ON THE OCCURRENCE OF INTERCELLULAR PECTIC WARTS IN COMPOSITAE [1]

Sherwin Carlquist [2]

IN A NUMBER of vascular plants, protuberances of various shapes characteristically occur on the outer surface of parenchyma cell-walls facing intercellular spaces. As the review of Kisser (1928) shows, these structures have been demonstrated in stem, petiole, or lamina of various ferns and of a small number of Equisetaceae, Cycadaceae, Taxaceae, and Angiospermae. They have been found also in aerial roots of orchids (Noack, 1892) and palms (Jost, 1887) and in the seed coats of Leguminosae (Mattirolo and Buscalioni, 1889). Kisser (1928) was unable to find any of these structures, which he terms "Pektinwarzen" on account of their chemical composition, in the Compositae he investigated. During a survey of the anatomy of the genus *Fitchia* and other members of the tribe Helianthеae (Compositae), the writer encountered such pectic warts in certain tissues of *Fitchia speciosa* Cheeseman and *Wyethia ovata* T. & G. Because these pectic warts represent a new record and differ in several respects from those described by Kisser and others, a description of these, together with photomicrographs—seemingly the first published of pectic warts—appeared desirable. Although inconspicuous and perhaps rare in vascular plants, intercellular pectic warts represent a neglected phenomenon which requires explanation by students of cell wall structure.

MATERIALS AND METHODS.—Vegetative material of *Fitchia speciosa (Carlquist H29*[3]*)*, was fixed in a Carnoy's fluid (3 parts absolute ethyl alcohol: 1 part glacial acetic acid). Material of *Wyethia ovata (Carlquist 398*[3]*)*, was fixed in formalin-propionic-alcohol (Johansen, 1940, p. 42). For infiltration and embedding of both species, the tertiary butyl alcohol series of Johansen (1940, p. 130) was used. The sections of *Fitchia speciosa* (fig. 1–4) were stained by the tannic acid-ferric chloride schedule of Foster (1934). For sections of *Wyethia ovata*, a safranin-fast-green combination corresponding to Northen's modification of Foster's tannic acid-ferric chloride method (Johansen, 1940, p. 92) was employed. Although the dehydration entailed by the above microtechnical methods tends to shrink structures rich in pectic materials, comparison of fresh material with paraffin sections of *Wyethia ovata* revealed no appreciable differences. It seems likely that the swelling tendency of the weak acids employed in fixation may have compensated for the shrinking effect of the alcohols employed. That the structures reported here are indeed pectic in nature was demonstrated by application of microchemical tests. Pectic warts stained deeply with Ruthenium red and failed to stain with zinc chloride-iodine. Treatment with warm 0.5 per cent ammonium oxalate dissolved these structures.

DISTRIBUTION AND CHARACTERISTICS.—In *Fitchia speciosa*, pectic warts are abundantly developed in intercellular spaces of the petioles of adult leaves. They are most frequent in the middle portion of the length of the petioles, being scarce or completely absent toward the base of the petiole or near the lamina. A transection of a petiole taken approximately halfway between lamina and base (fig. 1) reveals a prominent outer cylinder of collenchyma, interrupted in places by spongy photosynthetic tissue underlying stomata (fig. 1, right). Toward the interior of the collenchyma are large intercellular spaces in which conspicuous pectic warts appear. Although thin-walled parenchyma with large intercellular spaces occurs in the center of the petiole, no pectic warts are found in that region. Thus, pectic warts in the petiole of *Fitchia speciosa* are restricted to the intercellular spaces adjacent to cells showing collenchymatic thickening. Ontogenetically, these warts appear only after development of intercellular spaces. The studies of Kisser (1928) on the development of pectic warts in spongy parenchyma of *Saxifraga sarmentosa* leaves showed increase in wart size and number during leaf enlargement. In *Fitchia speciosa*, on the contrary, size and number of warts seem primarily dependent on the thickness of the wall on which they occur. As fig. 2–4 show, numerous small warts (fig. 3) or fewer and larger protuberances (fig. 4) may be seen in the same petiole. Thin walls have numerous small warts (fig. 3) while relatively thick walls possess larger warts (fig. 4) which may fuse into coralloid structures often forming bridges across intercellular spaces. In their most extreme development, as shown in fig. 4 (lower left), such pectic intrusion may partially or entirely fill an intercellular space. There is an ontogenetic increase in deposition of pectic material during maturation of the petiole. In the nearly-occluded intercellular spaces, deposition of material keeps pace with increase in size of intercellular spaces. The smaller warts on thinner walls appear only after intercellular spaces have become prominent. During petiole elongation, the globular shape of warts is retained, with only the tapered basal portion of the wart (fig. 3, 4) evidencing the elongation of the underlying cell wall.

