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**Original Research**

# Can Integrating Morphology and Anatomy Contribute to Species Identification of *Salacia oblonga* Wall. and *S. reticulata* Wight in family Celestraceae?

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## ABSTRACT

***Purpose:*** *Due to the overexploitation of Salacia oblonga and S. reticulata, natural populations have declined and become near threatened. Limited information is available on these species for correct identification and variability. Correct identification and variability are crucial for conservation purposes. Therefore, morphological and anatomical studies were carried out on these two species to identify and reveal their variability.*

***Research Method:*** *A detailed vegetative (leaves, stem, root), fruit morphology and anatomical study of leaf, petiole, stem, and root using light microscopy and Scanning Electron Microscopy was undertaken to identify reliable, diagnostic features to differentiate the two species and study the diversity of these species correctly.*

***Findings and Values:*** *The key takeaways are leaf arrangement, leaf margin, natural colour of the stem, presence or absence of lenticels, external root colour, shape and colour of the mature and ripe fruits, and number of locules and ovules, which are critical vegetative and fruit morphological characters in field identification, distinguishing the species. The shape and wing extensions in the petiole, arrangement of the invaginated ends of the vascular bundle of the petiole and midrib, deposition of cuticular materials around stomata on the abaxial leaf surface, and shape of the stomata complex were important traits for taxonomic purposes. Using identified important morphological and anatomical characteristics, which are useful for identification in the field, a dichotomous key was constructed to separate the two species.*

**Keywords:** *Anatomy, Diagnostic features, Light microscopy, Salacia, SEM, Sri Lanka*

## INTRODUCTION

The principally pantropical family, Celastraceae R. Br., (Angiosperm Phylogeny Group 2016) consists of 98 genera with 1264 species of herbs, woody lianas, shrubs, and trees (Savinov 2006, Gomes & Lombardi 2010, Chinh *et al.* 2016). In Sri Lanka, this family comprises 12 genera and 23 species (Senaratna 2001). One of the most medicinally important genera in this family in Sri Lanka is *Salacia* (subfamily *Salacioideae*) with five species, namely *Salacia acuminatissima* Kosterm., *S. chinensis* L., *S. diandra* Thw., *S. oblonga* Wall. ex Wight (Himbutu) and Arn., and *S. reticulata* Wight (Kothala himbutu) (Senevirathne *et al.* 2019).

The geographic distribution and conservation status of all species of *Salacia* in Sri Lanka have been extensively documented (Senevirathne *et al.* 2019). There is a risk of extinction of these valuable germplasms; *S. acuminatissima* and

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*S. chinensis* are endangered (EN) and near threatened (NT) respectively, and *S. diandra* is a critically endangered (CE) species. *S. oblonga* and *S. reticulata* are near threatened (NT) (Senevirathne *et al.* 2019). Moreover, these species are restricted to a few forests and are rare.

*Salacia oblonga* and *S. reticulata* are widely used for the treatment of diabetic patients in Ayurveda medicine and are the focus of studies for diabetic management worldwide (Pushpakumara *et al.* 2002, Ratnasooriya *et al.* 2003, Collene *et al.* 2005, Flammang 2006, Jennifer *et al.* 2007, Chhetri *et al.* 2008, Arunakumara & Subasinghe 2010, Sekiguchi *et al.* 2010, Basu *et al.* 2013, Harinarayanan *et al.* 2017). *S. oblonga* and *S. reticulata* are terrestrial, woody, erect shrubs that appear similar (Figs. 1A - 1D). Identification and differentiation of *S. oblonga* and *S. reticulata* from each other, in the absence of flowering and fruiting materials, is difficult.

Vegetative and floral morphology of different genera in the family Celastraceae has been studied, for example, *Elaeodendron* (Mennega 1983, Archer & van Wyk 1998), *Maytenus* (Gosline & Cheek 2014), *Salacia* (Groppo *et al.* 2014), *Euonymus* (Yao *et al.* 2018). The importance of anatomical characters for Celastraceae taxonomy was confirmed by Den Hartog & Bass 1978.

Anatomical characters are valuable for differentiating and identifying different species, for example, *Maytenus* (Giménez *et al.* 2014, Duarte & Debur 2005, Kumawat *et al.* 2016, Harinarayanan *et al.* 2017), *Kokoona* and *Lophopetalum* (Jansen & Baas 1973, Den Hartog & Baas 1978), subfamily *Salacioideae* (Gomes & Lombardi 2010). The anatomy of the petiole of different species in the family (Jansen & Baas 1973, Gomes & Lombardi 2010), leaf (Gomes & Lombardi 2010), stem (Mohamad *et al.* 2013) and root (Gomes & Lombardi 2010) has been investigated.

Considering the value of vegetative and fruit morphological and anatomical characters for species differentiation in the family Celastraceae, the objectives of this research were to (a) Examine and describe the morphological and anatomical characteristics of fruits, leaves, the stem and roots of *S. reticulata* and *S. oblonga*, (b) Determine whether morphological and anatomical characters can be used to accurately identify and differentiate *S. reticulata* and *S. oblonga* in the absence of flowers and construct a key to identify species.

## MATERIALS AND METHODS

### *Sampling and fixation*

Leaf, stem, root, and fruit materials of *S. oblonga* and *S. reticulata* were collected from the National Research Medicinal Plant Garden in Haldummulla, Sri Lanka (6.7612° N, 80.9014° E). Populations of both species occur allopatrically and are separated from each other by more than 500 meters. Identification of specimens was confirmed by the late Prof. Piyal Marasinghe, former Director of the National Research Medicinal Plant Garden, Haldummulla, Sri Lanka. All the prepared herbarium specimens were deposited at the Department of Botany herbarium, University of Ruhuna.

For anatomical study, three leaf samples, stem, root and fruit materials were taken randomly from healthy individuals for each species. To ensure and avoid the effect of light conditions on field specimens, leaves were sampled only from sun-exposed branches of healthy individuals (Martin *et al.* 2020). Materials for anatomical study (leaves, stems, and roots) were fixed in FAA (Formaldehyde, Ethanol, Acetic Acid in 10% 50% 5% + 35% water) for 24–48 hrs (depending upon the thickness) and subsequently stored in 70% ethanol.

