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Cecidogenous *Crotonothrips* (Thysanoptera)—*Memecylon* interactions: Host relations, nutritive tissue, tissue dynamics and cecidogenetic patterns

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Abstract. The host relations of *Crotonothrips* with *Memecylon* on the criterion of gall formation appear interesting. In the light of the morphogenetic courses that the susceptible host organ, the leaf, show, an attempt has been made to assess their functional efficiency in terms of structural adaptations envisaging the organisation of a nutritive zone, and tissue dynamics taking *Memecylon edule*, *Memecylon lushingtonii*, and *Memecylon umbellatum* as models.

Keywords. *Memecylon*; *Crotonothrips*; gall; host relations.

1. Introduction

The cecidogenous association between *Memecylon* and *Crotonothrips* (Phlaeothripidae: Tubulifera) appears striking, since *Crotonothrips gallarum*, *C. coorgensis*, *C. dissimilis*, *C. memecylonicus*, and *C. dantahasta* inducing galls, that range from simple epiphyllous rolls to complex rosettes on *Memecylon* sp., *M. talbotianum*, *M. lawsonii*, *M. lushingtonii*, and *M. edule* respectively, are known from southern India (Ananthakrishnan 1976, 1978). Although this kind of a specialised botanical affinity is frequent among gall-thrips (Ananthakrishnan 1980), the intimate relationship of species of *Crotonothrips* with diverse species of *Memecylon* appears to indicate an important phase in host-relationship patterns of cecidogenous insects, essentially because of their basic trait of organising a specialised nutritive guild in the form of a gall. With this in full view, and also to evaluate comparatively the responses of the host plants to thrips in terms of the development of nutritive tissue and its dynamics in relation to cecidogenesis, an attempt is made here to study three representative types from this gall complex, sampling *Memecylon edule* galls caused by *Crotonothrips dantahasta*, *M. lushingtonii* galls made by *C. memecylonicus*, and *M. umbellatum* galls caused by an undetermined species of *Crotonothrips*. Galls of *M. edule* have been considered here because of their easy availability through the year locally, and the other two represent morphological extremes: *M. umbellatum* galls being simple rolls; *M. lushingtonii* galls being complex rosettes.

2. Materials and methods

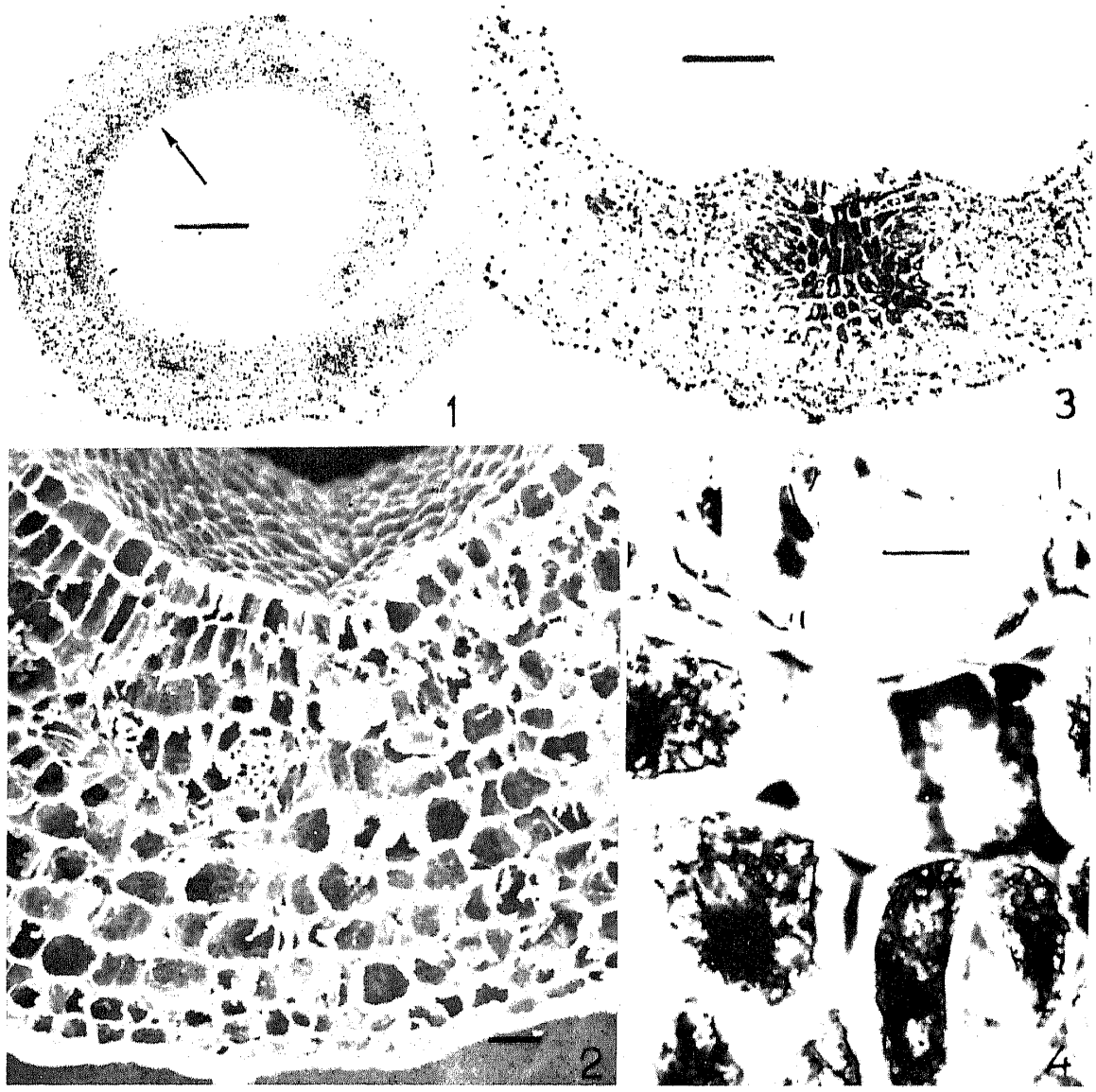
The materials were obtained from different localities of Tamil Nadu; *M. edule* from the plains of the city of Madras (MSL *ca*), and *M. lushingtonii* and *M. umbellatum* from higher elevations (Kolli Hill Ranges, Salem District, Tamil Nadu; 800 m *ca*) during

monsoon season (September–October 1984). The galls obtained in different developmental stages were graded considering the age of the gall-susceptible leaf and approximate population counts of the inhabiting thrips species, and were fixed in FAA. Through customary methods of dehydration, wax-embedding, cutting (6–8 μm), and staining with methylene blue-safranin combination, the material was prepared for microscopy. Unstained micropreparations were also made for observation under the phase contrast system. Necessary histochemical localisations have been made to confirm some of the observations (details indicated under Observations, wherever necessary). Scanning electron microscopy was also used, following the usual methods of critical point drying (using a Hitachi C. P. Drier), coating with gold, and observing in a Scanning Electron Microscope (Hitachi S-415) system at 15 KvA.

