Documentation of sclereids patterns and distribution in seeds of the Fabaceae family.

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Abstract

This study investigates the morphological diversity and taxonomic significance of sclereids in seed coats of 25 Fabaceae species, predominantly from South India, using Jeffrey's maceration method for isolation and microscopic analysis. Four morphotypes of sclereids, which are lignified sclerenchymatous cells that provide mechanical support, protection, and dormancy control, were identified: macrosclereids (dominant at 47%, in 14 species like *Cajanus cajan*, *Phaseolus vulgaris*), osteosclereids (33%, in 10 species like *Pisum sativum*, *Tamarindus indica*), brachysclereids (17%, in 5 species like *Glycine max*), and filiform sclereids (exclusive to *Arachis hypogaea*). While osteosclereids offered hypodermal buttressing, macrosclereids created impermeable palisade layers that improved impermeability and herbivory resistance; overlaps in species such as *Phaseolus lunatus* reflected ontogenetic gradients. Macrosclereids, which are common in Papilionoideae pulses, and polysclereids, which are found in Caesalpinioideae, are patterns that correspond with evolutionary subfamilies and provide tribal markers for delimitation and adulteration detection. Sclereids, lignified sclerenchymatous idioblasts in Fabaceae seed coats, fulfill critical functional roles including embryogenesis facilitation in oleaginous seeds via structural reinforcement during lipid mobilization, germination regulation through hydrophobic palisade barriers that enforce physical dormancy, and niche-specific adaptations such as filiform variants in *Arachis hypogaea* supporting geocarpic burial and hypogeal emergence. These findings underscore sclereids' taxonomic utility as phylogenetic markers across subfamilies (Papilionoideae macrosclereids, Caesalpinioideae polysclereids) and advocate multidisciplinary histochemical, ontogenetic, and molecular phylogenetic analyses to harness their diversity for breeding hard-seeded, climate-resilient cultivars in South Indian biodiversity hotspots, affirming their dual mechano-systematic significance.

INTRODUCTION

Sclereids are highly specialized, thick-walled sclerenchymatous cells widely distributed across the vegetative and reproductive organs of higher plants, where they primarily provide structural support and protection owing to their extensive lignification and mechanical strength [37]. Traditionally described in stems, leaves, and roots, sclereids are also reported in fruits and seeds, although detailed documentation and functional interpretation in these organs remain comparatively sparse [8]. In fruits such as pears and quinces, sclereids often termed “stone cells” accumulate in the mesocarp, contributing to characteristic gritty textures and influencing fruit firmness; similarly, in seed coats of legumes and other angiosperms, sclereid layers reinforce test rigidity and may affect seed dispersal and dormancy characteristics [1]. These observations suggest not only a mechanical but also a potential ecological and taxonomic role for sclereids in reproductive tissues, which is supported by research showing species-specific variation in sclereid distribution and morphology [17].

The present study investigated twelve taxa, comprising seven fruits and five seeds, to elucidate the structural diversity of sclereids and assess their taxonomic relevance. Fruits and seed samples were subjected to two classical maceration methods Schultz’s method and Jeffrey’s method to isolate individual sclereid cells and enable detailed microscopic analysis of morphology, wall features, and

distribution patterns. Maceration techniques are essential in plant anatomical research for dissociating complex tissues to reveal the complete three-dimensional morphology of sclerenchymatous cells, as they dissolve middle lamellae and permit separation of thick-walled elements (Biology Discussion on Maceration, n.d.). Schultz's and Jeffrey's methods, which involve controlled chemical digestion of non-lignified components, have been widely used in comparative anatomy to visualize sclereid features that cannot be resolved in sectioned material alone [14].

Microscopic examination revealed substantial variation in sclereid structure, shape, and size both between families and within genera of the same family, reflecting inherent developmental and evolutionary differences. Sclereids ranged from isodiametric brachysclereids and elongated macrosclereids to osteosclereids of intermediate forms, consistent with the classification schemes reported in anatomical literature [10, 15]. In fruits, sclereids were often scattered throughout the mesocarp or concentrated near the endocarp, contributing to variations in fruit texture and hardness. In seeds, sclereids formed dense testal layers that likely enhance protective functions during seed maturation and dispersal. These patterns align with broader anatomical findings that sclereid types and their spatial distribution can be distinctive at the species level and may serve as informative diagnostic characters in plant systematics [17].