### *Leaf clearing, sectioning, staining and light microscopy (LM)*

Approximately 2 × 2 cm pieces of the leaf blade, excluding the midrib, were used for leaf clearings. The samples were immersed in 10% potassium hydroxide overnight, transferred to fresh potassium hydroxide solution, and kept at room temperature. This was repeated

until samples became decolourized, after which they were washed thoroughly with deionized water, and treated with bleach (7% sodium hypochlorite). Cleared leaf samples were stained with 1% safranin to see stomata and epidermal cells. Freehand sections of the stem, roots, and leaves were taken. Histochemical tests were performed on transverse sections of leaves, roots, and stems, and radial and tangential sections of roots and stems. The slides were stained with Toluidine blue (TBO), and safranin and were observed using a Nikon Eclipse 50i compound microscope, and images were captured using Nikon NIS-Elements imaging software (Nikon Instruments Inc., Amsterdam, Netherlands).

### *Scanning electron microscopy (SEM)*

SEM (Tousimis, Rockville, USA) was used to study the surface micromorphology of leaves and anatomical features in roots and stems. Leaf samples (1 × 1 cm) and radial, tangential, and transverse freehand sections of root and stem materials were dehydrated in an alcohol series and then critical point dried with $CO_2$, at a critical point of approximately 35°C, around 1,200 psi (Anderson 1951). Samples were mounted on stubs with self-adhesive double-sided carbon discs. Leaf samples were mounted to observe abaxial and adaxial surfaces, sputter-coated with gold-palladium for 70s using a Leica EM SCD005 Gold Coater. Examination and documentation of images were conducted using an FEI Quanta 200 SEM/ESEM (FEI, Hillsboro, Oregon, USA) or a TM 3000 Hitachi TM-3000 Tabletop operated at 10 kV.

## RESULTS AND DISCUSSION

This study was carried out to determine whether *S. oblonga* and *S. reticulata* can be differentiated based on the morphological characters of fruits and vegetative morphological and anatomical features of leaves, stems and roots. Structural (morphology, anatomy and micromorphology – Table 1) aspects for different parts are presented. Observations alongside what has been reported previously in the literature as a combined result and discussion section are explained to avoid unnecessary repetition of information.

### *Leaf morphological features*

Both species have simple, opposite leaves. Leaf arrangement was usually distichous (opposite in one plane) in *S. oblonga* (Figs. 1A, 1B, Table 1) and decussate (opposite in two planes) in *S. reticulata* (Fig. 1C). The leaf margin in *S. oblonga* was usually entire (Figs. 1A, 1B), whilst sparsely spiny teeth were frequently observed along the leaf margin in *S. reticulata* (Figs. 1C, 1D). The leaf base was symmetrical in both species. In this study, observations showed that there is variation in leaf shape (*ovate*, *oblong*, *elliptical*) and leaf margin (*smooth to dentate*) within the same species (*S. reticulata* – Figs. 1C–1D). *Ovate* or *ovate-lanceolate*-shaped leaves have been described for *S. oblonga* in India (Harinarayanan *et al.* 2017), *elliptic*, *oblong*, or *obovate*, *entire*, or *serrate* (slightly toothed), with an *acute* or *rounded* apex, leaves of *S. kraussii* in South Africa (*Kisepa et al.* 2024).

The midrib was distinct externally in both species, with wing extensions and without extensions (Figs. 1A–1D). As there were leaf morphological variations within the species, leaf morphology alone may not be a reliable source of characters for species differentiation. However, combining leaf arrangement and leaf margin, in combination with other anatomical and morphological features (see below), can enhance the accuracy of species differentiation.

### *Fruit morphology*

There were clear distinctions in the morphology of fruits (Figs. 1E–1H, Table 1). Both species have *globose*, *baccate*, and *indehiscent* fruits with a mucilaginous edible pulp. The surface of the fruits of *S. oblonga* had constrictions (Fig. 1E, arrowhead) and a rough texture, while those of *S. reticulata* had a smooth fruit surface and had a neck (*pot shape* Figs. 1F, 1H, arrowhead) and were glossy in appearance (Figs. 1F and 1H). Immature fruits were green in both species and became orange-red in *S. oblonga* (Fig. 1G) and red in *S. reticulata* (Fig. 1H) when ripe. The surface texture and shape of the fruit had significant differences between the two species; fruits of *S. oblonga* have a rough texture with


**Figure 1: Morphological characters of *Salacia* species.** (A) Oppositely arranged, ovate leaves (opposite distichous) with obtuse leaf apex; (B) oppositely arranged, oblong leaves with acute leaf apex; (C) oppositely arranged, elliptical leaves (opposite distichous) with obtuse apex, dentate margin; (D) oppositely arranged, oblong leaves with acute leaf apex/obtuse, dentate margin; (E) globose fruit with constrictions (arrow points to constrictions in fruits); (F) red fruit, rounded base with a narrow neck; (G) orange-red ripe fruits; (H) dark red ripe fruits with a neck (arrow points to the neck of the fruit); (I) two-locular fruits; (J) one-seeded fruit; (K) ash-coloured bark with lenticels; (L) closer view of lenticels; (M) white-coloured bark; (N) orange-coloured roots; (O) yellow-coloured roots. Abbreviations used: So – *S. oblonga*; Sr – *S. reticulata*.

constrictions, while *S. reticulata* fruits have smooth and glossy surfaces, with a notable neck, making them distinguishable.

Two locules, with one ovule per locule, were observed in *S. oblonga* (Fig. 1I), whilst a single locule, with one ovule, was observed in *S. reticulata* in all fruit samples studied (Fig. 1J). Generally, Celastraceae are known to have red-orange coloured, indehiscent fruits with an edible pulp, few seeds and usually more than two ovules per locule (Simmons & Hedin 1999, Groppo *et al.* 2014, Kisepa *et al.* 2024). Single-seeded fruit has been observed in *Salacia chinensis* (Harinarayanan *et al.* 2017). However, more than five seeds have been observed from South Africa from *S. kraussii* (Kisepa *et al.* 2024).

Therefore, the number and arrangement of locules and ovules provide clear internal structural differences: *S. oblonga* has two locules, each containing a single ovule; *S. reticulata* has a single locule with one ovule. Fruit shape and number of locules could be used to distinguish *S. reticulata* from *S. oblonga*.