3. Observations

3.1 *Memecylon edule*

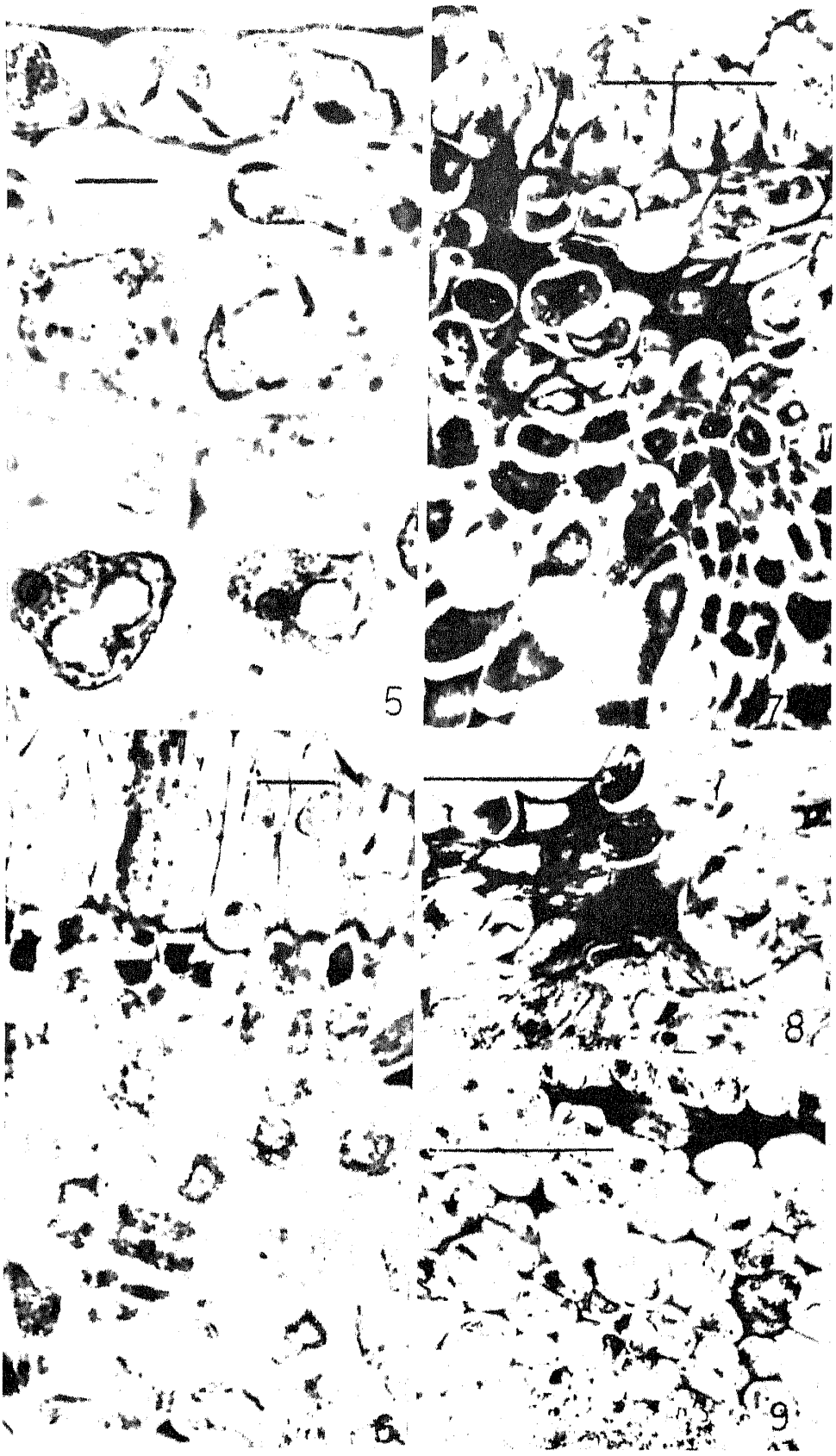
Crotonothrips dantahasta induce epiphyllous roll galls along the developing leaves of *M. edule*. On maturation (about 30 days), the galls become more pronounced with an enormous increase in the thickness of the gall-wall and a number of vertical infoldings, presenting a corrugated appearance. Both laminar halves roll tightly and independently on themselves towards the midrib. In young galls (2–3 days) thrips feed on specific areas along the upper side of the lamina closer to vascular traces (figures 1 and 2). The initial feeding impact involves the rupturing of 1–2 epidermal cells, and the resultant wounding stimulates a few surrounding epidermal cells and the immediate subjacent cells of the differentiating mesophyll to become metaplastic (figure 3); these cells show dense cytoplasm, characteristic of nutritive cells. The differentiation of these functionally specialised nutritive cells is of characteristic pattern that they are localised, involving only a few epidermal cells and 2–3 layers of cells lying immediately below (figure 4). These cells occurring along the direct line of feeding impact of thrips show abundant cytoplasm with numerous agglomerating vacuoles, and hypertrophied nuclei and nucleoli. The walls of these cells are abnormally and unevenly thickened with many irregular infoldings that occasionally show branching as well (figure 5). They do not appear to be of lignin (phloroglucinol test; Johansen 1940); the layers of these walls are shiny and crystalline under normal (figure 14) and phase contrast (figure 15) microscopy, but display characteristic striations and layering in their organisational patterns (figure 17). Not only hypertrophy and hyperplasia are well-manifest in the gall regions of the lamina, but also the total inhibition of differentiation of a dorsi-ventral leaf with 2 layers of palisade tissue and 5 layers of spongy mesophyll. The cells coming directly under the feeding stimulus of thrips show hypertrophy in the vertical axis, and these appear to arise from the primordial palisadic and epidermal cells. The succeeding layers of cells (5th-9th layers) of the upper mesophyll origin are hypertrophied more or less isodiametrically and display meristematism (figure 6). At this stage of gall development, the underlying 4th and 5th layers of cells show greater cytoplasmic specialisation than the cells lying above, suggesting the extension of the nutritive function to the underlying areas of the differentiating blade (figure 5). The lower spongy mesophyll contribute to the two layers of the lower gall lamina, that retain more or less their normal contour. Interestingly, the wall thickness of these cells is varying that the epidermal cells (1st layer) show 3–4 μm thickness; the second layer of nutritive



Figures 1–4. *Memecylon edule*; young gall (2–3 days old). **1.** T. S. Nutritive tissue (arrow) (bar = 200 μm). **2.** Stereoscan profile (bar = 100 μm). **3.** Differentiating nutritive tissue (bar = 100 μm). **4.** Feeding injury and nutritive tissue—enlarged (bar = 10 μm).

cells show 4–5 μm thickness while the third layer, with a remarkable drop to 1–2 μm, that gradually increases from the 4th layer onwards to 4 μm till the lower epidermis. In spite of this specific pattern in the thickness of wall in the nutritive and other mesophyll tissues nearer the feeding area, increase in wall thickness seems to be a general alteration in the morphogenetic gradient of the gall-susceptible leaf. This appears significant primarily because abnormally thick cell walls are evident even in non-gall regions of the leaf (figure 19), that show no other specific change except this.

The division patterns and the hypertrophy initiated by the feeding stimulus of thrips are so very characteristic that active division centres radiate in a vertical line till the mid-region of the gall mesophyll; at this point, this line takes a dialatory course that shows a 'fork'ing pattern extending upto the lower epidermis (figure 7). The neighbouring areas of this active meristem line are supported on either side (as in transverse sections) by



Figures 5–9. *Memecylon edule* gall (5–7 days old). **5.** Nutritive tissue very close to feeding injury area (subcellular specialisation evident) (bar = 10 μm). **6.** Lateral area of the nutritive area showing intense division activity (bar = 10 μm). **7.** Nutritive tissue showing part of the 'fork' as the stress region (bar = 50 μm). **8.** Necrosed zone—vertical pattern (bar = 50 μm). **9.** Necrosed zone—horizontal pattern (bar = 50 μm).

hypertrophy of mesophyll cells as well as of those at the farther regions of the gall mesophyll, i.e., beneath the 'fork'. The further growth of the gall is in conformity to this initial morphogenetic canalisation as regulated by the dissimination of the cecidogenetic gradient that originates at the feeding point—a region of constant injury and irritation. A weak but well-coordinated meristem gradient operates around the feeding site, contributing cells for upward growth, which is a distinct feature of this gall.