In their large size and extensive development, the petiolar pectic warts of *Fitchia speciosa* find a parallel, among plants in which this phenomenon

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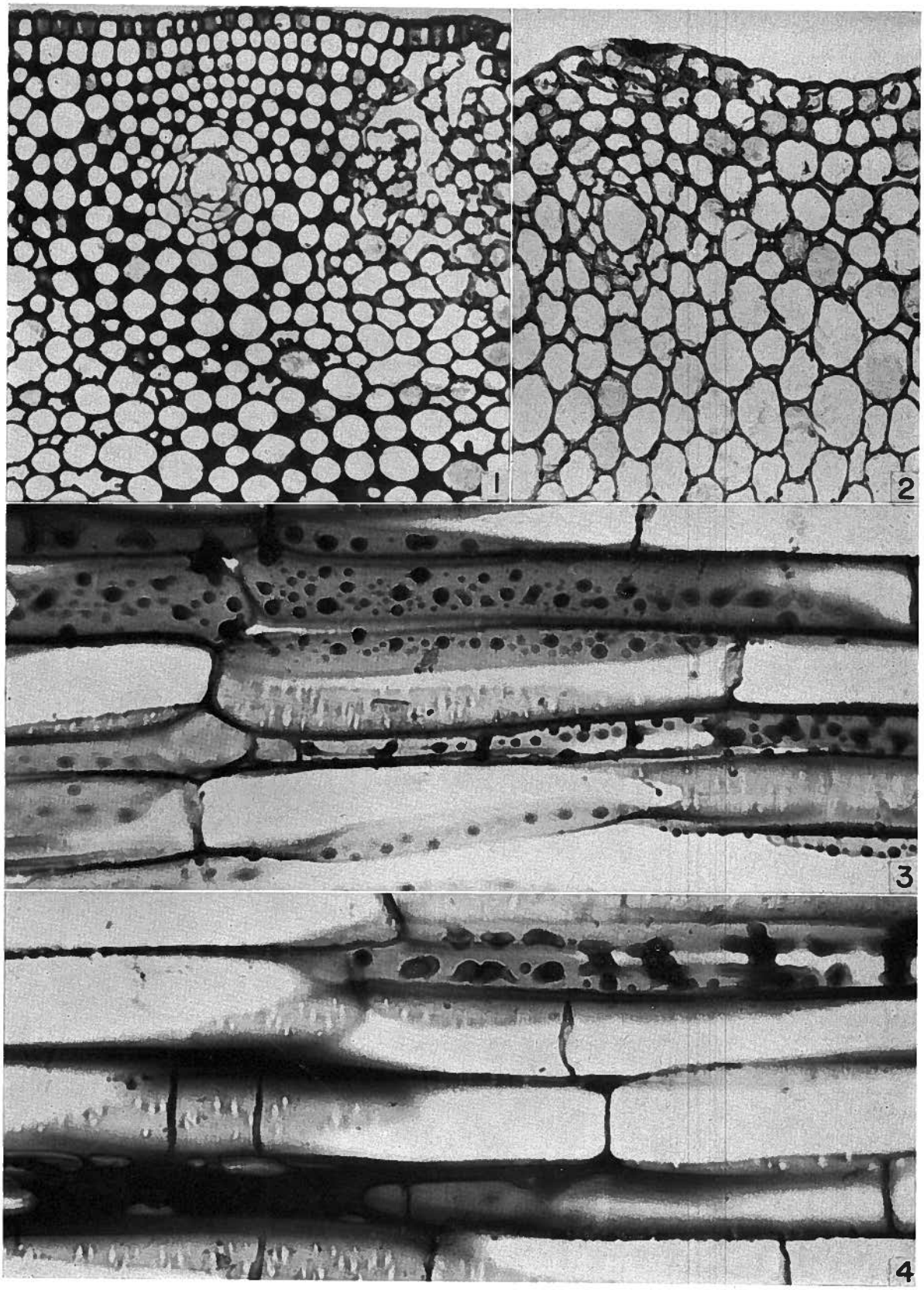
[3] Specimens of these collections have been deposited in the University of California Herbarium, Berkeley.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has been described, only in *Narcissus pseudo-narcissus* (Mangin, 1893), where they occur in the peduncle. In this species, however, they are described by Mangin as being gelatinous and unstable in shape. The tendency toward occlusion of intercellular spaces by pectic intrusions seen in *Fitchia speciosa* has not been found in any of the plants for which pectic warts have been reported.