Both species exhibit different fruit colouration upon ripening. *S. oblonga* shifts to an orange-

red colour while *S. reticulata* becomes red when ripe. The locules, locule number and arrangement of ovules can be considered key internal structural features that can help identify and differentiate the species.

According to the results and previous results, fruits are generally indehiscent with mucilaginous edible pulp and typically have red-orange-coloured ripe fruits with few seeds and more than two ovules per locule in the family Celastraceae. Therefore, the number of ovules, the number of locules, and the arrangement of ovules are key internal structural features that can be used to identify and differentiate between species.

Although both species share common traits with other members of the Celastraceae family, their fruit morphology, such as indehiscent fruits with mucilaginous pulp, reliable fruit morphological markers such as distinctiveness in fruit surface texture (*smooth* and *rough*), shape, and internal locule structure structures offers distinguishing *S. oblonga* and *S. reticulata* from other Celastraceae species (Nandikar 2021).

***Stem and root morphology***

A clear difference in the colour of the stem of the two species of *Salacia* was observed (Table 1, Figs. 4G–4L). The bark of *S. oblonga* was grey and lenticellate (Figs. 1K, 1L), whereas the bark of *S. reticulata* was white and without lenticels (Fig. 1M). Lenticellate stems with greyish to brownish bark have been recorded for the family (Archer & van Wyk 1998, Groppo *et al.* 2014).

A hard, orange inner bark and a rough, cracked outer bark have been observed in *Goupia glabra* (Celastraceae) (Carmo *et al.* 2016). Therefore, the grey lenticellate bark in *S. oblonga* versus the white bark without lenticels in *S. reticulata* provides a clear and practical distinguishing feature. Lenticellate bark is common within this family, and the white bark without lenticels in *S. reticulata* indicates a unique characteristic of this species.

**Table 1. Comparison of gross morphological characters of the two *Salacia* species (*S. oblonga* and *S. reticulata*) examined in this study, regarding the relevant figure number.** *Reliable diagnostic features that can be used to differentiate the two species.

| Characters | *S. oblonga* | Fig. No. | *S. reticulata* | Fig. No. |
|---|---|---|---|---|
| Leaves | | | | |
| *Arrangement | Opposite, distichous | 1A, 1B | Opposite, decussate | 1C, 1D |
| Apex | Obtuse, shortly acuminate | 1A, 1B | Obtuse, flat | 1C, 1D |
| Base | Acute | 1B | Acute | 1D |
| Shape | Ovate, oblong, ob-lanceolate | 1A, 1B | Oval, broadly elliptic, oblong | 1C, 1D |
| *Margin | Entire, smooth | 1A, 1B | Toothed | 1C, 1D |
| Fruits | | | | |
| Type | Baccate | 1E | Baccate | 1F |
| *Shape | Globose, without a prominent constriction | 1E, 1G | Globose with a narrow neck | 1F, 1H |
| *Colour when ripe | Orange-yellowish, edible pulp | 1G | Red, edible pulp | 1H |
| *No. of locules | Two | 1I | One | 1J |
| No. of seeds per locule | One | 1I | One | 1J |

| Characters | *S. oblonga* | Fig. No. | *S. reticulata* | Fig. No. |
|---|---|---|---|---|
| Stems | | | | |
| *Bark colour | Grey | 1K | White | 1M |
| *Lenticels | Prominent | 1L | Not obvious | 1M |
| Roots | | | | |
| *Colour | Orange | 1N | Yellow | 1O |
| Petiole | | | | |
| Shape | Oval | 2A | Roundish-to-semicircular | 2B |
| *Ridges on adaxial surface | Flattened or grooved, not prominent | 2A | Ridged, prominent | 2B |
| *Wing extension | Not noticeable | 2A | Noticeable/prominent | 2B |
| Sclerenchyma sheath | Noticeable/incomplete | 2C | Noticeable/incomplete | 2D |
| *Vascular bundle | U-shaped arc; invaginated ends towards middle with wide opening | 2A, 2C | C-shaped arc with convolute extremities and small opening | 2B, 2D |
| Lamina | | | | |
| *Vascular bundle | Irregular-shaped vascular system, open arc, invaginated ends towards base with narrow opening | 2E, 3A | V or reduced arc-shaped vascular system, no invagination, no narrow opening | 2F, 3B |
| Phloem | Continuous around xylem | 2E, 3A | Continuous around xylem | 2F, 3B |
| Epidermal pavement cells (adaxial) | | | | |
| Shape | Mostly round | 3C | Mostly irregular (round, elongated) | 3D |
| Epidermal pavement cells (abaxial) | | | | |
| Shape | Mostly sinuous | 3E | Mostly irregular (round, elongated) | 3F |
| Cuticular wax deposition (adaxial) | | | | |
| Pattern | Irregularly distributed cuticle materials | 3G | Irregularly arranged cuticle materials | 3H |
| Cuticular wax deposition (abaxial) | | | | |
| *Pattern | Rough, irregularly arranged | 3I | Smooth, arranged as blocks | 3J |
| Cuticular wax deposition around stomata | | | | |
| *Pattern | Irregularly deposited, crust-like appearance | 3I | Clearly arranged in blocks | 3J |
| Stomatal shape | | | | |
| *Shape | Circular or irregular anomocytic | 3D, 3I | Elliptical, anomocytic | 3F, 3J |

| Characters | *S. oblonga* | Fig. No. | *S. reticulata* | Fig. No. |
|---|---|---|---|---|
| Root | | | | |
| Periderm | Thick periderm outermost layer | 4A, 4B | Thick periderm outermost layer | 4D |
| Cortex | Dark brown coloured compounds (phenolic) in parenchyma cells | 4A, 4B | Light coloured compounds (phenolic) in parenchyma cells | 4D, 4E |
| Vessels | Arranged radially, single or rarely aggregated vessels, diffuse porous vessels and radial parenchyma | 4C | Arranged radially, single or rarely aggregated vessels, filled with light yellow phenolic compounds | 4F |
| Stem | | | | |
| Ground parenchyma | Dark brown colour phenolic compound deposits | 4H, 4I | Dark yellow colour phenolic compound deposits | 4J, 4K |
| Vessels | Solitary, rarely in groups of 2 to 3, diffuse-porous, slightly elliptical/slightly oblique to angular/oval in cross-section | 4I | Solitary, diffuse-porous, slightly elliptical/slightly oblique to angular/oval in cross-section | 4J |
| Primary xylem details | Vessels solitary and rarely in groups of 2 to 3 | 4G, 4I | Vessels solitary | 4J |
| Secondary xylem details | Vessels diffuse-porous and frequently slightly elliptical/slightly oblique to angular/oval in cross-section | 4I | Vessels diffuse-porous and slightly oblique to angular/oval in cross-section | 4J |