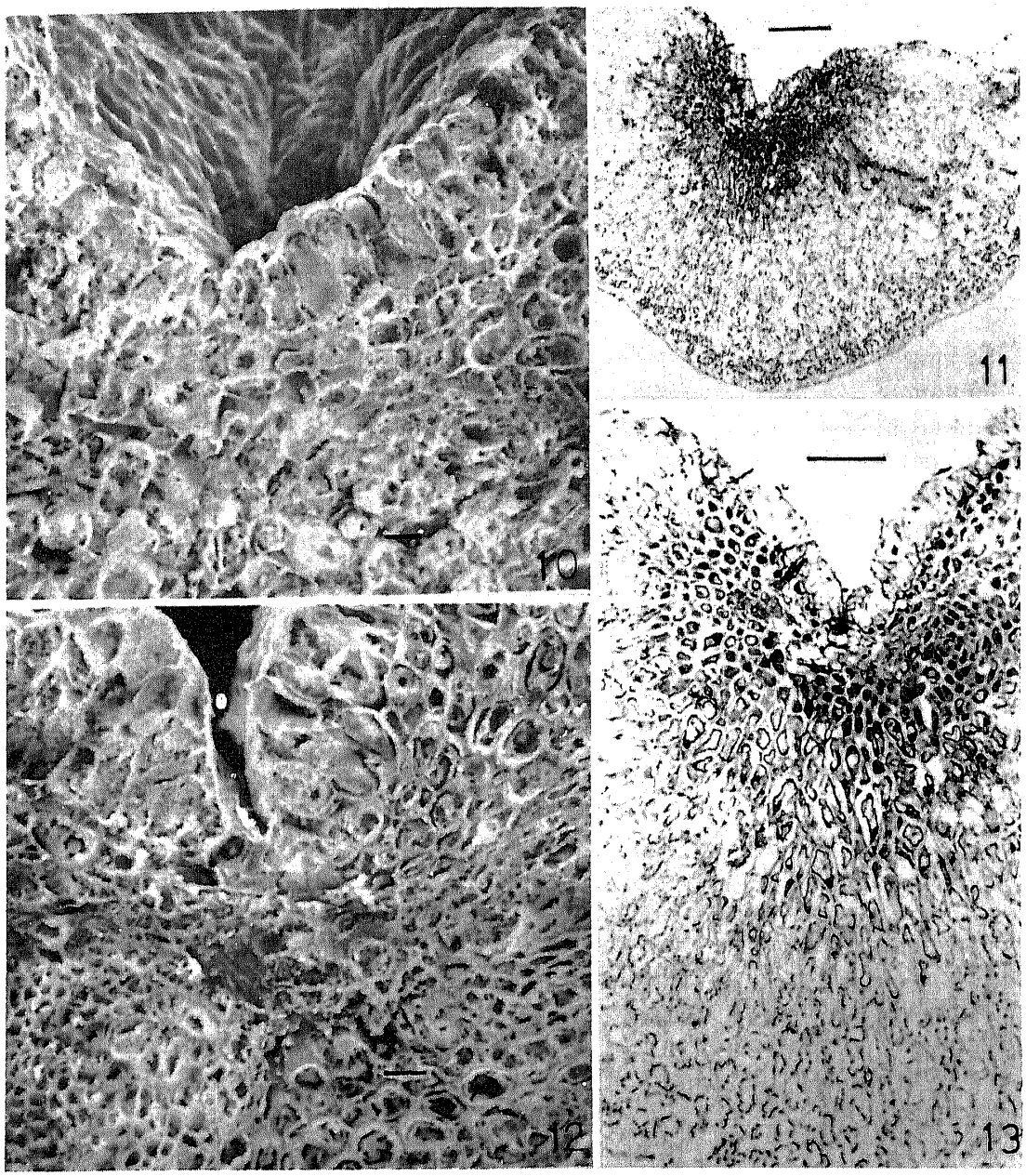
With ageing (6–9 days), the nutritive cells accumulate flavonolic and tanniniferous products as crystalline inclusions distributed especially along the tonoplast (tested by Lugol's iodine test and by the techniques of Mace and Howell (1974) for condensed tannin precursors); the galls attain an overall thickness of about 20 layers of cells with the nutritive tissue localised to 6–8 layers of cells from the upper epidermis. Simultaneously, around the feeding site, the upper mesophyll parenchyma and the upper epidermal cells display meristematic activity that contribute cells, enabling an upward growth of the gall tissue (figures 10, 11). At this stage, the nutritive cells of upper epidermal and palisadic origin continue to expand in the vertical axis, while the primordial palisadic cells show sporadic anticlinal divisions; very curiously, the nutritive (epidermal) cells show periclinal divisions contributing to the lateral, circumferential growth around the feeding site (figures 10,12,13). Although moderate division activity is evident along the cells of the upper mesophyll, the cells show enlargement in the tangential plane facilitating the further in-rolling of the lamina. The cells lying closer to the lower epidermis show anticlinal and periclinal divisions as well as stretching in the horizontal axis. Old galls (20–22 days) show an enormous increase in the tanniniferous products that almost occlude the cells.

Necrosis, an important cecidogenetic event in thrips gall systems, shows interesting patterns in its incidence. When feeding process is restricted to laminar areas and not directly on vascular regions, necrosed cells extend from upper epidermal cells to a few layers of mesophyll tissue below, extending in a vertical plane (figure 8). On the other hand, when feeding is restricted to vascular regions, necrosis of cells occurs along the upper-most layers of the mesophyll, excluding the epidermal cells, and extends in a horizontal axis (figure 9). This kind of a differential behaviour of the tissue of the same host organ appears unique.

Another outstanding feature of the nutritive tissue of the galls of *M. edule* is the development of a number peg-like ingrowths along the inner side of the wall that extend into the cytoplasm (figure 18), besides the thickening of the cell wall (figure 16). These ingrowths appear to be callosic and show compact distribution and close approximation to one another throughout the inner surface of the cell wall. Although the general thickening of the wall shows a varying profile, the intensity of the development and distribution of these wall ingrowths tends to decline towards the lower epidermis. In other words, these wall ingrowths are characteristic of the nutritive tissue, composed of the upper epidermal and a few subjacent mesophyll cells.

With the initiation of galls, the stomatal areas of the differentiating leaves show interesting responses. In very young galls (2–3 days) the epidermal cells closer to the stomatal pore show proliferation (figures 20,21), though localised, thereby the stomata are lifted-up (figure 22). With maturation of the galls, the guard cells of the stomatal pores located at the summits of the elevated areas, appear to have lost their characteristic profile and present themselves to be mere circular openings (figure 23). It is also apparent that these stomata have lost their basic function of opening and closing.

Very rarely, thrips have been observed to feed on the lower sides of the leaf, wherein, the entire sequences of events including the organisation of the nutritive tissue and

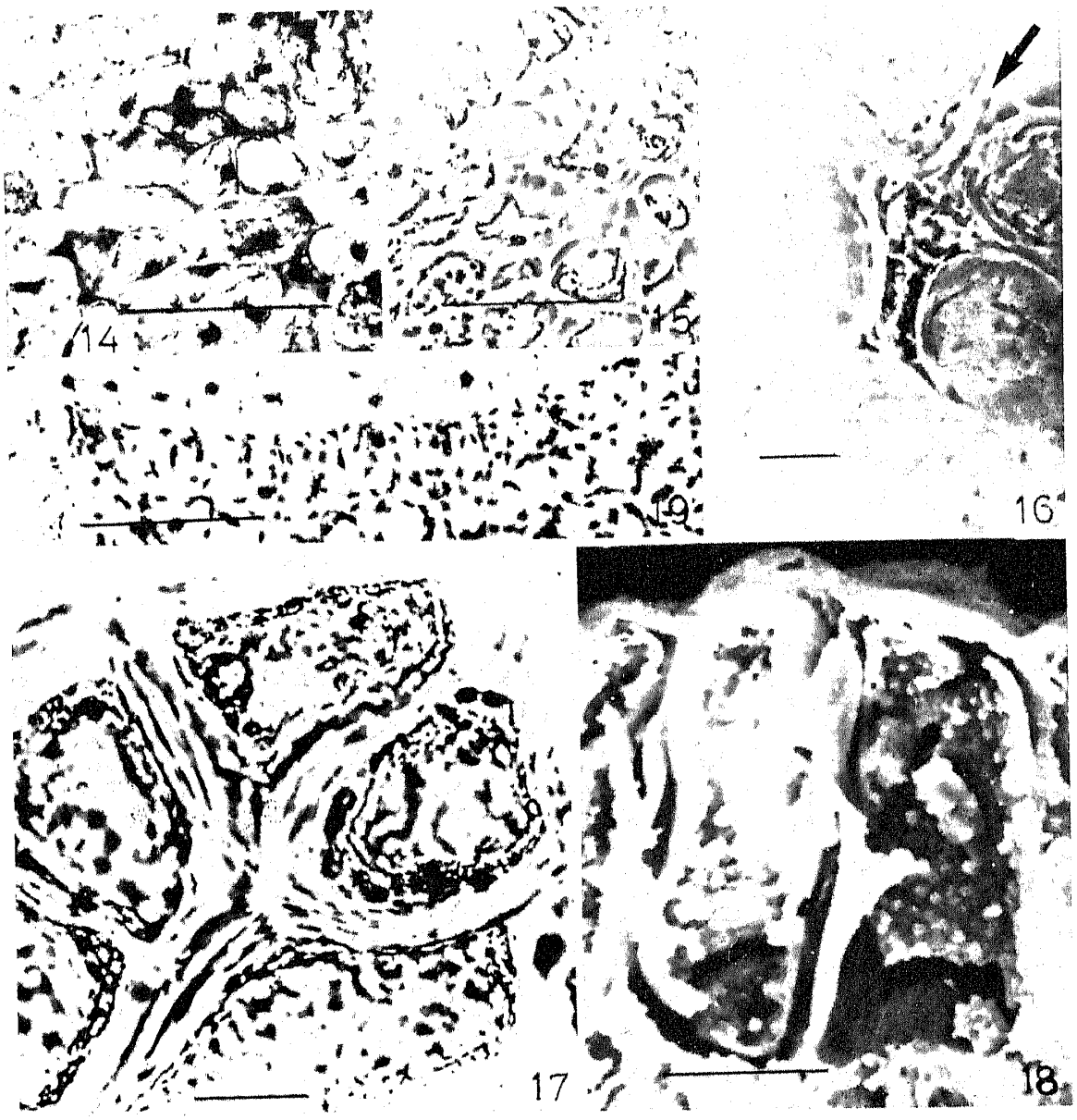


Figures 10–13. *Memecylon edule*; mature gall (5–7 days old). **10.** Stereoscan profile of the feeding zone showing circumferential growth (bar = 100 μm). **11.** Developing nutritive tissue (T.S.) (bar = 100 μm). **12.** Stereoscan profile—nutritive tissue (bar = 100 μm). **13.** Same stage as in figure 7 (T.S.) (bar = 100 μm).

proliferation are repeated in the same way as they normally would do on the upper side (figures 24,25).

