoma almost smooth [very finely granular]. Wide central rim representing cuticle at base of outer ledge distinct, also poral cutinisation. Guard cells with short incomplete rods and bars [B] at poles. ca. x 2150.

Stomata: Austrobaileyaceae, Gomortegaceae, Hernandiaceae
and Trimeniaceae

Inner surface of isolated cuticles.

133. Austrobaileya scandens. Anomocytic organisation [subsidiary cells not distinguishable]. Inner ledge [IL] prominent, wide; associated with cutinisation of guard cell inner walls at poles [obscuring T-pieces]. Reticulate protrusions [P] and depressions [D] of guard cell periclinal surface coarser than elsewhere. ca. x 1250.
134. Gomortega keule. Paracytic organisation [subsidiary cells distinct]. Subsidiary cells with lateral folds and evidence of secondary division. Guard cell periclinal cuticle finely granular, less complex than subsidiary cell ornamentation, with concentric striae. Guard cell polar T-pieces present [B]. ca. x 970.
135. Piptocalyx moorei. Subsidiary cell/surrounding cell flanges [SOF] Ω -undulate of deeper prominence than non-specialised cell flanges. Note presence of secondary flange [SF]. Guard cell/subsidiary cell flanges [GSF] especially low, curved. Cutinisation of guard cell inner walls obscuring T-pieces at poles. ca. x 1250.
136. Trimenia weinmanniaefolia. Subsidiary and guard cell periclinal surface with concentric striae, of particular prominence associated with subsidiary cells. Ridges smoother than furrows. Guard cells with polar thickening consisting of short incomplete rods. ca. x 1250.



in the other families. In members of the small families, the guard cell/subsidiary cell flange is a distinct anticlinal projection (curved) bounding the guard cell and is reminiscent of flanges of a non-specialised cell [see Text-Fig. 12]. However, in Lauraceae the flange associated with the guard and subsidiary cells merges without trace into the periclinal cuticle of the guard cell [see p. 212] producing a structure which is often 'wing'- or 'scale'-like in form and is, therefore, dissimilar to ordinary flanges [see Text-Fig. 13]. The Lauraceae cutinised portion of the guard cell (including GSF) never outlines a cell on the inner surface of the cuticle but arises at an angle on either side of the stomatal aperture. The extreme edge of this 'wing' corresponds to the guard cell/subsidiary cell flange and is usually tapered, e.g. in Alseodaphne oblanceolata (Fig. 125) and Systemonodaphne mezii although sometimes, it may be more blunt, as in Neocinnamomum spp. (Fig. 121).

In Lauraceae, the size and extent of cutinisation of the two parts (the guard cell/subsidiary cell flange and the periclinal cuticle) constituting the guard cell 'wing', determines its shape and size. The shape of these cutinised portions expressed in terms of a length:width ratio [Text-Fig. 15D] varies in surface view, from short and wide or obtuse, [1:w 1.6:1], in Cryptocarya ainikini to long and narrow or acute [1:w 21.0:1], in Cinnadenia paniculata. Most taxa have 'wings' with ratios of up to 6.0:1, for example, Aniba spp. [2.8:1] (Fig. 110), and Potameia spp. [5.7:1], although sometimes the cutinised parts are more acute, as in Apollonias arnottii [10.0:1] and Phoebe spp. [P. opaca 1:w 6.7:1; P. sheareri 1:w 9.0:1]. Eusideroxylon melagangai, with stomata on both surfaces possesses guard cell 'wings' of the obtuse form, especially so on the adaxial [adx. 1:w 1.3:1; abx. 1:w 2.7:1, i.e. adx. 'wing' is twice as obtuse as abx. 'wing']. The wing-like appendages may sometimes look narrower and more acute from above when they are orientated at a high angle [approaching 90°] to the periclinal surface. In any cuticle, a range of 'wing' orientations may be found; the length to width ratio must be based on dimensions taken

from cutinised portions which lie flat or almost so.

The polar tips of these 'wings', are often predominantly blunt, e.g. in Alseodaphne oblanceolata [Fig. 125] or more rarely, tapering, as in Laurus spp. [Figs 323, 324]. This aspect may depend, to some extent, on orientation of the guard cell 'wing' [best observed with S.E.M.]; the upright positions accentuating sharpness of the tip [see Fig. 109] and it also shows a degree of correlation with the main shape of the cutinised parts. Obtuse 'wings' (in flattened position) tend to be rounded at their tips, e.g. in Ocotea laevis (1:w 2.8:1) [Fig. 113] and the more narrow, elongate appendages regularly have pointed ends, such as in Neolitsea dealbata (1:w 10.0:1) [Fig. 130]. Of course, there are a number of exceptions, particularly amongst the obtuse 'winged' taxa, for example Nectandra pichurum (1:w 3.6:1) [Fig. 120] and Nothaphoebe umbelliflora (1:w 3.0:1) [Fig. 119], which possess conspicuously tapering 'wing' tips. Sometimes within one preparation tips may vary in shape, as in Nectandra salicifolia and Phyllostemonodaphne geminiflorum.

It may also be possible to detect some degree of curvature of the polar 'wing' tips: either inwards, e.g. in Endlicheria reflectens and Systemomodaphne mezii or, slightly outwards, as in Actinodaphne stenophylla and Endiandra kingsiana.

The lateral margins of the 'wings' are generally variously curved [convex] e.g. in Dehaasia caesia [Fig. 111] and Endlicheria piriformis [Fig. 114]. However, two rather interesting modifications occur: the curved outline may show a slight indentation in the mid-zone, which may perhaps be interpreted as a U-form undulation sinus, as in Dicypellium caryophyllatum [Fig. 117] or, the margin may be protruded into a tapering peg-like appendage in the middle region, e.g. in Cinnamomum oliverii [Fig. 124]. 'Wing' indentation appears to be only a predominant pattern, sometimes indistinguishable in certain 'wings' of a cuticle. The second modification, however, is a regular feature of all cutinised guard cell 'wing' parts

intraspecifically [see Figs 299, 300].

Occasionally, the 'wings' seem more or less straight at the margin, such as in Nectandra pichurim (Fig. 120).

12.5.2k POSITION OF GUARD CELL 'WING'

12.5.2k (i) WITH RESPECT TO APERTURE

'Wings' of Lauraceae members may be observed, particularly with scanning electron microscopy, to extend to varying lengths [l^1] when compared with the aperture length [l] (Text-Fig. 15D). The position of the guard cell 'wing' in relation to the aperture may thus be expressed in terms of the ratio $l:l^1$. The resulting values reveal that there are three main patterns: the aperture may be shorter than the 'wings', with a minimum of 0.4:1 [Alseodaphne oblanceolata: Fig. 125] for example, in Aniba megaphylla [$l:l^1$ 0.5:1] (Fig. 110); both aperture and 'wings' may be more or less similar in length, with ratios of approximately 1.0:1, e.g. in Dehaasia caesia (Fig. 111) and Nothaphoebe umbelliflora (Fig. 119) or, the aperture may be longer than the 'wings', with a maximum value of 1.5:1 [Mezilaurus lindaviana], such as in Potameia crassifolia [$l:l^1$ 1.1:1]. Most taxa have 'wings' which fall between the first two categories especially in the range 0.6 to 1.0, e.g. Laurus spp. [L. canariensis: 0.9:1, L. nobilis: 0.8:1] and Nectandra spp. [N. pichurum: 0.8:1; N. salicifolia: 0.7:1 (Fig. 120)]. Those of the adaxial stomata in Eusideroxylon melagangai [$l:l^1$: 0.7:1] (Fig. 115) are very similar in position with respect to the aperture to the abaxial (Fig. 116) and also occur within the commonest pattern group. Members of the third category are rare in comparison.

12.5.2k (ii) WITH RESPECT TO SUBSIDIARY CELL BOUNDARY

Guard cell 'wings' also extend to varying degrees [from pole to pole] across the subsidiary cell pair. Again a ratio, of wing length [l^1]:subsidiary cell length [l^2], is useful for demonstration of the variation. Average values range from when the wing length is about half the subsidiary cell pair length, minimum $l^1:l^2$ of 0.5:1,

in Dodecadenia grandiflora to when the wing length is approaching the subsidiary cell length, with a maximum value of 0.9:1, in Neocinnamomum caudatum [Fig. 121]. In the majority of taxa, 'wings' tend to be intermediate, i.e. between about 3/5 and 4/5 the subsidiary cell length [$1^1:1^2$ 0.6-0.8:1] such as in Nothaphoebe umbelliflora [$1^1:1^2$ 0.6:1] [Fig. 119], Sassafridium macrophyllum [$1^1:1^2$ 0.7:1] [Fig. 122] and Aiouea guianensis [$1^1:1^2$ 0.8:1]. Adaxial and abaxial guard cell 'wings' of Eusideroxylon melagangai also have values [0.6:1] in this same range.

More rarely 'wings' are in the $1^1:1^2$ ranges below 0.6:1, for example Dehaasia caesia [Fig. 111] and Dicypellium caryophyllatum [Fig. 117] [0.5:1], or above 0.8:1, as in Aniba megaphylla [0.9:1] [Fig. 110] and certain Ravensara spp. [R. aromatica $1^1:1^2$ 0.8:1, R. elliptica $1^1:1^2$ 0.9:1].

12.5.21 PRESENCE AND FORM OF POLAR THICKENING

Where the guard cells meet, the common wall may be thickened with cutin. This feature may only be observed in cuticular preparations of members of families related to Lauraceae where the guard cells are always distinctly delimited. In isolated cuticles of the latter family, the relevant portion does not remain [see p.224].

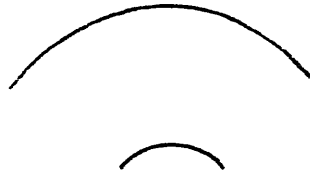
Various patterns of polar thickening may be detected as well as the situation where the common wall is not thickened, [Text-Fig. 17], e.g. in Gyrocarpus americanus and Illigera spp. [Figs. 132, 137].

The thickening may consist simply of a variously elongate, rod-like portion orientated along the wall from the aperture pole, or may consist of a rod plus a cross-piece or bar of various forms, situated at the guard cell pole.

Rods may occasionally be faint, marked only by beads of cutin in the S.E.M., as in Gomortega keule [Fig. 134] or more commonly, thin but continuous [a narrow ca. 0.4 μ m

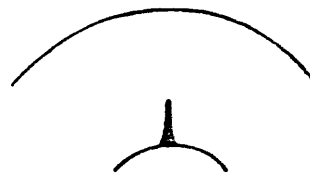
TEXT-FIGURE 17. Diagram showing patterns of polar thickening in guard cells [in families related to Lauraceae only]: rods, bars and T-pieces as seen on the inner surface of isolated cuticles by S.E.M.

A



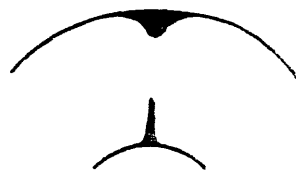
NONE

B



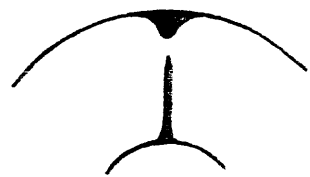
INCOMPLETE ROD

C



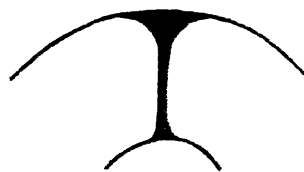
INCOMPLETE ROD (SHORT)
& BAR

D



INCOMPLETE ROD (LONG)
& BAR

E



COMPLETE ROD & BAR
= T-PIECE

solid line), e.g. in Hernandia spp. [Fig. 131] and Trimeria spp. [Fig. 136]. They may also sometimes be thick (a wide ca. 1.9 μm solid line), as in Austro-baileya scandens. Rods may be either complete, extending from the aperture to the guard cell pole to meet with a bar producing a 'T'-piece, e.g. in Piptocalyx moorei and Sparattanthelium guianense or incomplete, the cutin rod-thickening being confined to a portion of the common wall between the guard cells extending from the aperture side. Two main incomplete rod lengths may be recognised: short, which project just beyond the aperture pole to approximately $\frac{1}{4}$ common wall length, as in Hernandia olivacea [Fig. 131] and Trimeria weinmanniaefolia [Fig. 136] or long, extending almost to the guard cell pole, e.g. in Hernandia nymphiifolia and Trimeria papuana. Taxa with incomplete rods sometimes have, in addition, a bar at the pole of the guard cells, for example, in Trimeria papuana and Sparattanthelium tupiniquinorum [Fig. 138].

Occasionally, where thickening is in the form of a 'T'-piece, an extensive membrane-like structure seems to be associated with the 'T' obscuring its outline [see Figs 133, 135]. This could be produced by cutinisation of the inner walls of the guard cells at their ends. Observations of sections through the stoma provide evidence that this is so.

12.5.2m PERICLINAL SURFACE SCULPTURE

Where the outlines of guard cells are distinctly marked on the inner surface of a cuticle, as in all members of families related to Lauraceae, the periclinal region may easily be detected and its associated microrelief observed in the S.E.M. However, in Lauraceae, examination of the periclinal cuticle and assignation of types of sculptural elements present is difficult, due to its relatively small size and its gradation into the guard cell/subsidiary cell flange. The zone of the guard cell wings corresponding to the periclinal surface may be determined with the aid of transverse sections.

In the light microscope, the cuticle/cellulose wall

interface in this area appears even in all taxa, giving no indication of ornamentation, except in Austrobaileya scandens [Text-Fig. 21A]. However, scanning electron microscopy reveals that only a few Hernandiaceae, e.g. Gyrocarpus americanus, Illigera pentaphylla [Fig. 132] and Sparattanthelium guianense, lack any form of micro-relief in the periclinal region of the guard cell. In all others, even those taxa with smooth abaxial epidermal periclinal cuticle and many of those with both protrusions and depressions constituting the non-specialised cell periclinal sculpture, the surface is always ornamented with protrusions. A few species also show depressions, generally taxa in which the element occurs in the periclinal region of ordinary cells, for example in Austrobaileya scandens [Fig. 133], Dodecadenia grandiflora and Neocinnamomum spp. although this is not always so, as in Potameia spp. which exhibit an ornamentation of protrusions only.

The variation in ornamentation of the guard cell periclinal surface found within the assemblage may be most usefully described under the same headings used previously for inner periclinal surface sculpture [p. 127].

12.5.2m (i) SIZE OF ELEMENTS

Protrusions. These range in size from very fine [less than 0.2 μm , with a minimum of about 0.04 μm], e.g. in Endiandra spp. Gomortega keule [Fig. 134], Illigera pulchra [Fig. 137] and Ocotea guianensis to moderately coarse, with a maximum of 0.7 μm in Austrobaileya scandens [Fig. 133]. The protrusions of many taxa are never more than approximately 0.2 μm in diameter, such as those of Dehaasia caesia [ca. less than 0.2 μm -0.4 μm] [Fig. 111], Eusideroxylon spp. [ca. 0.2 μm or less [Figs 115, 116], Licaria spp. [ca. 0.2-0.4 μm], Systemonodaphne mezii [ca. 0.4 μm] and Urbanodendron verrucosum [ca. less than 0.2 μm] [Fig. 112]. There are exceptions, however, with some protrusions attaining a diameter of 0.5 μm , e.g. Cinnamomum camphora [Fig. 123], Dicypellium caryophyllatum [Fig. 117] [ca. 0.4-0.5 μm] Laurus spp. [Figs 323, 324] and

Trimenia weinmanniaefolia [Fig. 136] (ca. 0.2-0.5 μm).

Depressions. Diameter varies from very fine (less than 0.2 μm , as for protrusions), as in Neocinnamomum delavayi to coarse, with a maximum of about 1.1 μm , in Austrobaileya scandens [Fig. 133]. Again, like protrusions these depressions tend never to be more than approximately 0.4 μm ; e.g. Actinodaphne stenophylla [ca. 0.2 μm], Aiouea saligna [ca. 0.2 μm or less], Ravensara aromatica [less than 0.2 μm] and Sassafridium macrophyllum [ca. less than 0.2 μm - 0.4 μm].

Where both protrusions and depressions exist, the latter element type tends to be smaller in size than the former, except in Austrobaileya scandens [Fig. 133] which shows at least some depressions of larger dimensions than the protrusions.

12.5.2m (ii) DENSITY OF ELEMENTS. Individual or groups of elements, predominantly protrusions, may vary in their degree of separation on the guard cell periclinal surface. Frequently, the sculpture may be regarded as dense, for example in Aniba megaphylla [Fig. 110], Illigera pulchra [Fig. 137], Ocotea laevis [Fig. 113] and Piptocalyx moorei [Fig. 135]. In other taxa, elements are widely separated, such as in Cinnamomum iners, Gomortega keule [Fig. 134], Micropora curtisii [Fig. 126] and Ravensara pervillei. Many intermediates in sculptural density may be recognised between these two extremes, including that of Cinnamomum camphora [Fig. 123], Hernandia nymphiifolia, Persea americana and Phoebe sheareri [Fig. 128].

Elements may sometimes be separated to a greater degree in the region of the periclinal surface adjacent to the aperture than in the remainder of the guard cell cuticle as in Cinnamomum camphora [Fig. 123], Dehaasia caesia [Fig. 111] and Dicypellium caryophyllatum [Fig. 117]. More commonly, the reverse situation is detected, e.g. in Austrobaileya scandens [Fig. 133], Endiandra spp. and Potameia spp.

12.5.2m [iii] ARRANGEMENT AND FORM OF ELEMENTS

Protrusions. These are often found as individual granules on the guard cell periclinal surface, for example, in Gomortega keule (Fig. 134), all Hernandiaceae members with the element in this region (Fig. 138) and many Lauraceae, such as species of Cryptocarya, Endiandra and Neocinnamomum. Granules may be accompanied by clumps of protrusions in the periclinal area of the guard cells, in others, e.g. Dehaasia caesia (Fig. 111), Laurus spp. (Figs 323, 324) and Piptocalyx moorei (Fig. 135), or may be organised into reticula, as in Aniba megaphylla (Fig. 110), Ocotea laevis (Fig. 113), Systemonodaphne mezii and Trimenia weinmanniaefolia (Fig. 136). Protrusions arranged into clumps and reticula are occasionally observed on the guard cell periclinal surface, for example, in Persea spp., Phoebe sheareri (Fig. 128) and Sassafras albidum var. molle.

Individual protrusion elements tend always to be rounded when they occur in the guard cell periclinal area.

Depressions. When present, it is most usual to find these elements in the simplest form, pits. Only two other patterns may be detected: pits and clumps, in Alseodaphne semecarpifolia and reticula, in Austrobaileya scandens (Fig. 133).

Commonly, protrusions and depressions are organised to a similar level of complexity, when both are constituents of the guard cell periclinal microrelief, as in Alseodaphne spp., Austrobaileya scandens (Fig. 133) and Neocinnamomum spp. However, where they are not, the depressions often form simpler arrangements than the protrusions (d. pits; p. granules - clumps), e.g. in Aiouea saligna, Dodecadenia grandiflora and Ravensara aromatica.

12.5.2m [iv] PROMINENCE OF ELEMENTS. Cutin particles or groups of protrusions frequently appear rather smooth topped in the S.E.M. on the guard cell periclinal surface, for example, in Alseodaphne oblanceolata (Fig. 125),

Endlicheria piriformis (Fig. 114) and Eusideroxylon spp. (Fig. 115), particularly when densely arranged in a reticulum, such as in Licaria triandra, Nectandra salicifolia and Systemonodaphne mezii. Protrusions of greater prominence, producing a lumpy topography, may be found in a variety of taxa including Austrobaileya scandens (Fig. 133), Laurus spp. (Figs 323, 324) Mezilaurus lindaviana and Persea americana.

Depressions look especially deep on the guard cell periclinal surface of A. scandens (Fig. 133) and more shallow in most others with these elements, notably Neocinnamomum spp. (Fig. 121) (although this cannot be stated with certainty: see p. 140).

12.5.2m (v) SCULPTURAL DIFFERENCES BETWEEN NON-SPECIALISED CELL AND GUARD CELL PERICLINAL SURFACES

The sculpture of the periclinal surface of the guard cell may be similar to that of non-specialised cells in a restricted number of Lauraceae: Beilschmiedia madang, Cryptocarya alleniana, Phoebe opaca and Ravensara pervillei. In all others, differences between the periclinal microrelief of the two cell types may be detected. These may involve one or more of the four main factors (previously described on p.127) which influence the appearance of the constituent sculptural elements, particularly the size and arrangement of protrusions. Examples include Alseodaphne semecarpifolia [g.c. d. more complex], Aiouea saligna [g.c. d. finer & simpler], Austrobaileya scandens [g.c. p. & d. coarser; d. only more complex] (Fig. 133), Dehaasia caesia [g.c. p. finer & simpler] (Fig. 111), Dicypellium caryophyllatum [g.c. p. coarser] (Fig. 117), Nothaphoebe umbelliflora [g.c. p. more complex] (Fig. 119) and Sassafridium macrophyllum [g.c. p. coarser; d. finer].

12.5.2n PATTERN OF STRIAE ASSOCIATED WITH GUARD CELL

Examination of the outer side of isolated cuticles and portions of unmacerated leaf reveals that in Lauraceae, where the guard cell cuticle is visible due to the presence of a low subsidiary cell outer periclinal wall dome or a wide or a shallow stomatal pit (Figs 79, 81, 86, 96), the surface is smooth, i.e. striae (ridges or folds in

the cuticle] are absent. This is also the situation in some taxa of the related family Hernandiaceae, e.g. Illigera spp. [Figs 101, 102] and Sparattanthelium spp. In all others, a system of concentric rings of rounded ridges or striae with the aperture at its centre may be observed on the guard cell surface, particularly in isolated cuticular preparations. These striae tend to commence at the edge of the outer ledge furthest from the pore and continue outwards. Striae may vary in prominence from low, barely raised from the surface, such as in Gyrocarpus americanus and Trimenia weinmanniaefolia to high, with distinct ridges separated by deep furrows [dark in the S.E.M. and indicative of some depth], e.g. in Austrobaileya scandens [Fig. 83]. Intermediates in prominence may be recognised, in Gomortega keule [Fig. 84] and Trimenia papuana, for example.

The course described by the individual striae may be conspicuously undulate or wavy, especially those nearest to the subsidiary cell producing a wrinkled pattern, such as that shown by Austrobaileya scandens [Fig. 83], or striae may be straighter, e.g. in Gyrocarpus americanus, and Hernandia olivacea [Fig. 100]. The width or diameter of the striae may also be variable: occasionally, they may be fine, approximately 0.4-0.5 μm , as in Gyrocarpus americanus or more usually coarse, greater than 0.7 μm , e.g. Austrobaileya scandens [0.8-1.0 μm] [Fig. 83], Hernandia olivacea [0.7-0.9 μm], [Fig. 100] and Piptocalyx moorei [0.7-0.8 μm].

Guard cell striae are represented to varying degrees on the cuticle inner surface. They may sometimes be inconspicuous, as in Austrobaileya scandens [Fig. 133], Piptocalyx moorei [Fig. 135] and Trimenia papuana; rarely, more conspicuous on the inside than on the outside of the guard cell periclinal surface, e.g. in Trimenia weinmanniaefolia [Fig. 136], but may more often be similar in conspicuousness on both surfaces, as in striate Hernandiaceae and Gomortega keule [Fig. 134].

The alternating ridge and furrow system on the outside of the guard cell cuticle, in such taxa, corresponds to a furrow and ridge pattern respectively on the inner surface. At the apex of each internal ridge, the fine periclinal sculpture may occasionally be modified: it may appear smoother than the sides and basal region, e.g. in Trimenia weinmanniaefolia [Fig. 136].

12.5.2o GUARD CELL/SUBSIDIARY CELL FLANGE SCULPTURE

As in the case of the guard cell periclinal surface, in the S.E.M., the guard cell/subsidiary cell flange and its sculpture may only be distinguished with ease in species where the guard cell outlines are marked on the cuticle, that is, in all members of families related to Lauraceae. In the latter family, where the guard cell cutinised parts form a pair of wing-like appendages, the guard cell/subsidiary cell flange is located at the wing edge and it intergrades, without trace, into the periclinal surface of the rest of the wing. The area representing the flange on the wing may be estimated from leaf transverse sections. Light microscopic examination of the cuticle/cellulose wall boundary at the guard cell/subsidiary cell flange, in such preparations, show that it is even in most taxa, except Austrobaileya scandens [Text-Fig. 21A], Gomortega keule and Hernandia spp. [Text-Fig. 22A].

The scanning electron microscope, however, reveals that this specialised flange is completely unornamented in only two taxa, Gyrocarpus americanus and Systemonodaphne mezii. Most others have an ornamentation of protrusions on the guard cell/subsidiary cell flange, even species with smooth ordinary flanges and many of those where both element types are represented. Occasionally, protrusions and depressions may be detected on the guard cell/subsidiary cell flange surface, usually just in taxa where such elements occur on non-specialised flanges, e.g. Aiouea saligna, Austrobaileya scandens [Fig. 133], Endiandra spp. Illigera spp. [Figs 132, 137].

Variation in the appearance of the microrelief found on the guard cell/subsidiary cell flange surface in the

taxa examined may be best described under the same sections used for the periclinal sculpture.

12.5.2o (i) SIZE OF ELEMENTS

Protrusions. These range in size from very fine [diameter less than 0.2 μm , with a minimum of approximately 0.04 μm], as in Gomortega keule [Fig. 134], Licaria guianensis, Ocotea guianensis and Trimenia papuana to moderately coarse, with a maximum of up to 0.5 μm , e.g. in Dicypellium caryophyllatum [Fig. 117], Hernandia olivacea [Fig. 131] and Umbellularia californica. Most taxa exhibit protrusions of up to about 0.4 μm in diameter on the guard cell/subsidiary cell flange, such as Cinnamomum spp. [C. camphora: ca. 0.2-0.4 μm , other species: ca. less than 0.2 μm - 0.4 μm] [Figs 123, 124], Eusideroxylon spp. [ca. 0.2 μm or less] [Figs 115, 116], Piptocalyx moorei [ca. less than 0.2 μm] [Fig. 135] and Urbanodendron verrucosum [ca. less than 0.2 μm - 0.4 μm] [Fig. 112]. Certain others do, however, have some protrusions with greater dimensions, for example those with the maximum protrusion diameter mentioned above, Laurus spp. [Figs 323, 324], Sassafridium macrophyllum and Sparattanthelium tupiniquinorum.

Depressions. These vary in diameter from very fine [less than 0.2 μm , as protrusions] e.g. in Illigera pulchra [Fig. 137] and Neocinnamomum spp. [Fig. 121] to fine, with a maximum of about 0.4 μm , in Endiandra rubescens. The majority of taxa with these elements on the guard cell/subsidiary cell flange never have depressions greater than 0.2 μm in size, e.g. Actinodaphne stenophylla [ca. 0.2 μm], Austrobaileya scandens [Fig. 133], Hernandia olivacea [Fig. 131] [ca. 0.2 μm or less] and Ravensara aromatica [less than 0.2 μm].

In all cases where both protrusions and depressions constitute the sculpture of the guard cell/subsidiary cell flange, depressions are finer than protrusions.

12.5.2o (ii) DENSITY OF ELEMENTS. This, expressed in terms of the separation of individual or groups of sculptural components (primarily protrusions) may vary between taxa. Dense ornamentation is characteristic of the guard cell/subsidiary cell flange in many species, for example, in Austrobaileya scandens [Fig. 133], Dicypellium caryophyllum [Fig. 117], Illigera spp. [Figs 132, 137], Nothaphoebe umbelliflora [Fig. 119] and Trimenia papuana. Widely separated elements occasionally occur in others, such as Actinodaphne glomerata, Cinnamomum iners, Ravensara pervillei and Trimenia weinmanniaefolia [Fig. 136]. Sculpture somewhat intermediate in density may also be detected on this specialised flange in a number of different taxa, e.g. Endiandra rubescens, Laurus spp. [Figs 323, 324] and Potameia thouarsii.

12.5.2o (iii) ARRANGEMENT AND FORM OF ELEMENTS

Protrusions. A range of patterns may be seen on the guard cell/subsidiary cell flange. The simplest, granules, is most common in occurrence, being exhibited by many Lauraceae, such as Alseodaphne oblanceolata [Fig. 125], Cryptocarya spp. and Eusideroxylon spp. [Figs 115, 116] and some members of related families e.g. Gomortega keule [Fig. 134], Hernandia nymphiifolia and Piptocalyx moorei [Fig. 135]. Clumps of protrusions may be observed in addition to granules in others, including Alseodaphne semecarpifolia, Dehaasia caesia [Fig. 111], Laurus spp. [Figs 323, 324] and Sparattanthelium tupiniquinorum, and also occasionally reticula, as in Hernandia olivacea [Fig. 131] and Trimenia weinmanniaefolia [Fig. 136]. Clumps and reticula occur on the guard cell/subsidiary cell flange in a few taxa, Endiandra kingsiana and Illigera pulchra [Fig. 137] and a number show protrusions of the reticulate form only, such as Aniba megaphylla [Fig. 110], Austrobaileya scandens [Fig. 133], Licaria triandra and Ocotea laevis [Fig. 113]. Individual protrusions are always rounded.

Depressions. Generally, these are of pit-like form only on the guard cell/subsidiary cell flange, in those

taxa with this sculptural element. Clumps of pits may also be present in Endiandra rubescens.

When both element types are found together on this specialised flange, depressions are usually more simply organised than protrusions, except in Neocinnamomum spp. [Fig. 121] where the elements have a similar level of complexity.

12.5.2o [iv] PROMINENCE OF ELEMENTS. The S.E.M. shows this feature, particularly in the case of protrusions, to vary on the guard cell/subsidiary cell flange surface. Protrusion elements which barely protrude from the cutin matrix and, therefore, produce a rather smooth look to the sculpture, may sometimes be observed, for example in Endlicheria piriformis [Fig. 114], Hernandia nymphiifolia, Illigera spp. [Figs 132, 137] and Neocinnamomum caudatum [Fig. 121]. Other taxa possess prominent cutin particles or groups of protrusions which form a lumpy surface to the guard cell/subsidiary cell flange, such as in, Endiandra rubescens, Laurus spp. [Figs 323, 324], Micropora curtisii [Fig. 126] and Piptocalyx moorei [Fig. 135]. Protrusions of intermediate prominence may also occur, e.g. in Gomortega keule [Fig. 134], Hernandia olivacea [Fig. 131] and Hypodaphnis zenkeri.

Depressions of the guard cell/subsidiary cell flange in Endiandra rubescens appear especially deep and those in Neocinnamomum caudatum very shallow when compared with such elements of the same region in other species. Most taxa, however, seem to have shallow depressions and Austrobaileya scandens [Fig. 133] somewhat intermediate between the two extremes, although accurate estimation of depth is impossible in the S.E.M. [see p.140].

12.5.2o [v] SCULPTURAL DIFFERENCES BETWEEN NON-SPECIALISED AND GUARD CELL/SUBSIDIARY CELL FLANGES

The microrelief of the guard cell/subsidiary cell flange is similar in all respects to that of ordinary flanges in only one species, Beilschmiedia madang. In all others, the sculpture is different on the two flange types. Differences may be attributed to variation in one or more of the factors already described [see p.127],

which have a profound effect on the appearance of the ornamentation, especially element size and arrangement. Aspects of protrusions [p.] are responsible for much of the sculptural variation between the guard cell/subsidiary cell flange [GSF] and the non-specialised, epidermal flanges [OF]. Examples showing such differences include Gomortega keule [GSF. p. simpler] (Fig. 134), Illigera pentaphylla [GSF. p. coarser & simpler], Ocotea laevis [GSF. p. more complex] (Fig. 113), certain Persea spp. [P. chinensis & P. thunbergii: GSF. p. finer & simpler], Sassafras albidum var. molle [GSF. p. finer] and Urbanodendron verrucosum [GSF. p. coarser & more complex] (Fig. 112). Where depressions also exist and exhibit some differences, the resulting pattern on the guard cell/subsidiary cell flange [guard cell/ordinary cell flange in Austrobaileya] is even more dissimilar to that on ordinary flanges, as in Actinodaphne stenophylla [GSF. p. & d. coarser, p. simpler], Austrobaileya scandens [GSF. p. & d. finer, d. simpler] (Fig. 133), Dodecadenia grandiflora [GSF. p. simpler, d. coarser], Endiandra rubescens [GSF. p. & d. coarser, d. more complex], Hernandia olivacea [GSF. p. simpler, d. finer] (Fig. 131) and Neocinnamomum caudatum [GSF. p. & d. simpler, d. finer].

12.5.2p CONTINUITY OF GUARD CELL/SUBSIDIARY CELL FLANGE

The guard cell/subsidiary cell flange is continuous (uninterrupted) in almost all taxa, even in those with some form of discontinuity (gaps or pores) in the ordinary flanges. However, interruptions are present in the flange bordering the guard cells in Austrobaileya scandens (Fig. 133) and occasionally pores (1-2) may be detected at the edge of the wings [i.e. the guard cell/subsidiary cell flange region] in Dicypellium caryophyllatum. These features are also shown by non-specialised flanges in both taxa.

12.5.2q NATURE OF GUARD CELL/SUBSIDIARY CELL FLANGE APEX

The guard cell/subsidiary cell flange is more or less even at its apex in all taxa, regardless of the configuration shown by ordinary flanges.

12.5.3 SUBSIDIARY CELL CHARACTERS

12.5.3a HEIGHT IN T.S.

Thin transverse sections show that subsidiary cells may be of different heights, when measured from the highest point of projection of the subsidiary cell outer periclinal cuticle to the lowest point of the inner wall in the 'closed stoma' position. Average values range from 10.4 μm , in Illigera pulchra to 30.2 μm , in Aiouea guianensis, with various intermediates of, for example, 13.7 μm in Sparattanthelium guianense, 17.4 μm in Beilschmiedia madang [Text-Fig. 24A], 19.5 μm in Endlicheria piriformis, 23.4 μm in Hernandia olivacea [Text-Fig. 22A] and 27.1 μm in Laurus nobilis. The majority of taxa have subsidiary cells with an average height of 19.5 μm or less, as in Gyrocarpus americanus [ssp. africanus: 12.2 μm ; ssp. americanus: 12.8 μm] and Persea spp. [P. americana & P. chinensis: 15.9 μm ; P. thunbergii: 16.5 μm]. Some have taller subsidiary cells, e.g. Micropora curtisii (21.0 μm), Umbellularia californica (21.9 μm) and adaxial Eusideroxylon melagangai (21.4 μm). The latter contrasts with a shorter abaxial subsidiary cell height of 16.8 μm .

12.5.3b THICKNESS OF UNCUTINISED OUTER PERICLINAL WALL COMPARED WITH THICKNESS OF INNER WALL IN T.S.

When the thicknesses of both the uncutinised subsidiary cell outer periclinal and the inner walls are compared in transverse sections, two patterns of relative thickness may be recognised. Walls may be similar in thickness, as in many Lauraceae [see Text-Figs 21B, 23] e.g. Mezilaurus spp. and Persea spp. and most Hernandiaceae, such as, Illigera pentaphylla and Sparattanthelium spp. or, the outer periclinal wall may be conspicuously thicker than the inner wall, as in a number of Lauraceae, for example, Beilschmiedia madang [Text-Fig. 24A], Eusideroxylon zwageri [Text-Fig. 25A] and Ravensara pervillei [Text-Fig. 24B] as well as in several relatives, Gomortega keule, Illigera pulchra and Trimenia weinmanniaefolia.

In a few Lauraceae taxa, Endlicheria piriformis,

Laurus spp. and Micropora curtisii [all with the second type of subsidiary cell wall thickness], the outer periclinal wall is lignified.

12.5.3c CURVATURE OF OUTER PERICLINAL WALL IN T.S.

In transverse section, the subsidiary cell outer periclinal wall surface may be concave (sunken) to convex (domed). The curvature of this wall may be expressed in terms of a ratio; maximum height of the wall above (or below) the anticlinal borders (h): width across the subsidiary cell from the border with the guard cell to that with the surrounding cell (w) [see Text-Fig. 15A]. Taxa of families related to Lauraceae generally exhibit either concave subsidiary cells e.g. Gyrocarpus americanus [ssp. africanus: h:w 0.13:1; ssp. americanus: h:w 0.12:1] or more or less flat, such as Illigera spp. [I. pentaphylla: h:w 0.03:1, I. pulchra: h:w 0.07:1], Piptocalyx moorei [h:w 0.03:1] (Text-Fig. 22B) and Trimenia papuana [h:w 0.05:1]. However, there are a few examples with convex subsidiary cells, notably Hernandia spp. [H. nymphiifolia h:w 0.50:1], H. olivacea h:w 0.21:1] (Text-Fig. 22A). These are especially narrow and, therefore, have quite high h:w ratios.

All members of the Lauraceae possess the convex form of subsidiary cell outer periclinal wall surface [see Text-Figs 21B, 23, 24, 25]. Ratio values range from very low domed, maximum wall height above the anticlinal borders approximately 1/8 of the width across the subsidiary cell, as in Dehaasia caesia [h:w 0.12:1] to very high domed or distinctly papillate where the height is just greater than the subsidiary cell width from the guard cell border to that of the surrounding cell, e.g. in Ravensara aromatica [h:w 1.09:1]. Sometimes taxa have relatively low domed subsidiary cells of height up to ¼ width, as in Dicypellium caryophyllum [h:w 0.15:1], Eusideroxylon melagangai [adx. h:w 0.19:1; abx. 0.20:1] and Nectandra spp. [N. pichurim: h:w 0.22:1; N. salicifolia: h:w 0.16:1], but more commonly, the maximum height is between about ¼ and ¾ subsidiary cell width, for example, in Neocinnamomum spp. [N. caudatum h:w 0.20:1; N. delavayi: h:w 0.31:1] and Micropora curtisii [h:w 0.74: 1]. Occasionally, the

subsidiary cells are even more domed, with heights of more than $\frac{1}{2}$ width [up to 1.0:1], such as in Alseodaphne oblanceolata (h:w 0.95:1) and Pleurothyrium nobile (h:w 0.80:1).

The convexity of the outer periclinal wall of the subsidiary cell in T.S. in Lauraceae members and Hernandia spp. corresponds to their 'bulging' or prominence observed on the outer surface of isolated cuticles or whole leaf mounts in the scanning-electron microscope (e.g. Figs 85-90). On the inner cuticular surface, the dome is often represented by a hollow or scrobiculus, depending on its height and the area of the subsidiary cell involved in its formation (e.g. Figs 118, 119, 123, 127, 130). Such hollows, when h:w is greater than 0.22:1 are similar in type to those resulting from strongly domed or papillate cells in non-specialised regions [see p. 119].

12.5.3d DEPTH OF STOMATAL PIT (SUPRASTOMATAL CAVITY)

When the level of the guard cell periclinal surface is compared with that of the subsidiary cells, best seen in transverse section, three configurations may be recognised. The guard cell pair may be raised above the outer periclinal surface of the subsidiary cells as in most Hernandiaceae (except Hernandia spp.); both guard and subsidiary cells may be approximately level, as observed in members of the Trimeniaceae (e.g. Text-Fig. 22B) or, the guard cells may be sunken below the subsidiary cells, as in all Lauraceae (Text-Figs 21B, 23, 24, 25) and Hernandia spp. (Text-Fig. 22A). Where this third pattern occurs, a stomatal 'pit' is formed, lined by the subsidiary cell cuticle with the guard cell outer periclinal wall and cuticle producing the floor. The extent or depth of the pit (PD) [see Text-Fig. 15A] varies within the assemblage of taxa possessing this form of stomatal organisation, from very shallow (av. 0.61 μm), in Endiandra rubescens to very deep (av. 10.7 μm), in Aiouea guianensis. The pit is often between 2.5 μm and 5.2 μm deep, as in Neocinnamomum spp. (3.0 μm) and Potameia spp. (4.3 μm), although sometimes it may be deeper, up to 8.0 μm , e.g. in Alseodaphne spp. (A.

oblanceolata: 6.1 μm ; A. semecarpifolia: 6.7 μm) and Sassafridium macrophyllum (7.6 μm) or shallower than 2.5 μm , as in Dicypellium caryophyllum (1.8 μm), Eusideroxylon melagangai (adx. 2.1 μm ; abx. 0.9 μm) and Hernandia nymphiifolia (2.4 μm). More rarely, the stomatal pit may be even deeper than 8.0 μm , for example, in Actinodaphne glomerata (8.5 μm) and Laurus spp. (9.8 μm). When the stoma is raised or level with the subsidiary cells, the guard cells are clearly delimited in outer surface view (Figs 83, 84, 99-102). However, in the sunken form, the subsidiary cells commonly obscure the guard cell periclinal cuticle and outer ledges [e.g. Figs 87, 89, 90, 91, 106] unless the stomatal pit is shallow or wide [e.g. Figs 79, 81, 86, 93, 96].

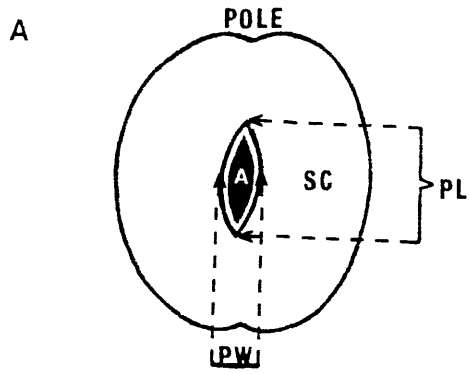
12.5.3e SHAPE OF STOMATAL PIT IN SURFACE VIEW

The opening of the stomatal pit (sunken stomata only) may vary in shape and size in surface view, and may be seen to most advantage with scanning electron microscopy. A ratio of 'pit' length [PL] to width [PW] may be used to demonstrate the range of variation [Text-Fig. 18A,B]. Three patterns emerge: the pit may be wider than long producing a wide, oval shape, with a minimum average value of 0.8:1 as in Aniba megaphylla and Systemonodaphne mezii; of more or less the same width and length giving a rather isodiametric shape [PL:PW 1:1], e.g. in Endlicheria spp. [E. piriformis: PL:PW 1.5:1, E. reflectens: PL:PW 1.2:1] (Fig. 79), and Eusideroxylon melagangai (adx. PL:PW 1.0:1; abx. PL:PW 1.1:1) (Fig. 96) or, longer than wide, resulting in various narrow oval, elliptical or slit-like shapes, with a minimum average length to width ratio of approximately 2.0:1, as in Endiandra spp. and a maximum of 14.3:1, in Lindera strychnifolia. The stomatal pit opening is usually of the third form [see Figs 87, 88, 89, 90, 91, 106, 108]. Most taxa have average PL:PW values in the lower end of the range, up to 6.0:1, e.g. Laurus spp. [L. canariensis 5.5:1, L. nobilis 5.2:1] and Neolitsea spp. (2.4:1), although there are a number of exceptions, such as certain Cinnamomum spp. [C. iners: PL:PW 14.1:1; C. oliverii: 9.6:1; C. pachyphylum: 6.9:1].

TEXT-FIGURE 18. Diagram of subsidiary cell features as seen from outer surface of cuticle by S.E.M.

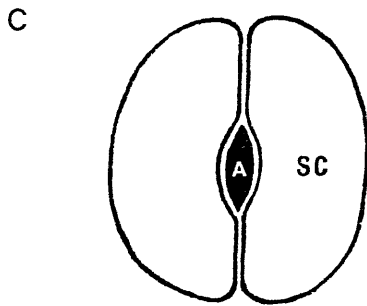
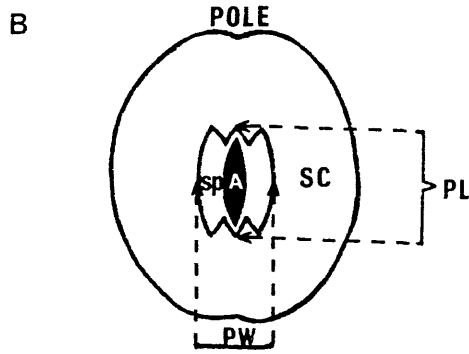
A,B. Shape of stomatal pit: A, elliptical; B, with tridentate ends.

C,D,E. Different degrees of prominence of ^{apparent} wall between adjacent subsidiary cells.



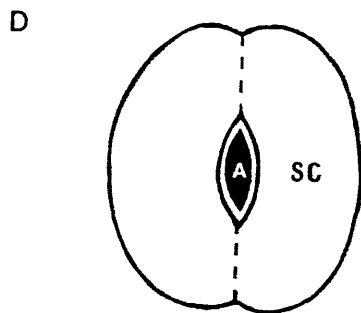
SHAPE OF STOMATAL PIT(sp)

PL:PW

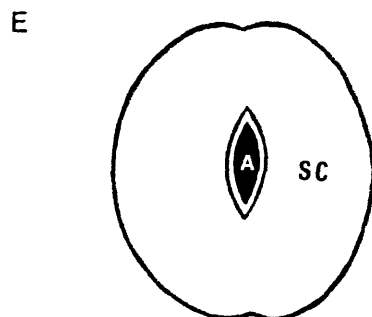


SUBSIDIARY CELL POLES

-DISCRETE



-PARTIALLY FUSED



-ENTIRELY FUSED

The lateral walls of the pit curve inwards in surface view and usually terminate bluntly at the poles, e.g. in Ravensara spp. [R. elliptica, R. pervillei] and Sassafridium macrophyllum (Fig. 106) or more rarely, sharply taper, as in Beilschmiedia micrantha (Fig. 88) and Licaria guianensis. However, the shape of the polar ends of the pit is not always distinct.

Those taxa with the more isodiametric stomatal pit opening may show a rather characteristic shaped polar pit wall which can be described as 'tridentate' since three rather pointed crests [inverted V s] are observed in surface view. Particularly good examples of this configuration are seen in Dicypellium caryophyllum, Endlicheria spp. (Figs 79, 80) and Eusideroxylon melagangai (Fig. 96).

12.5.3f DEFINITION OF WALL BETWEEN ADJACENT SUBSIDIARY CELLS AT THE STOMATAL POLES ON THE OUTER SURFACE

Scanning-electron microscopic examination of the subsidiary cell pair domes in taxa with sunken guard cells, reveals that, at the poles, the wall between adjacent subsidiary cells may be variously defined giving rise to different degrees of apparent fusion of the cells. Three main configurations may be recognised from whole leaf mounts and the outer surface of isolated cuticles (Text-Fig. 18 C-E). Subsidiary cell domes may be discrete at the poles, either widely separated as in Sassafras albidum var. molle (Fig. 85) and Umbellularia californica, or more usually situated closely together and sometimes just touching, with a well-defined wall between them, e.g. in species of Cinnamomum, Lindera and Persea; partly joined, with a distinct groove raised above the surface between the subsidiary cells at the poles, such as in Aniba spp., Ocotea laevis and Systemonodaphne mezii or, entirely joined at the poles, forming a ring around the stomatal pit, for example in Endlicheria spp. (Figs 79, 80), Eusideroxylon spp. (Figs 95, 96) and Licaria triandra. The third type described is of most common occurrence; the second is relatively rare.

In any cuticle, subsidiary cells may appear to be joined to different degrees so that there is more than one configuration [up to two] present. However, the majority of taxa [those mentioned above] show a predominance of one pattern. There are a few exceptions where this is more variable, as in Aiouea spp. [Fig. 82] and Laurus spp. [Figs 304, 316]. These have stomata of all three types.

The distinctiveness of the 'fusion' configurations is often enhanced by the prominence of the domes of the subsidiary cell outer periclinal wall and cuticle.

In all cases where the tridentate polar pit walls exist, the accompanying subsidiary cells appear to be fused into a ring.

12.5.3g ORIENTATION OF OUTER PERICLINAL WALL IN T.S.

Two aspects influence the shape of the subsidiary cell outer periclinal wall [apart from curvature of the wall itself]. These may be best seen in transverse sections.

12.5.3g (i) ANGLE RELATIVE TO BORDER WITH GUARD CELL

In taxa with sunken guard cells, the latter may or may not be over-topped by the subsidiary cells to varying extents. Part of the subsidiary cell outer periclinal wall, nearest to the guard cells forms the walls of the stomatal pit and these curve from the floor made by the guard cells to the pit mouth, often taking a recognisable sigmoid path e.g. in Aniba spp., Ravensara pervillei [Text-Fig. 24B] and Sassafridium macrophyllum.

The angle between the guard cell border and a tangent to the stomatal pit wall [see Text-Fig. 15A] gives some indication of the steepness of the subsidiary cell dome on the guard cell side and the degree of overhang, if only across the guard cells.

Four main angle configurations may be found: with acute angles less than 45° , resulting in no overhang of

the guard cells by the subsidiary cells and outward curving pit walls, with a minimum value of 23° , in Endiandra rubescens; acute angles more than 45° up to right angles of 90° , with no overhang and outward curving to more vertical stomatal pit walls, for example in Dicypellium caryophyllatum [53°] Hernandia olivacea [89°] [Text-Fig. 22A] and Phoebe opaca [90°]; angles more than 90° up to 135° , producing a slight to more distinct overhang of the guard cells, with inward curving pit walls, as in Licaria spp. [L. guianensis: 106.0° , L. triandra: 94.5°] and Lindera spp. [L. pulcherrima: 130.5° , L. strychnifolia 125.0°] or, angles of more than 135° , where the subsidiary cells often form a roof to the suprastomatal cavity due to the high degree of inward curvature of the pit walls, e.g. in Sassafridium macrophyllum [maximum of 158.5°].

Most taxa have subsidiary cells with some degree of overhang [more than 90°], especially in the range between 90° and 135° . Those with angles less than 90° are more rare in occurrence, particularly the very acute type exhibited by Eusideroxylon melagangai [adx. 32.0° ; abx. 42.0°] and Mezilaurus lindaviana [35.5°], for example.

Together with the depth of the stomatal pit, the above angle measurements may describe the pit shape. A wide range of patterns occur, such as very shallow with walls outward curving and no dome overhang [guard cell cuticle also exposed] e.g. in Endiandra spp. [Text-Fig. 23A]; very shallow with walls approximately vertical, slightly overhanging, as in Phyllostemonodaphne geminiflorum; moderate in depth with distinctly overhanging walls, e.g. in Aniba megaphylla; deep with vertical walls [guard cells obscured completely], as in Endlicheria piriformis; deep with conspicuously overhanging walls [roofed], e.g. in Sassafridium macrophyllum and very deep with slightly overhanging subsidiary cells, as in Aiouea guianensis.

Where guard cells are raised above a level with the subsidiary cells there is no stomatal pit so that its shape or wall pattern cannot be compared in such taxa.

However, the angle may indicate the slope of the subsidiary cell surface: downward, for example in Gyrocarpus americanus and Sparattanthelium spp. (raised stomata) and upward in those with level stomata, as in Piptocalyx moorei [Text-Fig. 22B].

12.5.3g (ii) ANGLE RELATIVE TO BORDER WITH SURROUNDING CELL

The angle between the level of the surrounding cell border and a tangent to part of the adjacent subsidiary cell outer periclinal wall (and cuticle) [see Text-Fig. 15A] reflects its steepness, a particularly important feature in taxa with domed or papillate subsidiary cells. The value is not usually 180° minus the angle of the subsidiary cell relative to the guard cell. It may be negative, indicating a downward slope from the surrounding cell border, with a maximum of -32.0° in Gyrocarpus americanus ssp. africanus, e.g. in certain Cinnamomum spp. [C. iners & C. pachyphyllum: -10.0° ; C. oliverii: -17.0°] [Text-Fig. 25B] and Phoebe opaca [-8.5°] or positive, suggesting an upward slope, with a maximum value of 67.0° in Aniba hostmanniana, as in Actinodaphne stenophylla [21.0°], Beilschmiedia madang [34.5°] [Text-Fig. 24A], Endlicheria spp. [E. piriformis: 50.5° ; E. reflectens: 45.0°], Nectandra spp. [N. pichurim: 5.0° ; N. salicifolia: 11.0°] and Piptocalyx moorei [1.0°] [Text-Fig. 22B].

Taxa with negative values for the angle between the level of the surrounding cell border and a tangent to the subsidiary cell may have basically concave subsidiary cells as in Gyrocarpus americanus ssp. africanus. Generally, they are variously convex (domed or papillate) and either curve downward from the level of the surrounding cell and others of the epidermis e.g. in certain Cinnamomum spp. [Text-Fig. 25B] or more usually, such subsidiary cells are concave towards the border with the subsidiary cell and then dome near the guard cell pair, as in Eusideroxylon zwageri [Text-Fig. 25A] and Phoebe opaca. This latter pattern may often be represented on the leaf or outer cuticle surface by a flat to sunken region in the outermost regions of the subsidiary cells with a rounded ridge or bulging area of various sizes located on either side of

the stomatal pit mouth [see Fig. 93].

12.5.3h PRESENCE OF POLAR PAPILLAE

In one Lauraceae taxon, Beilschmiedia madang, the polar ends of each domed subsidiary cell are extended into a globular papillate lobe, according to transverse sections [Text-Fig. 24A]. Surface views of the outer side of the isolated cuticle and the unmacerated leaf in the S.E.M. reveal that at the stomatal poles, a lobe from each of the two subsidiary cells has fused to form a polar papilla. Various degrees of fusion may be recognised in cuticle preparations ranging from a distinctly bilobed situation to totally fused, the papilla showing no evidence of its constituent lobes. Polar papillae give an almost colourless reaction in sections and cuticles when stained with Sudan IV (compared with the deep red of other cutinised parts) indicating the presence of extremely thin cutinisation over their surface.

12.5.3i MEDIAN PERICLINAL THICKNESS OF CUTICLE IN T.S.

Various patterns of cuticle thickness exist across the periclinal wall of subsidiary cells, in transverse section: the cuticle may be approximately the same thickness over the entire wall (increasing only at flanges), as in many Hernandiaceae and a few Lauraceae, e.g. Beilschmiedia micrantha and Micropora curtisii, or of differing widths over the wall, thinnest near to the guard cell then either (a) abruptly increasing at or near the dome crest, where subsidiary cells are strongly convex, with the maximum thickness towards the subsidiary cell/surrounding cell flange, as in Aniba megaphylla, Beilschmiedia madang [Text-Fig. 24A] and Systemonodaphne mezii, or (b) gradually increasing in thickness, but still thickest near to the flange between the surrounding and subsidiary cells, e.g. in Gomortega keule, Lindera pulcherrima, Litsea spp. and members of the Trimeniaceae [Text-Fig. 22B].

Shape and orientation of the inner surface of the subsidiary cell periclinal cuticle, due to the pattern of differential thickening together with prominence and direction of the outer wall, determines the position and

size of the hollow or scrobiculus [corresponding to the dome or papilla] of the subsidiary cell on the inside of cuticles. For example, in Endlicheria piriformis, the subsidiary cell is strongly domed with a periclinal cuticle of thickness type [a]. The resulting scrobiculus lumen is particularly narrow [0.9 μm] and tubular, orientated almost vertically in T.S. and may be observed with the scanning electron microscope to be a small, deep 'pit' in which the well-developed guard cell 'wings' are situated [see Fig. 114]. In Aniba megaphylla, with a similar subsidiary cell cuticle thickness configuration the dome is far less prominent on the outer surface, orientated at an obtuse angle to the guard cell border in section and the lumen is wider [2.4 μm] producing a much shallower, more conical-shaped scrobiculus which occupies a greater proportion of the subsidiary cell periclinal surface [Fig. 110].

Micropora curtisii, with the subsidiary cell cuticle of even thickness following a wide, domed outer surface in transverse section, appears correspondingly concave or sunken in the same region on the inner surface of the cuticle, in the S.E.M. [Fig. 126].

In Lindera pulcherrima which exhibits the type [b] cuticle thickness pattern over the subsidiary cells, the resulting scrobiculus is very like that of Micropora curtisii, except that it is deeper on the inner surface and occupies most of the subsidiary cell periclinal area. Mezilaurus itauba, with a very low backward directed dome located near to the guard cell, also has a type [b] cuticle thickness pattern over the subsidiary cells in section. In the S.E.M. the scrobiculus is narrow and shallow, the cuticle walls gently sloping outward to just beyond the guard cell 'wings'. The remaining periclinal cuticle is slightly convex due to a concave outer surface adjacent to the small dome.

Comparison of the average cuticle thickness measured in the middle of the periclinal surface of the subsidiary cell [Text-Fig. 15B, C] reveals that values

may vary between very thin (0.3 μm), such as in Beilschmiedia micrantha and Sassafras albidum var. molle and thick (9.4 μm) in Aiouea guianensis. Most taxa have a thin average median subsidiary cell periclinal thickness of 2.7 μm or less, e.g. Cinnamomum spp. [C. camphora: 0.6 μm ; C. iners & C. oliverii: 0.9 μm ; C. pachyphyllum: 1.1 μm] (Text-Fig. 25B), Laurus spp. [L. canariensis: 1.8 μm ; L. nobilis: 1.6 μm] and most Hernandiaceae [range 0.6-1.6 μm]. Exceptions include Eusideroxylon zwageri (6.2 μm) (Text-Fig. 25A), Hernandia olivacea (3.7 μm) (Text-Fig. 22A) and Trimenia weinmanniaefolia (3.3 μm).

Adaxial Eusideroxylon melagangai subsidiary cell median periclinal thickness (3.3 μm) also falls into this thicker category, unlike the abaxial (2.2 μm).

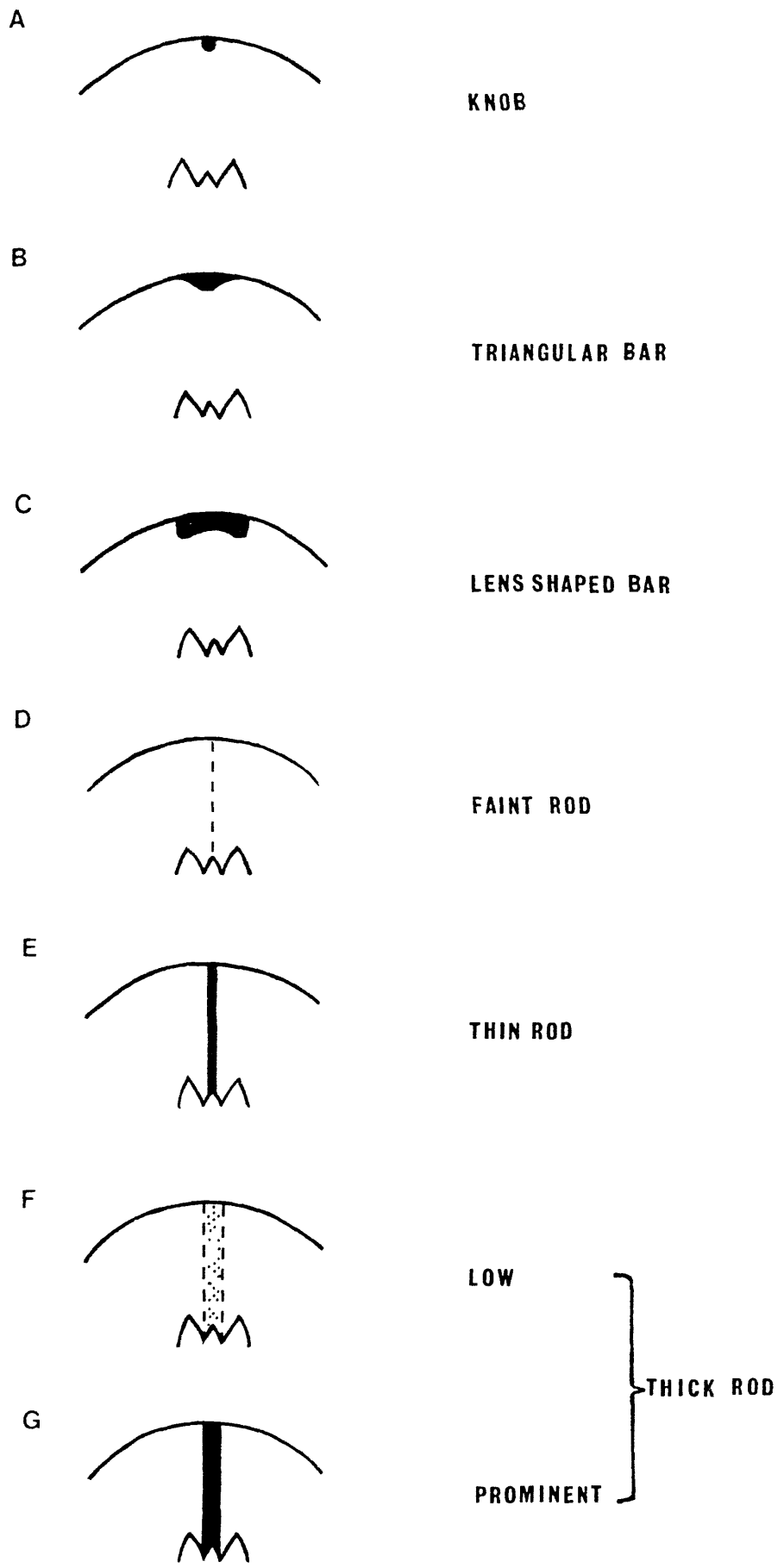
Subsidiary cell median periclinal cuticle is often thinner than the corresponding intercostal cuticle in the middle of the periclinal surface, such as in Beilschmiedia madang, Nothaphoebe umbelliflora and Ravensara pervillei although occasionally it is similar in thickness, e.g. in Persea americana and Piptocalyx moorei, or sometimes thicker than the corresponding intercostal cuticle, as in Aiouea guianensis and Eusideroxylon spp.

12.5.3j PRESENCE AND FORM OF POLAR THICKENING

In many Lauraceae, there appears to be a system of cutin thickening in the subsidiary cell polar region, similar to that which may occur in the guard cells in members of the related families. It may be associated with the common wall between the subsidiary cells and exists in a variety of patterns, most clearly observed with the S.E.M., based on one or more of four main configurations: lines, a rod, a crosspiece [bar] or apical knobs [see Text-Figs 19, 20].

In the first type (Text-Fig. 20), two lines of cutin commence from or near the guard cell 'wings' and run in

TEXT-FIGURE 19. Diagram showing basic patterns of polar thickening in subsidiary cells of Lauraceae: bars and rods as seen on the inner surface of isolated cuticles by S.E.M.



TEXT-FIGURE 20. Diagram showing basic patterns of polar thickening in subsidiary cells of Lauraceae: Lateral lines as seen on the inner surface of isolated cuticles by S.E.M.

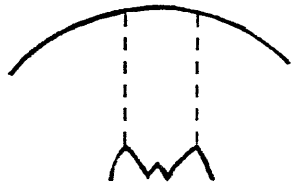
These may be found in association with rods/bars or both.

A



NONE

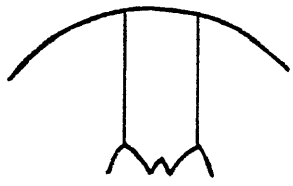
B



FAINT

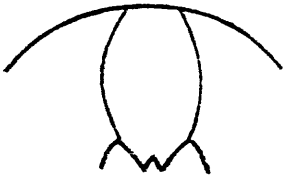
STRAIGHT/
LINEAR

C



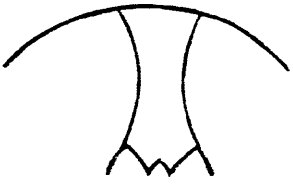
STRONG

D



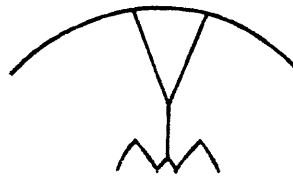
CONCAVE

E



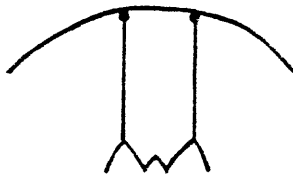
CONVEX

F



FUSED

G



APICALLY THICKENED

the same direction [side-by-side, but separated by a strip of periclinal cuticle] to terminate at two points in the subsidiary cell polar region on the subsidiary cell/surrounding cell flange. The strength or prominence of these lines, which may be described as 'lateral lines', is determined by the density of the constituent cutin; those of loosely packed granules are faintly delimited, for example, in Dicypellium caryophyllum [Fig. 117], Eusideroxylon spp. [Figs 115, 116] and Potameia spp., and those where the cutin is more solid are strongly marked, as in Endiandra spp. and Pleurothyrium spp. [Fig. 118]. Faint lines tend to be more common in occurrence than the strong form.

The direction taken by the lateral line pair may vary. Three patterns may be distinguished in the assemblage of taxa studied: lines may be occasionally concave, curving inward at the guard cell 'wings' and subsidiary cell poles, as in Endiandra rubescens, Nectandra spp. [Fig. 120] and Pleurothyrium spp. [Fig. 118], or sometimes straight or parallel, e.g. in Beilschmiedia spp., Nothaphoebe umbelliflora and Urbanodendron verrucosum [Fig. 112] or more commonly convex, curving outward at the guard cell 'wings' and subsidiary cell poles, such as in Dicypellium caryophyllum [Fig. 117] Eusideroxylon spp. [Figs 115, 116] and Potameia spp. The convex lateral lines of Aniba spp. are, in addition, fused part of the way down their course so that near to the 'wings' there is a single line [see Fig. 110].

In the second type of thickening [see Text-Fig. 19], the common wall of adjacent subsidiary cells appears to be thickened with cutin in the form of a rod. This is always raised to some extent above the periclinal surface, either to a low level [near to the surface], e.g. in Cinnamomum camphora [Fig. 123], Ocotea laevis [Fig. 113] and Umbellaria californica, especially when associated with lateral lines [at the centre of the pair], as in species of Beilschmiedia, Endiandra and Potameia, or to a conspicuously higher level, for example in Lindera spp., Neolitsea spp. [Fig. 130] and Persea spp.

As well as height differences between the rods, there is also variation in width [as seen from surface view] and three main size categories may be recognised: very narrow [ca. 0.02 μm], due to the presence of a single row of cutin granules or clumps, as in Beilschmiedia spp., Litsea meissneri [Fig. 109] and Ocotea laevis [Fig. 113]; thin [ca. 0.07 μm], the cutin forming a more or less solid rod, e.g. in Aiouea spp., Lindera spp. and Nothaphoebe heterophylla [Fig. 127] or, thick [ca. 0.20 μm], the rod being always solid cutin such as in, Apollonias arnottii [Fig. 129] and Phoebe sheareri [Fig. 128].

When present, rods are usually very narrow or thin.

The third type of subsidiary cell polar thickening consists of: occasionally a knob of cutin located at the point where the common wall abuts the subsidiary cell/surrounding cell flange, often associated with a very narrow, low rod as in species of Beilschmiedia and Potameia, or generally a wedge-shaped cross-piece, its widest part on the subsidiary cell/surrounding cell flange and the tapered end on the common wall region, part way towards the guard cell 'wings', for example, Endlicheria piriformis [Fig. 114], Laurus spp. [Fig. 323] and Persea spp. This form is often connected to a rod near the subsidiary cell poles giving a 'T'-shaped configuration. Another type of cross-piece is oblong and lens-shaped: concave where it abuts the subsidiary cell/ordinary cell flange and convex on the opposite side. It is only present in Dehaasia caesia [Fig. 111] and is not associated with any other subsidiary cell thickening pattern.

Where apical thickening occurs, small knobs of cutin may be found at the boundary between lateral lines and the subsidiary cell/ordinary flange, such as in species of Aniba [Fig. 110], Beilschmiedia, Eusideroxylon and Potameia or at the same position on the edge of a rod, e.g. in Endlicheria reflectens and Systemonodaphne mezii. This suggests that 'lateral line' thickening may be allied to the 'rod' form.

Within the Lauraceae, there are a few taxa which show no evidence of thickening in the polar or common wall regions of the subsidiary cells, for example, Alseodaphne oblanceolata (Fig. 125) and Hypodaphnis zenkeri.

12.5.3k TERRACING

In one Lauraceae taxon, Dehaasia caesia, the subsidiary cell inner periclinal surface regularly possesses a well-marked, concentric 'step' or terrace approximately half way across, with an indentation at each pole (between the cutin cross-piece and the aperture) (see Fig. 111). Thus, the guard cell 'wings' appear, in the S.E.M., to be on a higher plane than the periclinal cuticle surface of the epidermal cells and the outermost zone of the subsidiary cells. Transverse sections reveal that this phenomenon may occur due to the orientation and shape of the subsidiary cell periclinal cuticle: 'wings' are adjacent and above the very low subsidiary cell dome, a darkened area (shallow scrobiculus) in the S.E.M. The subsidiary cell inner periclinal cuticle abruptly increases in thickness (type a, p. 249) away from the 'wing', being checked approximately half way across the width at the point of a concavity or sunken area on the outer surface. Thereafter, the cuticle thickness of the subsidiary cell falls, producing a 'step' on the inner surface before increasing again, terminating in the subsidiary cell/surrounding cell flange. The location of the outer zone of the subsidiary cell below the inner is apparent rather than actual, according to the transverse section.

12.5.3l PRESENCE AND FORM OF FOLDING

The subsidiary cell outer periclinal cuticle is often unornamented or smooth, according to observations of leaf portions and the outer side of isolated cuticles, made using scanning electron microscopy. This is the case in most Lauraceae and a few Hernandiaceae, Illigera pulchra and Sparattanthelium spp. In other taxa, predominantly members of families related to the Lauraceae, the subsidiary cell cuticle surface is projected into a series of rounded ridges or folds (striae). Three patterns of

striae may be recognised: concentric, a system of discrete striae rings of increasing diameter extending across the subsidiary cell pair, commencing at the boundary between the guard and subsidiary cells, as in Hernandia spp. [Figs 99, 100], Piptocalyx moorei and Trimenia spp.; lateral, folds perpendicular to the long axis of the stomatal aperture which run across the width of the subsidiary cell, e.g. in Caryodaphnopsis spp. [Figs 248, 252], Gomortega keule [Fig. 84], Hypodaphnis zenkeri, Illigera pentaphylla [Fig. 101] and Litsea monopetala, sometimes accompanying the concentric type [in the outer zone of the cell], in certain Trimeniaceae [Piptocalyx moorei and Trimenia papuana]; and radiating, groups of striae which radiate from the guard cell pair like spokes of a wheel, only in Gyrocarpus americanus.

Of the three types, lateral folding occurs most commonly amongst the taxa and is the sole pattern found in Lauraceae. Concentric folding is very similar to the arrangement of striae sometimes seen on the outer surface of guard cells [see p.234].

Striae may vary in prominence from low, i.e. hardly raised from the surface, resulting in faint delimitation of folds], e.g. in Gyrocarpus americanus, Hernandia nymphiifolia [Fig. 99], Hypodaphnis zenkeri and Litsea monopetala, to high, with a distinct 'ridge and furrow' system, as in Caryodaphnopsis spp. [Figs 248, 252], Illigera pentaphylla [Fig. 101] and Trimenia papuana. Intermediates include the folding of Hernandia olivacea [Fig. 100] and Piptocalyx moorei. Most commonly, striae are low in prominence.

Individual striae tend to be either straight, as in Illigera pentaphylla [Fig. 101], or more usually, describe a slightly wavy course, for example, in Caryodaphnopsis spp. [Figs 248, 252] and Trimenia papuana. Fold prominence enhances the conspicuousness of the pattern observed.

The width of the subsidiary cell striae may also be

variable: from very fine, between ca. 0.4 and 0.9 μm , e.g. in Caryodaphnopsis spp. (ca. 0.5-0.9 μm), Gyrocarpus americanus (ca. 0.4 μm) and Illigera pentaphylla (ca. 0.5-0.7 μm) [Fig. 101] to coarse, more than 2.0 μm wide up to about 2.6 μm , as in Gomortega keule [Fig. 84], with assorted intermediates of, for example, very fine to fine, with a maximum diameter of approximately 1.5 μm , e.g. in Hernandia olivacea [Fig. 100]; fine (ca. 1.0-1.5 μm), such as, in Trimenia weinmanniaefolia; and fine to moderate, up to about 2.0 μm , e.g. in Trimenia papuana.

Striae are variously represented on the subsidiary cell inner cuticle surface by an alternating furrow and ridge pattern, as in the case of guard cell folds. Occasionally, they may be inconspicuous (indistinguishable) e.g. in Illigera pentaphylla [Fig. 132] and Piptocalyx moorei [Fig. 135], or less conspicuous than on the outer periclinal surface, as in Trimenia papuana (obscured by microrelief). Taxa in which striae are more prominent on the inside of the membrane, e.g. Trimenia weinmanniaefolia [Fig. 136] are rare. Usually, subsidiary cell folding is more or less similar in conspicuousness on both cuticle surfaces, as in most Hernandiaceae and all Lauraceae exhibiting this feature.

12.5.3m PERICLINAL SURFACE SCULPTURE

Surface views of cuticles show that subsidiary cells are clearly outlined in the same way on the inner side in all taxa, unlike the guard cell pair. In most Lauraceae, the subsidiary cell periclinal cuticle appears to be composed of two zones in the S.E.M.: (1) located nearest to the aperture and occupying varying proportions of the cell, usually sunken (concave), sometimes considerably so, corresponding to the dome or papilla of the cell and (2) situated outside (1) near to the subsidiary cell/surrounding cell flange, with a flat or slightly concave surface. There appears to be correlation between the conspicuousness of (1) and (2) and the form of the subsidiary cell dome. Where the latter is prominent, overhanging the guard cell to a high degree and the periclinal cuticle abruptly increases in thickness near to the dome apex [see

p. 249) before following a somewhat sigmoid direction to the flange, the zones are especially well-defined.

Some Lauraceae members possess distinct sculptural differences between [1] and [2] e.g. Cinnamomum camphora [Fig. 123], Dehaasia caesia [Fig. 111], Umbellularia californica and most particularly, Urbanodendron verrucosum [Fig. 112] whilst others, such as Neocinnamomum delavayi and Sassafridium macrophyllum [Fig. 122] do not. However, the nature of the microrelief of [1] may only be determined when the degree of concavity present within the area [equivalent to dome prominence] is low. When [1] is deeply sunken it is usually represented by a darkened or black region in the scanning-electron microscope so that resolution of any ornamentation is difficult or even impossible.

Therefore, in Lauraceae, only that part of the subsidiary cell designated zone [2] has been used for comparison of sculpture with that of the subsidiary cell periclinal surface in members of related families.

Light microscopic observations of the cuticle/cellulose wall boundary in transverse sections fail to reveal evidence of ornamentation in the periclinal region of the subsidiary cell in most taxa. However, there are a few examples with an uneven interface in this area such as Gomortega keule, Hernandia spp. [Text-Fig. 22A], Laurus spp. and Trimenia spp.

The scanning electron microscope shows that the subsidiary cell periclinal surface is unornamented in only a restricted number of taxa, including Caryodaphnopsis baviensis, Gyrocarpus americanus ssp. americanus, Licaria spp. and Nectandra spp. as well as in some examples whose other periclinal areas are always sculptured, notably those of Persea spp. Generally, when ornamentation is present, it takes the form of protrusions only, as in Aniba megaphylla [Fig. 110], Dehaasia caesia [Fig. 111] Hernandia nymphiifolia and all Trimeniaceae [Fig. 135], but more rarely, may also incorporate depressions, e.g.