The roots of *S. oblonga* were an intense orange (Fig. 1N), whilst those of *S. reticulata* were yellow and easily visible to the naked eye (Fig. 1O). Dark-to-light yellow, yellowish-brown, and pale-yellow external root colours have been observed in *S. chinensis*, *S. fruticosa* and *S. oblonga* respectively (Harinarayanan *et al.* 2017), making our observation of intense orange colour in *S. oblonga* a departure from what has been previously reported for this species. This intense colouration might be due to specific environmental factors and/or genetic variations, or could indicate a distinct subpopulation or ecotype within the species. The intense orange coloration of *S. oblonga* roots compared to the yellow roots of *S. reticulata* can serve as a reliable characteristic, especially when combined with other morphological features. In the field, the contrasting bark colours and textures (grey lenticellate for *S. oblonga* versus white without lenticels for *S. reticulata*) offer an immediate and practical way to distinguish these species.

### *Petiole anatomy and micromorphology*

In transverse section, the petiole was oval in *S. oblonga* (Fig. 2A) and roundish-to-semicircular in *S. reticulata* (Fig. 2B). On the adaxial leaf surface above the vascular region, a slightly flattened or grooved area was observed in *S.*

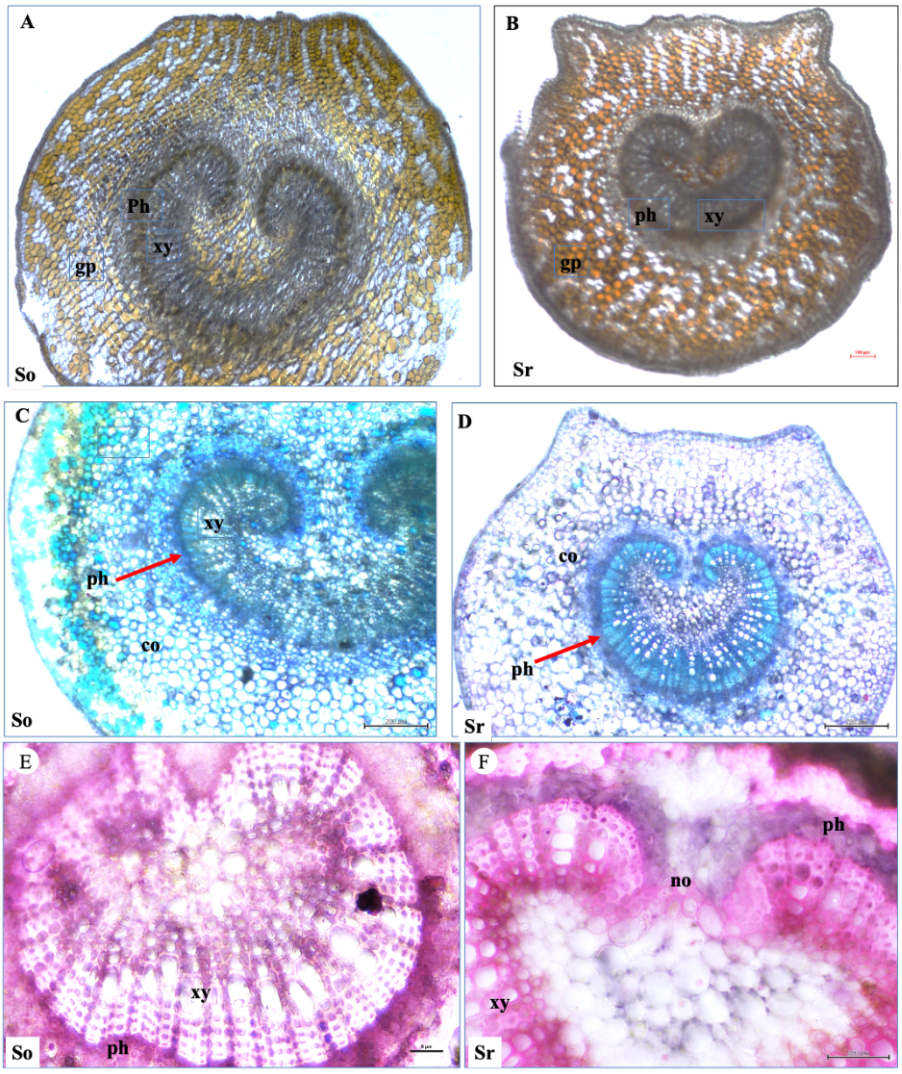



**Figure 2: Light micrographs of cross-sections through the vascular system of the petioles and leaf midrib of *S. oblonga* and *S. reticulata*.** (A) *S. oblonga*, oval shape contour, no winged extension but flat, slightly irregular on the upper surface of the petiole without staining shows the yellow colour pigments; (B) *S. oblonga* round shape contour with winged extension, flat, slightly irregular on the upper surface of the petiole, an open oval vascular system with clear convolute extremities, without staining shows the red/dark brown colour pigments; (C) *S. oblonga*, secondary compound bluish-green staining reaction with Toluidine Blue O (TBO) in almost throughout the ground parenchyma cells; (D) *S. reticulata*, secondary compound bluish-green staining reaction with TBO mainly around the xylem; (E) transverse section along the midrib of the leaf of *S. oblonga* stained with safranin, irregular shape vascular system, convolute extremities towards the base of the leaf and wide opening of the vascular system; (F) transverse section along the midrib of the leaf of *S. reticulata* stained with safranin, open V shape vascular system, neither invaginate ends towards the base of the leaf nor wide opening vascular system. Abbreviations used: So – *S. oblonga*; Sr – *S. reticulata*. Sub-Fig. letters, co – collenchyma; gp – ground parenchyma; no – narrow opening; ph – phloem; scl – sclerenchyma sheath; xy – xylem; wo – wide opening. Scale bar – 100 µm.