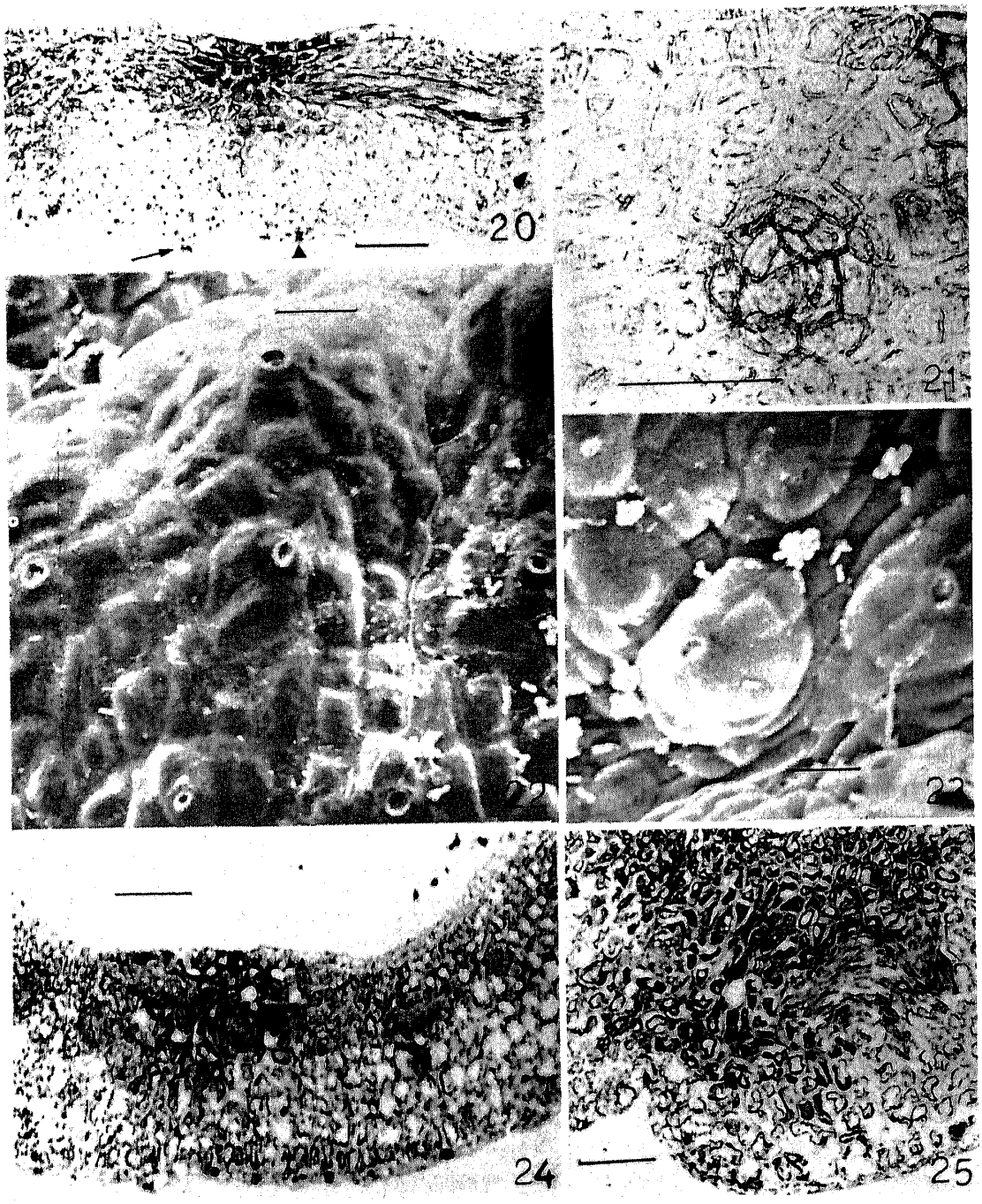
3.2 *Memecylon lushingtonii*

Crotonothrips memecylonicus induces more complex galls on the leaves of *M. lushingtonii*, than those of *M. edule*. The galls show greater morphological complexity



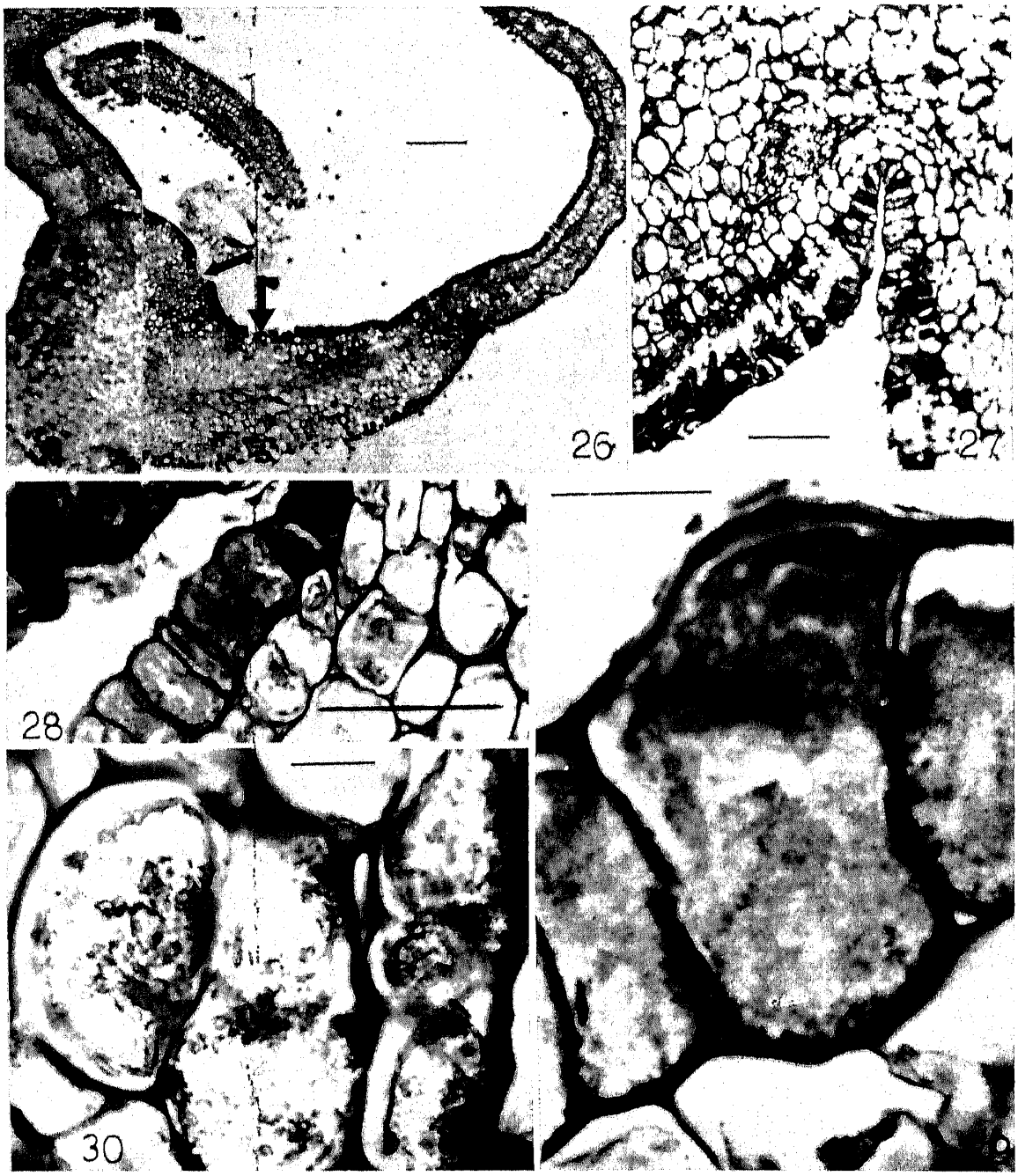
Figures 14–19. *Memecylon edule* gall (5–7 days old). **14** and **15.** Thickened cell walls of nutritive cells (bar = 50 μm). **16.** Enlarged view of the cell wall nature closer to the feeding area (arrow) (bar = 100 μm) (phase contrast microscopy). **17.** Macerated upper mesophyll cells closer to the feeding zone showing the cell wall nature (cf. striated nature) (bar = 10 μm) (phase contrast microscopy). **18.** Stereoscan profile of the nutritive (epidermal) cells showing peg-like wall ingrowths (bar = 10 μm). **19.** Thickened cell walls along the mesophyll regions of non-gall areas (bar = 100 μm).

in terms of rugosity and corrugations that the linear profile of the involved leaf is completely lost in the galling process, and the galls are characterised by a rosette-like appearance; interestingly, fusion of galled portions of the two oppositely placed leaves occurs, though infrequently, displaying a tendency to form 'closed' galls with a centrally placed insect chamber—an aspect extremely rare among thysanopterocecidia. Although, in principle, the galls are epiphyllous rolls, the intensity of rolling and the development of vertical partitions is great that the galls are unique.