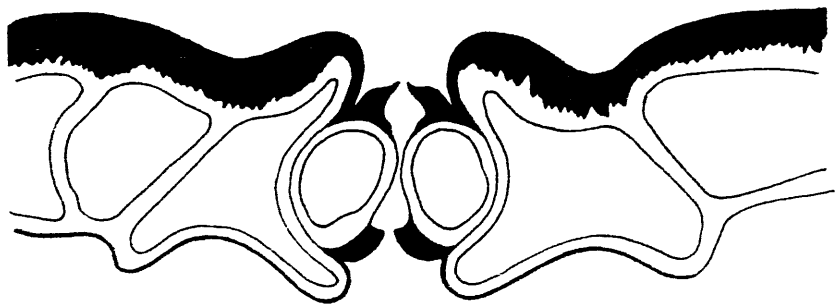
TEXT-FIGURE 21. Cuticle at the stoma in T.S.

- A. Austrobaileya scandens. Anomocytic. Level. With single cavity bounded by prominent outer and inner guard cell ledges. Stomatal flap present, restricted to inner cell wall just beyond inner ledge. Guard cell walls massively thickened. Guard cell/surrounding cell flange U-shaped. Cuticle/cellulose wall interface slightly uneven at stoma. Outer periclinal surface conspicuously folded or striate (except outer ledge). [See also Figs. 83 and 133].
- B. Umbellularia californica. Paracytic. Sunken. With distinct outer and inner cavities. Stomatal flap present, extending over subsidiary cell inner periclinal wall and sometimes beyond. Guard cell walls with very little thickening. Subsidiary cell outer wall not conspicuously thicker than inner. Guard cell/subsidiary cell flange V-shaped; subsidiary cell/surrounding cell flange U-shaped. Guard cell cuticle/cellulose wall interface even, subsidiary cell interface uneven. Outer periclinal surface smooth.

A



B

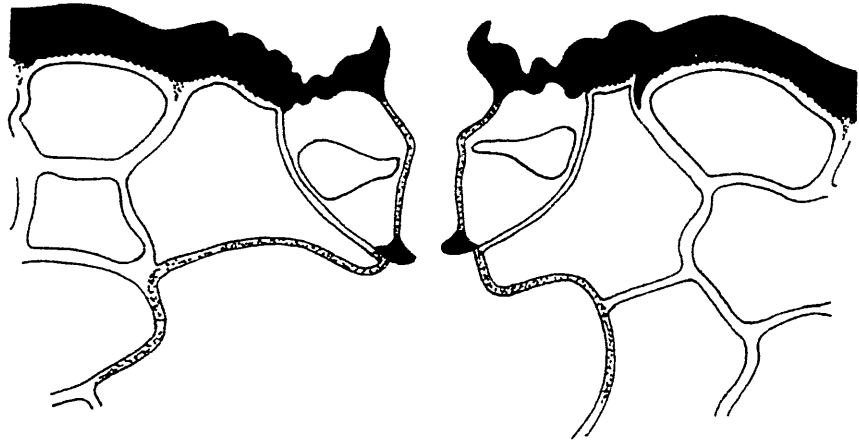


20 μm

TEXT-FIGURE 22. Cuticle at the stoma in T.S.

- A. Hernandia olivacea. Paracytic. Slightly sunken. Outer ledge prominent, incurved at base, outcurved at apex. Stomatal flap present, extending to inner wall of sub-epidermal cells [pink:stippled]. Poral wall of guard cell lightly cutinised [stippled]. Guard cell walls massively thickened. Guard cell/subsidiary cell flange U-shaped; subsidiary cell/surrounding cell flange V-shaped. Guard cell cuticle/cellulose wall interface even, folded; subsidiary cell interface slightly uneven, without folds. Outer periclinal surface of stomatal complex folded [striate]. [See also Figs. 98 and 131].
- B. Piptocalyx moorei. Paracytic. Level. Outer ledge incurved at base, outcurved at apex. Stomatal flap absent. Poral wall of guard cell lightly cutinised [stippled] except at pore 'lips' where cutinisation is more extensive [black]. Guard cell walls massively thickened. Flanges of stoma wide, V-shaped. Cuticle/cellulose wall interface even. Outer periclinal surface of stomatal complex smooth. [see also Fig. 135].

A



B

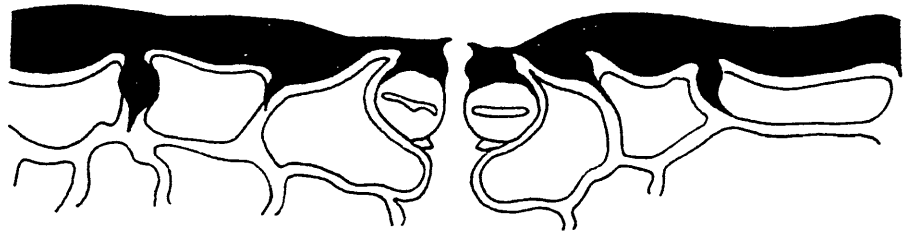


20 μm

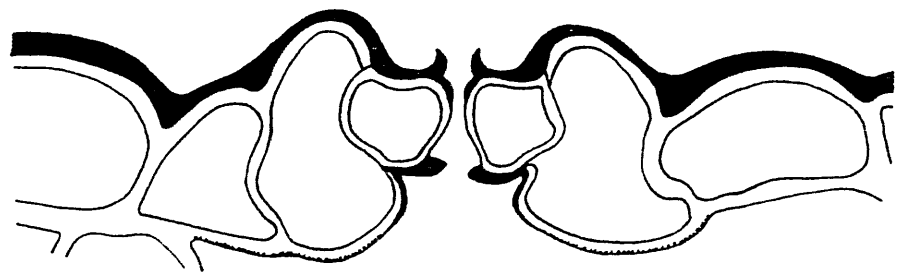
TEXT-FIGURE 23. Cuticle at the stoma in T.S.

- A. Endiandra kingsiana. Paracytic. Barely sunken. Very wide stomatal pit. Outer ledge straight. Stomatal flap absent. Upper guard cell wall massively thickened, lower wall moderately thickened. Inner ledge present, cutinisation not detected when stained with Sudan IV. Flanges of stoma V-shaped. Cuticle/cellulose wall interface even at stoma.
- B. Neocinnamomum caudatum. Paracytic. Sunken. Wide stomatal pit with outward sloping walls. Outer ledge outcurved. Stomatal flap present, lightly cutinised [stippled] extending over subsidiary cell inner periclinal wall. Guard cell walls with very little thickening. Inner ledge present, strongly cutinised [black]. Flanges of stoma U-shaped. Cuticle/cellulose wall interface even at stoma. Subsidiary cell secondarily divided [left]. [See also Fig. 121].

A



B

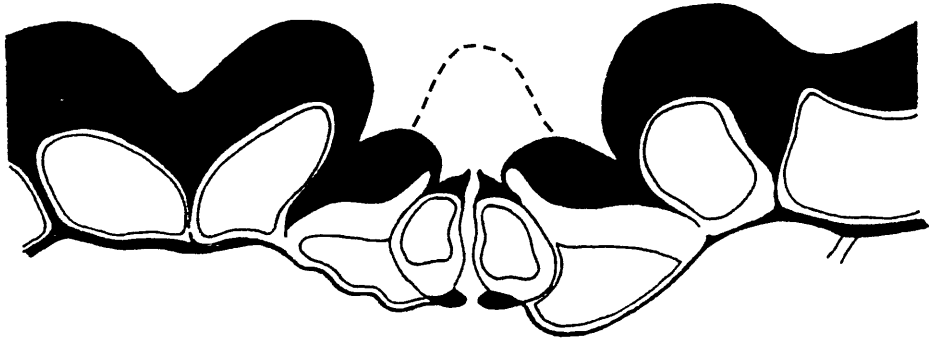


20 μm

TEXT-FIGURE 24. Cuticle at the stoma in T.S.

- A. Beilschmiedia madang. Paracytic. Guard cells and subsidiary cells sunken. Pit walls almost vertical. Note polar papilla of subsidiary cells [centre, broken lines]. Outer ledge outcurved. Inner ledge strongly cutinised. Stomatal flap present, extending over subsidiary cell inner periclinal wall and beyond. Upper guard cell wall with very little thickening, lower moderately thickened. Uncutinised subsidiary cell outer wall conspicuously thicker than inner wall. Flanges of stoma V-shaped. Guard cell/subsidiary cell flange very low, subsidiary cell/surrounding cell flange deep. Cuticle/cellulose wall interface even.
- B. Ravensara pervillei. Paracytic. Guard cells and subsidiary cells sunken. Cells adjacent to subsidiary cells obviously specialised [papillate]. Stomatal pit narrow, walls sigmoid [S-shaped]. Outer ledge straight. Inner ledge cutinised, less so [pink : stippled] than elsewhere [red]. Stomatal flap absent. Upper guard cell wall massively thickened and cutinised, lower with very little thickening. Uncutinised subsidiary cell outer wall conspicuously thicker than inner wall. Flanges of stoma moderate, V-shaped. Cuticle/cellulose wall interface even.

A



B

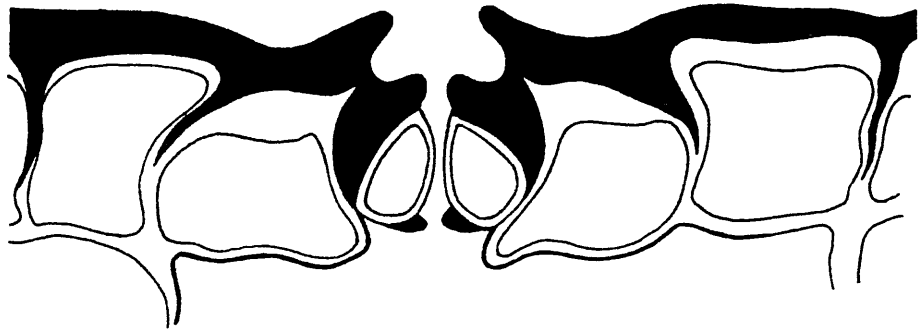


20 μ m

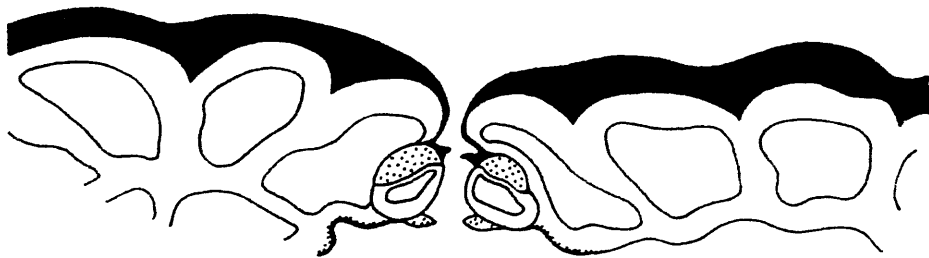
TEXT-FIGURE 25. Cuticle at the stoma in T.S.

- A. Eusideroxylon zwageri. Paracytic. Sunken. Outer periclinal wall of subsidiary cell projected into narrow papilla over guard cells. Papilla strongly cutinised, lacking lumen [therefore, no scrobiculus on inner surface of cuticle]. Outer ledge outcurved, blunt. Inner ledge strongly cutinised. Stomatal flap present, extending over subsidiary cell inner periclinal wall and beyond. Upper guard cell wall massively thickened, lower with very little thickening. Uncutinised subsidiary cell outer wall conspicuously thicker than inner. Flanges of stoma deep, V-shaped. Cuticle/cellulose wall interface even.
- B. Cinnamomium oliverii. Paracytic. Sunken. Outer periclinal wall of subsidiary cell curving downward from surrounding cells. Stomatal pit narrow, with sigmoid walls. Outer ledge small, incurved, tapering, strongly cutinised. Inner ledge and guard cell cuticle less well cutinised [stippled]. Stomatal flap present, covering subsidiary cell inner periclinal wall and sometimes beyond. Upper guard cell wall massively thickened, lower moderately thickened. Uncutinised subsidiary cell outer wall conspicuously thicker than inner. Flanges of stoma V-shaped. Guard cell/subsidiary cell flange moderate, subsidiary cell/surrounding cell flange very low. Cuticle/cellulose wall interface even.

A



B



20 μ m

in certain Cinnamomum spp. [except C. camphora] (Fig. 124), Hernandia olivacea (Fig. 131), Illigera spp. (Fig. 137) and Litsea umbellata.

Differences observed in the periclinal sculpture of the subsidiary cell within the taxa examined are most suitably described in the same way as the non-specialised periclinal ornamentation [p. 127].

12.5.3m (i) SIZE OF ELEMENTS

Protrusions. These range in diameter from very fine [less than 0.2 μm with a minimum of about 0.04 μm], such as in Gyrocarpus americanus ssp. africanus, Hypodaphnis zenkeri and Piptocalyx moorei (Fig. 135) to moderately coarse [with a maximum of approximately 0.9 μm], e.g. in Gomortega keule (Fig. 134) and Hernandia olivacea (Fig. 131). Subsidiary cell periclinal protrusions of most taxa tend to be no greater than about 0.5 μm in diameter, e.g. Aiouea saligna (ca. 0.4-0.5 μm), Dehaasia caesia (ca. less than 0.2 μm -0.4 μm) (Fig. 111), Nothaphoebe heterophylla (ca. less than 0.2 μm) (Fig. 127) and Trimenia papuana (ca. 0.2 μm or less). However, there may be at least some protrusions of coarser dimensions in a number of others, such as Aiouea guianensis (ca. 0.4-0.7 μm) Laurus spp. (e.g. L. canariensis: ca. 0.4-0.9 μm), Trimenia weinmanniaefolia (ca. 0.2-0.7 μm) (Fig. 136) and Urbanodendron verrucosum (ca. 0.4-0.7 μm) (Fig. 112).

Depressions. Where present, these vary from very fine [ca. less than 0.2 μm] e.g. in Illigera pentaphylla (Fig. 137), Litsea umbellata and Nothaphoebe heterophylla (Fig. 127) to moderately coarse [with a maximum of approximately 0.7 μm] in Aiouea guianensis. Subsidiary cell periclinal depressions are often no more than 0.4 μm in diameter, such as those of Alseodaphne spp., certain Cinnamomum spp. (C. iners, C. oliverii and C. pachyphyllum) (Fig. 124), Illigera pulchra (ca. 0.2 μm or less (Fig. 132) and Endiandra rubescens (ca. 0.2-0.4 μm). A few taxa have some depressions of larger size on the subsidiary cell periclinal surface: Hernandia olivacea (ca. 0.4-0.5 μm) (Fig. 131), Sassafridium macrophyllum (Fig. 122)

and Umbellularia californica (ca. 0.2-0.5 μm).

When both protrusions and depressions are present in the periclinal region of the subsidiary cell, depressions (d) are commonly finer than the protrusion elements (p) e.g. in Endiandra kingsiana (p. ca. 0.2-0.5 μm , d. ca. 0.2 μm or less), Hernandia olivacea (p. ca. 0.2-0.9 μm , d. ca. 0.4-0.5 μm) [Fig. 131], Illigera pentaphylla (p. ca. 0.2 μm or less, d. less than 0.2 μm) [Fig. 137] and Umbellularia californica (p. ca. 0.4-0.7 μm , d. ca. 0.2-0.5 μm). Sometimes, however, depressions and protrusions are of similar dimensions, such as those of Aiouea guianensis (ca. 0.4-0.7 μm), Illigera pulchra (ca. 0.2 μm or less) [Fig. 132] and Sassafridium macrophyllum (ca. 0.2-0.5 μm) [Fig. 122]. Occasionally, depressions are coarser than protrusions in the subsidiary cell periclinal areas, as in Cinnamomum iners (p. less than 0.2 μm , d. ca. 0.2 μm or less).

12.5.3m (ii) DENSITY OF ELEMENTS. This may vary between taxa. Individuals or groups of sculptural components are sometimes closely packed, producing a dense pattern in the subsidiary cell periclinal region, for example in Dicypellium caryophyllatum [Fig. 117], Endiandra spp., Illigera spp. [Figs 132, 137] and Trimenia papuana or, the elements may be more widely separated, as in Micropora curtisii [Fig. 126], Ravensara pervillei and Sassafras albidum var. molle. Many intermediate states of ornamentation density are found, e.g. in Hernandia nymphiifolia, Laurus canariensis, Sassafridium macrophyllum [Fig. 122] and Urbanodendron verrucosum [Fig. 112].

12.5.3m (iii) ARRANGEMENT AND FORM OF ELEMENTS

Protrusions. A variety of configurations may be observed on the periclinal surface of the subsidiary cell. Granules are often present, either alone, for example, in Aniba spp. [Fig. 110], Hernandia nymphiifolia, Laurus spp. [Fig. 323] and Trimenia papuana or less frequently, in association with more complicated aggregates: clumps, as in Dicypellium caryophyllatum [Fig. 117], Litsea meissneri [Fig. 109], Neocinnamomum caudatum [Fig. 121] and

Trimenia weinmanniaefolia [Fig. 136] or clumps and reticula, in Dehaasia cuneata only [Fig. 285]. Sometimes, the latter pattern may be found without granules, e.g. in subsidiary cells of Cinnamomum camphora [Fig. 123], Ocotea guianensis and Urbanodendron verrucosum [Fig. 112]. Reticulate protrusions, the most complex arrangement, are of common occurrence in the subsidiary cell periclinal region. Examples showing elements grouped in this way include a number of Lauraceae, such as Aiouea spp., Endiandra spp., Litsea umbellata and Sassafridium macrophyllum [Fig. 122] as well as various members of related families [but not in Trimeniaceae], e.g. Gomortega keule [Fig. 134], Hernandia olivacea [Fig. 131] and Illigera spp. [Fig. 137]. Individual protrusions tend to be rounded in most taxa, although occasionally, the filamentous form may be recognised, as in Illigera pulchra [Fig. 137] and Litsea umbellata or alternatively, some intermediate between the extremes, e.g. in Hernandia olivacea [Fig. 131].

Depressions. Where these are present, they are most often just pit-like in form, such as in Alseodaphne spp., Illigera spp., Lindera pulcherrima and Nothaphoebe heterophylla [Fig. 127]. Other taxa may possess pits together with additional depression arrangements: clumps, e.g. in Actinodaphne stenophylla, Cinnamomum oliverii [Fig. 124] and Cryptocarya ainikini or clumps and reticula, as in Cinnamomum pachyphyllum, Endlicheria piriformis [Fig. 114] and Ocotea guianensis on the subsidiary cell periclinal surface. Alternatively, clumped and reticulate depressions, for example those in Aiouea spp. and Endiandra spp. or reticula only, as in Hernandia olivacea [Fig. 131] and Sassafridium macrophyllum [Fig. 122], may occur more rarely without the pit-like form.

Depressions tend to be organised into less complex patterns than protrusions in the periclinal area of the subsidiary cell, where both elements constitute the surface ornamentation, as demonstrated by certain species of Cinnamomum [C. iners, C. oliverii and C. pachyphyllum], Endiandra and Illigera. There are a few exceptions however, in which the two element types form arrangements

of similar complexity, e.g. Cryptocarya ainikini, Hernandia olivacea [Fig. 131] and Phoebe sheareri [Fig. 128] or less frequently, where depressions are more complex than protrusions in Endlicheria piriformis [Fig. 114].

12.5.3m [iv] PROMINENCE OF ELEMENTS. This tends to be variable within the assemblage. Protrusions project very little from the cutin matrix of the subsidiary cell periclinal region in a number of species including Alseodaphne semecarpifolia, Dodecodenia grandiflora, Endlicheria piriformis [Fig. 114] and Neocinnamomum delavayi but more usually, are distinctly prominent, producing a highly textured surface, such as in Aiouea spp., Hernandia olivacea [Fig. 131], Sassafridium macrophyllum [Fig. 122] and Urbanodendron verrucosum [Fig. 112]. Various intermediates may be detected between the two extremes, for example, the subsidiary cell periclinal protrusions of Cryptocarya alleniana, Hernandia nymphiifolia and Umbellularia californica.

Most depressions appear shallow in the periclinal area of the subsidiary cell, particularly those of Lindera pulcherrima, Neocinnamomum spp. [Fig. 121] and Nothaphoebe heterophylla [Fig. 127], although they seem to be deep, in a few taxa, e.g. Aiouea guianensis, Hernandia olivacea [Fig. 131] and Sassafridium macrophyllum [Fig. 122]. However, estimation of depression depth is inaccurate and, therefore, unreliable from scanning electron microscopic observation [see p. 140].

12.5.3m [v] SCULPTURAL DIFFERENCES BETWEEN OTHER CELL AND SUBSIDIARY CELL PERICLINAL SURFACES. The periclinal microrelief of the subsidiary cell is always different in some respect from that of other cells [guard or ordinary cells] within a taxon. Differences may be detected in aspects [predominantly size and arrangement] of the sculptural elements, especially protrusions [p].

The periclinal ornamentation of the subsidiary cell [s.c.] may sometimes differ only from the sculpture in

the same area of non-specialised epidermal cells [o.c.] as in Dehaasia caesia [s.c. p. finer & more complex than o.c.] (Fig. 111), Hernandia nymphiifolia [s.c. p. finer] and Litsea umbellata [s.c. p. & d. finer], or more usually, from that of the guard cells, for example, in Caryodaphnopsis tonkinensis [s.c. p. coarser], Dicypellium caryophyllum [s.c. p. finer & simpler] (Fig. 117) and Ocotea laevis [s.c. p. coarser & simpler] (Fig. 113).

Most commonly, however, the microrelief is different on the periclinal surface of each cell type [subsidiary, guard and ordinary epidermal]. The resulting dissimilarities between the patterns detected in the periclinal region of the subsidiary cell and those of the other cells [o.c. or g.c.] may involve the same sculptural elements, frequently protrusions [p] only, such as in Laurus nobilis [s.c. p. finer than o.c.; simpler than g.c.] (Fig. 323), Litsea meissneri [s.c. coarser & more complex than o.c.; simpler than g.c.] (Fig. 109), Trimenia papuana [s.c. simpler than o.c.; coarser than g.c.] and Urbanodendron verrucosum [s.c. coarser & more complex than both o.c. & g.c.] (Fig. 112) or, occasionally both protrusions and depressions, for example Aiouea saligna [s.c. p. finer, d. coarser & more complex than o.c.; p. & d. coarser & more complex than g.c.], Neocinnamomum delavayi [s.c. p. finer & more complex, d. coarser than o.c.; p. coarser & more complex, d. coarser than g.c.] and Sassafridium macrophyllum [s.c. p. & d. coarser & more complex than o.c.; p. finer, d. coarser than g.c.] (Fig. 122). In a range of other taxa, variation between the ornamentation of the periclinal surface of the subsidiary cell and that of each of the other cells may be attributed to different component types, such as in Actinodaphne stenophylla [s.c. d. coarser & more complex than o.c.; p. & d. more complex, d. coarser than g.c.], Aiouea guianensis [s.c. d. coarser & more complex than o.c.; p. coarser & more complex than g.c.], Alseodaphne semecarpifolia [s.c. p. coarser than o.c.; p. finer & more complex, d. finer & simpler than g.c.], Endiandra kingsiana [s.c. p. coarser, d. finer & more complex than o.c.; p. coarser & more complex than g.c.],

Endlicheria piriformis [s.c. p. finer, d. more complex than o.c.; p. coarser than g.c.] [Fig. 114] and Illigera pulchra [s.c. p. & d. coarser than o.c.; p. coarser & more complex than g.c.] [Fig. 137].

12.5.3n THICKNESS OF CUTICLE AT SUBSIDIARY CELL/ORDINARY [SURROUNDING] CELL FLANGE IN T.S.

At the subsidiary cell/ordinary [surrounding] cell flange [SOF] the thickness of the cuticle, measured from the centre of the anticlinal border on the outer surface to the flange tip on the inner, in transverse sections [see Text-Fig. 15B, C], may vary. Average values range from 0.7 μm , in Micropora curtisii to 12.6 μm , in Aiouea guianensis. Many taxa have subsidiary cell/surrounding cell flanges of 4.9 μm or less: Hernandiaceae with the exception of Hernandia olivacea (up to 2.7 μm) [Text-Fig. 22A], a large number of Lauraceae, such as Hypodaphnis zenkeri (1.2 μm), Neocinnamomum spp. (3.9 μm) [Text-Fig. 23B] and Persea spp. [P. americana: 1.5 μm ; P. chinensis: 2.7 μm ; P. thunbergii: 2.4 μm] and some Trimeniaceae, e.g. Trimenia papuana (3.7 μm). Others have thicker cuticle at this flange, up to 9.8 μm , as in Eusideroxylon melagangai (adx. 9.8 μm ; abx. 9.0 μm), Nectandra spp. [N. pichurim: 6.1 μm , N. salicifolia: 7.0 μm] and Trimenia weinmanniaefolia (6.3 μm) and occasionally even more, for example, in Eusideroxylon zwageri (12.3 μm) [Text-Fig. 25A] and Potameia crassifolia (12.5 μm).

It is very rare for the cuticle thickness to be the same at all flanges in a preparation. Values for the three flange types [subsidiary cell/surrounding cell, guard cell/subsidiary cell and epidermal] are only similar in Litsea monopetala and Persea americana. Where dissimilarities occur, the cuticle thickness at the subsidiary cell/surrounding cell flange [SOF.] may differ from that at the ordinary flanges, such as in Hernandia nymphiifolia, Mezilaurus lindaviana and Persea chinensis, [SOF. thinner] or alternatively from that at the guard cell/subsidiary cell flange [GSF.], e.g. in Laurus nobilis, Litsea umbellata [SOF. thinner] and Sparattanthelium guianense [SOF. thicker].

More usually, differences in cuticle thickness may be detected at all flanges, as in Gomortega keule [SOF. thinner than OF.; thicker than GSF.], Nectandra spp. [SOF. thinner than OF. & GSF], Neocinnamomum spp. [SOF. thicker than OF & GSF.] and Systemonodaphne mezii [SOF. thicker than OF.; thinner than GSF.].

12.5.3o PROMINENCE OF SUBSIDIARY CELL/SURROUNDING CELL FLANGE IN T.S.

The degree to which the subsidiary cell/surrounding cell flange projects into the common wall between the subsidiary and surrounding cells is variable, particularly in the Lauraceae. In transverse section, it may sometimes be very low, extending only into the periclinal region above the anticlinal wall, as in Caryodaphnopsis spp., Laurus spp., and Micropora curtisii. More commonly, the subsidiary cell/surrounding cell flange may be low, protruding to the level where the anticlinal and periclinal walls meet, for example, in Dodecadenia grandiflora, Neocinnamomum spp. [Text-Fig. 23B] and Persea spp. or moderate, projecting to about halfway down the common anticlinal wall between the subsidiary and surrounding cells, as in species of Aniba, Endiandra [Text-Fig. 23A] and Ocotea.

This flange only rarely extends further, to where the inner periclinal wall of the subsidiary and surrounding cells meet the anticlinal [common] wall, resulting in the deep configuration, e.g. in Beilschmiedia madang [Text-Fig. 24A] and Eusideroxylon melagangai [adx.]. The subsidiary cell/surrounding cell flange of members of families related to Lauraceae is always either very low, such as in Gyrocarpus americanus ssp. africanus, Hernandia nymphifolia and Piptocalyx moorei [Text-Fig. 22B] or low, e.g. in Gomortega keule, Sparattanthelium spp. and Trimenia spp.

In a number of taxa, the subsidiary cell/surrounding cell flange is of similar prominence to all others [guard cell/subsidiary cell and epidermal] of the same cuticle surface, such as in Alseodaphne oblanceolata, Illigera pulchra, Ocotea spp. and Piptocalyx moorei. However, there are often differences; sometimes involving the prominence

of the flange between the subsidiary and surrounding cells [SOF] and that of the guard cell/subsidiary cell flange [GSF] only, e.g. in Alseodaphne semecarpifolia [SOF. deeper], Endlicheria spp. and Eusideroxylon melagangai [SOF. shallower] and Trimenia spp. [SOF. deeper] or that of just the epidermal flanges, as in Aniba spp. [SOF. deeper], Nectandra salicifolia and Ravensara elliptica [SOF. shallower], or of all other flanges [OF., GSF.] for example, in Beilschmeidia madang [SOF. shallower than OF.; deeper than GSF.], certain Cryptocarya spp. [C. ainikini & C. weinlandii [SOF. shallower than OF. & GSF.] and Phoebe sheareri [SOF. deeper than OF. & GSF.]

12.5.3p SHAPE OF SUBSIDIARY CELL/SURROUNDING CELL FLANGE

12.5.3p [i] IN TRANSVERSE SECTION. At the boundary between a subsidiary cell and an adjacent ordinary epidermal or surrounding cell, the cuticular layer may form either a V- or U-shaped anticlinal flange, in the same way as in other specialised and non-specialised regions [see p.142, 213]. The V-sectioned type of subsidiary cell/surrounding cell flange, which tapers in the S.E.M., is a regular feature of most Lauraceae, Gomortega keule and all Trimeniaceae but only a few Hernandiaceae, Illigera pentaphylla and Sparattanthelium guianense. The U-sectioned type, rounded [hemispherical] in the S.E.M., is shown by all other Hernandiaceae and a small number of Lauraceae, e.g. Hypodaphnis zenkeri, Litsea umbellata and Phoebe opaca. Generally, the subsidiary cell/surrounding cell flange is similar in shape to all others on the same surface. Sometimes, differences in form occur, most commonly between this specialised flange and either those of the ordinary epidermal cells, as in Dodecadenia grandiflora, Micropora curtisii and Sassafras albidum var. molle [SOF. V, OF. U] or more rarely, the guard cell/subsidiary cell flange, e.g. in Litsea umbellata [SOF. U, GSF. V]. Occasionally in T.S. the subsidiary cell/surrounding cell flange is dissimilar in outline from both of the other types of flange, such as in Hernandia olivacea [SOF. U, OF. & GSF. V] and Neocinnamomium spp. [SOF. V, OF. & GSF. U].

12.5.3p (ii) IN SURFACE VIEW. In the S.E.M., the subsidiary cell/surrounding cell flange may describe a straight, curved or undulate course, in the same way as ordinary flanges [see p. 143]. Most often this specialised flange is curved, with a single loop, for example, in many Lauraceae, such as Dehaasia caesia [Fig. 112], Nectandra pichurim [Fig. 120] and Nothaphoebe umbelliflora [Fig. 119], and all Hernandiaceae [Figs 131, 132, 137, 138]. Other configurations may also be recognised: straight to curved, in Lauraceae only, e.g. Eusideroxylon spp. [Figs 115, 116], Nothaphoebe heterophylla [Fig. 127] and Pleurothyrium cuneifolium [Fig. 118]; curved to U-undulate, as in Endlicheria piriformis [Fig. 114] and Neocinnamomum caudatum [Fig. 121] and undulate, with two or more loops of U-form, the second most common pattern, confined to Lauraceae members, e.g. Aniba megaphylla [Fig. 110], Phyllostemonodaphne geminiflorum and Systemonodaphne mezii, or, Ω -form, of rare occurrence, in Laurus spp. [Fig. 323], Micropora curtisii [Fig. 126] and Piptocalyx moorei [Fig. 135].

Undulation is generally most conspicuous on the side of the subsidiary cell/surrounding cell flange closest to the ordinary epidermal cells.

Cavities or hollows are common in the corners of the surrounding cells where they meet the subsidiary cells. They are also always present at each sinus when the subsidiary cell/surrounding cell flange is undulate. Cavities of various forms may be identified due to differing relationships between the width [determined by the undulation wavelength], and the height [controlled by the orientation of the flange to the periclinal surface at the sinus and flange depth]. Sometimes, they may be wider than high, giving a wide, shallow form such as in Aniba megaphylla [Fig. 110], Cryptocarya weinlandii and Litsea meissneri, but most often they are more or less equal in width and height, resulting in an isodiametric cavity shape, e.g. in Aiouea saligna, certain Cinnamomum spp. [C. oliverii & C. pachyphyllum], Micropora curtisii [Fig. 126] and Piptocalyx moorei [Fig. 135]. Very rarely, cavities are taller than wide, producing a characteristic column and arch pattern,

as in Aiouea guianensis and Cinnamomum iners, and these contrast with the cavities associated with non-specialised flanges, which are of the isodiametric type.

The subsidiary cell/surrounding cell flange is commonly similar in shape to the ordinary flanges, when viewed from above with light- or scanning electron-microscopy, for example, in Cinnamomum spp. (except in C. camphora), Illigera spp., Laurus spp. and Trimenia papuana. Sometimes, however, there are differences in the degree of undulation exhibited: e.g. the subsidiary cell/surrounding cell flange may be less undulate than those of the unspecialised cells, such as in Beilschmiedia madang, Dicypellium caryophyllatum (Fig. 117) and Endlicheria piriformis (Fig. 114).

12.5.3q CONTINUITY OF SUBSIDIARY CELL/SURROUNDING CELL FLANGE

12.5.3q (i) INTERRUPTIONS. The flange between the subsidiary cell and an abutting epidermal or surrounding cell may be uninterrupted along its length, for example, in Aniba spp. (Fig. 110), Eusideroxylon spp. (Figs 115, 116) and Piptocalyx moorei (Fig. 135) particularly when non-specialised flanges lack gaps, such as in Endiandra spp., Gyrocarpus americanus, Illigera pulchra and Nectandra spp. (Fig. 120) but sometimes also when they are interrupted, e.g. in Aiouea spp., Hernandia nymphiifolia and Pleurothyrium spp. However, most often this flange shows some degree of interruption. A number of categories may be recognised, very similar to those involving non-specialised flanges. The subsidiary cell/surrounding cell flange may be rarely interrupted, with never more than one gap per flange, as in Alseodaphne semecarpifolia, Cryptocarya alleniana, Illigera pentaphylla and Trimenia spp. (Fig. 136) or sometimes (about 50% subsidiary cell/surrounding cell flanges in the preparation) interrupted by one gap, very occasionally, as in Phyllostemonodaphne geminiflorum or more commonly by one or two gaps, e.g. in certain Cryptocarya spp. (C. ainikini & C. weinlandii), Dicypellium caryophyllatum and Lindera

strychnifolia, or by up to three gaps, such as, in Gomortega keule (Fig. 134), Lindera pulcherrima and some Persea spp. [P. americana & P. thunbergii]. A greater percentage of the flanges between the subsidiary and surrounding cells [75% or more] may be interrupted in other taxa and a range of numbers of gaps present exists: one gap or, one or two gaps per flange, rare within the assemblage, occurring just in Alseodaphne oblanceolata (Fig. 125) and Cinnadenia paniculata respectively, up to three gaps per flange, as in, Cinnamomum pachyphyllum, Laurus nobilis and Sassafras albidum var. molle; or most frequently, up to four gaps, e.g. in Dehaasia caesia (Fig. 111), Dodecadenia grandiflora and Phoebe sheareri (Fig. 128). Also of occasional occurrence are up to five gaps per flange, seen only in Umbellularia californica and between one and six gaps, in Hernandia olivacea (Fig. 131).

Those taxa in which the subsidiary cell/surrounding cell flange is clearly interrupted always possess non-specialised flanges with gaps. The subsidiary cell/surrounding cell flange most often displays fewer gaps per flange than the ordinary flanges, for example in Actinodaphne stenophylla, Dehaasia caesia, Laurus spp. and Lindera spp. However, sometimes the flanges between the subsidiary and surrounding cells may be interrupted to the same degree as non-specialised flanges, as in Endlicheria reflectens, Hernandia olivacea, Illigera pentaphylla and Umbellularia californica. Alternatively, the subsidiary cell/surrounding cell flange may occasionally possess more frequent gaps per flange than in non-specialised regions, such as in some Cryptocarya spp. [C. ainikini & C. weinlandii] and certain Persea spp. [P. americana & P. thunbergii].

There are never more than six gaps found in a subsidiary cell/surrounding cell flange, in contrast to the ordinary epidermal cell flanges which may have more than eight. In addition to breaks in the flange extending to the periclinal surface, there may also be partial gaps, which involve only part of the flange, just as in

non-specialised regions of a cuticle.

12.5.3q [ii] HOLES OR PORES. The subsidiary cell/surrounding cell flange may not be perforated at all in certain taxa, either when the ordinary flanges also lack pores, e.g. in Actinodaphne glomerata, Caryodaphnopsis spp. and Neocinnamomum spp. [Fig. 121] or when they are present, such as in Dehaasia cuneata [Figs 285, 286], Neolitsea spp. [Fig. 127] and Sparattanthelium guianense.

Commonly, holes perforate the subsidiary cell/surrounding cell flange either at the margin or somewhere in the body of the flange [see Figs 110, 117]. Just as in ordinary flanges [see p. 165], three main forms of pore may be identified, between which are many intermediates: tiny rounded channels, for example, in species of Alseodaphne, Endiandra and Lindera, also Sassafridium macrophyllum; round to oval, moderate sized pores, as in Cryptocarya spp. Endlicheria spp. and Urbanodendron verrucosum and large, round, oval or irregular shaped, window-like openings, e.g. in Beilschmiedia spp. Dicypellium caryophyllum and Mezilaurus lindaviana.

The first type is the most common pore form found in the subsidiary cell/surrounding cell flange of Lauraceae members and is the only configuration recorded in the single Hernandiaceae taxon, Illigera pentaphylla, with perforated flanges between the subsidiary and ordinary cells. In a cuticle preparation, it is quite common for the subsidiary cell/surrounding cell flange to show more than one pore type: moderate pores often being associated with tiny channels, as in Eusideroxylon spp., Nectandra spp. and Ocotea laevis. Less often, all three types may be recognised, e.g. in Dicypellium caryophyllum, Mezilaurus lindaviana and Ravensara elliptica, and even more rarely moderate together with large in Beilschmiedia spp.

When compared with the pore forms observed in ordinary flanges, those of the flanges between the subsidiary and surrounding cells are generally similar, e.g. in

Cryptocarya spp., Lindera spp., Nectandra spp. and Ravensara elliptica. However, sometimes there are differences. Commonly, less pore forms are found in the subsidiary cell/surrounding cell flange, such as in Aniba megaphylla, Endiandra spp. and Sassafridium macrophyllum, or occasionally more, for example in Mezilaurus spp.

The number of pores in the subsidiary cell/surrounding cell flange may vary and a range is usually observed in any cuticle preparation.

Most taxa with at least some perforate subsidiary cell/surrounding cell flanges have a maximum pore number between one and three per flange, as in Alseodaphne spp. [0-1], Nectandra spp. [0-2] and Ocotea laevis [0-3] [Fig. 113]. There are some examples, however, with up to four pores per subsidiary cell/surrounding cell flange, e.g. Beilschmiedia spp., Dicypellium caryophyllum [Fig. 117], Endiandra spp. and Eusideroxylon spp. No taxon has more than four pores in this flange. In non-specialised regions, flanges may sometimes have a greater number than this [maximum 5-8] per flange, as in Aniba megaphylla, Beilschmiedia spp. and Dicypellium caryophyllum. All such taxa, therefore, possess a greater perforation frequency in ordinary flanges than in those associated with the subsidiary and adjacent surrounding cells. Alternatively, pore frequency may either be similar in both the specialised and non-specialised flanges, e.g. in certain Cryptocarya spp. [C. ainikini & C. alleniana], Eusideroxylon melagangai (adx.). Illigera pulchra and Lindera pulcherrima, or be higher in the subsidiary cell/surrounding cell flange than in those of the ordinary epidermis, such as in Cryptocarya weinlandii, Endiandra spp. and Potameia crassifolia.

12.5.3r NATURE OF SUBSIDIARY CELL/SURROUNDING CELL FLANGE APEX

12.5.3r (i) FURROWING. The subsidiary cell/surrounding cell flange is always unfurrowed or 'single', even in taxa showing 'double' intercostal flanges.

12.5.3r (ii) IRREGULARITY/JAGGEDNESS. The margin of the flange associated with the subsidiary and surrounding cells, may be more or less even, in side view in the S.E.M. This commonly occurs when ordinary flanges also exhibit the even configuration, e.g. in various Lauraceae, such as Hypodaphnis zenkeri, Litsea umbellata and Neocinnamomum caudatum (Fig. 121), as well as some Hernandiaceae, for example, Gyrocarpus americanus, Hernandia nymphiifolia and Illigera pulchra (Fig. 137). The subsidiary cell/surrounding cell flange with an even margin is always either low or very low in prominence and may (in those taxa mentioned above) often also be U-sectioned.

Commonly, the subsidiary cell/surrounding cell flange margin exhibits some degree of irregularity, even when the unspecialised flanges of the epidermis do not, as in Caryodaphnopsis tonkinensis, Neocinnamomum delavayi and Sparattanthelium tupiniquinorum.

Irregularities vary from hardly discernible deviations from the horizontal about 0.10-0.18 μm , as in Mezilaurus itauba, Nothaphoebe heterophylla (Fig. 127) and Ravensara pervillei to distinct tooth-like projections with a maximum height of approximately 5.0 μm , in Beilschmiedia micrantha. A range of irregularity amplitude is always detected within a taxon and most often incorporates a minimum of less than 0.18 μm except in a few cases where the maximum is 1.1 μm or more, for example in Aniba megaphylla (min. 0.5 μm) (Fig. 110), Beilschmiedia micrantha (2.2 μm) and Endiandra spp. (0.4 μm). Generally, the subsidiary cell/surrounding cell margin has irregularities of up to about 1.0 μm , such as in Alseodaphne spp. [A. oblanceolata:max. 0.7 μm ; A. semecarpifolia: 0.4 μm] (Fig. 125), Illigera pentaphylla (max. 0.4 μm), Ocotea guianensis (max. 0.5 μm) and Trimenia spp. (max. 0.4 μm) (Fig. 136). However, a number of taxa show irregularities which project to a maximum in the range of 1.1 to 1.8 μm , e.g. Aniba spp. [A. hostmanniana:max. 1.4 μm ; A. megaphylla: 1.8 μm] (Fig. 110), Gomortega keule (max. 1.1 μm) (Fig. 134), Hernandia olivacea (max. 1.8 μm)

[Fig. 131] and Systemonodaphne mezii (max. 1.6 μm). Only occasionally, does the greatest irregularity amplitude exceed 1.8 μm . When this is the case, most commonly it is about 2.9 μm , as in Cryptocarya weinlandii, Endiandra rubescens, Ocotea laevis [Fig. 113] and Urbanodendron verrucosum [Fig. 112]. Sometimes, however, the maximum projection height is greater, such as 3.1 μm , in Dicypellium carophyllatum [Fig. 117] or less, 2.2 μm , in Endiandra kingsiana and Phyllostemonodaphne geminiflorum.

When compared with the results for intercostal regions, the amplitude of subsidiary cell/surrounding cell flange irregularities may be similar to those of ordinary flanges, for example, in Aniba spp., Beilschmiedia micrantha, Potameia crassifolia and Trimenia weinmanniaefolia; smaller, such as in Illigera pentaphylla, Lindera pulcherrima and Phyllostemonodaphne geminiflorum or greater, e.g. in Cryptocarya weinlandii, Ocotea laevis, Systemonodaphne mezii and Urbanodendron verrucosum. Where the latter trend occurs in Lauraceae, the irregularities of the subsidiary cell/surrounding cell flanges tend to be organised into more regular 'teeth', giving a frilly edge to the stomatal apparatus [see Figs 62, 112].

12.5.3r (iii) CORNER EXTENSIONS/PEGS. When the subsidiary cell/surrounding cell flange meets a flange of one of the adjacent ordinary cells, there may sometimes be deeper cutinisation than elsewhere. This phenomenon, producing cutin extensions or 'pegs', is not always easily distinguishable when the flange margin is uneven, in the same way as at the corners of ordinary cells. Particularly good examples of pegs associated with the subsidiary and surrounding cell flanges occur in Cryptocarya spp. [Fig. 62, centre], Illigera pentaphylla [Fig. 132], Hernandia olivacea [Fig. 131], Mezilaurus lindaviana, Pleurothyrium cuneifolium [Fig. 118], Ravensara spp., Sparattanthelium guianense and Trimenia spp. [Fig. 136].

Those taxa exhibiting ordinary flanges with corner extensions tend also to have pegs on the subsidiary cell/surrounding cell flange. Stomatal pegs appear more

prominent than those of non-specialised regions in most cases, except in the occasional taxon, such as Sassafridium macrophyllum.

12.5.3e SUBSIDIARY CELL/SURROUNDING CELL FLANGE SCULPTURE

The subsidiary cell/surrounding cell flange is defined on the inside of the cuticle in the same way as any ordinary epidermal flange, in all taxa, in contrast to the guard cell/subsidiary cell flange.

The interface between the cutinised layer and the cellulose cell wall at the subsidiary cell/surrounding cell flange in sections appears even in most species except in Gomortega keule, Hernandia spp. [Text-Fig. 22A] and Umbellularia californica [Text-Fig. 21B] when observed with light microscopy. However, the scanning electron microscope reveals that the surface of this flange is smooth only in a restricted number of taxa, e.g. in Gyrocarpus americanus ssp. americanus and Systemonodaphne mezii, when all other flanges are unornamented as well as in Caryodaphnopsis baviensis, Licaria spp. and Ravensara pervillei as on the ordinary flanges, although the guard cell/subsidiary cell flange is ornamented.

Protrusions are universally present in taxa when there is any sculpture on the subsidiary cell/surrounding cell flange, even when ordinary flanges are unornamented, e.g. in Aniba hostmanniana, Endlicheria reflectens and Nectandra salicifolia.

Depressions may also be detected in a range of species, including those of Aiouea, Cinnamomum [Fig. 124] and Neocinnamomum [Fig. 121] sometimes when absent on other flanges as in Cryptocarya weinlandii, Neolitsea dealbata and Umbellularia californica, or more commonly when absent only on the guard cell/subsidiary cell flange, e.g. in Illigera pentaphylla, Litsea umbellata and Nothaphoebe umbelliflora [Fig. 119].

Variation detected in the appearance of sculpture on the subsidiary cell/surrounding cell flange, within the

assemblage, may be described in sections in the same way as periclinal ornamentation [p. 127].

12.5.3s (i) SIZE OF ELEMENTS

Protrusions. These vary from very fine [less than 0.2 μm , with a minimum of ca. 0.04 μm] as in Dicypellium caryophyllatum [Fig. 117], Gyrocarpus americanus ssp. africanus and Nothaphoebe heterophylla [Fig. 127] to moderate [with a maximum of ca. 0.9 μm], in Apollonias arnottii [Fig. 129]. The subsidiary cell/surrounding cell flange protrusion diameters of many taxa fall in the range between the minimum and 0.5 μm e.g. in certain Cinnamomum spp. [all, except C. oliverii, ca. less than 0.2-0.4 μm], Dehaasia caesia [ca. 0.2-0.5 μm] [Fig. 111], Illigera spp. [ca. 0.2 μm or less] [Figs 132, 137] and some Persea spp. [P. chinensis & P. thunbergii; ca. 0.2-0.4 μm]. Other examples have some protrusions of greater size on this specialised flange, such as Caryodaphnopsis tonkinensis [ca. less than 0.2-0.7 μm], Laurus spp. [ca. 0.2-0.7 μm] [Fig. 323] and Trimenia weinmanniaefolia [ca. 0.4-0.7 μm] [Fig. 136].

Depressions. Where present on the subsidiary cell/surrounding cell flange, they range in size from very fine [less than 0.2 μm , with a minimum of approximately 0.04 μm] as in Aiouea spp., Illigera spp. [Figs 132, 137], Litsea umbellata and Sassafridium macrophyllum [Fig. 122], to fine [with a maximum of 0.4 μm], in Hernandia olivacea [Fig. 131]. Most taxa have depressions which are 0.2 μm or less in diameter, e.g. Endiandra rubescens [less than 0.2 μm], Lindera spp., Neocinnamomum spp. [ca. 0.2 μm or less] [Fig. 121] and Umbellularia californica [ca. 0.2 μm].

When the sculpture of this specialised flange incorporates both protrusions and depressions, the latter element type is usually of finer dimensions than the former. However, in a few species, Alseodaphne semecarpifolia, Lindera strychnifolia and Phoebe sheareri, protrusions and depressions are of similar size.

12.5.3s [ii] DENSITY OF ELEMENTS. This aspect varies between taxa. Dense sculpture is commonly found on the subsidiary cell/surrounding cell flange, as in Aiouea spp., Illigera pulchra [Fig. 137], Litsea umbellata and Piptocalyx moorei [Fig. 135]. Occasionally, the components are widely spaced, e.g. those of Cinnamomum iners and Mezilaurus lindaviana or sometimes, an intermediate state of sculptural density may be recognised on this specialised flange surface, such as in Dehaasia caesia [Fig. 111], Micropora curtisii [Fig. 126], Persea americana and Sassafras albidum var. molle.

12.5.3s [iii] ARRANGEMENT AND FORM OF ELEMENTS

Protrusions. These exist in a variety of forms on the subsidiary cell/surrounding cell flange. The simplest arrangement, granules, is of common occurrence and may constitute the entire microrelief of this specialised flange in some taxa, such as Aniba spp. [Fig. 110], Eusideroxylon spp. [Figs 115, 116], Gyrocarpus americanus ssp. africanus and Hernandia nymphiifolia, or may be accompanied by more complex groups: clumps, e.g. in Dehaasia spp. [Figs 111, 285, 286], Laurus spp. [Fig. 323], Piptocalyx moorei [Fig. 135] and Trimenia papuana or clumps and reticula, as in certain Lauraceae, for example Aiouea spp., Lindera strychnifolia and Neocinnamomum spp. [Fig. 121]. Clumped and reticulate protrusions may also be observed on the subsidiary cell/surrounding cell flange in a single Lauraceae taxon, Litsea umbellata. The most complicated protrusion pattern, consisting entirely of reticula, may be detected predominantly in members of families related to Lauraceae, e.g. Gomortega keule [Fig. 134], Illigera spp. [Figs 132, 137], Hernandia olivacea [Fig. 131] and Trimenia weinmanniaefolia [Fig. 136].

Individual protrusions are usually rounded in form, although the filamentous type sometimes occurs, as in Endiandra spp., Illigera spp. [Fig. 137] and Litsea umbellata or more rarely, an intermediate configuration, in Hernandia olivacea [Fig. 131].

Depressions. When these are present, they are generally of pit-like form only, for example, in Alseodaphne semecarpifolia, Hernandia olivacea [Fig. 131], Illigera spp. [Fig. 132, 137] and Litsea umbellata. A few taxa have depressions of more complex arrangement: Apollonias arnottii [clumps and reticula] [Fig. 129] and Endiandra kingsiana [pits and clumps].

Where the subsidiary cell/surrounding cell flange ornamentation is composed of both element types, depressions are usually arranged more simply than protrusions. However, in a few taxa, a similar level of organisation is attained, for example, in Cinnamomum iners, Endlicheria piriformis [Fig. 114] and Lindera strychnifolia.

12.5.3s [iv] PROMINENCE OF ELEMENTS. This is variable within the assemblage. Protrusions may hardly project at all from the cutin matrix of the flange, as in Aiouea spp. Dicypellium caryophyllatum [Fig. 117] and Sassafridium macrophyllum [Fig. 122] or at the other extreme, more often, are prominent, forming a distinctly textured surface, e.g. in Dodecadenia grandiflora, Laurus spp. [Fig. 323], Micropora curtisii [Fig. 126] and Sparattanthelium tupiniquinorum [Fig. 138]. A few examples with intermediate protrusion prominence are recognised, such as in Endiandra rubescens and Neocinnamomum caudatum [Fig. 121].

Subsidiary cell/surrounding cell flange depressions of Actinodaphne stenophylla and Apollonias arnottii [Fig. 129] look especially deep in the S.E.M., others less so, particularly those of Alseodaphne semecarpifolia, although details are impossible to obtain [see p.140].

12.5.3s(v) SCULPTURAL DIFFERENCES BETWEEN SUBSIDIARY
CELL/SURROUNDING CELL FLANGE AND OTHER
FLANGE SURFACES.

The sculpture found on the surface of the subsidiary cell/surrounding cell flange is similar to that of flanges elsewhere in a few taxa, Eusideroxylon spp. and Gyrocarpus americanus ssp. americanus. Others exhibit a variety of differences involving aspects, particularly size and arrangement, of the sculptural components. Sometimes, such dissimilarities occur between the ornamentation of the subsidiary cell/surrounding cell flange (SOF.) and that of either the ordinary flanges (OF.) such as, in Cinnamomum iners (SOF. p. coarser & simpler, d. finer), Cryptocarya ainikini (SOF. p. coarser) and Nothaphoebe umbelliflora (SOF. d. simpler), or more commonly, the microrelief of the guard cell/subsidiary cell flange, for example, in Ocotea laevis (SOF. p. finer & simpler) [Fig. 113], Piptocalyx moorei (SOF. p. coarser more complex) [Fig. 135] and Sassafras albidum var. molle (SOF. p. coarser). Most frequently the sculpture is different on all three flange types within a taxon. The resulting differences between the configuration on the subsidiary cell/surrounding cell flange and the others may involve the same sculptural elements; usually protrusions (p.) only, as in Cryptocarya weinlandii (SOF. p. coarser & more complex than on OF.; more complex than on GSF.), Dehaasia caesia (SOF. p. coarser than on OF. & GSF.) [Fig. 111], Hernandia nymphiifolia (SOF. p. finer & simpler than on OF.; coarser & simpler than on GSF.) and Sassafridium macrophyllum (SOF. p. more complex than on OF.; finer & simpler than GSF.) or occasionally, both protrusions and depressions, e.g. in Actinodaphne stenophylla (SOF. p. simpler, d. coarser than on OF.; p. & d. finer than on GSF.) and Neocinnamomum caudatum (SOF. p. coarser & simpler, d. simpler than on OF.; p. coarser & more complex, d. coarser than on GSF.). In

a number of taxa, however, different components of the microrelief are responsible for dissimilarities between the subsidiary cell/surrounding cell flange microrelief and ornamentation on each of the other two flanges, such as in Aiouea saligna (SOF. p. finer & simpler than on OF.; p. finer & more complex, d. finer than on GSF.), Apollonias arnottii (SOF. p. coarser & simpler, d. more complex than on OF.; p. coarser than on GSF.), Endiandra kingsiana (SOF. d. coarser & more complex than on OF.; p. & d. more complex, d. coarser than on GSF.), Hernandia olivacea (SOF. d. finer than on OF.; p. more complex, d. coarser than on GSF.) [Fig. 131] and Litsea umbellata (SOF. p. & d. finer, p. simpler than on OF.; p. finer & more complex than on GSF.).

12.5.3t SECONDARY ANTICLINAL DIVISIONS

Anticlinal divisions of the subsidiary cells parallel to the pore, which occurred after the formation of the stomatal complex [separation of guard cells from subsidiary cells] and may be designated secondary divisions, are present in most taxa. Such subdivision may be observed in either one or both subsidiary cells. At the junction between the resulting cells, the secondary flange is noticeably less prominent [see Gomortega keule: Fig. 134] and straighter [see Piptocalyx moorei: Fig. 135] than the primary flanges of the subsidiary cell, but always with similar surface sculpture.

In Trimeniaceae members, particularly Piptocalyx moorei, peculiar secondary anticlinal divisions may be seen in the subsidiary cells in addition to those parallel to the pore. These are orientated at an angle to the stomatal aperture and may sometimes even be perpendicular to it.

12.5.3u OBVIOUS SPECIALISATION OF ORDINARY [SURROUNDING] CELL ADJACENT TO SUBSIDIARY CELL

Specialisation of the ordinary cell adjacent to the subsidiary cell [parallel to the pore] may be recognised

distinctly in only a few Lauraceae taxa, Licaria guianensis and Ravensara pervillei [Text-Fig. 24B]. In these, the curvature of the outer periclinal wall of the cell next to the stomatal complex is considerably greater than that of other epidermal cells, when viewed in transverse section. The average value for the periclinal curvature of this cell in Licaria guianensis is 0.63:1 almost 5 times that of the ordinary cells. The corresponding value for Ravensara pervillei is 0.58:1, nearly 6 times the epidermal periclinal curvature. In surface view, these cells are clearly highly domed, kidney-shaped (reniform) and individually flanking and somewhat [4.0 μm] above the subsidiary cells in Licaria guianensis but providing a rather different configuration in Ravensara pervillei. The adjacent lateral cells here tend to form a wide irregular, basically dumb-belled ring overtopping the subsidiary cells with the stomatal complex, therefore, deeply sunken below in a 'pit' [of ca. 8.0 μm in T.S.] reminiscent of the stomatal pit.

The scanning electron microscope also reveals that in other Lauraceae taxa, the cells on either side [parallel to the pore] adjacent to the subsidiary cell pair are often particularly distinctive in form, similar in shape to those of Licaria guianensis mentioned above, curving towards the stomatal complex [see Fig. 80]. However, in transverse section, these cells are not obviously specialised in terms of periclinal curvature. Taxa with this characteristic appearance include Aiouea saligna [Figs 82, 89], Beilschmiedia madang, Licaria triandra and Nectandra spp.

The inner surface of cuticles of such examples suggests that these cells may sometimes, at least, be the result of secondary anticlinal divisions of the subsidiary cells [see Ocotea laevis: Fig. 113 and Sassafridium macrophyllum: Fig. 122].

12.5.3v NUMBER OF CELLS SURROUNDING STOMATAL COMPLEX

Surrounding the subsidiary cells there may be a varying number of epidermal cells outlined on isolated

cuticles and these may be best viewed in the light microscope or on the inner surface with the S.E.M. Within any cuticular preparation, a range of values for this feature may be observed, most commonly 4-5, e.g. in Aniba spp. (Fig. 110), Illigera pulchra and Pleurothyrium nobile, up to 6, as in Aiouea spp., Dehaasia spp. (Figs 111, 285, 286) and Phoebe sheareri (Fig. 128) or up to 7, for example, in Alseodaphne spp., Eusideroxylon melagangai [abx.], Nectandra spp. and Trimeniaceae members. Sometimes, there may be more than 7 cells found around the stomatal complex: occasionally up to 8 cells, such as, in Caryodaphnopsis spp., Endiandra spp. and Mezilaurus itauba, or more often up to 9, e.g. in Eusideroxylon melagangai [adx.] and E. zwageri, Hernandia olivacea [5-9] and Potameia crassifolia [8-9]. A few taxa, however, Litsea monopetala, Ocotea guianensis [6-10] and Pleurothyrium cuneifolium [7-10] (Fig. 118) have up to 10 cells surrounding the subsidiary cells and very rarely, there may be up to 12 cells [6-12] around the complex, as in Phoebe opaca.

The number of cells in this region may be influenced by cell size: where a large number are involved, these tend to be small.

12.6 CHARACTERS OF SPECIALISED CELLS : TRICHOMES

12.6.1 CHARACTERS OF NON-GLANDULAR TRICHOMES

These are unbranched, unicellular and simple [see Figs 10, 12, 14, 15, 16, 139, 140, 148] except in Piptocalyx moorei, where they appear to be bicellular.

12.6.1a OCCURRENCE

Simple hairs commonly occur on both leaf surfaces, for example, in Actinodaphne glomerata [Fig. 144], Litsea umbellata [Fig. 142], Ocotea laevis and Pleurothyrium spp. [Figs 2, 149, 150]. Sometimes, however, these hairs are confined to one side only, usually the abaxial, as in Aniba hostmanniana, Dehaasia caesia, Hernandia spp. and Ocotea guianensis [Fig. 141], but occasionally on the adaxial, e.g. in Dodecadenia grandiflora. More rarely, simple hairs appear to be entirely absent, such as in Aiouea guianensis.

12.6.1b FREQUENCY

The number of simple hairs per unit area (a field of view in a x 320 scanning electron micrograph, representing ca. 0.28 x 0.35 mm of surface) i.e. the frequency, is variable. Values range between very rare (one only), e.g. in Alseodaphne semecarpifolia, Illigera pentaphylla and Trimenia weinmanniaefolia and abundant (several hundred), as in certain surfaces of Ocotea guianensis [abx. 200-300] [Fig. 141] and Pleurothyrium cuneifolium [abx. 150-250] [Fig. 149]. Most taxa have up to 30 hairs per field, often never more than 10, such as Persea spp. and Sassafras albidum var. molle of the Lauraceae as well as all Trimeniaceae.

Although the frequency of simple hairs may be similar on both leaf surfaces, for example, in Aniba megaphylla [1], Cryptocarya weinlandii [1-3] and Trimenia papuana [2-3], it is more usual for differences to exist between the adaxial and abaxial. Generally, simple hairs are more frequent on the abaxial side of the leaf, such as in Gyrocarpus americanus [adx. 4-7; ssp. africanus abx. 60-70; ssp. americanus abx. 30-40], Litsea meissneri

Hairs: morphology

Outer surface: abaxial.

139. Gyrocarpus americanus ssp. americanus

Simple filiform hairs on and between minor vein (centre, left to right). Two distinct forms visible: very fine micro-hairs of high frequency and coarse macro-hairs [H] of low frequency. ca. x 140.

140. Sparattanthelium guianense

Simple filiform hairs in intercostal and costal regions. Note only one form distinguishable. ca. x 140.

141. Ocotea guianensis

Dense covering of very long simple hairs appressed to surface, obscuring it. Hairs all orientated in one direction. ca. x 140.

142. Litsea umbellata

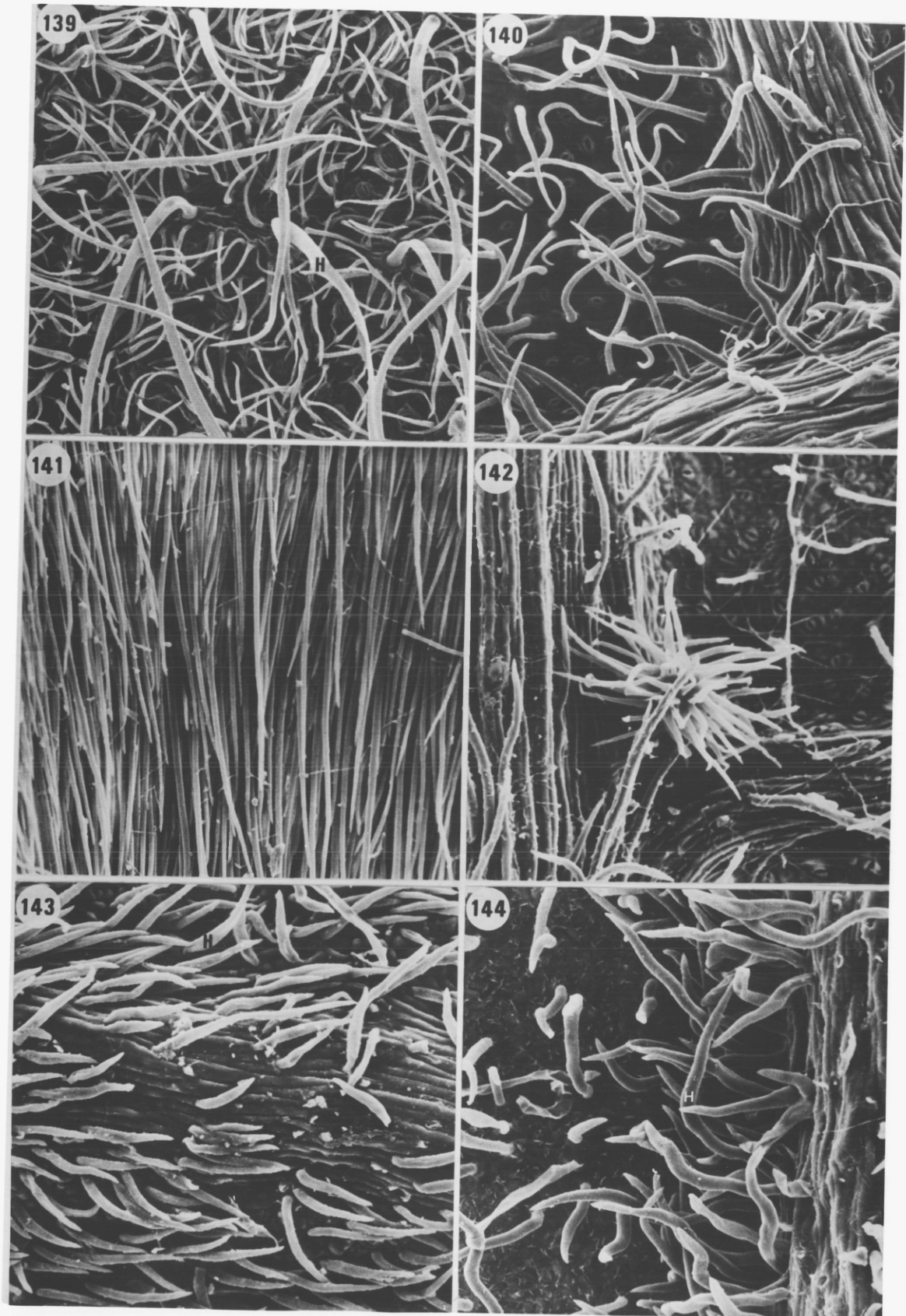
Tuft of hairs (possibly domatium) in axil between midrib and major vein. ca. x 140.

143. Litsea meissneri

Robust simple hairs [H] of high frequency in intercostal regions. Note most of hairs orientated in one direction. ca. x 150.

144. Actinodaphne glomerata

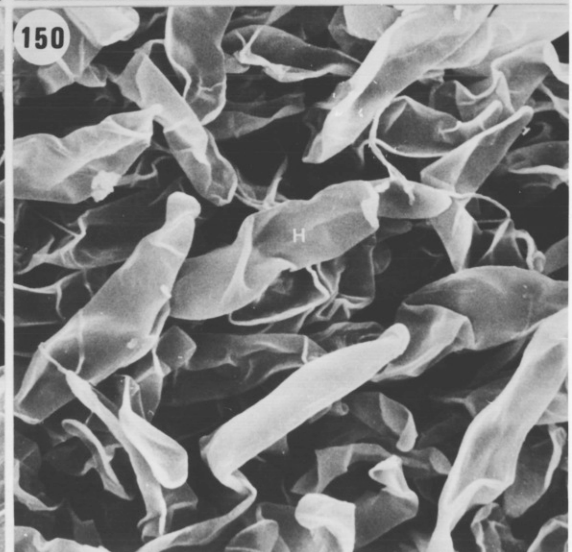
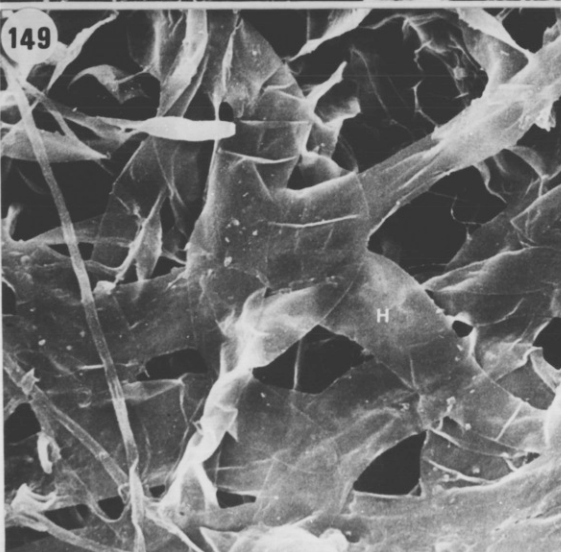
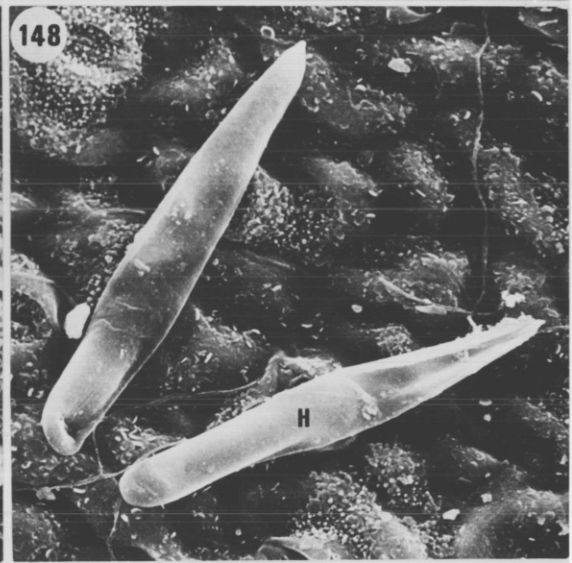
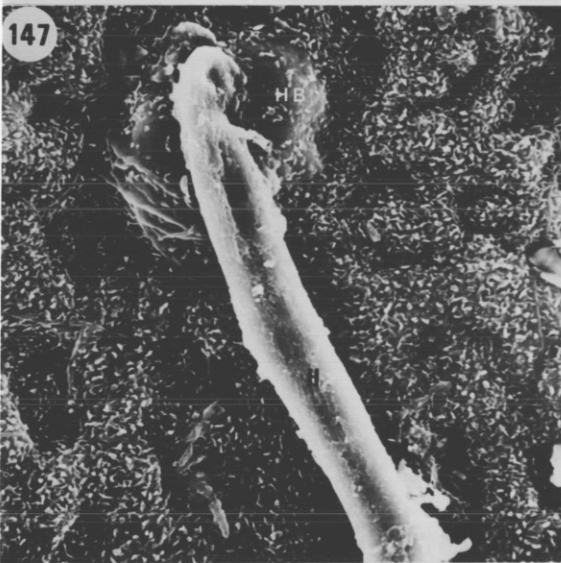
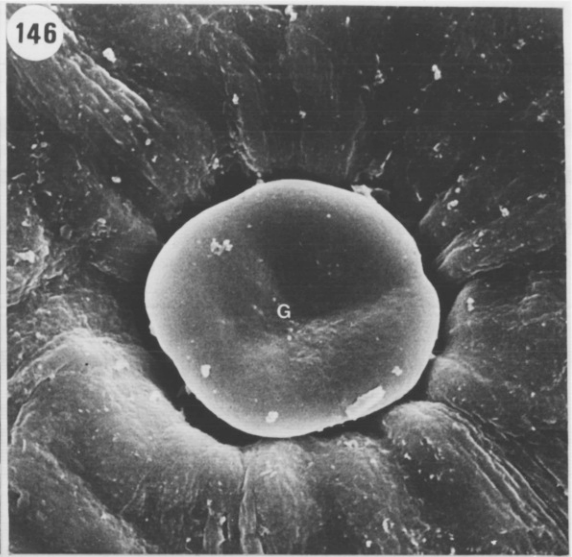
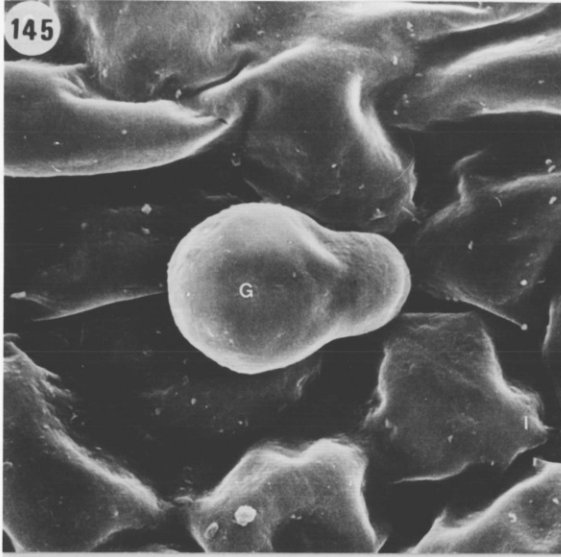
Simple hairs [H] especially associated with veins. ca. x 140.



Glands and hairs: morphology

Outer surface: abaxial.

145. Hernandia nymphiifolia. Pyriform gland body [G] located superficially in isolated cuticle. Note presence of five radiating basal cells. ca. x 1100.
146. Hernandia olivacea. Head of peltate gland [G] sunken, in isolated cuticle. Note striae radiating from gland pit. ca. x 1075.
147. Gomortega keule. Portion of long, simple hair [H] showing hair base [HB]. [First report of hairs in this species]. ca. x 530.
148. Neocinnamomum caudatum. Two simple hairs with short, robust bodies [H], closely appressed to surface due to pressing in herbarium. ca. x 545.
149. Pleurothyrium nobile. ca. x 575.
150. Pleurothyrium cuneifolium. ca. x 575.
Simple hairs [H] of high frequency forming a tomentum. Note especially flattened hair form in Fig. 149 and wrinkled hairs of Fig. 150. Probably due to herbarium treatment.



PORE = lumen of hair.

[adx. 1-2; abx. 21-34], Nectandra spp. [N. pichirum adx. 4-8, abx. 10-16; N. salicifolia: adx. 1-2; abx. 10-15] and Pleurothyrium spp. [P. cuneifolium adx. 15-20, abx. 150-250; P. nobile adx. 6-10, abx. 50-100]. However, in a few taxa, hairs are more abundant on the adaxial side, e.g. in Litsea umbellata [adx. 11-21; abx. 4-7], Potameia spp. [P. crassifolia adx. 20-25, abx. 1; P. thouarsii adx. 4-6, abx. 3-4] and Ravensara elliptica [adx. 11-15; abx. 6-8].

A greater number of hairs tend to be found on the veins than in between them. This is particularly noticeable on the adaxial surface, as in Apollonias arnottii, Mezilaurus itauba and Potameia thouarsii but sometimes may be especially distinct on the abaxial, e.g. Cryptocarya ainikini, Dehaasia caesia and Potameia crassifolia. Thus, when hairs are very rare they tend to be located entirely in costal regions, such as in Austrobaileya scandens, Gomortega keule [Fig. 147] and Dicypellium caryophyllum [abx. 1 hair].

12.6.1c PERSISTENCE IN CUTICLE PREPARATIONS

Commonly, simple hairs are represented only by their bases [a rimmed pore with radiating basal cells] in cuticle preparations [Figs 9, 11, 13]. However, in a few Lauraceae members hair bodies are of sporadic persistence. This may be observed on the abaxial surface alone, in Alseodaphne oblanceolata, Eusideroxylon melagangai, Licaria guianensis, Mezilaurus itauba and Nectandra salicifolia. Simple hair bodies are of more regular occurrence on the abaxial in the occasional Lauraceae taxon, e.g. Aniba hostmanniana and Litsea meissneri, and also in a number of Hernandiaceae, either mainly on the same surface [abaxial], as in Hernandia nymphiifolia, Illigera pentaphylla and Sparattanthelium guianense or rarely on cuticles of both sides of the leaf, in Gyrocarpus americanus.

The presence of hair bodies after maceration in some taxa is probably indicative of a thicker cuticle on the hairs.

In Piptocalyx moorei, the flask-shaped portion [basal hair cell] remains in isolated membranes.