Elsewhere in the plant body of *Fitchia speciosa*, intercellular protuberances were found only in the outer cortical regions of the seedling hypocotyl (fig. 2). Cells in this region have moderately thick primary walls, though no collenchymatic thickening is present. Protuberances in the form of single bridges across the spaces between cells may be found in this region.

In *Wyethia ovata*, pectic warts were found only along intercellular spaces in outer regions of the stem cortex (fig. 5). Although the cells on which they are borne have moderately thick primary walls, apparently no collenchymatic thickenings are present. These warts are smaller in size than those found in *Fitchia speciosa* petioles, though they have a similar knoblike shape. They appear when the tissues of the primary stem are reaching maturation, and persist during secondary growth. Older stems (fig. 6, 7) show a variety in size and form of such warts. In older stems these structures frequently form prominent bridges across the narrower portions of intercellular spaces. During the marked tangential stretching of cortical cell walls which accompanies secondary growth, the bases of these protuberances become distended (fig. 6) while the bridging connections between cells become strongly attenuated (fig. 7). Pectic warts were not found in stems of *Wyethia helenioides* or *W. angustifolia*.

DISCUSSION.—The information summarized by Kisser (1928) shows that while the morphology and chemical nature of pectic warts seems rather well understood, little is known concerning the systematic distribution of such structures, which have seemingly been overlooked in some plants. Likewise, suggestions as to the function of such structures, if any, or the reasons for their formation, are completely lacking. It seems likely that they have no mechanical function, because of the very plastic nature of their pectic composition and the mode in which they occur. Although they are associated with collenchyma in the petiole of *Fitchia speciosa*, they comprise only a small portion of the pectic wall materials present in this structure. Likewise, their occurrence in the very short "acaulescent" stems of *Wyethia ovata* suggests their lack of a mechanical function. The fact that they have been demonstrated repeatedly in certain species may indicate that they are characteristic of certain plants and do not represent a random development. It seems quite possible, as Kisser (1928) suggests, that different explanations underlie their occurrence in various groups.

Majumdar and Preston (1941) contend that extrusion of pectic materials into potential intercellular spaces constitutes the first stage of development of collenchymatic thickening. If they are correct in their interpretation, the condition shown in petioles of *Fitchia speciosa* could represent an instance in which this stage is greatly protracted. The development of individual warts in this species would be interpreted as an incomplete development of such intercellular space occlusion. Although normal collenchymatic thickening predominates in the petiole of *Fitchia speciosa*, careful examination of thickened areas at the interstices of some cells reveals that moderate wall thickening is present. The intercellular space between such cells has been entirely occluded by centrifugal extrusion of pectic materials, presenting the appearance of normal collenchyma.

Cognizance should be taken that *Fitchia speciosa* is apparently the first plant in which pectic warts have been reported to be associated with true collenchyma. All other instances could be interpreted as expressions of centrifugal pectic deposition accompanied by minimal centripetal deposition. This is opposed to normal primary cell wall formation in which thickening is almost exclusively centripetal. The reason for the pattern of pectic deposition in walls where pectic warts occur remains obscure. It would be of interest to know if extrusion of pectic warts is associated with thinner areas in the cell wall.

SUMMARY

Intrusions of pectic materials into intercellular spaces, forming structures to which the term "pectic warts" is applied here, are reported for the first time in Compositae. In *Fitchia speciosa*, they occur prominently in areas of petiolar collenchyma where large intercellular spaces are present, and less conspicuously in the cortical parenchyma of the seedling hypocotyl. A relation is suggested between size and number of warts and thickness of the wall on which they occur. Relatively smaller warts are found in the cortical parenchyma of *Wyethia ovata* stems. Warts in both species are found to undergo ontogenetic changes in size and shape. A possible relation is suggested between pectic warts, which are a centrifugal deposition, and the report of Majumdar and Preston that

Fig. 1–4. *Fitchia speciosa*.—Fig. 1. Transsection of petiole showing subepidermal collenchyma in which intercellular pectic warts occur; secretory canal above center. × 185.—Fig. 2. Transection of seedling hypocotyl, showing "bridges" across intercellular spaces near center of photograph; secretory canal at left. × 190.—Fig. 3, 4. Longitudinal section through petiole collenchyma. Fig. 3, 4, × 390.

