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Intercellular pectic protuberances in plants: their structure and taxonomic significance

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Abstract. The development, structure, histochemistry, distribution, and function of intercellular pectic protuberances (IPP) in vascular plants are reviewed on the basis of an extensive literature survey. This is supplemented by the first report of these structures in members of the Icacinaceae, based on a detailed anatomical study of leaf material of *Apodytes* and *Cassinopsis*. Development of IPP is usually associated with the formation of intercellular spaces during tissue expansion. Morphologically, four major categories of IPP are evident: scalae; strands; warts; and filaments. Ontogenetic pathways for these types are proposed. Copious pectin formation may result in a pectic sol, partially or completely filling the intercellular spaces. Although histochemical tests indicate that intercellular wall projections are predominantly pectic in composition, detailed comparative chemical studies are lacking. IPP are irregularly dispersed throughout the ferns, gymnosperms, dicotyledons and monocotyledons. A list of more than 200 plant species reported to have IPP is provided. Distribution data for flowering plants is plotted against Dahlgren's system of classification. Although IPP are generally diagnostic at the specific and sometimes the generic level, variation within families and orders seriously limits their taxonomic significance in higher categories. Their widespread distribution and morphological diversity suggest that IPP are of polyphyletic origin and thus not homologous in the different groups. If considered as a single category, the mere presence/absence of IPP is not useful in assessing taxonomic relationships. Assessed separately, filaments tend to be concentrated mainly in the ferns and monocotyledons. Unfortunately, research on IPP has not progressed far enough to give a complete picture; numerous gaps remain. The biological functions attributed to IPP are speculative and include involvement in apoplastic transport, cell-wall hydration, storage (e.g. carbohydrates, potassium), cell adhesion, and defence against pathogens. The possibility that they have no particular function cannot be ruled out. In almost all cases, experimental evidence for any of these functions is lacking.

Key words: Anatomy; Cell wall; Histochemistry; Icacinaceae; Leaf; Middle lamella; Pectin.

Introduction

During a comparative anatomical study of southern African Icacinaceae, we noted minute intercellular wall protuberances in the mesophyll of the leaves. The absence of these structures in some taxa and apparent constant presence in others, led us to question their chemical composition, ontogeny, function, and taxonomic significance. Histochemical tests showed that these protuberances consist mainly of pectic substances.

According to Kisser (1928), De Vriese and Harting (1853) were the first to report intrusions of pectic cell-wall material into intercellular spaces. The first detailed description of this phenomenon was given by Luerssen (1873, 1875) for the Marattiaceae and other ferns. Since then protuberances of various sizes, shapes

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and quantity have been reported to occur on the outer cell surface in a number of vascular plants (for reviews see Kisser, 1928; Branfoot, 1929; Carr and Carr, 1975). Surprisingly, with some exceptions (e.g. Carlquist, 1961; Esau, 1965; Ogura, 1972), this phenomenon is not mentioned in modern textbooks on plant anatomy (e.g. Metcalfe and Chalk, 1979; Mauseth, 1988; Fahn, 1990).

In earlier literature, much was written on the structure, development, and physico-chemical properties of intercellular pectic protuberances. Also, their occurrence in different locations within the plant, such as in the leaf, stem, root and seed, have been noted. Controversies over pectic cell-wall protuberances have revolved around three questions (Carr and Carr, 1975): a) do they form during or after intercellular space formation?; b) what do they consist of?; and c) what is their biological function? A variety of factors, including differences in distribution, shape, and physical properties, have led to the use of multiple designations by different authors. Names such as intercellular pectic strands, intercellular pectic warts, intercellular connections, intercellular mucilage, cuticularized threads ("Cuticularfäden"), filaments, pectic projections, lumps, bumps, and scala are found in the literature.

The introduction of sophisticated instruments and preparation techniques, such as freeze-drying, critical-point drying and the scanning electron microscope, have enabled workers like Carr and Carr (1975) and Carr *et al.* (1980a,b) to make significant contributions to our understanding of intercellular pectic structures. Although aspects of the morphology, development and chemical composition of intercellular protuberances are relatively well documented, their possible function and taxonomic significance remain obscure.

In this paper we report for the first time on the presence and structure of intercellular pectic protuberances in members of the Icacinaceae. We also review the characteristics and distribution of intercellular pectic protuberances in vascular plants on the basis of a comprehensive literature survey. The primary aim of this study is to evaluate the taxonomic significance of these structures.

Materials and Methods

Leaf structure was studied in eight species of *Apodytes* E. Mey. ex Arn., *Cassinopsis* Sond. and *Pyrenacantha* Hook., all taxa of the Icacinaceae from southern Africa (Table 1). Southern Africa is defined as the mainland region of the African Continent south of the Cunene/Zambezi rivers. Intercellular pectic protuberances were recorded only in members of *Apodytes* and *Cassinopsis*. Hence material of these two genera was studied in detail using light (LM), scanning electron (SEM) and transmission electron microscopy (TEM).

Unless stated otherwise, fresh leaves at various stages of development were either preserved in formalin-acetic acid-alcohol (FAA) (Johansen, 1940) or fixed in 2% glutaraldehyde in 0.1 M sodium cacodylate buffer at pH 7. Material was obtained from plants growing in botanical gardens and various natural populations.

LM Procedures

Small pieces of fixed or preserved leaf lamina were dehydrated, infiltrated and embedded in glycol methacrylate (GMA) (Feder and O'Brien, 1968). GMA sections, 3-5 μm thick, were cut on a Porter Blum MT-1 ultramicrotome, stained and, where appropriate, permanently mounted in entellan (Art. 7961, E. Merck, Darmstadt). The periodic acid-Schiff's reaction (PAS)

Table 1. *Members of Icacinaceae studied and voucher specimens. All are deposited in PRU*

Apodytes dimidiata E. Mey. ex Arn. subsp. *dimidiata*: *Potgieter 54, 56, 70.*
Apodytes sp. nov. A: *Van Wyk A405, A406, A1047, 10470.*
Apodytes sp. nov. B: *Van Wyk 1065, 2134, 2133.*

Cassinopsis ilicifolia (Hochst.) Kuntze: *Potgieter 69, 73, 74.*
C. tinifolia Harv.: *Potgieter 65; Van Wyk 10486, 10487, 10497*; *Van Wyk & Matthews 10489.*

Pyrenacantha grandiflora Baill.: *Potgieter 4, 9, 10, 11, 64.*
P. kaurabassana Baill.: *Potgieter 72.*
P. scandens Planch. ex Harv.: *Potgieter 58, 59, 61.*

was carried out according to Feder and O'Brien (1968), using 0.5% dinitrophenyl hydrazine in 15% acetic acid (for 30 min) as blocking agent. Following the PAS reaction, some sections were counterstained for 2 min in 0.05% toluidine blue O (Feder and O'Brien, 1968) in benzoate buffer at pH 4.4 (Sidman *et al.*, 1961).

For histochemical interpretation, GMA sections were also treated with one of the following compounds: Sudan black B (O'Brien and McCully, 1981); toluidine blue O (Feder and O'Brien, 1968); aniline blue (Jensen, 1962); acid fuchsin (O'Brien and McCully, 1981); ruthenium red (Johansen, 1940); potassium iodide-iodine (IKI) (Johansen, 1940); hydroxylamine-ferric chloride (Reeve, 1959a); IKI-H_2SO_4 (Johansen, 1940); and phloroglucinol (Johansen, 1940).

SEM Procedures

Two methods were used. In the first, fixed leaf fragments were dehydrated, infiltrated with liquid CO_2, subjected to critical-point drying, coated with gold, and examined with a Jeol JSM 840 SEM at 8kV. In the second, fresh leaf material was studied by cryoSEM. A piece of lamina was attached with silver cement to a stub and frozen in liquid nitrogen. The stub was transferred, in a nitrogen atmosphere, to a cold stage (-180°C) at the entry port of the SEM. After a delay of a few minutes for temperature equilibration, the leaf was fractured *in situ* with a knife blade and the clean-fractured surface examined on the cold specimen stage at 3kV.

TEM Procedures

Pieces (about 1 mm^2) of fixed or preserved leaf lamina were washed in 50% ethanol, then in bidistilled water, and fixed in 0.5% osmium tetroxide for 30 min. They were then dehydrated through an acetone series, embedded in quetol resin (Kushida, 1974), and sectioned at 73-93 nm thickness on an Ultracut E ultramicrotome. Sections were stained in aqueous uranyl acetate (10 min), followed by lead citrate (10 min) (Reynolds, 1963), and viewed with a Philips 301 TEM.