*oblonga*, whereas prominent ridges were seen in *S. reticulata* (Fig. 2B) in all samples examined.

*S. reticulata* possessed noticeable wing extensions toward the lamina, while no clear extensions were seen in *S. oblonga*.

### *Petiole anatomy and micromorphology*

Anatomical characteristics of the petiole were more or less similar in different regions of the petiole (base, middle, or apex) in both species (Figs. 2A, 2B). The oval shape of the petiole in *S. oblonga* contrasts with the roundish-to-

semicircular shape in *S. reticulata*, providing a clear morphological marker. The flattened or grooved adaxial surface in *S. oblonga* and the prominent ridges in *S. reticulata* above the vascular region are distinctive features that can aid in species differentiation. The presence of wing extensions in *S. reticulata* versus their absence in *S. oblonga* was another notable distinguishing feature (Table 1).

The epidermis in both species was typically one-layered (uniseriate) with rectangular or irregularly shaped cells. Beneath the epidermis, multiple layers of loosely arranged ground parenchyma were observed, rich in idioblasts that contained phenolic compounds. These compounds were stained with Toluidine blue, as shown in Figsures 2C and 2D. The vascular bundles were collateral and enclosed by a discontinuous sclerenchyma sheath in both species, but with differences in the median region (Figs. 2C, 2D). The vascular bundle was a U-shaped arc with clear invaginated ends in *S. oblonga* (Figs. 2A, 2C), whilst it was an oval-shaped arc with convolute extremities in *S. reticulata* (Figs. 2B, 2D). The U-shaped arc with invaginated ends in *S. oblonga* and the oval-shaped arc with convolute extremities in *S. reticulata* highlight differences in vascular structure. These configurations can be crucial for microscopic identification.

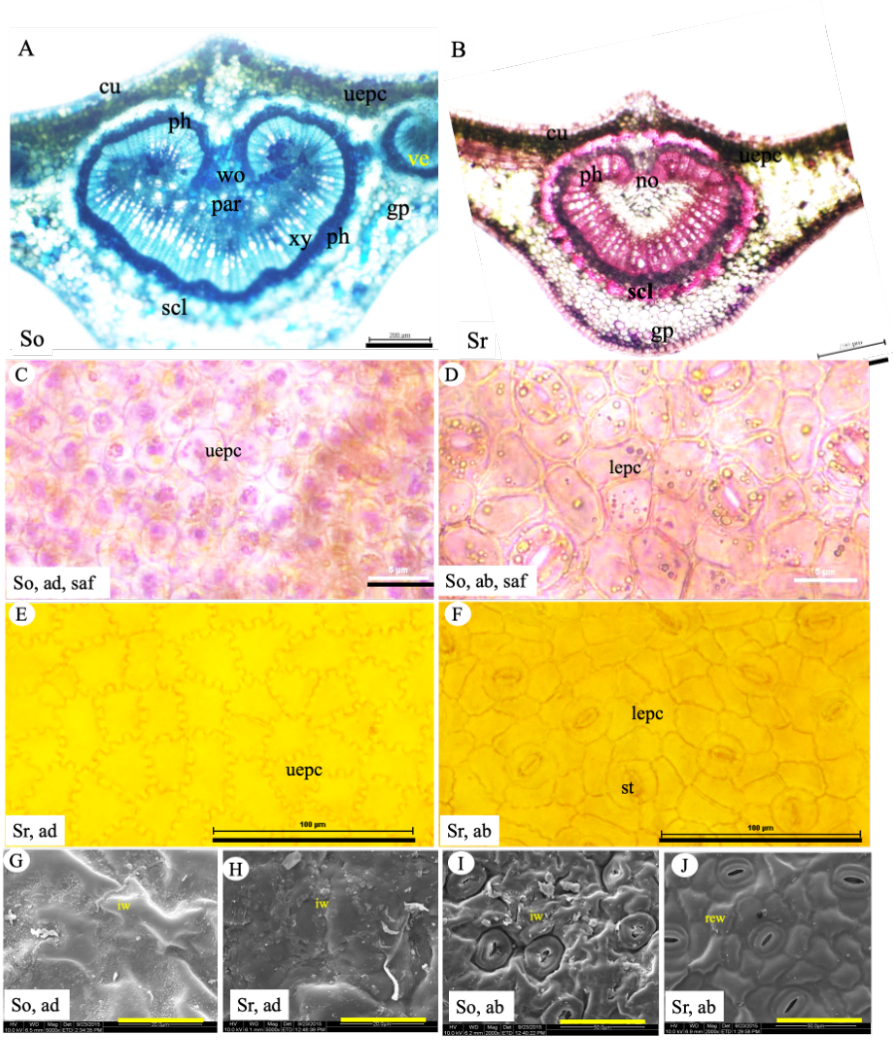
Radial rows of xylem cells were visible in both species (Figs. 2C–2D). Phloem tissue formed a continuous layer outside the xylem, but individual cells were not conspicuous. An incomplete sclerenchymatous sheath, with solitary or clustered sclereids and phenolic compounds in the petiole, has been reported in *Maytenus*, *Cheiloclinium*, *Peritassa* and *Tontelea* (Duarte & Debur 2005, Gomes & Lombardi 2010).

***Lamina anatomy and micromorphology***

Similarities and differences in anatomical and micromorphological structures of the two species of *Salacia* are summarised in Table 1. The midrib was raised on the adaxial leaf surface and prominently convex on the abaxial surface (Figs. 3A, 3B). The midrib occupies a large area of the lamina and is different in shape in the two species. It was irregular in outline, with invaginated ends of the vascular bundle in *S. oblonga* (Figs. 2E, 3A) and V-shaped or reduced arc-shaped in *S. reticulata* (Figs. 2F, 3B). In both species, a very clear, continuous phloem was present around the outside of the xylem, and a discontinuous sheath of sclerenchyma cells was around the vascular bundle (Figs. 3A–3B). The lamina was well-differentiated into palisade and spongy parenchyma regions. Both species had two layers of palisade parenchyma cells. The spongy parenchyma comprised 6–8 layers of loosely arranged, round to polygonal cells with abundant intercellular spaces.