Figures 20–25. *Memecylon edule.* **20.** Young gall (T.S.) showing hypertrophy of lower mesophyll and elevation of stomatal pores (arrow) (bar = 100 μm). **21.** Same as in figure 20; surface view (bar = 100 μm). **22.** Stereoscan view of the lower epidermis of young gall (bar = 100 μm). **23.** Same as in figure 22; old gall (bar = 100 μm). **24.** Old gall (20 days old) showing the accumulation of phenolic material in the erstwhile nutritive tissue (bar = 100 μm). **2.** Old gall; induction along the lower epidermis (bar = 100 μm).

Similar to the galls of *M. edule*, galls of *M. lushingtonii* are influenced by the feeding stimulus of thrips on the upper sides of the differentiating laminae (figure 26) of the two oppositely placed leaf primordia. As a result, the laminae begin to show inrolling, and begin to accommodate thrips by differentiating the nutritive tissue (figure 27), through



Figures 26–30. *Memecylon lushingtonii*; young gall (1–5 days old). **26.** Nutritive tissue (arrow) (bar = 200 μm). **27.** Feeding zone (bar = 100 μm). **28.** Differentiating nutritive tissue (bar = 100 μm). **29.** Nutritive (epidermal) cell (bar = 10 μm). 30. Nutritive (lower mesophyll) cell of 5 days old gall (cf. wall thickening).

identical morphogenetic processes as described for the galls of *M. edule*; but, significantly, a shallowing of the gall-lamina is evident in response to thrips feeding, besides organising the nutritive tissue by the metaplasia of the epidermal and subepidermal layers at specific areas (figure 28). The epidermal cells coming directly under the feeding impact, show enormous hypertrophy coupled with profound enlargement of the nucleus and nucleolus as well. The maximum hypertrophy level

appears nearly 6 times more than the hypertrophy level of the identical tissue in the galls of *M. edule*. The free regions of the nutritive (epidermal) cells along the adaxial leaf surface show profound cytoplasmic intensity, suggesting an active metabolic status (figure 29).

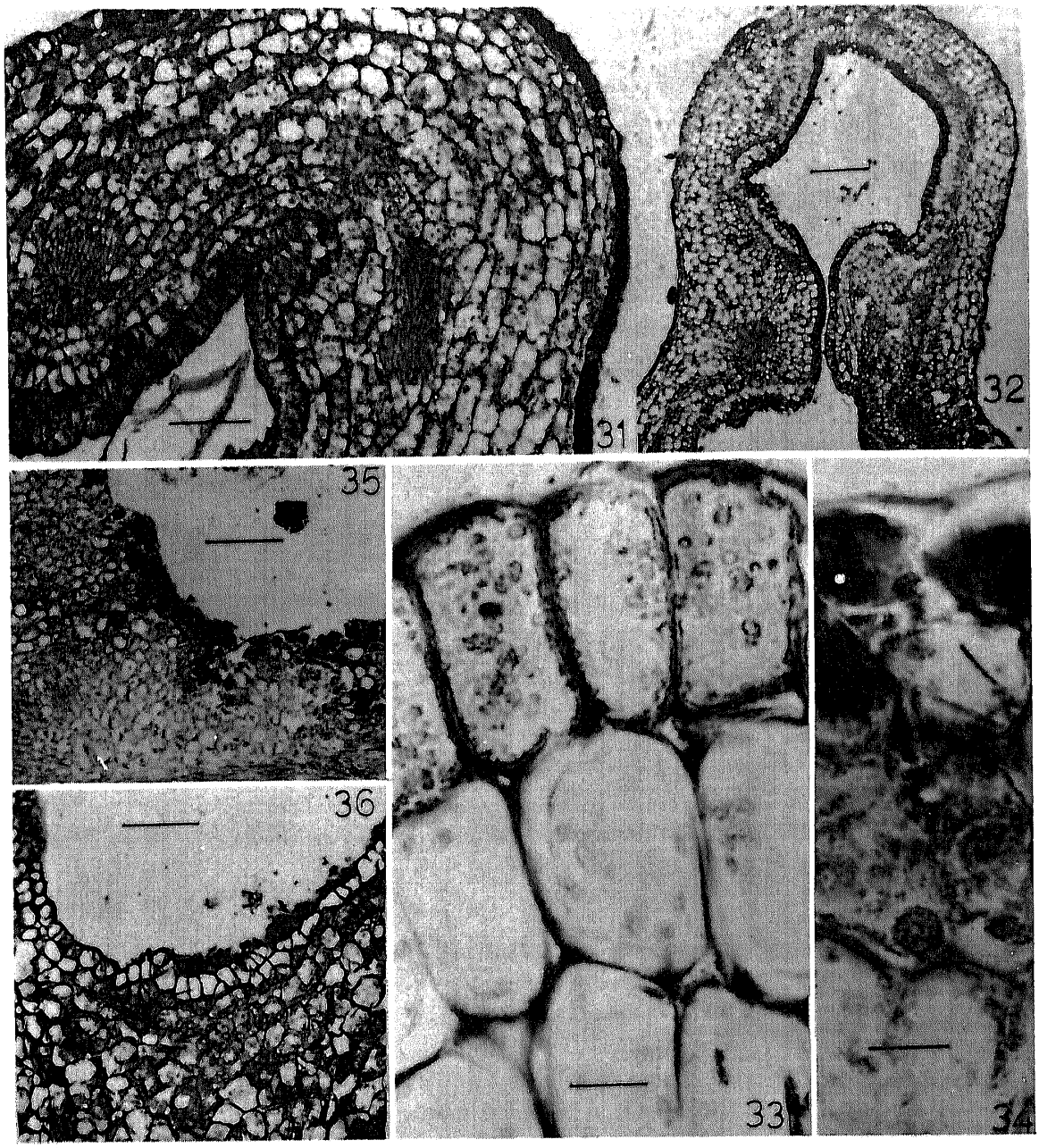
Within 4–5 days of galling, the nutritive area spreads to subjacent layers of the mesophyll as well, and at this stage, the nutritive cells (epidermal and upper mesophyll cells) begin to accumulate phenolic products as crystalline inclusions (figure 30). Although the accumulation of phenolic products is similar to the galls of *M. edule*, the time of initiation of this process appears within 5 days of gall initiation, which is much earlier than that of the galls of *M. edule*.

In spite of the basic processes of gall formation being similar to *M. edule*, the cecidogenetic gradient is distinctly of a specific pattern that proceeds as a straight line (as in transverse sections) up to the lower epidermis. The shallowing of the feeding area appears significant, supported by meristematic activity, though isolated, in the mesophyll regions closer to the upper and lower epidermises, on either flank of the feeding zone (figure 31). Among these, the division centres along the lower gall-line are more active, highlighting the major morphogenetic difference between the galls of *M. lushingtonii* and *M. edule*. Following the achievement of growth along the lower gall-line, the lateral (as in transverse sections) meristems in the upper zones, closer to this feeding areas become more active by adding cells to the formation of the pouch (figure 32). During late stages of gall ontogeny (20–22 days), the gall regions are enormously thickened with up to 50 layers of gall mesophyll with the characteristic shallowing of the gall-lamina, thus facilitating the formation of numerous pouches in the gall-system; this contributes to the profound increase in the surface area of galls, thereby providing a large nutritive area well-within the limited leaf-area.

With maturation, galls of *M. lushingtonii* too show abnormal wall thickenings with many warty wall ingrowths restricted to areas of nutritive cells (figure 33). Accumulation of tanniniferous material is yet another feature that characterises ageing of galls (figure 34), and the nutritive cells in particular that get occluded densely with phenolic material (figures 35,36,39).