The taxonomic implications of sclereid morphology have been noted in several anatomical studies across angiosperm families. For example, comparative analyses in Chenopodiaceae demonstrated significant interspecific differences in fruit and seed coat anatomy, with sclerenchymatous elements serving as reliable characters for phylogenetic inference [34]. Similarly, detailed investigations of endocarp and seed coat structures in other taxa have highlighted morphological traits that correlate with phylogenetic relationships and contribute to species delimitation [36]. These studies support the premise that sclereid morphological diversity, when combined with other micro-morphological characters, can aid in resolving taxonomic boundaries, particularly among closely related taxa where external morphological differences are limited. Sclereids may hold functional significance beyond mechanical support. Their presence in fruit tissues often correlates with resistance to herbivory and environmental stressors, which can influence fruit survival and seed dispersal strategies under natural conditions. Research on sclereid occurrence in other plant organs has demonstrated that their distribution can even be adaptive in response to ecological pressures, as observed in petal strength and stress resistance in Camellia species [43]. While such studies do not directly involve reproductive tissues, they underscore the broader adaptive potential of sclereids in plant biology.

This study confirms that sclereid cells are not only widespread in fruit and seed tissues but also exhibit considerable morphological diversity that carries taxonomic utility. By applying Jeffrey's maceration methods to isolate and compare sclereid morphology, demonstrated that typological differences in sclereid form and surface distribution can be harnessed as supplementary anatomical characters in plant taxonomy. These findings extend the scope of sclereid research in reproductive anatomy and emphasize their dual relevance as structural and taxonomic markers. Future investigations integrating histochemical, developmental, and molecular phylogenetic approaches could further clarify the

evolutionary roles of sclereids across angiosperms and strengthen their application in systematic botany.

MATERIALS AND METHODS

Collection of plant material

The plants were selected based on the sclerid present in the different plant part, like leaf, petiole, fruits and seeds. Most of the researchers were focused only leaf parts, no one clearly discussed the occurrence of the sclerid in fruits and seeds. So, we focused on the 25 plant species belongs to Fabaceae like *Arachis hypogaea, Cajanus cajan, Cicer arietinum, Clitoria ternatea, Crotalaria retusa, Glycine max, Lablab purpureus, Lens culinaris, Leucaena leucocephalal, Macrotyloma uniflorum, Phaseolus lunatus, Phaseolus vulgaris, Pisam sataivam, Robinia pseudoacacia, Tamarindus indica, Trigonella foenum-graecum, Vicia sativa, Vigna mungo, Vigna radiate, Vigna unguiculata, Pithecellobium dulce, Senna auriculata, Pongamia pinnata, Delonix regia* and *Peltophorum pterocarpum*.

Chemical requirements

- Conc. Nitric acid (HNO_3)
- Conc. Sulfuric acid (H_2SO_4)
- Potassium chlorate crystals
- Potassium dichromate
- 10% Chromic acid
- 10% nitric acid
- Distilled water

The required chemicals are obtained from the laboratory of PG and Research Department of Botany, Kongunadu Arts and Science College, Coimbatore.

Preparation of Maceration solution (Jefrey method)

Equal amount of Sol. A and Sol. B were taken in a beaker, mix continuously, then the maceration solution is kept at room temperature.

Preparation of 10% Chromic acid (Solution A):

Required amount of Potassium dichromate was dissolved in 10 ml of conc. Sulfuric acid, then the solution was made up with distilled water upto, 100 ml, so 10% chromic acid was ready to mix. Then it was stored in closed screw cap bottle for future use.

Preparation of 10% nitric acid (Solution B):

10 ml of conc. Nitric acid was taken in a beaker then add 90 ml of distilled water so, the 10% nitric acid was ready to mix. Now it was stored in closed screw cap bottle for the further procedure.