For polysaccharide detection we used a modification of the method described by Thiéry (1967): (1) fix fresh leaf material for 3 h in 2% glutaraldehyde in 0.1 M Na-cacodylate buffer (pH 7.2)——post fixation with osmium tetroxide is omitted; (2) embed in quetol and section material as described above; (3) treat sections with a 1% solution of periodic acid (PA) for 30 min; (4) wash thoroughly in bi-distilled water; (5) treat with 0.2% thiocarbohydrazide (TCH) in 20% acetic acid for 24 h; (6) soak in 20, 15, and 10% acetic acid for 20 min each; (7) wash in 5 and 2% acetic acid for 60 sec each; (8) rinse thoroughly in bi-distilled water; (9) stain sections with a 1% solution of silver proteinate for 30 min in darkness; (10) wash in bi-distilled water; (11) view under TEM. Control staining procedures followed the recommendations of Courtoy and Simar (1973), and are three-fold: (a) omit the PA treatment (steps 3 and 4); (b) omit the TCH treatment and subsequent acetic acid washings (steps 5, 6 and 7); (c) omit the staining with silver proteinate (steps 9 and 10).

Graphic Representation of Literature Survey

The distribution of pectic protuberances among the families of flowering plants is visually presented on diagrams based on the classification of Dahlgren (1980, 1983). The diagram used for the monocotyledons is reproduced from Dahlgren and Clifford (1982) and that for the dicotyledons from Dahlgren (1989, 1991).

Results and Discussion

Pectic Protuberances in southern African Icacinaceae

Intercellular, predominantly wart-like protuberances are present in the mesophyll of all investigated mature-leaf samples of *Apodytes* sp. B and *Cassinopsis* (Fig. 1, A & B). No protuberances were found in *Apodytes dimidiata* E. Mey ex Arn. and *Apodytes* sp. A, or any of the investigated species of *Pyrenacantha*. Results of different LM staining procedures are summarized in Table 2. Both ruthenium red and hydroxylamine-ferric chloride showed a positive reaction for pectin, which strongly supports the interpretation that these protuberances have a pectic composition. Too much weight should not, however be given to the results with ruthenium red, as this stain is not specific for pectic compounds. On the other hand, hydroxylamine-ferric chloride is specific for pectin and is therefore much more reliable. Positive staining (red to pink) with the PAS reaction and toluidine blue O further supports a pectic composition. Results of the other staining tests for various non-pectic compounds all proved negative.

A study of leaf development by SEM (Fig. 2, A-D) and TEM (Fig. 3, A-D), showed that pectic warts are established only after the formation and subsequent

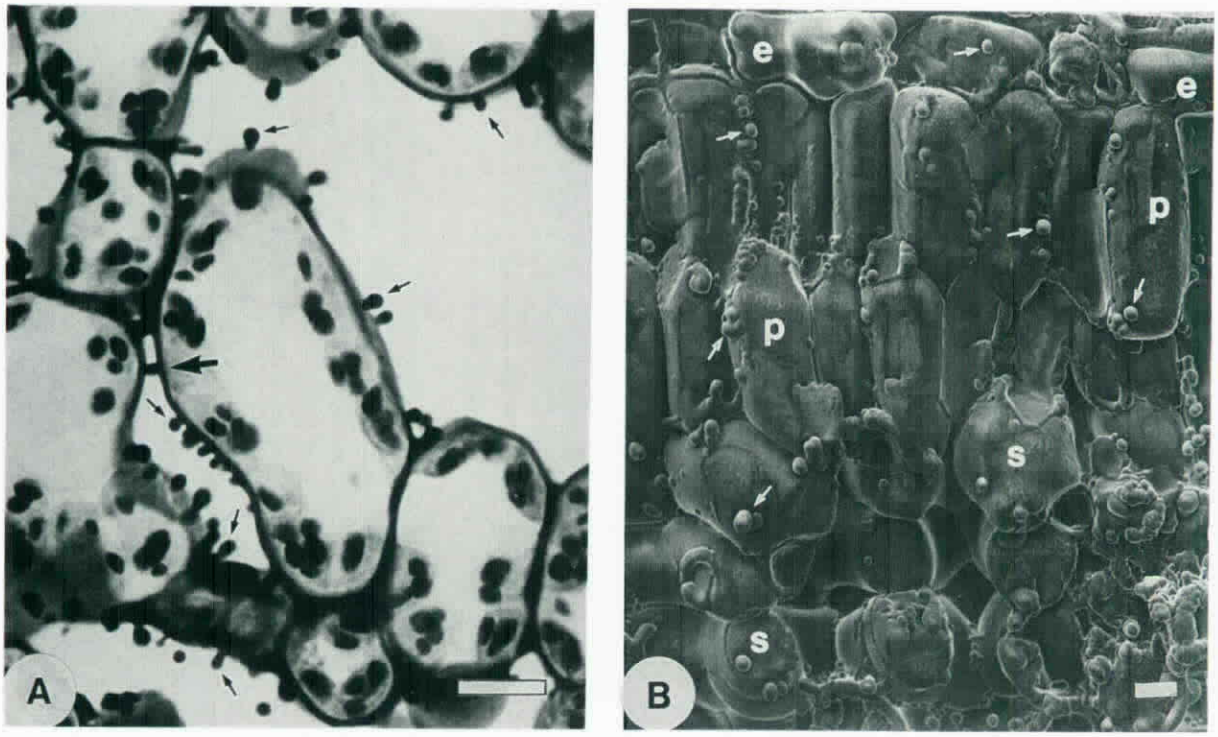

Fig. 1. Transverse sections of the leaf lamina of *Cassinopsis ilicifolia* (*Potgieter 73*). A, light micrograph of spongy parenchyma showing cell walls with numerous darkly stained (PAS/toluidine blue) intercellular pectic warts (small arrows) and very few pectic strands (large arrow); B, cryoSEM micrograph showing globular intercellular pectic warts (some arrowed) on the walls of epidermal (e), palisade (p), and spongy parenchyma (s) cells. Scale bars = 10 μm.

Table 2. *Histochemical reactions of intercellular wall protuberances in southern African Icacinaceae*

Stain	Test for:	Reaction
Sudan Black B	Fats, lipids & oils	–
PAS reaction	Starch & complex polysaccharides	Pink
Toluidine blue O	Wide spectrum, including pectins	Red
Aniline blue	Callose	–
Acid fuchsin	Proteins	–
Ruthenium red	Pectins	+
Hydroxylamine-ferric chloride	Pectins	+
IKI	Starch	–
IKI-H_2SO_4	Cellulose	–
Phloroglucinol	Lignin	–
Thiéry test	Polysaccharides	+

breakage of intercellular pectic strands. First appearance of pectic strands is associated with the formation of intercellular spaces, with the strands being, at least in part, the remnants of a well-developed middle lamella. In the young leaf these strands are more or less uniform in thickness and appear to be tightly stretched across the intercellular spaces. At their ends, the strands widen and merge smoothly with the cell wall to which they are attached. The strands, as well as the warts, are solid and there is no evidence of a cuticle. CryoSEM showed the pectic warts to have a more or less smooth outer surface (Figs. 1 B; 2, A–C). Very few pectic strands are found in the mature leaf, although warts (of different sizes in the same sample) are much