12.6.1d BODY TYPE

Simple hairs are always non-ornamented or smooth. Bodies vary in both length and width. Comparison of such dimensions between taxa has only been made from scanning electron micrographs of unmacerated leaf portions since hair bodies often become detached during cuticle isolation. However, measurement difficulties may still arise due to orientation of hairs to the surface, collapse of thin-walled hairs during drying of the plant specimen, shrinking both length and width [as in Fig. 2], density of hairs [frequency per unit area], particularly, if high so that individual bodies are difficult to distinguish due to overlap [Fig. 141] and body shape, especially if curled naturally or bent by pressing [Fig. 12]. Hairs vary in length from about 25 μm , as in Gyrocarpus americanus ssp. americanus and Mezilaurus itauba to 646 μm , in Piptocalyx moorei on the adaxial surface and from approximately 9 μm in Pleurothyrium cuneifolium to 566 μm , in Ocotea guianensis on the abaxial. Each taxon commonly exhibits a wide range of hair lengths, for example, Endlicheria reflectens [adx. ca. 54.3-311.4 μm ; abx. ca. 134.3-440.0 μm], Lindera strychnifolia [abx. ca. 211.4-508.6 μm], Mezilaurus lindaviana [adx. ca. 194.3-594.3 μm ; abx. ca. 117.1-525.7 μm] and Sassafras albidum var. molle [adx. ca. 80.0-251.4 μm ; abx. ca. 114.3-440.0 μm]. The maximum hair length is generally less than about 300 μm , particularly on the adaxial side of the leaf, although notable exceptions include some of the taxa mentioned above and Gyrocarpus americanus [abx. max. ca. 542.8 μm], Litsea umbellata [abx. max. ca. 377.1 μm] and Piptocalyx moorei [abx. max. ca. 520.0 μm]. A few have comparatively short hairs all less than 100 μm long, such as Aniba hostmanniana [abx. ca. 18.6-45.7 μm], Persea thunbergii [abx. ca. 18.6-85.7 μm] and Pleurothyrium cuneifolium [adx. ca. 44.0-45.3 μm ; abx. ca. 9.3-44.0 μm]. Other taxa possess hairs of intermediate lengths: up to approximately 200 μm , e.g. in Beilschmiedia madang [adx. ca. 74.3-131.4 μm ; abx. ca. 48.6-160.0 μm], Hypodaphnis

zenkeri [adx. ca. 151.4-165.7 μm ; abx. 45.2-134.3 μm] and Sparattanthelium tupiniquorum [adx. ca. 80.0-175.7 μm ; abx. ca. 71.4-140.0 μm], or with a maximum length between about 200 and 300 μm , as in Litsea meissneri [adx. ca. 28.6-271.4 μm], Litsea monopetala [abx. ca. 51.4-240.0 μm] and Sparattanthelium guianense [adx. ca. 171.4-297.1 μm ; abx. ca. 74.3-234.3 μm].

Hairs also show some variation in median width [Measured at half way along the hair length], ranging from approximately 4.3 μm , as in Dehaasia cuneata to 31.4 μm , in Trimenia papuana on the adaxial surface, and from about 2.8 μm , e.g. in Ocotea guianensis and Sassafridium macrophyllum to 28.6 μm , again in Trimenia papuana, on the abaxial. As with length, a range of widths may be detected within any taxon. This is especially great in hairs of the abaxial side of the leaf, such as in Beilschmiedia madang [ca. 11.3-23.0 μm], Gyrocarpus americanus [ssp. africanus ca. 5.7-14.3 μm ; ssp. americanus ca. 2.8-11.4 μm] and Nectandra pichurim [ca. 6.5-16.9 μm]. A number of taxa have hairs up to 10 μm in width on certain surfaces, e.g. in Aniba hostmanniana [abx. ca. 3.8-7.1 μm], Hypodaphnis zenkeri [adx. ca. 8.6-10.0 μm], and Nectandra salicifolia [abx. ca. 4.6-6.5 μm]. More commonly, the hairs may attain a width of between 10 and 20 μm , such as on some sides of the leaf in Endlicheria reflectens [adx. ca. 5.7-11.4 μm ; abx. ca. 8.6-11.4 μm], Mezilaurus lindaviana [adx. ca. 11.4-14.3 μm ; abx. ca. 11.4-17.1 μm] and Neocinnamomum caudatum [abx. ca. 12.8-14.3 μm]. Hairs more than 20 μm wide are found in only a few taxa, Beilschmiedia madang [adx. ca. 17.1-25.7 μm ; abx. ca. 11.3-23.0 μm] and Trimenia papuana [adx. ca. 25.7-31.4 μm ; abx. ca. 25.0-28.6 μm].

Since length and width of simple hairs varies, so also does the length:width ratio which is indicative of shape. Hairs may be between 2.0 [Mezilaurus itauba] and 56.6 [Piptocalyx moorei] times the width in length on the adaxial, and 2.6 [Cinnamomum iners] and 99.2 [Ocotea guianensis] times on the abaxial. Rather robust hairs with a low length:width ratio [l:w] are characteristic of

certain surfaces in Beilschmiedia madang [adx. 1:w 2.9-7.7:1.0; abx. 3.4-7.0:1.0] (Fig. 12), Caryodaphnopsis tonkinensis [abx. 1:w 2.2-8.1:1.0], Pleurothyrium cuneifolium [adx. 1:w 3.7-4.1:1.0; abx. 2.3-7.3:1.0] (Figs 2, 149) and Trimenia papuana [adx. 1:w 5.7-7.9:1.0; abx. 1:w 5.0-6.6:1.0]. Filiform hairs [high 1:w ratio] are a feature of some sides of the leaf in especially Gyrocarpus americanus [abx. max. ssp. africanus 1:w 37.9:1.0, ssp. americanus 47.6:1.0] (Fig. 139), Lindera strychnifolia [abx. max. 1:w 44.6:1.0], Litsea meissneri [adx. max. 1:w 47.6:1.0], Ocotea guianensis [abx. max. 1:w 99.2:1.0] (Fig. 141) and Piptocalyx moorei [adx. max. 1:w 56.6:1.0]. However, a wide range of hair shapes tends to occur in individual taxa.

With the exception of Gyrocarpus americanus ssp. americanus and Sassafras albidum var. molle, taxa have non-lignified hair bodies on the adaxial leaf surface. However, on the abaxial, lignification is much more common, for example in the Hernandiaceae Gyrocarpus americanus, Hernandia olivacea and Sparattanthelium guianense, and some Lauraceae e.g. Litsea spp. Mezilaurus lindaviana, Ocotea guianensis, Phoebe spp. Pleurothyrium spp. and Sassafras albidum var. molle. Lignin, with its strengthening properties, might be thought to assist persistence of hairs during maceration. However, hair bodies are generally found in those taxa which are non-lignified, except in Litsea meissneri. Thus, there appears to be little or no correlation between persistence of hairs in a cuticle and presence of lignin in the hair body.

12.6.1e GROUPING OF BASES

Bases are generally distributed singly in isolated cuticular preparations [see Figs 152, 153, 154]. Sometimes the rimmed pores may be paired [situated adjacent to one another and surrounded by a set of radiating basal cells, the constituent number being normally greater than around a single pore]. Such pore pairs always occur in a cuticle together with the solitary type and are confined to members of Lauraceae. Pairs are most often located only on the abaxial membrane, for example in,

Aniba hostmanniana, certain Cryptocarya spp. [C. alleniana & C. weinlandii], Nectandra spp. (Fig. 156) and Phoebe spp., but occasionally may be confined to the adaxial, as in Neocinnamomum delavayi, Neolitsea dealbata and Persea americana. Very rarely pairs occur in cuticles of both surfaces, as in Cinnamomum pachyphyllum and Mezilaurus lindaviana.

In a few Lauraceae taxa, Cinnamomum pachyphyllum, Litsea meissneri and Ocotea guianense, groups of three simple hair pores sometimes may also be observed (usually arranged in an irregular row flanked by basal cells rather than a cluster), on the abaxial only (see Fig. 155, right).

12.6.1f NUMBER OF BASAL CELLS SURROUNDING HAIR PORE

Solitary pores are universally present in all taxa with simple hairs and these can be used for comparative purposes. Thus, it may be observed that the number of basal cells radiating from this pore type may vary. In any cuticle preparation, a range of numbers exists which falls between four in Apollonias arnottii [adx.] and twelve in Endlicheria reflectens [abx.]. Commonly single pores are surrounded by up to seven basal cells, for example in Gomortega keule [abx. 6-7], Ocotea guianensis [abx. 4-6], Sassafras albidum var. molle [adx. 5-6; abx. 4-7] and Sparattanthelium spp. [S. guianense adx. 5-6, abx. 5-7; S. tupiniquinorum adx. 6-7, abx. 5-7]. There may also sometimes be hair pores with eight basal cells in certain taxa, on the adaxial membrane, as in some Cinnamomum spp. [C. iners 7-8; C. oliverii 5-8], Dodecadenia grandiflora [5-8] and Litsea spp. [L. meissneri 7-8; L. monopetala 6-8; L. umbellata 4-8], or on the abaxial, e.g. in Aniba hostmanniana [4-8], Ocotea laevis [6-8] and Ravensara spp. [R. elliptica & R. pervillei 4-8]. Occasionally, there are up to eight cells constituting the bases of single hairs on cuticles of both leaf surfaces, such as in Cinnamomum pachyphyllum and Cryptocarya alleniana [5-8]. A few examples with nine cells exist: on the adaxial, e.g. in Licaria guianensis and Nectandra pichurim [5-9] or more usually, on the abaxial cuticle, as in Caryodaphnopsis spp., Mezilaurus lindaviana and Sassafridium macrophyllum [6-9].

Simple hairs with more than nine basal cells are rare and occur predominantly in the families related to Lauraceae, in Gyrocarpus americanus ssp. africanus on the adaxial [7-11] (Fig. 154) and Trimenia spp. [T. papuana 5-10; T. weinmanniaefolia 6-11], on the abaxial.

The range of numbers of basal cells surrounding a single hair pore is often more or less similar on cuticles of the adaxial and abaxial surfaces of a taxon or shows a high degree of overlap. Occasionally there are more distinct differences, with more cells in bases of the adaxial hairs, such as Cinnamomum iners [adx. 7-8; abx. 5-7], Nectandra pichurim [adx. 5-9; abx. 4-6] and Nothaphoebe umbelliflora [adx. 6-7; abx. 4-6], or more commonly, more cells in bases of the abaxial simple hairs, Actinodaphne stenophylla [adx. 4-6; abx. 5-8], Endlicheria reflectens [adx. 5-6; abx. 4-12] and Neolitsea dealbata [adx. 4-6; abx. 5-9].

12.6.1g BASE TYPE

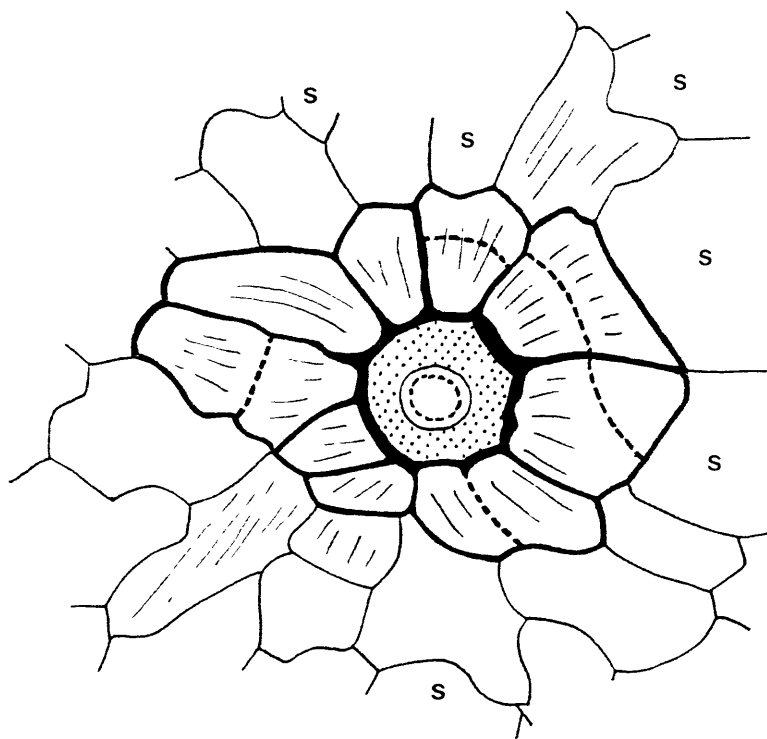
In the scanning electron microscope, most of the simple hair bases are similar in appearance; from an unmacerated leaf portion or the outside of an isolated cuticle, the base from which the main part of a body has become detached, consists of a central rounded pore opening [often bounded by a rim of body cuticle in a cuticular preparation] raised slightly above a ring of radiating basal cells [see Fig. 13]. On the inner surface of a cuticle, the pore is surrounded by a poral flange of varying prominence, depending on the depth to which the 'peg'-like foot of the hair penetrated in the leaf. This may sometimes be continuous with cutinisation covering all or part of the pore [the cutinised 'peg' end], for example, in Beilschmiedia micrantha (Fig. 153), Nectandra pichurim (Fig. 156) and Ocotea guianensis (Fig. 155). Basal cell form is more conspicuous on the inside of the cuticle than on the outside due to the presence of flanges. Those radiating from the pore [radial flanges] may gradually decrease in height [prominence] outwards. The basal cell/epidermal cell flanges are always similar to those of unspecialised cells. The basal cell periclinal and anti-

TEXT-FIGURE 26. Simple hair bases in isolated cuticles, as seen by light microscopy.

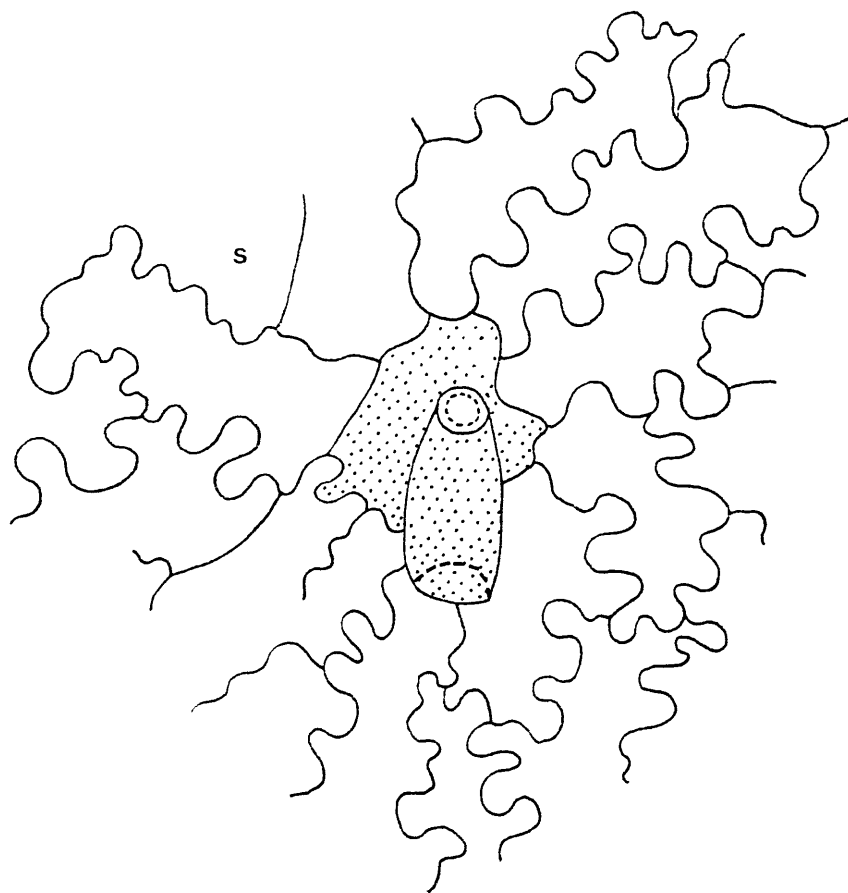
- A. Trimenia papuana [abx]. Base with strongly cutinised poral flange surrounding a less well cutinised poral rim [stippled], flanked by striate [parallel lines] basal cells of variable size and shape. Basal cell flanges deeper than those of non-specialised cells.
- B. Piptocalyx moorei [abx]. Lightly cutinised [stippled] base with conspicuous flask-shaped portion attached. Note thin poral flange around a thicker rim enclosed by a wide cutinised region and a ring of radially arranged basal cells.

Note s represents a stomatal complex.

A



B

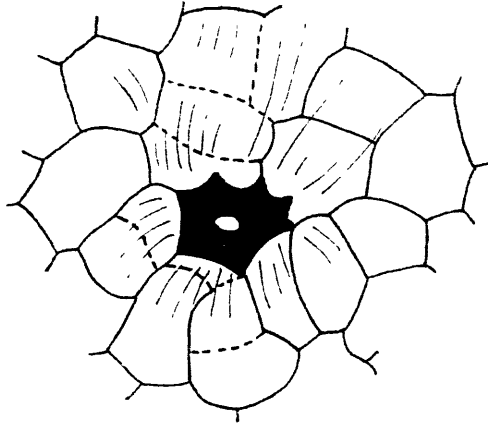


20 μ m

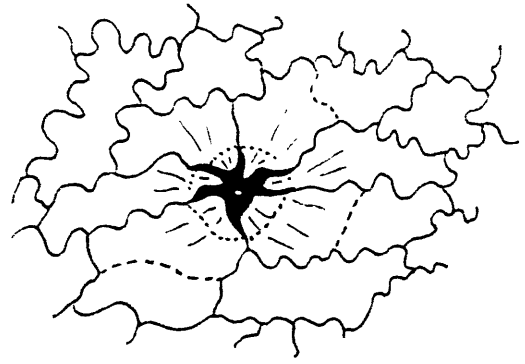
TEXT-FIGURE 27. Simple hair bases in isolated cuticles, as seen by light microscopy.

- A. Gomortega keule [abx]. Base with a thick, heavily cutinised poral flange surrounded by a ring of radiating basal cells which may possess secondary flanges (broken lines). Basal cells with radiating striae (parallel lines).
- B. Laurus canariensis [adx]. Base with a thick, well-cutinised poral flange as A but with deeper radial basal flanges near to the pore giving a stellate appearance.
- C. Alseodaphne oblanceolata [abx]. Base with a thin poral flange and within it, a faint poral rim.
- D. Sassafras albidum var. molle [abx]. Base with a thin poral flange, no visible poral rim, well cutinised radial basal flanges near the pore and an enlarged, lightly cutinised portion (stippled) of rounded outline (corresponding to basal part of the hair body) outside the poral flange.
- E. Sparattanthelium tupiniquinorum [adx]. Base with poral and radial flanges, thin and similar in thickness as well as prominence, to flanges of non-specialised cells.
- F. Neocinnamomum caudatum [abx]. Base with prominent cutinised foot, seen as a conical structure tapering from the cuticle surface. In situ, this would be embedded well down into the epidermis.

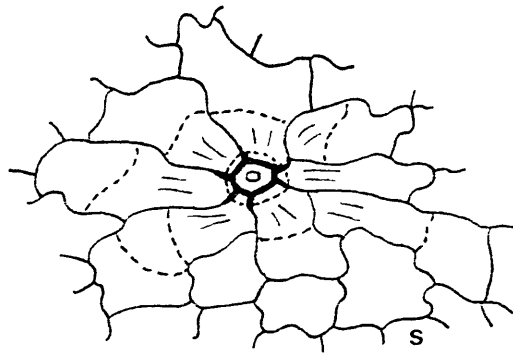
A



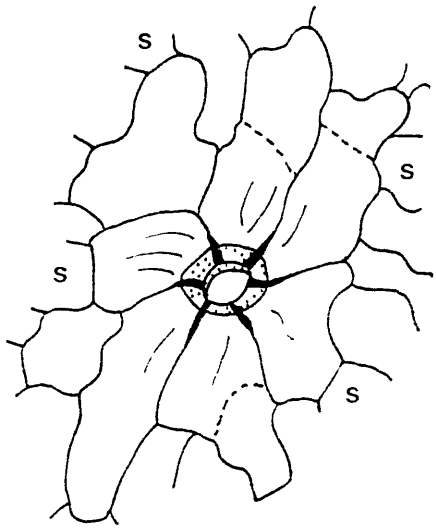
B



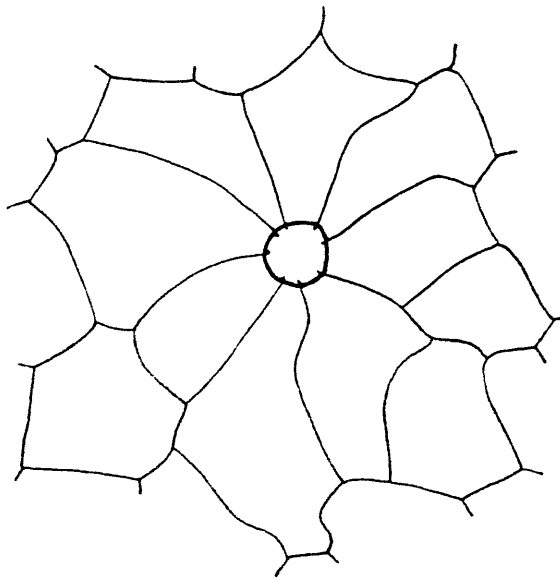
C



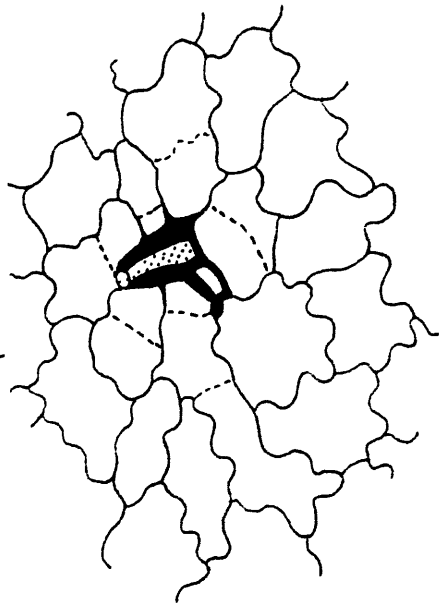
D



E



F



20 μm

clinal sculpture is also similar to elsewhere. The cutinised 'peg' end however, shows a smooth or finely granular microrelief.

Simple hair bases appear more variable in morphology, when viewed from above in cuticles, with the light microscope.

In Trimenia spp. alone, the bases are composed of a strongly cutinised poral flange (deep red in Sudan IV) ca. 1.8-3.6 μm wide, around a poral rim less well impregnated with cutin (pink), ca. 5.4-7.3 μm in width, flanked by two extremely irregular rings of different sized basal cells, the smallest of which are either located nearest to the pore or intermixed with somewhat larger cells similar to those of non-specialised areas (Text-Fig. 26A). Secondary flanges representing late divisions of individual cells further complicate the base pattern.

Piptocalyx moorei, of the same family, also has a distinctive base with a thin poral flange (of diameter ca. 0.5 μm) surrounding a thicker (2.0 μm) poral rim in the centre of a polygonal area which is more deeply cutinised than elsewhere. Attached to the base is a flask-shaped, cutinised portion, 45-50 μm in length (Text-Fig. 26B).

Many Lauraceae and members of related families possess much smaller bases with a thick, well-cutinised poral flange (thickness similar to the type described above, but appears thicker due to the smaller overall size of pore and flange) and thick radial basal flanges, which together form a star-shaped or stellate pattern of cutinisation (see Text-Fig. 27B). The poral rim is not visible. These bases are particularly common on both cuticles of species of Beilschmiedia, Cinnamomum (not C. pachyphyllum), Cryptocarya, Endiandra, Laurus, Ravensara and Sparattanthelium although they may occur on either the adaxial e.g. in Actinodaphne spp. Gyrocarpus americanus ssp. americanus and Sassafridium

macrophyllum, or more frequently on the abaxial, as in Endlicheria reflectens, Gomortega keule [Text-Fig. 27A] Hernandia spp., Nectandra spp. and Phoebe spp.

Others have bases with a somewhat thinner (ca. 0.9-1.8 μm) poral flange [staining red] and within it, a faint poral rim [pink], [Text-Fig. 27C], occasionally just on the adaxial cuticle, in Endlicheria reflectens, or on both sides, in Alseodaphne oblanceolata, Gyrocarpus americanus ssp. africanus and Nothaphoebe umbelliflora, but mainly on the abaxial only, as in Actinodaphne spp. Gyrocarpus americanus ssp. americanus, Litsea meissneri, Ocotea guianensis and Sparattanthelium guianense.

Another similar base lacks the poral rim and appears to have an enlarged cutinised [pink] portion with a rounded outline [part of the hair body] outside the poral flange [Text-Fig. 27D]. This form, like the last, is rare on the adaxial membrane, being found in only two taxa Aiouea saligna and Persea chinensis, and on the adaxial and abaxial, in Persea americana and Sassafras albidum var. molle. Examples with such bases confined to the abaxial cuticle include Beilschmiedia micrantha, Licaria guianensis and Persea thunbergii.

Bases in which the poral flange and radial flanges are of similar form [thickness and prominence] to flanges of non-specialised cells [Text-Fig. 27E] are uncommon, and are found in Austrobaileya scandens, Illigera pulchra [adx.] and Sparattanthelium spp. [abx.].

The cutinised 'peg' of the foot [the poral flange and its associated covering] may be especially prominent in a few taxa and may be detected as a conical structure, tapering away from the main cuticle surface [Text-Fig. 27F], [suggesting that the foot, embedded well down in the epidermis, is of smaller diameter than at the junction between the foot and the outside of the leaf [or cuticle]]. Examples, with such bases, are all found in the Lauraceae, either on the adaxial membrane, as in Actinodaphne glomerata and Nectandra pichurim or the abaxial, e.g.

in Hypodaphnis zenkeri and Neocinnamomum spp.

Taxa with lignified hair bodies [see p. 294] tend to also have bases showing evidence of lignification, for example, in Actinodaphne glomerata, Lindera strychnifolia and certain Persea spp. [P. americana & P. thunbergii], except in Endlicheria reflectens [abx.]. In a few taxa, lignin is confined to the hair bases, on the adaxial, in Aniba megaphylla and Mezilaurus lindaviana, or on the abaxial, e.g. in Cinnadenia paniculata, Cryptocarya alleniana and Sparattanthelium tupiniquinorum. It is generally more frequently found in bases on the abaxial leaf surface than on the adaxial, in the same way as for hair bodies.

12.6.2 CHARACTERS OF GLANDULAR TRICHOMES

12.6.2a OCCURRENCE

Glandular hairs are present in a very restricted number of taxa in the Hernandiaceae, i.e. species of Hernandia and Illigera over and between veins on both surfaces of the leaf, and in one Trimeniaceae taxon, Piptocalyx moorei on the abaxial. There is no evidence of such hairs in members of the Lauraceae.

12.6.2b TYPE

Three types of glandular hair may be distinguished from transverse sections and unmacerated leaf mounts viewed with light- and scanning electron-microscopy respectively: 'pyriform', inverse pear-shaped [ca. 30-40 μm long] as in Hernandia nymphiifolia [Text-Fig. 28B, Fig. 145] and Illigera spp.; 'peltate', flat-topped, mushroom form [ca. 20-30 μm long], characteristic of Hernandia olivacea [Text-Fig. 28A, Fig. 146] and 'digitate', elongate finger-like [ca. 70-100 μm long], as in Piptocalyx moorei [Text-Fig. 28C, D].

12.6.2c NUMBER OF CELLS IN BODY

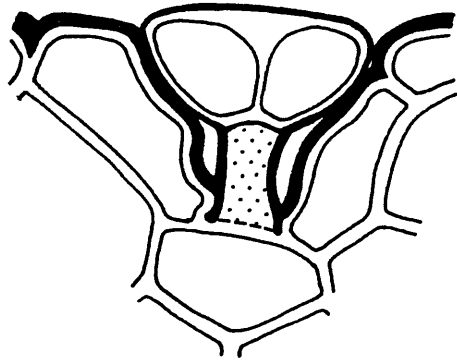
Pyriform and peltate glandular hairs possess a unicellular stalk and a one- (Hernandia nymphiifolia, Illigera pulchra) or two- (H. olivacea, I. pentaphylla) celled head. The head cells are arranged one above the other in the bicellular pyriform type [Text-Fig. 29B] and side-by-side in the peltate type [Text-Fig. 28A].

Digitate glandular hairs consist of either a flask-shaped basal portion [ca. 45-50 μm long] with a number [one or two] of cross walls terminated by a blunt ended cell [ca. 20-30 μm long] which tends to expand towards its tip [Text-Fig. 28C] or, a single flask-shaped cell [ca. 20-30 μm long] filled with brown-green contents in unstained sections attached to the base and an elongate body [ca. 60-70 μm long] of two or more cells that tapers to a point at its free end [Text-Fig. 28D].

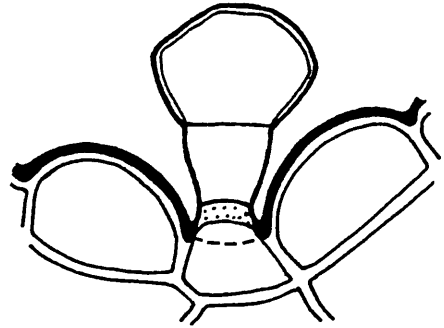
TEXT-FIGURE 28. Glandular hairs in transverse sections.

- A. Hernandia olivacea [adx]. Peltate gland consisting of bicellular head and a unicellular stalk. Gland base located at the bottom of a pit. Head raised slightly above level of epidermis [see also Figs. 146, 151 and Text-Fig. 29 D].
- B. Hernandia nymphiifolia [adx]. Pyriform gland consisting of unicellular head and stalk. Gland more or less superficial [see Fig. 145 and Text-Fig. 29C].
- C. Piptocalyx moorei [abx]. Digitate gland consisting of a bicellular basal portion and a unicellular head [contents brown-yellow before decolourisation].
- D. Piptocalyx moorei [abx]. Gland(?) consisting of a unicellular basal portion and a uniseriate bicellular head [contents as C]. Basal portion with starch grains.

A

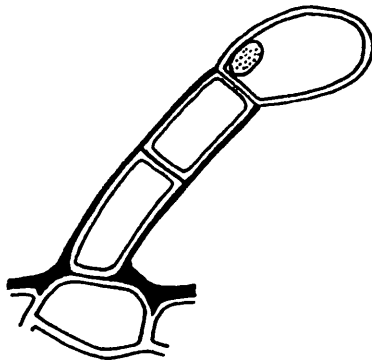


B

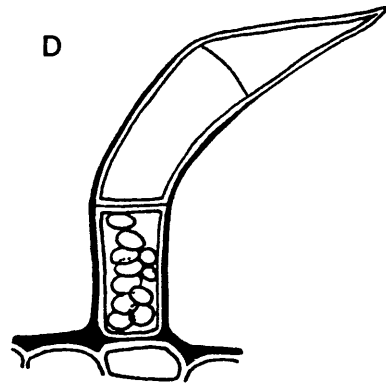


ca. 20 μm

C



D



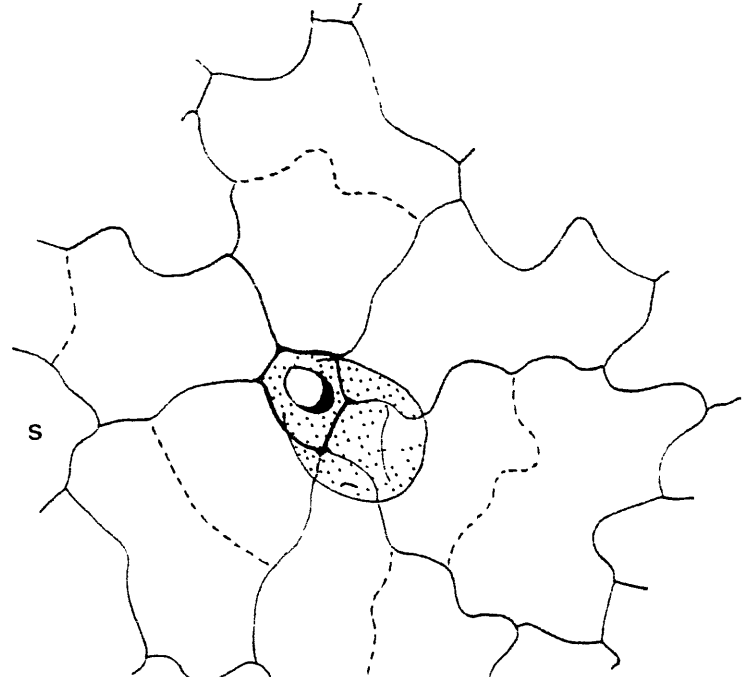
ca. 15 μm

TEXT-FIGURE 29. Glandular hairs in isolated cuticles, as seen by light microscopy.

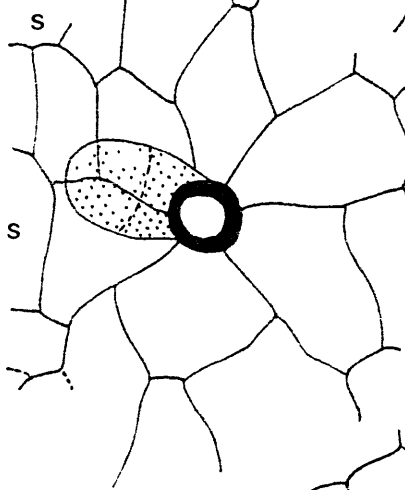
- A. Illigera pulchra [abx]. Superficial, pyriform type. Poral flange and gland body lightly cutinised. Basal cells often with secondary flanges [broken line].
- B. Illigera pentaphylla [abx]. Superficial, pyriform type. Poral flange heavily cutinised, gland body only lightly in comparison. Basal cells rarely secondarily divided.
- C. Hernandia nymphiifolia [adx] [cf. Text-fig. 28 B]. Superficial, pyriform type. Poral flange heavily cutinised and with pegs where it meets basal cell flanges. Gland body lightly cutinised. Basal cells often with secondary flanges.
- D. Hernandia olivacea [adx] [cf. Text-fig. 28 A]. Sunken, peltate type. Poral flange heavily cutinised, pegged; gland body lightly. Basal cells lining gland pit with radiating striae [parallel lines].

Note s represents stomatal complex.

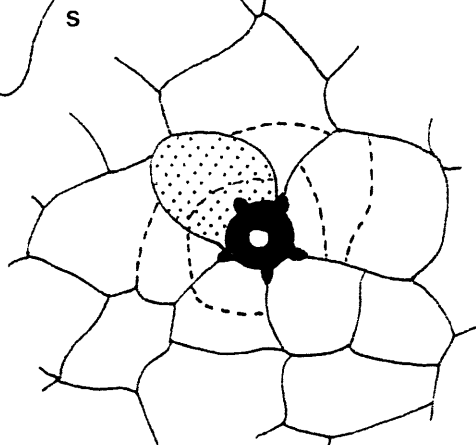
A



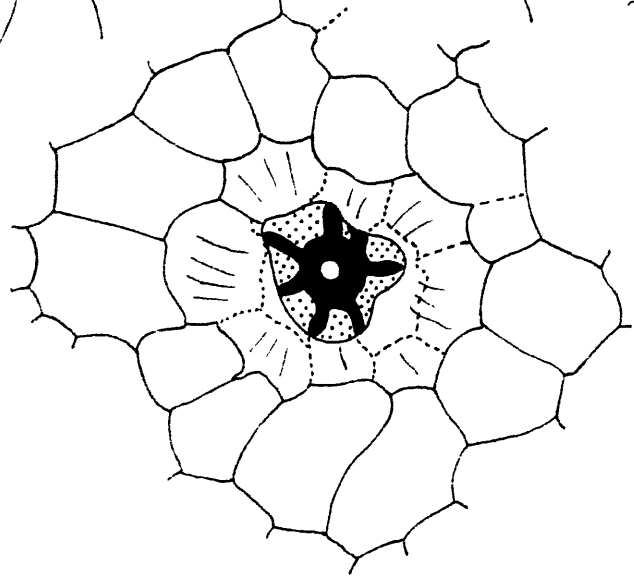
B



C



D



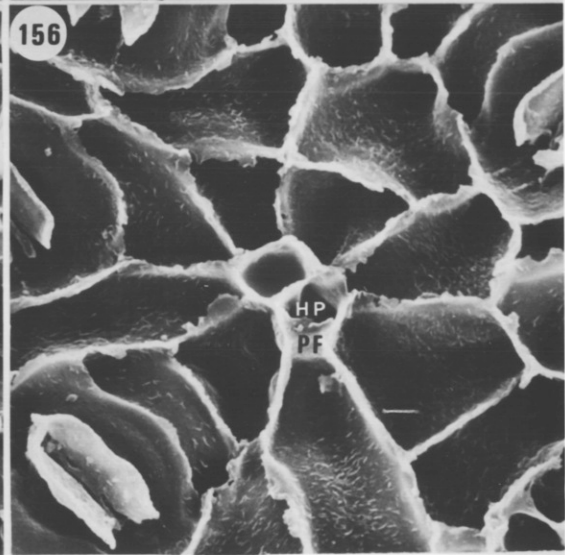
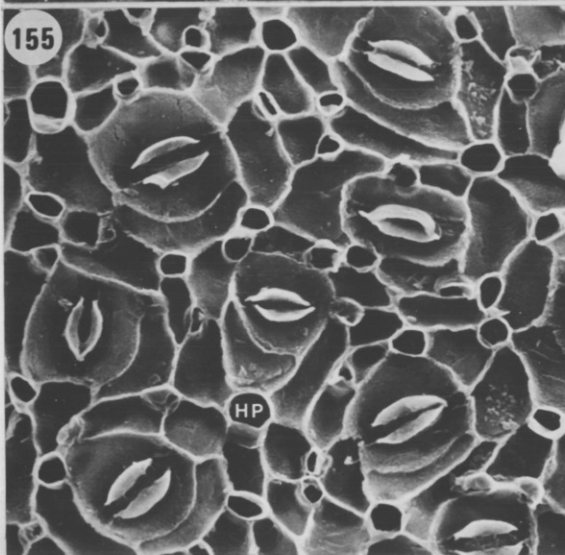
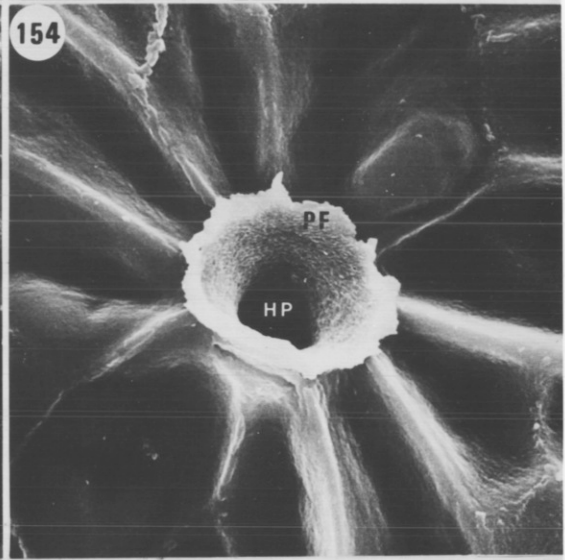
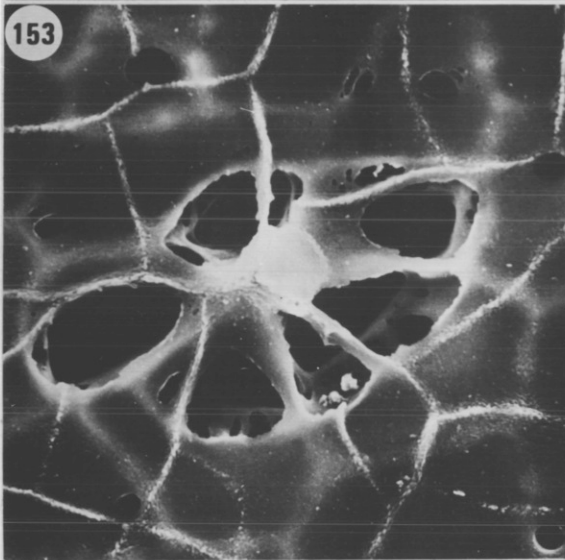
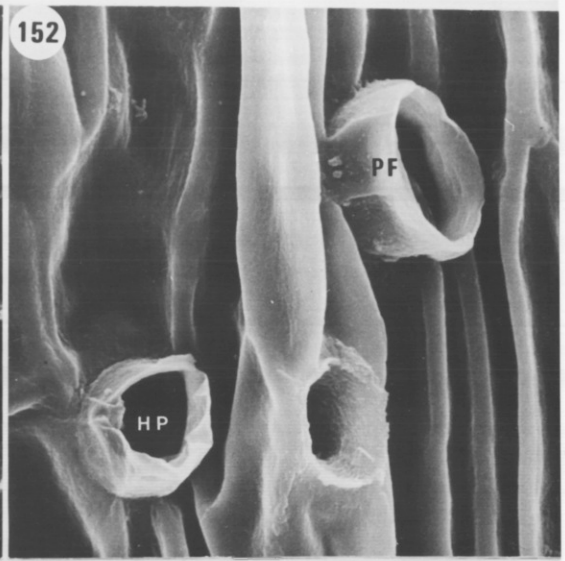
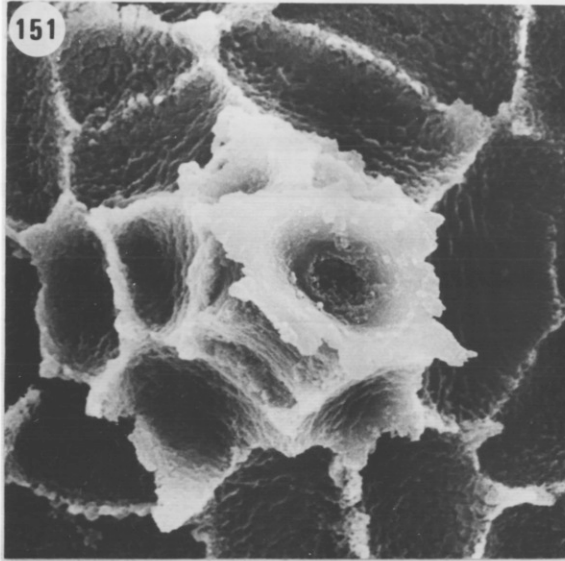
20µm

156. Nectandra pichurim. Double simple hair base in intercostal region. Note two hair pores (HP) each with poral flanges (PF) showing ring of 8 radiating basal cells, some of which have secondarily divided (e.g. top centre). Abx. ca. x 1060.

Hairs and glands: base morphology

Inner surface of isolated cuticles.

151. Hernandia olivacea. Base of peltate gland, projecting deeply due to many subdivisions of basal cells. Basal flanges particularly poral, deeper than ordinary epidermal flanges, with irregular margin and corner pegs. Pore occluded. Adx. ca. x 1065.
152. Gyrocarpus americanus ssp. africanus. Simple hair bases in costal area. Poral flange (PF) of variable form and prominence [compare that of top right to bottom centre]. May correspond to micro- and macro-hair types [see Fig. 139]. Hair pore (HP) distinct. Adx. ca. x 1065.
153. Beilschmiedia micrantha. Simple hair base in extensively cutinised epidermis. Basal cells with less cutin impregnation of inner periclinal wall. Basal cell flanges highly perforated, visible through gaps in cutinisation [e.g. right of centre]. Adx. ca. 1110.
154. Gyrocarpus americanus ssp. africanus. Simple hair base with conspicuously deeper poral flange (PF) compared with radiating basal cell flanges [very low]. Margin of poral flange jagged, basal cell flange margin even. Hair pore distinct (HP). Compare with Fig. 152. Adx. ca. x 1065.
155. Ocotea guianensis. Hair bases and pores (HP) of densely pubescent surface [see Fig. 141]. Hair pores distributed singly, in pairs or in threes. Closeness of hairs result in complex sharing of basal cells. Abx. ca. x 560.



12.6.2d CUTINISATION OF BODY

Pyriform and peltate glandular hair bodies are often represented in isolated cuticle preparations, particularly in Hernandia nymphiifolia [pyriform] and H. olivacea [peltate] [Text-Fig. 29]. The flask-shaped region of the digitate type also remains after maceration, but not the terminal cell or cells suggesting that cutinisation of this end region is considerably less than over the rest of the glandular hair. This is supported by the staining reaction of the cuticle on application of Sudan IV; almost colourless in the apical cell region and pink to red in the remaining areas of the hair. The bodies of pyriform and peltate hairs have a distinct cuticle with deeper cutinisation [red to deep red] towards the glandular hair base. Glandular hair bodies are never lignified.

12.6.2e POSITION OF BASE

The bases of pyriform and digitate hairs are clearly superficial, located level with the epidermal (and cuticular) outer periclinal surface when viewed in T.S. [Text-Fig. 28B, C, D]. In Hernandia olivacea, with peltate hairs, bases are conspicuously sunken [in a pit ca. 17-22 μm deep] [Text-Fig. 28A]. On the inner cuticle surface these bases are raised, with 2-3 tiers composed of subdivided basal cells increasing in height towards the strongly cutinised, 'stellate' pore rim [Fig. 151].

12.6.2f LIGNIFICATION OF BASE

Transverse leaf sections stained for lignin reveal that only the peltate glandular hairs of Hernandia olivacea possess lignified and, therefore, possibly mechanically strengthened bases.

12.6.2g INNER SURFACE MICRORELIEF OF BASE

The periclinal surface of the basal cells associated with glandular hairs usually shows the same composition, size, arrangement and form of sculptural components as that in ordinary cells. This tends to be the case with basal cell flange ornamentation and sometimes also that of the poral flange, such as in Illigera spp. However,

the latter flange may have a somewhat different sculpture of granules about 0.2-0.5 μm in diameter, in other taxa, e.g. Hernandia nymphiifolia [abx.] and H. olivacea [adx. & abx.] [Fig. 151].

A cutin extension or peg is generally present wherever the basal and poral flanges meet, except in Illigera pulchra.

Poral flanges are either of low prominence and narrow width with an even margin as in Illigera spp. or are deeper, exceeding both ordinary and basal cell flanges in prominence as well as being wide with a conspicuous irregular margin, e.g. in Hernandia nymphiifolia [abx.] and H. olivacea [adx. & abx.] [Fig. 151].

12.7 CHARACTERS OF SPECIALISED CELLS : CORK WARTS

In Lauraceae, groups of cells arranged in strict radial files, due probably to numerous successive anticlinal divisions during some stage in the development of the leaf, may be found scattered in isolated cuticle preparations mainly between veins [Figs 157-162]. Three types may be recognised: a group with a thin central periclinal region, which stains very pale pink with Sudan IV, in contrast to that of the surroundings, the cells radiating from it having flanges of similar prominence and thickness to ordinary flanges [Text-Fig. 30A], as in Dicypellium caryophyllum, Persea thunbergii and Systemonodaphne mezii; a group with a thin central periclinal cuticle and thick, deeply cutinised flanges bounding the central area, forming a strong polygonal outline, the flanges of the cells in the radial files and non-specialised areas being similar in form, for example, in Endiandra kingsiana [Text-Fig. 30B] and Persea americana, and the most common form, a group formed entirely of cells with very thick, heavily cutinised flanges, lacking a thin central region, e.g. in Actinodaphne stenophylla, Cinnamomum spp. [Fig. 160], Laurus nobilis [Text-Fig. 30C] and Nectandra salicifolia. Cuticle of the central area in the first two types is either amorphous or marked with very fine flanges.

Although such multicellular groups may occur on cuticles of both leaf surfaces, as in the taxa mentioned above, it is most usual for a type to be confined to either the adaxial membrane, as in Hypodaphnis zenkeri and Nothaphoebe spp. [first type], Endlicheria piriformis [second type] and Sassafras albidum var. molle [third type] or more frequently to the abaxial cuticle, for example, in Eusideroxylon spp. [first type], Neocinnamomum caudatum [second type] and Ocotea laevis [third type].

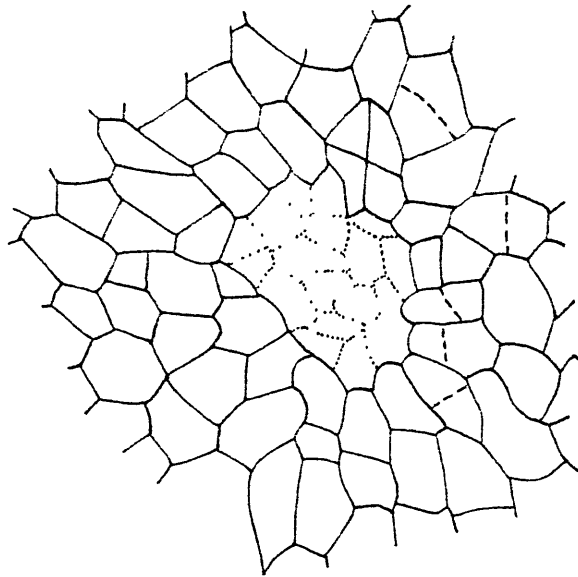
Generally, only one form of multicellular group is found in any taxon on a cuticle surface. Occasionally, however, two types may be detected within a taxon on different cuticles, as in Caryodaphnopsis baviensis [adx.

TEXT-FIGURE 30. Cork warts or related structures in isolated cuticles as seen by light microscopy.

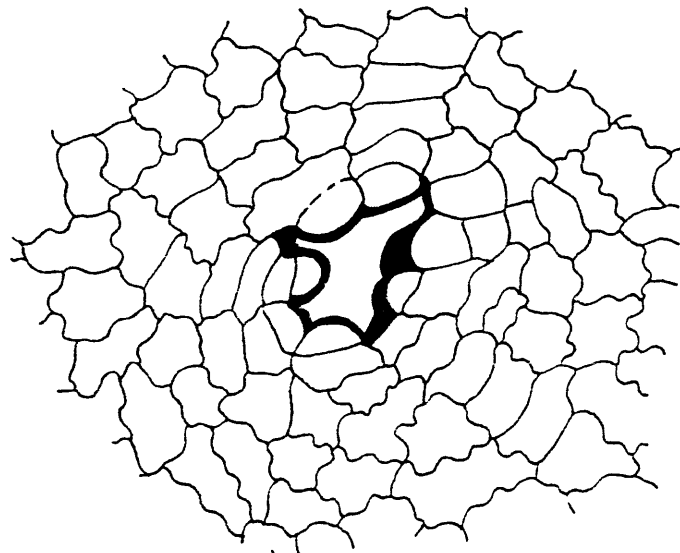
- A. Nothaphoebe heterophylla [adx]. Group with thin central periclinal region (with cell outlines dotted) and radial files of surrounding cells. Flanges of similar prominence and thickness to those of ordinary cells.
- B. Endiandra kingsiana [adx]. Group with thin central periclinal cuticle (as A) and thick, deeply cutinised flanges (black) bordering the central area. Flanges of radial files and non-specialised cells similar.
- C. Laurus nobilis [abx]. Group formed entirely of cells with very thick, heavily cutinised flanges. Note lack of thin central region.

Note s represents a stomatal complex.

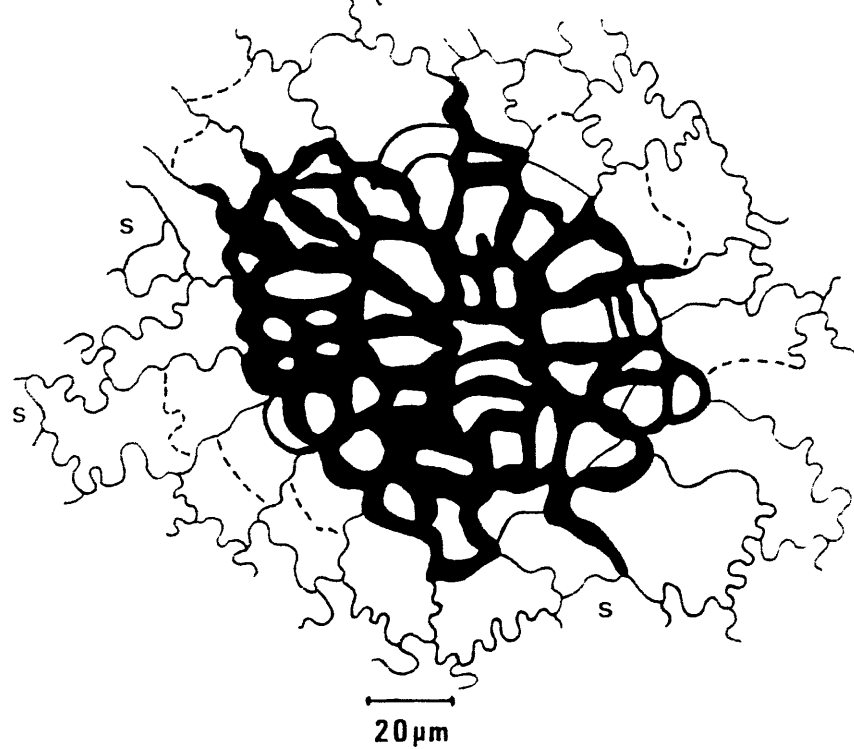
A



B



C



Cork warts and related structures

Inner surface of isolated cuticles.

157. Lindera pulcherimma

Group with thin central periclinal cuticle, lacking cell outlines bounded by a rim of especially deep and thickened flanges. Note radiating pattern of cells within group and presence of secondary flanges [e.g. centre left]. Adx. ca. x 545.

158. Lindera pulcherrima

Group similar to that shown in Fig. 157. Higher magnification to show details. Note distinct beaded secondary flanges [top right]. Abx. ca. x 1060.

159. Sassafridium macrophyllum

Group with thickly cutinised walls. Note some cutinisation of inner periclinal walls of cells in centre of group and presence of perforations of varying form. Adx. ca. x 1105.

150. Cinnamomum pachyphyllum

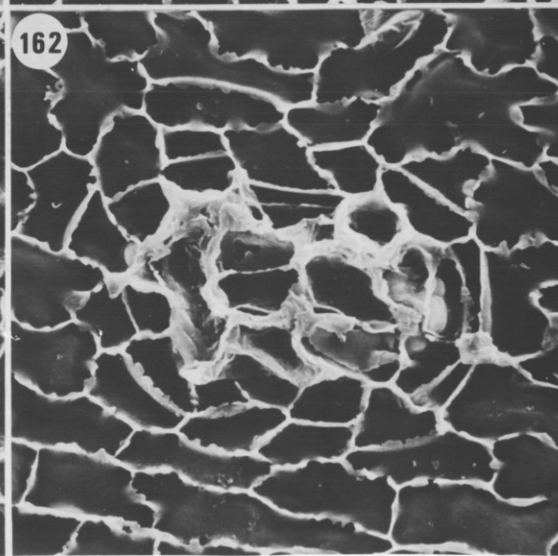
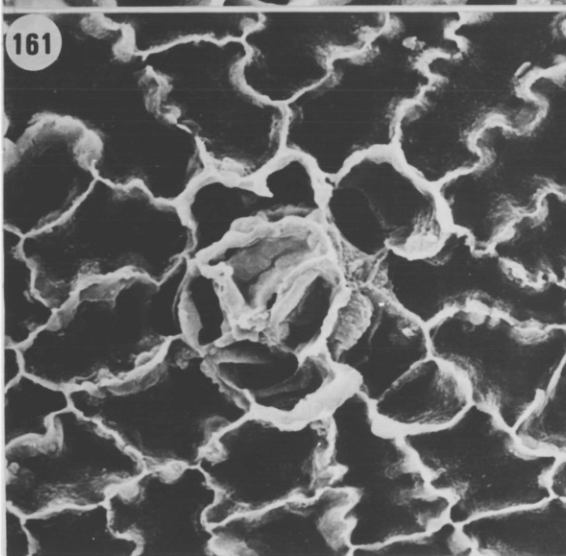
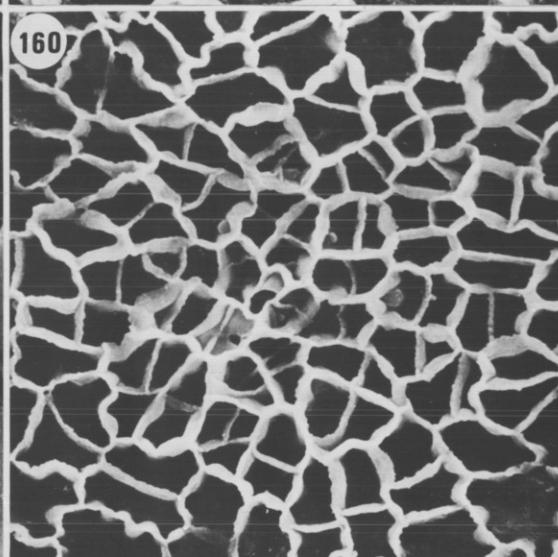
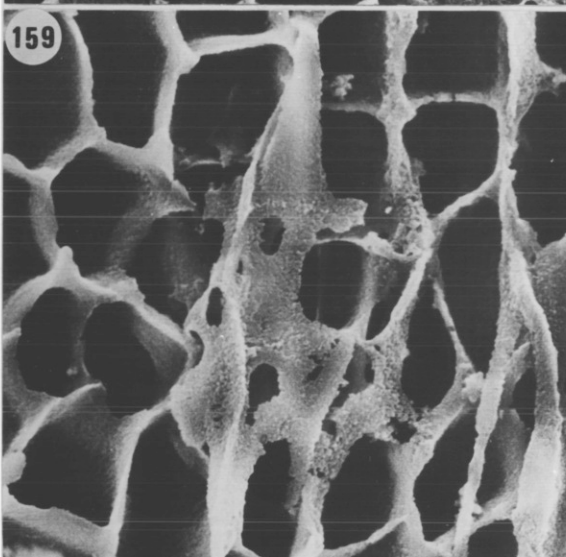
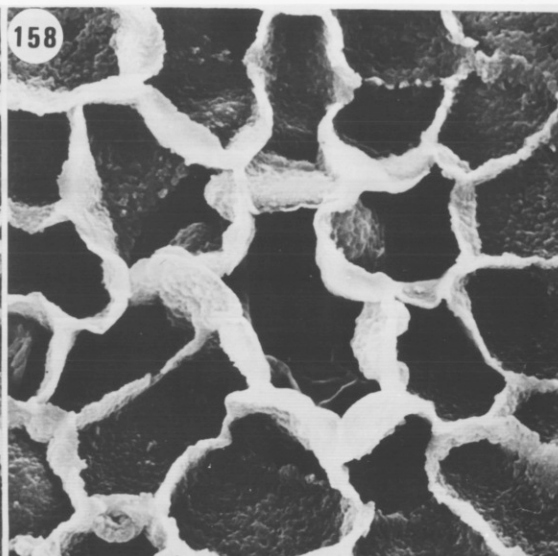
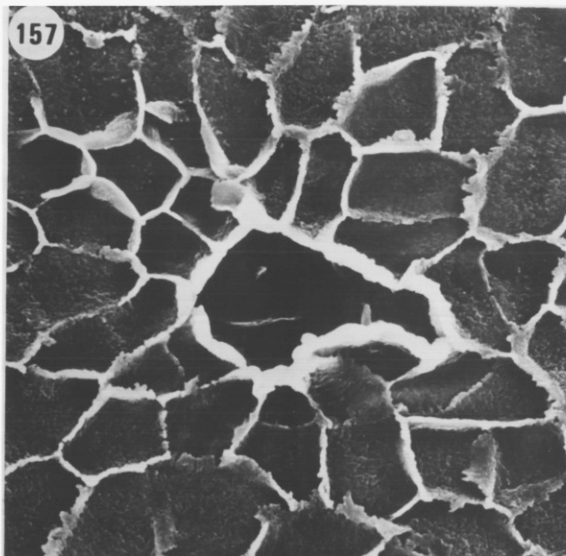
Large group similar to that in Fig. 159. Flanges noticeably less undulate than those of ordinary cells [bottom right]. Note absence of periclinal region with thin periclinal cuticle. Adx. ca. x 545.

161. Laurus canariensis

Group of similar type to that of Fig. 157. Central area obscured by cellular material. Adx. ca. x 535.

162. Aniba megaphylla

As Fig. 161. Abx. ca. x 545.



first type; abx. second] or on one cuticle, the abaxial, e.g. in Dicypellium caryophyllatum [first & third types]. Very rarely, all three types may be recognised, one form on the adaxial, two others on the abaxial, as in Pleurothyrium nobile [adx. second type; abx. first & third].

It would appear that these multicellular groups correspond to cork warts [small bodies of corky tissue] or to related structures, often produced in response to mechanical damage or wounds [see Stace, 1965a].

Whilst these groups are generally quite common in Lauraceae they are absent in many taxa including species of Alseodaphne, Cryptocarya, Dehaasia, Mezilaurus and Neolitsea.

12.8 CHARACTERS OF SPECIALISED CELLS : SECRETORY CELLS

Oil cells, thin-walled round to oval bodies of variable size surrounded by a specialised cell layer, are often scattered throughout the leaf in transverse section. When they are located at or near the outer surface of the epidermis in intercostal and minor costal areas, they may be represented in the isolated cuticle, as a central region from which five to seven basal cells radiate [similar to trichome bases]. Two main forms may be distinguished in the light- and scanning electron-microscope from surface view and inner cuticle surface respectively]: the first marked by a polygonal central outline [ca. 17-27 μm in diameter], sometimes associated with a rounded body [ca. 25-40 μm in diameter] presumably the oil cell itself, which appears as a greenish mass in the L.M., as on cuticles of both surfaces in all *Trimeniaceae* members [Text-Fig. 31A] and the abaxial only of *Gomortega keule* [Text-Fig. 31B, Fig. 163]. Alternatively, secretory cells may be defined by a rounded central outline [ca. 15-20 μm in diameter], which is never found in contact with cellular material in cuticular preparations, as in a few *Lauraceae*, only on the abaxial: in *Dodecadenia grandiflora*, *Nothaphoebe umbelliflora* [Fig. 165], *Sassafridium macrophyllum* and *Umbelularia californica* [Text-Fig. 31C, Fig. 166].

On the outer side of the cuticle or unmacerated leaf portion, oil cells may be recognised by their sunken central region [distinguishable from hair bases due to lack of a pore or opening], which is often particularly waxy in comparison with the surrounding 'basal' and non-specialised cells, e.g. in *Dodecadenia grandiflora* [Fig. 168] and *Piptocalyx moorei*, although there are exceptions, such as in *Nothaphoebe umbelliflora* [Fig. 167] and *Trimenia* spp. In addition, the first type of secretory cell has a prominent border outlining the central area and basal cells, whilst the second type possesses a sunken border over the associated anticlinal walls.

TEXT-FIGURE 31. Secretory cells in isolated cuticles as seen by light microscopy.

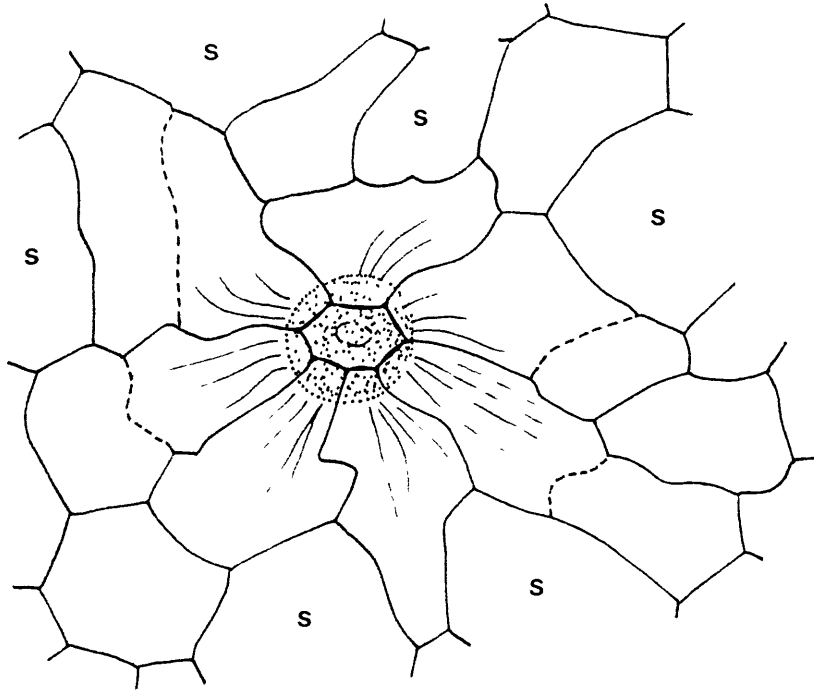
- A. Trimenia papuana [abx]. Secretory cell marked by a central polygonal outline associated [at a different focus] with a larger rounded mass [shown heavily stippled] and surrounded by a ring of radiating striate basal cells. Note basal cells sometimes with secondary flanges [broken lines].

- B. Gomortega keule [abx]. Secretory cell similar to A. [see also Fig. 163].

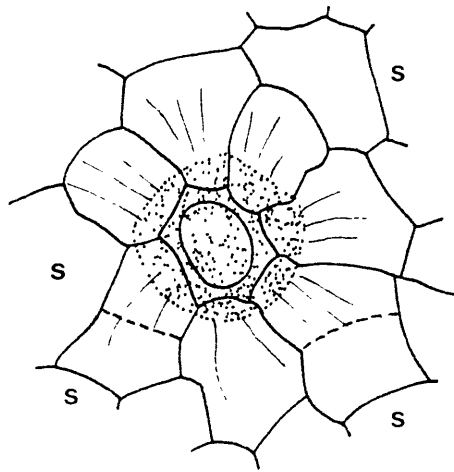
- C. Umbellularia californica [abx]. Secretory cell marked by a central rounded outline. Basal cells arranged as in A & B, but non-striate [see also Fig. 166].

Note s represents a stomatal complex.

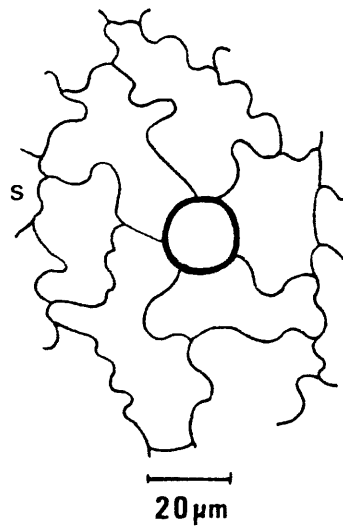
A



B



C



168. Dodecadenia grandiflora

As in Fig. 167. Concavity with dense wax granules
[scattered elsewhere]. Specialised cell outlines
faint. Abx. ca. x 2140.

Secretory cells

Outer and Inner surfaces. Figs. 163-166: Inner.

163. Gomortega keule

Secretory cell [type 1] in which central region is associated with rounded body X [collapsed] and surrounded by prominent border. Note ring of seven cells radiating from border. Flanges of surrounding cells and border with pegs. Secondary flanges present [bottom centre]. Abx. ca. x 1080.

164. Micropora curtisii

Secretory cell on vein. Central area [X] and border distinct. Flanges of surrounding cells conspicuously low and periclinal ornamentation of different form near border [i.e. granular to clumped protrusions rather than filamentous reticulate protrusions and pit-like to reticulate depressions]. Abx. ca. 1050.

165. Nothaphoebe umbelliflora

Secretory cell [type 2]. Periclinal surface of central area [X] smooth surrounding cells ornamented in same way as ordinary epidermal cells. Note prominent border with irregular margin. Abx. ca. x 1065.

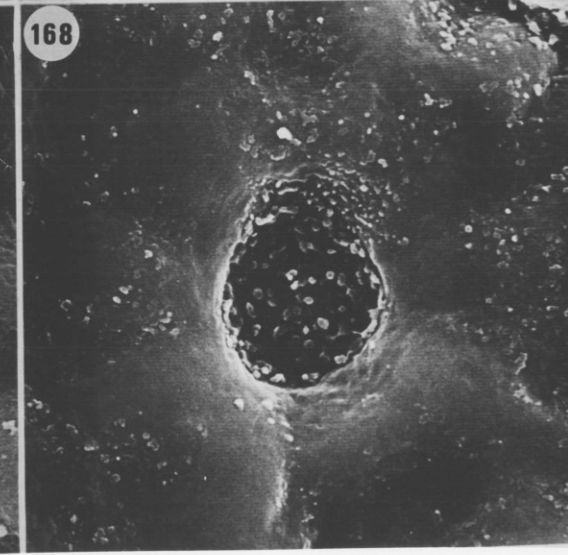
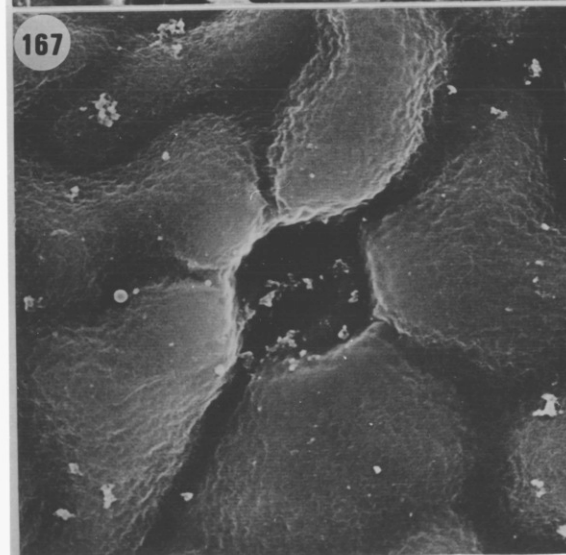
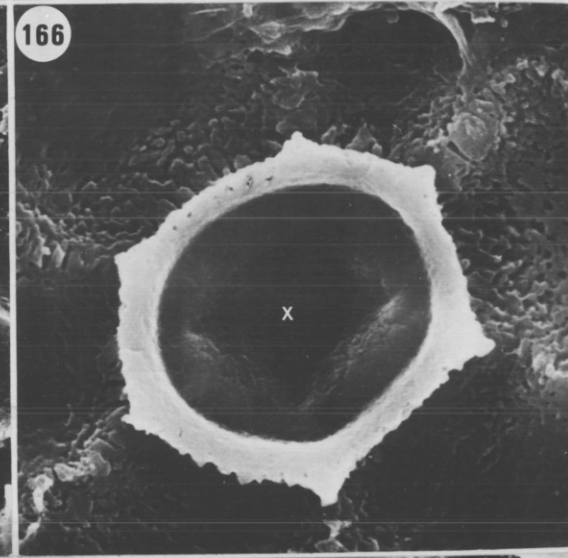
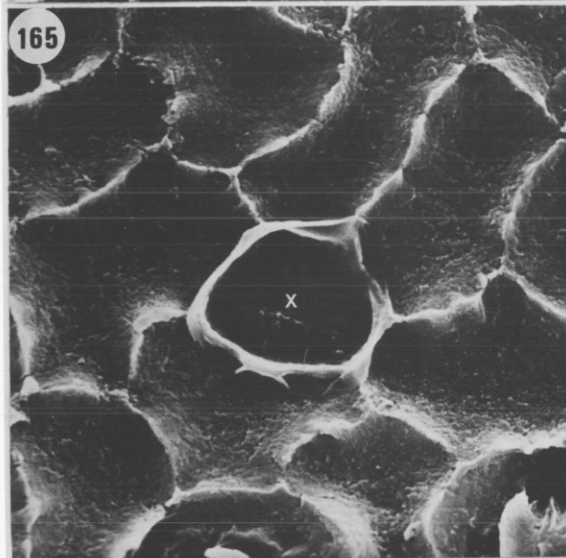
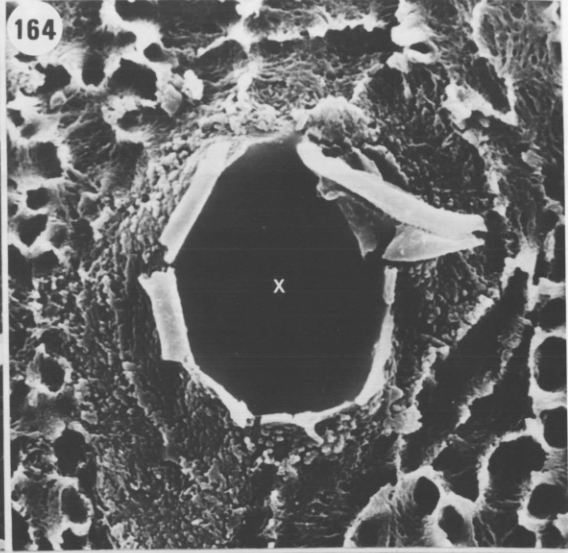
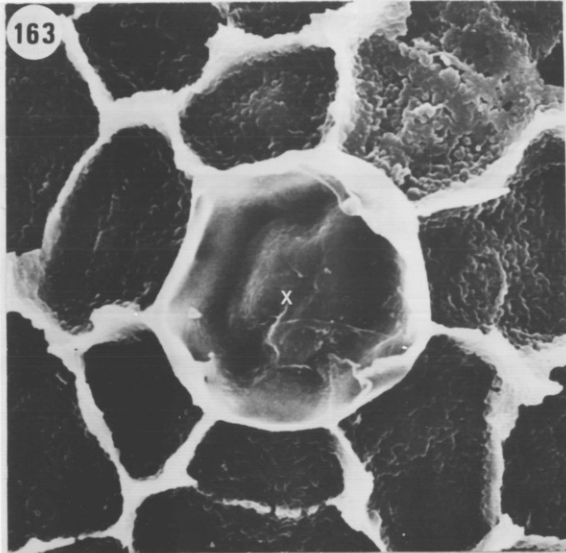
166. Umbellularia californica

As in Fig. 165. Border particularly well-developed with tapering pegs where surrounding cells radiate from it. Abx. ca. x 2015.

Figs. 167-168: Outer.

167. Nothaphoebe umbelliflora

Concavity corresponding to secretory cell [see Fig. 165] non-waxy. Specialised surrounding cells marked by sunken anticlinal borders, radiating from secretory cell. Abx. ca. x 1070.



On the inner cuticular surface, secretory cells are variable in appearance (Figs 163-166). In the first type, the specialised flanges are generally similar in prominence and thickness to non-specialised flanges, except in Piptocalyx moorei which has especially fine, low flanges round the central polygonal region. Where basal flanges meet the latter area of the cell in all taxa with this form of secretory cell, protruberances of cutin or pegs (similar to the pegs of ordinary anticlinal flanges) arise. Basal cells also possess such corner extensions in Gomortega keule (Fig. 163) and Trimenia spp. The central area of the secretory cell (x) has a relatively smooth periclinal surface in contrast to that of basal and non-specialised cells but flange sculpture and basal cell microrelief is always of the same type as that associated with ordinary cells.

The second type also possesses basal cells similar in form to other epidermal cells on the inside of the cuticle. However, the flange bordering the central region is usually deeper or more prominent than elsewhere, with a more irregular margin, e.g. in Nothaphoebe umbelliflora (Fig. 167). It may even be so deep that it flops over onto the surrounding basal cells, producing a thickened appearance in surface view, as in Sassafridium macrophyllum and Umbellularia californica (Fig. 166). Occasionally, this flange is of the same shape, sculpture and prominence as the basal and non-specialised flanges: U-sectioned, interrupted and very low, in Dodecadenia grandiflora. The periclinal surface of the central area (x) is smooth-finely granular in this form of secretory cell and may have peg-like extensions at the point where the basal cell flanges radiate out from the bordering flange, for example in Umbellularia californica (Fig. 166). Oil cells are non-lignified, with the exception of those in the latter species.

