

CONTRIBUTION OF ANATOMY TO THE SYSTEMATICS OF *ROTALA* L.
(LYTHRACEAE)

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ABSTRACT

Anatomical work done on the genus *Rotala* L. is reviewed and studies on the anatomy of adult stems and leaves and the SEM of the cuticle and stomata on leaves of 10 species of *Rotala* L., are presented. A 'key' based on anatomical features of diagnostic value is formulated to recognise the species from each other and the impact of such evidence on the infrageneric relationships, is discussed.

Detailed anatomical work done, involving the stems and leaves of adult plants belonging to eight species of *Ammannia* L. and 11 species of *Nesaea* Comm. ex Kunth has been presented by me earlier (Panigrahi, S.G., 1981; Panigrahi S.G., 1986). The work done similarly on 10 species of *Rotala* L., under the supervision of Prof. V. H. Heywood, University of Reading and of Dr. D. F. Cutler of the Jodrell Laboratory, Kew, U.K., between 1973 and 1975, is presented here.

Solereder (1908) and Metcalfe and Chalk (1950) have reviewed excellently the work done by various scientists involving both the woody and herbaceous genera of the family Lythraceae Juss. Yet, no one seems to have worked out the anatomy of any of the species of *Rotala* L. except Gunther (1905), who did not even name the species he worked with. Datta and Maiti (1968) studied the anatomy of two species, *Rotala pentandra* (Roxb.) Blatt. & Hallb. [as '*Ammannia pentandra* Roxb.=*Rotala rosea* (Poir.) C.D.K. Cook. and *Rotala indica* (Willd.) Koehne (as '*Ammannia peploides* Spreng.)']. Study of anatomy of as many as 10 species of *Rotala* L., is then, a major contribution to re-evaluate the infrageneric classification of Koehne (1903), based purely on gross morphological characters.

MATERIALS

Samples were taken from the specimens preserved in the Herbarium of the Royal Botanic Gardens, Kew, U.K. Details of sampling is summarised in Table 1 in Panigrahi (1979 a).

Salient anatomical features characteristic of the genus *Rotala* L. are presented below, followed by a 'key' for diagnosing anatomically the 10 species from each other. Impact of anatomy on the systematics and affinity of these taxa selected to represent one or the other of the sections of *Rotala* L. recognised by Koehne (1903), as visualised by taxonomists guided by the external morphology, both vegetative and reproductive, is discussed.

DIAGNOSTIC ANATOMICAL FEATURES OF
ROTALA L.

Stem in T. S. : *Outline* : Circular (Fig. 1A), squarish or rectangular (Fig. 2A, C) with or without shallow depressions or short elevations or even projections from the four corners (Fig. 2A). *Cuticle* : 2.5-6 μ m thick, smooth or with shallow depressions and striations, rarely strongly folded and ridged. *Papillae* absent or a few, rarely many, short, narrow when present, or sub-papillate. *Mucilage cells* absent or a few, generally small and rounded. *Epidermal cells* squarish, rectangular, angular or oval, 6-36 μ m high; outer walls generally flat, rarely con-

vex, anticlinal walls thin or thick, straight or more or less wavy, the inner walls thin. *Hypodermis* parenchymatous (Fig. 1A, B) or collenchymatous (Fig. 3A, D), 1-3-layered. *Cortex* aerenchymatous, 1-2 (rarely-3)-layered, air chambers generally large, regular, squa-