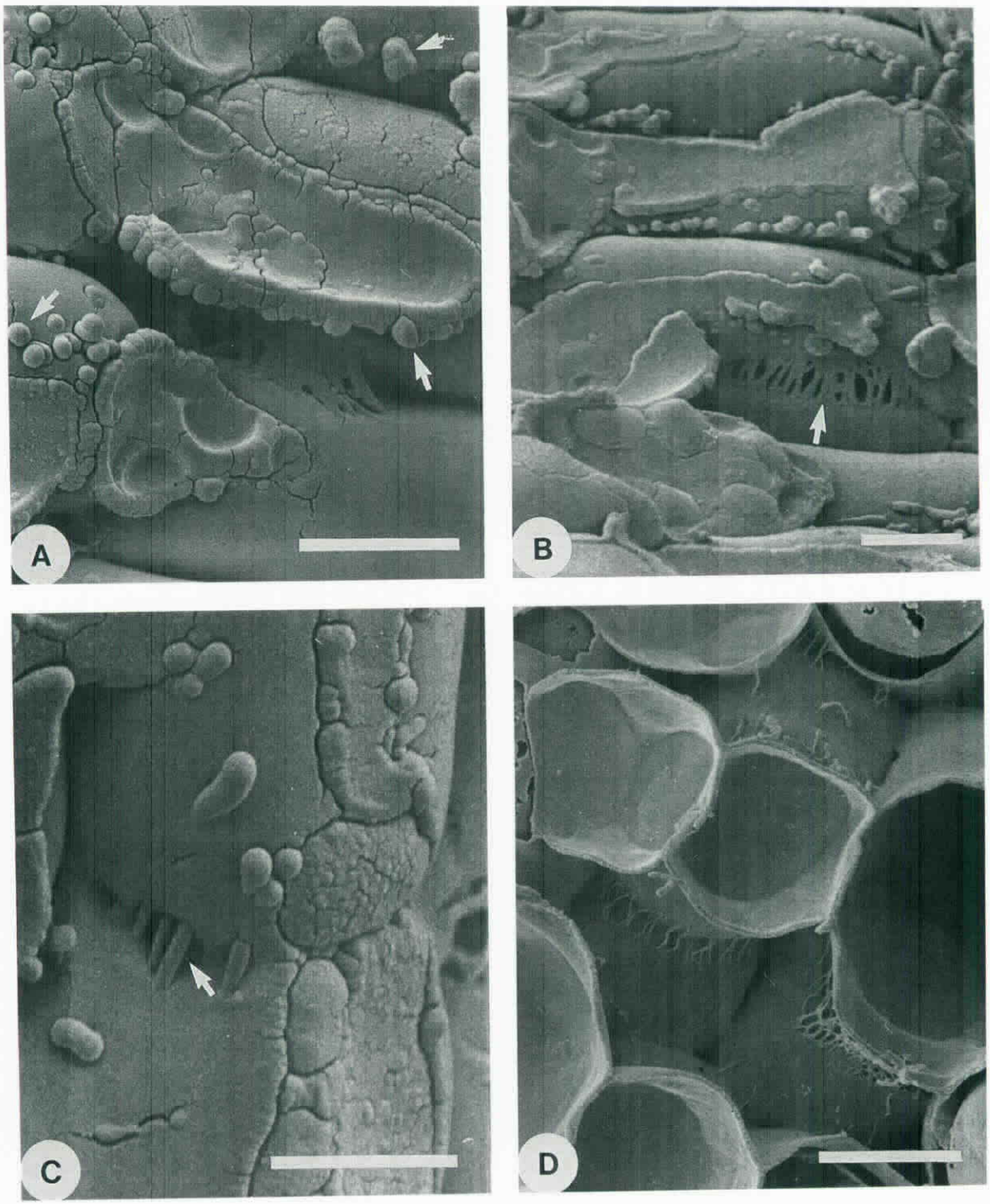

Fig. 2. Morphology of intercellular pectic protuberances as seen in transverse sections of the leaf lamina of *Cassinopsis ilicifolia* (*Potgieter 73*). A–C, cryoSEM micrographs. A, pectic warts (some arrowed); B, pectic strands approaching the scala arrangement (arrowed) as well as warts formed by the snapping and contraction of pectic strands during tissue expansion; C, pectic strands in the angle between two cells (arrowed) with warts on the exposed parts of the wall; D, critical-point dried spongy parenchyma showing pectic strands in the angle between adjacent cells (relatively small diameter of strands probably due to shrinkage caused in preparation). Scale bars = 10 μm.

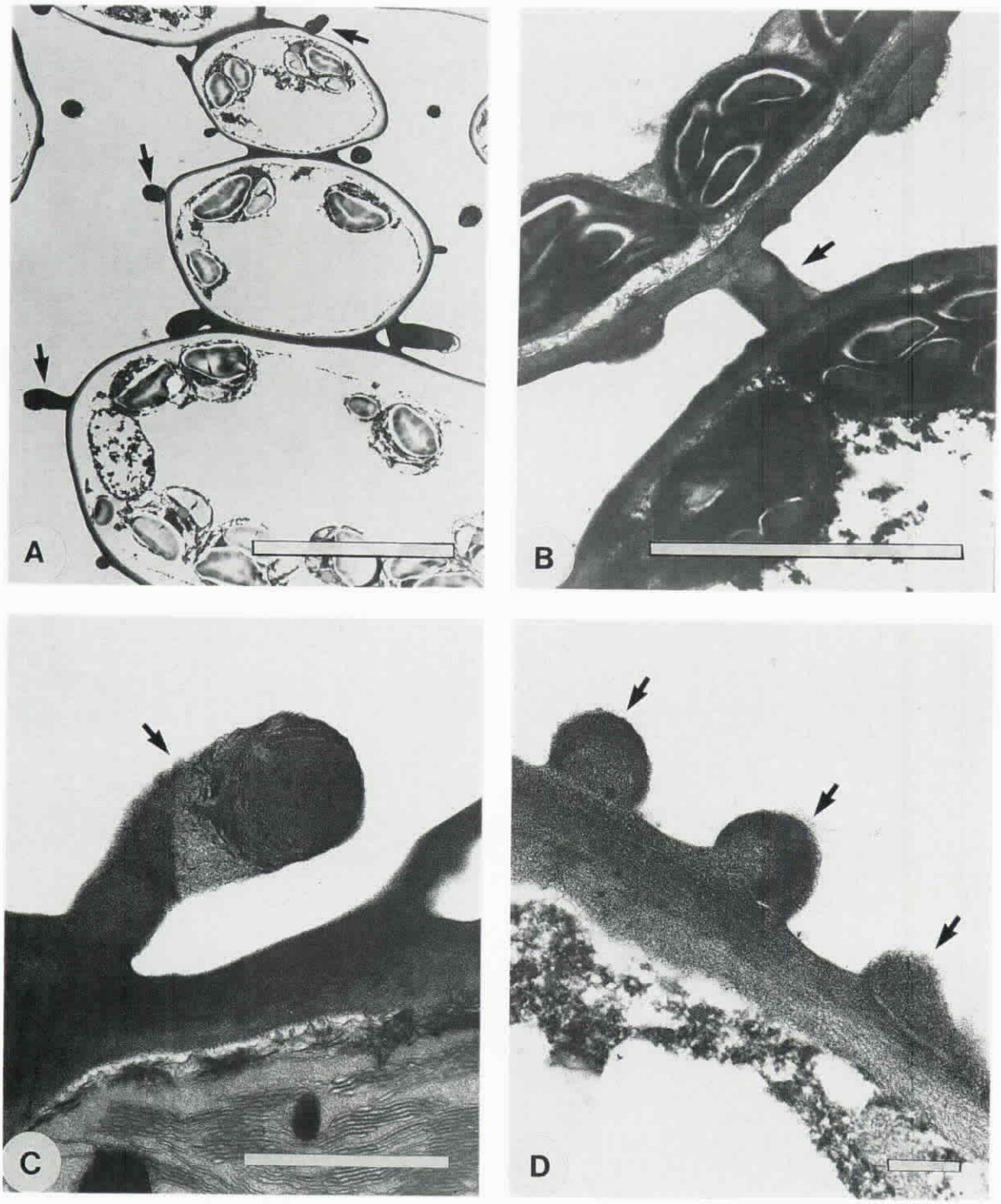

Fig. 3. TEM micrographs illustrating the structure of intercellular pectic protuberances in the spongy leaf parenchyma of *Cassinopsis ilicifolia* (*Potgieter 73*). A, low magnification showing pectic warts (some arrowed) ——note accumulation of pectic material at cell junctions; B, longitudinal section of a pectic strand (arrowed) between two cells; C, oblique transverse section of a pectic strand (arrowed); D, transverse section of pectic warts (arrowed)——note continuity with underlying cell wall. A, fixed in FAA; B–D, fixed in 2% glutaraldehyde. Scale bars of A & D = 10 μm, B = 0.23 μm, and of C = 1 μm.

in evidence. Warts are most common in the spongy parenchyma of the lamina, particularly towards the abaxial epidermis, although a few do occur in the palisade pa-renchyma (Fig. 1B).

Under TEM the internal structure of the warts is usually faintly fibrillar and layered (Fig. 3, B-D). There are no obvious pores in the cell wall through which the pectic substances can be secreted into the intercellular space. It is noticeable that the warts stain to the same density as the underlying cell wall (Fig. 3, C & D). A polysaccharide composition for the warts and strands was confirmed by the modified Thiéry staining. All controls were negative for polysaccharides, thus substantiating the results of the test.

Types of Intercellular Pectic Protuberances

We support the recognition of the three main morphological categories of pectic wall protuberances suggested by Carr and Carr (1975), namely, (1) *pectic scalae* (singular: *scala*), a regular ladder-like configuration of strands, all of relatively uniform thickness, extending between opposite cell walls, particularly common between cells in regularly arranged palisade mesophyll; (2) *pectic warts,* roughly spherical bodies projecting into the intercellular space, but not extending between opposite cells; and (3) *pectic filaments,* a dense mass of intercellular filaments or rod-like protuberances on the walls of cells, perhaps not always of pectin, but may include some pectinous material, either straight or curly, again not extending between opposing cells, recorded mainly in ferns, e.g. on walls of cortical parenchyma cells in the rhizome of *Pteridium esculentum* (Forst. f.) Nakai. To this we add (4) *pectic strands,* an irregular arrangement (compare scalae) of strands extending between opposite cell walls, which are particularly common in spongy mesophyll, and usually a developmental stage towards the formation of pectic warts (Fig. 4).

Although not a type of protuberance, a fifth category could be described as an *intercellular pectic sol*; a state in which the entire intercellular space, or just the connecting cell wall corners, becomes filled with a pectic matrix, a condition particularly associated with senescence in ripening fruit (Carré and Horne, 1927). Yet, Carlquist (1956) recorded a tendency towards occlusion of intercellular spaces by pectic intrusions in *Fitchia speciosa* Cheeseman (Asteraceae). This is due to a progressive increase in deposition of pectic material during maturation of the petiole. Pectic channels with abundant pectic sol were subsequently reported in the leaves of *Argyroxiphium* DC. (Carlquist, 1957).