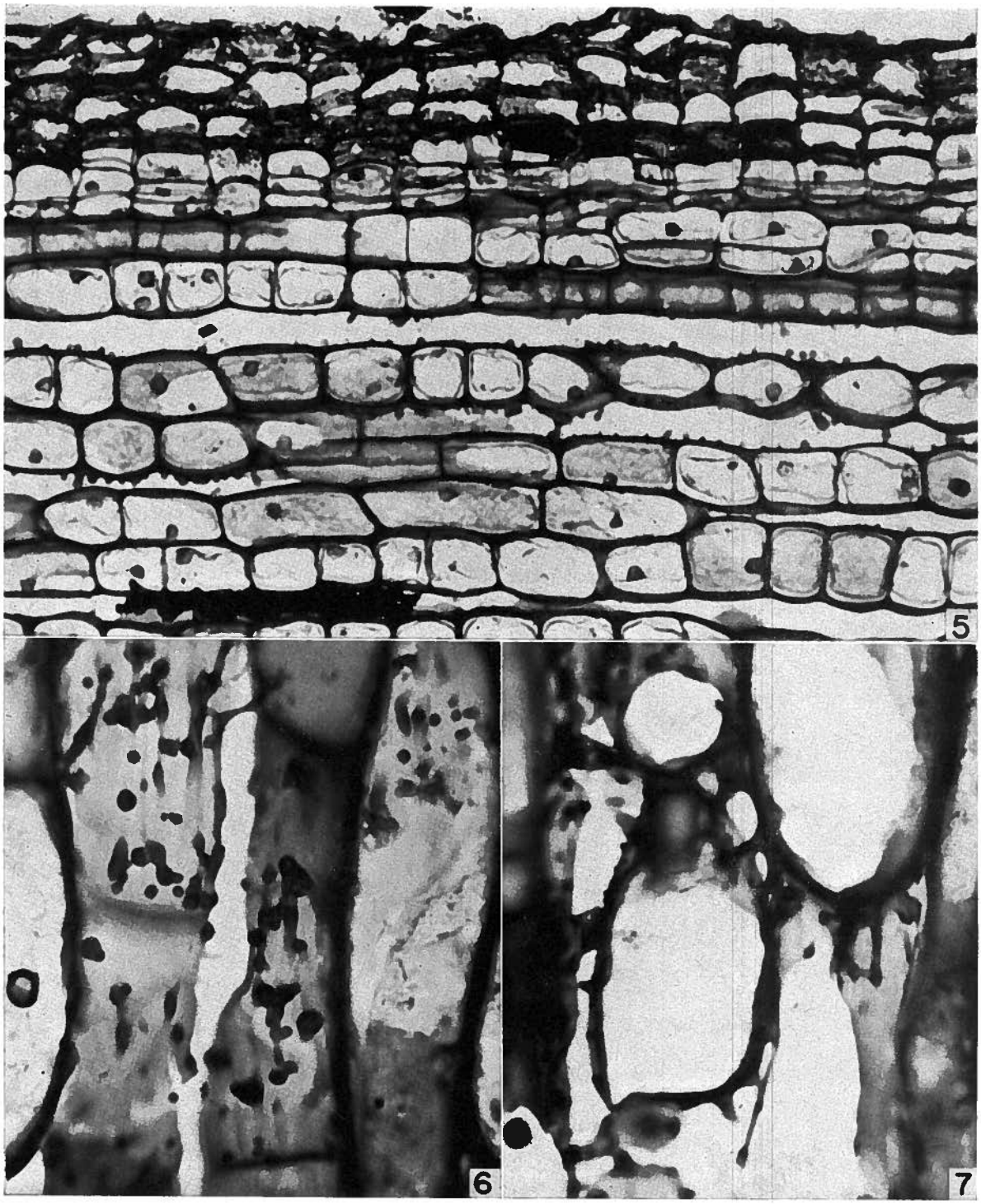

Fig. 5–7. *Wyethia ovata*, sections of stem.—Fig. 5, longitudinal section of a stem with little secondary growth. Periderm above; a carbonized resin deposit is seen in the intercellular space at left, below. × 200.—Fig. 6, 7. Areas from a transverse section of cortex of an older stem, showing pectic structures along the walls facing intercellular spaces. Fig. 6, 7, × 600.

collenchymatic thickening is initiated by filling of potential intercellular spaces by pectic materials. Although pectic extrusion may keep pace with intercellular space development in *Fitchia speciosa*, the phenomenon described here appears to be chiefly a deposition subsequent to the attainment of mature configuration by the primary wall and subsequent to the development of intercellular spaces.

THE CLAREMONT GRADUATE SCHOOL,
AND
DEPARTMENT OF BOTANY,
POMONA COLLEGE,
CLAREMONT, CALIFORNIA

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