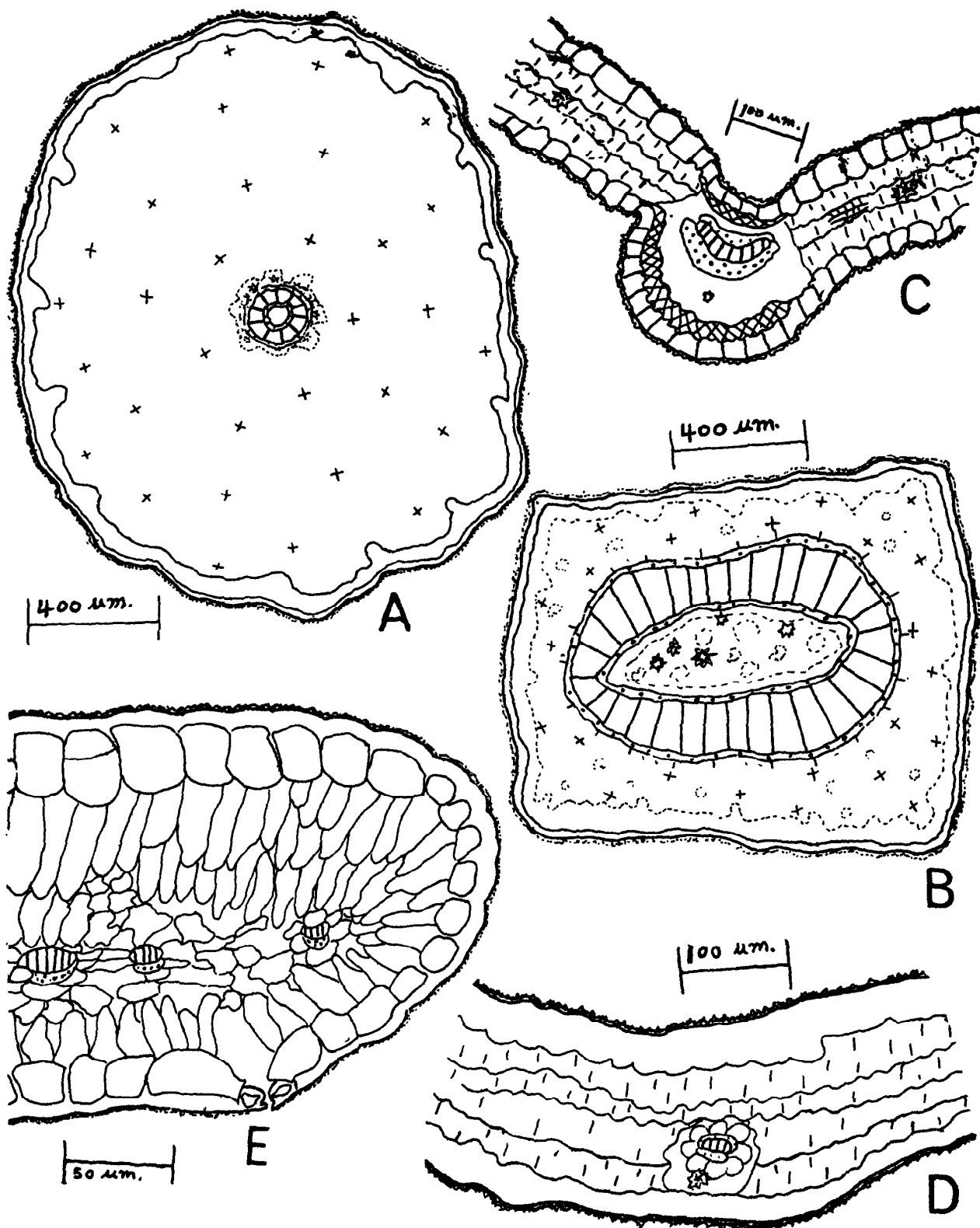


Fig. 1 (A-E) : Legend at the end of the article

rish, polygonal or radially elongated, generally 8-12 chambers in one layer; thin lining cells parenchymatous, large, round, oval or elongated (Plate 1A) [this type of aerenchyma is designated by me as TYPE A (cf. Panigrahi 1979)]; radial thickness of the cortex varies from $39\mu\text{m}$ in *Rotala serpyllifolia* to $828\mu\text{m}$ in *R. myriophylloides* (Fig. 1A), or broader than the xylem tissue of the same species. *Druses* and *crystals* a few to many, scattered or in groups of 2-6 (Fig. 2C); thick-walled cells scattered among the lining cells of the aerenchyma. *Endodermis* distinct with radial walls thickened as casparian strips. *Primary phloem fibres* generally absent, rarely present (Fig. 3A, depicted in thick-black circles or black-rods outside the external phloem ring). *External phloem ring* narrow and wavy in outline, as broad or broader than the *internal phloem ring*. Vascular tissue forms a continuous cylinder except for the leaf gaps; *xylem tissue* varies between $48\mu\text{m}$ to $310\mu\text{m}$ in radial thickness and is encircled by the external and internal phloem rings; cortex : xylem ratios vary between 0.312 : 1 (Fig. 3A) to 16.23 : 1 (Fig. 1A); xylem non-storeyed and diffuse with simple perforation plates; vessels solitary or in groups of 2-3, more or less evenly distributed, $15-36\mu\text{m}$ wide with vestured pits arranged alternately and long tails ending in a blunt apice; wood fibres more strongly developed in *Rotala ramosior* and *R. serpyllifolia* than in the other species of the genus; paratracheal parenchyma short, scattered in more or less regular bands, more abundant in *Rotala serpiculoides*. *Pith* hollow, parenchymatous with or without air spaces and fibres; crystals a few to many, solitary or in groups of 2-6 (Fig. 1B, Fig. 2A, C, Fig. 3A, D).

Leaf : Surface view : Epidermal cells 4-5-7-sided; isodiametric, rectangular elongated or polygonal, occasionally mixed with a few paired elongated or polygonal cells; outer walls more or less straight or wavy,

with or without *papillae*. *Mucilage cells* small, round or oval (Plate 1F, Fig. 2I). *Stomata* round or oval, occasionally elongated, surrounded by 4-6 cells, 1-16 per mm^2 on the adaxial and 3-26 per mm^2 on the abaxial surface; some stomata surrounded by three irregularly-shaped cells; unevenly thickened guard cells present in *Rotala serpyllifolia* (Plate 2D); cuticular pattern smooth with very broad shallow bands and a few elevated stomata as in *R. mexicana* (Plate 2A); cuticular pattern with ridges and furrows ridges of uneven thickness and irregular folds with smooth areas in between as in *R. diandra* (Plate 2B); cuticular pattern smooth with horizontally oriented striations and with boat-shaped depressed stomata as in *R. myriophylloides*; (Plate 2C); or of very short flakes overlying on one another and with both elevated and depressed stomata, as in *R. verticillaris* (Plate 2E). *Veins* vertically transcurrent, secondary veins parallel to the midrib, veinlets with 2-3 vein-endings present in each areole.

Leaf in T.S. Isobilateral (Plate 1D, F) (rarely tending to bifacial condition) or centric; *lamina* 57 to $270\mu\text{m}$ thick. *Outline* : oblong or elongated, generally narrow, straight or wavy with or without deep channels. *Cuticle* $3-13\mu\text{m}$ thick. *Epidermal cells* squarish, oval, angular or tabular, wide or narrow, $12-50\mu\text{m}$ on the adaxial surface and $15-50\mu\text{m}$ high on the abaxial surface. Papillae absent to a few, rarely many, $20-27\mu\text{m}$ long on the adaxial and $13-50\mu\text{m}$ on the abaxial surface (Fig. 2D, 3B). *Mucilage cells* round, oval (Plate 1D, F) or elongated on both surfaces or only on one surface or altogether absent; solitary or in groups 2-4, $10-65\mu\text{m}$ high on the adaxial and $10-60\mu\text{m}$ high on the abaxial surface (Plate 1D). *Stomata* raised, level or depressed with short blunt ledges. *Mesophyll* of large and elongated palisade cells with pointed ends, in 1-3 layers on the adaxial and small-celled, 1-layered (or rarely 3-layered) on the abaxial