Even within the four major groupings, minor variations do occur. For example, in the scalae group, the filaments can be rather distantly spaced, as in the stomata of *Vicia faba* L. (Carr *et al.,* 1980a), or they can be in a perforated curtain-like state as reported for species of *Eucalyptus* L'Hérit. (Carr and Carr, 1975). Variation of pectic warts includes a state such as that described for members of the Icacinaceae in the present study, to a state in which the pectic warts have droplets of oil adhering to them, or develop an internal vesicle (Davies and Lewis, 1981).

Chemical Composition and Properties of Pectin

The nomenclature of pectic substances has been very confusing at times. The word *pectin* has, for example, been loosely used to indicate any soft pectic substances (Sifton, 1945). According to Kertesz (1951), *pectic substances* constitute "...a group designation for those complex, colloidal carbohydrate derivatives which occur in, or are prepared from, plants...", whereas *pectin* is a general term designating "... those water-soluble pectinic acids of varying ester content and degree of neutralization which are capable of forming gels with sugar and acids under suitable conditions." Pectins are, in general, soluble in water and insoluble in organic solvents (Towle and Christensen, 1973). Pectins are also soluble under mildly acidic conditions at normal temperatures, but undergo depolymerization in a stronger acidic environment.

It is increasingly clear that pectic polysaccharides are not merely a jelly-like matrix found predominantly in the middle lamella, but substances of considerable chemical complexity, comprising a substantial, and orderly deposited, component of the cellulose-hemicellulose network in the cell wall (Brett and Waldron, 1990; Roberts, 1990). The three main classes of pectic polysaccharides isolated from primary cell walls are polygalacturonic acid (PGA), rhamnogalacturonan (RG)-I, and RG-II.

Pectin and pectic acids are reactive with a number of reagents and have been used as starting materials for a variety of useful derivatives (Branfoot, 1929; Kertesz, 1951; Towle and Christensen, 1973). The importance of pectin to the food industry (jams, jellies and preserves) lies in the ability of its solutions to yield

thermo-reversible gels.

Characteristics of Intercellular Pectic Protuberances

The known reactions of intercellular protuberances to different histochemical and other treatments are listed in Table 3. Our own range of tests on wall protuberances in the leaves of Icacinaceae (Table 2) are largely in agreement with the findings of other workers on pectic structures. Contrary to our findings, Carr and Carr (1975) reported pectic protuberances unstained by toluidine blue. Note, however, that the prolific filamentous intercellular protuberances of the ground parenchyma tissue in the stem of *Cocos nucifera* L., studied by Butterfield *et al.* (1981) and for which the results of several tests are reported in Table 3, might not be homologous with true pectic protuberances. In addition, certain ice crystal artifacts caused by water during cryoSEM may also closely resemble pectic warts in external morphology (Jeffree *et al.*, 1987).

Pectic protuberances are nearly always solid (Carr and Carr, 1975), and not covered by a cuticle (Carr *et al.*, 1980b) (Fig. 3). Near or in a stomatal aperture/cavity, protuberances may be coated with cutin (Heide-Jørgensen, 1978). The dubiously pectinous filaments in *Cocos nucifera* have a tranverse layered structure (Butterfield *et al.*, 1981). Pectic protuberances on wound callus cells of *Daucus carota* L. appear to have central lipidic cores (Davies and Lewis, 1981). A direct

Table 3. *Selective review of the reaction of intercellular wall protuberances to different histochemical treatments*

Treatment[a]	Reaction	Reference[d]
Ruthenium red	+	Heide-Jørgensen (1978)
Zinc-chloride-iodine	−	Carlquist (1956)
Warm 0.5% ammonium oxalate	Removed	Carlquist (1956)
Toluidine blue	−[c]	Carr and Carr (1975)
1% pectinase	Removed	Carr *et al.* (1980a)
IKI-H_2SO_4	Patchy	Davies and Lewis (1981)
Hydroxylamine-ferric chloride	−[c]	Davies and Lewis (1981)
Methylene blue	+	Davies and Lewis (1981)
Sudan IV[b]	Patchy	Davies and Lewis (1981)
Nile blue sulfate[b]	Patchy	Davies and Lewis (1981)
Osmium tetroxide[b]	−	Davies and Lewis (1981)
Periodic acid-Schiff	Pink	Butterfield *et al.* (1981)[e]
Cold 50% chromic acid	Removed	Butterfield *et al.* (1981)
Sodium hypochlorite	Removed	Butterfield *et al.* (1981)
Phloroglucinol-HCL	−	Butterfield *et al.* (1981)
Lignin pink	−	Butterfield *et al.* (1981)
75% H_2SO_4-iodine	−	Butterfield *et al.* (1981)
Cuprammonium hydroxide	−	Butterfield *et al.* (1981)
Aniline blue	−	Butterfield *et al.* (1981)
Hot water (1 h)	−	Butterfield *et al.* (1981)
Hot sodium chloride (1 h)	−	Butterfield *et al.* (1981)
Hot 10% KOH or NaOH (1 h)	−	Butterfield *et al.* (1981)
Cold 10% KOH or NaOH (48 h)	−	Butterfield *et al.* (1981)
Ethanol/methanol/benzene (refluxing for 24 h)	−	Butterfield *et al.* (1981)
0.5% ammonium oxalate, with or without prior acidification in 3% aqueous HCL	−	Butterfield *et al.* (1981)

[a]See Table 2 for tests performed during the present study.
[b]Test for projections containing vesicles and attached oil droplets.
[c]We have recorded a positive reaction in Icacinaceae (Table 2).
[d]Only relatively recent references are given.
[e]The intercellular protuberances in *Cocos nucifera*, tested by Butterfield *et al.* (1981) do not consist of pectin, although they may include some pectinous material.

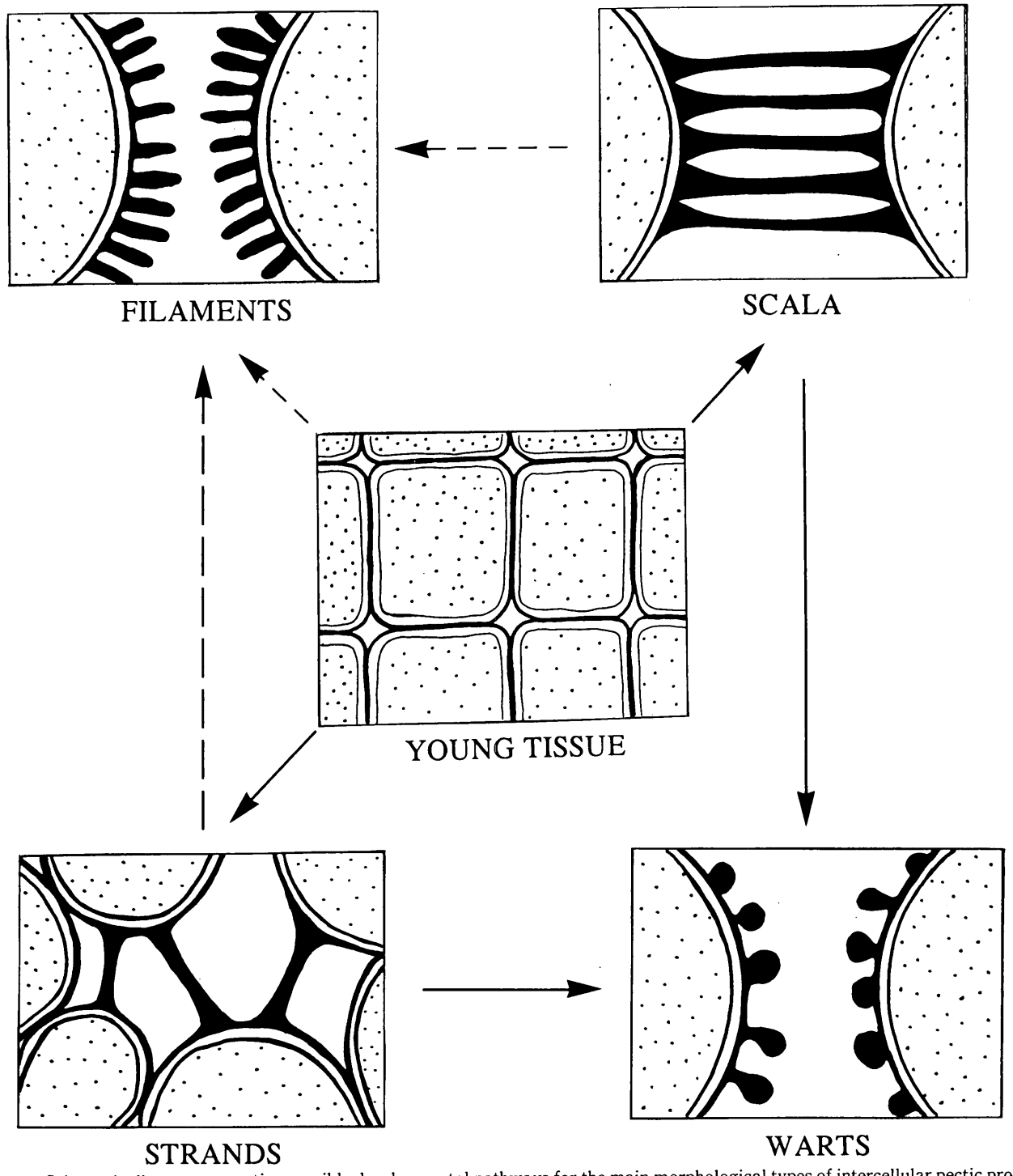

Fig. 4. Schematic diagram suggesting possible developmental pathways for the main morphological types of intercellular pectic protuberances during young tissue expansion. Solid-line arrows indicate pathways supported by ontogenetic evidence. In some cases, scalae, strands, and warts may co-exist (in various proportions) in the same tissue. The development of filaments is hypothetical, hence the use of dotted-line arrows. Indications are that, at least in some cases, filaments might not be homologous with the other forms of pectic protuberances. Excessive accumulation of pectic material may result in a pectic sol (not illustrated) partially or entirely filling the intercellular space. Protoplast of cells dotted; cell walls shown by two parallel lines; middle lamella shown as a heavy black layer; pectic protuberances black, continuous with middle lamella.