13.1 SPECIAL STUDY OF CASSYTHA

At maturity all members of the genus Cassytha are known to be long, thread-like, rootless, perennial, herbaceous, chlorophyllous twining plants without tendrils, bearing haustoria. Although generally described as parasites [Solereeder, 1908; Kostermans, 1957; Hutchinson, 1964; Kuijt, 1969; Weber, 1981] they must be at least partly autotrophic, according to Kienholz [1926] and may, therefore, be intermediate between an independent leafy climber and a complete parasite [McLuckie, 1924].

Leaves are reduced to minute (0.5-5.0 mm), sessile, basifixed, pubescent scales which lack chlorophyll and may be found arranged in spirals on the stem [where they seem to be caducus] and around the inflorescence [Weber, 1981] protecting the young buds [McLuckie, 1924]. The scales have a single median vascular strand [Kuijt, 1969; Weber, 1981] and a gland in the centre of the adaxial surface [Weber, 1981]. Kostermans [1957] considers that these scales are not 'proper' leaves and even bases his system of classification of the Lauraceae on this assumption.

Thus, the external and internal morphology of unmacerated stem portions and isolated cuticles respectively, was examined in two different species of the 'leafless' parasitic genus in order to compare their features, particularly those of stomata, with characters of leafy taxa and to ascertain the closeness of these rather odd plants to the main body of the Lauraceae.

In the following, features are described under similar headings to those used in section 12, to facilitate comparison.

13.1.1 CHARACTERS OF NON-SPECIALISED CELLS : GENERAL

13.1.1a SHAPE AND ARRANGEMENT OF CELLS

The outlines of cells on cuticle of C. filiformis are isodiametric to elongate, between 0.8 and 3.2 times longer than wide. Those of C. glabella are conspicuously elongate, 1.9 to 6.0 times longer than wide. All cells of both species are arranged end to end in approximately parallel rows along the length of the stem axis (Figs 177, 178). In C. glabella outlines appear rather rectangular in shape with many of the transverse flanges orientated horizontally [Fig. 178]. Cells tend to be more polygonal in C. filiformis with a greater proportion of oblique transverse flanges [Fig. 177]. Cell form and arrangement in stems of Cassytha spp. is reminiscent of costal cell morphology and organisation in leaves. There is, of course, no intercostal area in Cassytha. Secondary flanges are visible in C. filiformis only and sometimes occur parallel to the rows of cells.

13.1.1b SIZE OF CELLS

Cells are large with less than $10/\text{mm}^2$ [C. filiformis av. $6.2/\text{mm}^2$; C. glabella $4.2/\text{mm}^2$], unlike in most Lauraceae. Many taxa in the related families have cells of this size.

13.1.2 CHARACTERS OF NON-SPECIALISED CELLS : THE PERICLINAL WALL REGION

13.1.2a EXTENT OF PERICLINAL CUTINISATION

13.1.2a [i] THICKNESS OF PERICLINAL CUTICLE IN L.S.

Cuticle in the median periclinal zone has an average thickness of $6.4 \mu\text{m}$ in C. filiformis and somewhat less, $4.6 \mu\text{m}$ in C. glabella. Both values fall within the range detected for the character in leaves and may be described as moderate and thin respectively.

Special study of *Cassytha* spp.

Outer surface of stem: morphology.

169. *Cassytha filiformis*

Stoma with subsidiary cells apparently fused at poles to form a ring. Stomatal pit slightly longer than wide with tridentate polar ends, revealing guard cell periclinal surface and narrow outer ledge round aperture [A]. Densely covered with wax flakes [scales]. ca. x 1110.

170. *C. glabella*

Stoma with apparently discrete subsidiary cells. Stomatal pit widely elliptical showing guard cells, outer ledge and aperture [as *C. filiformis*] through opening. Wax covering scattered, of flakes as in Fig. 169. ca. x 1080.

171. *C. filiformis*

File of stomata arranged with apertures perpendicular to long axis of stem. ca. x 620.

172. *C. glabella*

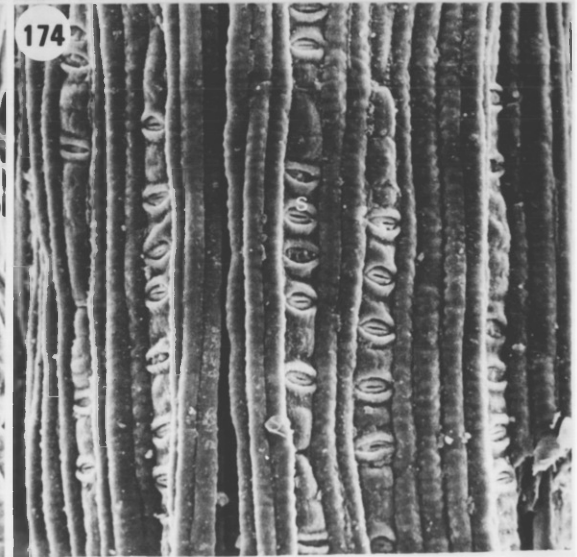
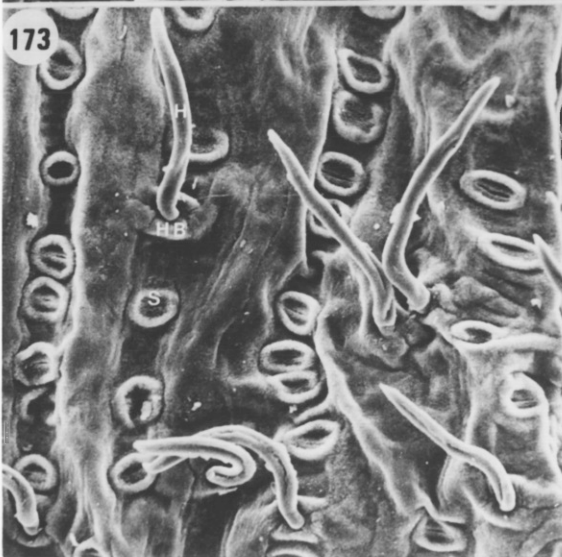
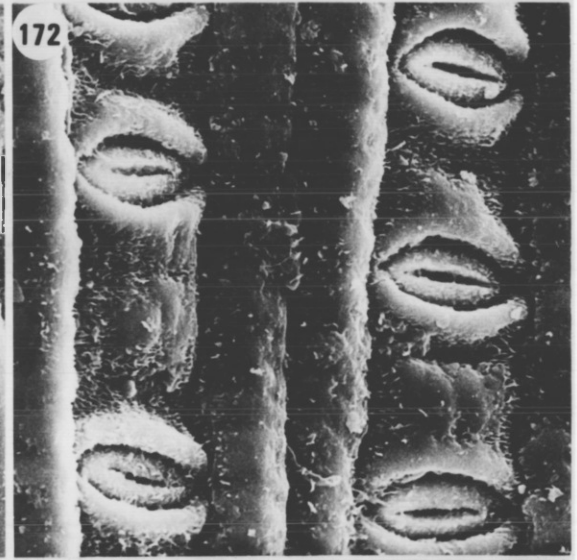
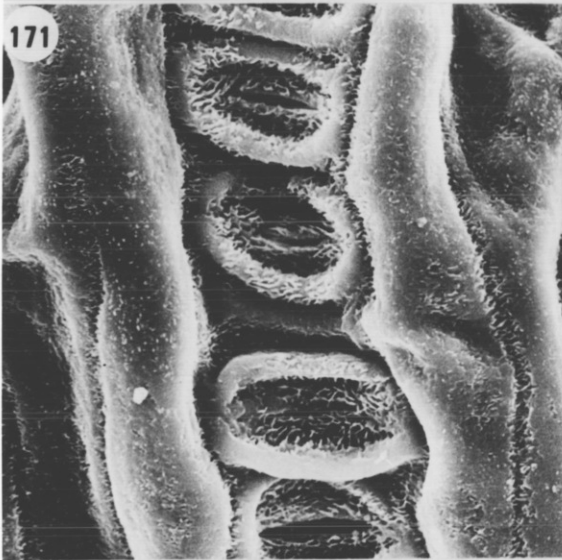
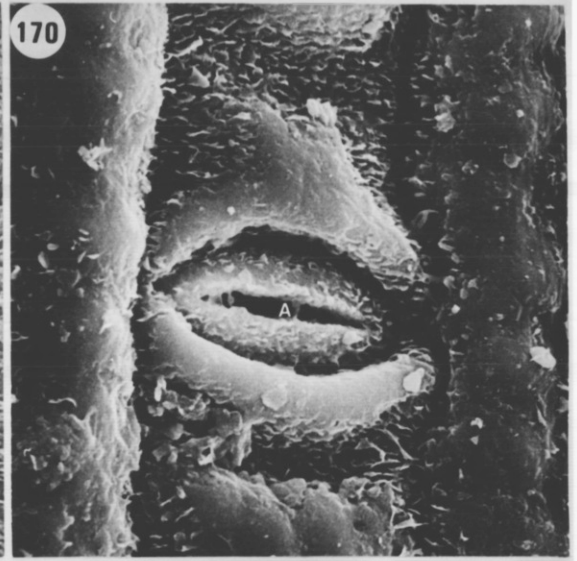
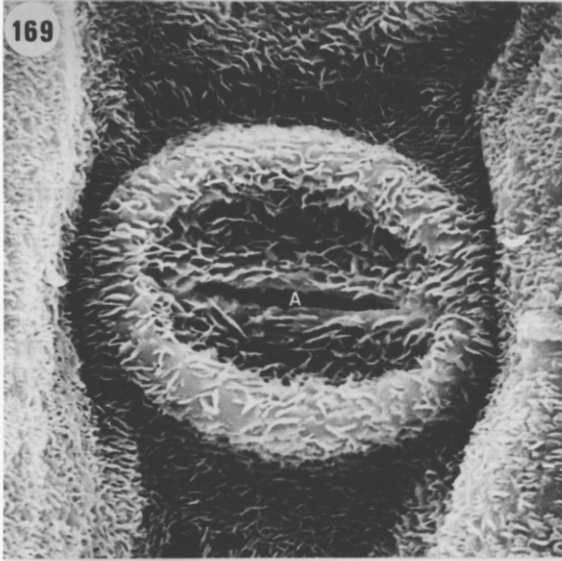
Stomata in files, as in Fig. 171. ca. x 535.

173. *C. filiformis*

Low power view of stem portion with rows of stomata [S] and scattered simple hairs [H] protruding from raised bases [HB]. Cell surface rather flat, anticlinal borders marked by shallow grooves. ca. x 135.

174. *C. glabella*

As Fig. 173. Note absence of hairs, greater convexity of cells and concavity of anticlinal borders. Stomata [S] smaller than in *C. filiformis* [Fig. 173]. ca. x 135.



Special study of Cassytha spp.

Inner surface of isolated stem cuticles.

175. C. filiformis

Stoma with obtuse wings [W], subsidiary cells bearing narrow depression corresponding to dome on outer surface [see Fig. 169] and polar thickening consisting of strong, convex lateral lines, a bar and a low, faint rod. ca. x 1060.

176. C. glabella

As Fig. 175. Wings narrower, less obtuse. Depression corresponding to dome of subsidiary cells occupying more of periclinal surface. Polar thickening as in Fig. 175. ca. x 1035.

177. C. filiformis

Flanges and periclinal surface of cells in non-stomatal regions. Cells short, elongate [1-3 times longer than wide]. Flanges [F] jagged, interrupted. Periclinal surface [PS] more or less smooth. ca. x 1030.

178. C. glabella

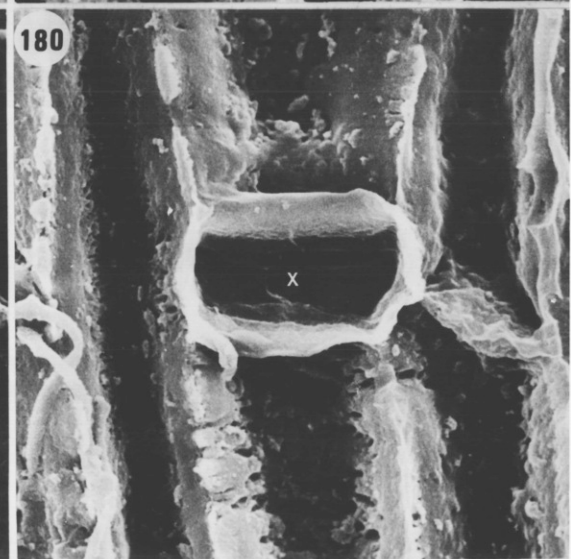
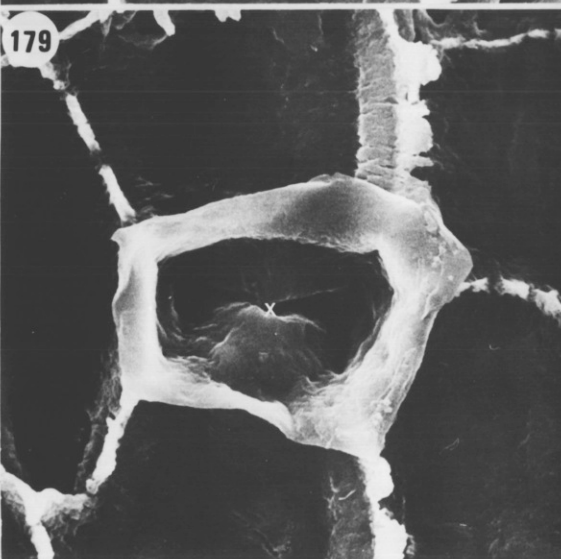
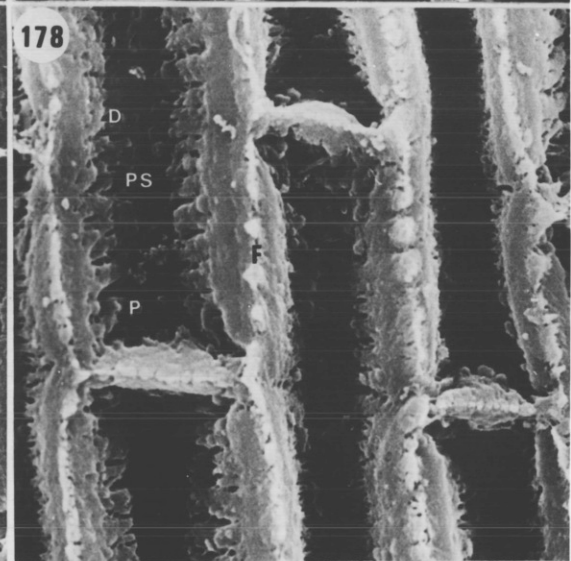
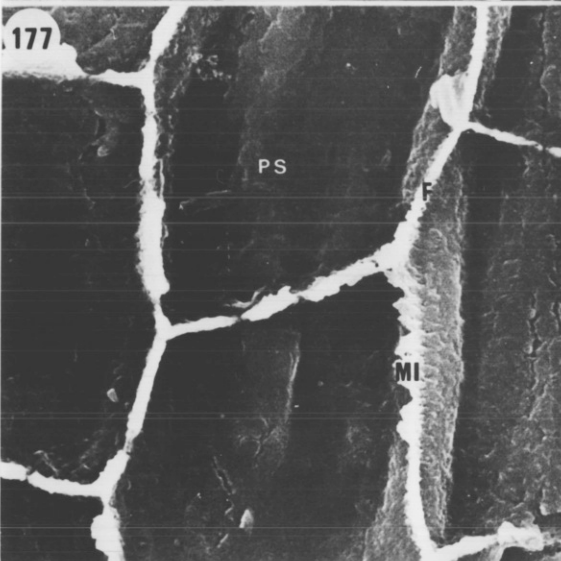
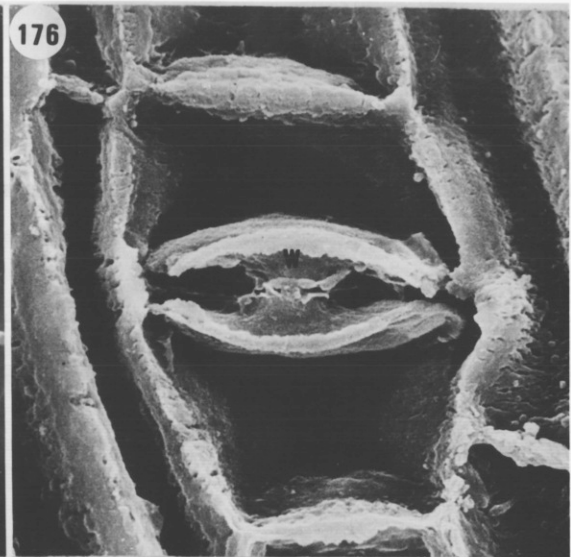
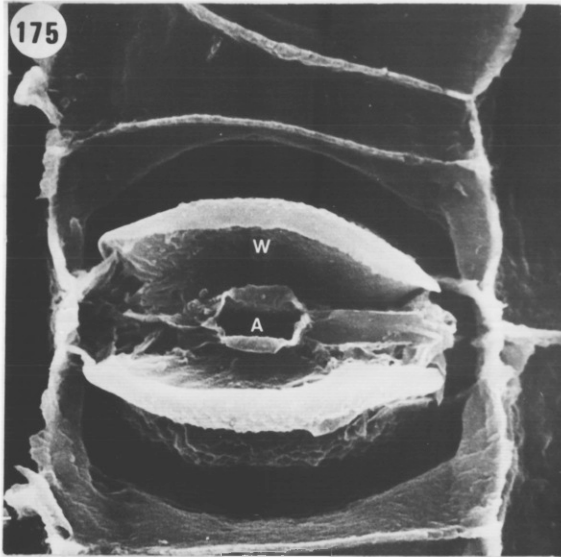
As Fig. 177. Cells narrow, elongate [2-6 times longer than wide]. Flanges jagged, interrupted. Periclinal surface very finely granular with dense fine to moderately coarse pit-like depressions. ca. x 1080.

179. C. filiformis

Secretory cell. Polygonal with thin central periclinal area [X] and especially prominent even-edged flanges. ca. x 1080.

180. C. glabella

As in Fig. 179. Similar to C. filiformis but smaller ca. x 1090.



13.1.2a (ii) EXTENT OF INNER PERICLINAL CUTINISATION

Cutinisation of the inner periclinal wall is absent, as in leaves of many other taxa.

13.1.2a (iii) PERICLINAL SUBDIVISION OF THE EPIDERMIS

This is also absent in both species, in accordance with the majority of the assemblage studied.

13.1.2a (iv). STAINING OF PERICLINAL CUTICLE IN L.S.

The cuticle is of the homogeneous type (so common in leaves) when stained with Sudan IV.

13.1.2b CURVATURE OF THE OUTER PERICLINAL WALL

The outer periclinal wall is convex [Figs 171, 172], most particularly in C. glabella (h:w 0.20:1.0; C. filiformis: h:w 0.09:1.0), the shape characteristic of abaxial leaf surfaces. On the inner side of cuticle of C. glabella, the periclinal region of each cell is increasingly sunken from the flanges and attains a maximum in the central most part corresponding to the doming of the outer surface (Fig. 178).

13.1.2c PATTERN OF FOLDING (STRIAE)

The outer surface of C. filiformis lacks ornamentation (i.e. is non-striate). C. glabella, however, possesses a series of solitary, more or less continuous parallel, straight lines, between ca. 0.7 and 1.3 μm in diameter, running along the stem axis (Fig. 172). These striae, which in form are reminiscent of those observed on veins of many Lauraceae and a few Hernandiaceae, are not represented on the inner side of the stem cuticle (Fig. 178).

13.1.2d. PERICLINAL SURFACE SCULPTURE

Under the light microscope, the cuticle/cellulose wall interface appears even. Scanning electron microscopic investigation of the inner surface reveals that the periclinal region is more or less smooth in C. filiformis (Fig. 177). In C. glabella, widely separated, fine (up to 0.2 μm), granular, round to filamentous protrusions may be observed together with a more predominant pattern of dense, pit-like to reticulate depressions, between about

0.2 and 0.5 μm in diameter [Fig. 178].

13.1.3 CHARACTERS OF NON-SPECIALISED CELLS : THE ANTICLINAL WALL REGION

13.1.3a DEVELOPMENT OF ANTICLINAL BORDERS

The anticlinal borders appear sunken (Figs 171,172), similar to those of abaxial costal cells in leaves of many taxa.

13.1.3b FLANGE FORM

13.1.3b (i) FLANGE SHAPE

In L.S., flanges are V-shape, the commonest form found in leaves.

13.1.3b (ii) VARIATION IN THE COURSE OF FLANGES

Flanges are predominantly straight (Figs 177, 178), in accordance with those of veins in leaves of a range of taxa.

13.1.3b (iii) FLANGE WIDTH

Flanges are moderately wide [C. filiformis: av. 4.3 μm ; C. glabella: 4.6 μm], unlike those of many of the assemblage.

13.1.3c EXTENT OF ANTICLINAL CUTINISATION

At the flange, the cuticle is of moderate thickness [C. filiformis: av. 12.2 μm ; C. glabella: 12.5 μm]. The flanges, themselves, are also intermediate in height, but taller in C. glabella (av. 7.9 μm) than in C. filiformis (5.8 μm) and project approximately half way down the epidermal anticlinal wall i.e. they are of moderate prominence.

13.1.3d CONTINUITY OF FLANGES

13.1.3d (i) INTERRUPTIONS. Flanges are frequently interrupted (75% or more with distinct gaps or breaks). Up to 6 gaps per flange may be detected in C. filiformis (Fig. 177) and up to 9, in C. glabella (Fig. 178). Such values are uncommon in leaves but do occur in a few taxa.

Partial gaps may also occur in some flanges, as in leaf cuticles.

13.1.3d (ii) HOLES OR PORES. These are found occasionally perforating only the main body of flanges up to 3 per flange in C. filiformis, no more than 2, in C. glabella. They are either tiny channels (Fig. 177) or round to oval, moderate sized holes, in the former species or just the minute form, in the latter. Such patterns are of regular occurrence in leaf flanges.

13.1.3e NATURE OF FLANGE APEX

13.1.3e (i) FURROWING. Flanges are 'single' (unfurrowed) (Figs 177, 178), as in most other taxa examined.

13.1.3e (ii) IRREGULARITY/JAGGEDNESS. The margin of flanges in both species may be described as uneven. Individual irregularities are often sharp or tooth-like, varying in height (amplitude) from less than 0.18 μm , like others in the assemblage with jagged flanges, to a maximum of about 3.6 μm in C. filiformis (Fig. 177) and 3.8 μm in C. glabella (Fig. 178). These values, for the greatest amplitude, lie more or less in the middle of the range detected in leaves.

13.1.3e (iii) CORNER EXTENSIONS/PEGS. In C. filiformis, on the inner cuticle surface, a peg or cutin extension may sometimes be detected at a cell corner, where flanges of adjacent cells meet. Corners are level in C. glabella.

13.1.3f FLANGE SCULPTURE

The cuticle/cellulose wall interface appears even at the flanges in the light microscope. However, in the S.E.M., the flange surface is ornamented in both species in contrast to the periclinal region [see p. 322]. In C. filiformis, dense reticula of rounded, moderate sized (ca. 0.4-0.5 μm) protrusions may be found (Fig. 177) and in C. glabella, very fine (less than ca. 0.2 μm) widely spaced, round - filamentous granules, accompanied by slightly coarser (0.2 μm or less) and denser, pit-like

depressions, reminiscent of the periclinal sculpture but finer [Fig. 178].

13.1.4 CHARACTERS OF NON-SPECIALISED CELLS : MISCELLANEOUS

13.1.4a EXTENT OF LIGNIFICATION

Lignin is absent in the epidermis of Cassytha.

13.1.5 CHARACTERS OF SPECIALISED CELLS : STOMATA

13.1.5a GENERAL CHARACTERS

13.1.5a [i] TYPE

Stomata are paracytic, with a pair of lateral subsidiary cells orientated parallel to the long axis of the pore, as in most taxa.

13.1.5a [ii] DISTRIBUTION

They are found all over the stem surface.

13.1.5a [iii] ARRANGEMENT

Stomata are organised in longitudinally running rows perpendicular to the long axis of the pore, generally separated by non-stomatal bands composed of unspecialised cells [Figs 173, 174], rather than at random.

13.1.5a [iv] DENSITY/FREQUENCY

The average number of stomata per unit area is very low: the value for C. filiformis [$121.8/\text{mm}^2$] is the same as the minimum found for abaxial leaf stomata, that for C. glabella [$95.7/\text{mm}^2$] is less, but greater than the adaxial average of Eusideroxylon melagangai. The correlation between stomatal size, dimensions of intervening cells and stomatal frequency is upheld in Cassytha spp. i.e. stomata are less frequent per unit area when they and the cells between them are large. The variation in stomatal frequency for each member of this genus is small [C. filiformis: $87.0-121.8-145.0$ per mm^2 ; C. glabella: $58.0-95.7-159.5$ per mm^2], in accordance with the trend

detected for the feature in leaves, when less than 580.0/mm².

13.1.5a [v] STOMATAL INDEX

Average values for stomatal index are moderate: 14.5 for C. filiformis, 16.3 for C. glabella and fall in the group of commonest average abaxial indices. The range of stomatal index values for C. filiformis [10.2-18.7] is encompassed by a wider range [8.5-22.0] in C. glabella, demonstrating further the greater usefulness of average indices for comparison. Cassytha spp. are examples of taxa with a low number of stomata per unit area and a comparatively high stomatal index due to the number of cells per unit area also being low.

13.1.5a [vi] SIZE

The stomatal apparatus is very large [ca. 41-50 µm] in diameter and in this feature Cassytha spp. closely resemble members of the family Trimeniaceae, rather than the Lauraceae.

13.1.5a [vii] NUMBER OF STOMATA IN CONTACT

In C. filiformis, subsidiary cells abut rather rarely onto those of adjacent stomata [70% areas examined lacking stomata in contact] in surface view. When subsidiary cells are adjacent, usually one or occasionally two stomata per unit area appear joined, resulting in an average of 0.37. The frequency is higher [1.00] in C. glabella [about 60% areas examined with stomata in contact] with mainly two stomata, rarely one, abutting onto another per unit area.

13.1.5a [viii] PRESENCE OF GIANT STOMATA

Giant stomata, several times larger in size than ordinary stomata are absent.

13.1.5a [ix] VEIN STOMATA AND ABNORMAL STOMATA

Stomata distributed on stems, such as these, may be considered to be vein stomata since vascular tissue runs down the centre of the axis.

Abnormal stomata have not been seen.

13.1.5b GUARD CELL CHARACTERS13.1.5b (i) SIZE IN L.S.

Individually, the guard cells are very large [14.7-15.9 μm] in diameter, when viewed in longitudinal section [due to arrangement, equivalent view to leaf T.S.], unlike those of most other taxa in the Lauraceae and related families. Only Austrobaileya scandens has a similar guard cell size.

13.1.5b (ii) EXTENT OF WALL THICKENINGS

Thin median longitudinal sections reveal that both the outer and inner walls of guard cells are massively thickened [see p. 200], so that the lumen is more or less centrally located and narrowly elongate. It is orientated obliquely in C. filiformis [upward towards the inner ledge], where the wall is thickened unevenly [least near the pore] and horizontally in C. glabella, due to even wall thickening. The configuration observed is similar to that in Endiandra rubescens, the only other Lauraceae member exhibiting such extensively thickened walls, certain Hernandiaceae, some Trimeniaceae and Austrobaileya scandens. The uneven thickening of the outer guard cell wall and, the lumen shape and orientation of C. filiformis most closely matches the patterns detected in Lauraceae, for example, in species of Licaria and Nectandra.

The thickenings of the guard cell are lignified.

13.1.5b (iii) CUTICLE THICKNESS

As in other Lauraceae, there is very little distinction between cutinisation of the outer ledge, that of the outer periclinal wall and the guard cell/subsidiary cell flange. The average periclinal thickness for the guard cell cuticle in C. filiformis is 13.4 μm and in C. glabella, 11.6 μm . This is considerably more than in any other taxon, even in the Lauraceae where the maximum thickness is 7.3 μm [adx. 7.6 μm]. Guard cells with a thick cuticle in leafy taxa have a particularly characteristic pattern of cutinisation [see p. 205]. This is also seen in Cassytha spp.

13.1.5b [iv] OUTER LEDGE FORM

The average length of the outer ledge in C. filiformis is moderate [4.6 μm] and in C. glabella, long [6.1 μm]. Similar dimensions only occasionally occur in Lauraceae, more regularly in related families. Neither average exceeds the maximum [11.9 μm] found in Austrobaileya scandens.

The base of the outer ledge is also wide in comparison with most taxa [C. filiformis: 7.6 μm ; C. glabella: 7.0 μm] except Austrobaileya scandens [8.5 μm].

The tendency of large guard cells to have a correspondingly large outer ledge also holds in stems.

The outer ledge of C. filiformis is basically obtusely triangular in shape [1:w 0.6:1.0], that of C. glabella is almost equilateral in outline [1:w 0.9:1.0]. These shapes are found most frequently in the Lauraceae. In both species, the base and apex of the outer ledge are outward curving, especially so in C. glabella and the extreme tip is conspicuously pointed, following the commonest trends within the assemblage.

The guard cell outer ledge is non-lignified, just as in the majority of taxa.

13.1.5b [v] INNER LEDGE FORM AND DEGREE OF CUTINISATION

The inner ledge of C. filiformis stains more deeply [red] than that of C. glabella [pink] indicating a higher level of cutinisation in the former than the latter species.

This ledge is obtuse [wider than long] and curves inward towards the inner cavity, in accordance with larger size leaf stomata. The inner ledge is prominent, being an average of 6.4 μm and 6.1 μm in length in C. filiformis and C. glabella respectively. Such prominence is achieved or exceeded in only a few Lauraceae, e.g. Aiouea spp., Litsea meissneri and Mezilaurus itauba and some of the related family members, Austrobaileya scandens, Gomortega

keule, Piptocalyx moorei and Trimenia weinmanniaefolia but not those of the Hernandiaceae.

In C. filiformis, the inner ledge appears larger in size than the outer ledge; the difference in C. glabella is less noticeable.

Both species have a non-lignified inner ledge.

13.1.5b (vi) PRESENCE OF OUTER AND INNER CAVITIES

Outer and inner cavities are defined by the guard cell outer and inner ledges respectively, in the same way as in leaf stomata of most taxa.

13.1.5b (vii) PRESENCE OF STOMATAL FLAP

A stomatal flap may be detected in longitudinal sections. This extends over part of the inner wall of the adjacent subsidiary cell near the inner ledge in C. glabella, but in C. filiformis, it covers the subsidiary cell wall and beyond to the inner wall of another epidermal cell. The flap stains red with Sudan IV indicating the presence of much cutin in C. filiformis and pink, when it is not so highly cutinised, in C. glabella.

13.1.5b (viii) THICKNESS OF CUTICLE AT GUARD CELL/ SUBSIDIARY CELL FLANGE

The average thickness of cuticle at this flange is very thick, particularly in C. filiformis (19.2 μm ; C. glabella: 14.3 μm) and the values exceed the maximum thickness for the same region in abaxial leaf stomata. Adaxial Eusideroxylon melagangai shows a greater average than C. glabella but not C. filiformis (15.9 μm).

13.1.5b (ix) PROMINENCE OF GUARD CELL/SUBSIDIARY CELL FLANGE

This flange is of moderate prominence in C. filiformis, like the ordinary flanges and low in C. glabella, less prominent than those of non-stomatal cells (moderate).

13.1.5b (x) SHAPE OF GUARD CELL/SUBSIDIARY CELL FLANGE
[IN L.S. AND SURFACE VIEW]

In profile, in the light microscope, the guard cell/subsidiary cell flange is V-shaped, similar to the ordinary flanges and to those of leaves in many taxa. The scanning electron microscope reveals that this flange is quite different in morphology to flanges elsewhere being 'wing'- or 'scale-like' [Figs 175, 176] just as is typically the case in Lauraceae leaf stomata (see p. 224). The extreme edge of the 'wing' corresponds to the guard cell/subsidiary cell flange, which tapers, as in many other Lauraceae taxa.

'Wings' are short and wide (obtuse) in surface view [1:w C. filiformis 3.8:1.0; C. glabella 5.2:1.0] and therefore correspond to the commonest wing form. The wing tips of C. filiformis are clearly blunt [Fig. 175] as in many leafy taxa; in C. glabella, tip shape is less easy to determine since the wings are characteristically orientated in an almost vertical position [Fig. 176]. Wing tips are also distinctly incurved, especially in C. filiformis (best observed in L.S.). The lateral margins of the 'wings' are curved, just as in most other Lauraceae.

13.1.5b (xi) POSITION OF GUARD CELL 'WING'

The wings extend beyond the aperture [Figs 175, 176] particularly in C. filiformis (aperture 1 : wing l^1 0.4:1.0). Those of C. glabella project to a lesser extent [1: l^1 0.75:1.0]. The pattern shown by these stem stomata, especially that in the latter species, is commonly found in leaf stomata of taxa in the same family.

The wing length l^1 is approximately 5/6 subsidiary cell length l^2 i.e. wing length approaches the subsidiary cell length. The value for C. glabella [0.8:1.0] is at the maximum of the most frequently occurring configurations, that for C. filiformis [0.84:1.0] is just outside and is, therefore, one of the rarer patterns [see p. 227].

13.1.5b [xii] PRESENCE AND FORM OF POLAR THICKENING OF GUARD CELLS

No polar thickening may be observed associated with guard cells in Cassytha spp., as in other Lauraceae [see explanation p. 227].

13.1.5b [xiii] PERICLINAL SURFACE SCULPTURE

The cuticle/cellulose wall interface in the periclinal region of the guard cell is even in both species in the light microscope. Scanning-electron microscopic examination of the same area reveals the presence of dense, granular protrusions, approximately 0.2-0.5 μm in diameter in C. filiformis [Fig. 175] and slightly less in C. glabella [ca. 0.2-0.4 μm] [Fig. 176]. This pattern contrasts with that found on the periclinal surface of non-specialised cells [see p. 322], as in the case of many leafy taxa.

13.1.5b [xiv] PATTERN OF STRIAE ASSOCIATED WITH GUARD CELL

In both species, a portion of the guard cell outer periclinal wall [and cuticle] is visible from above due to the stomatal organisation [Figs 169, 170]. This surface is smooth, lacking folding of any kind in C. filiformis. However, in C. glabella a series of fine, straight, lateral striae extend outward from the base of the outer ledge and are particularly conspicuous in isolated cuticle preparations [obscured by wax when unmacerated].

13.1.5b [xv] GUARD CELL/SUBSIDIARY CELL FLANGE SCULPTURE

The interface configuration and fine details of the microrelief at this flange are the same as those for the periclinal region of the guard cell [Figs 175, 176], a common feature in other Lauraceae. The pattern, again, is dissimilar to that of the ordinary flanges [see p. 324].

13.1.5c SUBSIDIARY CELL CHARACTERS13.1.5c (i) HEIGHT IN L.S.

Subsidiary cells are deep [av. C. filiformis 31.7 μm ; C. glabella 34.8 μm], exceeding the maximum average (30.2 μm in Aiouea guianensis) for leaf stomata.

13.1.5c (ii) THICKNESS OF UNCUTINISED OUTER PERICLINAL WALL COMPARED WITH THICKNESS OF INNER WALL IN L.S.

As in many taxa, the uncutinised portion of the subsidiary cell outer periclinal wall, is similar in thickness to the inner wall. The outer periclinal wall is also non-lignified.

13.1.5c (iii) CURVATURE OF OUTER PERICLINAL WALL IN L.S.

In these species, just as in all other Lauraceae, the subsidiary cell outer periclinal wall appears convex. That of C. glabella is more domed (h:w 0.55:1.0) than C. filiformis (h:w 0.35:1.0). This degree of doming falls within the commonest range of values for leaf stomata where the maximum wall height above the anticlinal border is between about $\frac{1}{4}$ and $\frac{3}{4}$ subsidiary cell width.

The convexity of the subsidiary cells in sections corresponds to their bulging or prominence from the stem surface in the S.E.M. [Figs 169, 170], in the same way as for leaf stomata.

On the inner surface of isolated cuticles, each subsidiary cell dome is represented by a single hollow [Figs 175, 176].

13.1.5c (iv) DEPTH OF STOMATAL PIT

The guard cells are sunken below the subsidiary cells, like those of Lauraceae leaf stomata. The average pit depth differs, however, in the two species examined: shallow [about 3.0 μm] in C. filiformis and moderate [6.4 μm] in C. glabella. The former has a pit of the commonest pattern, the latter the next most frequent type.

13.1.5c [v] SHAPE OF STOMATAL PIT IN SURFACE VIEW

In C. filiformis, the stomatal pit length slightly exceeds the width, giving a PL:PW ratio of 1.4:1.0 [approximately 1:1 - second pit type p. 243]. The pit of C. glabella is clearly wider than long, with PL:PW of 2.3:1.0 [third pit type] and is an example of the pit form of widest occurrence within the Lauraceae. The PL:PW values of both species are encompassed in the most common range for the ratio observed [up to 6.0:1.0] for Lauraceae leaf stomata.

The lateral walls of the stomatal pit curve inwards in surface view and terminate sharply at the poles in C. glabella (Fig. 170). In C. filiformis, however, as in those taxa with the more isodiametric stomatal pit opening on leaves, the polar walls are 'tridentate' (Fig. 169).

13.1.5c [vi] DEFINITION OF WALL BETWEEN ADJACENT SUBSIDIARY CELLS AT THE STOMATAL POLES ON THE OUTER SURFACE

Subsidiary cells of C. glabella are discrete, situated closely together at the poles, whereas those of C. filiformis are entirely joined, forming a ring [raised] around the stomatal pit, just as in leaf stomata of many Lauraceae, especially those with tridentate pit walls.

13.1.5c [vii] ORIENTATION OF THE SUBSIDIARY CELL OUTER PERICLINAL WALL IN L.S.

Longitudinal sections reveal that the subsidiary cell dome does not overhang the guard cell periclinal surface, since the angle between the guard cell border and a tangent to the stomatal pit wall is less than 90° [C. filiformis 48.0°; C. glabella 66.5°]. Thus, the entire guard cell surface is visible forming the floor of the stomatal pit, that is, the central region bounded by bulging subsidiary cells, in surface view [see Figs 169, 170]. This stomatal configuration is rare in leaf stomata.

The suprastomatal cavity, based on angle results stated above together with those on pit depth, is shallow in C. filiformis with outward curving walls and moderate

in C. glabella with less outwardly curving walls.

The angle between the level of the surrounding cell border and a tangent to part of the adjacent subsidiary cell outer periclinal wall (and cuticle) is positive, indicating an upward slope from the border [C. filiformis 40.0°; C. glabella 37.5°], as in most Lauraceae.

13.1.5c [viii] PRESENCE OF POLAR PAPILLAE

Polar papillae are absent.

13.1.5c [ix] MEDIAN PERICLINAL THICKNESS OF CUTICLE IN L.S.

The cuticle of the subsidiary cell is thinnest nearest to the guard cell (in L.S.). In C. filiformis the cuticle abruptly increases in thickness at the dome crest, the maximum occurring towards the subsidiary cell/surrounding cell flange. Cuticle thickness in C. glabella, however, appears to increase more gradually, but is still thickest near to the flange between the surrounding and subsidiary cells. Thus, the scrobiculus located on the inner surface of the subsidiary cell in C. filiformis is narrow and tubular in shape extending to some depth (due to dome prominence and orientation) and is clearly marked (Fig. 175). That of C. glabella appears to be less deep and to occupy more of the cell, although the scrobiculus boundary is sometimes ill-defined (Fig. 176).

Cuticle in the median periclinal zone of the subsidiary cells is thin [C. filiformis av. 2.1 µm; C. glabella 2.6 µm], as in leaf stomata of many taxa. This is considerably less than the corresponding non-specialised cell periclinal cuticle [C. filiformis 6.4 µm; C. glabella 4.6 µm], a common pattern within the assemblage examined.

13.1.5c [x] PRESENCE AND FORM OF POLAR THICKENING

Both species possess thickening at the subsidiary cell poles: a pair of strongly marked, convex lateral lines, a very narrow, low centrally placed rod and a wedge-shaped bar or cross-piece (Figs 175, 176). The resulting configuration is similar to that seen in a few other Lauraceae, e.g. Endiandra kingsiana and Litsea meissneri.

13.1.5c [xi] TERRACING

Subsidiary cells are not terraced.

13.1.5c [xii] PRESENCE AND FORM OF FOLDING

The subsidiary cell outer periclinal cuticle is unornamented [smooth] in C. filiformis similar to that in many taxa [Figs 169, 171]. C. glabella has a series of fine, straight, lateral folds or striae running across the width of the subsidiary cell, as over the guard cell [Figs 170, 172]. Striae are not present on the inner subsidiary cell surface [Figs 175, 176].

13.1.5c [xiii] PERICLINAL SURFACE SCULPTURE

The subsidiary cell periclinal cuticle is differentiated into two zones, as in most Lauraceae [see p. 258].

The interface between the cuticle and the cellulose wall in the periclinal region is even, just as that in other cell types, in the light microscope. The surface is also more or less smooth in the S.E.M., in C. filiformis [Fig. 175], in the same way as that of ordinary cells [Fig. 177] in this species. C. glabella, however, is ornamented with widely spaced, very fine [ca. 0.2 μm or less] granular protrusions and slightly coarser [ca. 0.4 μm or less] depressions of a pit-like-clumped arrangement [Fig. 176]. The latter pattern differs in only one aspect, depression arrangement [no reticula] from that observed in non-specialised periclinal areas [Fig. 178].

13.1.5c [xiv] THICKNESS OF CUTICLE AT SUBSIDIARY CELL/
ORDINARY [SURROUNDING] CELL FLANGE IN L.S.

The cuticle at this flange is moderately thick [C. filiformis av. 6.1 μm , C. glabella 7.3 μm] and is considerably thinner than the cuticle at either the guard cell/subsidiary cell flange or the flanges of non-stomatal cells.

13.1.5c [xv] PROMINENCE OF SUBSIDIARY CELL/SURROUNDING
CELL FLANGE IN L.S.

The subsidiary cell/surrounding cell flange is of low prominence, a pattern found in leaf stomata of many taxa.

The guard cell/subsidiary cell flange extends to a similar degree in C. glabella but not in C. filiformis [moderate]. Ordinary flanges are of deeper prominence [moderate] than the subsidiary cell/surrounding cell flange.

13.1.5c [xvi] SHAPE OF SUBSIDIARY CELL/SURROUNDING CELL FLANGE

In L.S., this flange is V-shaped. The pattern shown is the same as that of all other flanges in these species, and like the configuration observed most frequently amongst the taxa studied.

In the S.E.M., the subsidiary cell/surrounding cell flange describes a straight to slightly curved course [Figs 175, 176]. This pattern is characteristic of leaf stomata in certain other Lauraceae. The flange between the subsidiary and surrounding cells is more curved than ordinary flanges [straight only].

13.1.5c[xvii] CONTINUITY OF SUBSIDIARY CELL/SURROUNDING CELL FLANGE

In C. filiformis, the subsidiary cell/surrounding cell flange is not usually interrupted [Fig. 175]; when there is interruption, however, only one gap per flange may be detected. In C. glabella, the same flange is frequently interrupted by one or two gaps [a rare pattern in leaf stomata] [Fig. 176]. The subsidiary cell/surrounding cell flange is generally more continuous than an ordinary flange.

Tiny rounded channels, the commonest pore type found in leaf flanges may be present in this flange just as in non-stomatal flanges. C. filiformis does not exhibit the second form, round to oval, moderate sized perforations, in the subsidiary cell/surrounding cell flange. The frequency of pores in the latter flange is low in both species [0-1], in contrast to that of ordinary flanges, and the trend follows that detected in leaf stomata of other Lauraceae.

13.1.5c [xviii] NATURE OF SUBSIDIARY CELL/SURROUNDING
CELL FLANGE APEX

The subsidiary cell/surrounding cell flange is unfurrowed.

The margin of this flange is uneven in side view, in the S.E.M., particularly in C. filiformis [Fig. 175], where irregularities of up to 1.8 μm in amplitude may be observed. Irregularities at the margin in C. glabella may be smaller attaining a maximum height of 0.7 μm [Fig. 176], as in many other taxa. The amplitude of subsidiary cell/surrounding cell flange irregularities is less than those of non-stomatal flanges [second pattern recognised in leaves].

Especially deep, peg-like cutinisation occurs in C. filiformis, where the subsidiary cell/surrounding cell flange meets a flange of one of the adjacent ordinary cells [Fig. 175]. No pegs may be detected in C. glabella [Fig. 176].

13.1.5c [xix] SUBSIDIARY CELL/SURROUNDING CELL FLANGE
SCULPTURE

As with all other flanges, the cuticle/cellulose wall interface appears even at the subsidiary cell/surrounding cell flange, in the light microscope. Scanning electron microscopic observations reveal that this specialised flange is, in fact, ornamented; in C. filiformis with dense, moderate sized [ca. 0.4-0.5 μm] protrusions of granular-reticulate form [Fig. 175] and in C. glabella with more widely spaced, very fine [less than 0.2 μm] granules and somewhat coarser [ca. 0.4 μm or less], pit-like-reticulate depressions [Fig. 176]. These patterns are reminiscent of those found on ordinary flanges, particularly in the case of C. filiformis [see p. 324]. Depressions are of smaller dimensions and organised into less complex groups on unspecialised flanges than on the subsidiary cell/surrounding cell flange, in C. glabella.

13.1.5c [xx] SECONDARY ANTICLINAL DIVISIONS

Secondary divisions in the anticlinal plane, parallel to the pore, are present in some stomata. These usually occur in one of the subsidiary cell pair only. The resulting flange is noticeably less prominent and bears a more even margin, particularly in C. filiformis, than primary flanges. A peg may also be detected where the secondary flange meets the subsidiary cell/surrounding cell flange, in this species.

13.1.5c [xxi] OBVIOUS SPECIALISATION OF SURROUNDING CELL ADJACENT TO SUBSIDIARY CELL

The non-stomatal cell adjacent to the subsidiary cell [parallel to the pore] is not visibly specialised (in terms of greater periclinal curvature than other epidermal cells).

13.1.5c [xxii] NUMBER OF CELLS SURROUNDING STOMATAL COMPLEX

There are never more than 6 epidermal cells surrounding the stomatal complex. The range of most common occurrence in leaves is characteristic of C. glabella [4-5], whilst in C. filiformis 5-6 cells normally abut the stomatal complex. The small number of cells is to be expected since individual cell dimensions are large in Cassytha spp.

13.1.6 CHARACTERS OF SPECIALISED CELLS : TRICHOMES

13.1.6a CHARACTERS OF NON-GLANDULAR TRICHOMES

In Cassytha, such trichomes are unbranched, unicellular and simple, as in most of the pubescent taxa examined.

13.1.6a [i] OCCURRENCE

Simple hairs occur all over the stem surface in C. filiformis (Fig. 173). They are absent in C. glabella (Fig. 174).

13.1.6a [ii] FREQUENCY

Up to 4 hairs may be observed per field of view [at x 320] in C. filiformis. The frequency, therefore, is low and falls in the range most commonly found in leaves.

13.1.6a [iii] PERSISTENCE IN CUTICLE PREPARATIONS

Simple hairs in C. filiformis are represented only by their bases in isolated cuticles, as in the case of the majority of taxa with pubescent leaves.

13.1.6a [iv] BODY TYPE

Simple hair bodies are non-ornamented [smooth] in C. filiformis [Fig. 173], conforming to all other hairs of this type. They are intermediate in both length [ca. 145.7-231.4 μm] and width [11.4-14.3 μm]. In shape, C. filiformis hairs are also intermediate between the robust and filiform extremes [1:w 10.2-17.5:1.0].

Hair bodies of C. filiformis are non-lignified, like those of many other taxa.

13.1.6a [v] GROUPING OF BASES

Simple hair bases in C. filiformis are generally distributed singly in cuticular preparations. Occasionally the bases may be paired.

13.1.6a [vi] NUMBER OF BASAL CELLS SURROUNDING HAIR PORE

4-5 cells constitute the hair bases in C. filiformis. They radiate from the pore in much the same way as basal cells of costal hairs in leaves.

13.1.6a [vii] BASE TYPE

In C. filiformis the base from which a hair body has become detached, is reminiscent of all others found on leaf surfaces when viewed with scanning electron microscopy. The basal cells, however, tend to bulge or protrude more above the surrounding cells than in most taxa. They also possess fine radial striae on the outer side. On the inner cuticle surface, the poral flange is continuous with cutinisation covering the pore and the radial flanges gradually decrease in prominence outwards. All sculptural features are similar to those of non-stomatal cells. The

cutinised 'peg' end exhibits a smooth to finely granular microrelief, a common configuration in leaves.

In the light microscope, the bases of the simple hairs of C. filiformis have a thick, well cutinised poral flange as well as thickened radial basal flanges, and thus appear stellate in form, as do those on leaf surfaces of many other taxa. Such bases are non-lignified in C. filiformis.

13.1.6b CHARACTERS OF GLANDULAR TRICHOMES

13.1.6b (i) OCCURRENCE

Glandular hairs are absent, as in all other Lauraceae.

13.1.7 CHARACTERS OF SPECIALISED CELLS : CORK WARTS

No evidence of cork warts has been found.

13.1.8 CHARACTERS OF SPECIALISED CELLS : SECRETORY [OIL] CELLS

Oil cells are represented in the stem cuticles within and between stomatal bands of both species. In the light- and scanning electron-microscopes, these secretory cells are much like the second type described on p. 313. However, in Cassytha spp. they are always of greater diameter, approximately 31.1-34.3 μm in C. filiformis and 25.7-31.4 μm in C. glabella. These secretory cells are particularly abundant in C. glabella.

On the outer side of the cuticle or unmacerated stem portion, oil cells are exactly like the second type of leaf secretory cells in form. On the inner cuticular surface, this is also the case [Figs 179, 180]. The bordering flange is deep [especially in C. filiformis] so that it flops over onto the surrounding basal cells, producing a thickened or polygonal appearance in surface view [Fig. 179]. The margin of this flange contrasts greatly with the other very irregular flanges, since it

is more or less even (see Figs 175, 177). The periclinal surface of the central secretory cell area is almost smooth (the normal configuration for all oil cells). Peg like-extensions are absent at the point where the basal flanges radiate out from the flange bordering the secretory cell.

Oil cells are also non-lignified, as in most taxa.

13.2 SPECIAL STUDY OF THE ABAXIAL SURFACE IN CARYODAPHNOPSIS

Whole leaf mounts [Fig. 185] and isolated cuticles [Fig. 186] of the abaxial surface of Caryodaphnopsis tonkinensis have a rather complicated, reticulum-like appearance in the S.E.M. Two levels of surface may be detected: (1) the outermost, consisting of a dense network of anastomosing parts and (2) the inner, at a lower level of focus, which is seen only through gaps of various shapes and sizes, in (1). However, the precise organisation constituting this surface pattern is not clear from such direct observation.

Further attempts have been made to elucidate the structure, using other preparation techniques prior to examination with scanning electron microscopy.

13.2.1 SELLOTAPE PULL [See p. 92].

This method, previously used with some success in gymnosperms by Alvin [per. comm.] for removing 'alveolar material' i.e. a layer probably consisting of polymerised wax lying outside the cuticle itself, leaves only an imprint on the sellotape of the costal and inter-costal areas [Fig. 183]. The leaf portion from which the tape has been pulled remains unchanged in its reticulate appearance indicating that alveolar material is not responsible for the surface configuration.

13.2.2 TRANSVERSE SECTIONS [See p. 90,91].

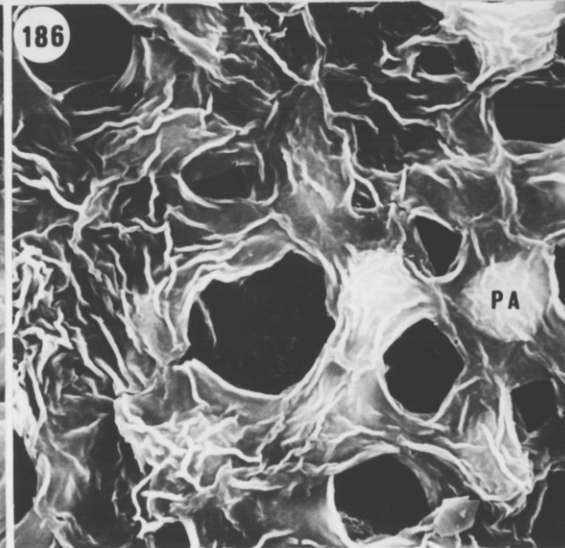
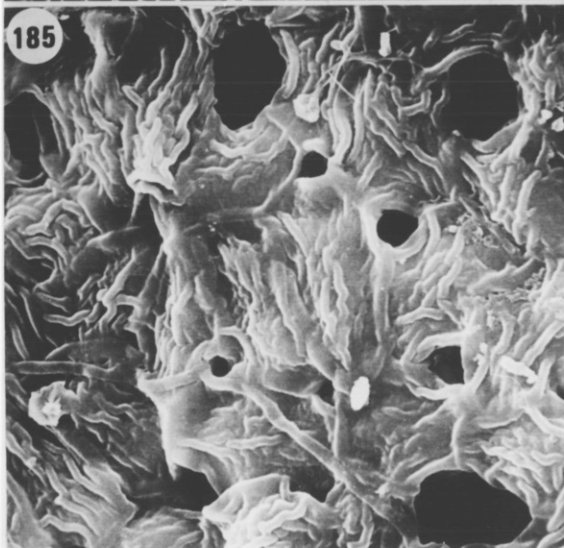
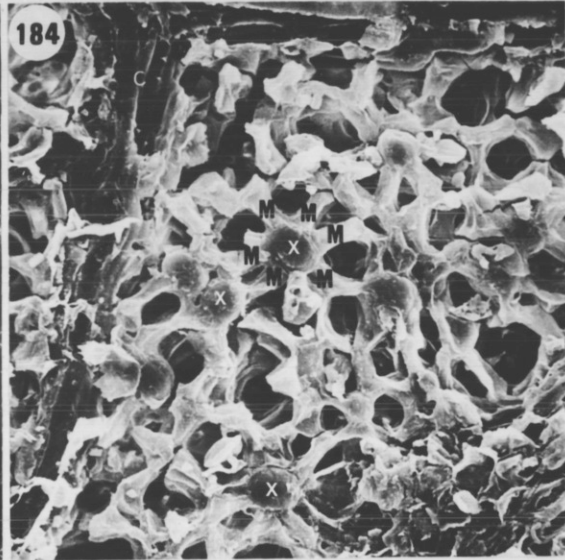
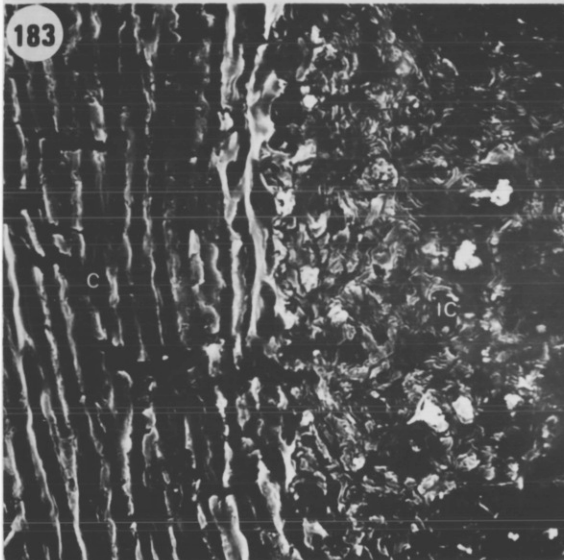
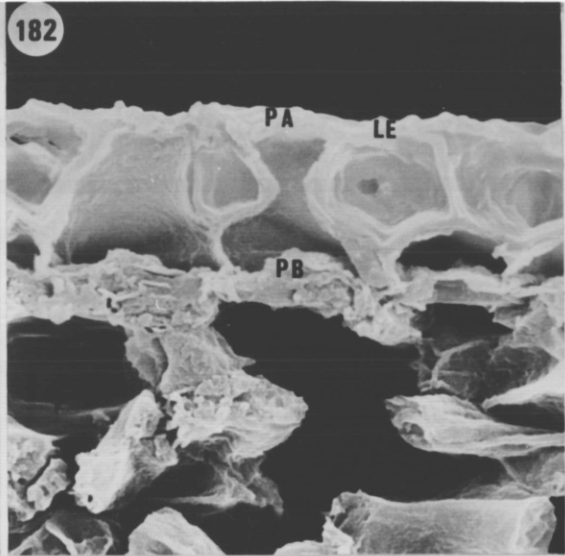
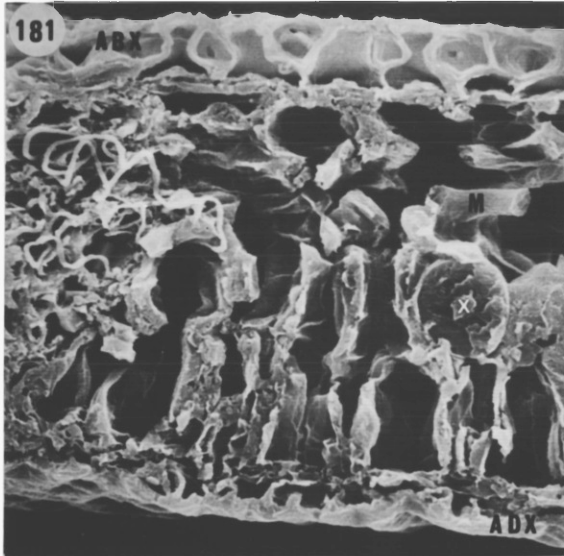
Thick [60-80 μm] sections of leaves [Figs. 181 & 182] show the epidermis to be composed of columnar cells each with an expanded base and apex. The latter appears sometimes to fuse with apices of neighbouring epidermal cell via lateral extensions. Other information regarding cell arrangement is difficult to ascertain by this technique.

13.2.3 SURFACE SCRAPES [See p. 92].

Most veins are unchanged by this method [Fig. 184]. In non-vein areas, only mesophyll cells, arranged in a

Special study of the abaxial epidermis of *Caryodaphnopsis*
tonkinensis

181. Thick transverse section of leaf, showing modified abaxial epidermis [ABX] and position of mesophyll [M] and secretory cell [X] revealed in surface scrape [Fig. 184]. ca. x 510.
182. Thick transverse section of leaf. High power view of Fig. 181. Note distinct columnar form of epidermal cell with expanded base [PB] and apex [PA]. Also note lateral extensions [LE] linking apices of neighbouring cells. ca. x 1155.
183. Inprint on sellotape showing costal [c] and intercostal [i.c.] areas prepared using sellotape pull technique. ca. x 300.
184. Result after surface scrape. Note veins [c] remain unchanged. Mesophyll cells [M] occur between veins, arranged in stellate manner around secretory cell [X]. ca. x 250.
185. Unmacerated leaf portion showing surface with complicated, reticulum-like appearance interspersed by gaps of varying shapes and sizes. ca. x 985.
186. Isolated cuticle retaining complex form shown in Fig. 185. ca. x 1015.



stellate manner around cells with dense contents [possibly secretory], are revealed. The surface scrapes result in the removal of the whole of the epidermis and, therefore, cannot be of use in determination of its structure. They do, however, suggest that fine paradermal sections, taken at a higher level, may be useful for structural interpretation.

13.2.4 PARADERMAL SECTIONS [See p. 91,92]

Thin [10-15 μm] surface sections clearly demonstrate the exact organisation of the epidermis. These have been cut and mounted in two ways to obtain details of all aspects of the arrangement: [a] from outside inwards to the base of the cells [Figs 187-192] and [b] from inside outwards to the cell apices [Figs 193-198].

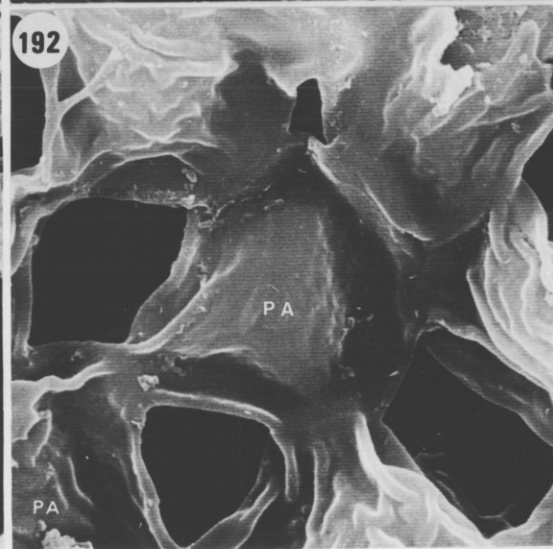
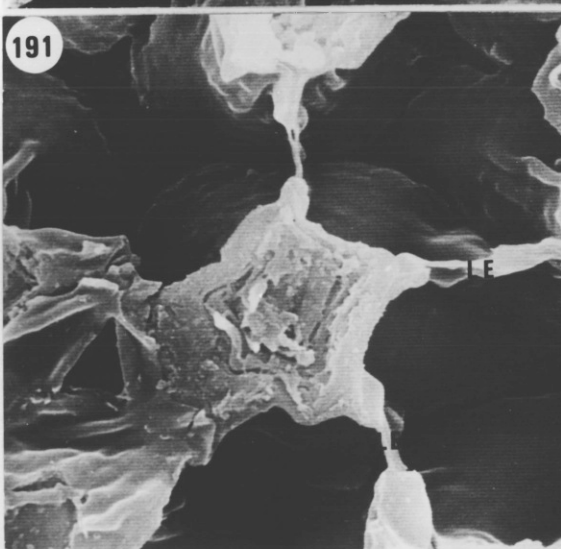
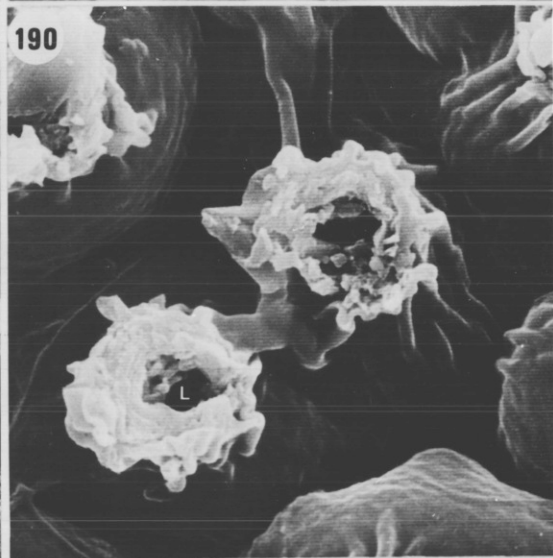
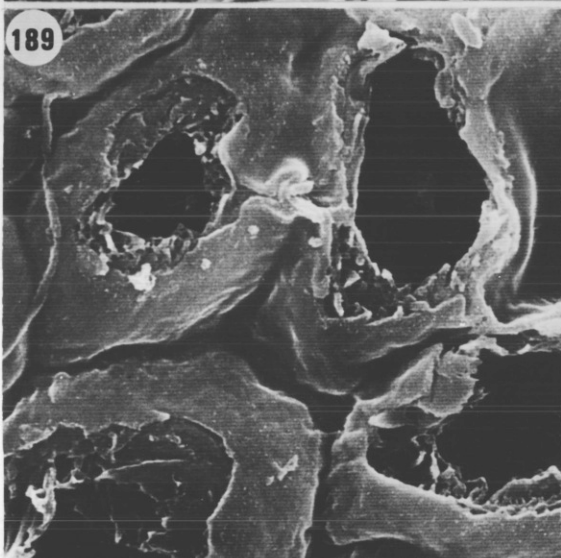
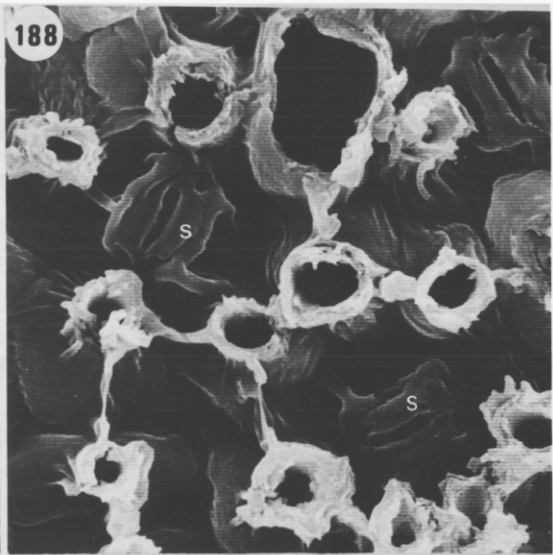
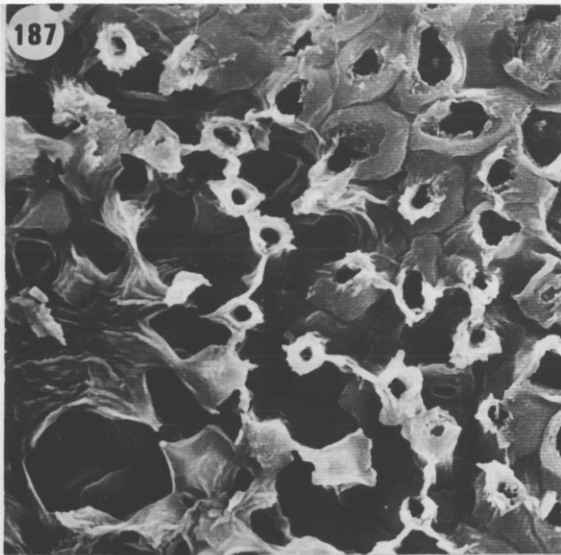
13.2.4a The flattened, striate, polygonal apex of each epidermal cell is normally fused to varying numbers of neighbouring cell apices at certain points around its edge [Fig. 192]. Where there is no fusion, gaps of various shapes and sizes occur in the surface. The cells are distinctly joined by lateral extensions [Fig. 191]. Below the apex, each cell decreases in diameter forming a columnar portion, rounded in cross section, with a thick, striate wall surrounding a comparatively small lumen [Fig. 190]. Towards the base, the cells abruptly expand outward and assume a striate, polygonal, tabular form [Fig. 189]. Low-power observations reveal that stomata are located amongst rings of between 5 and 8 of these cells at this level [Fig. 188]. Thus, in the leaf, the stomata are situated well beneath the actual leaf surface in discontinuously 'roofed' cavities.

13.2.4b Below the epidermis, the mesophyll cells radiate from presumed secretory cells [as detected by surface scrapes]. Stomata, each with a pair of guard cells and two laterally placed subsidiary cells, may also be seen above and between these mesophyll groups [Fig. 195]. At the same level as the stomata, cut basal portions of the epidermal cells may be recognised. These are short, polygonal in shape and concave with a single centrally

Special study of the abaxial epidermis of *Caryodaphnopsis tonkinensis*.

Paradermal sections: outside to inside.

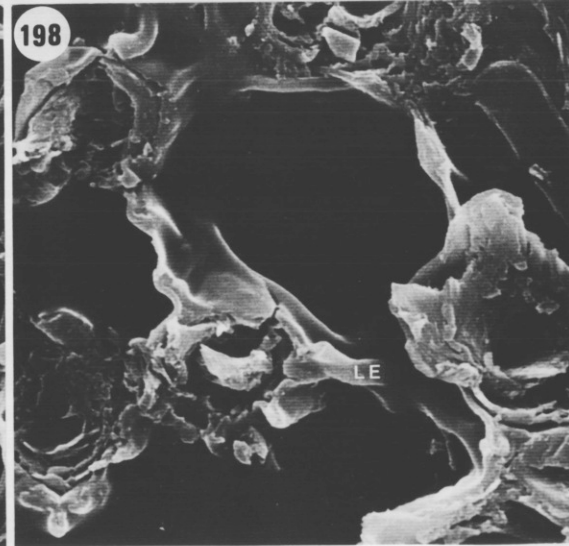
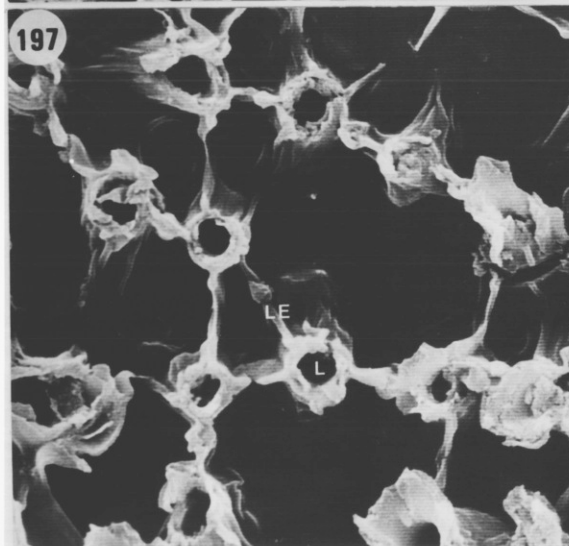
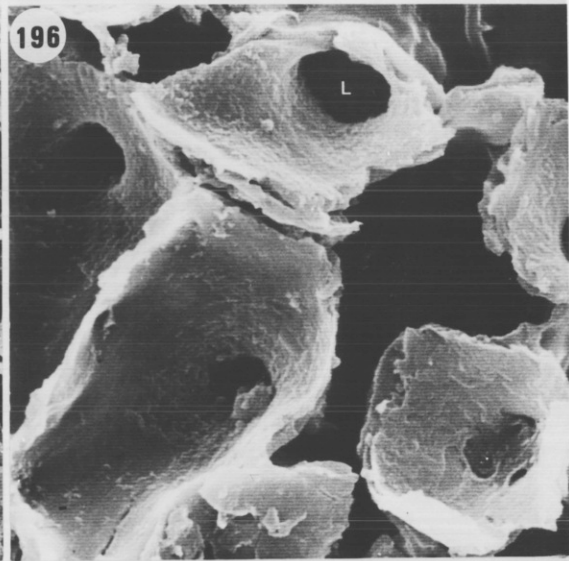
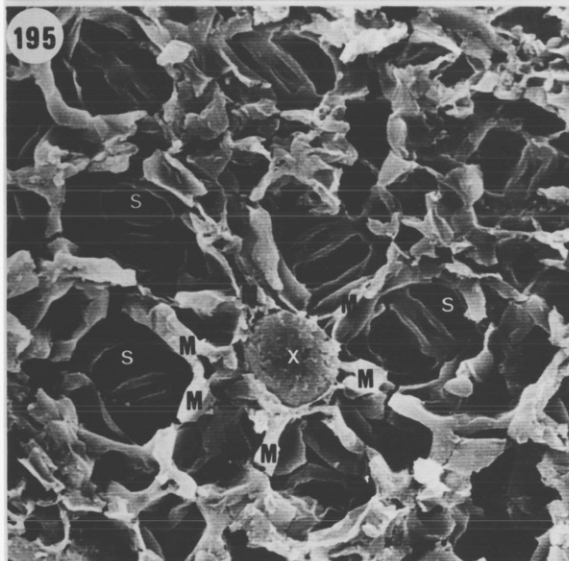
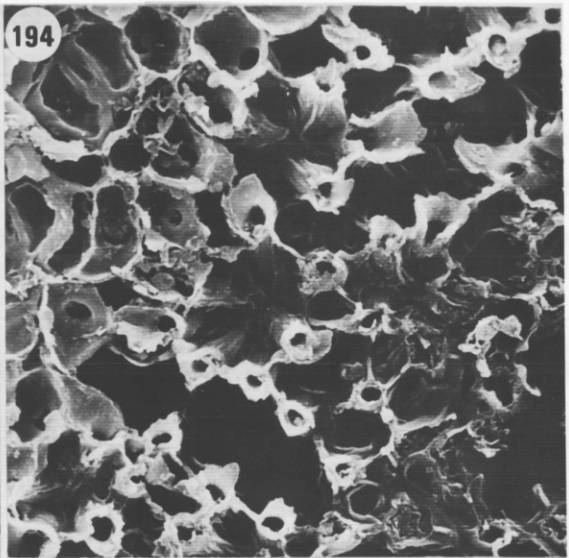
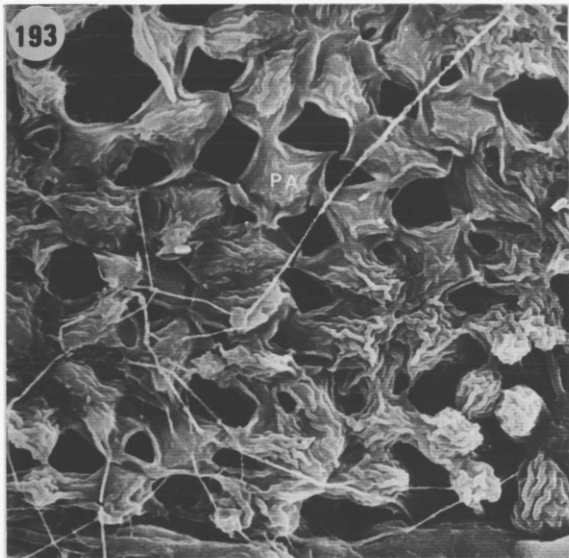
187. General view of paradermal section. Low power.
ca. x 570.
188. Portion revealing location of stomata [S].
ca. x 1095.
189. Cut basal parts of cells. ca. x 2250.
190. Cut columnar part of cells, round in cross section with thick, striate wall surrounding comparatively small lumen [L]. ca. x 2200.
191. Cells cut at apex, showing distinct lateral extensions [LE] joining apices of nearest neighbours.
ca. x 2220.
192. Uncut portion, but still demonstrating fusion of apices [PA]. ca. x 2175.



Special study of the abaxial epidermis of *Caryodaphnopsis tonkinensis*.

Paradermal sections: inside to outside.

193. General view of uncut epidermis. Low power.
ca. x 525.
194. General view of paradermal section. Low power.
ca. x 560.
195. Portion revealing position and arrangement of groups of mesophyll (M) around single secretory cell (X) [as in Fig. 184] and location of stomata (S).
ca. x 1115.
196. Cut basal portions of epidermal cells each with single centrally located depression (L) corresponding to lumen of columnar part. ca. x 2140.
197. Cut columnar region of cells [see Fig. 190], with distinct lumen (L). ca. x 1060.
198. Cut apices, in isolation. Note their flattened, polygonal outline and lateral extensions (LE) linking adjacent apices. ca. x 2185.



located depression corresponding to the lumen of the columnar portion of the cell [Fig. 196]. Below this, the cells suddenly decrease in diameter and assume the columnar form recognised in [a] [Fig. 197]. At the top of each column, the cells again expand to form a flat, polygonal apex which is always linked to a number of other similar apices by lateral extensions, as in [a] [Fig. 198].

The abaxial epidermis of Caryodaphnopsis tonkinensis, therefore, consists of densely packed, coronulate, striate papillae which often fuse at the apices, interspersed by deeply sunken stomata.