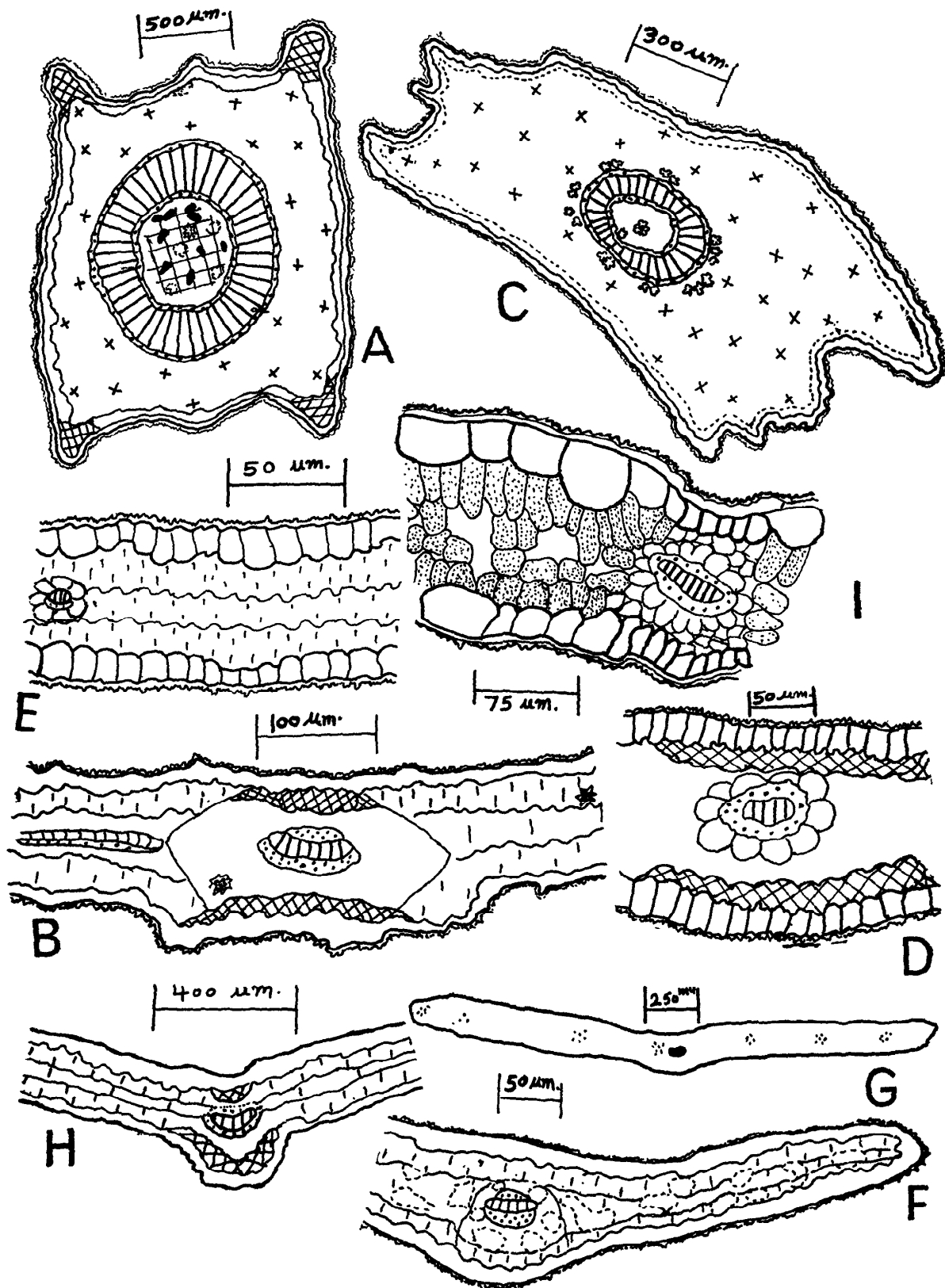


Fig. 2 (A-I) : Legend at the end of the article

surface (Plate 1D, F; Fig. 2I); spongy tissue 1-2-layers in between the palisade layers, variously-shaped; irregular air spaces present or absent, or as in the case of *Rotala myriophylloides*, with centric leaf (Panigrahi and Panigrahi, 1977). *Mesophyll* homogeneous comprising loosely arranged round chlorenchymatous cells and air spaces; crystals, as in the stem, a few to many, solitary or in groups. *Midrib* indistinct or conspicuous (Fig. 3F), trapezoid (Fig. 2B) or rectangular in shape or semi-circular (Fig. 1C, 3F) or oval (Fig. 2H) on the abaxial side; collenchymat-

ous (Fig. 2D) or parenchymatous (Fig. 2F, I), both adaxially and abaxially. *Bundle sheath* distinct with large parenchymatous cells (Plate 1D, F), rarely indistinct, air spaces of different shapes present or absent, crystals and druses a few. *Vascular bundle* small, oval (Fig. 2F), round or crescentiform (Fig. 3F), 28-70 μ m thick in the middle. *Margin* narrow and obtuse; bordering cells 3-7, oval or squarish, more or less thick-walled, smooth; mechanical tissue present or absent (Plate 1E).

KEY TO THE TEN SPECIES OF *ROTALA* L.