relationship between protuberance size and number, and the thickness of the wall on which they occur, has been discussed (Carlquist, 1956; Butterfield *et al.*, 1981). Eletron probe analysis strongly suggests the presence of potassium and calcium within the filamentous protuberances of *Cocos nucifera* (Butterfield *et al.*, 1981). Carr *et al.* (1980a) provide evidence that palisade pectic scalae are depleted of calcium, at least in the mature fully-formed condition.

Development of Intercellular Pectic Protuberances

The development of the main categories of pectic protuberances as well as their possible inter-relationships are schematically shown in Fig. 4. Unfortunately, the ontogeny of pectic protuberances has hitherto been studied in very few taxa. Hence the diagram presented here is, in part, hypothetical.

During tissue expansion intercellular spaces are formed as a result of the pulling apart of cells. Most pectic protuberances are undoubtedly formed during this stage, with the bulk of their pectinous substance clearly derived from the middle lamella. Carr *et al.* (1980a) speculated that, where the middle lamella pectin is cross-linked by calcium, intercellular spaces will not form. Where the middle lamella pectin is not cross-linked with calcium, the pectin will eventually be stretched into a curtain and finally into regular pectic scalae or irregular strands. Observations by Carr and Carr (1975) suggest that these extended strands are under tension. As tissue development proceeds, these cylindrical connections (strands) may rupture as the tissue attains its maximum expansion. A consequence of this rupture is the formation of globules (pectic warts) which remain on the opposing walls of the separated cells. Our own work has clearly shown that pectic warts in the Icacinaceae are derived from pectic strands, the warts representing a later stage of development. This might explain Kisser's (1928) observation that pectic warts, in spongy parenchyma of *Saxifraga sarmentosa* L. leaves, show an increase in wart size and number during leaf enlargement. Carlquist (1957) suggests that the abundant pectic sol in leaves of *Argyroxiphium* represents an extreme stage of development of pectic warts——still present in the pith of the stem.

In contrast to the scalae, strands, and warts, the mode of development of pectic filaments is still very uncertain; hence the dotted-line arrows in Fig. 4. There is no conclusive evidence that the bulk of the filaments in, for example *Pteridium, Cocos,* or the very regular rod-like protuberances in *Equisetum* L. (Chauveaud, 1902) and members of the Marattiaceae (Luerssen, 1873, 1875), are derived simply from the fracturing of pectic strands connecting adjacent cells during tissue expansion. It has been suggested that at least some of these filaments may be derived from extracellular materials laid down after intercellular space formation (Carr and Carr, 1975; Butterfield *et al.*, 1981). Circumstantial evidence suggests that, over an extended period (possibly the whole life of the palm), the filaments in *Cocos nucifera* increase in number and grow by accretion at one or other of their ends (Butterfield and Meylan, 1980; Butterfield *et al.*, 1981).

Distribution and Taxonomic Significance

Following a comprehensive literature review, Kisser (1928) cites references to pectic warts ("Pektinwarzen") in a large number of plant species, and also makes his own additions to the list of taxa. An updated list, in which we have incorporated a number of subsequent references to pectic protuberances, is presented in Table 4. Most of the reports taken from Kisser (1928) have been followed back to their original source. This information is graphically portrayed for dicotyledons and monocotyledons in Figs. 5 & 6 respectively. This list of taxa with intercellular pectic protuberances is undoubtedly incomplete due to the following factors. Firstly, most workers do not recognize these structures for what they are, and thus do not report them. Secondly, the small dimension of pectic protuberances makes them difficult to detect, particularly with the light microscope. Thirdly, the anatomy of the majority of plant species is either unknown, or has not yet been studied in detail.

In spite of the scanty information available (Table 4), it is clear that intercellular pectic protuberances in plants have a wide distribution with respect to taxon, organ/tissue type, ecological preference and biogeography. Similar inductions were also made by Carr *et al.* (1980b) and Carlquist (1956). This wide distribution among vascular plants limits the use of pectic protuberances as taxonomic markers to characterize higher taxonomic categories. The great variability of many families and orders implies that parallel origin or loss of pectic protuberances must have been rampant in the evolutionary history of the vascular plants. It is therefore clear that these structures, when considered

Table 4. *Distribution of intercellular pectic protuberances in vascular plants*

Taxon[a]	Type of protuberance[b]	Organ/Tissue[c]	Reference
FERNS & FERN ALLIES			
ASPLENIACEAE			
Asplenium bulbiferum	+	P	Luerssen (1875)
A. dimorphum	+	P	Luerssen (1875)
A. marginatum	+	P	Luerssen (1875)
A. mollissimum	W?	P	Kisser (1928)
A. musaefolium	W?	P	Kisser (1928)
A. nidus	+	L	Luerssen (1875)
A. vulgare	+	+	Luerssen (1875)
BLECHNACEAE			
Blechnum brasiliense	W	P	Gardiner (1885), Mangin (1893)
B. cartilagineum	+	P	Luerssen (1875)
B. procerum	+	P	Luerssen (1875)
Woodwardia lunulata	+	P	Luerssen (1875)
W. radicans	+	P	Luerssen (1875)
CYATHEACEAE			
Cyathea aspera	+	P	Luerssen (1875)
C. australis	+	P	Luerssen (1875)
C. dealbata	+	P	Luerssen (1875)
C. excelsa	W	L	Hannig (1898)
C. glauca	+	P	Luerssen (1875)
C. imrayana	+	Lenticel	Hannig (1898)
C. loddigesii	+	P	Luerssen (1875)
C. radens	+	P	Luerssen (1875)
C. spectabilis	+	P	Luerssen (1875)
DAVALLIACEAE			
Davallia pyxidata	+	RH	Luerssen (1875)
DENNSTAEDTIACEAE			
Hypolepis repens	+	+	Luerssen (1875)
Lindsaea repens	+	P	Luerssen (1875)
Pteridium esculentum	F	L	Carr and Carr (1975)
DICKSONIACEAE			
Cibotium glaucescens	+	P	Luerssen (1875)
C. schiedei	+	P	Luerssen (1875)
Dicksonia antarctica	+	P	Luerssen (1875)
DRYOPTERIDACEAE			
Cystopteris fragilis	+	P	Luerssen (1875)
Didymochlaena lunulata	+	P	Luerssen (1875)
Dryopteris falcatum	+	P	Luerssen (1875)
D. filix-mas	W	P	Luerssen (1875), Gardiner (1885)
D. proliferum	+	P	Luerssen (1875)
Onoclea sensibilis	+	P	Luerssen (1875)
O. struthiopteris	+	P	Luerssen (1875)
Polybotrya acuminata	+	P	Luerssen (1875)
P. cervina	+	P	Luerssen (1875)
EQUISETACEAE			
Equisetum arvense	W	ST	Mangin (1893)
E. hyemale	W	ST	Mangin (1893)
E. limosum	W	ST	Mangin (1893)
E. maximum	W	ST	Mangin (1893)
E. palustre	F	ST	Vidal (1896)
E. ramosissimum	W	ST	Mangin (1893)