The outline of the epidermal cells differed between the two species on the adaxial surface (Fig. 3C, Fig. 3E) and the abaxial surface (Figs. 3D–3F). In *S. oblonga*, adaxial epidermal cell walls were mostly round (Fig. 3C) and abaxial epidermal cell walls were irregular/straight/slightly curved (Fig. 3D). In *S. reticulata*, adaxial epidermal cell walls were strongly sinuous (Fig. 3E) and abaxial epidermal cell walls were irregular/straight, slightly curved, or slightly sinuous (Fig. 3F). The epidermis was uniseriate and the varied cell wall outlines (irregular, straight, slightly curved in *S. oblonga* vs. slightly sinuous in *S. reticulata*) provide and indicate additional identifying features, clear micromorphological differences (Figs. 3C–3F).

A very few, unbranched, non-secretory, tiny trichomes were present on the abaxial surface of *S. oblonga*. These trichomes were curved at the end and formed a hook-like structure. The presence of hook-like trichomes in *S. oblonga* may play a role in defence against herbivory or aid in reducing water loss by trapping moisture. The absence of these trichomes in *S. reticulata* indicates a possible divergence in defence mechanisms or microenvironmental adaptations. Anatomical characteristics, such as venation, vascular bundles, collenchyma, and stomata, have been used to study the taxonomy of Celastraceae (Chinh *et al.* 2016). Den Hartog & Bass (1978) supported the expansion of Celastraceae based on stomatal types and crystals in the leaf epidermis. Similar characteristics, such as raised midrib, polygonal




**Figsure 3:Light microscopic (LM) and scanning electron microscopic (SEM) views of the leaf anatomy of *S. reticulata* and *S. oblonga*.** (A) transverse section along the midrib of the leaf of *S. reticulata* showing vascular arrangement; (B) transverse section along the midrib of the leaf of *S. oblonga* showing vascular arrangement; (C) LM view of adaxial leaf surface of *S. oblonga* after staining with safranin, highlighting upper epidermal pavement cells; (D) LM view of abaxial leaf surface of *S. oblonga* stained with safranin, showing lower epidermal pavement cells; (E) LM view of adaxial leaf blade surface of *S. reticulata*, unstained; (F) LM view of abaxial leaf blade surface of *S. reticulata*, unstained; (G) SEM view of adaxial leaf surface of *S. oblonga* showing wart-like wax deposits; (H) SEM view of adaxial leaf surface of *S. reticulata* showing irregularly arranged cuticle; (I) SEM view of abaxial leaf surface of *S. oblonga* showing irregularly arranged cuticle surrounding the stomata; (J) SEM view of abaxial leaf surface of *S. reticulata* showing regularly arranged cuticle surrounding the stomata. Abbreviations used: So – *S. oblonga*; Sr – *S. reticulata*; ab – abaxial; ad – adaxial; cu – cuticle; gp – ground parenchyma; lepc – lower epidermal pavement cells; iw – irregular wax deposits; no – narrow opening; par – parenchyma; ph – phloem; rew – regularly deposited wax; sb – satellite bundle; scl – sclerenchyma sheath; uepc – upper epidermal pavement cells; wo – wide opening; xy – xylem. Scale bars – 5 µm (C, D); 20 µm (G–J); 100 µm (E, F); 200 µm (A, B).

epidermal cells, dorsiventral mesophyll, and sclerenchymatous sheath, have been observed in *Maytenus ilicifolia*, but differences from our study species include the presence of five strata of palisade parenchyma and a biconvex midrib (Duarte & Debur 2005). The leaves of both *S. oblonga* and *S. reticulata* were hypo-stomatic with randomly distributed stomatal complexes located at the same level as the other epidermal cells (Fig. 3D, Fig. 3F) or partially hidden in crypts (Fig. 3I, Fig. 3J). Hypo-stomatic stomata have also been observed

in the genus *Putterlickia* (Celastraceae) (Jordaan & Wyk 1998). Whilst we did not observe adaxial stomata, they have been reported in some genera including *Anthodon*, *Apodostigma*, *Bhesa*, *Campylostemon*, *Denhamia*, *Hippocratea*, *Lophopetalum*, *Maytenus*, *Plenckia*, *Pristimera*, and *Siphonodon* (Den Hartog & Bass 1978). The stomatal complexes were circular or irregular in *S. oblonga* (Fig. 3D, Fig. 3J) and elliptical in *S. reticulata* (Fig. 3F, Fig. 3J). In the equatorial region, the stomatal complex was irregular in *S. oblonga* and narrow in *S. reticulata* (Fig. 3D, Fig. 3F). Stomatal complexes were anomocytic with four to six subsidiary cells (Fig. 3D, Fig. 3F, Fig. 3J). Cuticular reinforcement in the stoma region was observed in *S. oblonga* (Fig. 3I). A variety of stomatal complexes (e.g., anisocytic, anomocytic, cyclocytic, bi- and/or tricyclic, laterocytic, paracytic, parallelocytic, helicocytic) have been reported in some genera of Celastraceae (Den Hartog & Bass 1978).

***Leaf epicuticular waxes***

The cuticle was wavy and highly sinuous on both abaxial and adaxial surfaces in both species (Figs. 3G–J). The adaxial surface of both species was rich in irregularly deposited cuticular waxes that gave the leaf an irregular, rough, and rugged appearance (Figs. 3G–J). Differences in cutinized thickenings on the outer periclinal walls of the two species were observed on both abaxial and adaxial surfaces. On the abaxial surface, cuticular wax was irregularly distributed in *S. oblonga* (Fig. 3G), deposited as blocks, and in a regular pattern around the stomata in *S. reticulata* (Fig. 3J). The cuticular ornamentation and distribution patterns of the waxes serve as distinguishing features for species identification. These micromorphological characteristics provide valuable insights into taxonomic identification and ecological adaptations. The distinct patterning of cuticular wax in *S. reticulata*, especially around the stomata, may be an adaptation to optimize gas exchange and minimize water loss, while the irregular arrangement in *S. oblonga* could help protect the stomatal openings from excess water loss or pathogen entry. The adaxial surface of both species, rich in cuticular waxes, contributed to the irregular, rough, and rugged appearance of the leaf (Fig. 3G, Fig. 3J). This sinuous nature likely enhances flexibility and strength, protecting the leaf from damage and desiccation. The thick, rugged cuticle and wax deposits likely play significant roles in reducing water loss, shielding against UV radiation, and providing a barrier against pathogens. Variations in wax deposition patterns and cuticle structure between the two species suggest adaptations to different ecological niches. No comparable data were found for other *Salacia* species; however, the presence of a thick cuticle has been reported for *Maytenus* (Celastraceae) (Gomes & Lombardi 2010).