- 1a. Hypodermal collenchyma present only on the adaxial side of the leaf-midrib or wholly absent:
 - 2a. Leaf isobilateral; cortex with one layer of squarish or polygonal air spaces and either narrower than or twice as broad as the xylem tissue; bundle sheath without air spaces:
 - 3a. Stem hypodermis parenchymatous but midrib hypodermis collenchymatous; epidermal cells without periclinal division (i.e. all 1-layered); cortex narrower than or equal to xylem-tissue in radial thickness; pith hollow; 3-6 stomata per mm² on the abaxial side (Fig. 1C) .. *Rotala mexicana*
 - 3b. Stem hypodermis collenchymatous, but midrib hypodermis parenchymatous; some epidermal cells of the leaf with periclinal division (i.e. some cells 2-layered); cortex almost twice as broad as the xylem tissue; pith with air spaces and fibre cells; 16-18 stomata per mm² on the abaxial side (Fig. 1D, E) .. *Rotala verticillaris*
 - 2b. Leaf homogenous; cortex with 2-3 layers of polygonal air spaces and ca. 16 times broader than the xylem tissue (Fig. 1A); bundle sheath with air spaces .. *Rotala myriophylloides*
- 1b. Hypodermal collenchyma present on both the abaxial and adaxial sides of the leaf-midrib (Fig. 1C; Fig. 3B, F):
 - 4a. Cortex : xylem ratio more than one:
 - 5a. Stem hypodermis parenchymatous and interrupted by air spaces; cortex less than 250 μ m in radial thickness (Fig. 1B) .. *Rotala serpiculoides*
 - 5b. Stem hypodermis collenchymatous, or aerenchymatous, but not interrupted by air spaces; cortex more than 300 μ m in radial thickness:
 - 6a. Pith with air spaces; papillae present:
 - 7a. Stem hypodermis collenchymatous; cortex about three times broader than the xylem tissue in radial thickness (Plate 1A); midrib semi-circular on the abaxial side and a shallow depression on the adaxial side (Fig. 1C); margin without any collenchymatous tissue .. *Rotala rosea*
 - 7b. Stem hypodermis collenchymatous at the corners only (Fig. 2A); cortex about one and a-half times broader than the xylem tissue in radial thickness; midrib trapezoid (Fig. 2B); impressed both on the abaxial and adaxial sides; margin with 4-5-layered collenchymatous tissue. (plate 1E) .. *Rotala diandra*
 - 6b. Pith without air spaces; papillae generally absent:
 - 8a. Stem more or less rectangular; leaf epidermal cells rectangular in T. S.; cortex with 2-3 layers of squarish air spaces and about seven times as broad as the xylem tissue; pith parenchymatous (Fig. 2C, D, F) .. *Rotala tenella*
 - 8b. Stem circular; leaf epidermal cells rectangular in T. S.; cortex with 2-3 layers of large, polygonal, radially elongated air spaces and about 13 times as broad as the xylem tissue (Plate 1B); pith parenchymatous with central collenchyma (Fig. 2G, H, I) .. *Rotala filiformis*
 - 4b. Cortex : xylem ratio less than one:
 - 9a. Xylem tissue somewhat broader than the cortex in radial thickness; primary phloem fibres absent; mesophyll and midrib with air spaces; mucilage cells solitary; papillae many on the leaf epidermis (Fig. 3D, E) .. *Rotala ramosior*
 - 9b. Xylem tissue almost three times as broad as the cortex; primary phloem fibres present (Fig. 3A); mesophyll and midrib without air spaces; mucilage cells in groups; papillae absent on the leaf epidermis (Plate 1D; Fig. 3A, B, C) .. *Rotala serpyllifolia*

SYSTEMATIC ANATOMY OF THE TEN SPECIES OF *ROTALA* L.

Koehne (1903) divided the genus *Rotala* L. into two sections, viz. *Hippuridium* and *Enantirotala*, the former characterised by verticillate or alternate leaves with axillary flowers, calyx always appendiculate; and the latter with typically decussate leaves and calyx sometimes exappendiculate. On the basis of presence or absence of collenchyma in the hypodermis of the stem and on the adaxial sides of the leaf-midrib, we may re-group the ten species of *Rotala* into two major sections, corresponding roughly with the two sections recognised by Koehne on gross morphology. *Rotala mexicana* with leaves 3-6 per whorl, flowers axillary and sessile, petals 0, etc., is referred to subsect. 1 *Hypobrichiastrum*; *Rotala verticillaris* and *Rotala myriophylloides* with flowers in racemes or in terminal spikes and persistent petals etc., are included in the subsect. *Eurotala*. A reference to the 'Key' based on anatomy, however, shows that *R. verticillaris* and *R. mexicana* are more close to each other by sharing between them isobilateral leaves and characters of cortical aerenchyma, bundle sheath without air spaces, the relative width of the cortex vis-a-vis the xylem tissue and scale-like cuticular ornamentation, than they are to *Rotala myriophylloides*, the latter possessing a $\pm$ homogenous leaf, a cortex with many layers of polygonal air spaces as aerenchymatous tissue, air spaces in 2-3 layers around the midrib vascular bundle, the cortex 16 times as broad as the xylem tissue in radial thickness and cuticular ornamentation comprising broad ridges and furrows. Besides, *R. myriophylloides* has a stem with parenchymatous hypodermis, pronounced development of the cortex (ca 828 μ m) in radial thickness, reduced vascular tissue (ca 80 μ m), pith cavity, stomata 10-14 mm² on the abaxial side of the aerial leaf. *Rotala verticillaris*, in contrast, has a stem with collenchymatous hypodermis, cortex ca 300 μ m vis-a-vis xylem tissue ca 150 μ m, pith

with scattered air spaces and fibre cells and stomata 1-18 per mm² on the abaxial side of the leaf surface. Therefore, the grouping of the two species in the same subsection *Eurotala* is hardly supported by their anatomy.

Rotala serpiculoides, the sole representative of the subsect. 5. *Serpiculopsis* is characterised by the calyx without appendages, cymose inflorescences and flowers without petals. Anatomically, it also stands apart by its parenchymatous stem hypodermis interrupted by air spaces and pith and mesophyll of leaf with air spaces.