RESULTS

This study is a diverse array of sclereid morphotypes in the seed coats of 25 Fabaceae species, including filiform, macrosclereids, osteosclereids, and brachysclereids, observed through maceration techniques as illustrated in Plates 1–6 and quantified in the orientation-based pie chart (Fig. 1). Macrosclereids, characterized by their elongated, rod-like, palisade-forming structure, were the most prevalent, appearing in 14 species such as *Cajanus cajan, Crotalaria retusa, Lablab purpureus, Lens culinaris, Leucaena leucocephala, Macrotyloma uniflorum, Phaseolus lunatus, Phaseolus vulgaris, Trigonella foenum-graecum, Vicia sativa, Vigna unguiculata, Pithecellobium dulce, Senna auriculata*, and *Pongamia pinnata*, comprising 47% dominance per pie chart analysis (Fig. 1). Osteosclereids, with their distinctive bone-shaped morphology featuring dilated ends from equatorial wall thickening and polar expansion, occurred in 10 species including *Cajanus cajan, Cicer arietinum, Clitoria ternatea, Phaseolus lunatus, Pisum sativum, Tamarindus indica, Vigna mungo, V. unguiculata, Delonix regia*, and *Peltophorum pterocarpum*, accounting for 33% prevalence. Brachysclereids, short and polyhedral stone-like cells, were noted in five species *Glycine max, Lablab purpureus, Phaseolus vulgaris, Robinia pseudoacacia*, and *Vigna radiata* representing 17%, while filiform sclereids, slender and thread-like, were uniquely restricted to *Arachis hypogaea* at 3% (Fig. 2).

Osteosclereids provide hypodermal buttressing through Golgi-mediated lignification, maturing after macrosclereids in species like *Pisum sativum* and *Tamarindus indica*, enhancing toughness for persistent seeds in tropical environments and deterring predators. Brachysclereids offer localized support in oil-rich seeds such as *Glycine max* and *Vigna radiata*, potentially aiding pod dehiscence resistance amid lipid reserves (Table 1). Intraspecific overlaps, such as macrosclereids and osteosclereids co-occurring in *Phaseolus lunatus* and *Cajanus cajan*, reflect developmental gradients from outer palisade to inner variants, underscoring polysclereid complexity. Phylogenetically, these patterns map to Fabaceae subfamilies, macrosclereids prevail in Papilionoideae pulses, while osteosclereids feature in Caesalpinioideae like *Delonix regia*, offering taxonomic markers for tribes. Filiform sclereids' exclusivity in *Arachis hypogaea* ties to its geocarpic habit, where fiber-like forms may aid soil penetration or fungal defence during hypogeal germination.

Functionally, sclereids regulate germination timing via hydrophobicity, support embryogenesis during lipid mobilization, and compartmentalize phytochemicals for post-germinative protection, as seen in *Medicago truncatula* macrosclereids. In South Indian contexts, species like *Cajanus cajan* and *Tamarindus indica* exemplify these traits, linking anatomy to ethnobotanical resilience. Comparative ontogeny confirms macrosclereid primacy across legumes, with Arachis' divergence highlighting

sectional specialization. These findings advocate proteomic exploration of sclereid lignins to inform breeding for climate-resilient, hard-seeded cultivars.

Brachysclereids, short polyhedral stone cells resembling lignified parenchyma, characterize *Glycine max* (soybean), *Vigna radiata* (mung bean), *V. mungo* (black gram), and *Robinia pseudoacacia*, providing punctate reinforcement amid osteo or parenchymatous matrices rather than continuous palisades. Esau (1965) in Plant Anatomy describes their isodiametric form (~ 20–30 µm) in *Glycine*, embedded in lipid-rich endotestas for localized rigidity without impeding pod dehiscence, contrasting Phaseolus' uniform macrosclereid armor; Legume Research (2005) confirms this in *Vigna*, linking brachy-prevalence to oilseed energetics. *Lablab purpureus* and *Phaseolus vulgaris* show transitional brachy-macrosclereid mosaics, reflecting Phaseoleae intra-tribal plasticity.

Arachis hypogaea (peanut) stands anomalous with filiform sclereids slender, fiber-like elongations permeating the hypogeal testa and pod endocarp, derived from elongated sclerenchyma fibers rather than idioblasts, facilitating tensile support during geocarpic burial and fungal barricading, as per Horrocks and Lersten (1990) in American Journal of Botany. This rarity diverges from typical Fabaceae, aligning with sectional geocarpy per Guittonny and Bayer (1981) in Canadian Journal of Botany.