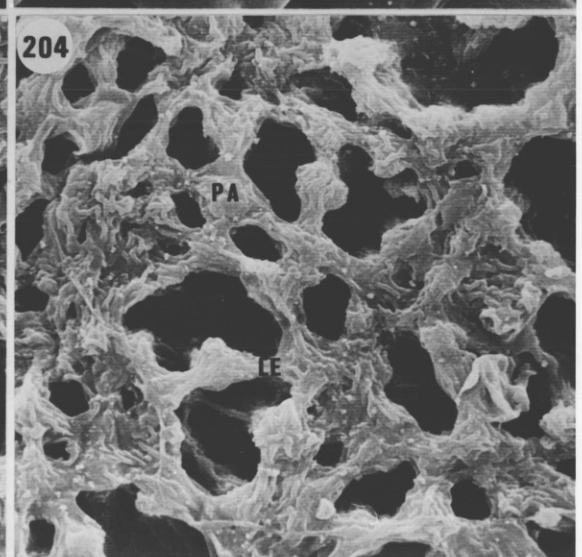
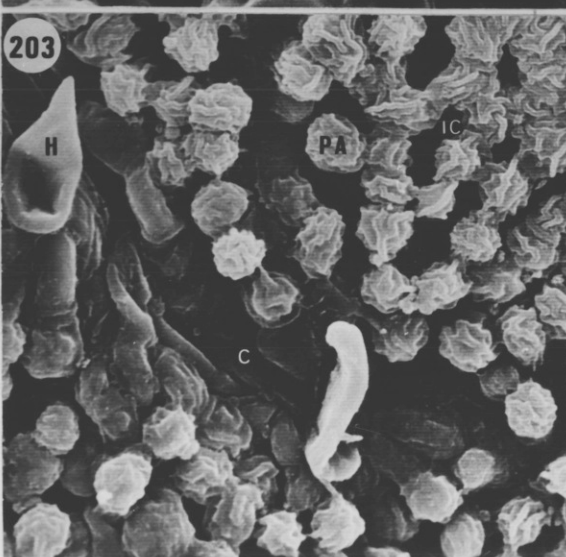
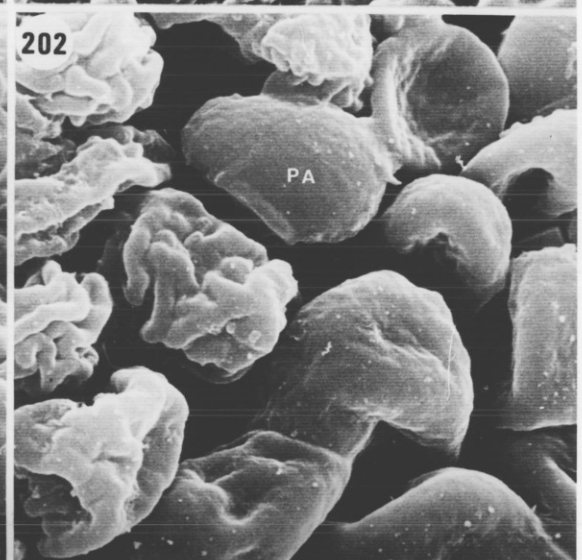
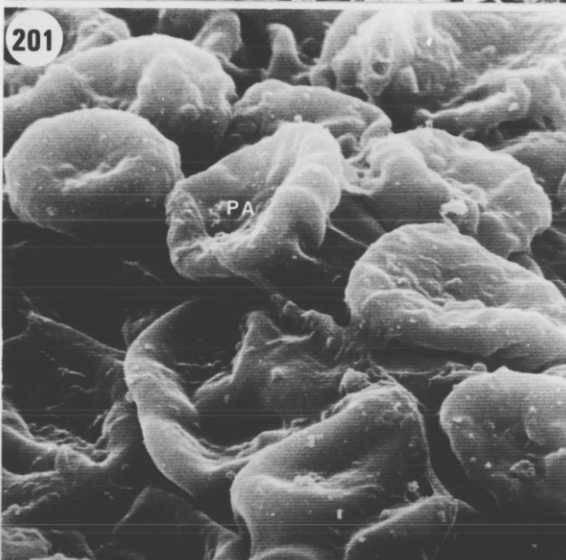
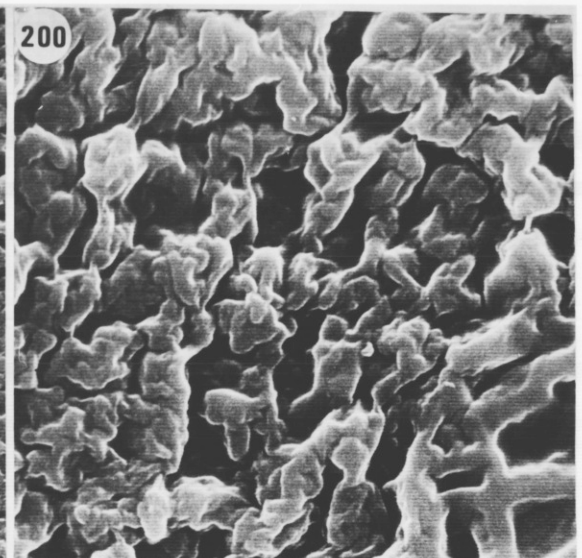
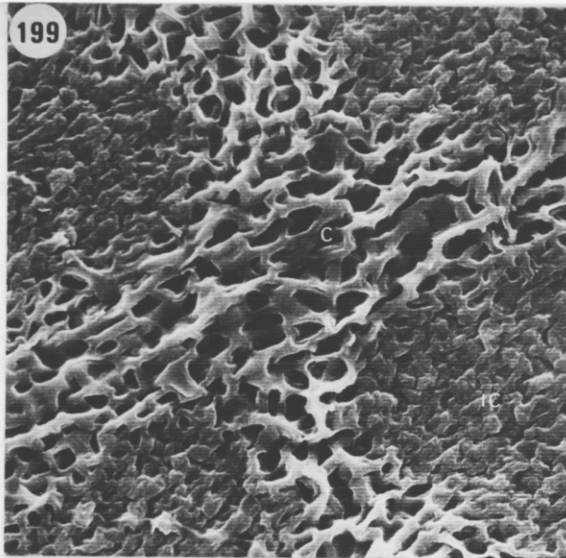
The basic configuration described is shown by all but specimen [5] [Fig. 242], although there is some minor variation in the size and prominence of cells as well as in the degree of fusion of the cell apices among other specimens [Figs 241, 243, 245]. However, according to observations made of other features [5] has clearly been misidentified. Hence, the epidermal structure is consistent and characteristic of the species. It may, in addition, be a feature of the genus since a second species, C. baviensis also exhibits a similar abaxial pattern [Fig. 246].

The papillate structure is not always evident in the very young leaves from the top of the shoot [Figs 199, 200]. Only concave cells with raised borders representing veins may be clearly visible, separating regions composed of slightly convex, irregularly undulate cells. In other leaves taken from near the shoot apex, the surface is projected into papillae which, individually, commonly remain separate from others, particularly near costal areas and occasionally, fuse apically in the centre of the intercostal regions. Striae also appear more well-developed away from the veins. Sometimes at the leaf apex, papillae may have flattened apices [Fig. 201] but more usually these cells are rather globular in form [Figs 202, 203]. The margin of larger leaves just below the end of the shoot tends to exhibit a rather open network of

Special study of the abaxial epidermis of *Caryodaphnopsis*
tonkinensis

Young leaves: development of surface.

199. Portion of abaxial surface of young leaf showing costal [c] and intercostal [i.c.] areas. Note lack of papillae. Low power. ca. x 560.
200. High power view of intercostal region shown in Fig. 199, demonstrating highly wrinkled topography, but no papillae. ca. x 2160.
201. High power view of surface in apical region of young leaf removed from just below end of shoot. Papillae with flattened apices. ca. x 2165.
202. High power view of surface in mid-zone of same young leaf shown in Fig. 201. Papillae more globular in form, some [on left of Fig.] conspicuously striate. ca. x 2200.
203. Base area of very small, young leaf showing most papillae to have discrete globular apices [PA]. Note stoma located below general level of epidermis [below PA]. ca. x 570.
204. Margin of larger young leaf sample from same specimen as Fig. 203 showing rather open network of papillae with especially elongate lateral extensions [LE] linking adjacent apices [PA]. ca. x 535.



papillae with especially elongate lateral apical extensions (Fig. 204). The rest of the surface shows the dense pattern so characteristic of the mature leaf specimens.

Thus, although the developmental sequence is difficult to ascertain from dried material, it would seem that the complicated epidermal configuration in C. tonkinensis develops through a number of stages: firstly, an initial simple stage with slightly convex, irregularly wrinkled cells; secondly, a stage with more prominent, predominantly discrete and globular papillae, and thirdly, a stage of increasing complexity by flattening and increasing the area of the apices, and by development of lateral extensions which may join a number of papillae together.

13.3 SPECIAL STUDY: PRELIMINARY INVESTIGATION OF INTRASPECIFIC VARIATION

Unmacerated leaf portions [for the outer surface] and isolated cuticles [for the inner surface] of different specimens representing five species have been examined to ascertain the extent of variability that may occur intraspecifically, particularly in features of the inner cuticular surface.

13.3.1 BEILSCHMIEDIA MADANG

Six different specimens [numbered 1-6] have been examined [see p. 471].

13.3.1a OUTER SURFACE. A high degree of similarity is shown particularly in the case of the adaxial [Figs 205-210] where the only difference is the presence of simple hairs in [3]. Abaxial dissimilarities include the distinctiveness of cell outlines in intercostal regions [sutures more sunken in [3]], stomatal size [smaller in [3]], size and form of wax associated with polar papillae [Figs 217-222] and frequency of simple hairs [lowest [2], intermediate [5] and [6], highest [1], [3] and [4]] [see Figs 211-216].

13.3.1b INNER SURFACE. The adaxial [Figs 223-228] and the abaxial [Figs 229-234] cuticles also exhibit basic similarity between specimens. Nevertheless, some variation is apparent, mainly due to differences in the extent to which the inner periclinal wall of the epidermis is cutinised. This is most evident in costal regions. Over adaxial veins, in [2], [4] and [6], cutinisation extends across the entire wall except for small perforations [1-2 per cell]. In [1] and [3], the inner periclinal wall is only partially cutinised. Specimen [5] seems to have a slightly different pattern of cutinisation to the others, with irregular patches extending below the epidermis, predominantly in the anticlinal walls but also in the periclinal which are, therefore, highly perforated with small, regular round or oval pores [Fig. 227]. The inner periclinal wall of abaxial costal cells in [2] is entirely

Intraspecific variation in *Beilschmiedia madang*

Outer surface: adaxial.

205. Specimen 1. ca. x 240.

206. Specimen 2. ca. x 250.

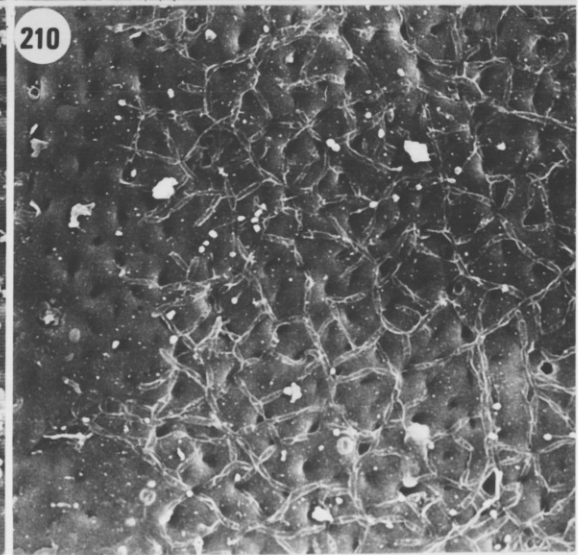
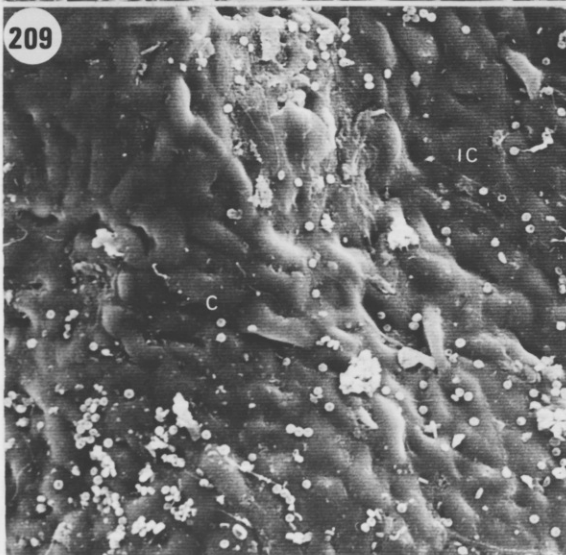
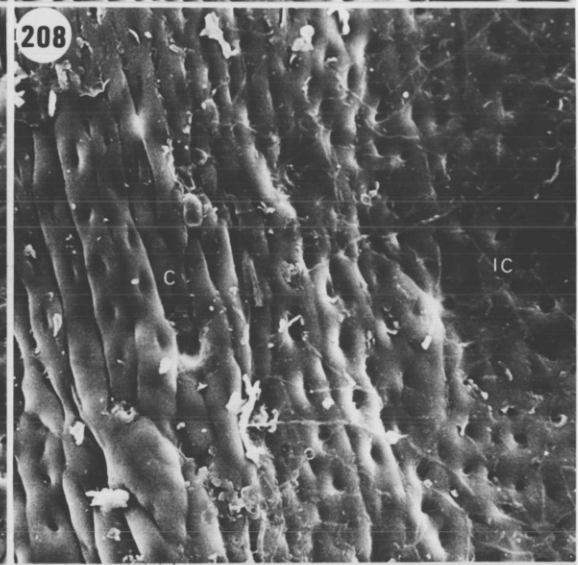
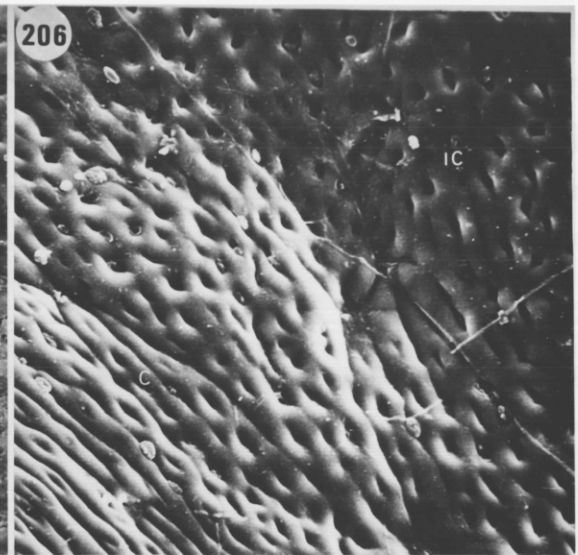
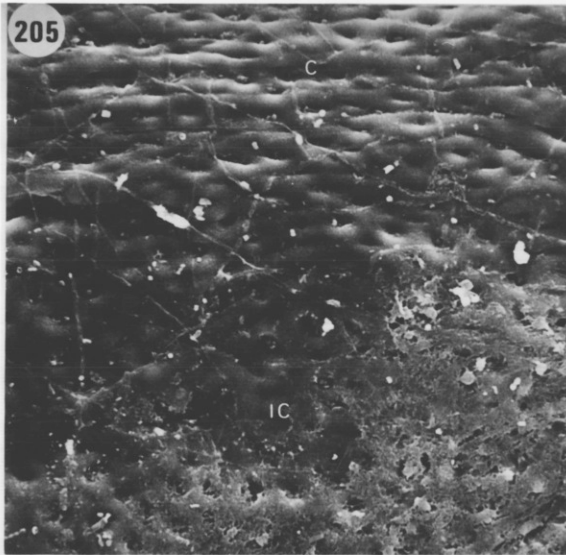
207. Specimen 3. ca. x 285.

208. Specimen 4. ca. x 280.

209. Specimen 5. ca. x 280.

210. Specimen 6. ca. x 280.

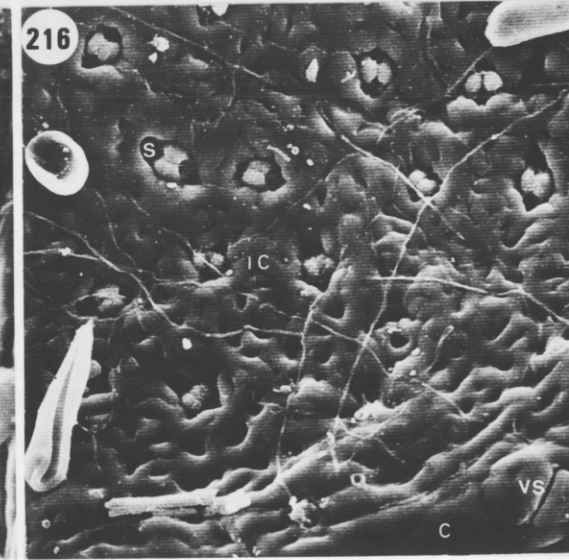
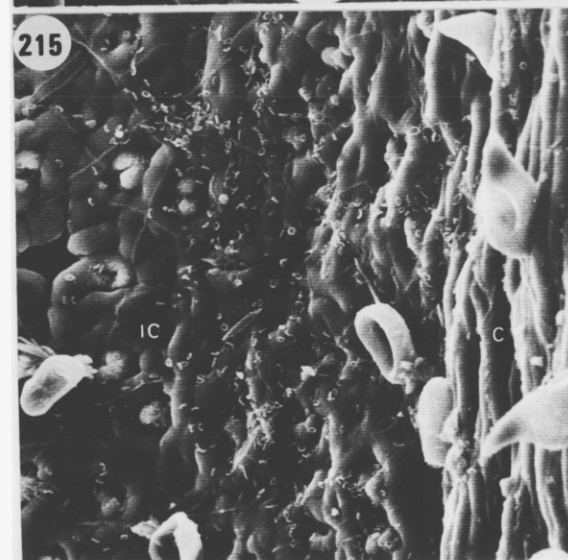
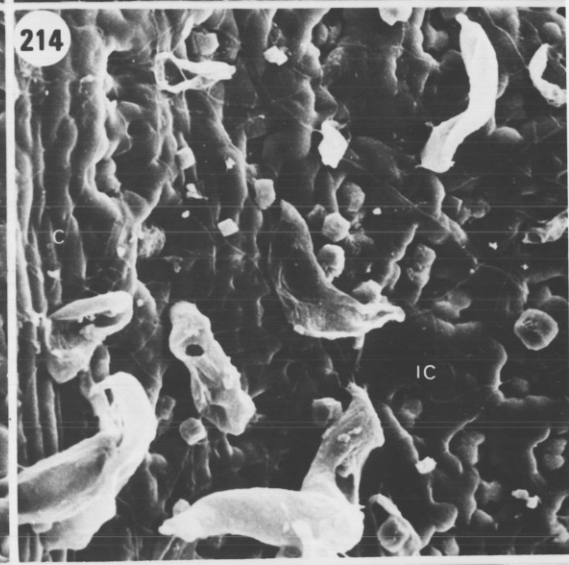
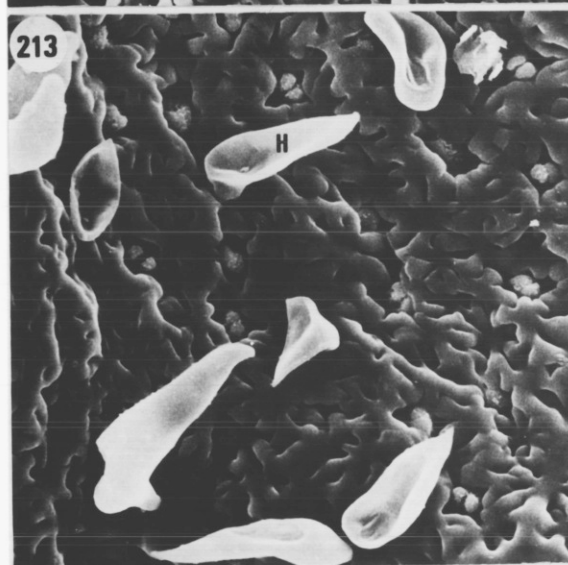
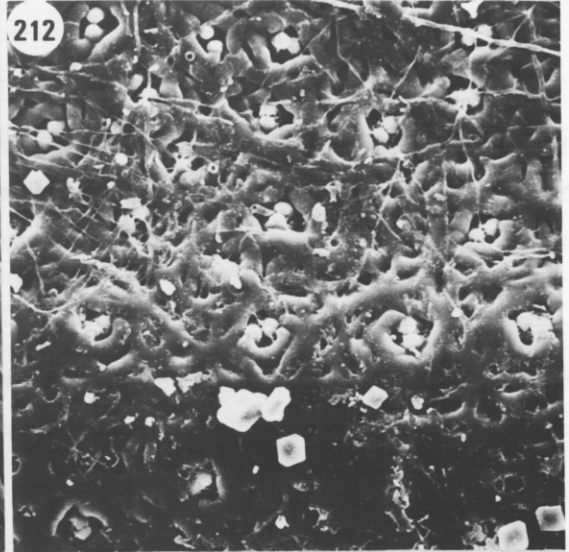
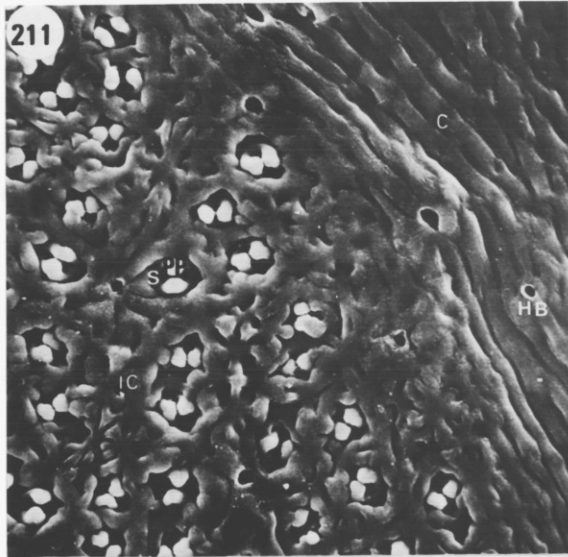
Note high level of similarity between specimens. Only difference is presence of simple hairs in Specimen 3. See Fig. 12.



Intraspecific variation in *Beilschmiedia madang*

Outer surface: abaxial.

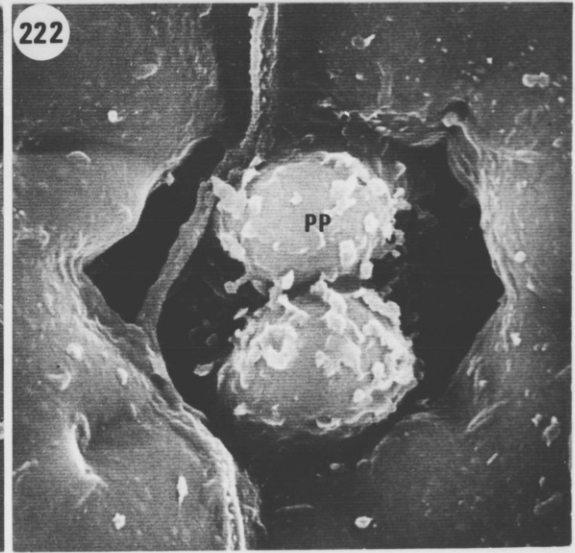
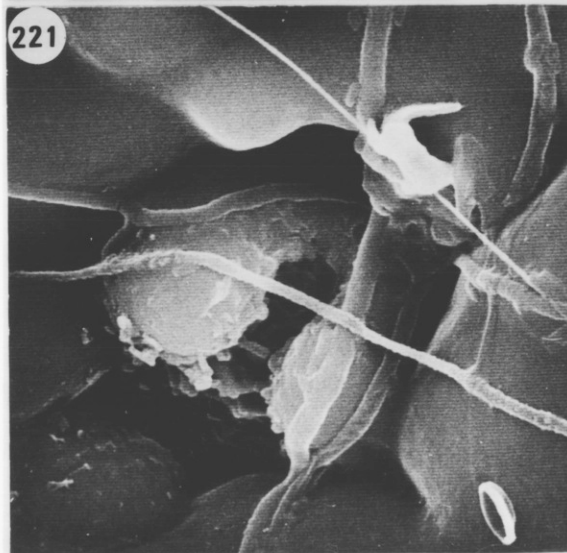
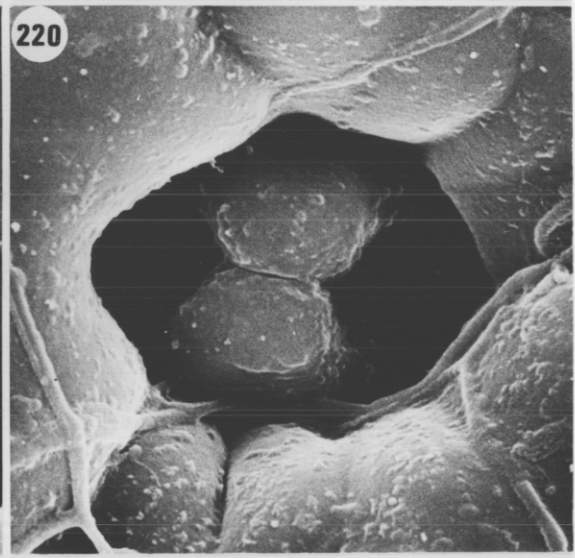
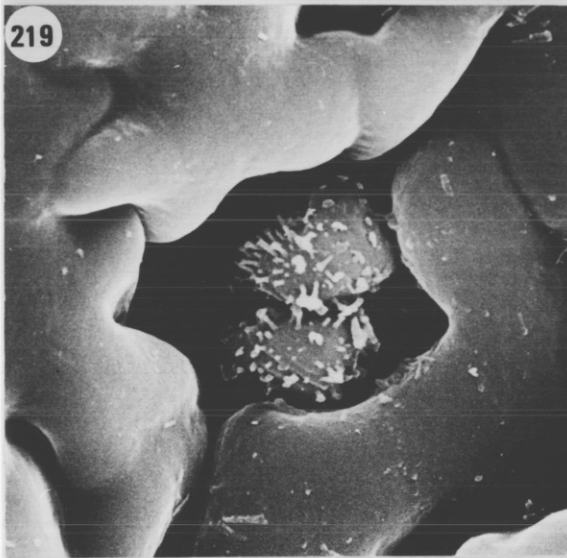
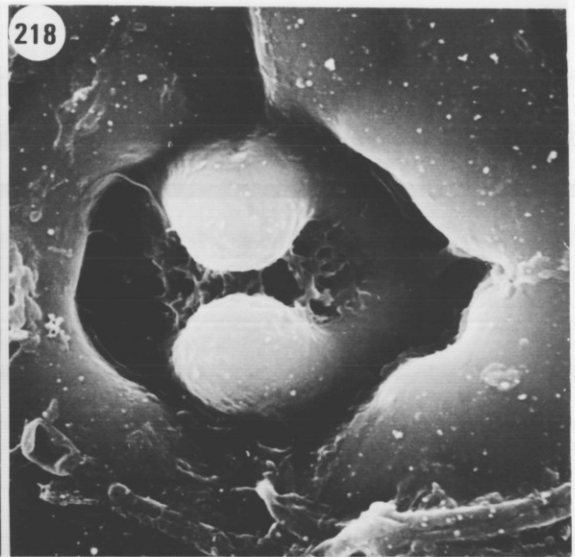
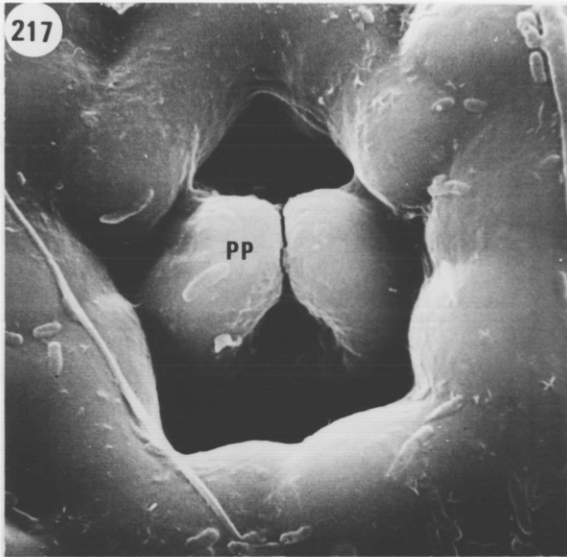
211. Specimen 1. Note high frequency of simple hairs, represented here by bases (HB) in isolated cuticle. ca. x 265.
212. Specimen 2. Note low frequency of simple hairs (H). ca. x 250.
213. Specimen 3. Note particularly distinct concavity of intercostal anticlinal borders in this specimen compared with others. Hair frequency as specimen 1. ca. x 295.
214. Specimen 4. Hair frequency as specimens 1 and 3. ca. x 285.
215. Specimen 5. Note intermediate frequency of simple hairs. ca. x 275.
216. Specimen 6. Hair frequency as specimen 5. ca. x 275.



Intraspecific variation in *Beilschmiedia madang*

Outer surface: stomata.

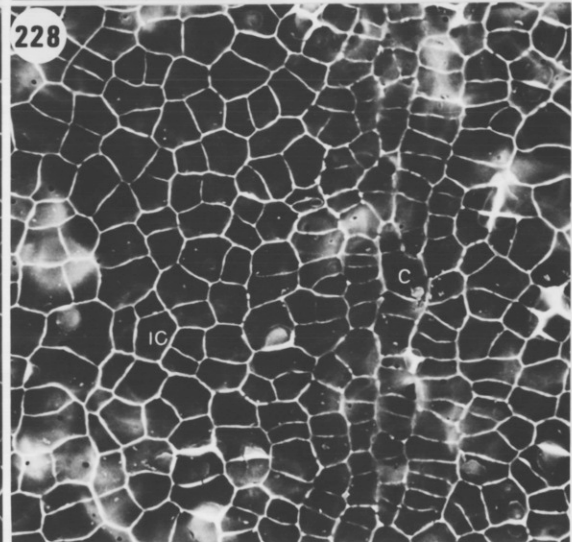
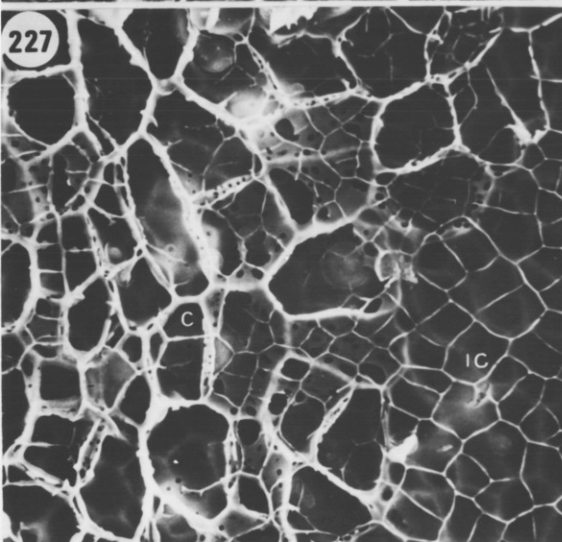
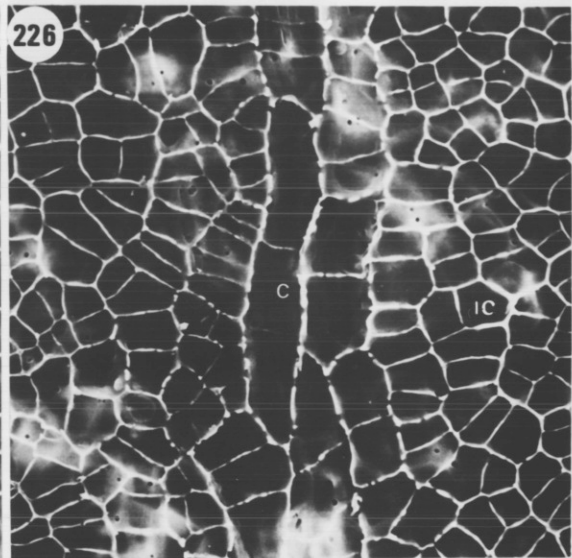
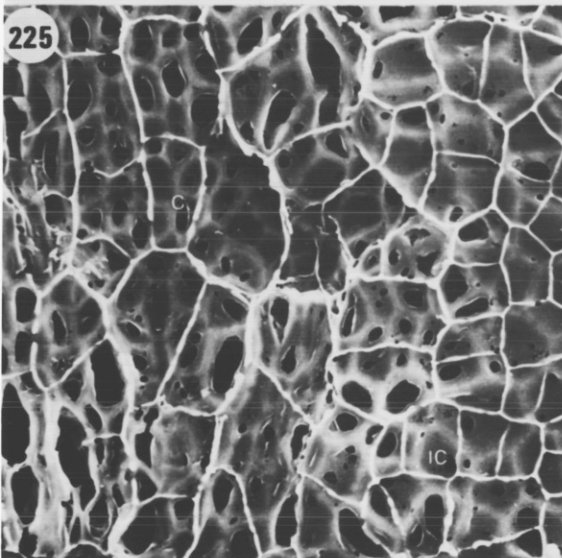
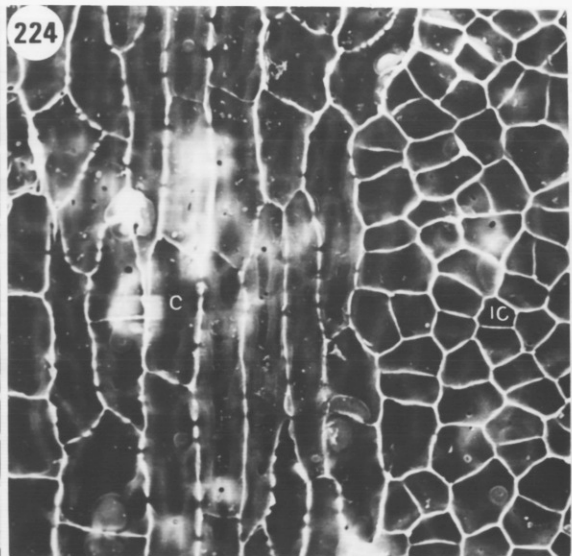
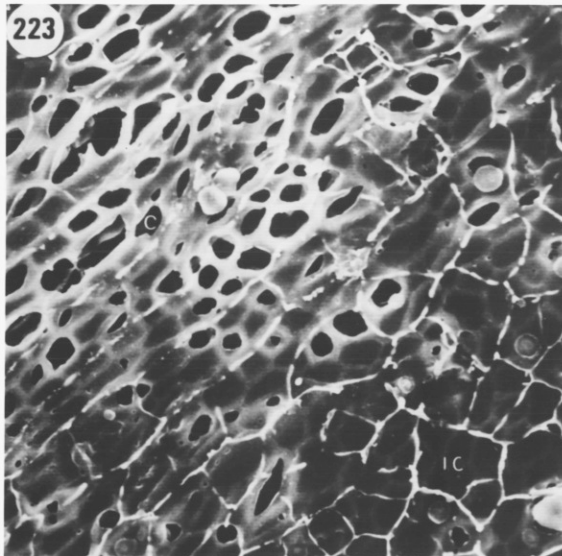
217. Specimen 1. Stoma with subsidiary cell periclinal surface prolonged into lobes, two of which are fused at each of the stomatal poles to form a papilla. Polar papillae with very little wax. ca. x 2000.
218. Specimen 2. Wax on polar papillae, scattered, finely granular. ca. x 2010.
219. Specimen 3. Note smaller stomatal size than in other specimens. Also different wax form [rodlets] associated with polar papillae. ca. x 2215.
220. Specimen 4. Wax similar to specimen 2 [Fig. 218], larger. ca. x 2250.
221. Specimen 5. Wax on polar papillae in form of flakes. ca. x 2140.
222. Specimen 6. Wax similar to specimen 5 [Fig. 221], more prominent and abundant. ca. x 2120.



Intraspecific variation in *Beilschmiedia madang*

Inner surface of isolated cuticles: adaxial.

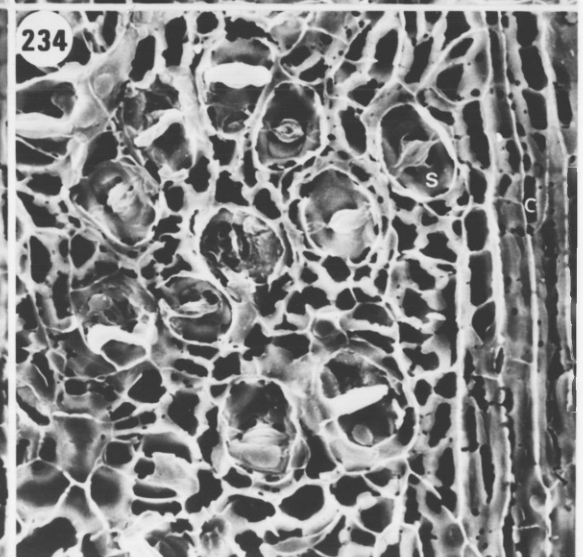
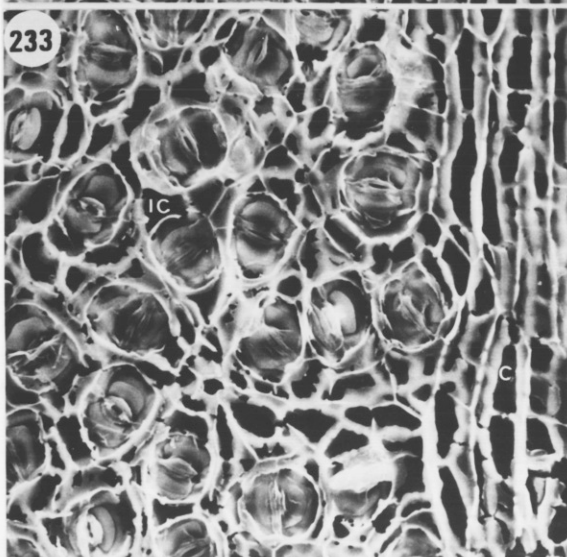
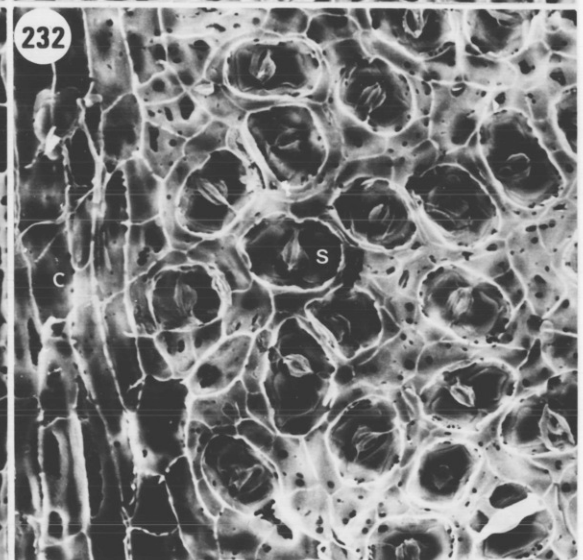
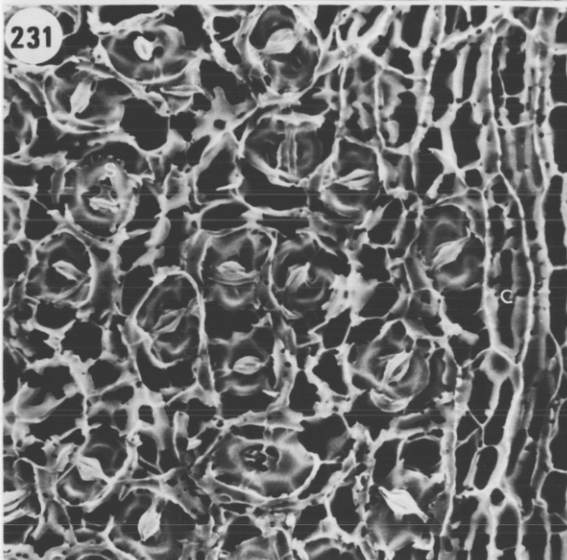
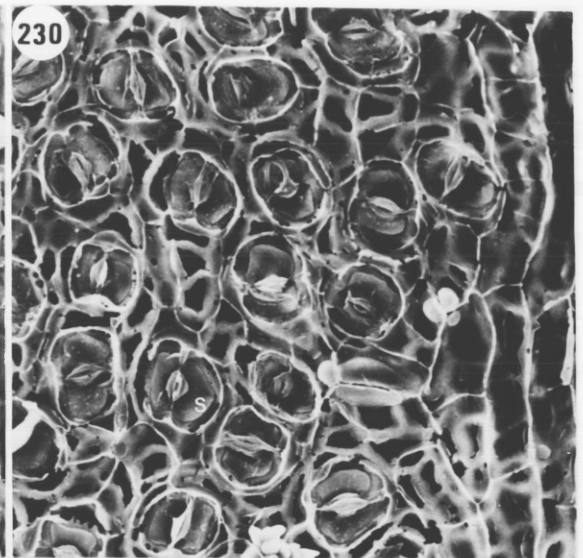
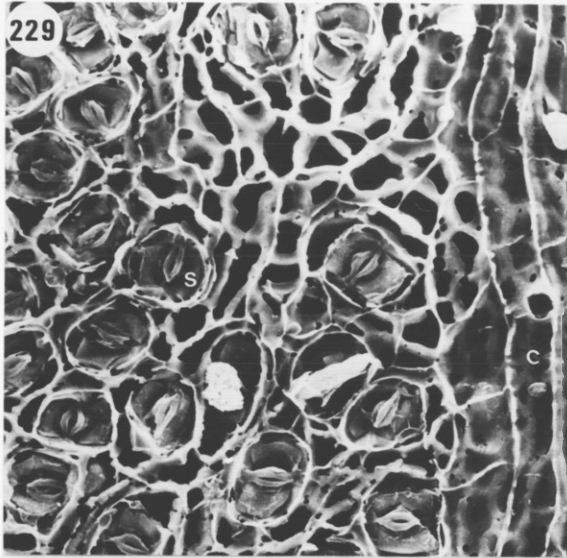
223. Specimen 1. Inner periclinal wall partially cutinised, particularly in costal region [c]. ca. x 255.
224. Specimen 2. Cutinisation extending over entire inner periclinal wall, perforated by 1-2 small round holes [pores] in all regions. ca. x 265.
225. Specimen 3. As specimen 1 [Fig. 223]. Less cutinised in intercostal region [i.c.]. ca. x 260.
226. Specimen 4. As specimen 2 [Fig. 224]. ca. x 250.
227. Specimen 5. Cutinisation deeper than other specimens some extending well into hypodermis particularly in the anticlinal plane. ca. x 275.
228. Specimen 6. As specimens 2 and 4. ca. x 270.



Intraspecific variation in *Beilschmiedia madang*

Inner surface of isolated cuticles: abaxial.

229. Specimen 1. Cutinisation extending over entire periclinal wall, perforated, in costal regions; confined to cell edges in intercostal. Stomata [S] also deeply cutinised. ca. x 275.
230. Specimen 2. As specimen 1 [Fig. 229]. ca. x 270.
231. Specimen 3. Inner periclinal cutinisation confined to cell edges ['borders']. Note frilly appearance of borders due to frequent occurrence of pores. ca. x 275.
232. Specimen 4. Costal and intercostal inner periclinal wall almost entirely cutinised, perforated. ca. x 270.
233. Specimen 5. As specimen 3 [Fig. 231]. ca. x 275.
234. Specimen 6. As specimens 3 and 5. Costal cells [c] with more inner periclinal cutinisation. ca. x 265.



cutinised except for varying numbers of holes [1-9 per cell], [1] [4] and [6] to a slightly lesser degree, with [3] and [5] the least, cutinisation being confined to that part of the wall nearest to the epidermal flanges, resulting in 'borders'. The latter, in [3] look especially uneven or frilly due to the presence of more pores at the edge of this cutinisation than in other specimens.

In intercostal areas of the adaxial in [2], [4], [5] and [6], the entire inner periclinal wall is cutinised and perforated by small, round holes [1-2 per cell]. Sometimes in [1] and often in [3], less of this wall is cutinised so that the surface appears to have perforations of widely differing size and shape. On the abaxial, in the same region, cutinisation extends over all of the inner periclinal wall and is perforated by holes [1-9] only in [4]. Other specimens have cutinised 'borders'.

Minor intraspecific dissimilarities may be attributed to differences in the degree to which the hypodermis is marked [adx. least [1], most [5]] and in the amount of inner periclinal cutinisation of the basal cells of simple hairs [abx. most [2] & [4], either entirely perforated by a few small holes or slightly less with round or oval pores of various sizes; intermediate [1] & [5]; least [3] & [6], with pored 'borders' only].

13.3.2 CARYODAPHNOPSIS TONKINENSIS

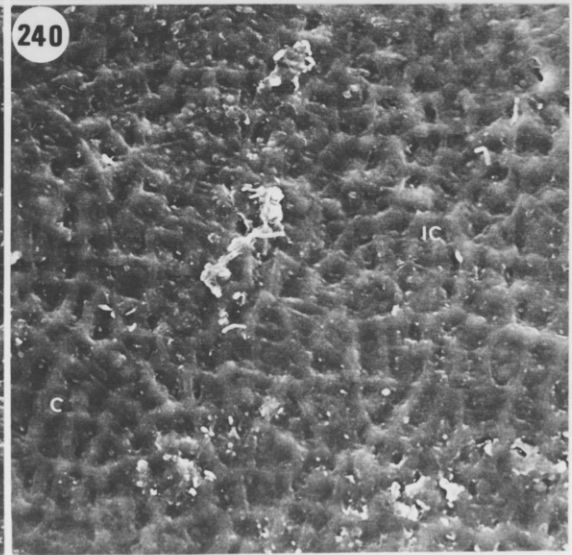
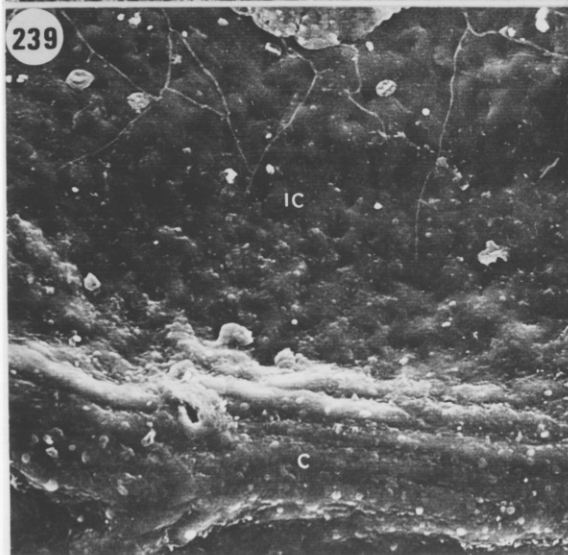
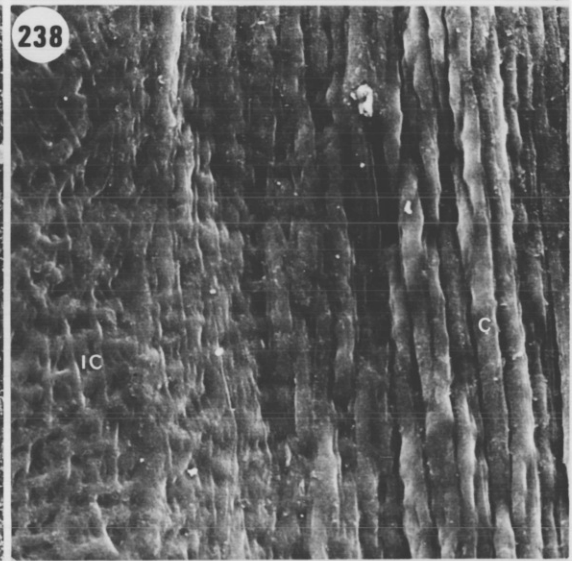
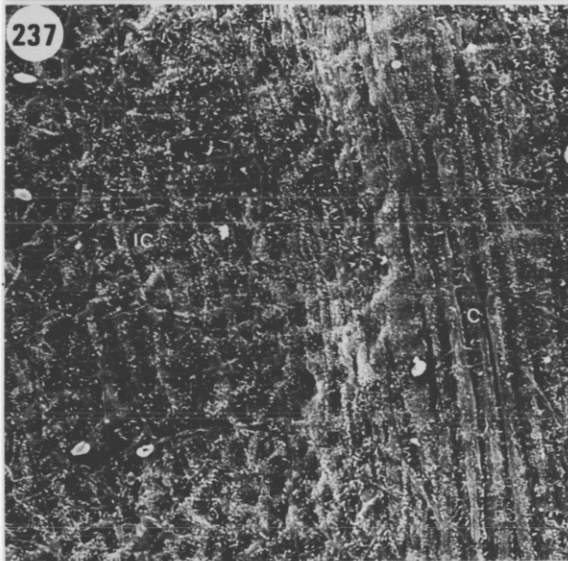
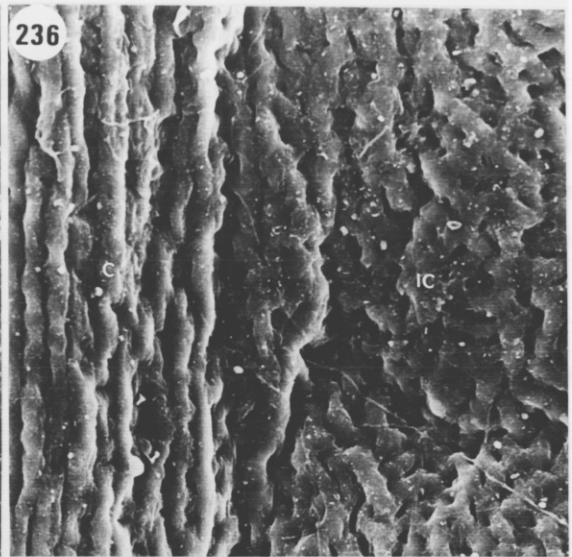
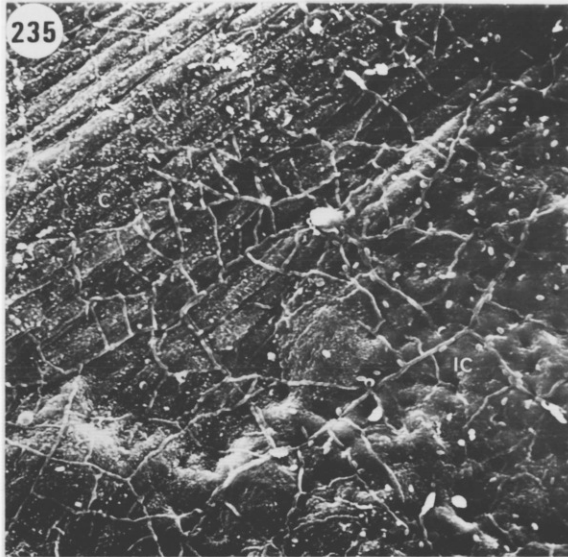
Seven different specimens [numbered 1-7] have been examined [see p. 471, 472]. However, there is much evidence, including details of leaf shape, venation as well as cuticular features, indicating that [5] has been determined incorrectly [see Figs 239, 242, 250, 253, 254, 259, 260]. Therefore, it has been disregarded in the description given here.

13.3.2a OUTER SURFACE. All specimens are very similar [Figs 235-238; 241, 243-245; 247-249, 251]. A few dissimilarities are distinguishable involving width and prominence of anticlinal borders [greater in [2]]:

Intraspecific variation in *Caryodaphnopsis tonkinensis*

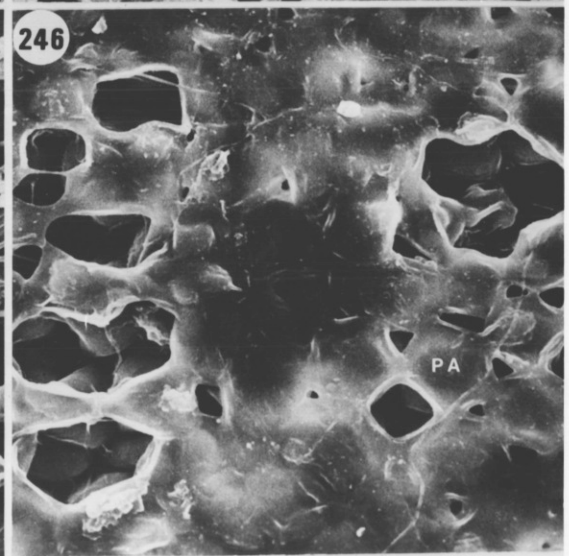
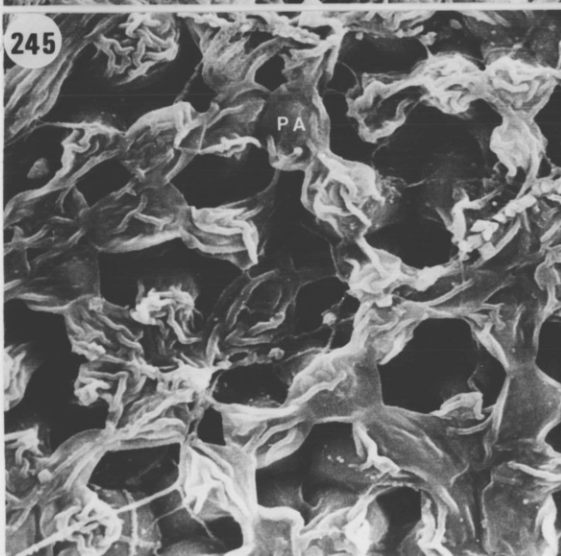
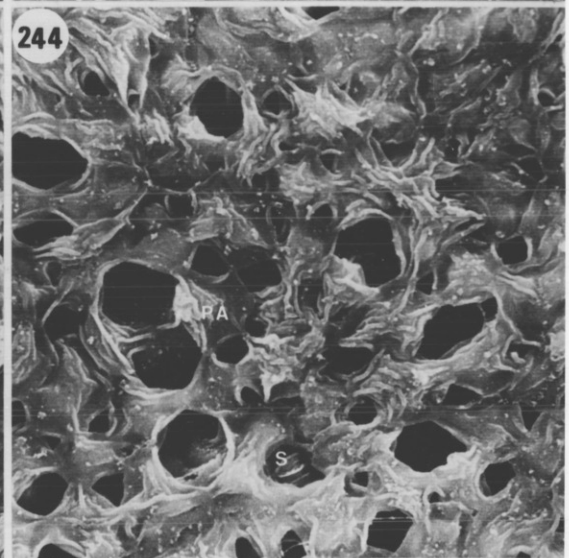
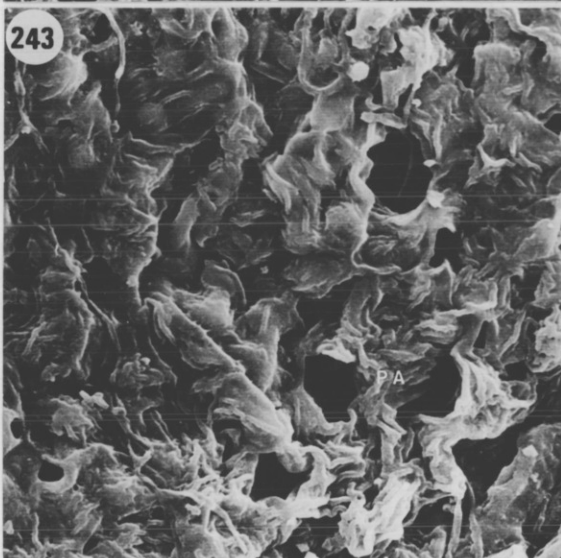
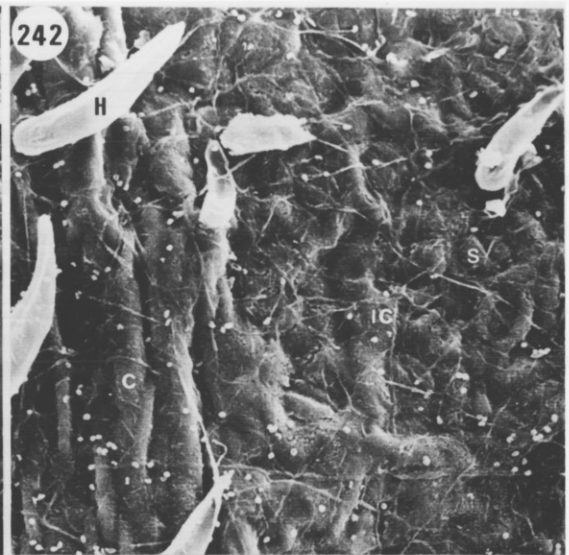
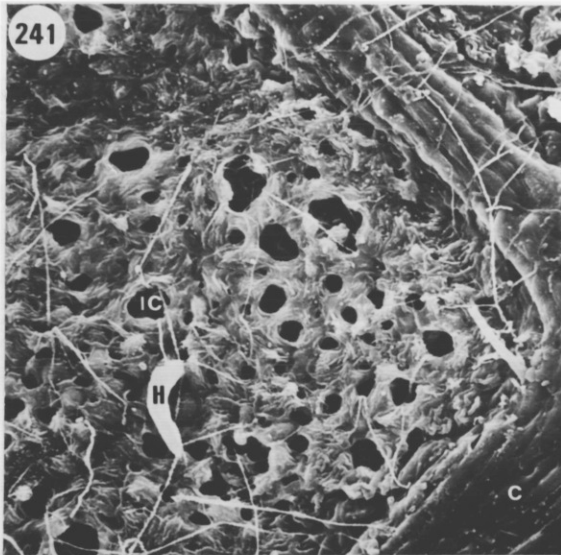
Outer surface: adaxial intercostal [i.c.] and costal [c] areas.

235. Specimen 1. With wax and dense network of fungal hyphae [anastomosing threads]. ca. x 265.
236. Specimen 2. Note especially prominent and wide anticlinal borders. ca. x 270.
237. Specimen 3. Note dense covering of wax [small flakes]. ca. x 270.
238. Specimen 4. Very little wax. ca. x 275.
239. Specimen 5.
Unknown taxon. Appearance of surface basically similar to that of *Caryodaphnopsis* specimens. ca. x 270.
240. *Caryodaphnopsis baviensis*
For comparison. Very like *C. tonkinensis*. ca. x 265.



Intraspecific variation in *Caryodaphnopsis tonkinensis*

- 241, 242. Outer surface: abaxial intercostal (i.c.) and costal (c).
241. Specimen 1. Papillate cells only in region of major vein (c). ca. x 255.
242. Specimen 5. Unknown taxon. Non-papillate in all areas. Stomata level with epidermis. Surface extensively encrusted with wax. Clearly unlike *Caryodaphnopsis*. ca. x 265.
- 243-246. Outer surface: abaxial intercostal.
243. Specimen 2. Note high degree of fusion of papillae apices (PA) as in specimen 1 (Fig. 241). ca. x 540.
244. Specimen 3. Showing papillae with intermediate state of apical fusion. [Compare with Figs. 243 and 245]. ca. x 540.
245. Specimen 4. Papillae apices with least fusion. ca. x 560.
246. *Caryodaphnopsis baviensis*
For comparison. Less striate. Papillae fused to a high degree at apices. Like *C. tonkinensis*. ca. x 555.



Intraspecific variation in *Caryodaphnopsis tonkinensis*

Outer surface: stomata.

247. Specimen 2. ca. x 2135.

248. Specimen 3. ca. x 2150.

249. Specimen 4. ca. x 2140.

251. Specimen 7. ca. x 2205.

Guard cell cuticle [including narrow outer ledge] visible around aperture. Subsidiary cell outer periclinal cuticle with lateral striae, domed. Especially clear in Fig. 248. Stoma sunken below level of epidermis in pit which may be partially covered [roofed] by fused apices [PA] of surrounding papillate cells [Figs. 247, 249, 251]. Little wax.

250. Specimen 5.

Unknown taxon.

Guard cell cuticle not exposed. Overlapped by conspicuously domed subsidiary cell [SC] outer periclinal wall. Abundant wax. Dissimilar to stoma of *Caryodaphnopsis*. ca. x 2150.

252. *Caryodaphnopsis baviensis*

For comparison. Very similar to *C. tonkinensis*.

Outer ledge more prominent. Subsidiary cell dome located less centrally, nearer to guard cell cutinised parts. ca. x 2130.

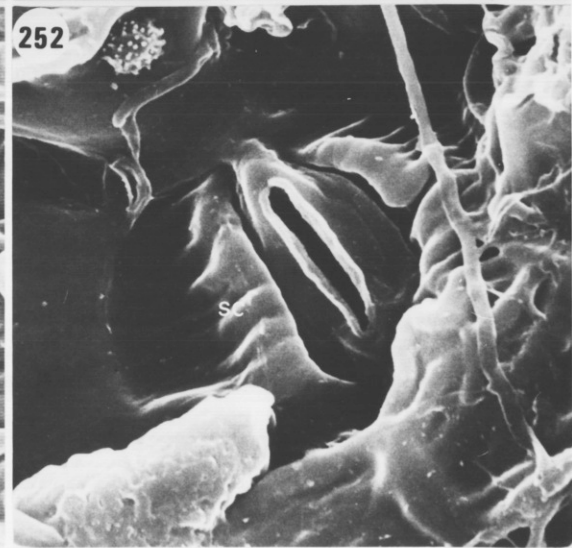
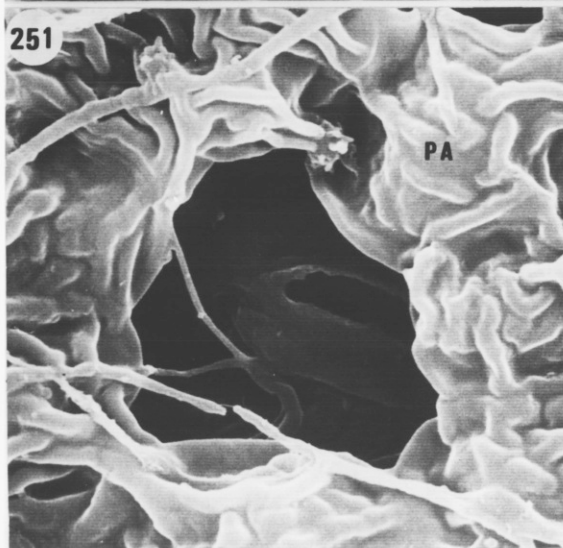
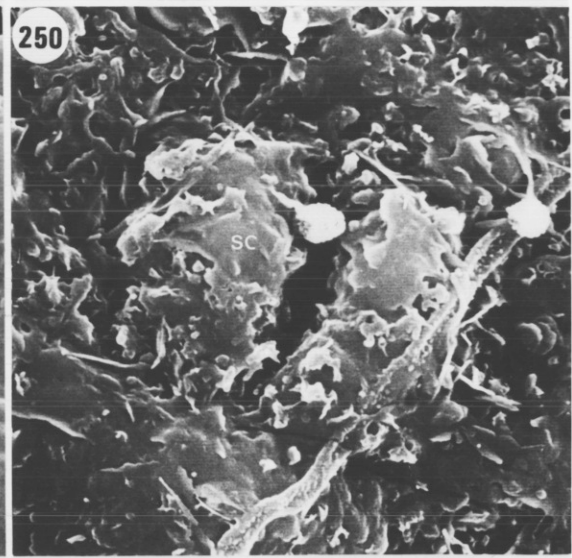
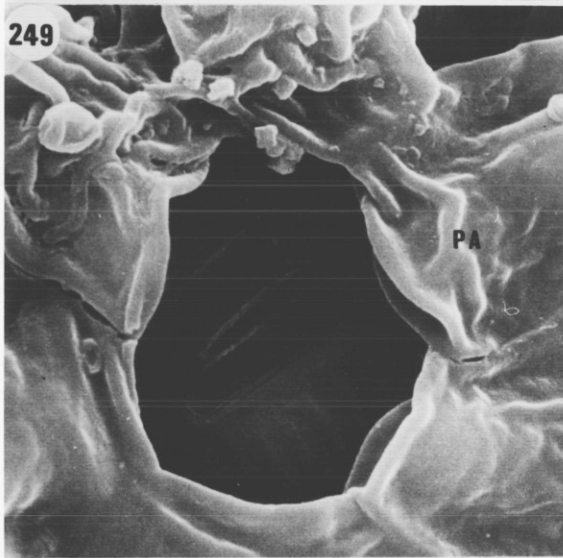
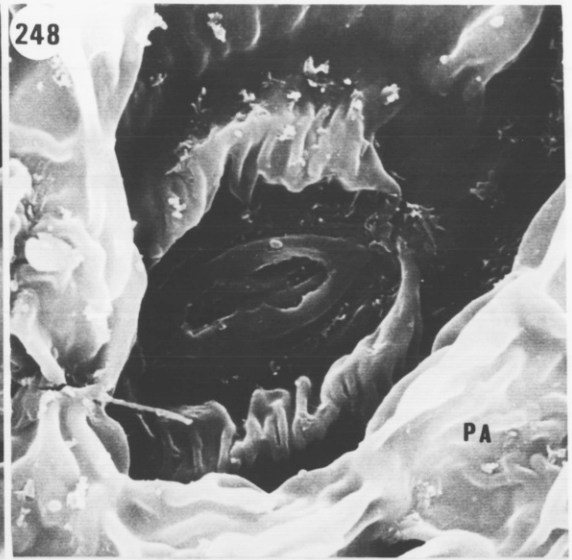
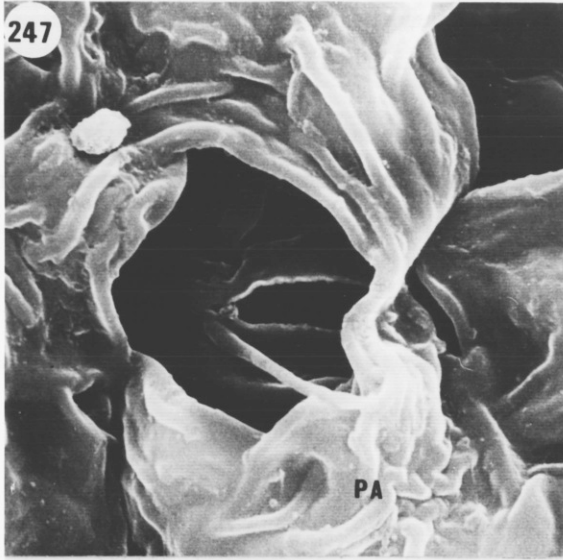


Fig. 236) on the adaxial and definition as well as fusion of papillae [most (1): Fig. 241 and (2): Fig. 243; intermediate (3): Fig. 244, (6) and (7); least (4): Fig. 245] on the abaxial.

13.3.2b INNER SURFACE. Adaxial [Figs 255-258] and abaxial [Figs 261-264] cuticles of all specimens are almost identical. Despite this basic similarity, some variation is observed. This involves features of individual cells, their flanges, periclinal sculpture, striae, stomata and hairs.

Cells vary in size on the adaxial; those of (6) are slightly smaller [Fig. 255] and intercostal cells of (7) slightly larger than in the other specimens [Fig. 257]. There may also be a difference in the periclinal concavity of cells [adx. c. (6) more than others]. Flange shape differs, on the adaxial: flanges of (1) are straight to curved occasionally U-undulate over veins, those of (2), (3), (4), (6) and (7) are predominantly straight. The degree of flange margin irregularity tends to vary between specimens, particularly on the adaxial and differences are variable over and between veins [adx. i.c. least irregular (1), (2), (6) and (7), most (3) and (4); c. least (1), (3), (6) and (7), intermediate (4), most (2); abx. c. least (1), (2), (3), (4) and (7), most (6)]. On the adaxial, the frequency of flange interruptions is somewhat dissimilar, being lowest in (1) and (6), intermediate in (4) and (7), and highest in specimens (2) and (3). Periclinal protrusions exhibit size differences in costal regions on the abaxial surface [minor veins fine (1), (2) and (3), more coarse (4), (6) and (7); major veins especially fine in (6)]. Protrusions also show variable prominence [those of (6): Fig. 256, are shallow or indistinct in all areas of the adaxial compared with others e.g. (7): Fig. 258 [distinct]]; (4) has more rounded protrusions over veins.

Depressions [scrobiculi] corresponding to the external papillae differ in diameter i.e. the proportion of the cell occupied [i.c. least (1) and (6): Fig. 264, most

Intraspecific variation in *Caryodaphnopsis tonkinensis*

Inner surface of isolated cuticles: adaxial.

253. Specimen 5.

Unknown taxon. Intercostal [i.c.] and costal [c] areas. Low power cells conspicuously U-undulate with highly jagged flanges, unlike *Caryodaphnopsis*. ca. x 280.

254. Specimen 5.

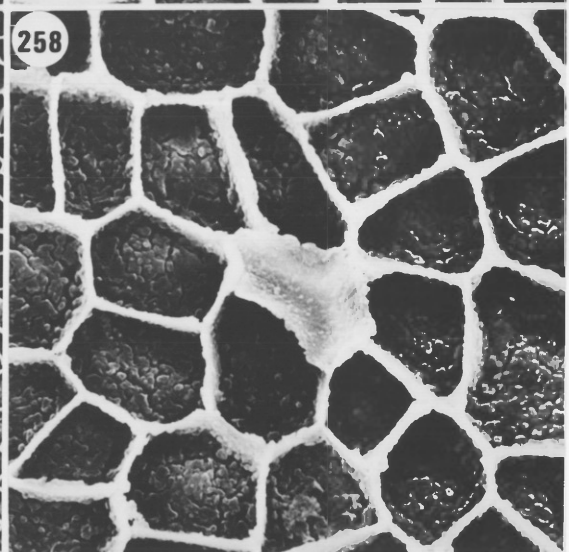
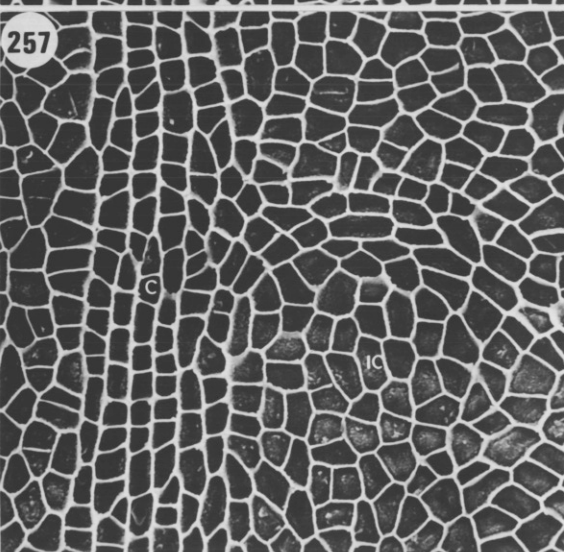
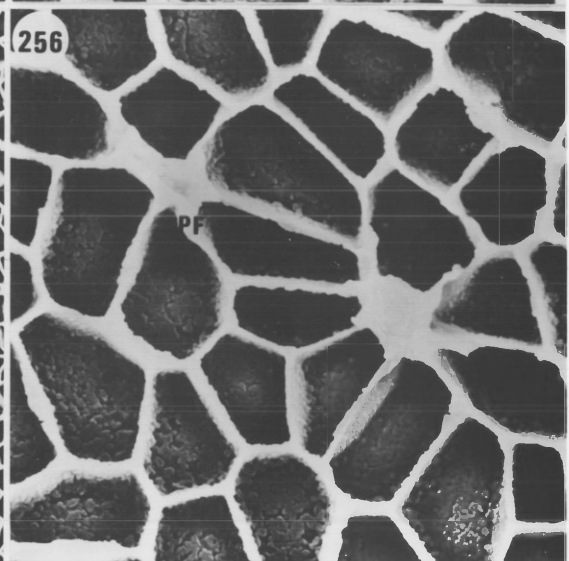
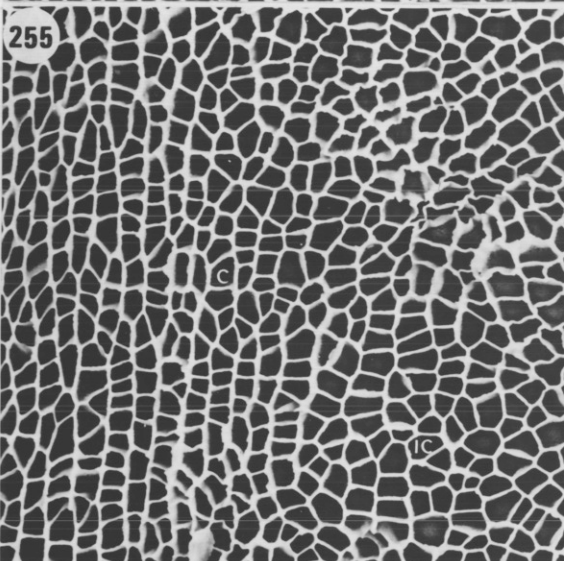
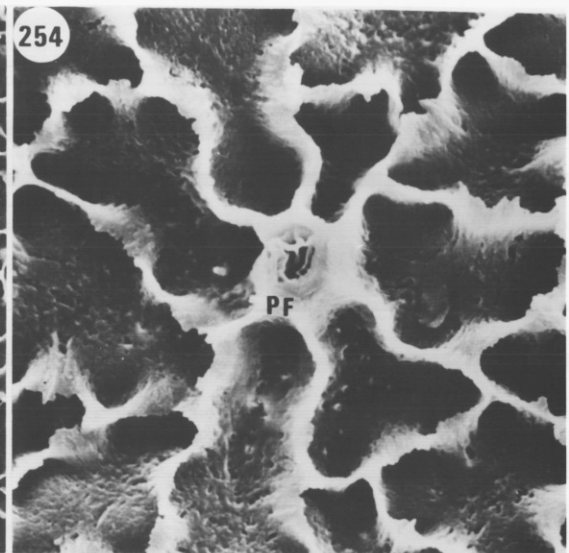
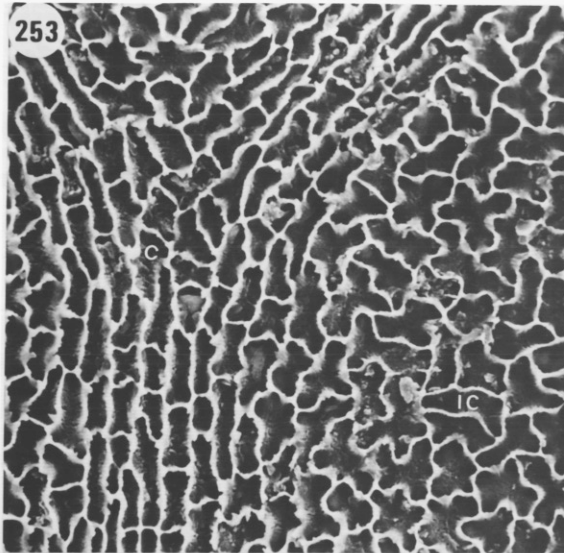
Unknown taxon. Fine details of simple hair base [i.c.]. Arrangement as in *Caryodaphnopsis*. However, basal cell flanges U-undulate with cavities, jagged, periclinal surface with fine reticulum of filamentous protrusions and pit-like to clumped depressions. ca. x 1060.