Rotala rosea of subsect. 6 *Sellowia* is one of several species sharing with subsect. 7 *Suffreniopsis* its axillary solitary flowers. Whereas the former subsection has its calyx appendages subulate, flowers 3-or 5-or 6-merous, rarely 4-merous, and 1, 5, or 6 stamens, the latter subsection has its calyx appendages 0, flowers 4-merous and stamens 5 per flower. Anatomically, *R. rosea* shares its collenchymatous hypodermis of the stem and broader cortex (ca 300 μ m) and pith with air spaces with *R. diandra* of subsect. *Suffreniopsis*, but it differs from the latter in having its pith largely collenchymatous, but without pith fibres, cortex almost three times as broad as the xylem tissue, midrib semi-circular and leaf-margin without any mechanical tissue. Thus, Koehne's (1903) merging of *Tritheca pentandra* (Roxb.) Miq. (= *Rotala rosea*) is fully supported by anatomy. *R. diandra*, on the other hand, has its stem hypodermis collenchymatous only at the corners, pith collenchymatous only at the centre, cortex only 1½ times broader than the xylem tissue, midrib trapezoid, leaf-margin collenchymatous and a cuticular pattern comprising an irregular network of mounds with sharper folds. *R. diandra* differs from two other species of the subsect. 7, viz. *R. tenella* and *R. filiformis* by the presence of air spaces in the pith and of many papillae on the leaf epidermis, *R. tenella* and *R. fili-*

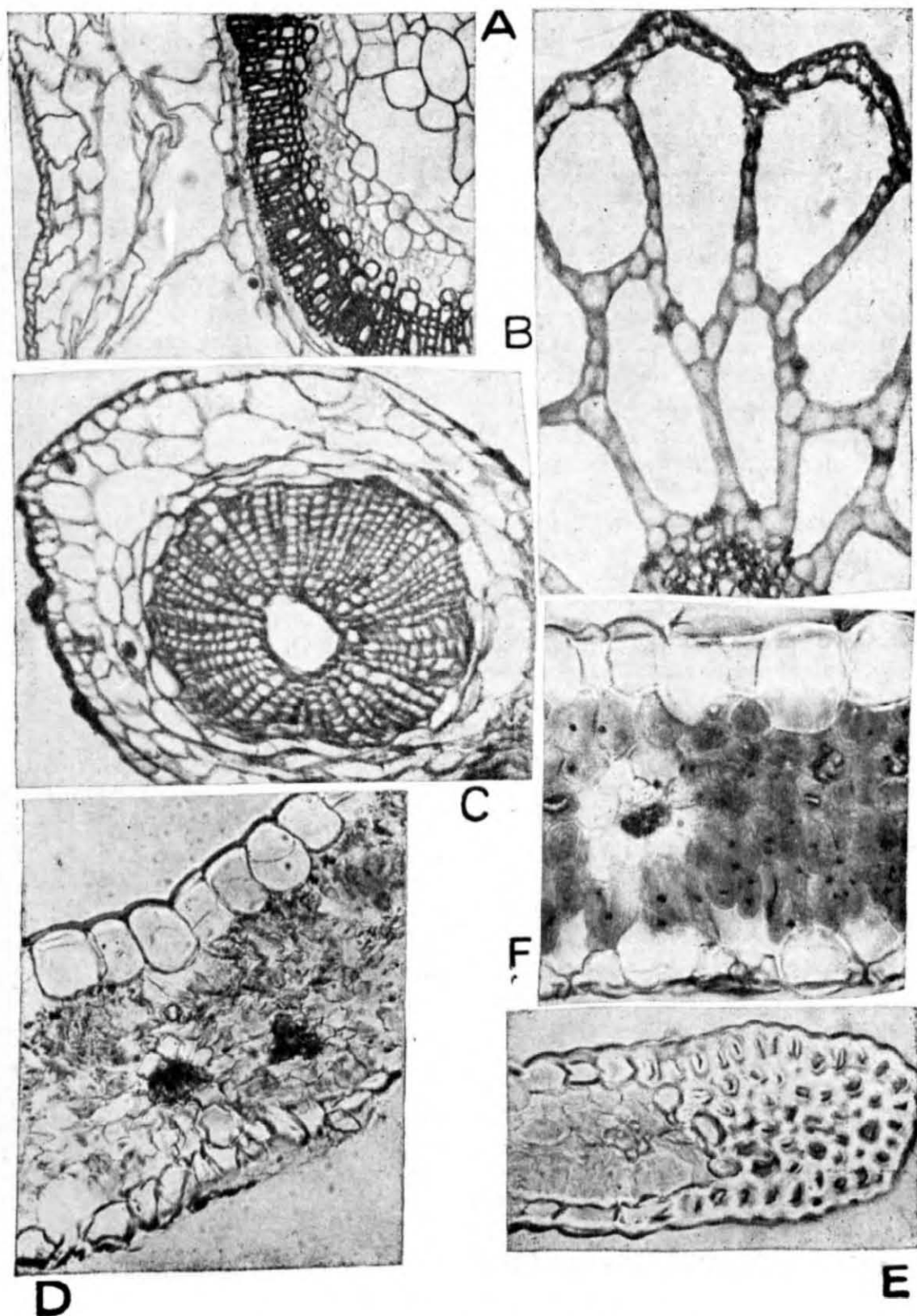
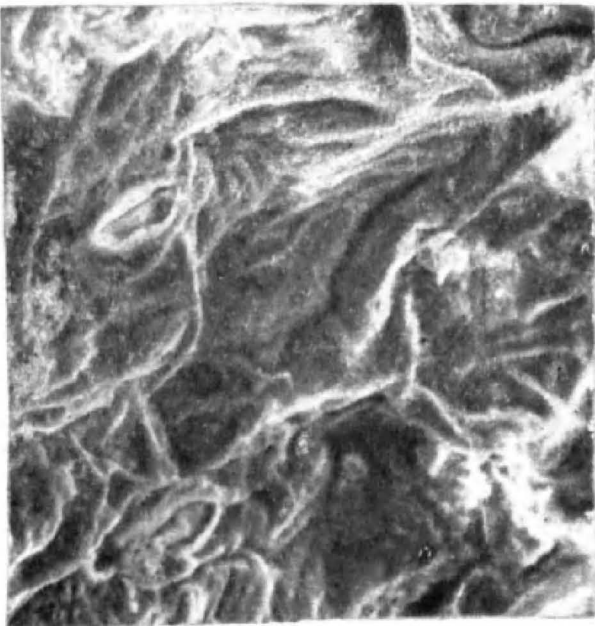
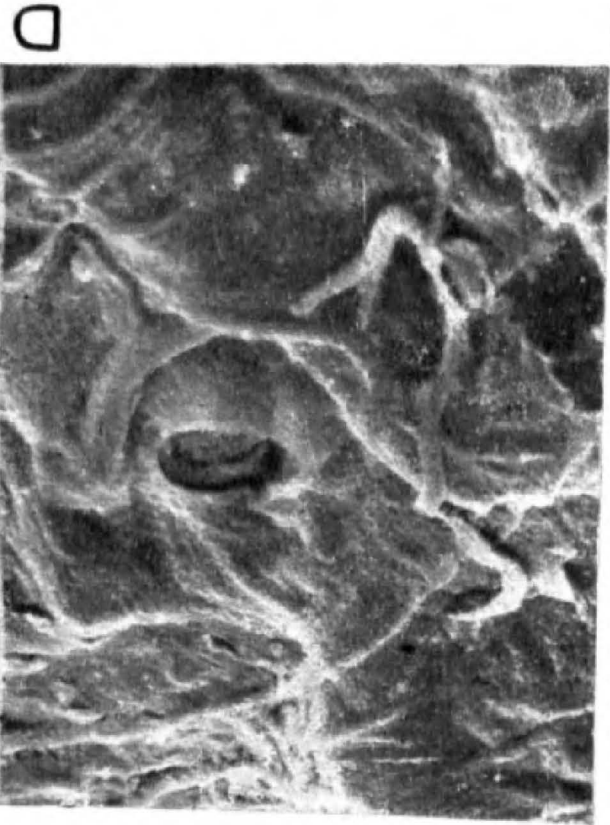
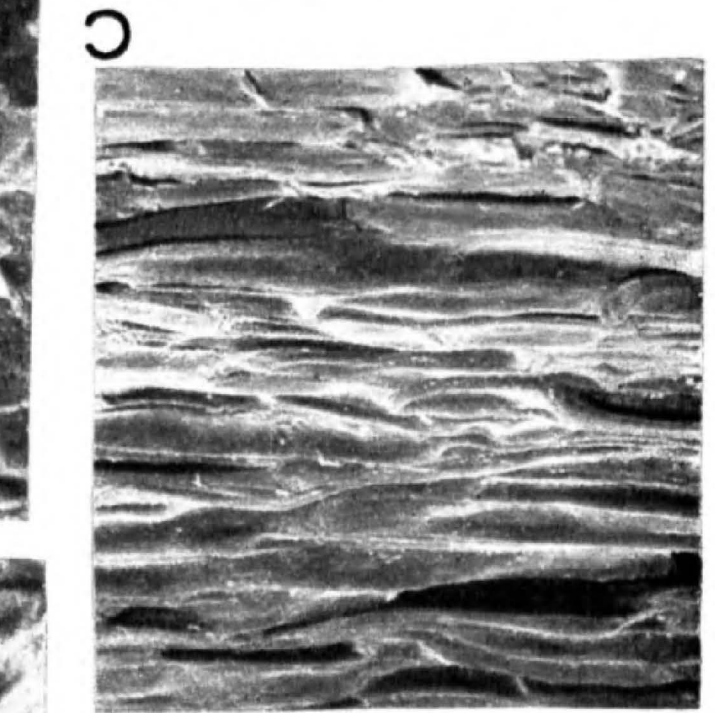
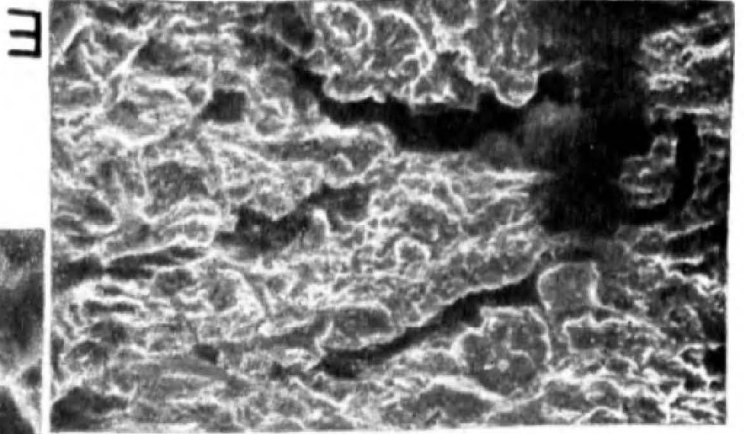