Old galls (18–20 days) show peculiar cellular behaviour, that the cells of the lower mesophyll layers (derivatives of the primordial spongy mesophyll cells) retain their normal morphology (under galled conditions), while the upper epidermal cells and the subjacent layers of the mesophyll (the erstwhile nutritive cells) show stretching along the horizontal axis, and develop, as a result, large intercellular spaces (figure 37). This appears significant, and is obviously due to dehydration and subcellular molarity changes within gall systems, particularly in the upper layers closer to the insect chamber, coordinating with the ceasing of the feeding stimulus. This facilitates the unrolling of the laminae that have rolled-in tightly, thus enabling the easier migration of thrips populations built-up within the galls.

Rarely, galls of *M. lushingtonii* show meristematic activity in the circumferential area of the feeding spot of young galls, which results in the development of covering 'lip-like' growths enclosing a large insect cavity (figure 38). Besides this, some of the other salient aspects that appear interesting in these galls are: (i) development of nutritive cells in regions closer to lower mesophyll, but adjoining vascular tissues (figure 40); (ii) total inhibition of the differentiation of sclereids that are characteristic of the normal leaves of *Memecylon* (figure 41); and (iii) differentiation of the mesophyll parenchyma cells into tracheary elements, thus contributing to the proliferation of the vascular tissues in gall system (figure 42).



Figures 31–36. *Memecylon lushingtonii.* **31.** Differentiating gall-leaf (T.S.) (1–5 days old) showing the shallowing of the lamina. Proliferation evident along the upper mesophyll (bar = 100 μm). **32.** Mature gall (T.S.) (5–10 days old) with a well-developed, centrally placed insect chamber (bar = 200 μm). **33.** Mature gall–nutritive tissue (bar = 10 μm). **34.** Old gall (20 days old)—nutritive tissue (cf. upper epidermal cells accumulate tannin) (bar = 10 μm). **35.** Old gall (25 days old); intense accumulation of tannin material (bar = 100 μm). **36.** Old gall—region closer to erstwhile nutritive tissue; proliferation and emptying of cells evident (bar = 100 μm).

3.3 *Memecylon umbellatum*

Crotonothrips sp. induces epiphyllous roll galls on the leaves of *M. umbellatum*. Compared to *M. edule* and *M. lushingtonii* galls, these galls are very simple, displaying inrolling with moderate blister-like swellings along the lower surface of the leaf.

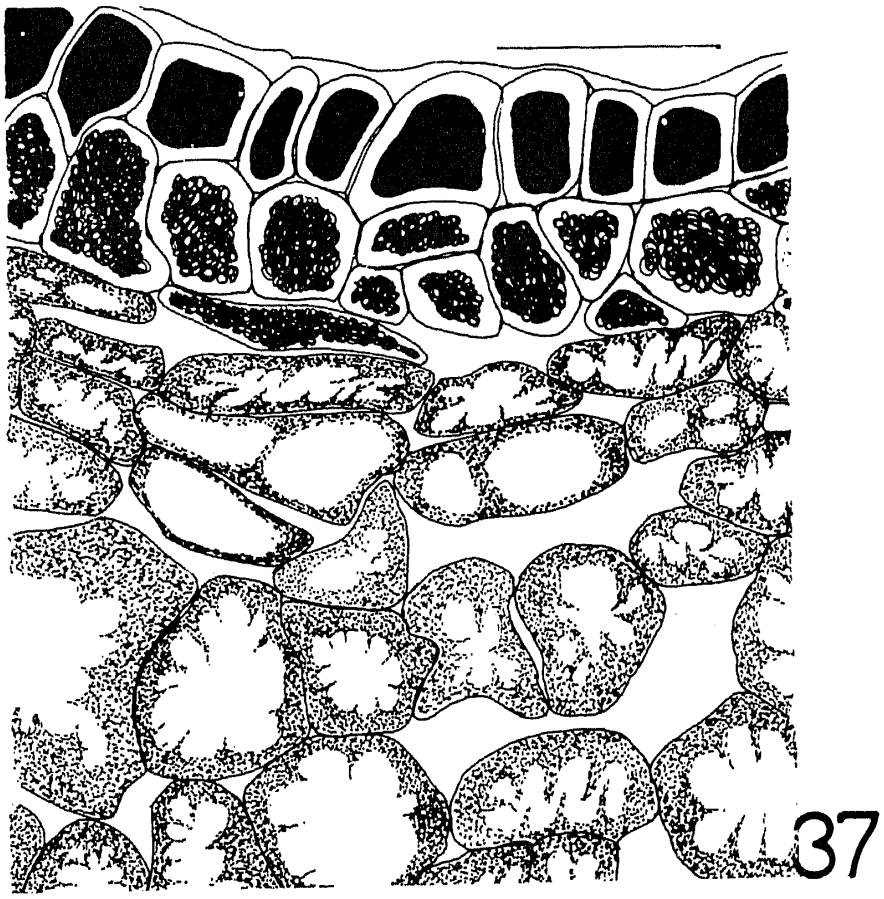
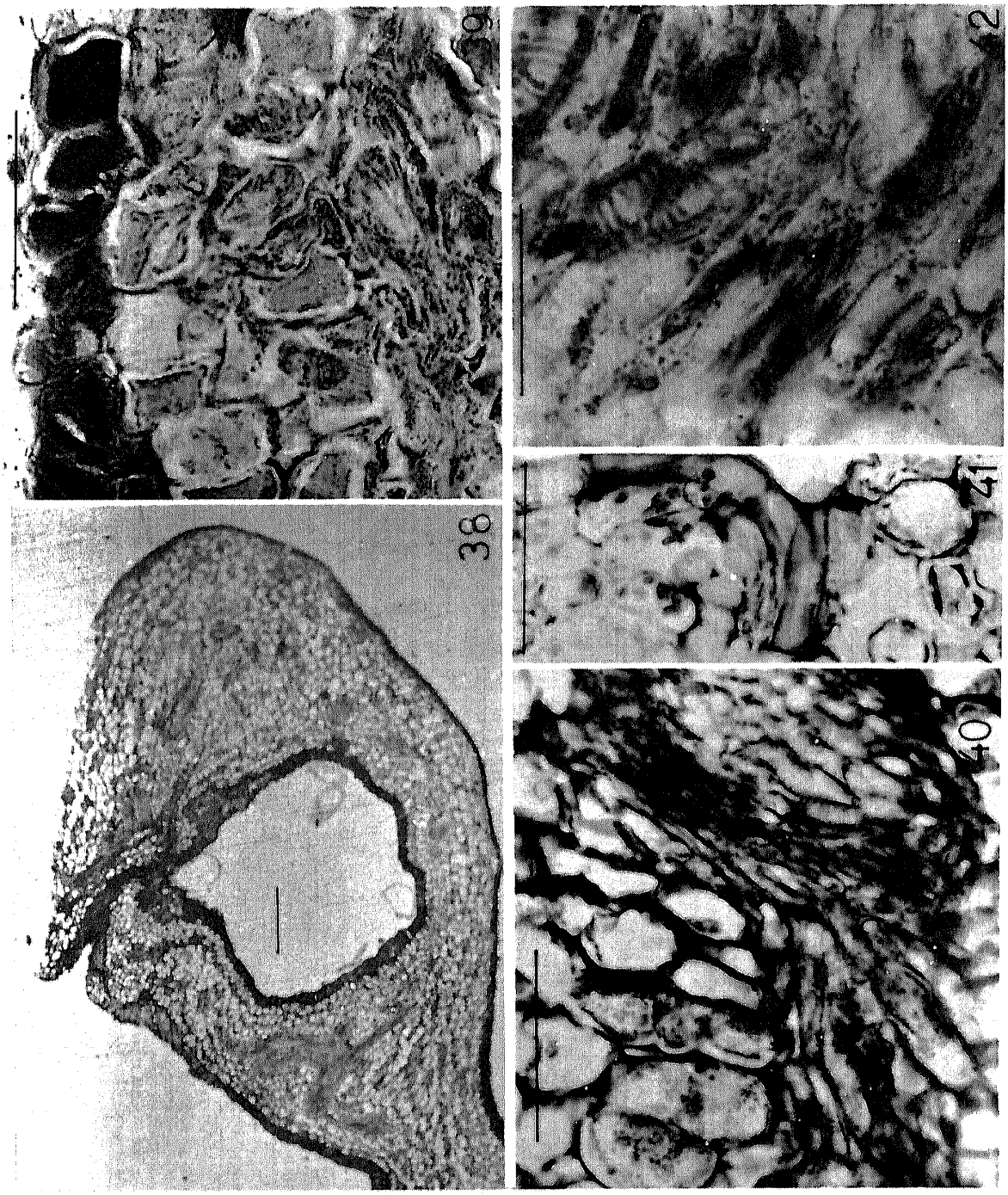


Figure 37. Old gall of *Memecylon lushingtonii*; some of the mesophyll cells showing lateral expansion and development of intercellular spaces.