***Root anatomy***

No differences were observed in the root anatomy of the two study species (Figs. 4A–F). The outermost cork consisted of irregular-to-rectangular-shaped, thick-walled cork cells arranged in five to six compact layers. This robust, multi-layered cork likely protects the inner root tissues from mechanical injury, pathogens, and water loss. The irregular-to-rectangular shape of these cells may confer additional structural strength and flexibility. Uniseriate xylem rays were observed. Vessels were solitary, rarely in groups of two to three, and arranged radially in both species (Fig. 4C, Fig. 4F). This configuration might be an adaptation to optimize water uptake and minimize the risk of embolism (air bubble formation) within the vessels. The solitary and radial arrangement of vessels is typical of many woody plants and contributes to efficient transport of water and nutrients from the root to the rest of the plant. The presence of annual rings in the xylem was observable but not distinct (Fig. 4C, Fig. 4F). Even if not distinct, this suggests some level of growth periodicity, likely influenced by environmental factors such as seasonal changes. However, the lack of distinctness might indicate a less pronounced variation in growth rates compared to other species that experience more distinct seasonal changes. Similar root anatomy has been observed in *Salacia macrophylla* (Mohamad *et al.* 2013), and a multi-storied suberized cork consisting of rectangular-shaped cells with highly thickened lower tangential walls has been observed in *S. chinensis* (Harinarayanan *et al.* 2017).

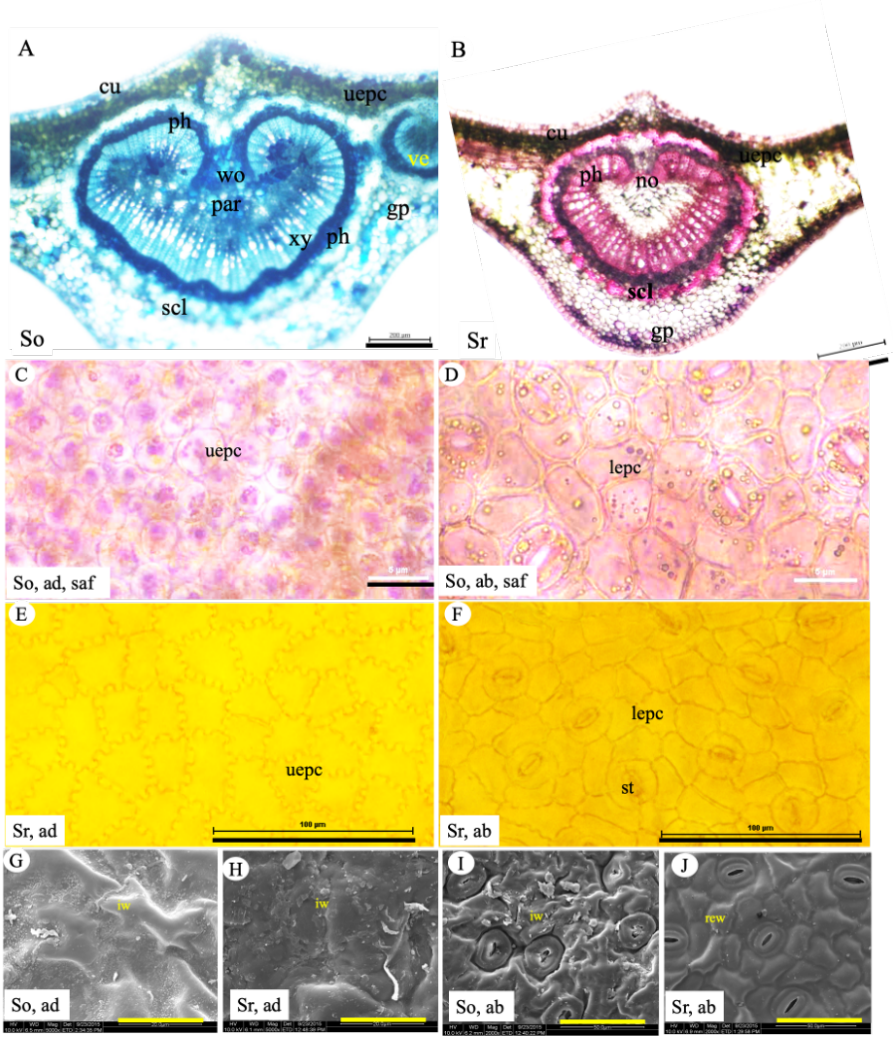



**Figure 4. Light microscopic (LM) view of root and stem anatomy of *Salacia* without staining.** (A) transverse section (TS) of root of *S. oblonga*; (B) TS of root of *S. oblonga* showing light-coloured idioblasts; (C) TS of root of *S. oblonga* showing uniseriate ray parenchyma and isolated vessels; (D) TS of root of *S. reticulata* overview; (E) TS of root of *S. reticulata* showing dark-coloured idioblasts; (F) TS of root of *S. reticulata* showing uniseriate ray parenchyma, isolated vessels, and vessel idioblasts; (G) TS of stem of *S. oblonga*; (H) TS of stem of *S. oblonga* showing light-coloured idioblasts; (I) TS of stem of *S. oblonga* showing uniseriate ray parenchyma, isolated vessels, and idioblasts of pith parenchyma cells; (J) TS of stem of *S. reticulata* overview; (K) TS of stem of *S. reticulata* showing light-coloured idioblasts; (L) TS of stem of *S. reticulata* showing uniseriate ray parenchyma and isolated vessels; (M) simple wall pitting and scalariform perforation plates of *S. oblonga*; (N) longitudinal section showing alternate thickenings in vessel elements in *S. reticulata*; (O) tracheid with scalariform thickenings of *S. oblonga*; (P) tangential longitudinal section (TLS) of *S. oblonga* revealing tracheid with spiral thickening. Abbreviations used: So – *S. oblonga*; Sr – *S. reticulata*; ab – abaxial; ad – adaxial; brp – biseriate ray parenchyma; id – idioblasts; urp – uniseriate ray parenchyma; v – vessels. Scale bars – 20 µm (O, P); 50 µm (M, N); 100 µm (A–L).