Table 4. *Continued*

Taxon[a]	Type of protuberance[b]	Organ/Tissue[c]	Reference
E. sylvaticum	F	+	Vidal (1896)
E. trachyodon	W	ST	Mangin (1893)
E. variegatum	W	ST	Mangin (1893)
GYMNOGRAMMACEAE			
Gymnogramma japonica	+	P	Luerssen (1875)
MARATTIACEAE			
Angiopteris crassipes	F	L	Schenck (1886)
A. evecta	W, F	L, P, ST, R	Carr & Carr (1975), Kühn (1889), Schenck (1886), Hannig (1898)
A. longifolia	F	L	Schenck (1886)
A. teys-manniana	F	L	Schenck (1886)
A. willinkii	F	L	Schenck (1886)
Danaea elliptica	W	L, P	Luerssen (1873)
Kaulfussia aesculifolia	F	L	Luerssen (1873)
K. assamica	W	L, P, ST	De Vriese and Harting (1853)[d], Luerssen (1873), Kühn (1889)
Maratia alata	W	L	Kühn (1889)
M. cicutaefolia	F	L, P, ST, R	Luerssen (1873), Schenck (1886)
M. fraxinea	F	L, P, ST	Schenck (1886), Kühn (1889)
M. kaulfussii	F	L	Schenck (1886)
M. laxa	F	L	Luerssen (1873), Schenck (1886)
M. verschaffeltii	+	L	Hannig (1889)
M. weimannifolia	F	L	Schenck (1886)
NEPHROLEPIDACEAE			
Nephrolepis davallioides	+	P	Luerssen (1875)
OLEANDRACEAE			
Oleandra hirtella	+	RH	Luerssen (1875)
OPHIOGLOSSACEAE			
Helminthostachys zeylanica	W	ST	Kühn (1889)
Ophioglossum vulgatum	+	P	Luerssen (1875)
OSMUNDACEAE			
Osmunda cinnamomea	+	P	Luerssen (1875)
O. regalis	+	P	Luerssen (1875)
Todea barbara	+	P	Luerssen (1875)
POLYPODIACEAE			
Leptochilus axillaris	+	RH	Luerssen (1875)
Phegopteris hexagonoptera	+	P	Luerssen (1875)
P. vulgaris	+	P	Luerssen (1875)
Platycerium alcicorne	+	P	Luerssen (1875)
Polypodium geminatum	+	RH	Luerssen (1875)
P. leiorrhizum	+	RH	Luerssen (1875)
P. lingua	+	RH, P	Luerssen (1875)
P. percussum	+	RH, P	Luerssen (1875)
P. vulgare	ST	L	Stevens and Martin (1977)
PTERIDACEAE			
Acrostichum conopodium	+	P	Luerssen (1875)
A. flagelliferum	+	P	Luerssen (1875)
A. lingua	+	P, RH	Luerssen (1875)
Cheilanthus falcatus	+	P	Luerssen (1875)
C. rotundifolius	+	P	Luerssen (1875)
Pteris aquilina	F, ST	P	Mangin (1893)
P. aguilina var. *esculenta*	+	P	Luerssen (1875)

Table 4. *Continued*

Taxon[a]	Type of protuberance[b]	Organ/Tissue[c]	Reference
P. aurita	+	RH, P	Luerssen (1875)
P. longifolia	+	P	Luerssen (1875)
GYMNOSPERMS			
ARAUCARIACEAE			
Agathis australis	ST	W	Bolton *et al.* (1975)
A. robusta	ST	W	Bolton *et al.* (1975)
A. vitiensis	ST	W	Bolton *et al.* (1975)
Araucaria angustifolia	ST	W	Bolton *et al.* (1975)
A. cunninghamii	ST	W	Bolton *et al.* (1975)
CYCADACEAE			
Cycas revoluta	W	P	Mangin (1893)
PINACEAE			
Picea abies	SC, S	B	Parameswaran (1976)
Tsuga canadensis	W	L	Fisher and Dengler (1977)
ZAMIACEAE			
Macrozamia spiralis	SC	L	Carr *et al.* (1980b)
ANGIOSPERMS: DICOTYLEDONS			
AMARANTHACEAE			
Iresine brilliantissima	ST	L	Carr *et al.* (1980a)
APIACEAE			
Daucus carota	W	R	Davies and Lewis (1981)
Oenanthe aquatica	ST	L	Heide-Jørgensen (1978)
APOCYNACEAE			
Carissa grandiflora	W	L	Poulsen (1917)[d]
AQUIFOLIACEAE			
Ilex aquifolia	SC	L	Carr *et al.* (1980b)
ARALIACEAE			
Fatsia japonica	W?	P	Kisser (1928)
ASCLEPIADACEAE			
Araujia sericofera	SC	L	Carr *et al.* (1980b)
ASTERACEAE			
Anthanasia parvifolia	ST	L	Heide-Jørgensen (1978)
Argyroxiphium caliginii	SO	L	Carlquist (1957)
A. grayanum	SO	L	Carlquist (1957)
A. sandwichense	W	L	Carlquist (1957)
A. virenscens	SO	L	Carlquist (1957)
Fitchia speciosa	W	ST, SE, P	Carlquist (1956)
Helianthus annuus	SC	L	Carr *et al.* (1980a)
Petasites hybridus	SC	L	Carr *et al.* (1980b)
Wyethia ovata	W	S	Carlquist (1956)
BERBERIDACEAE			
Berberis vulgaris	SC	L	Carr *et al.* (1980b)
BETULACEAE			
Betula pendula	SC, W	L	Matyssek *et al.* (1991), Scheidegger *et al.* (1991)
BRASSICACEAE			
Kohlrabi sp.	W	T	Vochting (1908)[d]
BUXACEAE			
Buxus sempervirens	W?	L, P	Kisser (1928)

Table 4. *Continued*

Taxon[a]	Type of protuberance[b]	Organ/Tissue[c]	Reference
CHENOPODIACEAE			
Atriplex spongiosa	SC	L	Troughton and Donaldson (1972), Carr and Carr (1975)
ERICACEAE			
Arctostaphylos officinalis	W?	L, P	Kisser (1928)
Erica vestita	W?	L, P	Kisser (1928)
Rhododendron indicum	W?	L, P	Kisser (1928)
EUCRYPHIACEAE			
Eucryphia sp.	SC	L	Carr *et al.* (1980b)
EUPHORBIACEAE			
Euphorbia wulffeni	SC	L	Carr *et al.* (1980b)
FABACEAE			
Baptisia exaltata	+	S	Schips (1983)
Ervum lens	+	S	Schips (1983)
Trigonella foenum-graecum	+	S	Schips (1983)
Vicia faba	ST	L	Carr *et al.* (1980a), Schips (1893)
GESNERIACEAE			
Saintpaulia ionantha	SC	L	Carr *et al.* (1980b)
HIPPOCASTANACEAE			
Aesculus hippocastanum	W	C	Losch (1916)
ICACINACEAE			
Apodytes sp. nov. B	W	L	Present study
Cassinopsis ilcifolia	W	L	Present study
Cassinopsis tinifolia	W	L	Present study
LENTIBULARIACEAE			
Pinguicula vulgaris	SC	L	Carr *et al.* (1980b)
LOGANIACEAE			
Buddleja davidii	SC	L	Carr *et al.* (1980b)
MYOPORACEAE			
Myoporum insulare	SC	L	Carr *et al.* (1980b)
MYRTACEAE			
Eucalyptus gomphocephala	ST	L	Carr and Carr (1975)
E. gummifera	ST	L	Carr *et al.* (1980b)
E. wandoo	ST	L	Carr and Carr (1975)
NYMPHAEACEAE			
Nuphar luteum	W	C	Van Alten (1910)
OLEACEAE			
Ligustrum lucidum	W	L	Poulsen (1917)[d]
L. ovalifolium	W?	L, P	Kisser (1928)
Olea curopaea	SC	L	Carr *et al.* (1980b)
ONAGRACEAE			
Fuchsia hybrida	ST	L	Carr *et al.* (1980a)
PLANTAGINACEAE			
Plantago media	SC	L	Carr *et al.* (1980b)
POLYGONACEAE			
Muehlenbeckia adpressa	SC	L	Carr *et al.* (1980b)
PROTEACEAE			
Hakea suaveolens	ST	L	Heide-Jørgensen (1978)

Table 4. *Continued*

Taxon[a]	Type of protuberance[b]	Organ/Tissue[c]	Reference
RANUNCULACEAE			
Aconitum gracile	W?	L, P	Kisser (1928)
A. haematum	W?	L, P	Kisser (1928)
A. napellus	W?	L, P	Kisser (1928)
A. neomontanum	W?	L, P	Kisser (1928)
A. paniculatum	W?	L, P	Kisser (1928)
A. strictum	W?	L, P	Kisser (1928)
A. virgatum	W?	L, P	Kisser (1928)
Anemone hepatica	W?	L, P	Kisser (1928)
Helleborus abchasicus	W?	L, P	Kisser (1928)
H. atrorubens	W?	L, P	Kisser (1928)
H. corsicus	W?	L, P	Kisser (1928)
H. cyclophyllus	W?	L, P	Kisser (1928)
H. dumetorum	W?	L, P	Kisser (1928)
H. foetidus	W?	L, P	Mangin (1893), Kisser (1928)
H. intermedium	W?	L, P	Kisser (1928)
H. kochii	W?	L, P	Kisser (1928)
H. macranthus	W?	L, P	Kisser (1928)
H. multifidus	W?	L, P	Kisser (1928)
H. niger	W?	L, P	Kisser (1928)
H. occidentalis	W?	L, P	Kisser (1928)
H. odorus	W?	L, P	Kisser (1928)
H. purpurascens	W?	L, P	Kisser (1928)
H. vesicarius	W?	L, P	Kisser (1928)
H. viridis	W?	L, P	Kisser (1928)
ROSACEAE			
Eriobotrya japonica	W?	L, P	Kisser (1928)
Prunus persica	W	F	Reeve (1959b)
Pyrus malus	W	L	Carr *et al.* (1980b)
RUTACEAE			
Dictamnus albus	W?	L, P	Kisser (1928)
SAXIFRAGACEAE			
Saxifraga cartilaginea	W?	L, P	Kisser (1928)
S. cotyledon	W?	L, P	Kisser (1928)
S. hypnoides	W?	L, P	Kisser (1928)
S. geum-haworthii	W?	L, P	Kisser (1928)
S. sarmentosa	W	L, P	Kisser (1928)
SOLANACEAE			
Lycopersicon esculentum cv.	W	C	Jeffree and Yeoman (1983)
TAXACEAE			
Taxus baccata	W	L	Mangin (1893)
THYMELAEACEAE			
Daphne laureola	W?	L, P	Kisser (1928)
D. mezereum	W?	L, P	Kisser (1928)
VERBENACEAE			
Avicennia marina	SC	L	Carr *et al.* (1980b)
VISCACEAE			
Viscum album	W?	L, P	Kisser (1928)