Plate 1 (A-F) : Legend at the end of the article

Plate 2 (A-E) : Legend at the end of the article



A

B

E

D

formis differ from each other in the development of their cortex vis-a-vis the xylem tissues, parenchymatous pith with or without central collenchyma, outline of the stem and of epidermal cells, as set out in the indented 'KEY'.

Rotala ramosior, restricted to the New World, and one of the two species of subsect. *Borykiniopsis*, may be distinguished from all other species of the sect. *Enantirotala* by its low cortex : xylem ratio (0.774 : 1), absence of primary phloem fibres, collenchymatous

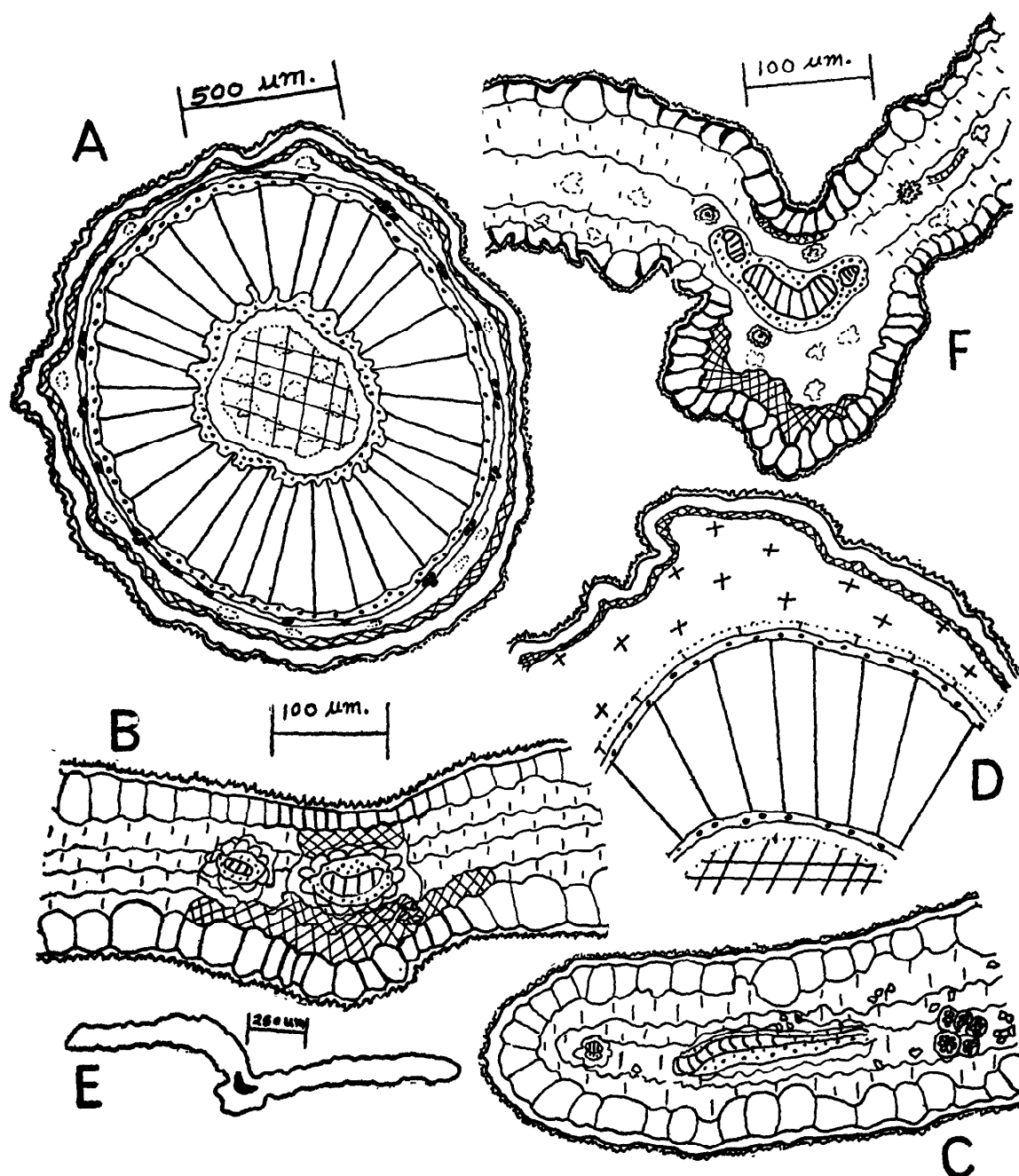
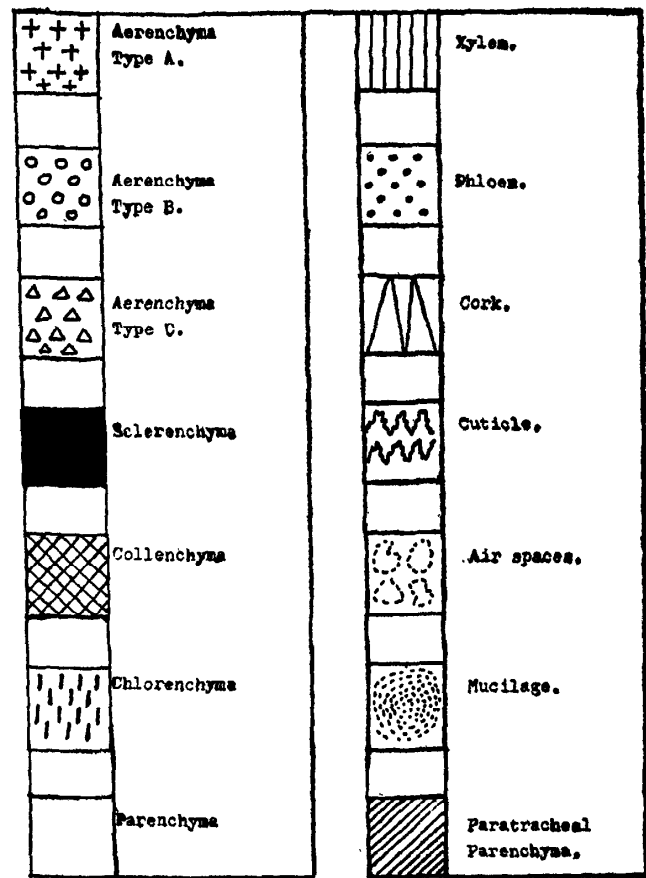


Fig. 3 (A-F) : Legend at the end of the article

pith without air spaces, but mesophyll and bundle sheath with air spaces, papillae many and solitary mucilaginous cells in the epidermis of the leaf.

Rotala serpyllifolia, assigned to subsect. *Mirkooa*, is characterised by racemose inflorescence, as opposed to the cymose or axillary, solitary flowers characteristic of subsect. 6 *Sellowia* and of subsect. 7 *Suffreniopsis*. Anatomically, *R. serpyllifolia* also stands out within the genus *Rotala* L. by the cortex/xylem ratio (0.312 : 1), cortex with a narrow band of irregularly air spaces, presence of primary phloem fibres, and air spaces in the collenchymatous pith, presence of 3-4 mucilage cells in groups, and an unusual cuticular pattern with shallow mounds with reticulate configuration.