Interestingly, the galls of *M. umbellatum* are identical to the galls of *M. edule* in their developmental patterns, although the proliferation pattern, supportive hypertrophy, organisation of the nutritive tissue (figures 43, 45, 46, 48) are evident in a minified scale. The circumferential growth around the feeding site is similar to that of *M. edule*. Investigations on the epidermises of differentiating galls show moderate proliferation around the feeding site (figure 44), while with maturation, the epidermal cells, a little away from the puncture area, that correspond to the circumferential growth area, show enormous hypertrophy to a magnitude of 14–15 times with normal division activity (figure 47). The hypertrophy pattern is less-manifest in regions closer to the puncture area and more intense at regions away, showing a sequential increase.

Old galls (20–25 days old) are characterised by the accumulation of tannin material in the nutritive cells that gradually extends to the deeper mesophyll (figure 49), similar to

Figures 38–42. *Memecylon lushingtonii*. **38.** Mature gall showing tendency to develop labial covering growth (bar = 200 μm). **39.** Old galls—accumulation of tanniniferous and flavanolic material in the nutritive tissue (bar = 50 μm). **40.** Mature gall—nutritive tissue closer to vascular strands (bar = 50 μm). **41.** Normal leaf—sclereids (bar = 50 μm). **42.** Gall (5–10 days old); proliferation of interfascicular parenchyma and transformation into tracheary elements (bar = 50 μm).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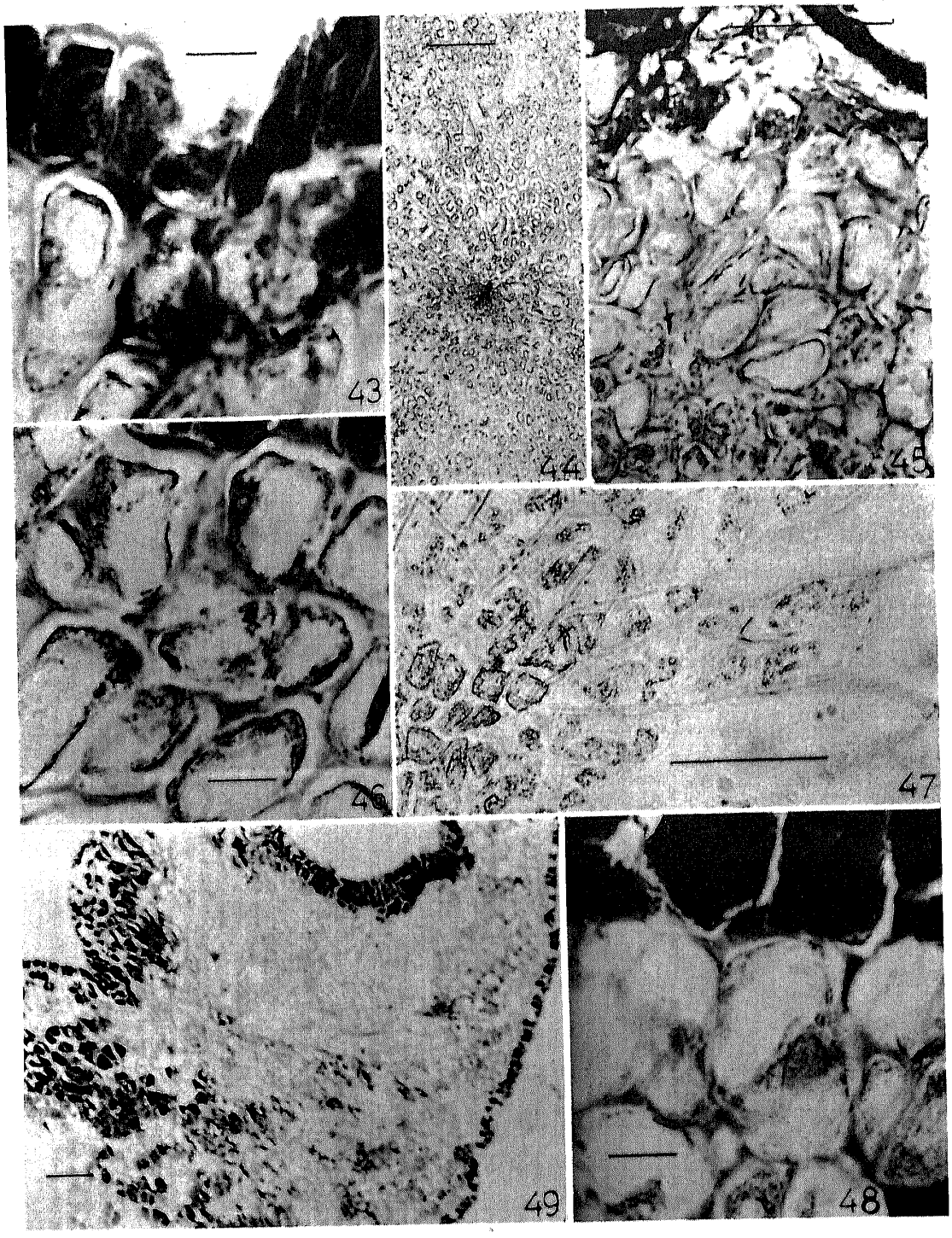

Figures 43–49. *Memecylon umbellatum*. **43.** Young gall (1–3 days old)—feeding damage and initiation of nutritive cells (bar = 10 μm). **44.** Young gall; surface view of the circumferential growth around the feeding site (radial pattern of epidermal proliferation) (bar = 100 μm). **45.** Young gall—lateral aspects of the feeding area showing proliferation (bar = 50 μm). **46.** Mature gall (5–8 days old); nutritive tissue (bar = 10 μm). **47.** Mature gall; surface view of the epidermal hypertrophy (bar = 50 μm). **48.** Mature gall (8–10 days old); cells near the nutritive area (wall thickening is less intense) (bar = 10 μm). **49.** Old gall (20 days old) (bar = 100 μm).

the other two galls. In the mid-mesophyll areas, no significant hypertrophy and development of intercellular spaces is evident as in the galls of *M. lushingtonii.*

4. Discussion

By preferring the leaves of *Memecylon*, species of *Crotonothrips* have, in principle, a fundamentally identical cecidogenetic behaviour; yet, the developmental patterns in terms of specific responses of the host plants are distinct. Based on the degree of complexity, *umbellatum* galls appear to be the simplest of the three, showing a simple external form and developmental events, while the galls of *lushingtonii* present themselves to be of the complex type in form, organisation, and development; tendency to develop covering 'lip-like' growth as well as closed galls, a character more-frequent among the galls of Homoptera and Diptera, appears important. Galls of *edule* provide sufficient scope to be recognised as an intermediate type.

Gall induction by thrips is a specific, population-regulated phenomenon (Ananthakrishnan 1984; Raman and Ananthakrishnan 1984). *Crotonothrips–Memecylon* interactions indicate a successful interlinking of the collective feeding effort of the building populations of thrips species with the responses of the host in terms of developmental adjustments, thus rendering each gall system as a functionally effective one. For instance, with ageing, galls of *M. lushingtonii* show highly specialised patterns of tissue behaviour that lead to the loosening of the compact system enabling the easier migration of *Crotonothrips memecylonicus.* Interestingly, this kind of a host behaviour is lacking in the galls of *edule* and *umbellatum*, wherein the systems are less compactly in-rolled. Although the precise physiological nature of the tissue involved is not known, the functional moderation as evident in the structural adjustments of *M. lushingtonii* galls, facilitating the temporal expansion along the horizontal axis of particular tissue is unique.