Table 4. *Continued*

Taxon[a]	Type of protuberance[b]	Organ/Tissue[c]	Reference
VITACEAE			
Vitis vinifera	W	P	Mangin (1893)
ANGIOSPERMAE: MONOCOTYLEDONS			
AGAVACEAE			
Yucca filamentosa	W?	L, P	Kisser (1928)
Y. gloriosa	W?	L, P	Kisser (1928)
AMARYLLIDACEAE			
Narcissus pseudonarcissus	SC	L	Carr *et al.* (1980b)
ARACEAE			
Arum maculatum	W?	L, P	Kisser (1928)
A. sanctum	SC	L	Carr *et al.* (1980b)
ARECACEAE			
Cocos nucifera	W, F	S	Butterfiels *et al.* (1981), Scheidegger *et al.* (1991)
Phoenix dactylifera	W	RE	Jost (1887)
P. farinifera	W	RE	Jost (1887)
Rhophalostylis sapida	F	L	Butterfield *et al.* (1981)
COMMELINACEAE			
Callisia fragens	ST	L	Stevens and Martin (1977)
Commelina communis	ST	L	Stevens and Martin (1977)
Palisota barteri	ST	L	Stevens and Martin (1977)
Tradescantia pallida	ST	L	Stevens and Martin (1977)
T. virginiana	ST	L	Stevens and Martin (1977)
ERIOCAULACEAE			
Paepalanthus sp.	W	L	Poulsen (1888)[d]
LILIACEAE			
Scilla bispanicus	SC	L	Carr *et al.* (1980a)
ORCHIDACEAE			
Cephalanthera rubra	F	RE	Noack (1892)
Epipactis latifolia	F	RE	Noack (1892)
E. palustris	F	RE	Noack (1892)
E. rubescens	F	RE	Noack (1892)
Paphiopedilum bellatulum	W	L	J.R. Lawton (pers. com. 1991)
P. insigne	W	L	J.R. Lawton (pers. com. 1991)
P. lawrenceanum	W	L	Lawton and Coetzee (1991)
POACEAE			
Bambusa sp.	SC	L	Carr *et al.* (1980b)

[a]Species names unchanged, except for correction of obvious typographical errors. No attempt has been made to resolve the nomenclature of the taxa mentioned in the original reports (therefore names not necessarily currently in use). Older reports rarely mention the placing of voucher specimens in herbaria. Hence it is impossible to know the exact taxon in question. Families for ferns and gymnosperms follow Kramer and Green (1990). Spelling of generic names follows Mabberley (1987). Family placement for angiosperms is based on Dahlgren (1980) and Dahlgren & Clifford (1982).

[b]F=filaments; SC=scalae; SO=sol; ST=strands; W=warts; +=present (type ambiguous/not specified). Only predominant state(s) listed.

[c]C=callus; F=fruit; L=leaf/frond; P=petiole; R=root; RE=aerial root; RH=rhizome; S=seed; SE=seedling; ST=stem; T=tuber; W=wood; +=present (organ/tissue not specified).

[d]Information from Kisser (1928).

as a single morphological category, are not useful in assessing taxonomic relationships, except that the shared ability to produce intercellular pectic protuberances might reflect a former common ancestry for the major groups of vascular plants.

If different morphological types of pectic protuberances had been plotted in Figs. 5 & 6, would this have given rise to a different pattern? Unfortunately, in most cases the information available on pectic protuberances is too vague to unequivocally assign them to a particular morphological class. Moreover, Kisser (1928), in his review on the subject, described all pectic protuberances reported at that stage as "Pektinwarzen", including some known to be filaments and strands. Despite the scanty morphological evidence, there seems to be a tendency for the distribution of filaments to be concentrated in the ferns and monocotyledons, but the phylogenetic significance of this observation can not yet be adequately assessed. There is clearly a need to reinvestigate most of the species included in Table 4, and to classify their pectic protuberances into more homogeneous (and hopefully homologous) structural and chemical categories.

Kisser (1928) cautiously concluded that pectic protuberances might be of taxonomic value at the specific and generic levels, but stressed the need for the investigation of many more taxa. Whereas protuberances were present in all but one of the 16 species of *Helleborus* L. (Ranunculaceae) he investigated, they were absent in members of the related genera *Coptis* Salisb. and *Eranthis* Salisb. Carlquist (1956) noted that pectic warts (and for that matter, intercellular projections) have been repeatedly demonstrated in certain species, indicating that these structures are characteristic of certain taxa and do not represent a random development. This is supported by our observation that in members of the Icacinaceae the presence/absence of pectic protuberances are constant for a species. It would, however, seem that species with pectic protuberances do have a propensity for either scalae, strands, warts, or filaments to be exclusively or predominantly present at the mature stage. The reason for this remains unknown, but it is most likely due to differences in the physico-chemical properties of the pectinous material. Carr *et al.* (1980b) also suggest that pectic scalae are likely to occur in leaves of those species in which a regular palisade layer is formed, irrespective of taxonomic affinity or ecological preference. It seems that, although the mere presence/absence of intercellular projections are, as a rule, not of any taxonomic significance at the family or higher level, they do have diagnostic value at the species and possibly genus, level. In Hawaiian Asteraceae, amorphous intercellular pectic secretions have proved to be of systematic value in distinguishing *Wilkesia* A. Gray from *Argyroxiphium* DC. (Carlquist, 1957).

It is a mystery why only some species, and not all, have intercellular pectic projections. In addition to possible differences in the chemical composition of the pectin (particularly the relative abundance of the pectic polysaccharides PGA, RG-I, and RG-II), the explanation might lie in the fact that the amount of pectin relative to other cell wall components may differ substantially between taxa (Thornber and Northcote, 1961; Milton, 1991). It would be informative to have quantitative data to be able to compare the amount of pectin produced by plants with intercellular protuberances with those in which these structures are absent.

Function of Intercellular Pectic Protuberances

Carlquist (1956) remarked that it is very likely that these structures have no significant function, because of their composition and the mode in which they occur. In this connection Heide-Jørgensen (1978) considers it a casual structure of no harm to the plant, produced as a mechanical consequence of intercellular space formation. If these protuberances have any biological function, it is still merely speculative.

Noack (1892) suggested an absorptive function for the intercellular "slime" strands of orchid roots. Majumdar and Preston (1941) contend that intrusion of pectic material into intercellular spaces constitutes the first stage in the development of collenchyma thickening. One of the most often cited functions is that of involvement in the adhesion of cells, by forming bridges between adjacent cells. Davies and Lewis (1981) suggest that the protuberances associated with multi - vesiculate bodies ("lomasomes") may be involved in the secretion of an oily water-impermeable barrier at the surface of wound callus cells in *Daucus carota,* or be engaged in suberization or defence. Regarding the latter aspect, pectic materials have well-established roles in many types of host-parasite interactions (e.g. Zhang *et al.*, 1990 and references therein).