255. Specimen 6. As fig. 253. Flanges predominantly straight with few irregularities. Note slightly smaller size of cells compared with Specimen 7, [Fig. 257]. ca. x 275.

256. Specimen 6. As Fig. 254. Periclinal protrusions moderate, shallow or indistinct, reticulate with fine clumped to reticulate depressions. Note deep poral cutinisation [PF] of hair base. ca. x 1060.

257. Specimen 7. As Fig. 253. Larger cells than in Specimen 6 [Fig. 255]. ca. x 275.

258. Specimen 7. As Fig. 254. Periclinal protrusions distinct. Poral cutinisation of hair base shallow compared with that in specimen 6 [Fig. 256]. ca. x 1065.



Intraspecific variation in *Caryodaphnopsis tonkinensis*

Inner surface of isolated cuticles: abaxial.

259. Specimen 5.

Unknown taxon. Intercostal [i.c.] and costal [c] areas. Low power. Note conspicuously interrupted, jagged flanges of low prominence [i.c. and c]. Subsidiary cells non-striate; 'wings' sometimes present, obtuse. ca. x 275.

260. Specimen 5.

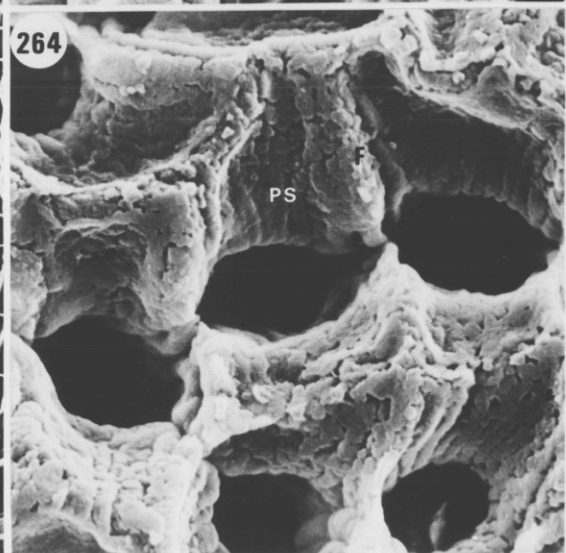
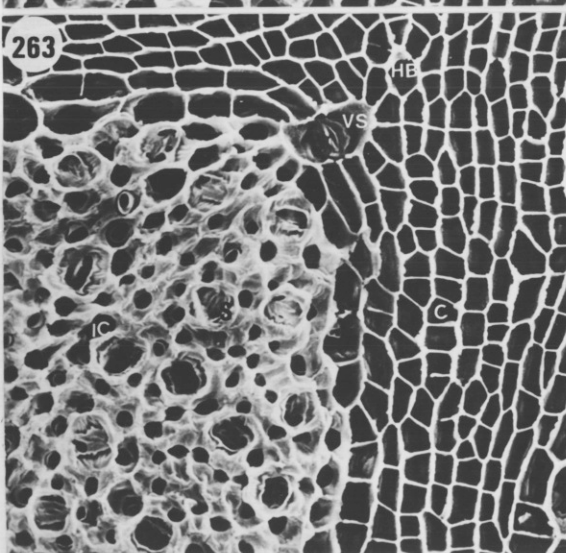
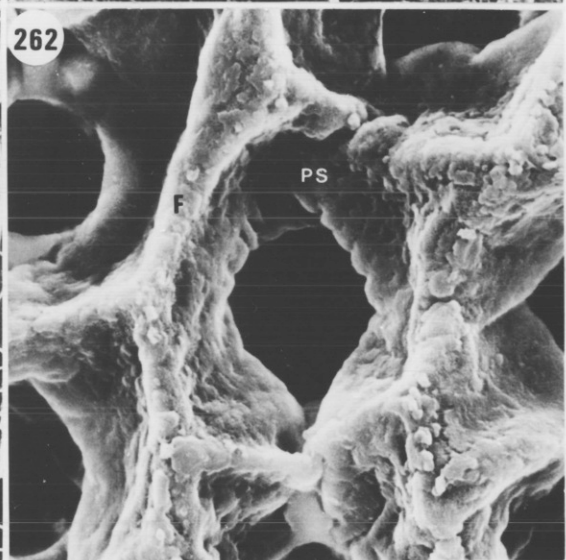
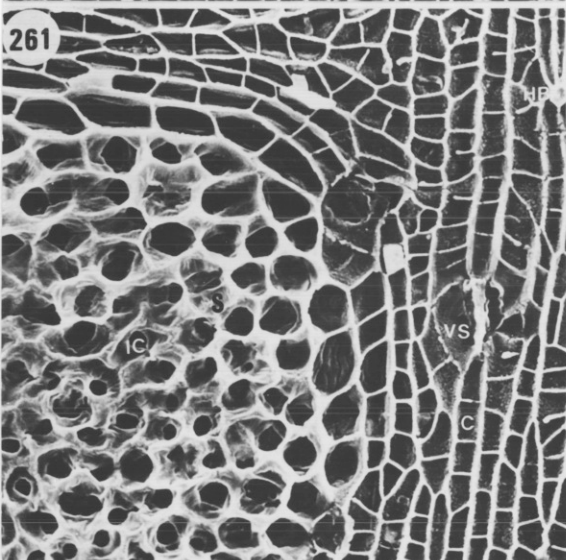
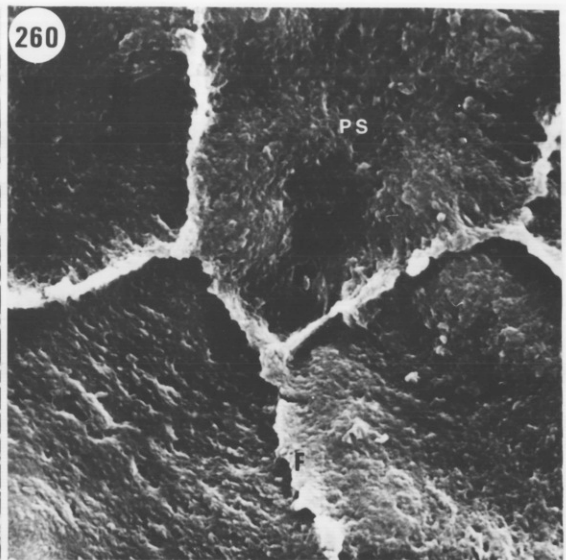
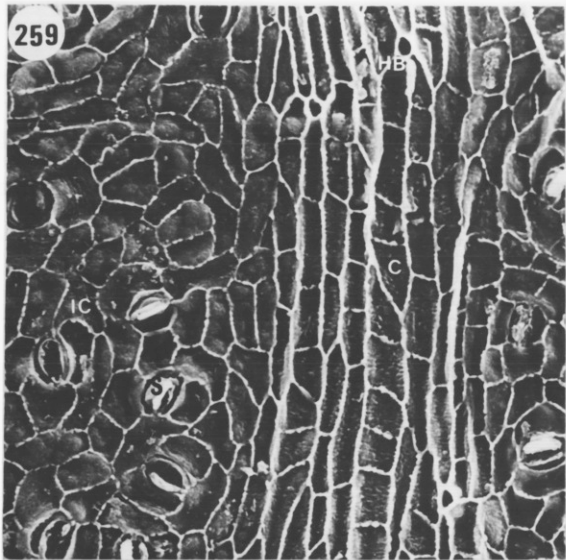
Unknown taxon. Fine details of flanges and periclinal surface in intercostal cells. No scrobiculus in periclinal region [PS], ornamentation of fine filamentous reticulate protrusions and very fine to fine pit-like to clumped depressions. Flanges interrupted, jagged. ca. x 2120.

261. Specimen 4. As Fig. 259. Showing very low intercostal flanges and moderate costal flanges with even margins. Cells scrobiculate in intercostal areas only. Subsidiary cell cuticle with lateral striae. 'Wings' removed by maceration. Note presence of enlarged vein stoma [VS]. ca. x 275.

262. Specimen 4. As Fig. 260. Conspicuous scrobiculus in periclinal region [PS] of cell. Flanges very low with sculpture of fine to moderately coarse clumped or reticulate protrusions. Periclinal surface of fine granules. ca. x 2125.

263. Specimen 6. As Fig. 259. Similar to specimen 4 [Fig. 261]. ca. x 270.

264. Specimen 6. As Fig. 260. Note scrobiculus occupies less of cell than in specimen 4 [Fig. 262]. Inner surface [PS] with prominent striae. ca. x 2140.



[2], [3], [4]: Fig. 262 and [7]; c. least [1], [4], [6] and [7]; most [2] and [3]] on the abaxial. Striae exhibit dissimilarities in shape on minor veins (more convolute and irregular [3]; longitudinal, straight in others) and prominence in between veins [greater in [6]: Fig. 264]. Stomata tend to vary in size [larger [2] and [7], up to 1½ times those of e.g. [1] and [4]]. Differences are also evident in aspects of the subsidiary cells: texture of the periclinal ornamentation [smooth [1], [3] and [4], granular [2], [6] and [7]] and definition of internal lateral striae [indistinct [1], slightly prominent [3], moderate prominence [4], most prominent [6] and [7]].

Certain features of hairs and the cells associated with them are variable: on the adaxial, the degree of poral cutinisation [least deep [4], deep [2], [3] and [7]: Fig. 258, most deep [1] and [6]: Fig. 256]; on the abaxial, basal cell shape [longer than broad [1], [3] and [4], more polygonal [2], [6] and [7]], periclinal concavity [less in [3]], prominence of basal cell striae [more prominent in [3], especially so in [6]] and scrobiculi [less concave: [3], moderate: [4] and [7], very concave: [1], [2] and [6]], as well as the development of the scrobiculi around the bases [less prominent in [3]].

13.3.3 DEHAASIA CUNEATA

Five different specimens (numbered 1-5) have been examined [see p. 472, 473].

13.3.3a OUTER SURFACE. The abaxial surface again, shows a high level of similarity, except in aspects of papillae [Figs 271-276]: size [smaller in [4]], shape [oval [4], round all others] and prominence [less in [4]], wax: form [flakes [1], flakes and needles [2] and [3], needles [4] and [5]], size [finest [4], intermediate [3] and [5], coarsest [1] and [2]] and density [least [3], intermediate [1] and [2], most [4] and [5]] and hairs: frequency [lowest [5], intermediate [1] and [3], highest [2] and [4]]. The adaxial surface appears rather different in all specimens [Figs 265-270]. Various factors contribute to such dissimilarity including differences in periclinal

Intraspecific variation in *Dehaasia cuneata*

Outer surface: adaxial intercostal [i.c.] and costal [c] areas.

265. Specimen 1.

Periclinal surface concave. Anticlinal borders raised. Striae inconspicuous. Simple hairs rare. ca. x 265.

266. Specimen 1.

Isolated cuticle. Showing more clearly concavity of cells and raised anticlinal borders. ca. x 260.

267. Specimen 2.

Periclinal surface convex. Anticlinal borders slightly sunken. Surface with fine low striae. Simple hair frequency as in specimen 1 [Fig. 265]. ca. x 275.

268. Specimen 3.

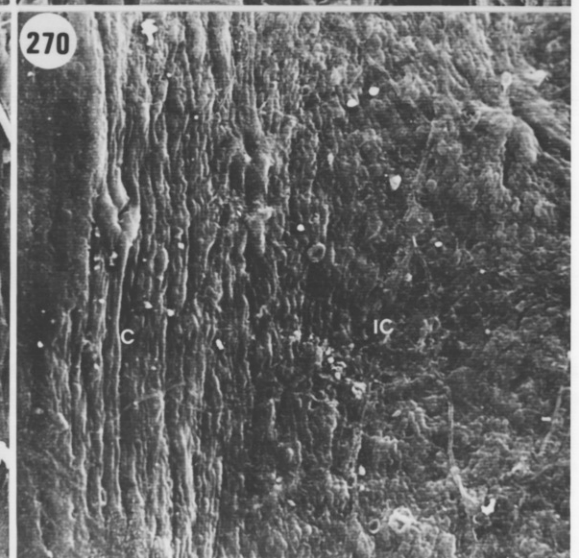
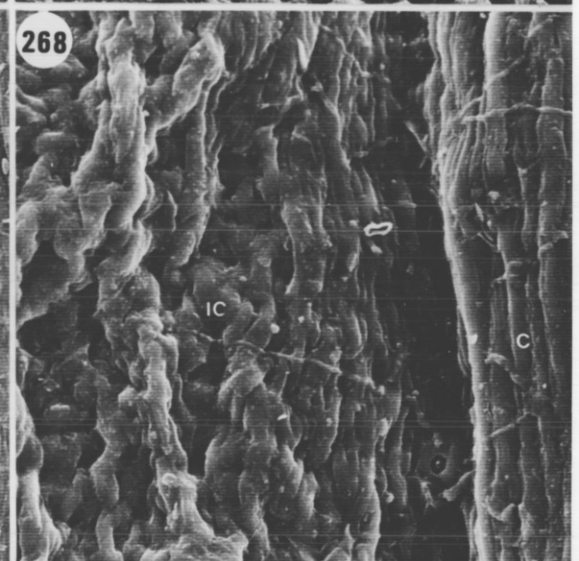
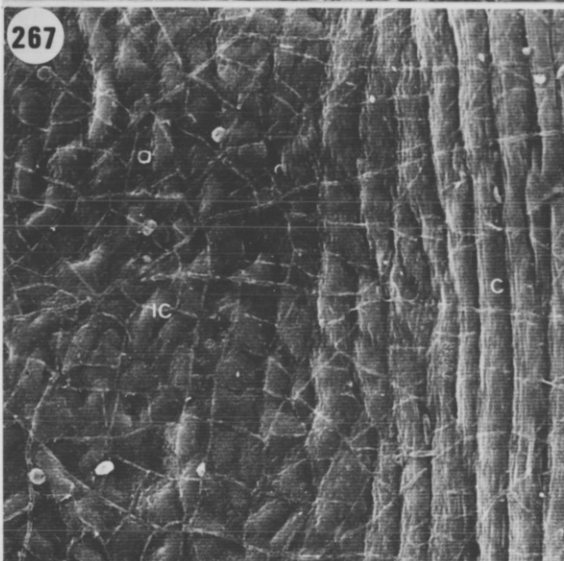
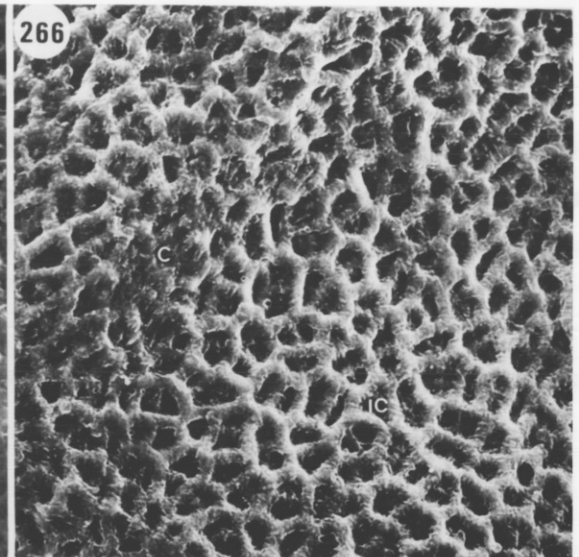
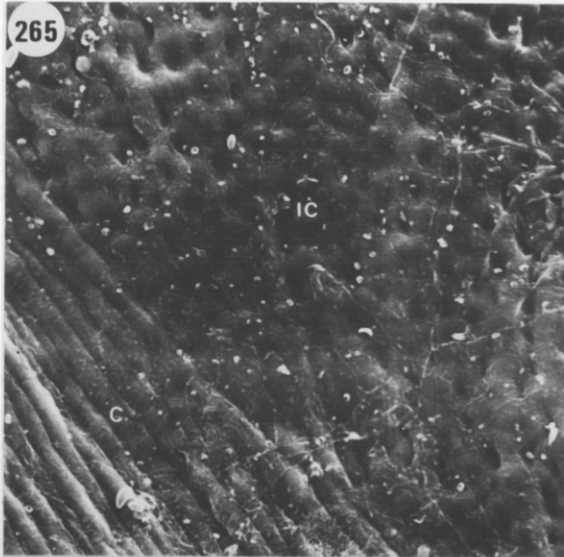
As specimen 2 [Fig. 267] but anticlinal borders more deeply sunken. Surface coarsely wrinkled. Simple hair frequency as in specimen 1. ca. x 285.

269. Specimen 4.

Periclinal surface almost flat. Anticlinal borders slightly sunken. Striae inconspicuous. Simple hairs abundant. ca. x 280.

270. Specimen 5.

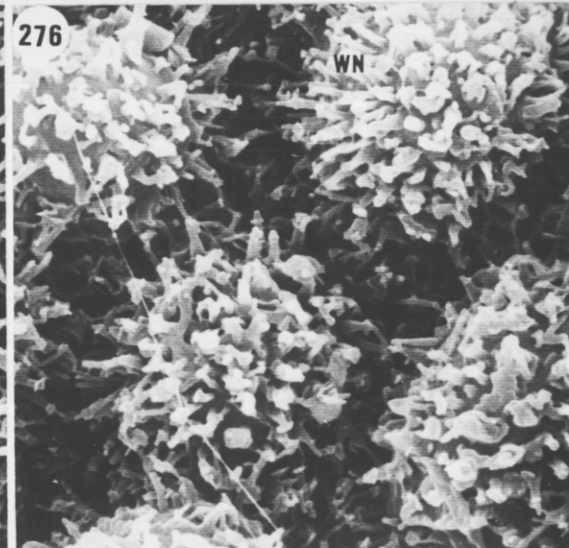
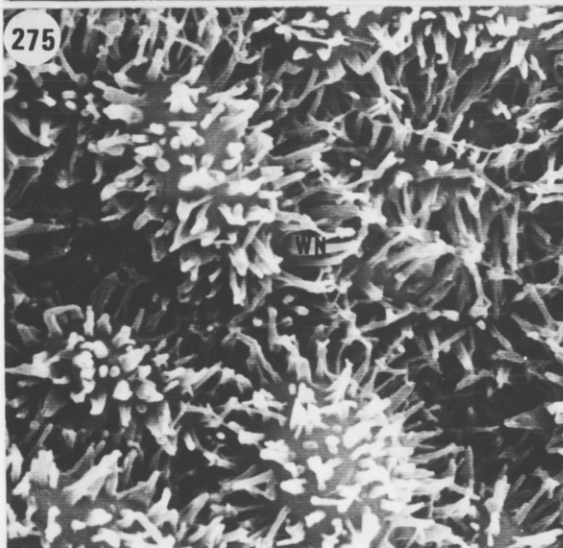
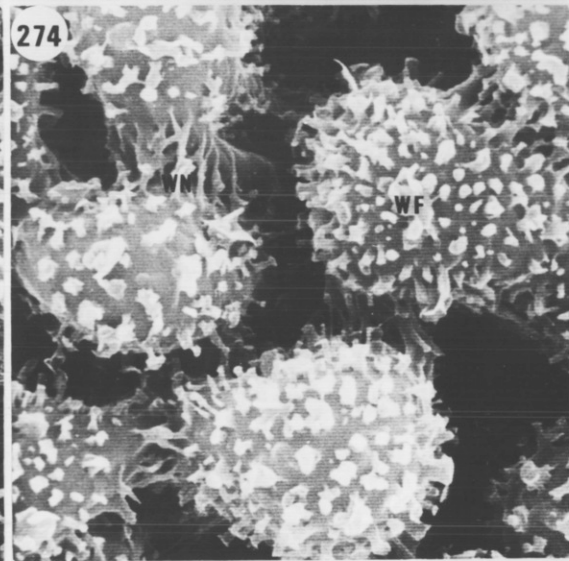
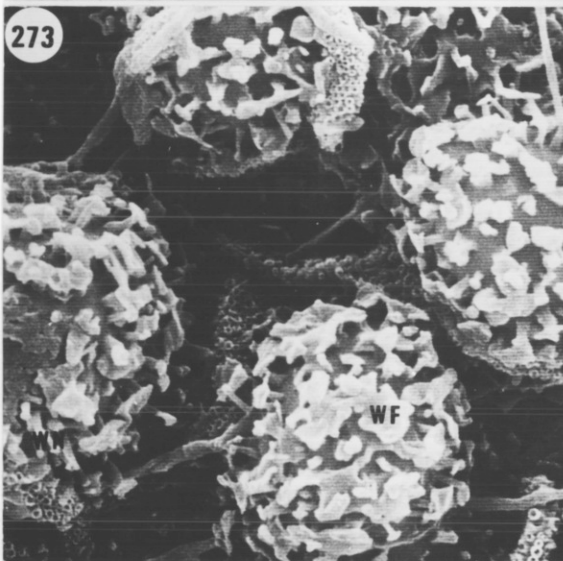
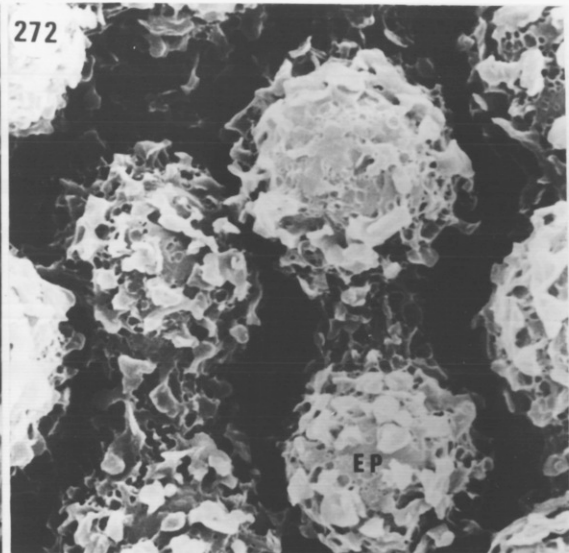
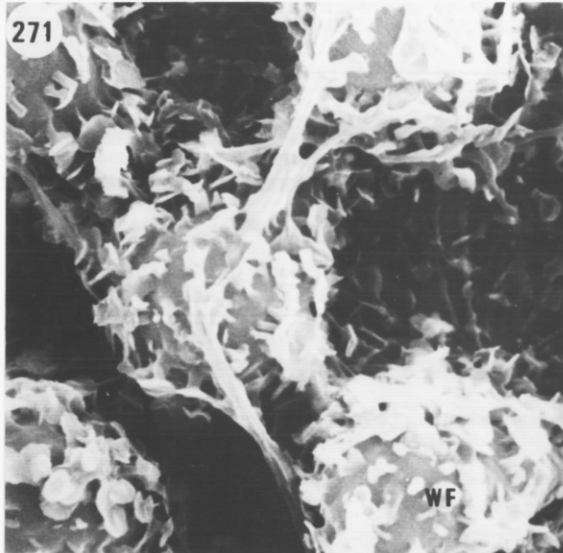
Periclinal surface convex. Anticlinal borders slightly sunken. Surface with fine, prominent striae. Simple hair frequency as in specimen 1. ca. x 280.



Intraspecific variation in *Dehaasia cuneata*

Outer surface: papillae of abaxial.

271. Specimen 1. Papillae round, globular with covering of coarse wax flakes [WF]. ca. x 2065.
272. Specimen 1.
Isolated cuticle. Note that much wax is insoluble. Also de-waxing causes wax to change slightly in form and produces a bubbled appearance. ca. x 2045.
273. Specimen 2. Papillae as in Fig. 271 but with covering of wax flakes [WF] and a few needle-like rodlets [WN] which project outward from the papillae. ca. x 2215.
274. Specimen 3. Similar to specimen 2 [Fig. 273] but with finer flakes and more abundant needle-form rodlets. ca. x 2120.
275. Specimen 4. Papillae oval, globular with dense covering entirely of wax needles. ca. x 2220.
276. Specimen 5. Papillae as specimen 1 [Fig. 271]. Wax as specimen 4 [Fig. 275] but considerably coarser. ca. x 2195.



curvature of cells [concave (1), almost flat (4), convex (2), (3) and (5)], anticlinal border configuration [raised (1), slightly sunken (2), (4) and (5), conspicuously sunken (3)], size and prominence of striae or wrinkles [inconspicuous (1) and (4); fine, low (2); fine, prominent (5); coarse, prominent (3)] and frequency of simple hairs [abundant (4), rare in others].

13.3.b INNER SURFACE. Adaxial [Figs 277-282] and abaxial [Figs 283-288] cuticles are similar in most features in all specimens. There are, however, quite a wide range of characters which show intraspecific variation: aspects of whole cells, flanges, periclinal ornamentation, striae, stomata and hairs.

Cells tend to vary in size on both surfaces [adx. smallest: (1), (4): Fig. 281, and (5), intermediate: (3) Fig. 279], largest, twice the size of the smallest (2): Fig. 277; abx. smallest (3): Fig. 284, intermediate (1), (4) and (5): Figs 283, 284, 287, 288; largest, more than twice the smallest size (2)]. Adaxial periclinal curvature is noticeably different in (3) [convex: Figs 279, 280] from that of the other specimens [concave: Figs 277, 281, 282, 288]. Flanges vary slightly in prominence; on the adaxial those of (5) are predominantly deep, whereas flanges in (1), (2), (3) and (4) are moderate-deep. On the abaxial, intercostal flanges look deeper in (2) than in the others. Flange shape differs on the abaxial in intercostal areas [straight-curved, no cavities (3): Fig. 284, U-undulate at base, straight at apex, with cavities at undulation sinuses (2) and (5): Fig. 288, no cavities (4): Fig. 287; U-undulate, with cavities (1): Fig. 283]. Abaxial costal flanges are slightly different in thickness in (2) [less wide] than in other specimens.

The margin configuration of flanges varies somewhat; on the adaxial, (3) [Figs 279, 280] has more or less even flanges in contrast to other specimens [irregular, especially (2): Fig. 277, 278] and on the abaxial, major vein flanges have less prominent irregularities in (2). Aspects of flange continuity are variable: the type of

Intraspecific variation in *Dehaasia cuneata*

Inner surface of isolated cuticles: adaxial.

277. Specimen 2.

Intercostal [i.c.] and costal [c] areas. Cells large: twice size of those shown in specimen 4 [Fig. 281]. Periclinal surface concave. Flanges occasionally interrupted with 1 gap. Perforations present. ca. x 275.

278. Specimen 2.

Fine details of flanges and periclinal surface in costal region. Flanges [F] with uneven margin. Periclinal surface with very fine to fine granular protrusions and pit-like or clumped depressions. ca. x 2135.

279. Specimen 3.

As Fig. 277. Cells of intermediate size [compare with Figs. 277 and 281]. Periclinal surface convex. Flanges frequently interrupted with 1 or 2 gaps. Perforations absent. ca. x 270.

280. Specimen 3.

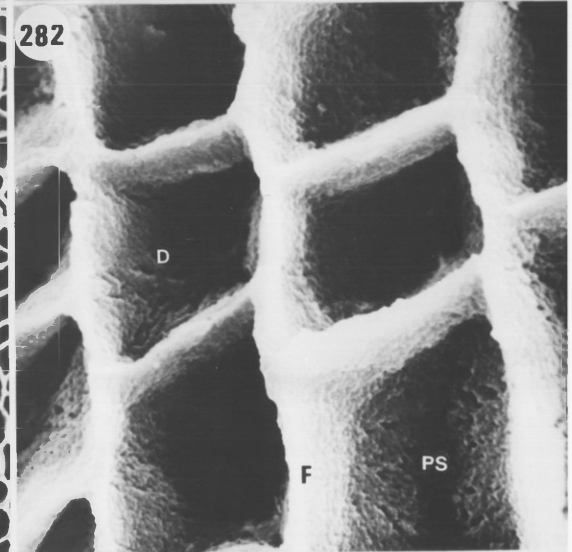
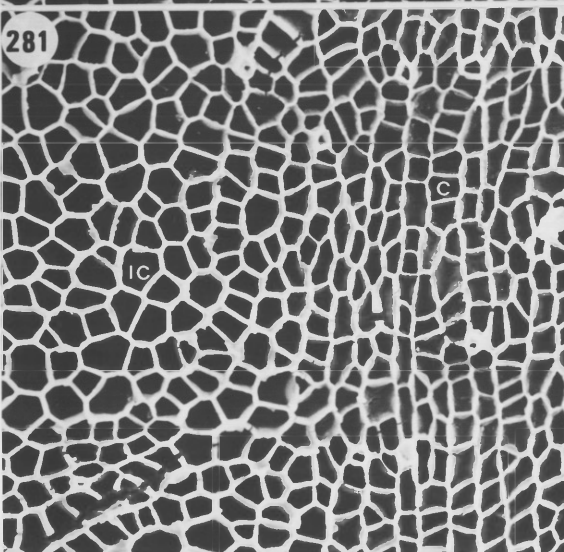
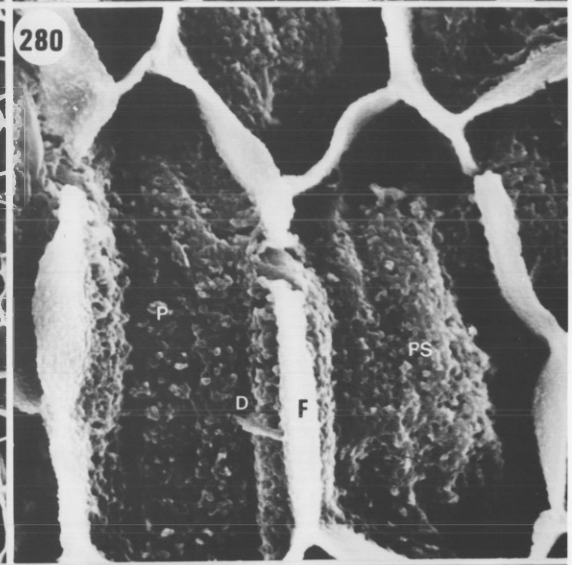
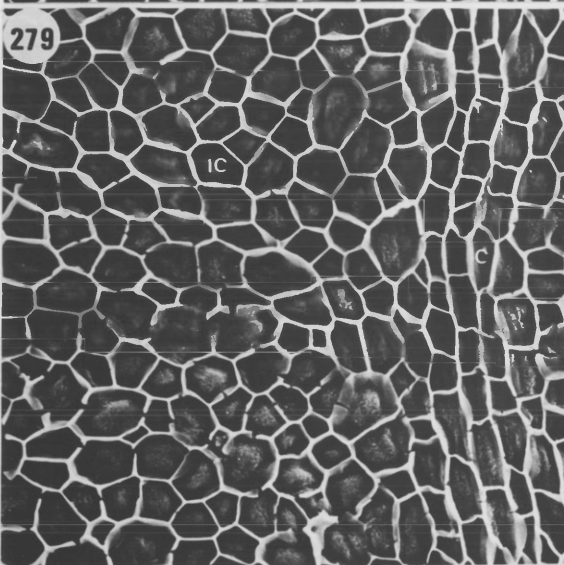
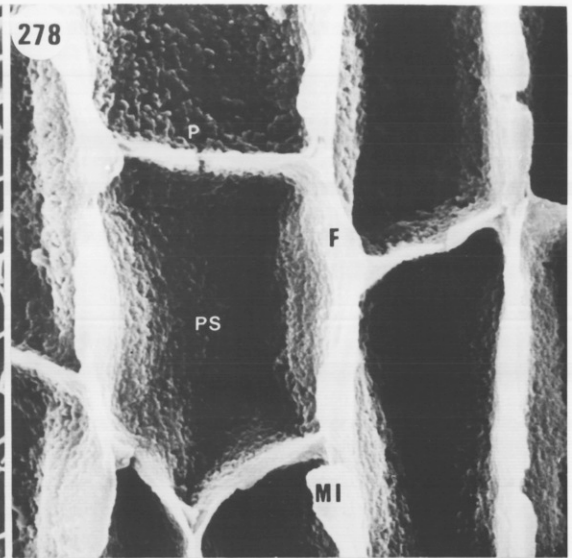
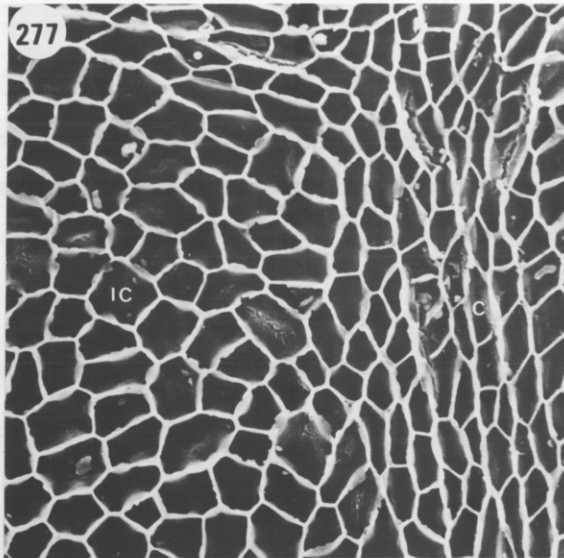
As Fig. 278. Flanges with more or less even margin and distinct interruptions. Periclinal surface [PS] with fine reticulate protrusions and pit-like or clumped depressions [D]. ca. x 2145.

281. Specimen 4.

As Fig. 277. Cells small. Periclinal surface as specimen 2. Flanges sometimes interrupted with 1 gap. Perforations present. Note frequent occurrence of hair bases compared with other specimens [see also Fig. 269]. ca. x 270.

282. Specimen 4.

As Fig. 278. Flanges with uneven margin. Periclinal surface with very fine granular protrusions and fine pit-like or clumped depressions. ca. x 2135.



268. Specimen 5.

As Fig. 283. Cell size as specimen 1. Intercostal flanges U-undulate at base, straight at apex, with cavities; occasionally interrupted with 1 gap. Scrobiculi of moderate prominence. Between $\frac{1}{2}$ and $\frac{3}{4}$ cell diameter forming scrobiculus. ca. x 285.

Intraspecific variation in *Dehaasia cuneata*

Inner surface of isolated cuticles: abaxial.

283. Specimen 1.

Intercostal [i.c.] and costal [c] areas. Cells of intermediate size. Intercostal flanges U-undulate, with cavities; sometimes interrupted by 1-2 gaps. Scrobiculi deep, especially in non-vein regions. Less than $\frac{1}{2}$ cell diameter contributing to each scrobiculus. ca. x 255.

284. Specimen 3.

As Fig. 283. Cells small. Intercostal flanges straight to curved, without cavities; sometimes interrupted, as specimen 1. Scrobiculi deep. Most of cell forming scrobiculus. ca. x 270.

285. Specimen 5.

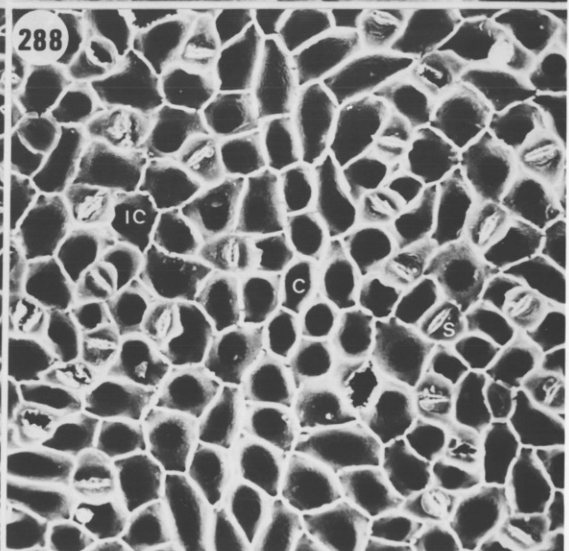
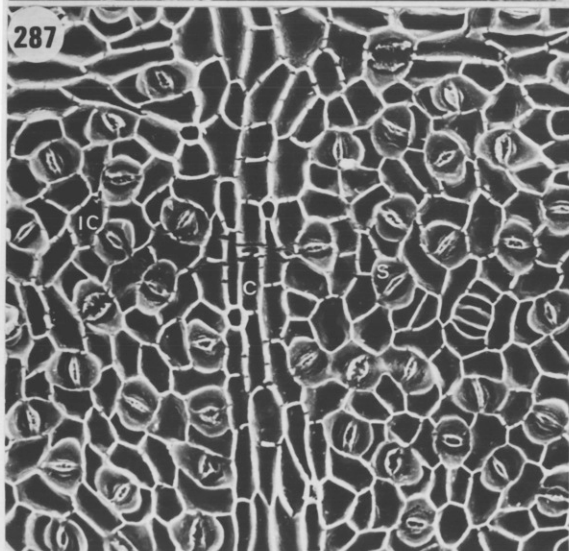
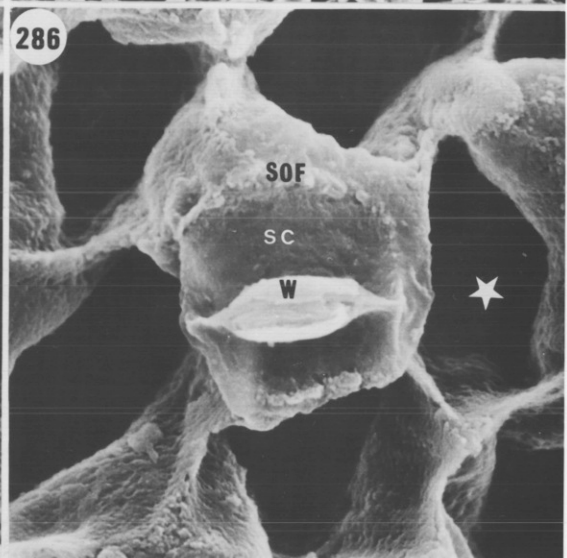
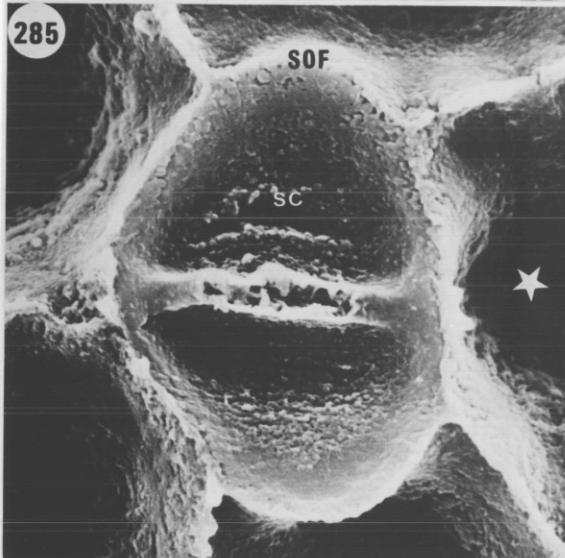
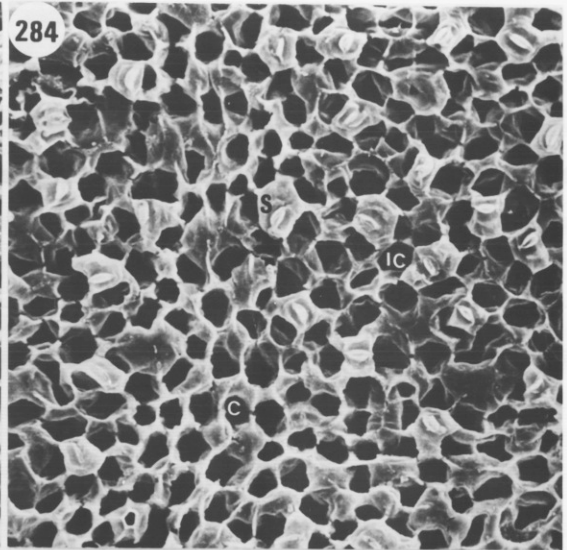
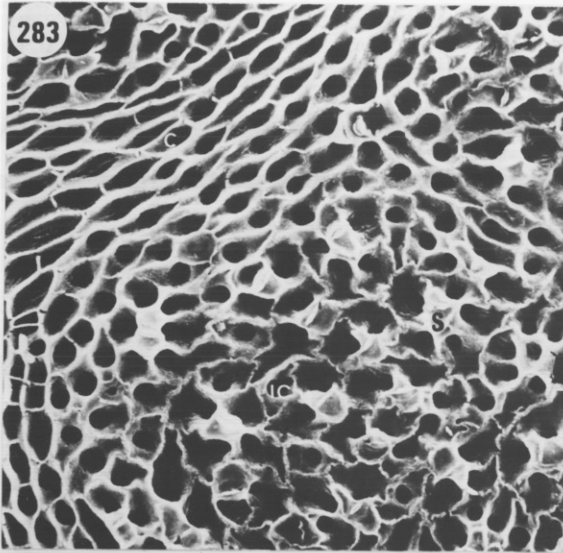
Stoma. Subsidiary cell periclinal surface concave. Note wings [W] of guard cell removed by maceration. Subsidiary cell periclinal ornamentation of fine granular or clumped protrusions. ca. x 2185.

286. Specimen 3.

As Fig. 285. Subsidiary cell [SC] periclinal surface more or less flat. Stomatal complex appears to be slightly raised above level of epidermal cells. Subsidiary cell periclinal ornamentation of finer protrusions than in Fig. 285. ca. x 2125.

287. Specimen 4.

As Fig. 283. Cell size as specimen 1. Intercostal flanges U-undulate at base, straight at apex, without cavities; frequently interrupted with 1-3 gaps. Scrobiculi shallow. Between $\frac{1}{2}$ and $\frac{3}{4}$ cell diameter contributing to scrobiculus. ca. x 285.



adaxial discontinuity [gaps & pores (1), (2), (4) and (5); gaps only (3) and the frequency of discontinuities [adx. low, occasionally with one gap/flange (1) and (2), intermediate (4) and (5), most; sometimes with 1-2 gaps/flange (3): Figs 279, 280; abx. low, occasionally with one gap/flange (5), intermediate: (1), (2) and (3), most, frequent with 1-3 gaps/flange (4)].

Dissimilarities may also be detected in periclinal ornamentation. On the adaxial, differences occur in depression size [especially wide in (5) and protrusion arrangement [granules (1), (2), (4) and (5), reticula (3): Fig. 280] over veins and on the abaxial, protrusion size [fine (1), (2), (4) and (5), coarse (3)]. A few features of scrobiculi are seen to vary intraspecifically: prominence in abaxial intercostal and costal regions [shallow (4), moderate (2) and (5), deep (1), particularly in non-vein areas and (3)] and area of cell occupied by depression corresponding to papilla [least, central circumscribed portion only of less than $\frac{1}{2}$ cell diameter (1), intermediate (2), (4) and (5); most, almost all of cell diameter (3)]. The delimitation of striae on the inner surface of adaxial veins tends to show variation [inconspicuous (1), (2), (4) and (5), conspicuous (3)].

Aspects of the stomatal complex exhibit dissimilarities between specimens: subsidiary cell concavity [convex or flat (3), concave (2), (4) and (5), especially so in (1)] and position when compared with intercostal cell level [raised in (3) only: Fig. 286].

A number of features of hairs also display differences. On the adaxial, basal cells differ in periclinal curvature [convex (3), concave (1), (2), (4) and (5)], their flanges vary in margin configuration [even (3), irregular in others] and type of discontinuity present [gaps only (3), gaps & pores in others], and their periclinal surface exhibits sculptural dissimilarities [reticula (3), granules in others]. On the abaxial, basal cell flanges vary in prominence [(2) less than (1), (3), (4) and (5)] and shape [straight-curved, no cavities (1), (3), (4)

and [5], U-undulate at base, straight-curved at apex, with cavities in undulation sinuses [2]]. In addition, a slight difference in basal cell periclinal sculpture size is detected [finer in (2) than others] as well as variation in prominence of scrobiculi [very shallow (2) and (5), shallow (4), moderate (1), deep (3)].

13.3.4 CINNAMOMUM OLIVERII

Two different specimens [numbered 1: tropical and 2: subtropical] have been examined [see p. 472].

13.3.4a OUTER SURFACE. This looks identical, except for a slightly flatter adaxial surface in (2) than in (1) [Figs 289-294].

13.3.4b INNER SURFACE. The adaxial [Figs 295-296] and the abaxial [Figs 297-300] cuticles of the two specimens show a high level of similarity. However, some differences may be seen. These involve various aspects of flanges, the periclinal surface and simple hair bases. Flange prominence is dissimilar in (1) and (2), being greater in (1) than (2) on the adaxial in all regions and the reverse [more in (2) than (1)], on the abaxial in minor vein and intercostal areas. Flanges also vary in shape: those of the adaxial non-vein cells are more undulate in (2) than (1), and abaxial vein flanges are similarly different in (1) from (2). A further difference is connected with flange form: (2) exhibiting some grooved or 'double' flanges in places on the adaxial, in contrast to (1) which has 'single' flanges only.

Specimen (2) differs from (1) in two features of the abaxial intercostal periclinal ornamentation: protrusion size [(2) finer than (1)] and form [(2) less rounded or flatter than (1)].

The number of hair bases per unit area, i.e. frequency, is dramatically different in the two specimens on the adaxial being considerably greater in (1) [20 bases/field at x 160] [Fig. 296] than in (2) [2 bases/field] [Fig. 295]. Basal cell flange prominence and shape are variable: the

Intraspecific variation in *Cinnamomum oliverii*

Outer surface.

289. Specimen 2.

Adaxial intercostal [i.c.] and costal [c] areas.
ca. x 285.

290. Specimen 1.

As Fig. 289. Note greater convexity of cells than
in specimen 2 [Fig. 289]. ca. x 280.

291. Specimen 2.

Abaxial intercostal [i.c.] and costal [c] areas.
ca. 275.

292. Specimen 1.

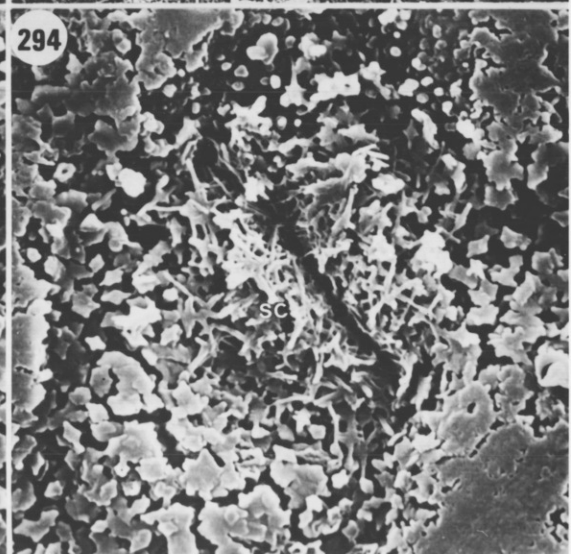
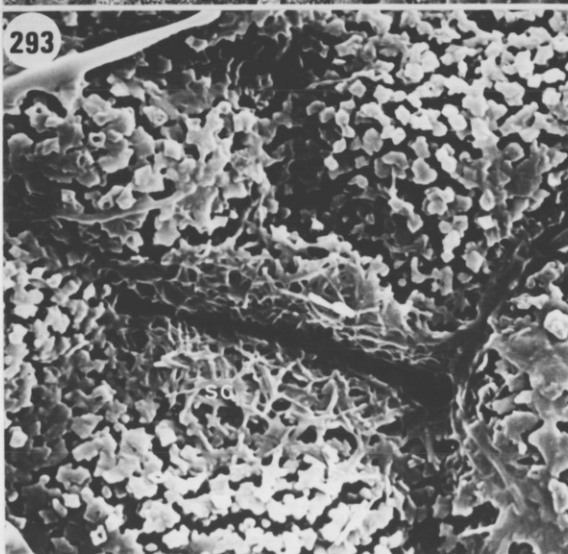
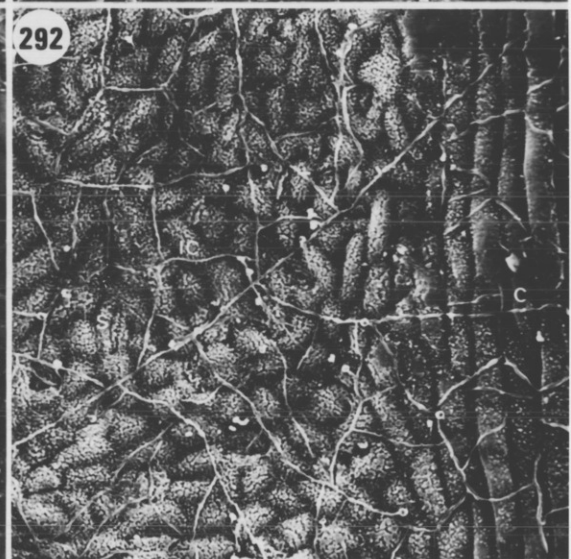
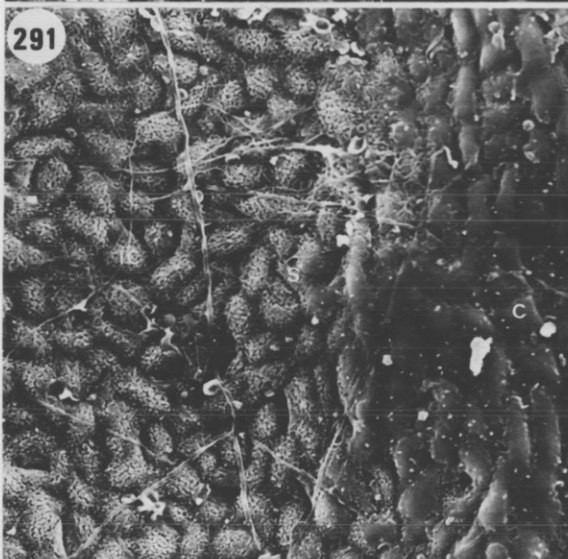
As Fig. 291. Very similar to specimen 2 [Fig. 291].
ca. x 270.

293. Specimen 2.

Stoma with apparently discrete subsidiary cells
densely covered with wax rodlets [in contrast to
granules and platelets of surrounding cells].
Note narrow stomatal pit not revealing guard cells.
ca. x 2215.

294. Specimen 1.

As Fig. 293. ca. x 2215.



Intraspecific variation in *Cinnamomum oliverii*

Inner surface of isolated cuticles.

295. Specimen 2.

Adaxial intercostal [i.c.] and costal [c] areas.

Note few hair bases [HB]. ca. x 155.

296. Specimen 1.

As Fig. 295. Note abundant hair bases, particularly associated with veins. ca. x 150.

297. Specimen 2.

Adaxial costal flanges and periclinal surface. Flanges [F] low, periclinal ornamentation of moderately coarse reticulate protrusions [P] and pit-like to reticulate depressions [D]. ca. x 2185.

298. Specimen 1.

As Fig. 297. Flanges of slightly deeper prominence than in specimen 2 [Fig. 297]. ca. x 2185.

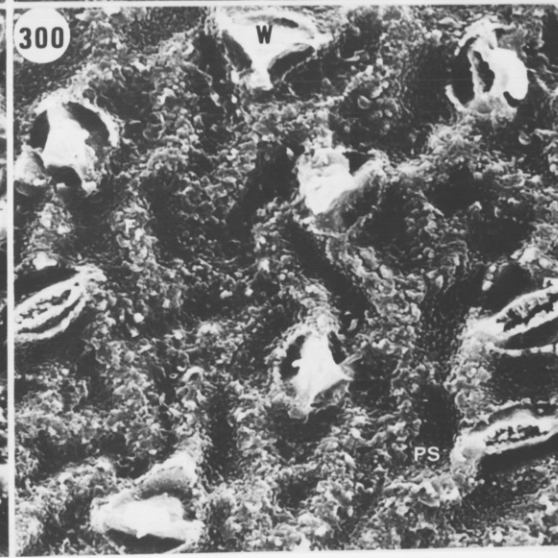
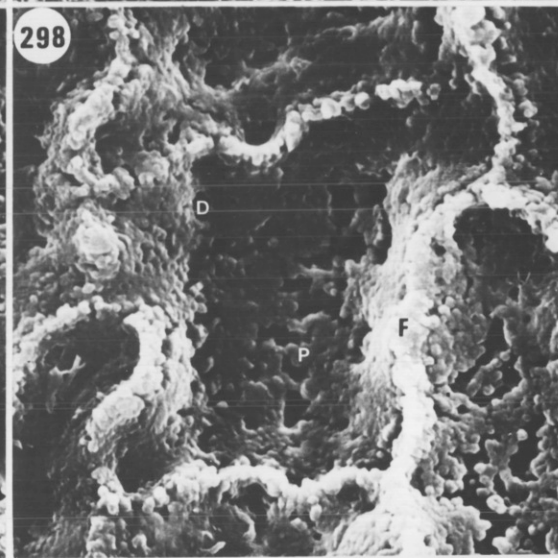
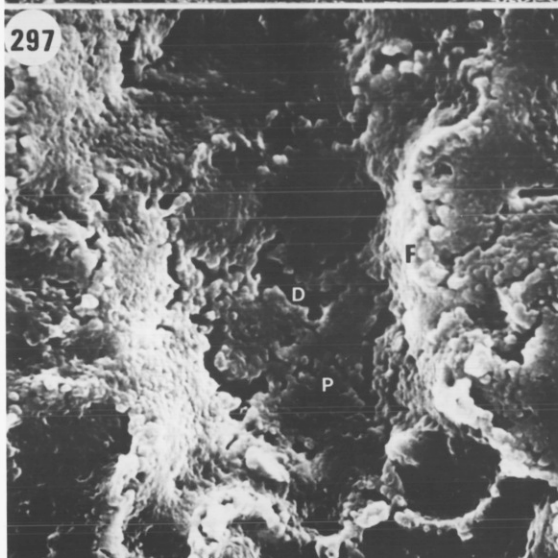
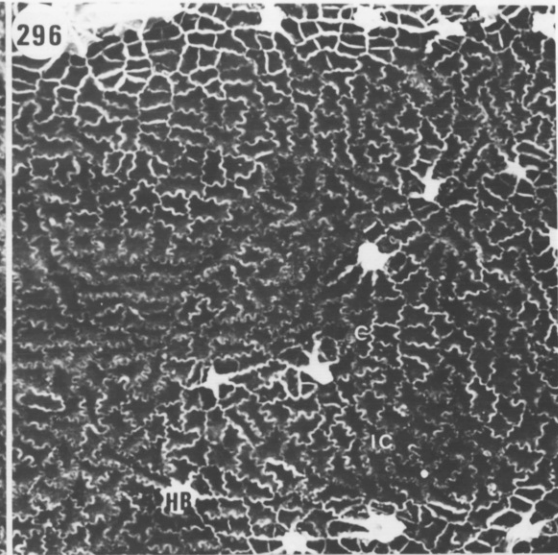
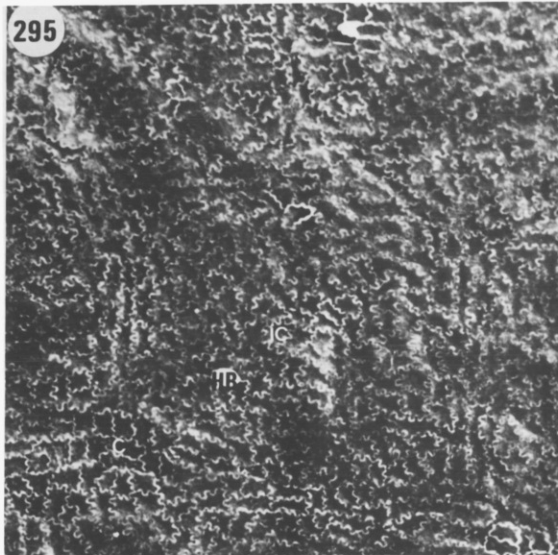
299. Specimen 2.

Abaxial intercostal area showing stomata with conspicuously pegged guard cell wings [W].

ca. x 575.

300. Specimen 1.

As Fig. 299. Periclinal protrusions slightly coarser and more prominent than in specimen 2 [Fig. 299]. ca. x 565.



flanges of hairs on the adaxial tending to be less prominent and those of abaxial hairs less undulate, in [2] than [1]. The periclinal curvature of all basal cells in [2] also differs from that of those in [1] [more concave in the former, especially when secondarily divided].

13.3.5 LAURUS CANARIENSIS

Two different specimens [numbered 1: L. azorica and 2: L. canariensis] have been examined [see p. 473].

13.3.5a OUTER SURFACE. The two specimens are almost identical. Differences may, however, be detected mainly on the adaxial [Figs 301-302] involving vein prominence, cell convexity, concavity of borders and abundance of wax [in all cases more in [2] than [1]]. Abaxial dissimilarities are concerned with frequency of simple hairs [greater in [2] than [1] and wax form [(1) flakes, (2) granules] [Figs 303-306].

13.3.5b INNER SURFACE. Adaxial [Figs 307-308] and abaxial [Figs 309-312] cuticles of [1] and [2] are similar in many features. Nevertheless, some dissimilarities occur; the majority being concerned with aspects of flanges. Minor differences involve periclinal ornamentation and cell size. Variation in flange prominence may be detected: on the adaxial, the flanges of [2] are less prominent than those of [1], on the abaxial, [2] has flanges of deeper prominence than [1]. Flange shape also differs in the two specimens: [2] shows more undulate adaxial flanges, particularly in intercostal areas than [1], but less undulate flanges in abaxial costal regions. The form of these undulations is dissimilar in [1] from [2], the former possessing non-vein flanges with a buttress and cavity organisation on the adaxial surface, unlike [2], and the latter having more rounded undulate sinuses to flanges over major abaxial veins.

Various aspects of periclinal sculpture exhibit differences: on the adaxial, composition [(1) protrusions only, (2) protrusions and depressions], protrusion size

Intraspecific variation in *Laurus canariensis*

Outer surface.

301. Specimen 1.

Adaxial intercostal [i.c.] and costal [c] areas.
ca. x 280.

302. Specimen 2.

As Fig. 301. Note greater vein prominence, cell convexity, concavity of anticlinal borders and abundance of wax than in specimen 1 [Fig. 301].
ca. x 280.

303. Specimen 1.

Abaxial intercostal [i.c.] and costal [c] areas.
Note concentration of wax on subsidiary cells of stomata. ca. x 275.

304. Specimen 2.

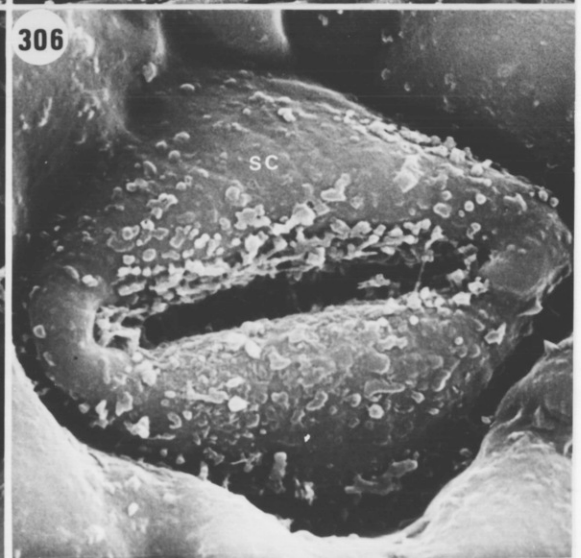
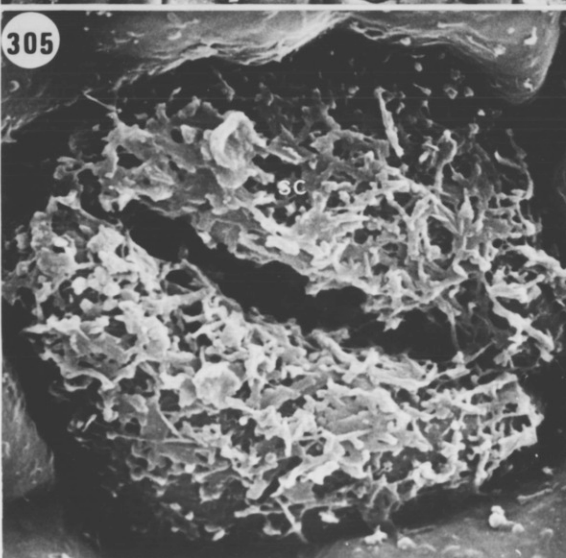
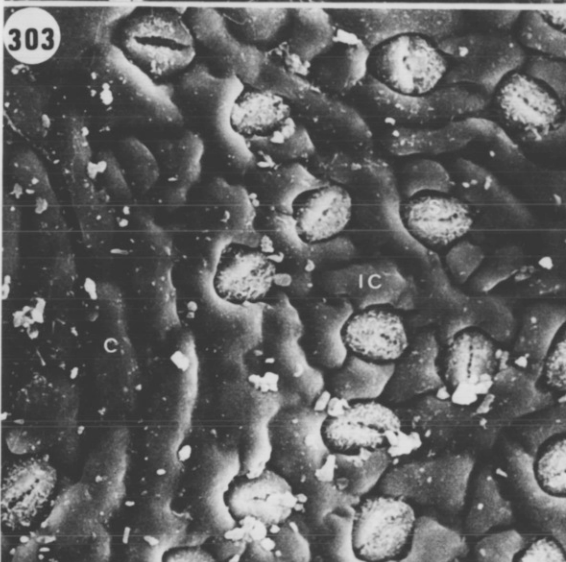
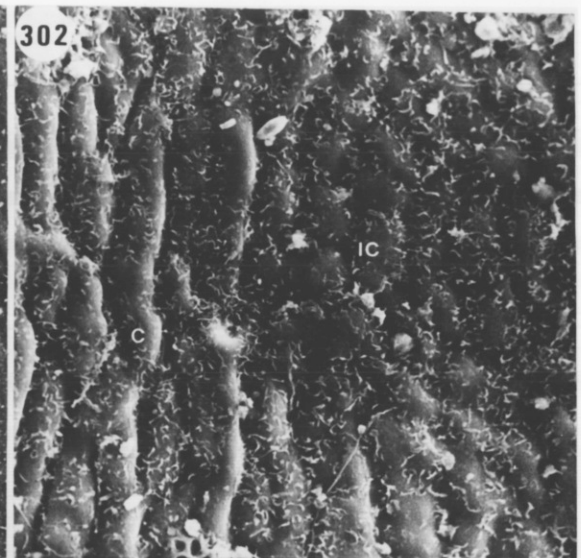
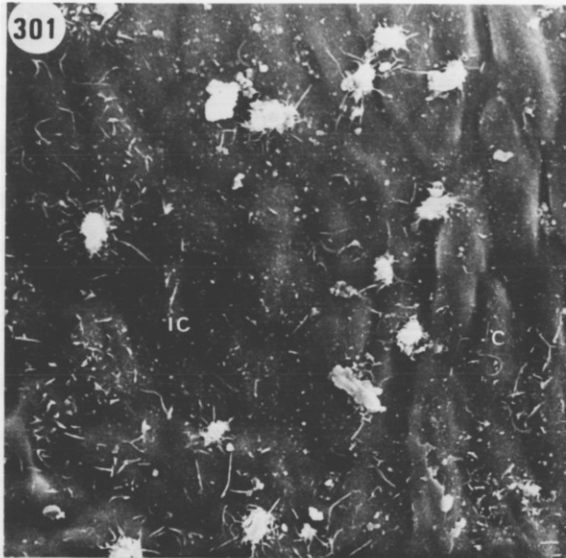
As Fig. 303. ca. x 275.

305. Specimen 1.

Stoma. With triangular, domed subsidiary cells densely covered by wax rodlets. Stomatal pit narrow, elongate; not revealing guard cells. ca. x 2125.

306. Specimen 2.

As Fig. 305. Similar configuration to specimen 1 [Fig. 305] but wax clearly of different form [granules]. ca. x 2200.



Intraspecific variation in *Laurus canariensis*

Inner surface of isolated cuticles.

307. Specimen 1.

Fine details of adaxial intercostal flanges and periclinal surface. Note distinct cavities in sinuses of undulation in flanges. Periclinal ornamentation of granular protrusions. ca. x 1095.

308. Specimen 2.

As Fig. 307. Note flanges less prominent, more undulate than in specimen 1 (Fig. 307). Periclinal ornamentation of reticulate protrusions and pit-like depressions. Protrusions radiating from undulation sinuses, which have conspicuous smooth surface. ca. x 1055.

309. Specimen 1.

Abaxial intercostal [i.c.] and costal [c] areas. ca. x 140.

310. Specimen 2.

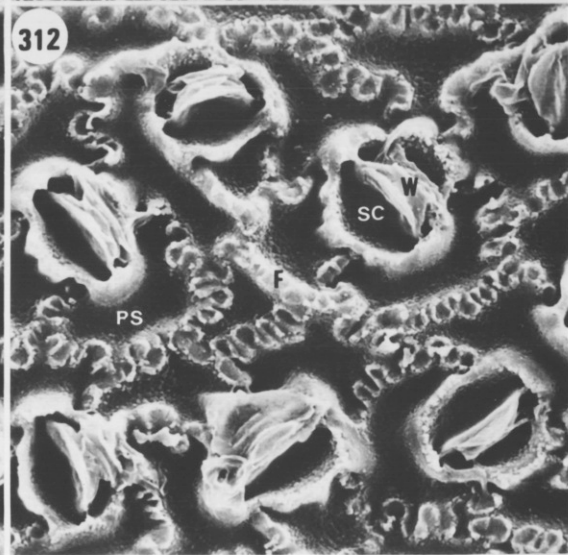
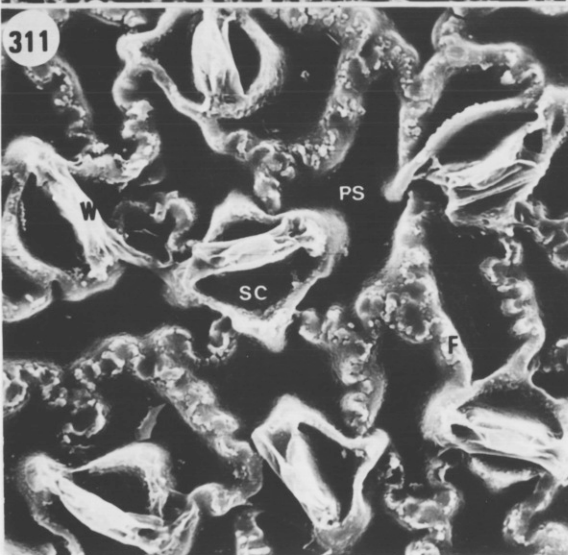
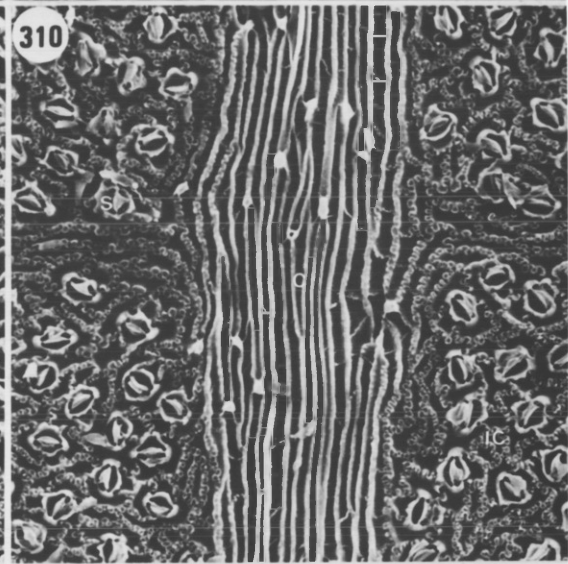
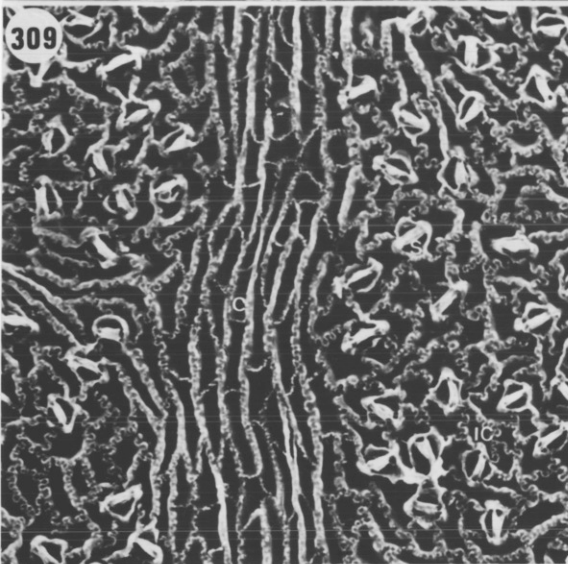
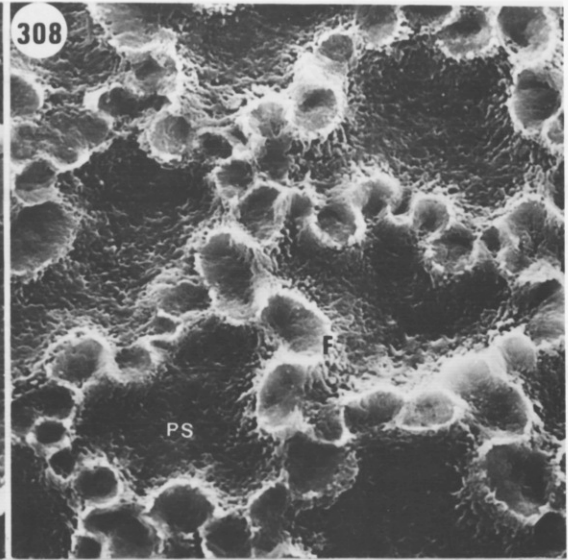
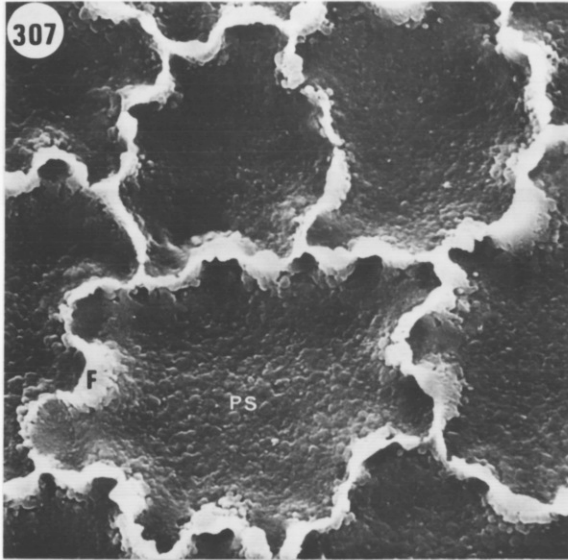
As Fig. 309. Flanges [especially costal] more prominent and more undulate [except costal] than in specimen 1 (Fig. 309). ca. x 135.

311. Specimen 1.

Stomata with triangular subsidiary cells [SC]; narrow, elongate guard cell wings [W] sometimes associated with portions of stomatal flap. Note T-form of subsidiary cell polar thickening. ca. x 540.

312. Specimen 2.

As Fig. 311. Note greater prominence of periclinal protrusions associated with stomata and non-specialised cells in this specimen. ca. x 555.



Intraspecific variation in *Laurus nobilis*

Outer surface of fresh and dried material.

313. Specimen 1.

Adaxial intercostal [i.c.] and costal [c] areas.
ca. x 265.

314. Specimen 2.

As Fig. 313. Note slightly greater cell convexity
than in specimen 1. [Fig. 313]. ca. x 260.

315. Specimen 1.

Abaxial intercostal [i.c.] and costal [c] areas.
ca. x 275.

316. Specimen 2.

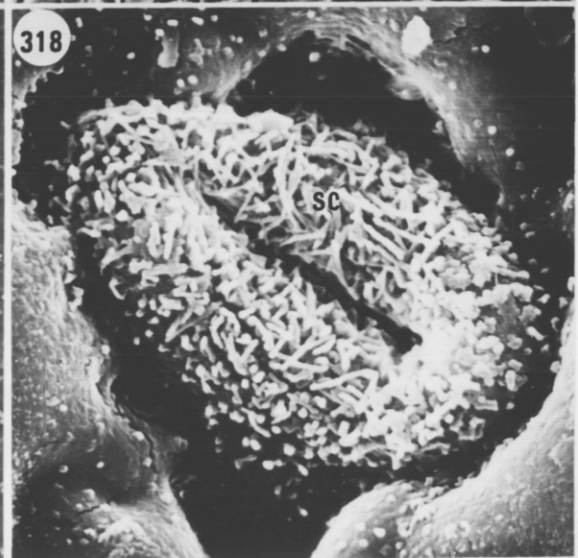
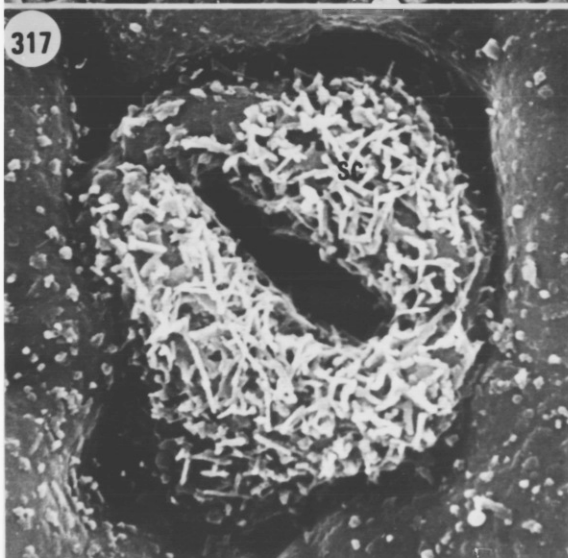
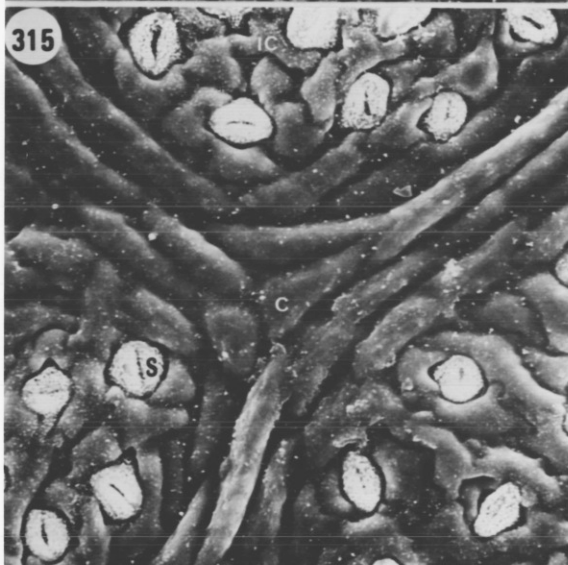
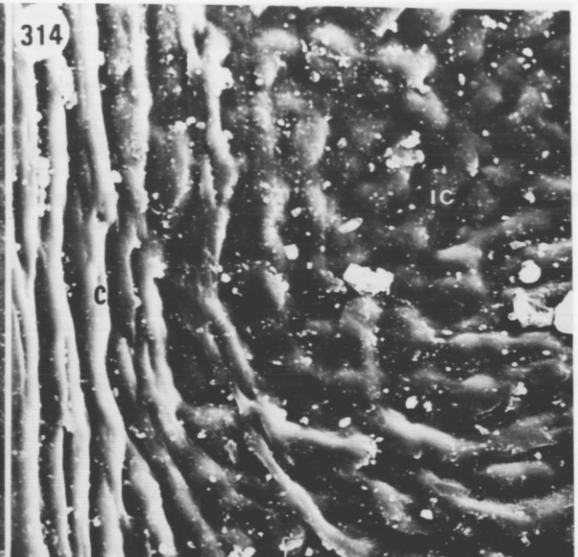
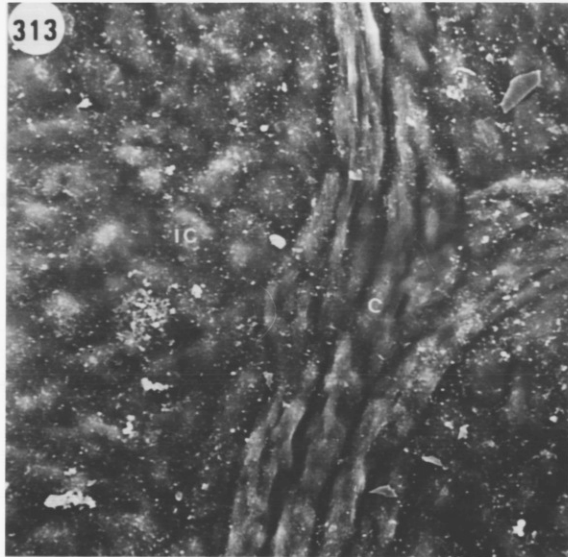
As Fig. 315. Note slightly greater cell convexity
and more sunken anticlinal borders than in specimen 1
[Fig. 315]. ca. x 275.