To sum up, the species included in the Sect. *Enantirotala*, with the exception of *R. ramosior*, from a natural group, anatomically as well, and are easily set apart from the species of the Sect. *Hippuridium*.



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LEGEND OF THE FIGURES/PLATES

Fig. 1 (A-E.) : A. *Rotala myriophylloides* Welw. ex Hiern : T. S. stem showing reduced vascular tissue and large cortex. B. *Rotala serpiculoides* Welw. ex. Hiern : T. S. stem hypodermis parenchymatous ; aerenchyma of type 'A', cortex : xylem ratio more than 1 ; pith with druses and air spaces. C. *R. serpiculoides* Welw. ex Hiern : T. S. leaf showing pronounced midrib with collenchymatous tissue both on the abaxial and adaxial sides ; phloem surrounding the reduced arch-shaped vascular bundle and druses in the mesophyll of the isobilateral leaf. D. *Rotala verticillaris* L. T. S. isobilateral leaf showing reduced vascular tissue surrounded by phloem and a parenchymatous bundle sheath and few druses. E. *R. verticillaris* : T. S. leaf showing leaf-margin with vascular bundles of the veins ; some epidermal cells transversely divided and stomata and a thick cuticle.

Fig. 2 (A-I) : A. *Rotala diandra* (F. v. Muell.) Koehne : T. S. stem showing collenchymatous tissue in the angular projections ; phloem surrounding the xylem tissue both externally and internally ; collenchymatous pith with stone cells, druses and air spaces. B. *Rotala diandra* : T. S. leaf (isobilateral) with hypodermal collenchymatous tissue on both abaxial and adaxial sides of the midrib and druses scattered. C. *Rotala tenella* (Guill. et Perr.) Hiern : T. S. Stem more or less rectangular ; cortex about seven times as broad as the xylem tissue ; pith parenchymatous and with a few druses ; a layer of druses surround the vascular tissues. D. *R. tenella* : T. S. Leaf-midrib with hypodermal collenchyma on both sides and parenchymatous bundle sheath surrounding the concentric vascular bundle. E. *R. tenella* : T. S. leaf lamina with reduced vascular bundle of the vein ; isobilateral leaf. F. *R. myriophylloides* : T. S. Leaf showing isobilateral nature and abundant air spaces and reduced leaf-midrib. G. *R. filiformis* (Bellardi) Hiern : Leaf-outline and H. showing the T. S. leaf-midrib with hypodermal collenchyma on both the abaxial and adaxial sides and isobilateral leaf. I. Showing enlarged view of the leaf lamina.

Plate 1 (A-F) : A. *Rotala rosea* (Poir.) C. D. K. Cook. T. S. stem showing hypodermal collenchyma, two layers of squarish air spaces ; pith collenchyma with air spaces. ($\times 500$) ; B. *Rotala filiformis* (Bellardi) Hiern (*R. congolensis* Fernandes & Diniz) T. S. Stem (a sector) showing 2 or 3 layers of polygonal air spaces and reduced xylem tissue ($\times 500$). C. *Rotala mexicana* Chamm. & Schlecht. : T. S. stem showing pronounced development of xylem tissue, 1-2 layers of polygonal air spaces and hollow pith and a distinct endodermis ($\times 125$). D. *Rotala verticillaris* L. T. S. leaf with periclinal division of some cells of the upper epidermis, midrib hypodermis parenchymatous, parenchymatous bundle sheath and nearly isobilateral leaf ($\times 500$). E. *Rotala diandra* (F. v. Muell.) Koehne : T. S. leaf-margin with collenchymatous tissue ($\times 500$). F. *Rotala serpyllifolia* (Roxb.) Brem. : T. S. leaf isobilateral nature, group of mucilage cells, stomata and parenchymatous bundle sheath ($\times 500$).

Plate 2 (A-E) : (S. E. M. of the leaf surface to show the epidermis and cuticular ornamentation and stomatal ledges etc.). A. *Rotala mexicana* : Cuticular pattern- smooth with very broad shallow bands and a few elevated stomata ($\times 1,000$). B. *Rotala diandra* : Cuticular pattern ridged and furrowed ; ridges of uneven thickness and irregular folds with smooth areas in between ($\times 1,000$). C. *Rotala myriophylloides* : Cuticular pattern smooth with horizontal oriented striations and with boat-shaped depressed stomata ($\times 1,000$). D. *Rotala serpyllifolia* : Cuticular pattern of mounds, irregularly-shaped and spirally arranged cuticular layers and a sunken stoma with overarching edges of the cuticular ramparts ($\times 1,000$). E. *Rotala verticillaris* : Cuticular pattern of very short flakes overlying on one another and with both elevated and depressed stomata ($\times 1,000$).

Fig. 3 (A-F) : A. *Rotala serpyllifolia* (Roth) Brem. : T. S. stem showing a pronounced collenchymatous layer of hypodermis ; large xylem tissue and primary phloem fibres and pith collenchymatous with air spaces in between. B. *Rotala serpyllifolia* : T. S. Leaf with hypodermal collenchyma on both the abaxial and adaxial sides, parenchymatous bundle sheath, a few druses and highly developed papillae on the epidermal tissue. C. *R. serpyllifolia* T. S. Leaf showing the marginal end a part of lamina with abundant druses and isobilateral nature. D. *Rotala ramosior* (L.) Koehne : T. S. stem (one sector) with a ring of hypodermal collenchyma, aerenchyma of type 'A' and collenchymatous pith. E. *R. ramosior* : Leaf in out-line, and F. T. S. leaf-midrib region showing pronounced projection on the dorsal surface, hypodermal collenchyma more developed on the projected side ; druses and air spaces.