The hydrophilous nature of pectins has led to the suggestion that the pectic component of the cell wall

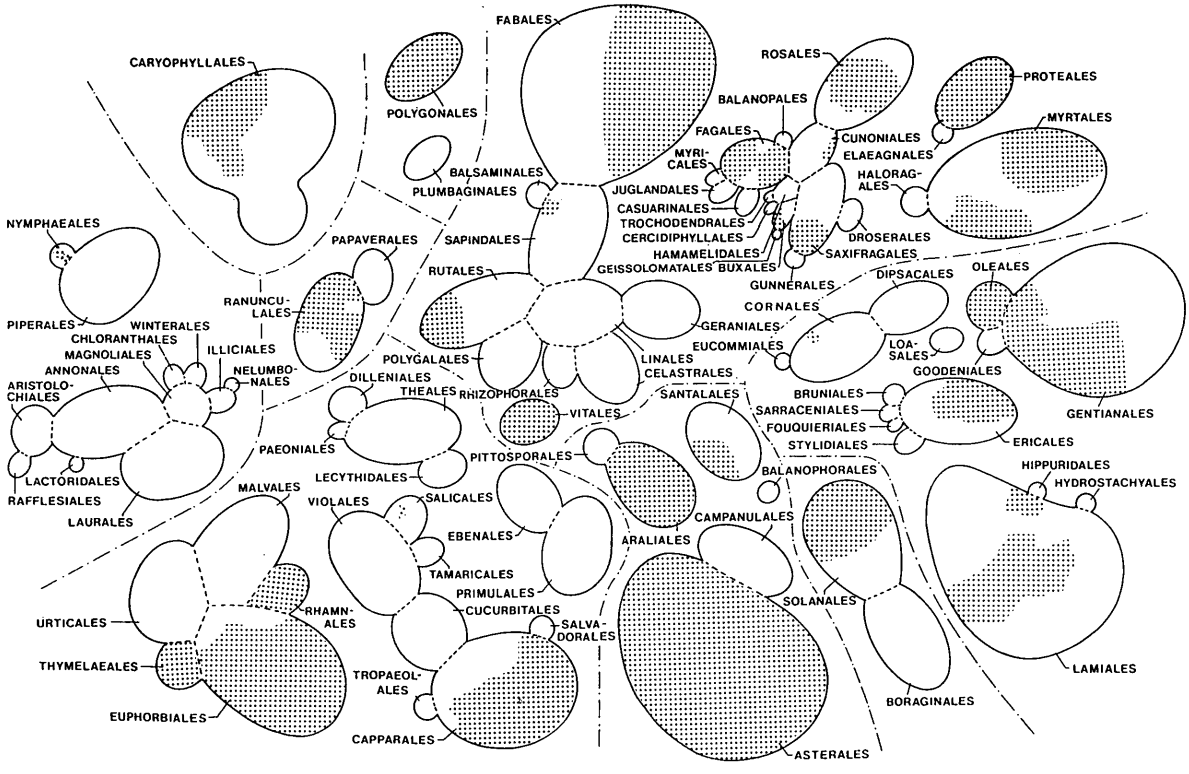

Fig. 5. Known distribution of intercellular pectic protuberances (presence indicated by dots) among dicotyledonous families. Position of families and orders follows Dahlgren (1989, 1991).

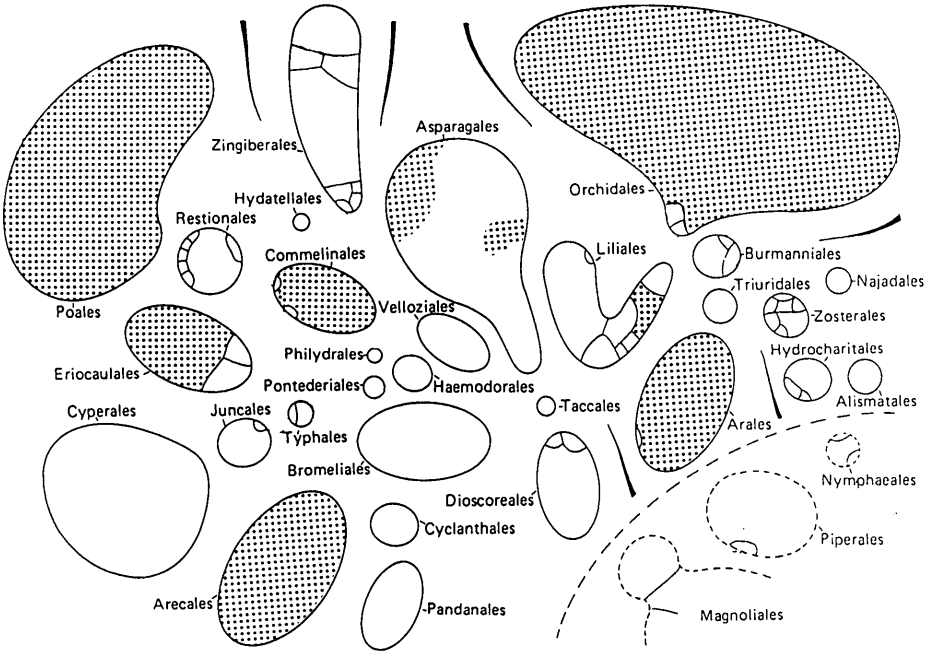

Fig. 6. Known distribution of intercellular pectic protuberances (presence indicated by dots) among monocotyledonous families. Position of families and orders follows Dahlgren and Clifford (1982).

may passively regulate the hydration of the wall according to the ecological availability of water (Frey-Wyssling, 1976). Pectic strands could also have an effect on lateral water conduction, as they enlarge the surface area of the cell wall. Carr *et al.* (1980b) consider it possible that pectic strands function in providing an apoplastic pathway for ionic movement, particularly of potassium ions. It is also likely that the strands have transport and storage roles for potassium (Carr *et al.*, 1980b). Heide-Jørgensen (1978) notes that pectic strands may have some value in lateral water conduction within the mesophyll. As pectic warts do not stretch between cell walls, it is unlikely that this type of protuberance is significantly involved in conduction or adhesion.

It is also plausible that these pectic structures may store carbohydrates or other substances. It is generally accepted that at least some cell-wall polysaccharides function as reserves in vegetative tissue, the catabolism of such polysaccharides contributing to processes such as resynthesis of cell-wall components and respiration (Labavitch, 1981; Brinson and Dey, 1985).

Conclusions

Hitherto nearly all tests indicate that intercellular wall protuberances in plants are predominantly pectic in composition. Morphologically, four major categories of pectic protuberances are evident: scalae, strands, warts, and filaments. Development of these structures is usually associated with the formation of intercellular spaces. Our own observations on members of the Icacinaceae strengthen the notion that pectic strands and scalae form as a consequence of intercellular space formation. In this family, pectic warts develop as a consequence of the snapping and retraction of stretched pectic strands during tissue expansion.

Intercellular pectic protuberances are of widespread occurrence among vascular plants. Their seemingly erratic distribution at higher taxonomic levels suggests that these structures have little or no taxonomic significance at and above the family level. It must, however, be emphasized that protuberances showing morphological resemblance may not necessarily be anatomically, ontogenetically, or chemically similar. In view of the very scanty available information, we might well be comparing non-homologous structures.

Although few studies comment on infraspecific variability in the occurrence and distribution of pectic protuberances, available evidence supports their diagnostic value at the species level. Indications are that the presence/absence of pectic protuberances might also be constant for some genera. There is nevertheless a need for more anatomical surveys to assess natural variability at these lower taxonomic levels.

After more than a hundred years of investigation, and despite the use of increasingly sophisticated techniques, the precise biological function, if any, of intercellular pectic protuberances still eludes us. Likely hypotheses would include involvement in aspects such as apoplastic transport, cell-wall hydration, carbohydrate storage, cell adhesion, or a role in defence against pathogens. There is a need for experimental data to test these hypotheses.

Progress in the chemistry and physiology of the so-called extracellular matrix has been very slow. The growing realization that there are often striking chemical and quantitative differences in cell wall components between different groups of plants, and the recent discovery of several macromolecules which are preferentially localized to intercellular spaces (reviewed by Roberts, 1990), offers considerable prospects for future comparative research. This will hopefully contribute to a better understanding of the composition, function, and taxonomic significance of what are currently rather crudely identified as intercellular pectic protuberances.

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植物的細胞間果膠突起之構造與分類意義

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以廣泛的文獻調查爲基礎，我們對維管束植物的細胞間果膠突起 (IPP) 的發育、結構、組織化學、分布及功能做了回顧。根據我們對 Apodytes(柴龍樹屬)和 Cassinopsis 葉片材料之詳細解剖研究，本文並首次報導茶葉茱萸科植物的此類構造，作爲補充的資料。IPP 的發育通常和組織在擴展時細胞間隙的形成有關。IPP 可依形態而明顯區別爲四類：梯形、束狀、瘤狀、和絲狀。本文對於各種形態 IPP 的發生步驟提出見解。大量的果膠產生可以導致果膠體的形成，而局部或完全地充滿細胞間隙。雖然組織化學的試驗顯示細胞間壁突起在成份上是以果膠爲主，更深入的化學研究則尚闕如。IPP 不規則地分布於蕨類植物，裸子植物，集子葉和單子葉植物。本文列舉 200 種以上經報導具 IPP 的植物，雖然 IPP 在種或者有時候屬的類階上通常是好的分類性狀，但在科和目的類階則因多變異而嚴重地限制其分類價值。IPP 的普遍性分布和多變的形態顯示他們的多源性，因此在不同的植物類羣並非同源。如果僅就 IPP 的有無做爲單一的分類標準，來評估分類羣關係是行不通的；若分開來看，絲狀形者主要集中於蕨類植物和單子葉植植物。可惜的是，關於 IPP 的研究尚未進展到足以提供一幅完整的圖案，還有相當多的空白有待填充。關於 IPP 在生物學上的功能：包括非原質體的運輸、細胞壁的水合作用、儲藏(如碳水化合物，鉀)、細胞的粘連、及抗病作用等多屬臆測，並無法排除他們沒有特定功能的可能性，有關其功能的任何說法皆乏實驗證據。