317. Specimen 1.

Stoma. With triangular domed subsidiary cells
densely covered with wax rodlets. Note granular
nature of wax on ordinary epidermal cells. Stomatal
pit narrow, elongate; not revealing guard cells.
[Compare with Fig. 305]. ca. x 2050.

318. Specimen 2.

As Fig. 317. ca. x 2075.



Intraspecific variation in *Laurus nobilis*

Inner surface of isolated cuticles from fresh [1] and dried [2] material.

319. Specimen 1.

Fine details of adaxial intercostal [i.c.] and costal [c] areas. Flanges U- Ω -undulate. Flange and periclinal ornamentation of granules. ca. x 620.

320. Specimen 2.

As Fig. 319. [Note cracks not part of sculpture, probably due to over maceration]. ca. x 595.

321. Specimen 1.

Abaxial intercostal [i.c.] and costal [c] areas. ca. x 265.

322. Specimen 2.

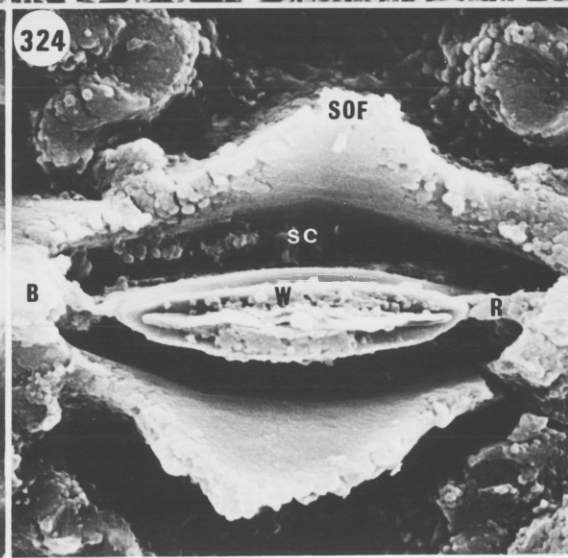
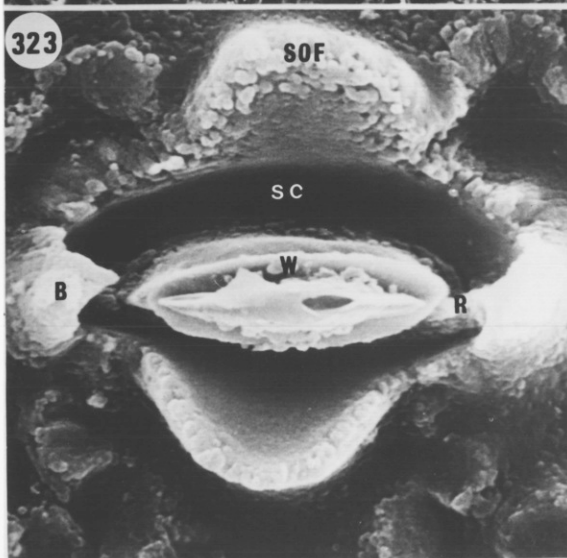
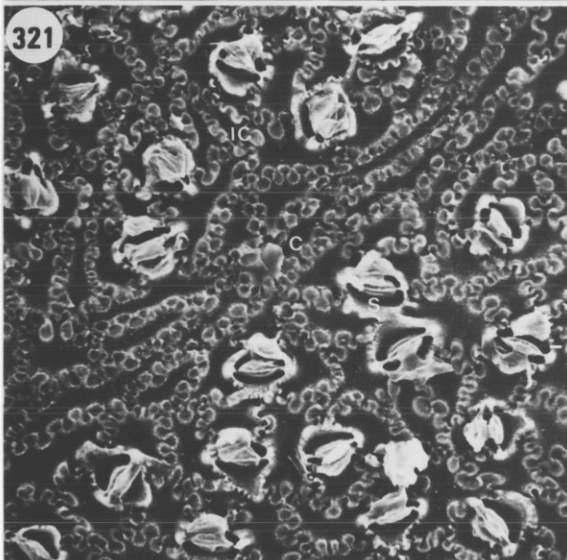
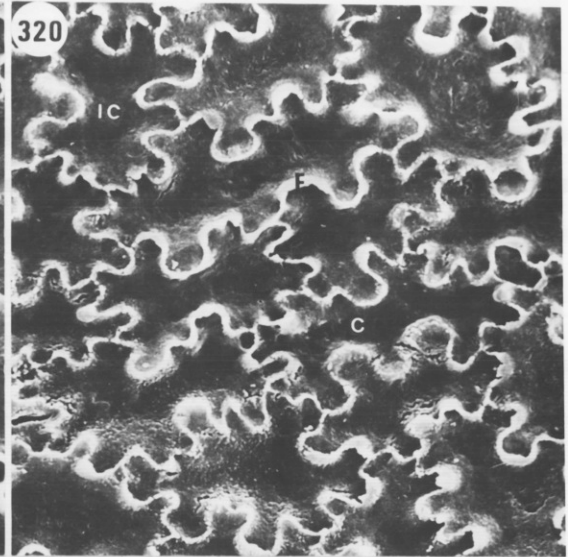
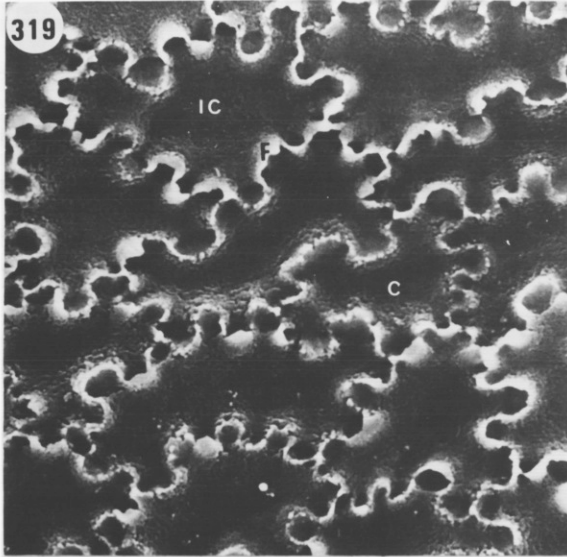
As Fig. 321. ca. x 270.

323. Specimen 1.

Stoma with triangular subsidiary cells [SC] bearing depression corresponding to dome on outer surface. Subsidiary cell/ordinary cell flange [SOF] undulate. Guard cell wings [W] narrow, elongate. Note polar thickening composed of rod [R] and bar [B], associated with subsidiary cells. ca. x 2095.

324. Specimen 2.

As Fig. 323. ca. x 2010.



[[2] finer than [1]] and protrusion arrangement [[2] reticula, radiating from undulation crests; [1] granules] and on the abaxial, protrusion prominence [[2] more than [1]] and arrangement over veins [[2] granules-reticula, [1] granules].

In addition, cell size differs in [1] from [2] on the adaxial cuticle, the former being of larger dimensions than the latter.

13.3.6 LAURUS NOBILIS

Two specimens (numbered 1: fresh and 2: dried) have been examined [see p. 473] to ascertain the extent of variation caused by using the two types of source material.

13.3.6a OUTER SURFACE. Unmacerated leaf portions are very similar in morphology [Figs 313-318]. The cells of [2] appear slightly more convex than [1], with more well-defined [sunken] sutures at the cell borders.

13.3.6b INNER SURFACE. Both the adaxial [Figs 319, 320] and the abaxial [Figs 321-324] cuticles of the two specimens are identical.

Thus, there are no significant differences between fresh and dried material of a species.

13.3.7 ATTEMPT TO RELATE INTRASPECIFIC DIFFERENCES WITH ENVIRONMENT

An attempt was made to relate intraspecific differences in Beilschmiedia madang, Caryodaphnopsis tonkinensis and Dehaasia cuneata with dissimilarities in soil and altitude, using the limited data regarding these aspects supplied by collectors on the labels of the herbarium specimens from which samples had been removed. Features unique to individual specimens were noted. Trends involving these characters and certain environmental conditions e.g. high altitude, extreme base-rich soil, were then sought.

BEILSCHMIEDIA MADANG

Specimen 1. Sandy ridges. Unique features: none.

Specimen 2. Low ridge, sandy loam soil, 30m. Unique features: costal cutinisation deeper and trichome frequency lower on abx.

Specimen 3. Hilly loam with coral limestone, 30m. Unique features: intercostal cutinisation less and trichome frequency greater on adx.; anticlinal borders more sunken and stomata smaller on abx.

Specimen 4. Marshy, on white sand soil, 5m. Unique features: intercostal cutinisation deeper and costal flanges more perforated on abx.

Specimen 5. Sandy (granitic soil), 50m. Unique features: hypodermal flanges more prominent and costal cutinisation deeper on adx.

Specimen 6. Sandy clay (skeletal) soil, 650m. Unique features: none.

CARYODAPHNOPSIS TONKINENSIS

Specimen 1. Coral limestone, 150m. Unique features: flanges more undulate on adx.; lateral striae less prominent on abx.

Specimen 2. Primary forest, soil black, near river bank. Unique features: anticlinal borders wider and more sunken, costal flanges more irregular on adx.

Specimen 4. Sandstone ridge, 40m. Unique features: costal flange irregularity different (intermediate) and poral cutinisation of trichomes shallower on adx.; papilla apices less fused, costal periclinal protrusions more rounded and prominence of internal lateral striae different (moderate) on abx.

Specimen 6. 850 ft. Unique features: slightly smaller cells, costal cells more concave in periclinal region and periclinal protrusions less prominent (indistinct) on adx.; costal flanges more irregular, major vein periclinal protrusions smaller, intercostal and trichome base striae more prominent on abx.

Specimens 3 and 7. No habitat details, therefore, no comparison made.

DEHAASIA CUNEATA

Specimen 1. Sandy granitic soil, 20m. Unique features:

periclinal wall more concave and anticlinal borders of different shape [raised] on adx.; wax of different form [flakes], flanges more undulate, intercostal scrobiculi deeper, occupying less of cell, subsidiary cell concavity greater and basal cell scrobiculi of different prominence [moderate] on abx.

Specimen 2. Sandstone ridge, 40m. Unique features: cells larger and flanges more irregular on adx.; intercostal flanges deeper, costal flanges narrower, flanges less irregular, striae of different prominence [low], basal cell flanges less prominent and more undulate, and basal periclinal sculpture finer on abx.

Specimen 3. Limestone, 400m. Unique features: anticlinal borders more sunken, cells of different size [intermediate], periclinal wall of different shape [convex], flange margin more even, flange discontinuity type different [gaps], gap frequency greater, periclinal protrusions more complex and coarse, costal striae more conspicuous and all striae more coarse on adx., density of wax on papillae less, cells smaller, intercostal flanges less undulate, intercostal scrobiculus prominence greater, area of cell occupied by scrobiculus more, costal striae more conspicuous, subsidiary cells less concave, position of subsidiary cells with respect to surface different [raised], basal cells of trichomes with different periclinal curvature [convex], form of flange margin [even], type of flange discontinuity different [gaps] and more complex periclinal sculpture on abx.

Specimen 4. Ridge, loam soil containing lime, 30m. Unique features: cells less concave and trichomes more frequent on adx.; papillae smaller size, less prominent, of different shape [oval] with wax of smaller size, intercostal flanges more undulate, gaps more frequent, scrobiculi less prominent and prominence of trichome basal cells different [shallow] on abx.

Specimen 5. Sandy loam soil. Unique features: flanges deeper, periclinal depressions wider and striae finer as well as more prominent on adx.; gaps less frequent and trichomes of lower frequency on abx.

Specimens collected from plants in the more extreme conditions i.e. high altitude or base-rich soil tend to show most unique features, particularly in Dehaasia cuneata [3]. Leaves from some limestone specimens e.g. in Beilschmiedia madang [3] and D. cuneata [3] have more sunken anticlinal borders than others. D. cuneata [4], also from similar soil conditions, differs most particularly intraspecifically in anticlinal border configuration but shows a different degree of concavity. Base-rich specimens of Caryodaphnopsis tonkinensis [1] and D. cuneata [3,4] exhibit dissimilarities in flange undulation. Certain specimens of these taxa [1 and 3 respectively] differ in striae prominence. In all cases, these specimens do not show a consistent degree or level of variation. This is likewise so in high altitude specimens of C. tonkinensis [6] and D. cuneata [3] which exhibit differences in cell size, periclinal curvature and flange margin irregularity. Such specimens are, however, constant in the degree of striae prominence shown when compared with others of the same species. The two specimens of C. tonkinensis [4] and D. cuneata [2] from a sandstone ridge at 40m are unique in their flange irregularity and prominence of striae. No definite relationships between intraspecific variation and the environment can be recognised from this preliminary work.

14. NUMERICAL METHODS

14.1 SELECTION OF OPERATIONAL TAXONOMIC UNITS

Eighty-eight operational taxonomic units (OTUs) were selected. These, with the exception of two which were stem portions of Cassytha spp., were represented by mature leaf samples of species or subspecies primarily from the Lauraceae (74 named species, 1 unknown in 40 genera) but also from the families Austrobaileyaceae (1 species in 1 genus), Gomortegaceae (1 species in 1 genus), Hernandiaceae (6 species in 3 genera, 2 subspecies of 1 species in another genus) and Trimeniaceae (3 species in 2 genera) which have been considered to be closely related to Lauraceae (Hutchinson, 1959; 1964; Cronquist, 1968; Takhtajan, 1966, 1969, 1980; Thorne, 1968, 1976; Stebbins, 1974; Dahlgren, 1980). The list of OTUs is given in tables II-IV of results.

14.2 SELECTION OF CHARACTERS

The characters chosen for inclusion were derived from those aspects described in the main part of this study (see Section 12). Thus, the list is composed mainly of cuticular features obtained by examination of isolated cuticles with both scanning electron- and light-microscopy, from unmacerated leaf portions viewed with the S.E.M. and transverse sections observed with the light microscope. A large proportion of characters relate to aspects of the inner cuticular surface. A few features are characteristic of the stoma as seen in T.S. and contribute strongly to interspecific differences. The presence of lignin was also included.

14.3 SCORING OF CHARACTERS

The variability of features was first determined both within each sample and between all OTUs. Those characters showing no variation between members of the assemblage were then discarded. Each feature is a unit character, i.e. describing one different aspect/attribute of an OTU.

Adaxial and abaxial features were organised into two subsections in the tables corresponding to characters of

the intercostal and costal regions, since each of these areas may exhibit a different combination of features.

Characters may be either quantitative [measurement] or qualitative [descriptive]. Quantitative states were expressed, increasing numerically either in a linear form, advancing in equal increments, or in a non-linear mode, where the preceding increment is doubled. The linear form was used for most measurements; the non-linear mode was only applied to characters where the values increased exponentially, e.g. those concerning angles or ratios. Qualitative character states were assigned as consistently as possible, increasing numerically with increasing complexity or prominence of the feature or with increased development of a more 'advanced' form of structure. Multi-state characters were scored from 1 [lowest state] to n [maximum nth state]. Bistate qualitative features were recorded as 1 [absence] or 2 [presence]. Where no equivalent structure was present for scoring, no comparison was possible and a score of 9 was ascribed.

14.4 SELECTION OF CHARACTERS FOR PRELIMINARY ANALYSIS

A total of 381 characters [83 adx. i.c., 51 adx. c., 86 abx. i.c., 47 abx. c., 114 stomatal] were scored. The sheer volume of such data posed great problems of storage, time and manipulation for the computer. Therefore, a subset of data was selected for a preliminary analysis. 114 stomatal features [35 quantitative, 79 qualitative: see Table IV] were chosen for this because the stoma seems to be the most informative part of the cuticle and is also the main aspect of the leafless Cassytha which can be strictly compared with other Lauraceae. It appears likely that stomata are especially useful for inferring taxonomic relationships since stomatal organisation in Lauraceae is distinct and different from that in other related families. 40 characters of the abaxial intercostal inner cuticular surface [12 quantitative, 28 qualitative] were chosen in addition [see Table V]. These were selected on the basis of being most likely to occur on the inside of any abaxial cuticle accompanying stomata.

14.5 MULTIVARIATE ANALYSIS

The coded data for the 114 stomatal and 40 abaxial intercostal inner surface features was punched on 80 column Fortran cards using an IBM machine. Two cards were prepared for each OTU; one for characters 1-80 inclusive, the other for 81-154.

Two standard methods of analysis may be applied, [1] principal co-ordinates analysis and [2] cluster analysis [C.A.].

Principal co-ordinates analysis works on a similarity matrix between OTUs. It utilises Gower's similarity coefficient [see Gower, 1971] and ordines OTUs in Euclidean space. The distribution of OTUs may be plotted using the principal axes of variation (I and II, or n, usually up to V). This type of analysis is particularly suited mathematically to data expressed in both binary and multistate terms, unlike principal components analysis [P.C.A.] which has commonly been used in numerical work. Principal co-ordinates analysis, like P.C.A., is useful for detecting major clusters and gradients in the data set.

Cluster analysis brings together into clusters those OTUs whose members have the highest similarity. The clusters are then arranged in a hierarchic taxonomic dendrogram based on successive linkages formed between nearest neighbours at decreasing levels of similarity of Euclidean distance, with groups or phenons defined by an overlay of horizontal lines drawn at the various levels of similarity [Sokal & Rohlf, 1962]. This dendrogram may be subject to some distortion, given by the cophenetic correlation coefficient, as well as some simplification. C.A. is not thought to be a reliable method to indicate major clusters but it is valuable for revealing fine details at high levels of similarity [i.e. at the dendrogram tips].

Since the methods of analysis clearly have different optimum uses, both were applied to the data.

The principal co-ordinates analysis program was

prepared by Dr. D.H. Dalby with the assistance of Professor R.G. Davies, who also wrote the cluster analysis program HYCLUS. Both analytical programs were converted to Fortran 77 and run on the Cyber 855 computer at the Imperial College Computer Centre by Dr. D.H. Dalby.

Initially, OTUs were ordinated using principal co-ordinates analysis only and their distribution was plotted on axes I and II (Text-Fig. 32). Since major groupings were not evident, it was possible that some characters were causing unnecessary 'noise' in the system (i.e. certain small differences in some features had been over-emphasised by the assignation of too many states and were leading to greater apparent than actual dissimilarity between individual OTUs). Thus, any affinities between genera were difficult to detect due to the often wide separation of species within them. Therefore, a second subset of characters was selected. 60 stomatal features (9 quantitative, 51 qualitative: asterisked in Table IV) were chosen by finding the commonest characters for which scores were constant for all members of a genus (i.e. in 26 or more genera). Monospecific genera and those represented by only one species [7] could not be included. Principal co-ordinates analysis and cluster analysis was applied to the new data set. OTUs were ordinated in a plot on axes I and II by principal co-ordinates and clustered in a dendrogram by C.A. (See Text-Figs 33,34).

14.6 DESCRIPTION OF CHARACTERS AND STATES

In the following character description, features and states have been assigned Arabic numerals. However, states appear in parenthesis (brackets). Note, all costal characters have been taken from veins of constant size (6-8 cells wide) since variation in width of veins may induce cell shape modifications. This size occurs most commonly in preparations.

CHARACTERS OF NON-SPECIALISED CELLS

Nos. 1-4. From isolated cuticles viewed by light microscopy.

1. Cell frequency. Expressed as average number of cells per unit area in 16 randomly selected grid squares [each 1.8 mm²]. Stomatal complex omitted where present. Basal cells and hair pores included. i.c. only.
States: [1] 16.6-96.9; [2] 97.0-177.3;
 [3] 177.4-257.7; [4] 257.8-338.1

2. Cell shape. Form of 10 cells in representative area, determined by length to width ratio of longest, narrowest cell and shortest, widest cell. i.c. and c.
States: [1] Predominantly isodiametric to short polygonal. l:w = 2 or less:1 [usually 1-2:1];
 [2] Mixture of types [1] and [3], l:w = less than 2:1 to more than 2:1 [i.e. no predominant shape];
 [3] Predominantly elongate polygonal, l:w = more than 2:1 [up to 10:1].

3. Course of flanges [i.e. degree of undulation].
 Predominant pattern noted. Where two occur, forms averaged. Where no predominance exists, all types averaged. To cater for intermediates between basic types, 0.5 scores designated. All scores doubled for computation. i.c. and c.
States: [2] straight; [3] straight-curved; [4] curved;
 [5] curved-U-undulate; [6] U-undulate;
 [7] U-undulate-Ω-undulate; [8] Ω-undulate.

4. Flange width. At base where anticlinal flange meets periclinal surface. Measured under x 100 objective. 5 readings made with flange margin over centre of flange [see Text-Fig. 2 B, for T.S. view]. i.c. and c.
States: [1] 1.5-3.3 units; [2] 3.4-5.2; [3] 5.3-7.1;
 [4] 7.2-9.0; [5] 9.1-10.9; [6] 11.0-12.8
 [1 unit = 0.571 μm].

Nos. 5-30. Determined from camera lucida drawings prepared under x 100 objective [1 unit = 0.61 μm].

5. Curvature of outer periclinal wall. Shape expressed in terms of ratio $\frac{c-g}{e-f}$, where c-g is maximum height of wall above or below anticlinal borders and e-f is width across cell from border to border [see Text-Fig. 2 B]. Results of 5 cells averaged. Non-linear scale of scoring adopted for convex shapes due to exponential increase of values. i.c. and c.
States: [1] Concave-flat; [2] Convex 0.01-0.08; [3] 0.09-0.23; [4] 0.24-0.52; [5] 0.53-1.09.

6. Dome/papilla type. Abx. i.c. only.
States: [1] With globular [rounded] crown [e.g. Figs. 13-18, 271-276]; [2] With coronulate [frilly, flattened] crown [e.g. Figs. 241-246, Text-Fig. 11]; [9] No comparison, where domes/papillae absent, i.e. when periclinal curvature is less than 0.23.

7. Area of outer periclinal wall involved in papilla formation. Abx. i.c. only.
States: [1] Central circumscribed area of wall forming dome/papilla; [2] All of wall forming dome/papilla; [9] no comparison [see 6].

8. Shape of anticlinal borders. Assigned to nearest configuration. i.c. and c.
States: [1] Sunken [e.g. Text-Fig. 8, Figs 4 and 6]; [2] Flat; [3] Raised [e.g. Text-Fig. 10 B].

9. Extent of cutinisation with respect to outer periclinal wall. Expressed in terms of ratio $\frac{c-h}{c-d}$, where c-h is cuticle thickness in middle of outer periclinal wall and c-d is total wall [and cuticle] thickness in same region [see Text-Fig. 2B]. Calculated for 5 cells. Results averaged. i.c. and c.
States: Text-Fig. 3. [1] 0.09-0.31; [2] 0.32-0.54; [3] 0.55-0.77; [4] 0.78-1.00.

10. Average median thickness of periclinal cuticle.
 Thickness c-h measured in units in middle of outer periclinal wall in 5 cells. Results averaged i.c. and c.
States: [1] 0.5-4.5; [2] 4.6-8.6; [3] 8.7-12.7; [4] 12.8-16.8;
11. Lateral extent of cutinisation with respect to inner periclinal wall. Predominant pattern assigned by inspection. i.c. and c.
States: Text-Fig. 4. [1] None; [2] Intermittent: irregular distribution of patches and corners; [3] Corners: regular and of frequent occurrence; [4] Corners and intermittent; [5] Corners and some cutinisation [discontinuous] across wall; [6] Corners and entire inner periclinal wall laterally.
12. Presence of total cutinisation of anticlinal wall.
 Adx. i.c. only.
States: [1] Absent; [2] Present [see Text-Fig. 8 A]
13. Presence of periclinal subdivision of epidermis. i.c. and c.
States: [1] Rare or absent; [2] Sometimes or frequently present [see Text-Fig. 9A].
14. Thickness of cuticle at non-specialised flange.
 Thickness a-b [Text-Fig. 2 B] measured in units from outer periclinal cuticle in middle of anticlinal border along centre of cutinisation to tip of flange, using flexible scale. 5 measurements averaged. i.c. and c.
States: [1] 0.5-8.0 units; [2] 8.5-16.0; [3] 16.5-24.0; [4] 24.5-32.0; [5] 32.5-40.0; [6] 40.5-48.0; [7] 48.5-56.0.
15. Flange prominence. Depth to which flange extends in epidermal anticlinal wall. i.c. and c.
States: Text-Fig. 6. [1] Very low - flange not reaching to top of anticlinal wall; [2] low-flange

extending to top of anticlinal wall; [3] moderate - flange reaching about half way down anticlinal wall; [4] deep-flange extending to inner periclinal wall; [5] extensive - anticlinal cutinisation extending to subepidermal layer.

16. Flange shape in profile. i.c. and c.
States: [Text-Fig. 10] [1] Blunt, U-shaped, [2] Tapering/sharp, V-shaped.
17. Staining reaction of cuticle. Number of layers distinguishable when cuticle is stained with Sudan IV. i.c. and c.
States: [1] Homogeneous - 1 layer, equally well-cutinised; [2] Heterogeneous - 2 layers, one [inner] less cutinised than the other [outer] [See Text-Fig. 8].
18. Configuration of cuticle/cellulose wall interface. Degree of unevenness depicted at boundary between cuticle and cellulose wall in periclinal region. i.c. and c.
States: [1] Even, interface more or less straight; [2] slightly uneven, interface with tiny irregularities, up to 1 mm in drawings [x 100 objective] [e.g. Text-Fig. 7A]; [3] Very uneven, interface with large irregularities, more than 1 mm in height in drawings [x 100 objective] [e.g. Text-Fig. 7B].

Nos. 19-30 Extent of lignification. Ascertained by testing T.S. with phloroglucinol and concentrated HCl [p.91]. i.c. only. Scored separately according to location since different combinations occur.

19. Presence in whole epidermis.
20. Presence in papillae.
21. Presence in outer periclinal wall.
22. Presence in inner periclinal wall.

23. Presence in lower part of anticlinal wall.
24. Presence in part of subepidermal anticlinal wall.
25. Presence in hypodermis.
26. Presence in hair bodies.
27. Presence in hair bases.
28. Presence in gland bases.
29. Presence in secretory cells.
30. Presence in cells at ends of sclereids.
States: [1] Absent [no colouration]; [2] present [pink-dark purple red].

Nos. 31-37. From unmacerated leaf portions and isolated cuticles observed with S.E.M.

Nos. 31-36. Epidermal striae [outer surface] i.c. and c.

31. Presence of striae.
States: [1] Absent; [2] Present.
32. Size of striae. Measured in units from $\times 640$ micrographs. 1 unit = 1.54 μm .
States: [1] Less than 1.0 unit; [2] 1.1-2.0; [3] 2.1-3.0; [4] 3.1-4.0; [9] No comparison, where striae absent.
33. Fusion of striae.
States: [1] Solitary, predominantly separate, without lateral fusion; [2] Network, fusing laterally to varying degrees [e.g. Fig. 5]; [9] No comparison [see 32].
34. Orientation of striae.
States: [1] Random, multi-directional [Fig. 5]; [2] Parallel, orientated in one specific direction;

34. Continued...
[9] No comparison [see 32].
35. Continuity of striae across cell.
States: [1] Discontinuous - not continuous over more than 1 cell; [2] Continuous - over more than 1 cell; [9] No comparison [see 32].
36. Shape of striae.
States: [1] More or less straight; [2] Undulate; [9] No comparison [see 32].
37. Development of veins on outer surface. Degree to which veins delimited on adx. at x 320.
States: [1] Veins difficult to differentiate from i.c. regions [i.e. indistinct]; [2] Veins easily recognised and differentiated from i.c. regions [i.e. distinct].
- Nos. 38-67. From inner surface of isolated cuticles observed with scanning electron microscopy.
- Nos. 38-44. Fine sculpture of periclinal surface of non-specialised cells. i.c. and c.
38. Presence of protrusions [cutin particles protruding from cutin matrix].
States: [1] Absent; [2] Present.
39. Form of protrusions. Where two forms occur, intermediate state assigned. Scores doubled for computation.
States: [2] Rounded; [3] Rounded-filamentous; [4] Filamentous [elongate, thread-like]; [9] No comparison, where protrusions absent.
40. Pattern of protrusions. All patterns present recorded. Average noted. Scores doubled for computation.
States: [Text-Fig. 5] [2] Granules; [3] Granules-clumps; [4] Clumps [of granules]; [5] Clumps-reticula; [6] Reticula [granules tending to form networks]; [9] No comparison [see 39].

41. Size of protrusions. Measured in units [1 unit = 0.36 μm] from micrographs using templates of increasing diameter drawn on tracing paper.
States: [1] Distinct cutin particles up to 0.50 units in diameter; [2] 0.51-1.00; [3] 1.01-2.00; [4] 2.01-4.00; [9] No comparison [see 39].
42. Presence of depressions [pits left by removal of cellulosic fibres from cutin matrix].
States: [1] Absent; [2] Present.
43. Pattern of depressions. All patterns present recorded. Average noted. Scores doubled for computation.
States: [Text-Fig. 5] [2] Pit-like; [3] Pits-clumps; [4] Clumps of pits; [5] Clumps-reticula; [6] Reticula [pits tending to form networks]; [9] No comparison, where pits absent.
44. Size of depressions. Measured in units in same way as protrusions [see 41].
States: as 41.
45. Presence of striae on inner surface. i.c. and c.
States: [1] Absent; [2] Present.
- Nos. 46-51. Fine sculpture of non-specialised flanges. Measured and scored in same way as characters 38-44 for periclinal sculpture of non-specialised cells.
- Nos. 53-58. Continuity of non-specialised flanges.
[a] Perforations/pores (holes through flange, at edge or in body). i.c. and c. [Figs. 55-58].
53. Presence of pores in flange body [whole pores].
54. Presence of pores at flange edge [half pores].
States: [1] Absent; [2] Present.

55. Type of pore [perforations in body only]. All patterns recorded from micrographs. Average noted. Scores doubled for computation.
States: [2] Tiny rounded channels, ca. 0.05-0.09 μm in diameter with lumina difficult to resolve even at high power in S.E.M; [3] Tiny-moderate; [4] Moderate, round to oval pores, ca. 0.18-0.36 μm in diameter, with distinct lumina; [5] Moderate-large round, oval or irregularly shaped, window-like openings, ca. 0.90-2.50 μm in diameter; [9] No comparison, where pores absent.
56. Frequency of pores. Number of perforations found per flange. Range of values noted. Categories based on maximum frequency per flange.
States: [1] 1-3; [2] 4-6; [3] 7-9; [4] 10-12; [5] 13-15; [9] No comparison [see 55]
- [b] Interruptions/gaps [breaks in flange from margin to periclinal surface] i.c. and c. [Figs. 59, 60].
57. Presence of gaps.
States: [1] Absent; [2] Present.
58. Frequency of gaps. Number of interruptions per flange. Range of values noted. Categories based on maximum number found per flange and percentage of flanges interrupted.
States: [1] Rare, up to 3/flange; [2] Some [50%] to frequent [75% or more], 3-4/flange; [3] Frequent [75% or more] occasionally some, 5-7/flange; [4] Frequent [75% or more], 7-8/flange; [5] Frequent, more than 8/flange; [9] No comparison, where gaps absent.
59. Presence of double flanges. Presence of groove/furrow in middle lamella region of flanges [see Figs. 39, 67]. i.c. and c.
States: [1] Absent; [2] Present.

60. Presence of triple flanges at cell corners.
 Presence of two grooves either side of middle lamella [see Fig. 68]. Adx. only.
States: [1] Absent; [2] Present.
61. Flange shape at cell corners. Presence of lateral thickening at junction of flanges at corners of cells [independent of scrobiculi]. i.c. and c.
States: [1] Lumen outline angular, thickening absent; [2] Lumen outline rounded, thickening present.
62. Presence of cutin extension/peg at corner where non-specialised flanges meet. i.c. and c. [see Figs. 69-72].
States: [1] Absent; [2] Present.
- Nos. 63-64. Margin of non-specialised flange. i.c. and c. [Figs. 61, 63-66].
63. Form of margin.
States: [1] Even, regular; [2] Uneven, irregular [with jagged outline].
64. Amplitude of margin irregularities. Size of irregularities determined from micrographs. Unevenness due to nature of sculpture and small irregularities at margin of larger uneven portions or teeth not included. Maximum height of teeth from crest to base measured in units [1 unit = 0.36 μm] at $\times 2500$.
States: [1] 0.5-2.5 units; [2] 3.0-5.0; [3] 5.5-7.5; [4] 8.0-10.0; [5] 10.5-12.5; [9] No comparison, when margin even.
65. Presence of cavities in curved to undulate flange type. Presence of hollow at each undulation crest in flanges. i.c. and c. [All taxa with at least some curved/undulate flanges].
States: [1] Absent; [2] Present [e.g. Figs. 39-41].

66. Presence of secondary flanges. Presence of secondary divisions of cells each marked by especially low flange orientated across cell [see Fig. 70]. Adx. only. States: [1] Absent; [2] Present.
67. Development of veins on inner surface. Determined and scored in same way as character 37.

STOMATAL FEATURES

Subsidiary cell characters scored as [9], by convention, in Austrobaileya scandens, due to anomocytic stomatal arrangement.

Nos. 68-75. From light microscopic observations of isolated cuticles.

68. Type of stomata.
States: [1] Anomocytic; [2] Paracytic.
69. Distribution of stomata.
States: [1] On one leaf surface [abx], [2] On both leaf surfaces [abx. and adx]; [9] No comparison, on stem [in Cassytha].
70. Arrangement of stomata.
States: [1] Not regularly arranged [random]; [2] Regularly arranged [in rows].

Nos. 71-72. Number of stomata.

71. Stomatal density. Average number of complexes per grid square from 16 randomly selected grid squares [each 1.8 mm²].
States: [1] 1.5-10.4; [2] 10.5-19.4; [3] 19.5-28.4; [4] 28.5-37.4.
72. Stomatal index. Average $\frac{S}{E + S} \times 100$, where S = total number of stomata, E = total number of epidermal cells per grid square from 16 randomly selected grid squares.

72. Continued.....
States: [1] 0.7-6.9; [2] 7.0-13.2; [3] 13.3-19.5;
 [4] 19.6-25.8.
73. Size of stomatal apparatus. Size range estimated from camera lucida drawings (x 10 objective) of complexes in 16 randomly selected grid squares, using circles of varying diameters [1 unit = 8 μ m].
States: [1] 1-2 units; [2] 2-3; [3] 3-4; [4] 4-5.
74. Number of stomata in contact. Average number of times subsidiary cells of adjacent stomata touch [i.e. are contiguous] per grid square from 16 randomly selected grid squares.
States: [1] 0.00-0.89; [2] 0.90-1.79; [3] 1.80-2.69;
 [4] 2.70-3.59; [5] 3.60-4.49; [6] 4.50-5.39.
75. Presence of giant stomata.
States: [1] Absent; [2] Present [e.g. Figs.103,104].
- Nos. 76-85. From S.E.M. observations of isolated cuticles.
76. Presence of striae on outer surface of guard cell.
States: [1] Absent; [2] Present [concentric type].
77. Course of subsidiary cell/surrounding cell flange in surface view. Determined and scored in the same way as character 3.
78. Presence of subsidiary cell polar papillae.
States: [1] Absent; [2] Present [see Text-Fig. 24 A].
- Nos. 79-82. Striae on outer surface of subsidiary cell.
79. Presence of striae.
States: [1] Absent; [2] Present.
- Nos. 80-82. Type of striae.
80. Concentric.

81. Lateral.

82. Radiating.

States: [1] Absent; [2] Present; [9] No comparison where non-striate.

83. Degree of prominence of wall between adjacent subsidiary cells as seen in surface view.

States: [see Text-Fig. 18 C-E]. Subsidiary cells [1] Discrete, wall prominent; [2] Partially discrete, wall less prominent or of variable prominence; [3] Apparently fused, wall invisible.

Nos. 84-85. Stomatal pit features. [see Text-Fig.18 A,B].

84. Shape of pit in surface view. Expressed in terms of length PL: width PW ratio. Average calculated from measurements of 5 stomata. Non-linear scale of scoring adopted due to exponential increase of values.

States: [1] 0.7-1.2; [2] 1.3-2.3; [3] 2.4-4.4; [4] 4.5-8.5; [5] 8.6-16.6; [9] No comparison, where pit absent.

85. Presence of tridentate polar pit walls.

States: [1] Absent; [2] Present; [9] No comparison [see 84].

Nos. 86-114. From camera lucida drawings of transverse sections of representative stomata prepared under x 100 objective and observed by light microscopy. [1 unit = 0.61 μ m].

86. Guard cell size. Assigned to nearest size range using circles of varying diameter defined by radius aid.

States: [1] 3-5 units; [2] 5-7; [3] 7-9; [4] 9-11; [5] 11-13.

Nos. 87-88. Extent of thickening of guard cell walls.

87. Extent of thickening of upper wall of guard cell.

88. Extent of thickening of lower wall of guard cell.

Treated separately since degree of thickening may differ between upper and lower walls. Determined by ratio

$$\frac{\text{wall thickness}}{\frac{1}{2} \text{ guard cell height}}$$

States: [see Text-Fig. 14]. [1] Very little, between 0 and 1/3 wall thickened; [2] Moderate, between 1/3 and 2/3 wall thickened; [3] Massive, between 2/3 and 1 wall thickened.

Nos. 89-90. Thickness of guard cell cuticle.

89. Thickness of guard cell periclinal cuticle.

Measured in units in region b (Text-fig. 15 B,C).

States: [1] 0.5-5.5 units; [2] 6.0-11.0; [3] 11.5-16.5; [4] 17.0-22.0.

90. Thickness of cuticle at guard cell/subsidiary cell flange. Measured in region GSF (Text-Fig.15B,C).

States: [1] 0.5-8.0 units; [2] 8.5-16.0 [3] 16.5-24.0; [4] 24.5-32.0.

91. Prominence of guard cell/subsidiary cell flange.

Approximate depth estimated by inspection and compared with depth where guard cell meets inner periclinal wall of subsidiary cell.

States: [1] Very low, between 0 and ¼ depth; [2] Low, between ¼ and ½ depth; [3] Moderate, between ½ and ¾ depth; [4] Deep, between ¾ and 1 depth.

92. Shape of guard cell/subsidiary cell flange. Scored in same way as character 16.

93. Length of guard cell outer ledge. Length l measured in units half way along width at base of ledge to tip [see Text-Fig. 16 A].

93. Continued....
States: [1] 1.0-5.0 units; [2] 5.5-9.5;
 [3] 10.0-15.0; [4] 15.5-19.5.
94. Width at base of guard cell outer ledge. Width W measured in units across base of outer ledge where ledge projects from guard cell to where it apparently meets wall lining outer stomatal cavity [see Text-Fig. 16 A].
States: [1] 1.5-4.5 units; [2] 5.0-8.0 [3] 8.5-11.5;
 [4] 12.0-15.0.
- Nos. 95-96. Curvature of outer ledge.
95. Curvature of outer ledge apex.
96. Curvature of outer ledge base.
- Treated separately as patterns at base and apex may differ. Configuration assigned by inspection.
States: [see Text-Fig. 16 B-E]:
 [1] Incurved; [2] Straight; [3] Outcurved.
97. Degree of cutinisation of guard cell inner ledge . Indicated by intensity of colour reaction when stained with alcoholic Sudan IV.
States: [1] Colourless [least cutinised];
 [2] Pink; [3] Red [most cutinised].
98. Prominence of guard cell inner ledge . Length l measured in units from lowermost point of projection on guard cell inner periclinal wall to tip of ledge [see Text-Fig. 16 A]. Used in preference to median length since it is more variable between taxa.
States: [1] 1.5-6.5 units; [2] 7.0-12.0;
 [3] 12.5-17.5; [4] 18.0-23.0.
99. Presence of outer and inner cavities.
States: [1] Absent [e.g. Text-Fig. 21 A];
 [2] Present [e.g. Text-Fig. 21 B].

100. Depth of stomatal pit (suprastomatal cavity).
 Determined by measuring depth in units, from highest point reached by subsidiary cell outer periclinal wall to where guard cell meets subsidiary cell [see Text-Fig. 15 A].
States: Guard cells [1] Raised, $h =$ positive; [2] Level, $h = 0$; [3] Sunken, $h =$ negative 0.5-4.5 units; [4] Sunken, $h =$ negative 5.0-9.0, [5] Sunken, $h =$ negative 9.5-13.5; [6] Sunken $h =$ negative 14.0-18.0.
101. Presence of stomatal flap.
States: [1] Absent; [2] Present.
102. Subsidiary cell height. Measured in units from highest point reached by subsidiary cell outer periclinal wall to lowest point attained by subsidiary cell inner periclinal wall.
States: [1] 18.0-27.5 units; [2] 28.0-37.5; [3] 38.0-47.5; [4] 48.0-57.5.
103. Thickness of uncutinised subsidiary cell outer periclinal wall compared with thickness of subsidiary cell inner periclinal wall.
States: [1] Not obviously thickened; [2] Obviously thickened.
104. Curvature of subsidiary cell outer periclinal wall.
 Concavity to convexity expressed in terms of ratio $h:b$, where h is maximum height of subsidiary cell wall above [or below] anticlinal borders (AB) and b is width across subsidiary cell from border with guard cell to border with surrounding cell [see Text-Fig. 15 A]. Scored in same way as character 5.
105. Orientation of subsidiary cell periclinal wall relative to guard cell in sunken stomata. Representing degree to which subsidiary cells over-top guard cells. Indicated by angle between guard cell border and tangent to stomatal pit wall (a_1 in Text-Fig. 15 A). Measured using protractor.

105. Continued....
States: [1] 3.5-42.0°; [2] 42.5-81.0°; [3] 81.5-120.0°; [4] 120.5-159.0°; [9] No comparison, where stomata not sunken.
106. Orientation of subsidiary cell periclinal wall relative to surrounding cell in sunken stomata.
 Angle between level of surrounding cell border and tangent to part of adjacent subsidiary cell outer periclinal wall (and cuticle) (a_2 in Text-Fig. 15 A), reflecting steepness. Measured using protractor.
States: [1] -17.0-0.0°; [2] 0.5-17.5°; [3] 18.0-35.0°; [4] 35.5-52.5°; [5] 53.0-70.0°; [9] No comparison [see 105].
- Nos. 107-108. Thickness of subsidiary cell cuticle [1 unit = 0.61 μm].
107. Median thickness of subsidiary cell periclinal cuticle. Measured in units in region c, [Text Fig. 15 B,C].
States: [1] 0.5-4.5 units; [2] 4.6-8.6; [3] 8.7-12.7; [4] 12.8-16.8.
108. Thickness of cuticle at subsidiary cell/surrounding cell flange. Measured in units in region SOF, [Text-Fig. 15 B,C].
States: [1] 0.5-8.0 units; [2] 8.5-16.0; [3] 16.5-24.0.
109. Prominence of subsidiary cell/surrounding cell flange. Approximate depth of flange in wall between subsidiary cell and surrounding cell estimated by inspection. Scored in same way as character 15.
110. Shape of subsidiary cell/surrounding cell flange
 Scored in same way as character 16.

111. Obvious specialisation of surrounding cell adjacent to subsidiary cell.
States: [1] Not obviously specialised;
 [2] Obviously specialised [with greater periclinal curvature than other ordinary cells.
- Nos. 112-114. Lignification of stomata.
112. Presence of lignin in guard cell thickenings.
113. Presence of lignin in guard cell outer ledges.
114. Presence of lignin in subsidiary cell outer periclinal wall. Scored in same way as characters 19-30.
- Nos. 115-181. From inner surface of isolated cuticles viewed with scanning electron microscopy.
- Nos. 115-119. Form of guard cell 'wing'. In Lauraceae only.
115. Shape of guard cell 'wing'. Expressed in terms of ratio $l_1:w$, where l_1 is wing length and w is wing width at widest point [see Text-Fig. 15 D].
 Measured from micrographs. Average of 5 calculated.
States: [1] 1.3-5.2; [2] 5.3-9.2; [3] 9.3-13.2;
 [4] 13.3-17.2; [5] 17.3-21.2; [9] No comparison, in families related to Lauraceae.
116. Shape of guard cell 'wing' tip.
States: [1] Pointed/sharp [e.g. Figs. 119, 120];
 [2] Blunt/rounded [e.g. Fig. 113]; [9] No comparison [see 115].
117. Presence of peg on 'wing' margin.
States: [1] Absent; [2] Present [e.g. Fig. 124];
 [9] No comparison [see 115].

118. Prominence of guard cell 'wing' beyond aperture.
 Determined from ratio $l:l_1$, where l is aperture length and l_1 is wing length [see Text-Fig. 15 D]. Measured from micrographs. Average of 5 calculated. States: [1] 0.40-0.68; [2] 0.69-0.97; [3] 0.98-1.26; [4] 1.27-1.55; [9] No comparison [see 115].
119. Prominence of guard cell 'wing' relative to subsidiary cell boundary. Expressed by ratio $l_1:l_2$, where l_1 is wing length and l_2 is subsidiary cell polar length [see Text-Fig. 15 D]. Measured from micrographs. Average of 5 calculated. States: [1] 0.47-0.61; [2] 0.62-0.76; [3] 0.77-0.91; [9] No comparison [see 115].
- Nos. 120-123. Guard cell polar thickening. [see Text-Fig. 17, Figs. 131-138].
120. Presence of polar thickening in guard cells.
States: [1] Absent; [2] Present; [9] No comparison, where guard cells not marked on cuticle, i.e. in Lauraceae.
121. Type of polar thickening.
States: [1] Incomplete rod; [2] Incomplete rod and bar; [3] Complete rod and bar [= T-piece]; [9] No comparison [see 120].
122. Width of polar rods.
States: [1] Faint [broken line of cutin particles, diameter ca. less than 1.0 μm , commonly 0.50-0.75 μm]; [2] Thin [unbroken line, diameter same as [1]]; [3] Thick [unbroken line, diameter ca. 1.0 μm or more, commonly 2.0 μm]; [9] No comparison [see 120].
123. Length of incomplete rods.
States: [1] Short [ca. 1/3 distance between aperture and pole; [2] Long [ca. 2/3 distance between aperture and pole]; [9] No comparison [see 120].

- Nos. 124-130. Fine sculpture of periclinal surface of guard cell. Measured and scored in same way as characters 38-44.
131. Presence of striae on inner surface of guard cell.
Scored as character 45.
- Nos. 132-138. Fine sculpture of guard cell/subsidiary cell flange. Measured and scored in same way as characters 38-44.
139. Presence of gaps [interruptions] in guard cell/subsidiary cell flange.
States: [1] Absent; [2] Present.
- Nos. 140-151. Subsidiary cell polar thickening [see Text-Figs. 19, 20].
140. Presence of polar lateral lines [cutin lines].
States: [1] Absent; [2] Present.
141. Strength of polar lateral lines.
States: [1] Faint (broken line of cutin particles); [2] Strong (unbroken line of cutin); [9] No comparison, where lines absent.
142. Shape of polar lateral lines in surface view.
States: [1] Concave, incurved from 'wing' tip to pole; [2] Straight, with no deviation from 'wing' tip to pole; [3] Convex, outcurved from 'wing' tip to pole; [9] No comparison [see 141].
143. Presence of fusion of polar lateral lines.
States: [1] Absent (not fused); [2] Present (fused about half way between 'wing' tip and pole); [9] No comparison [see 141].
144. Presence of polar rods [centrally placed rod-like thickening orientated along common wall between adjacent subsidiary cells].
States: [1] Absent; [2] Present.

145. Width of polar rods. Scored in same way as character 122. [9] No comparison, where rods absent.

146. Height of polar rods.

States: [1] Low, barely raised above periclinal surface [almost level]; [2] Prominent, conspicuously raised above periclinal surface; [9] No comparison [see 145].

147. Presence of polar bars [cutin cross-piece located at poles, at 90° to common wall between subsidiary cells].

States: [1] Absent; [2] Present.

Nos. 148-158. Type of polar bar.

148. Knob-type.

149. Triangular.

150. Lens-shaped.

States: [1] Absent; [2] Present; [9] No comparison, where bars absent.

151. Presence of apical thickening of subsidiary cell [knob-like thickening at point where lateral lines, or bars meet subsidiary cell/surrounding cell flange.

States: [1] Absent; [2] Present.

Nos. 152-158. Fine sculpture of periclinal surface of subsidiary cell. Measured and scored in same way as characters 38-44.

Nos. 159-160. Scrobiculi [depressions corresponding to dome/papilla externally].

159. Presence of conspicuous scrobiculus on subsidiary cell inner surface.

States: [1] Absent; [2] Present.

160. Percentage of subsidiary cell forming scrobiculus.
Expressed by ratio of maximum diameter of scrobiculus to maximum diameter of subsidiary cell in half subsidiary cell pair. Measured approximately from micrographs.
States: [1] 1-25%; [2] 26-50%; [3] 51-75%; [4] 76-100%; [9] No comparison, where scrobiculus not defined.
- Nos. 161-164. Subsidiary cell striae [inner surface].
Recorded separately since outer and inner surfaces may differ. Described and scored in same way as characters 79-82.
165. Presence of terraced subsidiary cell [with 'step' on inner surface].
States: [1] Absent; [2] Present [see Fig. 111].
166. Presence of secondary division of subsidiary cell at angle to pore.
States: [1] Absent; [2] Present.
- Nos. 167-173. Fine sculpture of subsidiary cell/surrounding cell flange. Measured and scored in same way as characters 38-44.
- Nos. 174-178. Continuity of subsidiary cell/surrounding flange. Measured and scored in same way as characters 53-58.
- Nos. 179. Presence of peg at corner where surrounding cell flange meets subsidiary cell/surrounding cell flange. Scored in same way as character 62.
- Nos. 180-181. Margin of subsidiary cell/surrounding cell flange. Described and scored in same way as characters 63-64.

TRICHOME FEATURES

Nos. 182-185. From unmacerated leaf portions/isolated cuticles viewed with S.E.M.

Nos. 182-194. Simple hairs [non-glandular].

182. Presence of two distinct simple hair forms. Presence of micro- and macro-hairs on unmacerated leaf [see Fig. 139].

States: [1] Absent; [2] Present; [9] No comparison, simple hairs absent.

183. Persistence of simple hairs in cuticle preparations. Expressed in terms of frequency of persistence of hair bodies in isolated cuticles.

States: Hair bodies [1] never persistent [bases only detected]; [2] sometimes persistent [bases and portions of bodies detected]; [3] usually persistent [portions and whole bodies detected]; [9] no comparison [see 182].

184. Presence of simple hair bases.

States: [1] Absent; [2] Present.

185. Frequency of simple hair bases. Number of hair bases per unit area [micrograph of field of view at x 320]. Range found from unmacerated leaf portions, outside and inside of isolated cuticles. Non-linear scale adopted due to exponential increase of values.

States: [1] 1-11; [2] 12-32; [3] 33-73; [4] 74-154; [5] 155-315; [9] No comparison [see 182].

Nos. 186-194. From isolated cuticles viewed with light microscopy.

Nos. 186-193. Type of simple hair base. Presence of one or more types described below.

186. Type 1. [see Text-Fig. 27 D].
187. Type 2. [see Text-Fig. 27 A,B].
188. Type 3. [see Text-Fig. 27 C].
189. Type 4. [see Text-Fig. 27 F].
190. Type 5. [see Text-Fig. 27 E]. Poral flange rounded.
191. Type 6. As 5, except poral flange polygonal.
192. Type 7. [see Text-Fig. 26 A].
193. Type 8. [see Text-Fig. 26 B].

States: [1] Absent; [2] Present; [9] No comparison [see 182].

194. Number of simple hairs occurring together.
 Represented by number of hair pores occurring together sharing basal cells.
States: Hair pores [1] solitary [single]; [2] sometimes in pairs [also solitary]; [3] sometimes in three [also solitary and pairs]; [9] no comparison [see 182].

Nos. 195-198. From isolated cuticles observed by light- and scanning electron-microscopy as well as transverse sections.

195. Presence of glandular hairs.
States: [1] Absent; [2] Present.

Nos. 196-198. Type of glandular hair body.

196. Pyriiform [see Text-Figs 28 B, 29 A-C and Fig. 145].
197. Peltate [see Text-Figs 28 A, 29 D and Fig. 146].

198. Digitate [see Text-Fig. 28 C,D].

States: [1] Absent; [2] Present; [9] No comparison, where glands absent.

No. 199. From T.S. leaf viewed with light microscopy.

199. Position of glandular hair base.

States: [1] Superficial, more or less level with outer surface [Text-Fig. 28 B]; [2] Sunken conspicuously located in pit, well below outer surface [Text-Fig. 28 A]; [9] No comparison [see 198].

Nos. 200-206. From isolated cuticles viewed with light microscopy.

CORK WART FEATURES

200. Presence of cork warts. Recognised as groups of cells arranged in strict radial files.

States: [1] Absent; [2] Present.

Nos. 201-203. Type of cork wart.

201. Type 1. [see Text-Fig. 30 A].

202. Type 2. [see Text-Fig. 30 C].

203. Type 3. [see Text-Fig. 30 B].

States: [1] Absent; [2] Present; [9] No comparison, where cork warts absent.

SECRETORY CELL FEATURES

204. Presence of secretory cells. Recognised as a rounded/polygonal central area with very thin cuticle, bounded by distinct flange and ring of basal cells.

States: [1] Absent; [2] Present.

Nos. 205-206. Type of secretory cells.

205. Type 1. [see Text-Fig. 31 C].

206. Type 2. [see Text-Fig. 31 A,B].

States: [1] Absent; [2] Present; [9] No comparison,
where secretory cells absent.

14.7 RESULTS

14.7.1 PRINCIPAL CO-ORDINATES ANALYSIS

The distribution of OTUs based on both character subsets is very complicated.

In the 154 character analysis using all stomatal and 40 selected abaxial cuticular inner surface features [Text-Fig. 32], Lauraceae [closed circle] are distributed throughout the diagram, but predominantly in the right half. Related families are scattered in the left half; the Gomortegaceae [open circle 75] and Trimeria spp. [open square 76, 77] being most closely associated with Lauraceae; the Hernandiaceae [open triangle], except Sparattanthelium guianense [86], located towards the far left with Gyrocarpus americanus subspecies [80, 81] distinct from other family members in the lower left region and Austrobaileyaceae [open hexagon 79] occupying an isolated position in the bottom left-hand corner.

Within the Lauraceae, species of a genus [where more than one has been studied] sometimes fall close together indicating high interspecific affinity, e.g. in Aiouea [3,4], Caryodaphnopsis [12,13], Endiandra [28,29], Eusideroxylon [32,33], Laurus [35,36], Nectandra [47,48], Neocinnamomum [49,50] and Potameia [65,66]. In other genera, however, constituent species are widely separated suggesting a less strong interspecific relationship, as in Alseodaphne [5,6] and Nothaphoebe [53,54] on axis I; Actinodaphne [1,2], Beilschmiedia [10,11], Lindera [39,40], Mezilaurus [44,45] and Phoebe [60,61] on axis II or, Litsea [41-43] and Ravensara [67-69] on both principal axes. In Persea, two species P. chinensis and P. thunbergii [58,59] appear very closely related. The third species, P. americana, is somewhat separated from them on axes I and II showing that within a genus some species exhibit greater interspecific affinity than others.

The genus Litsea [41-43] forms a wide triangular distribution in the centre of the diagram and provides a reference point for assigning possible generic relation-

TEXT-FIGURE 32. Principal co-ordinates analysis OTUs.
Distribution obtained from analysis of all stomatal
characters and selected abaxial intercostal inner cuticular
features.

Open hexagon = Austrobaileyaceae

Open circle = Gomortegaceae

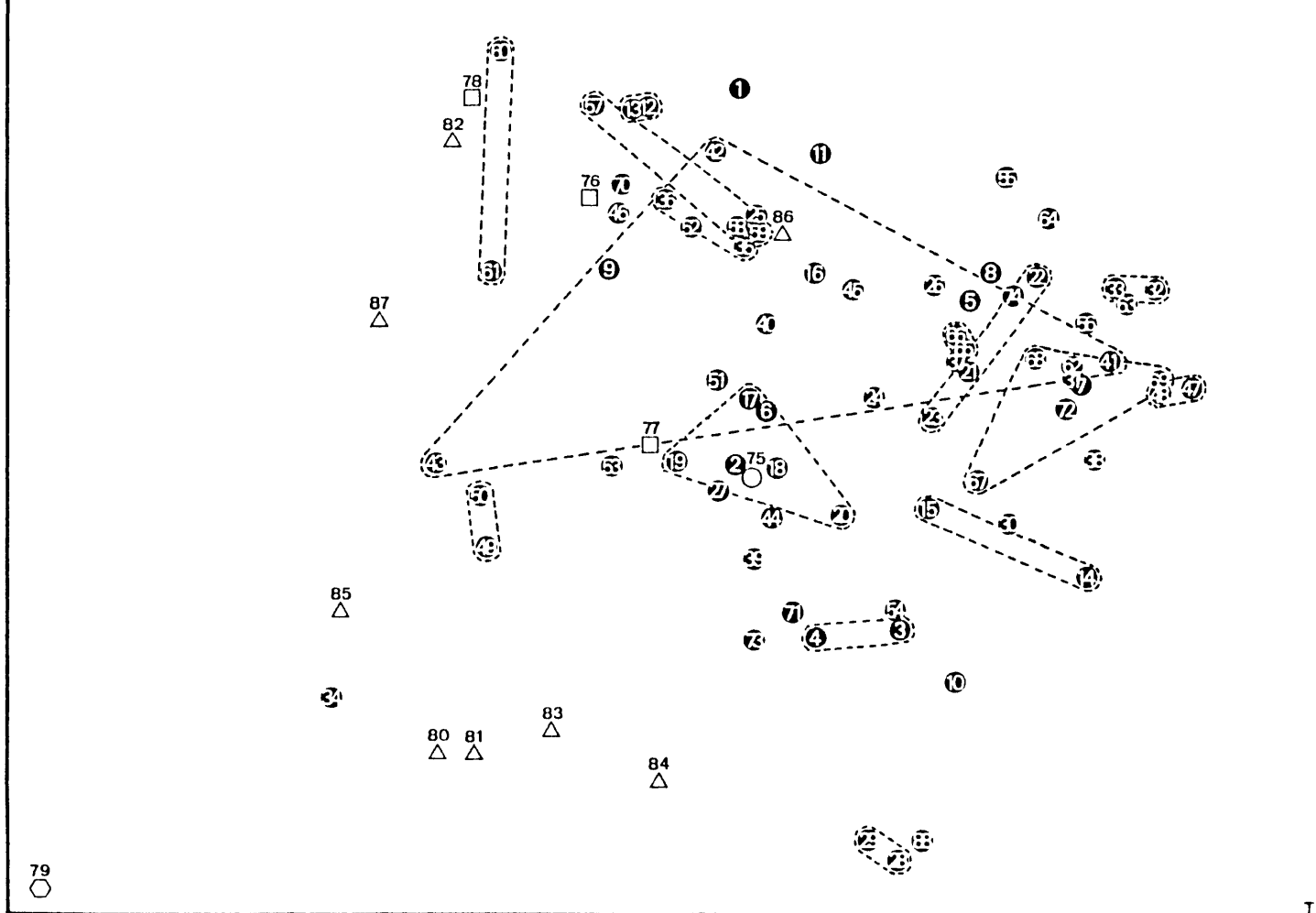
Open triangle = Hernandiaceae

Closed circle = Lauraceae

Open square = Trimeniaceae

[Numbers correspond to those of OTUs in Tables II-IV].

II



I

ships within the Lauraceae. At the top of the triangle (near L. monopetala [42], Persea [57-59] may be found. Adjacent, outside the Litsea distribution, occurs Caryodaphnopsis [12,13], Micropora [46], Sassafras [70] and, further to the left, Phoebe [60,61].

Neocinnamomum [49,50] falls below L. umbellata [43] on the extreme left of the Lauraceae group as does Hypodaphnis [34] even more remote amongst the Hernandiaceae.

In the lower centre of the diagram (and along the base of the Litsea 'triangle') occurs a triangular area formed by three of the four representatives of Cinnamomum [17-20]. [18 falls inside this zone]. Also in the same region, are Lindera [39,40] and Mezilaurus [44,45]. Below the Cinnamomum group fall Dodecadenia [27], Nothaphoebe [53,54], Sassafridium [71], Umbellularia [73] and finally, furthest away, Aiouea [3,4]. Endiandra [28,29] and the unknown taxon [88] are distributed at the very bottom of the diagram, well separated from other Lauraceae.

Near to L. meissneri [41] at the right corner of the Litsea triangle, two other areas are formed by species of respectively Cryptocarya [21-23] above and Ravensara [67-68] below. Phyllostemonodaphne [62] and Systemonodaphne [72] fall within the region bounded by Ravensara. Nectandra [47,48] is positioned close by to the left of this group. Beneath Ravensara lies Cassytha [14,15]. Just above L. meissneri, near Cryptocarya, Ocotea [55,56], Pleurothyrium [63,64] and Eusideroxylon [32,33] are found. Closely associated with Cryptocarya is Urbanodendron [74]. Aniba [78], Endlichera [30,31] and Licaria [38,39] are also distributed in this left 'corner' region near to L. meissneri.

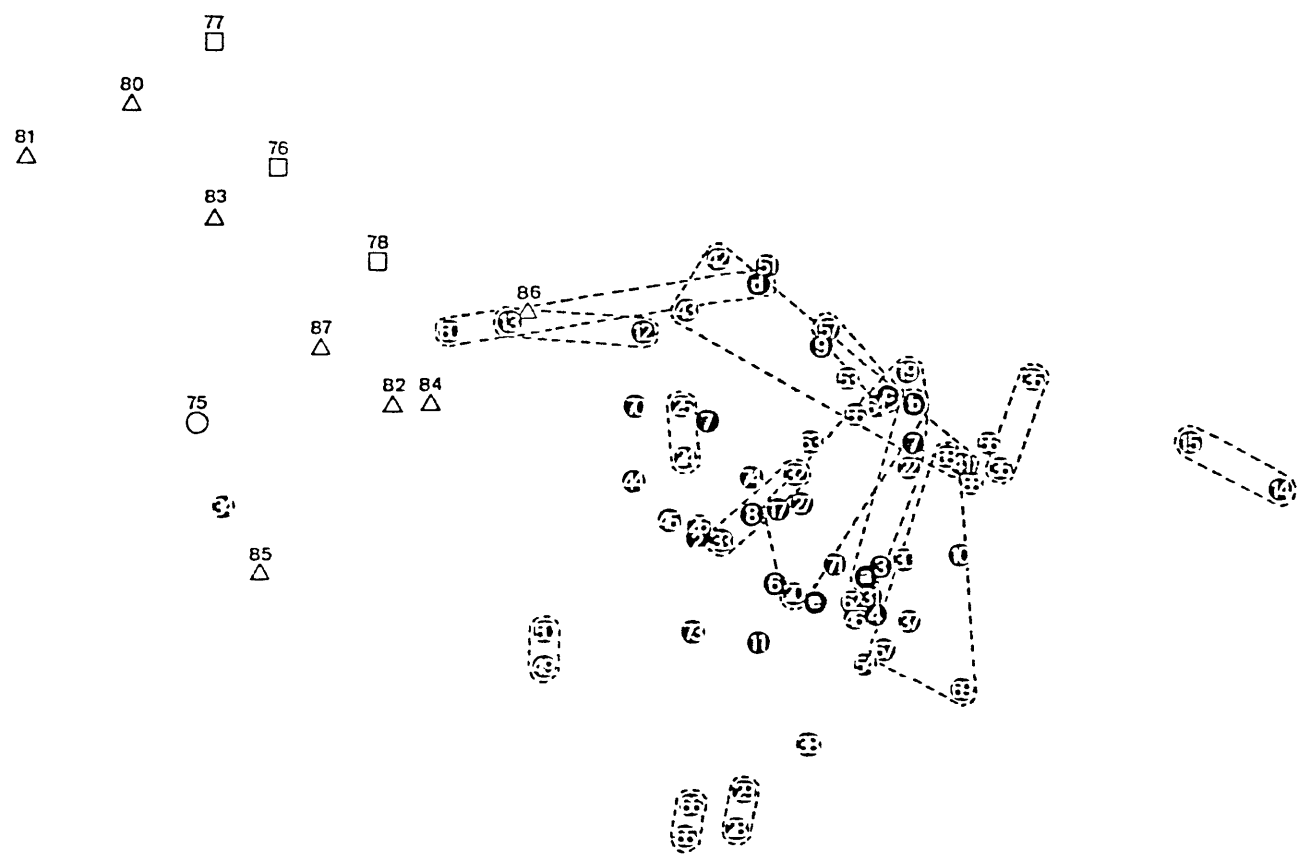
Within the area bounded by Litsea, fall Laurus [35,36] very close to Persea, Dicypellium [26] and Potameia [65, 66] especially, near to Cryptocarya and Alseodaphne [5,6], Dehaasia [24,25] and Cinnadenia [16] in the centre zone. The widely separated species of Actinodaphne [1,2] and Beilschmiedia [10,11] fall in the central region

TEXT-FIGURE 33. Principal co-ordinates analysis OTUs.
Distribution obtained from analysis of 60 selected stomatal
characters.

[symbols representing families as in Text-figure 32].

a	=	21,72
b	=	23,18
c	=	16,39,40,58,59
d	=	1,52,61
e	=	47,48

II



79
○

I

of the diagram.

In the 60 character analysis based on selected stomatal features only [Text-Fig. 33] the Lauraceae have been drawn together almost entirely in the right half of the diagram, away from members of related families on the left. Trimeniaceae form a distinct group at the periphery of the upper left quarter with Piptocalyx [78] more closely related to Lauraceae than Trimenia [76,77]. Gomortegaceae falls to the far left of centre in the upper quarter separated from most Lauraceae, except Hypodaphnis zenkeri [34], by Hernandiaceae. The latter family has a scattered distribution with Gyrocarpus americanus subspecies [80,81] separate from other members in the top left-hand corner and Illigera [84,85] left of centre. Sparattanthelium guianense [86] is closest to the main Lauraceae group. Austrobaileyaceae [79] again, is isolated in the bottom left-hand corner, even further from the rest of the assemblage than in the 154 character analysis.

By selecting characters which show generic constancy in this analysis, some unrelated Lauraceae taxa have identical values on axes I and II, i.e. Cryptocarya ainikini [21] and Systemonodaphne mezii [72] [a]; Cryptocarya weinlandii [23] and Cinnamomum iners [18] [b]; Cinnadenia paniculata [16], Lindera spp. [39,40], Persea chinensis and P. thunbergii [58,59] [c]; Actinodaphne glomerata [1], Neolitsea dealbata [52] and Phoebe sheareri [61] [d]; Nectandra spp. [47,48] [e]. These taxa are obviously not the same in all other micromorphological features, only those chosen for use in the analysis. This is, perhaps, the main disadvantage of the selection technique applied.

The distribution of Lauraceae OTUs based on 60 stomatal characters is similar in some ways to that involving 154 characters. It demonstrates, particularly, the isolation of Hypodaphnis [34] from other family members and its affinity with the Hernandiaceae to the left of the diagram. It also supports the segregation of

Neocinnamomum [49,50], Endiandra [28,29] and most especially Cassytha [14,15]. Phoebe [60,61] and Caryodaphnopsis [12,13] more or less retain their general position to the left of the Litsea 'triangle', also Cryptocarya [21-23] and Ravensara [67-69] to the right and Umbellularia [73] in the lower centre.

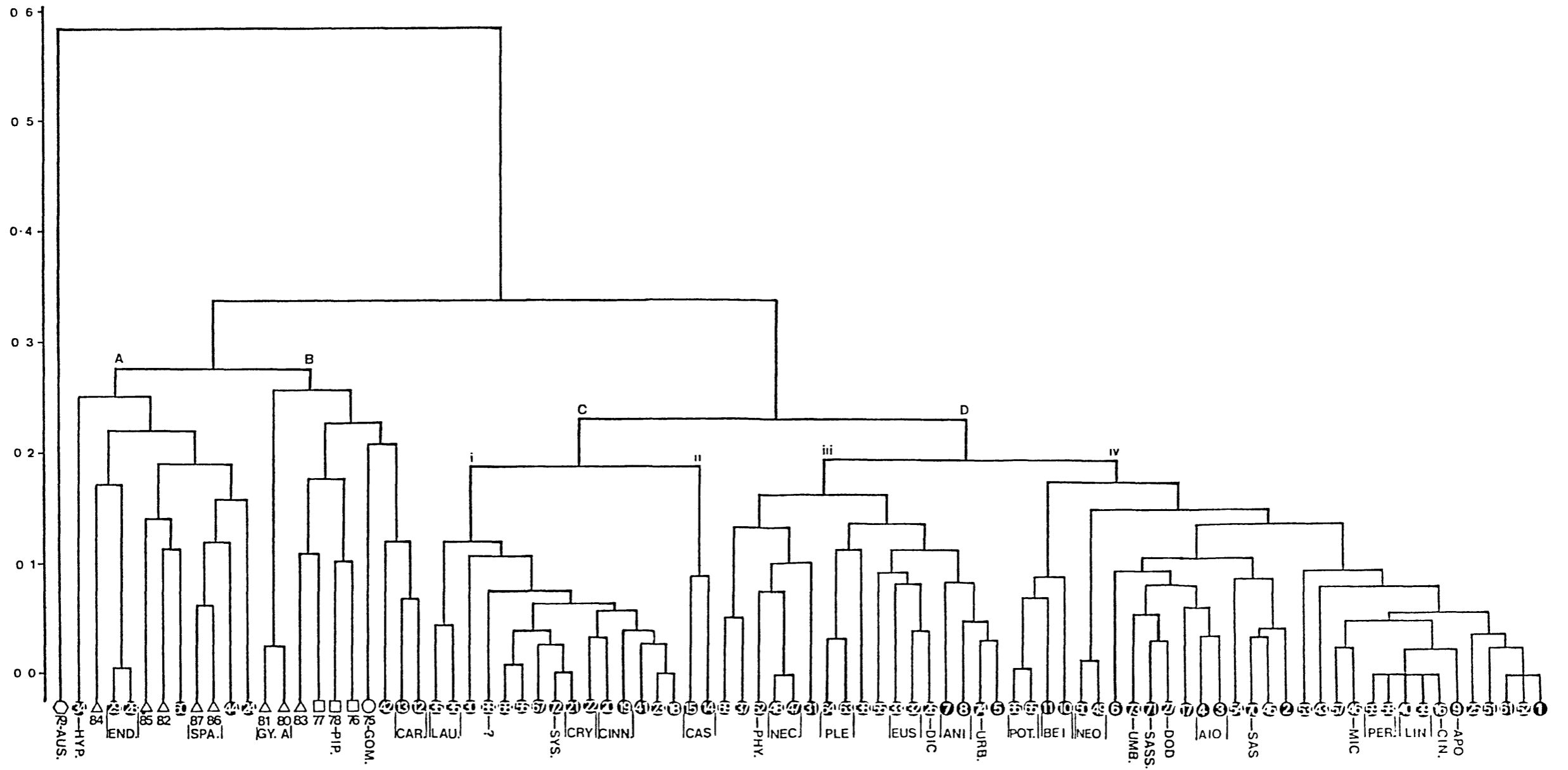
Some of the group that are bounded by Litsea in the 154 character analysis fall outside in that based on 60 characters, e.g. Dehaasia [24,25] and Dicypellium [26] in the centre of the diagram and most particularly Laurus [35,36] to the right of L. meissneri [41]. Cinnamomum [17-20] is distributed closer to Cryptocarya. Eusideroxylon [32,33] is found in the centre of the diagram near to Urbanodendron [74] unlike in the 154 character analysis where it appears discretely above the right-hand corner of the Litsea distribution along with Ocotea and Pleurothyrium. The latter two genera, however, are still located in this general area although no longer separated. Persea [57-59] is located nearer to L. meissneri [41] than to L. monopetala [42] in this analysis. The unknown taxon [88], close to Endiandra [28,29] in the 154 character analysis, falls slightly to the right of L. meissneri [41] and well away from Endiandra, especially on axis II, when fewer characters are utilised.

In general, the distribution based on the subset of 60 stomatal features gives good separation of the related families from the Lauraceae but does not give a clear representation of the sub-divisions present within this family. Clusters of genera seem more evident when the larger subset of data is analysed.

14.7.2 CLUSTER ANALYSIS

The dendrogram resulting from the analysis of 60 selected stomatal characters [Text-Fig. 34] shows that at a very low level of similarity Austrobaileya scandens [open hexagon 79] separates off from all other OTUs [see extreme left]. The remainder of the assemblage is further divided into two main clusters: the left, containing members of the related families [i.e. Gomortegaceae,

TEXT-FIGURE 34. Cluster Analysis dendrogram based on 60 selected stomatal characters. [OTUs numbered according to Table II].



Hernandiaceae and Trimeniaceae] as well as a few Lauraceae [closed circles] and the right, composed entirely of Lauraceae.

Each of these clusters are also divided into two subclusters [A and B, C and D]. Those on the right, C and D, are further separated into smaller clusters, [i] and [ii], [iii] and [iv] respectively. [i] includes most of the Cinnamomum, Cryptocarya and Ravensara species examined also Laurus spp. [35,36] and Systemonodaphne mezii [72]; [ii] comprises of Cassytha spp. [14,15] only; [iii] contains members of such genera as Aniba [7,8], Dicypellium [26], Eusideroxylon [32,33], Licaria [37,38], Nectandra [47,48], Phyllostemonodaphne [62], Pleurothyrium [63,64] and Urbanodendron [74], and [iv] incorporates species of Actinodaphne [1,2], Aiouea [3,4], Apollonias [9], Beilschmiedia [10,11], Cinnadenia [16], Dodecadenia [27], Lindera [39,40], Micropora [46], Neocinnamomum [49,50], Neolitsea [51,52], Nothaphoebe [53,54], Persea [57-59], Potameia [65,66], Sassafras [70], Sassafridium [71] and Umbellularia [73], amongst others. Due to the method of character selection some OTUs are shown as identical [i.e. with a y value of 0.0]. These OTUs also have the same position in the principal co-ordinate analysis involving these 60 characters.