One of the basic and major demands of insect-induced gall systems is to offer nutritional facility to the gall making organisms. Galls of *edule*, *lushingtonii*, and *umbellatum* provide excellent examples for this cecidogenetic requirement, as a highly specialised nutritive tissue is initiated in these galls, firstly in response to the feeding stimulus, and secondly to the consequent injury and irritation. A purposeful combination of these enables the primordial host tissue to turn metaplastic and display signs of enlargement and occasional proliferation and thus become tissues of special nature with abundant food reserves (Raman and Ananthakrishnan 1983; Gopinathan 1984). Significantly, this tissue shows a series of specialised responses in conjunction with the process of ageing. Initially, the nutritive cells accumulate more and more of cytoplasmic reserves, and within about 7 days, tanniniferous material appear indicating the gradual transformation of this tissue into a non-functional one. But the spread of this subcellular specialisation to the lower mesophyll cells, concurrently with the accumulation of flavanolic and tanniniferous material in the upper mesophyll cells suggests that thrips are able to obtain a continuous supply of nutrition throughout their period of stay within gall systems. Intense accumulation of the phenolic substances in the nutritive cells upon ageing and ultimately senescence, that takes about 25 days in all the three gall systems, synchronises with the general pattern of life-cycle duration of species of *Crotonothrips.*

Histogenetic studies describe how a shift in the direction of division activity is

initiated during cecidogenesis. These also underline the nature of the feeding stimulus that initiates and directs 'new' courses of differentiation. Although growth in terms of hypertrophy and hyperplasia is localised to specific areas of the gall-susceptible leaf, there is an overall impact evident in the total leaf: (i) normal differentiation course is inhibited, thus the whole leaf retains tissues in their primordial profile; (ii) abnormal wall thickenings develop throughout the blade; and (iii) gall-susceptible leaf rolls on itself, although the intensity of rolling varies with species.

Investigations on the growth processes shed considerable light on the tissue behaviour as altered in the cecidogenetic system. Under the general circumstances that the host organ is a leaf, the gall susceptible hosts belong to the genus *Memecylon*, and the gall inducing agents belong to the genus *Crotonothrips*, the gall formation process and the end-products display a highly varied and eventful course of differentiation and growth. This aspect becomes all the more significant essentially because the localised effect of the reaction processes underscores the need to modify the innate rules that govern the orientation patterns of cell division and hypertrophy, so that the tissue geometry, and in effect, the organ symmetry are maintained. Alteration in the course of morphogenetic events to neutralise the stress created by the cecidozoa is obvious by the creation of new, active division centres at specific localities of the organ, and the rest of the system being supported by activities such as cell enlargement, and subcellular adjustments that include wall ingrowths and thickenings, as well as cytoplasmic specialisation as evident in the nutritive cells. Interestingly, the stress areas show varying profiles in the analysed gall systems: *edule* and *umbellatum* galls show an inverted 'Y' pattern, while *lushingtonii* system shows an 'I' pattern, which necessarily predict the further course of morphogenetic events to achieve the ultimate gall-form

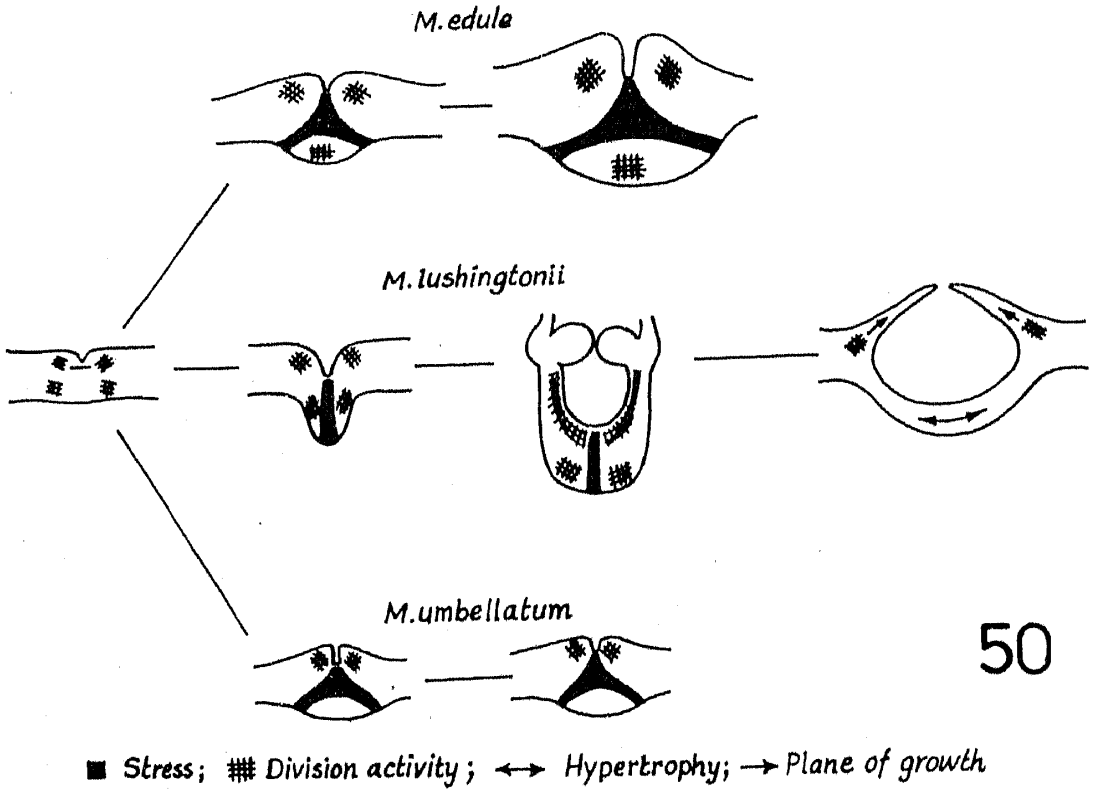

Figure 50. Schematic representation of cecidogenetic pattern in the three types of galls.

(figure 50). The inverted 'Y' course activates the circumferential growth around the feeding site, and the 'I' course initiates the shallowing of the gall lamina, although in either case, the basic objective of the gall system seems to provide scope for the development of vertical partitions in the rolled leaf, thereby increasing the nutritive surface area well within the limited leaf area. The 'I' and 'Y' patterns of stress situations also indicate very interesting cellular behaviour as well, wherein each constituent cell is moderately hypertrophied in the vertical axis, corresponding to the flow pattern of the cecidogenetic gradient. On the whole, as evident in transverse sections, these gall systems do not sacrifice their bilaterally symmetrical organisational pattern, but broadly, there is an overall exaggeration in cell dimensions at particular areas, and more subtly, there are a number of specific developments that contribute to the spatial organisation of a leaf as a compensated system of a gall suiting the needs of an alien genome.

Every cell participating in cecidogenesis shows a distinct pattern of hypertrophy; though differing in magnitude and intensity, each cell largely conforms to the type of the primordial tissue from which it has originated: cells of palisadic origin show hypertrophy in the vertical axis; cells of spongy mesophyll origin show isodiametric hypertrophy. This tissue behaviour suggests that thrips are able to destabilise the normal polarity gradient only partly. Similarly, the cells of the upper epidermis of *edule* and *umbellatum* show profound meristematic activity enabling the upward circumferential growth; on the other hand, proliferation of the upper epidermis in the galls of *lushingtonii* is minimal, primarily because the galling process involves a greater developmental stress towards shallowing. While such is the morphogenetic course involving a significant divergence in the behavioural trends the upper epidermal and associated mesophyll cells, the lower epidermal and allied mesophyll cells display identical behavioural patterns in all the three species, that the stomatal areas and subjacent mesophyll cells show hypertrophy and proliferation to such an extent that the stomatal pores are elevated from the normal levels indicating the possible development of a water stress. The loss of the contour of guard cells, and the pores remaining open throughout, suggest the functional status of these in aiding the transpirational processes to get over the water stress developed from within, probably as a consequence of gall development. Further, the modification of form of these stomatal pores indicate the establishment of new polarity axes and new courses of differentiation at regions farther away from the stimulus area. Besides these behavioural adjustments in the tissue systems, the development of wall thickening, that shows varying profiles, appears interesting. Probably because the intensity of thickening increases with ageing in cells, thus reducing the surface area, these cells develop peg-like ingrowths that enable an increase in the surface area. Higher rates of incidence of this subcellular differentiation nearer the feeding site and a gradual decrease towards the lower mesophyll support this contention. In all the three species, differentiation of tracheary elements by the hyperplasia of interfascicular parenchyma as well as the total inhibition of sclereid differentiation are evident; the latter becomes extremely important as normal leaves of all the species of *Memecylon* are characterised by the incidence of different kinds of sclereids (Rao 1957). A positive reaction of the gall tissue showing the induction of tracheary elements and a simultaneous negative response of inhibition of the formation sclereids support the idea that cytodifferentiation stems from epigenetic modifications (Davidson 1968; Maresquelle 1980) as these appear as directed changes, although the question relating to the reversibility potential of these

cells needs to be investigated. However, the cytodifferentiation patterns regulating cell behaviour involving structural and functional changes create difficulties in establishing a causal relationship with the stimulus from the gall maker, since the activity patterns towards changes in polarity axes are moderate in some areas, but strong in some other areas.

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