***Stem anatomy***

The stems of *S. oblonga* and *S. reticulata* were rectangular or circular in cross-section. A thick cuticle indicates adaptations for reducing water loss and protecting the stem from environmental stressors such as UV radiation, pathogens, and physical damage. A simple glabrous epidermis with a thick cuticle was observed (Figs. 4G, 4H, 4J, 4K). The cortical cells consisted of thin-walled parenchyma cells with dark-coloured phenolic deposits in both species. The vascular bundle consisted of phloem and xylem arranged as a closed cylinder traversed by narrow, uniseriate or biseriate rays (Fig. 4L).

Predominantly uniseriate rays were present in *S. oblonga* (Fig. 4I), but both uniseriate and biseriate rays were observed in *S. reticulata*. Both species primarily had solitary vessels, but vessels in groups of two or three were occasionally observed in *S. oblonga* (Fig. 4I).

Vessels were diffuse-porous and frequently slightly elliptical to slightly oblique, angular, or oval in cross-section (Figs. 4I, 4L). Simple perforation plates with a highly reduced border were exclusively scalariform (Fig. 4M). Inter-vessel pits were non-vestured. Simple vessel-ray pits have been observed in *Elaeodendron* (Xinying *et al.* 1990). Vessels had alternate thickenings (Fig. 4N). Fibres were non-septate in both species, with scalariform (Fig. 4O) and spiral (Fig. 4P) thickenings, in agreement with what has been reported in the family (Giménez *et al.* 2014, Carmo *et al.* 2016). Growth rings were absent or hardly observed, probably due to the absence of clear seasonal variations in Sri Lanka (Figs. 4G, 4J).

Characters such as distinct growth rings, thick-walled fibres, diffuse-porous solitary vessels, simple perforations, alternate pits, and non-septate fibres have been observed in several species of *Maytenus* (Giménez *et al.* 2014). Solitary, diffuse vessels have been observed in *Maytenus* and other Celastraceae (Duarte & Debur 2005, Joffily *et al.* 2007). The wood anatomical features of the two *Salacia* species were similar to those of other genera and species of the family Celastraceae.

***Dichotomous key to separate the species***

1. Opposite, distichous leaf arrangement, obtuse, shortly acuminate leaf apex, acute leaf base ..... go to 3

2. Opposite, decussate leaf arrangement, obtuse, flat leaf apex, acute leaf base ..... go to 4

3. Ovate, oblong, ob-lanceolate leaf shape, entire, smooth leaf margin ..... go to 5

4. Oval, broadly elliptic, oblong leaf shape, toothed leaf margin ..... go to 6

5. Globose, without a prominent constriction fruit shape ..... go to 7

6. Globose with a narrow neck fruit shape ..... go to 8

7. Orange-yellowish, edible pulp fruit colour when ripe, two locules per fruit, one seed per locule ..... go to 9

8. Red, edible pulp fruit colour when ripe, one locule per fruit, one seed per locule ..... go to 10

9. Grey stem bark, prominent stem lenticels, inside stem orange colour ..... go to 11

10. White stem bark, no obvious stem lenticels, inside stem yellow colour ..... go to 12

11. No noticeable wing extension on the petiole ..... go to 13

12. Prominent wing extension on petiole ..... go to 14

13. Oval petiole outline in cross-section, noticeable/incomplete sclerenchyma sheath ..... go to 15

14. Roundish-to-semicircular petiole outline in cross-section, noticeable/incomplete sclerenchyma sheath ..... go to 16

15. U-shaped arc with invaginated ends towards the middle of the petiole and a wide opening vascular bundle ... go to 17

16. C-shaped arc with convolute extremities and a small opening vascular bundle ..... go to 18

17. Irregularly shaped, open arc with invaginated ends and narrow opening vascular bundle in the lamina; phloem continuous around the xylem ... go to 19

18. V- or reduced arc-shaped vascular bundle, no invaginated ends or narrow opening; phloem continuous around the xylem ..... go to 20

19. Adaxial epidermal pavement cells mostly round, abaxial epidermal pavement cells mostly irregular; irregularly distributed

cuticular wax on adaxial; rough, irregularly arranged wax on abaxial; irregularly deposited crust-like wax around stomata ..... go to 21

20. Adaxial epidermal pavement cells mostly sinuous, abaxial epidermal pavement cells mostly irregular; irregularly distributed cuticular wax on adaxial; smooth, block-arranged wax on abaxial and around stomata ..... go to 22

21. Circular or irregular, anomocytic stomata; tiny hooked hairs ..... go to 23

22. Elliptical, anomocytic stomata; hairs absent ..... go to 24

23. Dark brown phenolic compounds in root cortex; solitary or rarely aggregated diffuse-porous vessels and radial parenchyma ..... go to 25

24. Light yellow phenolic compounds in root cortex; solitary or rarely aggregated diffuse-porous vessels with light yellow phenolic deposits and radial parenchyma ..... go to 26

25. Dark brown phenolic deposits in stem ground parenchyma; solitary vessels, rarely in groups of two or three; diffuse-porous vessels, slightly elliptical/oblique/angular/oval *S. oblonga*

26. Dark yellow phenolic deposits in stem ground parenchyma; solitary vessels; diffuse-porous vessels, slightly oblique to angular .....*S. reticulata*

## CONCLUSION

These results highlight the role of anatomy and vegetative morphology as an important tool in taxonomic studies of the genus *Salacia*. Several reliable vegetative morphological characters (shape and colour of fruits, number of locules and seeds, stem bark colour, root colour, presence or absence of lenticels) can be used to distinguish *S. oblonga* and *S. reticulata* in the field without flowers. Anatomical features such as wing extensions, shape and arrangement of invaginated ends of the vascular bundle of the petiole and lamina, deposition of cuticular materials around the stomata on the lower leaf surface, and shape and arrangement of the stomata can also differentiate the two species. Correct identification is essential for conservation purposes.

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