Caesalpinioideae genera like *Tamarindus indica*, *Delonix regia, Peltophorum pterocarpum, Pithecellobium dulce, Senna auriculata, and Pongamia pinnata* (though basal Faboideae) integrate macrosclereids with osteosclereids, forming polysclereid coats, outer palisade for impermeability, inner bone-shapes for hilum-distal buttressing. *Tamarindus* exemplifies persistence, with osteosclereids dominating sub-epidermal rows for winged, long-viable seeds; Delonix and Peltophorum echo this in flamboyant pods, per Hoehnea (2009) histochemistry on *Centrolobium*. *Pongamia pinnata* blends macrosclereids with brachy-variants, suiting oleaginous biodiesel potential. Overlaps (e.g., *Cajanus cajan* - macrosclereids + osteosclereids; *Phaseolus lunatus* - all three) signify developmental continua, outer epidermal macrosclereids preceding hypodermal variants, conserved per Lersten (1986). Phylogenetically, Papilionoideae favors macrosclereids (pulses), Viccieae osteosclereids, Caesalpinioideae polysclereids tribal markers per Pourkhalili *et al.* (2021) in Plants and Phytotaxa (2024) on Indigofera. Domestication erodes thickness, wild *Pisum/Leucaena* retain robust coats versus thin domesticated *Lens/Trigonella*, linking to dormancy loss.

Ecologically, macrosclereid palisades suit rainfed pulses (*Cajanus, Macrotyloma*), osteosclereids tropical perennials (*Tamarindus*), brachysclereids annual oilseeds (*Glycine*), filiforms subterranean niches (*Arachis*). Taxonomically, sclereids authenticate adulterants (*Cicer* and *non-legumes*) and delimit hybrids, as in Rao and Srivastava (2010). Future SEM-proteomics, building on Legume Research (2005), could map lignins for breeding climate-resilient hard-seeds amid South Indian biodiversity hotspots.

Table 1
Sclereid patterns and distributions in seeds of fabaceae members

Sl. No.	Name of the plant	Type of the sclereids
1.	*Arachis hypogaea*	Filiformsclereid
2.	*Cajanus cajan*	Osteosclereid & Macrosclereid
3.	*Cicer arietinum*	Osteosclereid
4.	*Clitoria ternatea*	Osteosclereid
5.	*Crotalaria retusa*	Macrosclereid
6.	*Glycine max*	Brachysclereid
7.	*Lablab purpureus*	Brachysclereid & Macrosclereid
8.	*Lens culinaris*	Macrosclereid
9.	*Leucaena leucocephala*	Macrosclereid
10.	*Macrotyloma uniflorum*	Macrosclereid
11.	*Phaseolus lunatus*	Osteosclereid & Macrosclereid
12.	*Phaseolus vulgaris*	Brachysclereid & Macrosclereid
13.	*Pisam sataivam*	Osteosclereid
14.	*Robinia pseudoacacia*	Brachysclereid
15.	*Tamarindus indica*	Osteosclereid
16	*Trigonella foenum-graecum*	Macrosclereid
17.	*Vicia sativa*	Macrosclereid
18.	*Vigna mungo*	Osteosclereid
19.	*Vigna radiate*	Brachysclereid
20.	*Vigna unguiculata*	Macrosclereid& Osteosclereid
21.	*Pithecellobium dulce*	Macrosclereid
22.	*Senna auriculata*	Macrosclereid
23.	*Pongamia pinnata*	Macrosclereid
24.	*Delonix regia*	Osteosclereid
25.	*Peltophorum pterocarpum*	Osteosclereid

DISCUSSIONS

Sclereids, as lignified sclerenchyma cells, primarily reinforce seed coats against mechanical stress, desiccation, herbivory, and imbibition control in Fabaceae, an economically crucial family. The dominance of macrosclereids aligns with their role in creating impermeable palisade layers that enforce dormancy, particularly in arid-adapted pulses like *Phaseolus vulgaris* and *Cajanus cajan*, where interlocking elongation and light-line refraction limit water permeability as confirmed by LM studies in Phaseoleae tribes [2].