Also, because of the way in which the characters were selected, it is to be expected that individual species of a genus [where more than one has been studied] should pair together in the dendrogram. This is the case with species of Endiandra [28,29], Neocinnaomomum [49,50], Pleurothyrium [63,64] and Potameia [65,66] at very high levels of similarity and species of Aiouea [3,4], Caryodaphnopsis [12,13], Cassytha [14,15], Laurus [35,36] and Sparattanthelium [86,87] at slightly lower levels. The two subspecies of Gyrocarpus americanus also pair as anticipated.

Often, however, an individual species of one genus is most similar in the selected characters to one or more non-related species. Pairing may, therefore, involve

members of two different genera in the same family, e.g. Trimenia papuana [76] and Piptocalyx moorei [78] of the Trimeniaceae; Ravensara elliptica [68] and Ocotea laevis [56], and Persea americana [57] and Micropora curtisii [46] of the Lauraceae. Alternatively, a pair may comprise of representatives of two different families suggesting strong interfamilial affinity. In subcluster A of the main left cluster, Hernandia nymphiifolia [82] of the Hernandiaceae is most similar to Phoebe opaca [60] of the Lauraceae. In subcluster B, H. olivacea [83] pairs with Trimenia weinmanniaefolia [77] of the Trimeniaceae.

Species of a genus, although not both pairing immediately together, do sometimes fall in the same small cluster, such as Aniba spp. [7,8] with Urbanodendron verrucosum [74] and Alseodaphne oblanceolata [5], Eusideroxylon spp. [32,33] with Dicypellium caryophyllum [26] in [iii] and Beilschmiedia spp. [10,11] with Potameia spp. [65,66] in [iv].

In other cases, individual species of a genus occur in the same subcluster, e.g. Illigera spp. [84,85] in A of the main left cluster, Licaria spp. [37,38] in D [iii] and Persea spp. [57-59] in D [iv] of the main right cluster.

Sometimes, species of a genus are widely separated on the basis of these characters, such as Dehaasia caesia [24] in subcluster A and D. cuneata [25] in D [iv], Hernandia olivacea [83] in subcluster B and H. nymphiifolia [82] in A of the main left cluster, and Endlicheria piriformis [30] in subcluster C [i] and E. reflectens in D [iii] of the main right cluster.

Certain OTUs seem to occupy isolated positions within the subclusters, notably Hypodaphnis zenkeri [34] in subcluster A and Gyrocarpus americanus subspecies [80,81] in B of the left main cluster, also Laurus spp. [35,36] in subcluster C [i] and most particularly Cassytha spp. in its own subcluster [C[ii]], species of Potameia [65,66] and Beilschmiedia [10,11] as well as Neocinnamomum

[49,50] in D [iv].

In general, Lauraceae and the related families, except Austrobaileyaceae, show quite a high degree of similarity. Although members of a genus may resemble each other in the selected stomatal characters and pair together, sometimes an individual species is more similar to a non-related species than to another of the same genus or even family. Clusters of genera are more evident within the Lauraceae using this type of analysis than when principal co-ordinates are employed.

15. GENERAL DISCUSSION WITH SUGGESTIONS FOR FURTHER WORK

Five angiosperm families are represented in this study: Austrobaileyaceae, comprising of large climbing shrubs to high climbing lianas from Australia; Gomortegaceae, trees from Chile; Hernandiaceae, tropical trees, shrubs and some lianas; Lauraceae, tropical and subtropical trees and shrubs with a few parasitic climbers and Trimeniaceae, tropical trees and shrubs.

Despite the apparent homogeneity sometimes seen in leaf macromorphology of these Laurales, scanning electron- and light-microscopic investigations have revealed a wealth of micromorphology in cuticles of selected taxa. The value of the cuticle as a source of ^{taxonomically useful} characters in seed plants is well known [Florin, 1931; Stace, 1965a; Boulter, 1971; Dilcher, 1974; Barthlott & Ehler, 1977; Wilkinson, 1979; Barthlott, 1981; Oladele, 1981, 1983b] and results of the present study support this view.

The wide range of micromorphological features found may be divided into two main categories based on cell type: non-specialised and specialised. The first category is made up of characters of intercostal and costal areas describing general aspects of cells [size, shape and arrangement], the periclinal wall region [degree of cutinisation, curvature, pattern of folding, fine sculpture] and the anticlinal wall region [development of anticlinal borders, extent of cutinisation, flange shape in T.S. and surface view, flange width, continuity, margin form and fine sculpture]. The second category comprises stomatal, trichome, cork wart and secretory cell features. Stomata vary in a number of general ways: in type [including giant, vein and abnormal forms], distribution, arrangement, density/frequency, index, size and degree of contiguity. Other aspects varying between taxa involve guard cells e.g. size, extent of wall thickening and cutinisation [including stomatal flap], outer and inner ledge form, presence of outer and inner cavities, type of polar thickening, pattern of folding, fine sculpture of periclinal and anticlinal surfaces, as well as flange shape, continuity and margin form. Alternatively,

interspecific variation may concern subsidiary cell characters such as, height, curvature and orientation of the outer periclinal wall in T.S., degree of cutinisation, depth of stomatal pit, definition of wall at poles on outer surface, presence of polar papillae, type of polar thickening [in Lauraceae only], terracing, pattern of folding, fine sculpture of periclinal and anticlinal surfaces, flange shape, continuity and margin form and presence of secondary anticlinal divisions. Trichome features showing differences include occurrence, type, frequency, persistence in cuticle preparations, body form, degree of cutinisation, base type, grouping, number of constituent cells and position with respect to leaf surface. Cork warts and secretory cells vary in occurrence, distribution, type and extent of cutinisation.

Rather few cuticular characters have been described in members of the families related to Lauraceae, by previous workers. In Austrobaileyaceae, details of ridging/folding of the abaxial cuticle [Bailey & Swamy, 1949; Metcalfe & Chalk, 1950], degree of cutinisation [Bailey & Swamy, 1949], stomatal type, distribution, size [Metcalfe & Chalk, 1950; Roth, 1981] and shape [Metcalfe & Chalk, 1950] are known in addition to absence of trichomes [Roth, 1981].

Features recorded in Gomortegaceae include cell shape [Roth, 1981], course of anticlinal walls, stomatal type, distribution [Solereeder, 1908; Metcalfe & Chalk, 1950; Roth, 1981] and occurrence of secondary divisions of subsidiary cells parallel to the pore [Solereeder, 1908; Metcalfe & Chalk, 1950], absence of trichomes [Solereeder, 1908; Metcalfe & Chalk, 1950; Uphof, Hummel & Staesche, 1962; Roth, 1981] and presence as well as shape of secretory cells [Solereeder, 1908; Metcalfe & Chalk, 1950].

In Trimeniaceae, information has been provided concerning cell size [Hobein, 1888; Solereeder, 1908; Metcalfe & Chalk, 1950], course of anticlinal wall [Money, Bailey & Swamy, 1950], stomatal type [Hobein, 1888; Solereeder, 1908; Beauvisage, 1920; Metcalfe & Chalk, 1950; Stern, 1954; Rodenburg, 1971; Roth, 1981], presence and type of trichomes

[Hobein, 1888; Solereder, 1908; Metcalfe & Chalk, 1950; Money, Bailey & Swamy, 1950; Uphof, Hummel & Staesche, 1962; Roth, 1981; Wilkinson per. comm.], trichome frequency [Rodenburg, 1971] and arrangement of basal cells [Roth, 1981] and presence of secretory cells [Hobein, 1888; Solereder, 1908; Perkins, 1925; Metcalfe & Chalk, 1950].

Characters of the Hernandiaceae previously recognised include presence of secondary periclinal divisions [cutinised] in the epidermis, occurrence and type of papillae [Solereder, 1908; Metcalfe & Chalk, 1950], stomatal type [Solereder, 1908; Metcalfe & Chalk, 1950; Kubitski, 1969; Roth, 1981] and distribution [Solereder, 1908; Metcalfe & Chalk, 1950], presence, type, shape and cellular composition of trichomes [Solereder, 1908; Metcalfe & Chalk, 1950; Uphof, Hummel & Staesche, 1962; Kubitski, 1969; Roth, 1981] as well as presence, type [Solereder, 1908; Kubitski, 1969] and shape [Metcalfe & Chalk, 1950] of secretory cells.

Whilst most of the results given by previous workers concerning cuticle characters of these related families are in accordance with those found in this study, there are some notable inconsistencies. In the present investigation, Austrobaileya scandens is seen to have a hypostomatic leaf. However, others [Metcalfe & Chalk, 1950; Roth, 1981; Wilkinson per. comm.] have detected stomata on both leaf surfaces [scattered on adx., abundant on abx.]. A single hair base has also been found, contrary to observations made by Roth [1981].

Hairs are reported to be absent in Gomortega keule. Nevertheless, this study has revealed the rare occurrence of simple unicellular, non-glandular trichomes on the abaxial side of the leaf. The peculiar secondary divisions described in subsidiary cells by Solereder [1908] and later by Metcalfe & Chalk [1950], occurring at right angles to the pore, have not been observed. Similar divisions are present, however, in Trimeniaceae [Piptocalyx moorei].

Metcalfe & Chalk [1950] inferred that cells of Tri-
menia and Piptocalyx spp. are small in the description given for Monimiaceae under which Trimeniaceae was then classified. On the contrary, cells are rather large in

comparison with those of most other taxa studied. These authors also suggested that trichomes in the two genera are non-glandular. The present investigation and subsequent work by Wilkinson (per. comm.) has revealed the presence of distinctly glandular forms. Roth [1981] mentioned that basal cells around trichome pores are randomly arranged in Piptocalyx moorei. This cannot be confirmed by results of this study since basal cells clearly have a radiating arrangement. In addition, Roth stated that trichomes are unicellular in Piptocalyx. However, some trichomes seem to be bicellular whilst others have bodies comprising of more than two cells.

Most workers believe stomata to be paracytic in Illigera and Hernandia and anomocytic in Gyrocarpus and Sparattanthelium (Hernandiaceae). The present investigation reveals the usual presence of a very narrow, faintly marked subsidiary cell either side of the guard cells in the latter two genera. Therefore, these stomata may also be considered paracytic. Roth [1981] recorded absence of stalked glands in Hernandia. According to Kubitski [1969] and results of the present study, such glands are common to many species of the genus.

A range of cuticular characters have been observed previously in Lauraceae. Details of cells: shape [Dubard & Dop, 1907; Bandulska, 1926, 1928; Santos, 1930; Marlier-Spirlet, 1945; Occhioni & Souza, 1948; Kasapligil, 1951; Kostermans, 1957; Shakryl, 1965; Imkhanitskaya, 1966; Ferguson, 1974b; Pal, 1978], size [Santos, 1930; Marlier-Spirlet, 1945; Occhioni & Souza, 1948; Kasapligil, 1951; Ferguson, 1974b; Fishbeck & Kummerow, 1977], distinctiveness of veins [Occhioni & Souza, 1948; Imkhanitskaya, 1966; Pal, 1978], degree of cutinisation/outicle thickness [Dubard & Dop, 1907; Teschner, 1923; Bandulska, 1926, 1928; Santos, 1930; Marlier-Spirlet, 1945; Occhioni & Souza, 1948; Kasapligil, 1951; Kostermans, 1957; Imkhanitskaya, 1966; Fishbeck & Kummerow, 1977; Pal, 1978] and modification when associated with sclereids [Dubard & Dop, 1907] are known.

Features of the periclinal wall region recorded by previous workers include nature of cuticle surface: absence of striae [Solereder, 1908; Pal, 1978], presence of delicate punctations [Solereder, 1908; Teschner, 1923; Marlier-Spirlet, 1945; Metcalfe & Chalk, 1950; Kostermans, 1957], warts [Kostermans, 1973] and granulation [Imkhanitskaya, 1966], occurrence of domes [Kostermans, 1973] or papillae [Petzold, 1907; Solereder, 1908; Teschner, 1923; Bandulska, 1928; Santos, 1930; Occhioni & Souza, 1948; Metcalfe & Chalk, 1950; Kostermans, 1957; Imkhanitskaya, 1966; Kubitski & Renner, 1982] as well as their form [Kubitski & Renner, 1982].

Aspects of the anticlinal wall already considered concern shape of anticlinal borders [Fishbeck & Kummerow, 1977], course of anticlinal wall in surface view [Petzold, 1907; Solereder, 1908; Bandulska, 1926, 1928; Santos, 1930; Marlier-Spirlet, 1945; Occhioni & Souza, 1948; Metcalfe & Chalk, 1950; Kasapligil, 1951; Kostermans, 1957, 1973; Shakryl, 1965; Imkhanitskaya, 1966; Ferguson, 1974b; Pal, 1978], thickness/width of wall [Bandulska, 1926, 1928; Santos, 1930; Marlier-Spirlet, 1945; Kostermans, 1957; Imkhanitskaya, 1966], wall striation/pitting [Bandulska, 1926; Santos, 1930] and shape of anticlinal cutinisation in T.S. [Imkhanitskaya, 1966; Fishbeck & Kummerow, 1977].

Various stomatal features have been noted previously in Lauraceae: those pertaining to the entire complex such as, type [Petzold, 1907; Solereder, 1908; Bandulska, 1926, 1928; Occhioni & Souza, 1948; Metcalfe & Chalk, 1950; Kostermans, 1957, 1973; Pal, 1978; Roth, 1981], distribution [Dubard & Dop, 1907; Petzold, 1907; Solereder, 1908; Teschner, 1923; Bandulska, 1926, 1928; Santos, 1930; Marlier-Spirlet, 1945; Metcalfe & Chalk, 1950; Kasapligil, 1951; Kostermans, 1957, 1973; Imkhanitskaya, 1966; Ferguson, 1974b; Pal, 1978; Roth, 1981; Kubitski & Renner, 1982] including on veins [Kasapligil, 1951; Pal, 1978], arrangement [Pal, 1978], density/frequency [Petzold, 1907; Marlier-Spirlet, 1945; Kasapligil, 1951; Fishbeck & Kummerow, 1977; Pal, 1978] and striation pattern [Petzold, 1907; Kubitski & Renner, 1982], as well as characters of guard

and subsidiary cells.

Guard cell features include position with respect to epidermis [Guttenburg, 1907; Petzold, 1907; Solereder, 1908; Bandulska, 1926, 1928; Santos, 1930; Marlier-Spirlet, 1945; Metcalfe & Chalk, 1950; Kasapligil, 1951; Kostermans, 1957], distinctiveness [Solereder, 1908; Bandulska, 1926, 1928; Santos, 1930; Kostermans, 1957], shape in T.S. [Bandulska, 1926] and surface view [Marlier-Spirlet, 1945; Kasapligil, 1951], size [Bandulska, 1926; Santos, 1930; Marlier-Spirlet, 1945; Kasapligil, 1951; Litke, 1966; Ferguson, 1974b], presence of thickened poral rim [Bandulska, 1926, 1928], inner ledge [Guttenburg, 1907] and ridge-like processes [Petzold, 1907; Metcalfe & Chalk, 1950; Kostermans, 1957], presence of scales [the cutinised part of the guard cell], their shape, [Bandulska, 1926, 1928; Marlier-Spirlet, 1945; Imkhanitskaya, 1966] and persistence in cuticle preparations [Bandulska, 1926].

Characters of subsidiary cells described in the literature concern position with respect to the pore [Petzold, 1907; Solereder, 1908; Teschner, 1923; Bandulska, 1926, 1928; Santos, 1930; Marlier-Spirlet, 1945; Kostermans, 1957], shape of outer periclinal wall and cuticle [Guttenburg, 1907; Marlier-Spirlet, 1945; Kasapligil, 1951], shape in surface view [Bandulska, 1928; Imkhanitskaya, 1966], size [Bandulska, 1926; Kasapligil, 1951] and degree of development of thickening at poles [Bandulska, 1926, 1928; Marlier-Spirlet, 1945].

The nature of cells surrounding the complex has also been mentioned: position with respect to subsidiary cells [Santos, 1930; Marlier-Spirlet, 1945], presence of papillae [Bandulska, 1926; Kubitski & Renner, 1982], cell size, arrangement, number and wall form [Bandulska, 1926, 1928].

Features of trichomes given previously include type [Petzold, 1907; Solereder, 1908; Santos, 1930; Metcalfe & Chalk, 1950; Kostermans, 1957; Pal, 1978; Aleykutty & Inamdar, 1980; Roth, 1981; Kubitski & Renner, 1982],

distribution [Dubard & Dop, 1907; Occhioni & Souza, 1948; Kostermans, 1973; Pal, 1978; Lu, 1979; Kubitski & Renner, 1982], density/frequency [Bandulska, 1928; Santos, 1930; Occhioni & Souza, 1948; Kostermans, 1957, 1973; Wofford & Pearman, 1975; Pal, 1978], size [Wofford & Pearman, 1975; Pal, 1978; Kubitski & Renner, 1982], shape [Santos, 1930; Occhioni & Souza, 1948; Imkhanitskaya, 1966; Wofford & Pearman, 1975; Pal, 1978; Lu, 1979; Aleykutty & Inamdar, 1980; Kubitski & Renner, 1982], tip form and nature of body surface [Aleykutty & Inamdar, 1980], number of cells in body [Petzold, 1907; Solereder, 1908; Teschner, 1923; Santos, 1930; Occhioni & Souza, 1948; Metcalfe & Chalk, 1950; Kostermans, 1957; 1973; Imkhanitskaya, 1966; Wofford & Pearman, 1975; Pal, 1978; Aleykutty & Inamdar, 1980; Roth, 1981], wall thickness [Solereder, 1908; Teschner, 1923; Santos, 1930; Metcalfe & Chalk, 1950; Kostermans, 1957, 1973; Imkhanitskaya, 1966; Pal, 1978; Aleykutty & Inamdar, 1980], presence of septa [Petzold, 1907], degree of cutinisation [Imkhanitskaya, 1966; Aleykutty & Inamdar, 1980], occurrence of bases [Bandulska, 1926; Imkhanitskaya, 1966; Ferguson, 1974b], form [Bandulska, 1926; Imkhanitskaya, 1966], size, frequency, distribution [Bandulska, 1926] and arrangement of basal cells [Roth, 1981].

Details of other specialised structures known in Lauraceae concern cork warts: presence [Mez, 1889; Solereder, 1908] and secretory cells: presence [Dubard & Dop, 1907; Petzold, 1907; Solereder, 1908; Lehmann, 1925; Leeman, 1928; Metcalfe & Chalk, 1950; Kasapligil, 1951; Kostermans, 1957; Imkhanitskaya, 1966; Pal, 1975], shape [Müller, 1905; Dubard & Dop, 1907; Petzold, 1907; Solereder, 1908; Lehmann, 1925; Leeman, 1928; Metcalfe & Chalk, 1950; Kostermans, 1957; Pal, 1975], size [Kasapligil, 1951] and extent of cutinisation [Petzold, 1907].

In general, results of the present study agree with those of other workers. However, as in the case of the related families some discrepancies are noted in cuticle morphology of Lauraceae.

Solereder [1908] asserted that anticlinal walls

[= flanges] are only rarely undulate. However, undulation seems to be a common phenomenon in many taxa according to this and most other work [e.g. that of Bandulska, 1926; Santos, 1930; Marlier-Spirlet, 1945; Kostermans, 1957; Pal, 1978].

Pal (1978) believed Lauraceae stomata to be anomocytic in type. All earlier workers recognised distinct subsidiary cells and considered the organisation as paracytic. The present study clearly demonstrates that Pal's interpretation is incorrect and supports the widely held view.

Leaves of Lauraceae have been regarded as hypostomatic. This appears to be the usual situation although one taxon examined, Eusideroxylon melagangai, also had stomata scattered on the adaxial surface.

In the past, difficulties in determining which part of the stomatal complex corresponds to the 'scale' [sensu Bandulska, 1926] seem to have been experienced. Both Bandulska (1926) and Marlier-Spirlet (1945) correctly illustrated these structures in surface view but due to poor or incomplete drawings of sections, caused some ambiguity. Bandulska, in particular, inferred that scales were outgrowths of subsidiary cells in Aniba. In Neolitsea apoensis, she showed the guard cell outer ledge and other cutinised parts to represent the scales. Within the text, this author also stated that guard cells were 'scale covered'. The present investigation clearly demonstrates that scales [here called 'wings'] comprise of the cutinised portion of the guard cell i.e. the periclinal cuticle and anticlinal flange between the guard and subsidiary cells. These structures lie on the inner surface of the isolated membrane and are not visible on the outside of the leaf in an unmacerated specimen.

The ring of cells found girdling accessory [= subsidiary] cells in some species of Cinnamomum by Bandulska (1928) were not observed in recent work by Kubitski & Renner (1982). Results of the present study confirm this finding.

Most workers have described trichomes of Lauraceae as simple and unicellular. However, Aleykutty & Inamdar [1980] have recorded the occasional presence of three other forms: bicellular, peltate and vesicular in certain species of Cinnamomum, Litsea and Neolitsea respectively. Only simple, unicellular trichomes have been detected in the Lauraceae investigated in this study.

Roth [1981] mentioned that hair base cells were characteristically randomly arranged in the family. Such a result cannot be confirmed, since these cells are always radially organised around a trichome pore in the taxa examined in the present work.

The cuticle of unspecialised cells is smooth, according to Solereder [1908]. Nevertheless, striae have been found on some surfaces of Caryodaphnopsis [abx.] and Persea [adx.] species. Especially fine striation also appears common to the costal region of most taxa, but is only distinguishable in the S.E.M.

Very little is known of the cuticular anatomy of the scale-like, non-photosynthetic 'leaves' in Cassytha, the genus of parasitic climbers. A few facts, however, have been given by Weber [1981] concerning veins [presence], trichomes [type, arrangement and distribution] and glands [presence and distribution]. Details of the stem are better documented. Features recorded pertain to cells: shape and degree of cutinisation [McLuckie, 1924; Metcalfe & Chalk, 1950; Weber, 1981]; stomata: type [Metcalfe & Chalk, 1950], arrangement [Solereder, 1908; McLuckie, 1924; Metcalfe & Chalk, 1950; Kuijt, 1969; Weber, 1981], position with respect to leaf surface [McLuckie, 1924; Metcalfe & Chalk, 1950], orientation of pore [Petzold, 1907; Solereder, 1908; McLuckie, 1924; Metcalfe & Chalk, 1950; Kuijt, 1969; Weber, 1981] and presence of outer ledge [McLuckie, 1924; Metcalfe & Chalk, 1950; Kuijt, 1969; trichomes: presence [McLuckie, 1924; Aleykutty & Inamdar, 1980] and form [Aleykutty & Inamdar, 1980] and secretory cells: occurrence and type [Hackenburger, 1889; Solereder, 1908]. Inconsistencies have not been detected between results provided

by these workers and those of the present study regarding such characters in Cassytha.

Thus, the investigation described in this thesis represents a more comprehensive examination of the cuticle in members of the five angiosperm families than ever attempted previously and supplements our existing knowledge of features of the outer cuticular surface by many characters of the inner side of the membrane, most of which have never before been recognised in these plants. Prior to this work, it had not been established with certainty in angiosperms whether the inner cuticular surface would provide any additional features to those found on the outer side although it had been suggested as a possibility by Wilkinson [1979] on the basis of her own studies and those of Lange [1969], Baker [1970, 1971] and Barthlott & Ehler [1977]. This fact and, therefore, the taxonomic potential of the inside of the membrane has been known for some time, however, in gymnosperms [Boulter, 1971; Stockey & Taylor, 1978a; Miranda & Chaphekar, 1980; Oladele, 1981, 1983b].

Since a range of basic characters such as cell shape, flange course and periclinal curvature may be detected on the inner cuticular surface together with a great range of microrelief [secondary] ornamenting these 'primary' structures, it is reasonable to propose that such features may be classified in the same way as characters of the outer surface, according to the scheme devised by Barthlott & Ehler [1977] and reported in Barthlott [1981]. In their system, all inner surface features were considered secondary in nature.

Thus, the grades of inner surface micromorphology recognised in the present investigation are: 1, primary, including cell shape and size, course and width of flanges, anticlinal and periclinal extent of cutinisation, flange margin form [irregularity, grooving, corner extensions], flange continuity and periclinal curvature, and 2, secondary, superimposed on 1, consisting of anticlinal and periclinal sculpture [protrusions, depressions] and folding. It could be argued that flange margin form falls

in a further category [between 1 and 2] since it deals with a particular part of the flange, the edge, which could be thought of as superimposed on the main body of the flange.

The sculptural patterns of the periclinal surface on the inside of the cuticle are particularly varied and, therefore, interesting accounting for many interspecific differences. This ornamentation must be described as fully as possible since it may, as in gymnosperms, be of taxonomic importance, especially as preliminary studies have revealed very little intraspecific variation in aspects of the sculpture. Oladele [1981], although successfully assigning periclinal ornamentation in Cupressaceae and Taxodiaceae to three types [fine, moderate and coarse] by comparison, recommended a more detailed treatment. The many patterns found in the selected Laurales suggest that Oladele was correct in his conclusion. Thus, in this study ornamentation has been described by dealing separately with composition, size and arrangement of elements i.e. protrusions/depressions [easily determined], sculptural density and element prominence [more difficult and sometimes impossible to define]. A more workable system might be developed to advantage using only those aspects which may be distinguished with relative ease, perhaps by combining the schemes previously devised by Miranda & Chaphekar [1980] and Oladele [1981].

In order to understand the many periclinal sculptural patterns and perhaps ascertain any function they might have in situ, studies devoted to the development of some of the different configurations are urgently required. Holloway [1982] has shown that six types of cuticle may be recognised on the basis of their element [lamellae/fibrillae] content in the T.E.M. It would be interesting to ascertain whether each of these types has a characteristic form of periclinal sculpture in the S.E.M. It may be that the particular chemical components of a cuticle influences the fine relief seen. Baker [1971] has already given some evidence of this.

As stated by Oladele [1981] for gymnosperms, further

developmental investigations are required in angiosperms to determine why some taxa have certain features and others not, e.g. flange margin irregularity, perforations or interruptions, furrowing and differing sculpture in different cell types. Detailed studies of the development of specialised papillae in Beilschmiedia madang [on subsidiary cells] and Caryodaphnopsis tonkinensis [on ordinary epidermal cells] may also prove to be of interest as may be that of the different external forms of subsidiary cells in Lauraceae i.e. where subsidiary cells appear discrete, or partially or entirely fused at the poles.

In order to interpret the wealth of features revealed by microscopical techniques, this work has shown that it is necessary to build up a three-dimensional picture of cuticle structure. S.E.M. of unmacerated portions of leaf or isolated cuticles gives topographical details of the individual outer and inner surfaces but often not how the two sides relate to each other. Transverse and paradermal sections through the leaf provide the important 'missing link', particularly in determination of stomatal organisation, complex epidermal morphology [as in Caryodaphnopsis] and the pattern of cutinisation when extensive.

In general, the cuticular membrane remains unchanged during isolation [from both fresh and dried material] when chromium trioxide solution is utilised, as found by Oladele [1981]. However, the steady state achieved in gymnosperms resulting in 'a steady and consistent state of surface sculpture' [Oladele, 1981], first described by Alvin & Boulter [1974], is apparently not attained in angiosperms. When a flowering plant cuticle is ready for examination in the S.E.M., most parts tend to be fully macerated although regions [usually odd cells or more usually stomata] may be detected which are slightly over-macerated [identified e.g. by removal of the cutinised guard cell wings in Lauraceae] or, undermacerated [i.e. complete with adhering cellulosic material, such as part of the stomatal flap] with a glazed appearance. It is desirable to obtain a cuticle which reveals the true cuticular microrelief when inner surface features are to

be described so that careful examination of the membrane is necessary throughout maceration using light microscopy to obtain the cuticle at the optimum stage for observation in the S.E.M. The correct state of maceration in angiosperms seems to be only recognised by experience.

When interpreting cuticular structure, the few artifacts arising as a result of the dewaxing and isolation processes, must be appreciated and taken into consideration. Dewaxing of the leaf sample with chloroform and cyclohexane prior to maceration to reveal underlying surface features [see p. 88] does not always appear entirely effective, leaving behind in certain cases (e.g. in Aniba hostmanniana, Licaria guianensis and Ravensara pervillei) a bubbled appearance due to rings of undissolved wax. Sometimes dewaxing hardly affects the waxy surface at all [notably in Alseodaphne semecarpifolia and Dehaasia cuneata : abx.] or only modifies its form (e.g. from rods or rods and flakes to granules as in Lindera strychnifolia and Cinnadenia paniculata respectively). Application of another solvent such as ether or an ether/chloroform mixture is suggested as an alternative.

Removal of the underlying wall by maceration often causes domed or papillate surfaces to collapse, especially when the cuticle is thin, preventing a true representation of the periclinal curvature. This type of surface could be critical point dried according to techniques described by Cohen & Shaykh [1973] and Lewis & Nemanic [1973].

The use of concentrated nitric acid towards the end of the isolation process [see p. 89] seems to result in flecks, particularly on the inner surface of certain cuticles (e.g. shown in Figs 71, 118, 120). These flecks may either be undissolved wall material or some reaction product of the cuticle itself (perhaps due to degradation by the acid). It is best, therefore, to use only chromium trioxide solution which does not give flecking.

As in gymnosperms [Oladele, 1981], the present study shows that each flowering plant species has a characteristic

assemblage of features. In some cases, however, certain characters appear to be unique, such as presence of polar papillae arising from subsidiary cells in Beilschmiedia madang (other Lauraceae have lateral domes/papillae); presence of stomata on the adaxial leaf surface in Eusideroxylon melagangai; presence of large, solid, dome-like extension to subsidiary cell, best seen in T.S. in E. zwageri (usually periclinal projections of subsidiary cells are hollow and represented to some degree on the inner surface unless very low in prominence); and presence of anomocytic stomata in Austrobaileya scandens (the other taxa all having paracytic stomata).

A few features seem to be characteristic of all members examined of certain genera, e.g. adaxial patterns of cutinisation in Beilschmiedia spp., where the entire epidermis is cutinised, and in Eusideroxylon spp. in which flanges associated with sclereids are particularly prominent (and lignified) compared with those of ordinary epidermal cells; grooved, cavity and buttress flange type in Endiandra spp. and papilla form (coronulate, striate, lobed with distinct lumen, often joined at the apices by cutinised extensions of the lobes, forming roofed chambers in which stomata may be located) in Caryodaphnopsis spp. These characters may, indeed, distinguish the entire genus but more species will have to be studied before this can be established with any certainty. Desch (1941), however, maintains that in Lauraceae, no well-defined generic anatomical features can be discerned because of the considerable variation in structure which exists both within a species and a genus.

Intraspecific studies involving gymnosperms, have revealed a remarkable constancy in cuticular features, particularly those of the inner surface (Miranda & Chaphekar, 1980; Oladele, 1981, 1983b; Alvin, Dalby & Oladele, 1982) within a given species. In angiosperms, however, previous work has reported a number of differences between entities of a species (see Review p.62-70). The preliminary investigation in this study based on cuticles of certain Lauraceae has shown that specimens of a species tend to exhibit a high degree of basic similarity. There

are, nevertheless, some small dissimilarities, a result which is in accordance with the findings of Pearson & Brown [1932] and Dadswell & Eckersley [1940] based on examination of wood. In general, the outer surface of the cuticle shows fewer of these differences than the inner and the adaxial side less than the abaxial [not surprisingly since more features exist and may vary on the inner and abaxial surfaces].

Slight variation in the degree of periclinal curvature, configuration of the anticlinal borders and aspects of hairs [presence and frequency] appears to be most often responsible for such small external intraspecific differences on the adaxial, although features of surface ornamentation [striae size and prominence] and wax [abundance] may be contributory factors in some species. Hair frequency may also be somewhat variable on the abaxial as well as characters concerned with wax, particularly form and size. Where surfaces are papillate, different specimens seem to vary slightly in size, shape or prominence of the papillae together with definition or fusion of the apices. Stomatal size and the distinctiveness of cell outlines may more rarely differ intraspecifically.

On the inner cuticular surface, small differences in the extent of periclinal and anticlinal cutinisation [predominantly of the epidermis but occasionally also of the hypodermis], flange shape and form [especially aspects of undulation, continuity and margin], periclinal curvature and ornamentation [element composition, size, prominence, arrangement and form] and most particularly features of hair bases, contribute mainly to variation between species. As on the abaxial outer surface, characters associated with papillae represented by scrobiculi [diameter and prominence] may also vary somewhat intraspecifically. Variability in a number of stomatal features is responsible for minor differences in the abaxial inner cuticle surface amongst specimens: complex size, subsidiary cell periclinal curvature and ornamentation, definition of subsidiary cell striae and position of subsidiary cell compared with intercostal cell level. Other assorted characters may less

commonly exhibit small dissimilarities e.g. cell size [adx. & abx.], flange thickness [abx.], flange furrowing [adx.], shape and prominence of striae [adx. & abx.] and basal cell size and striation [abx.].

The total effect of these dissimilarities on the appearance of the cuticle is, in fact, slight so that any entity may easily be assigned to its species.

The above differences are consistent with many of the results of previous workers [see Review p.62-70] and may be due to genetic variation or may relate to the season in which the specimens were collected, the position of the leaves on the tree or shrub or the environmental regime [light, temperature, altitude, soil and atmospheric moisture] in which the specimens were located.

Studies attempting to correlate intraspecific differences with environmental factors such as soil and altitude, using the limited details supplied by collectors, are unfortunately inconclusive. Although certain entities differ somewhat from others in a species e.g. Dehaasia cuneata [3] from limestone at 400m and Caryodaphnopsis tonkinensis [6] from 260m, it is generally not clear whether or not the differences are a consequence of variation in environmental factors. Expected dissimilarities based on the previous literature [see Review p. 66-70] are not usually detected, except smaller cells in the high altitude Caryodaphnopsis tonkinensis specimen. Some of the differences involve periclinal curvature and striation, aspects which are known to be affected by levels of illumination and soil and atmospheric moisture. Details of these are not given by collectors. Thus, more habitat information is really required for satisfactory elucidation of the effect of the environment on cuticular features.

Preliminary studies involving numerical analyses of subsets of the 381 character data set have shown that family separation may be achieved [principal co-ordinates] and subgrouping within the Lauraceae is possible [cluster analysis]. This suggests the potential of such cuticular

features, particularly those of the stomatal complex [which predominantly comprise the subsets], in taxonomy for classification as well as identification. Certain workers investigating gymnosperm cuticles e.g. Boulter [1971] have also found the stoma to be especially valuable. Comparison of analyses of different subsets of characters, such as those of the inner or abaxial surfaces, may further complement the present study.

The Austrobaileyaceae [represented by Austrobaileya scandens] is especially distinct from other Laurales, occupying an isolated position in both analyses. This result is consistent with current beliefs regarding the family derived from studies of pollen morphology and floral characteristics [see Money, Bailey & Swamy, 1950; Walker, 1976; Endress, 1980; Endress & Honegger, 1980]. Recently, Austrobaileyaceae has been described as being somewhat intermediate between the Magnoliales and Laurales [Takhtajan, 1983] although previously it had been placed both nearer [Endress, 1980] and in [Cronquist, 1981] the Magnoliales. It would, perhaps, be of interest to extend the work of Baranova [1972] and Bongers [1973] by examining some members of this group in the same way as Austrobaileya scandens and compare their cuticle characters with those of this taxon by numerical methods, to ascertain the degree of its affinity with them.

Hypodaphnis zenkeri also appears distinct in the analyses falling well away from other Lauraceae, near to certain Hernandiaceae. The placement of this species is in accordance with the findings of Richter [1981], based on wood anatomy. H. zenkeri, in addition, seems to be the only Lauraceae with an inferior ovary in its flower [Kostermans, 1938] another feature found in all Hernandiaceae.

The two groupings [Hernandia & Illigera, Gyrocarpus & Sparattanthelium] recognised within the Hernandiaceae on the basis of pollen morphology, mode of anther dehiscence, vascularisation of ovaries and nature of perianth by Guillaumin [1948], Money, Bailey & Swamy [1950], Novák [1954],

Takhtajan [1966], Thorne [1968] and Willis [1974] are not distinguishable when subsets of cuticular characters [mainly stomatal] are considered. The taxonomic treatment [single family of discrete genera] of Pax [1891], Corner [1952], Benson [1957], Emberger [1960], Engler [1964], Cronquist [1968], Keng [1969], Kubitski [1969] and Hutchinson [1973] is, therefore, favoured.

Results of the present study seem to agree in many ways with those obtained by numerical analysis of features of Hernandiaceae flowers [including glands], fruits, leaf venation and leaf macromorphology conducted by Chuah [1975]: the two species of Sparattanthelium pair together at a relatively high level of similarity, Gyrocarpus americanus remains distinct from other members on a separate limb of the diagram and Hernandia peltata [= nymphiifolia] falls in the same subcluster as Illigera pentaphylla [suggesting a relationship between Hernandia and Illigera, contrary to the work of Shutts [1959, 1960]]. Although Sparattanthelium also appears with these latter taxa in this subcluster, members of the genus are more like I. pentaphylla than H. nymphiifolia in the present investigation. Chuah, however, shows Sparattanthelium to be less similar to I. pentaphylla than H. nymphiifolia.

The cluster analysis shows that Gomortega keule [Gomortegaceae] and Trimeniaceae members are closely allied. This is in accordance with recent work by Takhtajan [1983] who noted their relationship through Monimiaceae. In fact, Piptocalyx and Trimenia have sometimes been considered as genera within this family [see Heywood, 1979]. Generally, however, they are thought to constitute a separate family group, the Trimeniaceae [Hutchinson, 1964; Cronquist, 1968, 1981; Takhtajan, 1969, 1983].

Stern [1955] asserted that the systematic position and relationships of Gomortega have been uncertain since the genus was first described by Ruiz & Pavòn [1794]. He also recognised two main ideas regarding affinities of this genus: the first, with Monimiaceae [Philippi, 1868; Mez, 1889; Engler & Diels, 1938; Kostermans, 1952] supported by

details of wood anatomy [Garratt, 1934; Bailey & Swamy, 1948] and pollen morphology [Erdtman, 1952] and the second, with Lauraceae [Nees von Esenbeck, 1836; Endlicher, 1836-1840; Bentham & Hooker, 1862-1883]. Doubt has been expressed, however, as to whether Gomortega could be included in the Lauraceae due to its ovary form [3-celled] [Philippi, 1864-1865; Baillon, 1871], the presence of abundant endosperm [Philippi, 1864-1865] and the more advanced xylem type [Stern, 1955], although Metcalfe & Chalk [1950] have recorded a distinct resemblance between gomortegaceous and lauraceous wood and the spines of Gomortega pollen are known to be reminiscent of those found in the Lauraceae [Walker, 1976].

In the present investigation, G. keule is distributed amongst Lauraceae members in the 154 character principal co-ordinates analysis, suggesting a close affinity with them. However, when fewer characters are analysed in the same way, this taxon remains discrete. Such a position corresponds well with the view of Reiche [1876] who established Gomortega within a separate family, the Gomortegaceae.

Numerical studies reveal that within the Lauraceae, members of some genera [e.g. Aiouea, Caryodaphnopsis, Endiandra, Laurus, Neocinnamomum, Potameia] appear very similar in their cuticular characters whilst those of others [such as Actinodaphne, Beilschmiedia, Litsea, Mezilaurus, Nothaphoebe, Phoebe, Ravensara] are quite dissimilar and often resemble a non-related taxon more closely than another species of the same genus. This situation is well known from work based on other features [e.g. wood anatomy] by Hooker [1885], Mez [1889], Macbride [1931], Janssonius [1934], Record & Hess [1943] and Kostermans [1952] and has led to the conclusion that many lauraceous genera are somewhat artificial. Although certain workers have mentioned which genera show artificiality, for example Mez [1889] [Persea, Phoebe, Nectandra and Ocotea], generalisations may be rather unwise particularly when only a restricted assemblage of taxa especially of the larger genera has been examined, as in the present investigation.

Thus, whereas Lauraceae species seem easily characterised and, therefore, identified by their cuticular anatomy, genera often appear to be hard to define making determination difficult, as recognised by Record & Hess [1943] from wood features but contrary to recent observations made by Swart & Van der Walt [1985]. These workers were only able to determine genera [Beilschmiedia, Cryptocarya and Ocotea].

Numerical work also shows that there is some grouping of genera in the Lauraceae. This appears rather complex due to taxa commonly seeming more similar to non-related species than to others in the same genus (as mentioned above). Four main groups are suggested by cluster analysis corresponding to subclusters i, ii, iii and iv.

In i, Laurus spp. pair off on a separate limb from a large cluster composed of species of a number of genera e.g. Cinnamomum, Cryptocarya, Ravensara and Systemonodaphne. Most previous workers have considered Laurus to be related to Lindera [see Table VI], also Richter [1981] from wood features. A few have noted its affinity with other genera, in addition, such as Litsea [Nees von Esenbeck, 1836; Bentham & Hooker, 1862-1883; Hutchinson, 1964], Umbellularia [Bentham & Hooker, 1862-1883; Hutchinson, 1964], Actinodaphne, Sassafras [Bentham & Hooker, 1862-1883] and Dodecadenia [Hutchinson, 1964]. Lindera in the present study, however, is located well away from Laurus in sub-cluster iv together with most of Laurus' other supposed relatives [based on inflorescence, anther and fruit features]. Thus, cluster analysis results do not appear to support the existing taxonomy in this respect, neither does the corresponding principal co-ordinates analysis. Nevertheless, when 154 characters are considered Lindera strychnifolia, Litsea monopetala and Sassafras albidum var. molle fall near to Laurus.

The other members of i have a range of affinities in the different Lauraceae classification [Table VI]. Cinnamomum is grouped with Cryptocarya and Ravensara, amongst others, according to Bentham & Hooker [1862-1883]

but is more usually placed separately from these genera [Pax, 1891; Kostermans, 1957; Hutchinson, 1964]. Systemonodaphne is generally incorporated in another group with genera such as Aiouea, Aniba, Endlicheria, Phyllostemonodaphne and Urbanodendron. The 154 character principal co-ordinates analysis shows Cryptocarya to be distributed close to Ravensara away from Cinnamomum and Systemonodaphne mezii to be quite near Aniba hostmanniana, Endlicheria reflectens and Phyllostemonodaphne geminiflorum. These results seem more in agreement with previous taxonomic beliefs.

The unknown taxon also occurs in subcluster i, on a separate limb from other members. It is, therefore, clearly a Lauraceae and incorrectly identified as Caryodaphnopsis tonkinensis since this falls with non-Lauraceae in cluster B to the left of the dendrogram. Affinities of the unknown taxon are variable depending on the type of analysis and the character selection on which this is based. It is closest to Endiandra spp. when all stomatal and some abaxial intercostal inner surface features are used for the principal co-ordinates analysis and near Litsea meissneri on the basis of selected stomatal characters. If all 381 cuticular features were to be analysed, the unknown taxon might more easily be assigned to a genus.

Subcluster ii consists only of Cassytha. This genus of parasites without proper photosynthetic leaves, is clearly closely related to Lauraceae, despite its isolated position. Lindley's [1853] proposal of segregation of these unusual plants from the family, therefore, cannot be supported. Instead, retention of Cassytha in Lauraceae is favoured. This conclusion is in accordance with the view held by Nees von Esenbeck [1836] and most subsequent workers including Bentham & Hooker [1862-1883], Meissner [1864], Mez [1889], Pax [1891], Mirande [1905], Kostermans [1957], Sastri [1962] and Hutchinson [1964]. Since Cassytha is somewhat discretely placed in the cluster analysis (and in the principal co-ordinates distribution), this genus might occupy a separate subgroup within the family. This appears consistent with its placement in most

classifications, e.g. in a different tribe [Nees von Esenbeck, 1836; Bentham & Hooker, 1862-1883; Pax, 1891; Hutchinson, 1964], suborder [Meissner, 1864; Mez, 1889] or subfamily [Kostermans, 1957] from the rest of the Lauraceae [Table VI].

In the cluster analysis, Cassytha shows affinities with the large subcluster i, containing all Cryptocarya species examined as well as members of various other genera [see p. 441]. According to Kostermans (1957), Cassytha approaches Cryptocarya most closely in floral organisation. There is also some evidence for this relationship from both embryology [Sastri, 1962] and studies of the perianth enclosing the fruit [Kuijt, 1969]. Cuticular features, however, do not indicate such strong affinity with Cryptocarya alone.

Subcluster iii consists of two smaller clusters. One incorporates Nectandra and Phyllostemonodaphne together with individual species of Endlicheria, Licaria and Ravensara. The other is composed of Aniba, Dicypellium, Eusideroxylon, Pleurothyrium and Urbanodendron as well as single species of Alseodaphne, Licaria and Ocotea. Again, classifications vary in their placement of these genera [Table VI]. Nectandra is commonly grouped with Dicypellium. Sometimes both are classified with Aniba, Licaria, Ocotea and Urbanodendron in one tribe, the Perseae [Mez, 1889], or with Eusideroxylon, Ocotea and Pleurothyrium [Apolloniae] away from Aniba, Endlicheria, Licaria, Phyllostemonodaphne and Urbanodendron [Cinnamomeae] [Hutchinson, 1964]. Kostermans (1957), on the other hand, places most of the subcluster iii representatives in the two sub-tribes of the Cinnamomeae i.e. a: Dicypellium, Nectandra, Ocotea and Pleurothyrium; b: Aniba, Endlicheria, Licaria, Phyllostemonodaphne and Urbanodendron. Eusideroxylon is placed on its own in sub-tribe a of the Cryptocaryeae. The principal co-ordinates analysis based on 154 features provides further evidence of the relationship between all subcluster iii genera. They tend to be distributed in and around the right-hand corner of the 'Litsea triangle' [along with Cryptocarya and Ravensara : sub-tribe b in

Kostermans's Cryptocaryeae].

The largest subcluster, iv, bears Potameia and Beilschmiedia on a separate limb as well as Neocinnamomum in a similar arrangement, branching off from two smaller clusters. One of these comprises of Aiouea, Dodecadenia, Sassafras, Sassafridium, Umbellularia and individual species of the genera Actinodaphne, Alseodaphne, Cinnamomum, Mezilaurus and Nothaphoebe. The other small cluster includes Apollonias, Cinnadenia, Lindera, Micropora, Neolitsea and Persea together with single species of Actinodaphne, Dehaasia, Litsea, Nothaphoebe and Phoebe.

In classification systems of Lauraceae [Table VI], Potameia is regularly grouped with Beilschmiedia and Dehaasia, often also with other subcluster iv members, Apollonias [Bentham & Hooker, 1862-1883; Kostermans, 1957; Hutchinson, 1964], Aiouea [Bentham & Hooker, 1862-1883; Pax, 1891; Hutchinson, 1964], Micropora [Pax, 1891; Hutchinson, 1964] and Mezilaurus [Kostermans, 1957; Hutchinson, 1964]. The principal co-ordinates analyses give very little support to any of these proposed affinities except Beilschmiedia with Aiouea in that based on 154 features .

Neocinnamomum and Sassafridium are considered synonymous with Cinnamomum [Hutchinson, 1964]. On the basis of cuticular characters, it appears that Neocinnamomum, with its discrete position in both the cluster and principal co-ordinates analyses [also in Richter's (1981) wood anatomical studies], should merit full generic status. The situation is not so clear regarding Sassafridium.

Umbellularia is usually classified with Sassafras [Nees von Esenbeck, 1836; Bentham & Hooker, 1862-1883; Mez, 1889; Pax, 1891; Kostermans, 1957]. Sometimes it is grouped with Actinodaphne [Pax, 1891; Kostermans, 1957], Lindera, Litsea [Mez, 1889; Hutchinson, 1964], Persea and Phoebe [Pax, 1891]. All these genera are represented in subcluster iv. In the 154 character principal co-ordinates analysis Umbellularia falls closest to Sassa-

fridium macrophyllum and Aiouea spp. (as in the cluster analysis) suggesting their affinity but not confirming previous taxonomic views.

Dodecadenia is thought to be related to Umbellularia by Hutchinson [1964] and to Actinodaphne, Lindera and Litsea by Nees von Esenbeck, 1836]. Cluster analysis results seem consistent with these beliefs, particularly those of Hutchinson. In the principal co-ordinates analysis using 154 features, Dodecadenia grandiflora is distributed very close to Actinodaphne stenophylla and in the same general region (below centre of the 'Litsea triangle') as Umbellularia californica and Lindera pulcherrima.

Persea is grouped with Phoebe in most Lauraceae classifications. Both these genera, besides falling in the same subcluster in the dendrogram, also appear quite near each other in the 154 character principal co-ordinates distribution, at the top of the 'Litsea triangle'. Other members of subcluster iv located in this area include Apollonias arnottii, Dehaasia cuneata, Micropora curtisii and Sassafras albidum var. molle.

The affinities of Cinnadenia seem uncertain, according to Kostermans [1973]. Its inflorescence type, general flower composition, thickness of fruit pedicel and presence of small cupula suggests that it should be placed near Cinnamomum. Nevertheless, there are a number of differences: size of anthers, location of stamens and pistils and frequency of glands in the flower. These indicate affinity with Ocotea. The presence of large staminodes prevents its inclusion within the genus. This investigation shows Cinnadenia to resemble a variety of taxa in cuticle micro-morphology including those mentioned by Kostermans: Lindera spp., Persea spp. (cluster analysis), Cinnamomum pachyphyllum, Pleurothyrium nobile, Ocotea guianensis (60 character principal co-ordinates) and Mezilaurus lindaviana (154 character principal co-ordinates). No definite conclusions can, therefore, be made regarding the taxonomy of Cinnadenia. This may, however, be resolved by further numerical work

using a different selection of features or a larger data set.

A few genera fall away from other Lauraceae, most notably Hypodaphnis in all analyses even though it has the guard cell 'wing' stomatal organisation so characteristic of the family. Kostermans [1957] gives Hypodaphnis the separate status of Tribe V in his classification, which appears more in keeping with the results of the present study than Hutchinson's [1964] proposal of its inclusion in Tribe IV, the Cinnamomeae, along with such genera as Cinnamomum, Dicypellium, Eusideroxylon, Nectandra, Nothaphoebe, Persea, Phoebe and Pleurothyrium.

In the cluster analysis, Endiandra pairs with a Hernandiaceae member. The same genus occupies a somewhat isolated position in both principal co-ordinates analyses being associated only with Potameia and the unknown taxon in the distributions based on 60 and 154 characters respectively. Endiandra and Potameia are often placed in the same tribe [see Nees von Esenbeck, 1836; Bentham & Hooker, 1862-1883; Kostermans, 1957; Hutchinson, 1964]. They also show affinities on the basis of wood anatomy [Richter, 1981] and the siliceous inclusions in the xylem [Richter, 1979] together with Beilschmiedia. It would be interesting to discover what features make Endiandra so distinct. With further application of numerical techniques this might be ascertained.

Caryodaphnopsis spp. are clustered with non-Lauraceae in the dendrogram. However, this genus falls near Phoebe and Persea in the 60 and 154 character principal co-ordinates analyses respectively, members of the same tribe, the Cinnamomeae, according to Hutchinson [1964]. Caryodaphnopsis is even described as a synonym for Persea [Kostermans, 1957]. Airy-Shaw [1940] states that the constituent species had previously been referred to the genus Nothaphoebe on account of their 4-locellate anthers and minute outer perianth segments, although in most other characters they differ widely. The leaves, for instance, resemble certain species of Cryptocarya e.g. C. laevigata

and most other flower and fruit features are closest to those of Dehaasia. It is no wonder Airy-Shaw felt that Caryodaphnopsis' affinities are not very clear and a 'rational revision of the entire Lauraceae necessary' before it can be assigned to a tribe. Recent work involving wood [Richter, 1981] and its included crystals [Richter, 1979] has indicated, just as the present investigation, that C. tonkinensis is somewhat unique in the family.

Although results of the preliminary numerical studies suggest intergeneric relationships within the Lauraceae and in some cases support existing taxonomic views regarding affinities of individual genera, it is not possible to produce any system of classification from them. However, further analytical work involving all cuticular characters [381] obtained from the taxa investigated could provide valuable assistance to the taxonomist interested in improving Lauraceae systematics, especially if the results are used in association with data obtained from previous studies of the same [Anzotegui, 1979: not available in U.K.] and other aspects of the plants e.g. venation [Rieger & Fourniero, 1982], wood [see Metcalfe & Chalk, 1950 for references also Stern, 1954; Richter, 1981], crystalline and siliceous inclusions of wood [Richter, 1979], bark sclerenchyma [Bamber & Summerville, 1979], secondary metabolites [Gottlieb, 1972; Gottlieb & Kubitski, 1981] and other chemicals [Hegnauer, 1966], embryological development [Endress, 1972] and fossil remains [Shakryl, 1979].

The wealth of cuticular characters, particularly of the inner side of the membrane, revealed by this study may not only be useful for identification of extant angiosperm species but may have further application in palaeobotany. Leaves are often represented solely by their cuticles in fossil deposits [see Bandulska, 1926, 1928; Dilcher, 1964, 1974] so every available feature should really be utilised for correct assignation of familial affinities. Kovach & Dilcher [1984] have recently shown the potential of descriptions of the outer and inner surfaces of dispersed cuticles from the Eocene of North America. Although a

great number of the inherent characters were not included, connections between the fossils and present-day families were established. Certain membranes with stomata were assigned to the Lauraceae (e.g. Claibornicutis undulata, Piliparicutis claibornensis and Saxonicutis eocenica) and one even to the genus Ocotea [P. obtusifolia]. Experience gained from the present study, especially regarding the stomatal organisation within the family, permitted similar conclusions to be made. Membranes without stomata were clearly more difficult to assign.

Since the Lauraceae are an important fossil group, occurring widely in Central Europe and North America from the Cretaceous to Middle Tertiary eras (de Wit, 1963), detailed descriptions of extant species obtained from cuticular studies such as the present investigation would greatly assist palaeobotanists, particularly if a data bank of information was set up on computer (see Hill, 1980) similar to the U.S.G.S. system for leaf architecture (Spicer, per. comm.)

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17. APPENDIXMATERIALS: TABLE 1LAURACEAE

- Actinodaphne glomerata [Bl.] Nees; Sabah, K.Muroh, 44718, 27/9/1965, [K].
- A. stenophylla Thw; Ceylon, N.Balakrishnan, NBK 333, 8/5/1971, [K].
- Aiouea guianensis Aublet Hb.Kunth ex; British Guiana, N.Y.Sandwith, 326, 23/9/1929, [K].
- A. saligna Meissn; Brazil, G.C.G.Argent in Richards, 6901, 10/9/1968, [K].
- Alseodaphne oblanceolata [Merr] Kosterm.; Sabah, A.Gibot, 41650 NT13, 24/5/1964, [K].
- A. semecarpifolia [Wall.ex Nees]Nees; Ceylon, N.Wirawan, R.G.Cooray & N.Balakrishnan, 15/7/1969, [K].
- Aniba hostmanniana [Nees] Mez; E.Trop.S.America, W.A.Engler & H.S.Irwin, 46473, 17/8/1961, [K].
- A. megaphylla Mez; E.Trop.S.America, B.Maguire, J.P.Schulz, T.R.Soderstrom & N.Holmgren, 54415, 31/7/1963, [K].
- Apollonias arnottii Nees; India, A.Kostermans, 26199, 22/6/1976, [K].
- Beilschmiedia madang Bl.; [1] Malay Islands, A. Kostermans, 12507, 15/7/1956, [K].
- B. madang [2] Borneo, A.Kostermans, 4319A, 11/10/1950, [K].
- B. madang; [3] E.Borneo, A.Kostermans, 5809, 18/7/1951, [K].
- B. madang; [4] Borneo, A.Kostermans, 7741, 5/8/1952, [K].
- B. madang; [5] Bangka, A.Kostermans & Anta 794, 19/9/1949, [K].
- B. madang; [6] Sarawak, P.S.Ashton, 18403, 6/4/1963, [K].
- B. micrantha Merr.; Malay Islands, E.Banang, 51960, 17/6/1965, [K].
- Caryodaphnopsis baviensis [Lec.] A.Shaw; Annam, Poilane, 31451, 22/2/1941, [L].
- C. tonkinensis [Lec.] A.Shaw; [1], Malay Islands, A. Kostermans, 5320, 19/6/1951, [K].

- C. tonkinensis; [2] N.Borneo, J.Ahwing, 34917, 23/2/1963, [K].
- C. tonkinensis; [3] N.Borneo, D.L.Nicholson, SAN 26379, 3/7/1961, [K].
- C. tonkinensis; [4] E.Borneo, A.Kostermans, 9515, 27/5/1954, [K].
- C. tonkinensis; [5] Malay Islands, J.D.Mamit, S 35178, 25/9/1974, [K].
- C. tonkinensis; [6] Bukit Selebor, I.Paie, S 28085, 28/9/1968, [K].
- C. tonkinensis; [7] S.E.Borneo, E.G.Sauveur, K33, 20/10/1950, [K].
- C. tonkinensis; [8] Bukit Selebor, I.Paie, S 28034, 26/9/1968, [K].
- C. tonkinensis; [9] Borneo, A.Kostermans, 6899, 13/5/1952, [K].
- Cassytha filiformis L; Aldabra S.Isl. S.A.Renvoize, 1119, 24/2/1968, [K].
- C. glabella R.Br.; Australia, H.I.Aston, 613, 14/9/1960, [K].
- Cinnadenia paniculata (Hookn F) Kosterm.; Assam, N.L.Bor, 42, 30/11/1935, [K].
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- C. oliverii F.M.Bailey; [1] Australia, B.Hyland, 4502 R.F.K. 29/4/1981, [A].
- C. oliverii; [2] Australia, A.G.Floyd, AGF 1516, 10/7/1980, [N].
- C. pachyphyllum Kosterm.; Siam, A.F.G.Kerr, 15433, 20/4/1928, [K].
- Cryptocarya ainikini Kosterm.; Soloman Islands, I.Gafui & collectors, 16316, 26/8/1969, [K].
- C. alleniana C.T.White; New Guinea, R.Pullen, 7611, 17/6/1969, [K].
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- D. cuneata; [2] E.Borneo, A.Kostermans, 9540[9534],
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- D. cuneata; [5] E.Borneo, A.Kostermans, 10.027,
22/2/1955.
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9810, 1887, [K].
- Dodecadenia grandiflora [Wallich ex Nees] Nees, India
R.N.Parker, 3329, 20/4/1936, [K].
- Endiandra kingsiana Gamble; E.Borneo, A.Kostermans, 13737,
9/9/1957, [K].
- E. rubescens Blume ex; S.Borneo, A.Kostermans, 8021,
30/7/1953, [K].
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A.G.H.Daniels & F.P.Jonker, 847, 7/8/1959, [K].
- E. reflectens [Nees] Mez; E.Trop.S.America, S.J.Wilson-Browne,
WB 104/5647, 9/1948, [K].
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2/4/1948, [K].
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18/9/1960, [K].
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41416, 29/7/1959, [K].
- Laurus azorica [Seub.] Franco; [1] Canary Islands, Bramwell,
364, 9/11/1968 [R].
- L. canariensis Bark.-Webb & Barth; [2] Canary Islands,
K.Lems, 2222, 17/8/1954, [R].
- L. nobilis L.; Great Britain, C.D.Faggetter, 10/1980, [C].
- Licaria guianensis Aublet; Trinidad, A.Kostermans, A.15018,
7/1959, [K].
- L. triandra [Sw.] Kosterm.; Dominican Republic, José de Js
Jiménez, 1395, 14/5/1947, [K].
- Lindera pulcherrima [Wall.] Benth.; Assam, Capt.F.
Kingden Ward, 8072, 12/4/1928, [K].
- L. strychnifolia [S.et Z.] Villar; Anhwei, K.S.Chow, 136,
1973, [K].
- Litsea meissneri Hook.F.; Ceylon, A.Kostermans, 25417,
18/8/1972, [K].

- L. monopetala [Roxb.] Persoon; Indo-China, M.Poilane, 10873, 13/6/1924, [K].
- L. umbellata [Lour.] Merr.; Malay Peninsula, J.C., 1617, 16/8/1967, [K].
- Mezilaurus itauba [Meissner] Taubert.ex; E.Trop.S.America, A.Ducke, 681, 22/3/1941, [K].
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- Nectandra pichurim [R.& P.] Mez; Brazil, N.T.Silva, 57828, 17/10/1963, [K].
- N. salicifolia [H.B.K.] Nees; Mexico, E.Matuda, 16391, 24/9/1946, [K].
- Neocinnamomum caudatum [Wall.] Merrill; India, Mrs. N.E.Parry, 1343, 2/1938, [K].
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- Neolitsea cassia [L.] Kosterm.; Ceylon, A.Kostermans, 23429, 10/5/1969, [K].
- N. dealbata [R.Br.] Merr.; Australia, S.T.Blake, 2074, 13/12/1930, [K].
- Nothaphoebe heterophylla Merr.; N.Bornea, J.Ahwing, 34946, 3/3/1963, [K].
- N. umbelliflora [Bl.]Bl.; Java, A.Kostermans, 20, 2/11/1960, [K].
- Ocotea guianensis Aublet; Brazil, J.A.Ralter, R.Role Santos, R.Souza & R.A.de Castro, R/204, 26/4/1968, [K].
- O. laevis Kosterm; Madagascar, R.Capuron, 11.756 SF, 2/1955, [K].
- Persea americana Miller; Great Britain, C.D.Faggetter, 10/1980.
- P. chinensis [Champ.ex Benth.]Pax; Hong Kong, S.Ying Hu, 10581, 4/7/1970, [K].
- P. thunbergii [Sieb.Zucc.] Kosterm.; Hong Kong, S.Ying Hu, 6937, 5/4/1969, [K].
- Phoebe opaca Bl.; N.Borneo, D.Brand, 31010, 18/9/1962, [K].
- P. sheareri [Hemsley] Gamble; Kwangtung, W.T.Tsang, 21328, 31/4/1932, [K].

- Phyllostemonodaphne geminiflorum [Meissn.] Kosterm.;
Brazil, J.G.Richlmann, 889, 17/11/1925, [K].
- Pleurothyrium cuneifolium Nees; Peru, G.Klug, 3116,
7/1933, [K].
- P. nobile A.C.Smith; Brazil, B.A.Keukoff, 4800, 13/6/1933,
[K].
- Potameia crassifolia Kosterm.; Madagascar & Muscarine
Isl. R.Capuron, 9059, 23/11/1954, [K].
- P. thouarsii Roem. & Schultes; Madagascar & Muscarine Isl.
Lam & Moeuse 5702, 4/12/1938, [K].
- Ravensara aromatica Sonn.; Madagascar & Muscarine Isl.
R. Capuron, 26858 SF, 6/5/1969, [K].
- R. elliptica Kosterm.; Madagascar & Muscarine Isl. R.Capuron,
26852 SF, 11/1968, [K].
- R. pervillei [Baillon] Kosterm.; Madagascar & Muscarine Isl.
R. Capuron, 26852 SF, 5/1969, [K].
- Sassafras albidum var. molle [Raf.] [Nutt.] Nees; North
America, Anon, H3246/63 18, 14/6/1903, [K].
- Sassafridium macrophyllum Rose; Mexico, H.S.Gentry, 1478,
8/7/1935, [K].
- Systemonodaphne mezii Kosterm.; Suriname, H.S.Irwin, G.T.
Prance, T.R.Soderstrom & N.Holmgren, 55719, 15/9/1963,
[K].
- Umbellularia californica [HK.& Arn.] Nutt.; Great Britain,
C.D.Faggetter, 10/1980, [C].
- Urbanodendron verrucosum [Nees] Mez.; Brazil, Riedel,
479.1141, 1867, [K].

AUSTROBAILEYACEAE

- Austrobaileya scandens C.T.White; Australia, C.T.White,
10734, 9/1936, [K].

GOMORTEGACEAE

- Gomortega keule I.M.Johnston; Chile, F.G.Meyer, 9741,
3/1/1966, [K].

Hernandia nymphifolia = H. nymphaefolia

HERNANDIACEAE

- Gyrocarpus americanus Jacq. ssp. africanus; Rhodesia,
G. Pope, H. Biegd & E. Russel, 1437, 29/1/1975, [K].
- G. americanus Jacq. ssp. americanus; New Guinea, R. Pullen,
6808, 25/4/1967, [K].
- Hernandia nymphiifolia (Presl) Kub. [peltata Meissn.]
Solomon Islands, I. Gafui & collectors, BSIP 15451,
14/7/1969, [K].
- H. olivacea Gillespie; Fiji, A. Nasogiri, FD 57,
11/9/1973, [K].
- Illigera pentaphylla Welw.; Cameroons & Congo, A. J. M.
Leeuwenberg, 6164, 17/7/1965, [K].
- I. pulchra, Bl., Malay Islands, Drs. V. Leeuwen-Reynvaan,
14194, 2/5/1932, [K].
- Sparattanthelium guianense Sandwith; Brazil, G. T. Prance,
P. J. M. Maas, D. B. Woolcott, D. F. Coelho, O. P. Monteiro &
J. F. Ramos, 15362, 17/10/1971, [K].
- S. tupiniquinorum Mart.; Brazil, M. Silva & R. Souza, 2321,
19/8/1969, [K].

TRIMENIACEAE

- Piptocalyx moorei F. Muell.; Australia, R. Schodde, 5119,
19/10/1966, [K].
- Trimenia papuana Rindl.; New Guinea, L. J. Brass, 29569,
14/5/1959, [K].
- T. weinmanniaefolia Seeman; Samoan Islands, E. Christophersen
& E. P. Hume, 2074, 15/7/1931, [K].

KEY TO SOURCES:

- A. C.S.I.R.O. Herbarium, Atherton, Queensland,
AUSTRALIA.
- C. Chelsea Physic Garden, London, ENGLAND.
- K. Herbarium, Royal Botanic Gardens, Kew, ENGLAND.
- L. Herbarium, Leiden, NETHERLANDS.
- N. New South Wales, AUSTRALIA.
- R. Herbarium, University of Reading, ENGLAND.

TABLE V. Details of 40 selected abaxial intercostal inner surface features of the cuticle used for numerical analysis.

ANALYSIS NO.	DESCRIPTION NO.	ANALYSIS NO.	DESCRIPTION NO.
115	4	135	51
116	3	136	52
117	15	137	53
118	∅	138	55
119	45	139	56
120	∇	140	57
121	61	141	58
122	7	142	59
123	38	143	63
124	39	144	64
125	40	145	62
126	41	146	66
127	42	147	184
128	43	148	185
129	44	149	194
130	46	150	195
131	47	151	199
132	48	152	203
133	49	153	205
134	50	154	206

NOTE

2 characters [11 & 6] were re-defined to facilitate application to inner surface of isolated membranes.

∅ 118 presence of cutinisation of inner periclinal wall of epidermis

∇ 120 presence of scrobiculi on inner surface

STATES: [1] absent; [2] present

TABLE VI. CLASSIFICATION SYSTEMS FOR LAURACEAE (1836-1964)

1. Nees von Esenbeck (1836)

Tribe I.	Cinnamomeae	:	<u>Cinnamomum</u> .
Tribe II.	Camphoreae	:	<u>Camphora</u> [= <u>Cinnamomum</u>].
Tribe III.	Phoebeae	:	<u>Apollonias</u> , <u>Phoebe</u> .
Tribe IV.	Perseae	:	<u>Persea</u> , <u>Machilus</u> [= <u>Persea</u>] <u>Boldu</u> [= <u>Beilschmiedia</u>], <u>Alseodaphne</u> , <u>Hufelandia</u> [= <u>Beilschmiedia</u>].
Tribe V.	Cryptocaryeae	:	<u>Endiandra</u> , <u>Beilschmiedia</u> , <u>Cecidodaphne</u> [= <u>Cinnamomum</u>], <u>Cryptocarya</u> , <u>Caryodaphne</u> [= <u>Dehaasia</u>], <u>Aganthophyllum</u> [= <u>Ocotea</u>], <u>Mespilodaphne</u> [= <u>Ocotea</u>].
Tribe VI.	Acrodiclidia	:	<u>Aydendron</u> [= <u>Endlicheria</u> , <u>Aniba</u>], <u>Evonymodaphne</u> [= <u>Licaria</u>] <u>Acrodiclidium</u> [= <u>Licaria</u>], <u>Misanteca</u> [= <u>Licaria</u>].
Tribe VII.	Nectandreae		
	Subgenus A	:	<u>Potameia</u> .
	Subgenus B	:	<u>Nectandra</u> .
Tribe VIII.	Dicypellia	:	<u>Dicypellium</u> , <u>Petalanthera</u> [= <u>Ocotea</u>], <u>Pleurothyrium</u> .
Tribe IX.	Oreodaphne	:	<u>Teleiandra</u> [= <u>Ocotea</u>], <u>Leptodaphne</u> [= <u>Ocotea</u>] <u>Aiouea</u> , <u>Goeppertia</u> [= <u>Endlicheria</u>], <u>Haasia</u> [= <u>Dehaasia</u>], <u>Oreodaphne</u> [= <u>Ocotea</u>], <u>Camphoromoea</u> [= <u>Ocotea</u>], <u>Ocotea</u> , <u>Gymnobalanus</u> [= <u>Ocotea</u>].

- Tribe X. Flaviflorae : Sassafras, Benzoin [= Lindera].
- Tribe XI. Tetrathereae : Cyclicodaphne [= Litsea], Tetranthera [= Litsea], Polyadenia [= Lindera], Laurus, Lepidadenia [= Litsea].
- Tribe XII. Daphnidia : Dodecadenia, Actinodaphne, Daphnidium [= Lindera], Litsaea [= Litsea].
- Tribe XIII. Cassyteeae : Cassyta [= Cassytha].
- Genus incertum : Adenostemon [= Gomortega], Gomortega, Keulia [= Gomortega].
2. Bentham & Hooker [1862-1883]
- Tribe I. Perseaceae: : Cryptocarya, Ravensara, Apollonias, Beilschmiedia, Dehaasia, Aiouea, Potameia, Endiandra, Eusideroxylon, Cinnamomum, Persea, Dicypellium, Nectandra.
- Tribe II. Litseaceae : Sassafras, Actinodaphne, Litsea, Umbellularia, Lindera, Laurus.
- Tribe III. Cassytheae : Cassytha.
3. Meissner [1864]
- Suborder I. Laurineae.
- Tribe I. Perseaceae: : Cinnamomum, Alseodaphne, Phoebe, Persea, Haasia [= Dehaasia], Apollonia [= Apollonias].
- Tribe II. Cryptocaryeae : Cryptocarya, Endiandra, Aiouea, Acrodiclidium [= Licaria].
- Tribe III. Oreodaphneae : Dicypellium, Nectandra, Sassafras.

- Tribe IV. Litseaceae.
- Sub-tribe I. Tetrantherae : Actinodaphne, Litsea.
- Sub-tribe II. Daphnidiaceae : Laurus, Lindera.
- Suborder II. Gynocarpeae.
- Suborder III. Cassytheae
4. Mez [1889]
- Suborder I. Laureae.
- Tribe I. Perseeae : Cryptocarya, Aiouea, Aniba, Persea, Ocotea,
Dicypellium, Urbanodendron, Acrodiclidium
[= Licaria], Endlicheria, Phoebe, Nectandra.
- Tribe II. Litseae : Litsea, Sassafras, Umbellularia, Benzoin
[= Lindera].
- Suborder II. Cassytheae : Cassytha.
5. Pax [1891]
- Subfamily I. Persoideae
- Tribe I. Cinnamomeae : Cinnamomum, Persea, Phoebe, Ocotea,
Umbellularia, Nectandra, Dicypellium.
- Tribe II. Eusideroxyloideae : Eusideroxylon.
- Tribe III. Litseae : Sassafras, Actinodaphne, Litsea.
- Subfamily II. Lauroideae
- Tribe I. Apollonieae : Apollonias, Dehaasia, Hexapora [= Micropora],
Beilschmiedia, Aiouea, Potameia.
- Tribe II. Cryptocaryeae : Cryptocarya, Ravensara.
- Tribe III. Acrodiclidieae : Endiandra, Acrodiclidium [= Licaria].
- Tribe IV. Laureae : Benzoin [= Lindera], Laurus.

- Tribe V. Cassytheae : Cassytha.
6. Kostermans [1957] [also in Bernardi, 1962]
- Subfamily A. Lauroideae.
- Tribe I. Perseae
- Sub-tribe a. Perseineae : Persea, Phoebe.
- Sub-tribe b. Beilschmiediineae : Apollonias, Dehaasia, Beilschmiedia, Endiandra, Mezilaurus, Hexapora (= Micropora), Potameia.
- Tribe II. Cinnamomeae.
- Sub-tribe a. Cinnamomineae : Ocotea (+ Nectandra + Pleurothyrium) Cinnamomum, Actinodaphne, Sassafras, Umbellularia, Dicypellium.
- Sub-Tribe b. Anibineae : Aiouea, Aniba, Endlicheria, Licaria, Urbano-dendron, Systemonodaphne, Phyllostemonodaphne.
- Tribe III. Litseae
- Sub-tribe a. Litseineae : Litsea, Neolitsea.
- Sub-tribe b. Lauriineae : Lindera, Laurus.
- Tribe IV. Cryptocaryeae
- Sub-tribe a. Eusideroxylineae : Eusideroxylon.
- Sub-tribe b. Cryptocaryneae : Cryptocarya, Ravensara.
- Tribe V. Hypodaphneae : Hypodaphnis.
- Sub-family B. Cassythoideae : Cassytha.

7. Hutchinson (1964)

- Tribe I. Apollonieae : Apollonias, Thouvenotia [= Beilschmiedia], Beilschmiedia, Systemonodaphne, Dehaasia, Urbanodendron, Aniba, Nobeliodendron [= Licaria], Aiouea, Phyllostemonodaphne, Brassioidendron, [= Beilschmiedia], Micropora, Endiandra, Licaria, Potameia, Misanteca [= Licaria], Mezilaurus, Syndiclis [= Potameia], Endlicheria.
- Tribe II. Cryptocaryeae : Cryptocarya, Ravensara.
- Tribe III. Sassafrideae : Sassafras, Sassafridium [= Cinnamomum], Actinodaphne.
- Tribe IV. Cinnamomeae : Phoebe, Persea, Nothaphoebe, Pleurothyrium, Nectandra, Synandrodaphne [= Nectandra], Dicypellium, Cinnamomum (+ Neocinnamomum), Cardiodaphnopsis [= Caryodaphnopsis] Machilus [= Persea], Ocotea, Stemmatodaphne [= Alseodaphne], Hypodaphnis, Eusideroxylon.
- Tribe V. Litseae : Dodecadenia, Umbellularia, Litsea, Neolitsea, Lindera, Laurus, Iteadaphne [= Lindera] Valvanthera.
- Tribe VI. Cassytheae : Cassytha