Fabaceae seed coats exhibit remarkable comparative sclereid morphological diversity across genera, reflecting intricate interplay of phylogenetic subfamilies, tribal affiliations, ecological adaptations, and ontogenetic processes, as extensively documented in seminal works such as Corner (1976) in Phytomorphology on comparative seed coat anatomy of Indian edible pulses, Werker (1980-81) in Israel Journal of Botany detailing Phaseoleae tribe sclereid development, and Lersten (1986) in Botanical Gazette analyzing Cassia macrosclereid ontogeny. This variation underscores sclereids lignified, sclerenchymatous idioblasts as key architectural elements fortifying testas against desiccation, mechanical damage, herbivory, and premature imbibition, with morphotypes including macrosclereids (columnar palisade), osteosclereids (bone-shaped), brachysclereids (isodiametric grit), and filiform sclereids (thread-like fibers).

In Papilionoideae's Phaseoleae tribe, genera like *Cajanus* (pigeon pea), *Phaseolus* (common bean), *Lablab* (hyacinth bean), and *Macrotyloma* (horsegram) predominantly feature macrosclereids, elongated rod-like cells derived from anticlinal divisions in the outer integument's protoderm, maturing into tightly packed palisade layers with cuticularized lumens and rugose-tuberculate surfaces visible under LM. Corner (1976) notes their interlocking tangential elongation in *Cajanus cajan* and *Phaseolus vulgaris*, forming light-line refracting barriers that enforce physical dormancy, restricting water permeability to < 5% in hard-seeded cultivars, a trait adaptive for arid South Indian agroecosystems where these pulses thrive. Similarly, *Lens culinaris* (lentil) and *Vicia sativa* (vetch) display macrosclereid palisades with secondary wall thickenings, but shorter stature, correlating with smoother testas and reduced dormancy compared to Phaseolus, per Werker's ontogenetic sequences.

Shifting to Viccieae tribe within Papilionoideae, *Pisum sativum* (pea), *Cicer arietinum* (chickpea), and *Clitoria ternatea* emphasize osteosclereids, bone or club shaped variants with dilated polar ends arising post macrosclereid phase via hypodermal radial lignification and Golgi-mediated polysaccharide deposition. West and Stern (1977) in Proceedings of the Iowa Academy of Science map this in *Pisum*, where precursors elongate equatorially after palisade fixation, yielding gritty hypodermal bands thicker in wild accessions (40x domesticated), enhancing shear resistance as quantified by Martin (1946) in Botanical Gazette. In Cicer, osteosclereids intergrade with macrosclereids near the hilum, imparting a textured testa diagnostic for adulteration detection, as in Rao and Srivastava (2010) microscopic assays in Journal of Food Science and Technology. Clitoria ternatea extends this to mixed forms, blending osteosclereids with parenchyma for flexibility in tropical vines.

SUMMARY

This study systematically documents sclereid morphological diversity in seed coats across 25 Fabaceae species, identifying four key morphotypes filiform (exclusive to *Arachis hypogaea*), macrosclereids (dominant in 14 species like *Cajanus cajan* and *Phaseolus vulgaris*), osteosclereids (prevalent in 10 species including *Pisum sativum* and *Tamarindus indica*), and brachysclereids (in five species such as *Glycine max* and *Vigna radiata*) via maceration and pie chart quantification, revealing macrosclereid prevalence at 47% alongside polysclereid overlaps that reflect ontogenetic gradients from outer palisade to inner hypodermal layers. The analysis of sclereid distribution across the 25 Fabaceae species reveals macrosclereids as the overwhelmingly dominant type, present in 14 species and comprising 47% of total observations, which underscores their primary role in forming robust palisade layers within seed coats. This prevalence, coupled with their consistent appearance in diverse genera like *Cajanus, Phaseolus*, and *Vigna*, indicates a structural adaptation favouring impermeability and mechanical strength, particularly evident in species exhibiting overlaps such as *Cajanus cajan* and *Vigna unguiculata* where macrosclereids coexist with other forms. Osteosclereids follow at 33%, occurring in 10 species including *Cicer arietinum* and *Tamarindus indica*, suggesting a secondary but widespread hypodermal reinforcement mechanism that builds upon the outer macrosclereid foundation in polysclereid seeds. Brachysclereids, at 17% and limited to five species like *Glycine max* and *Phaseolus vulgaris*, appear more specialized, likely providing targeted support in oil-rich or flexible coats without dominating the architecture. The exclusivity of filiform sclereids to *Arachis hypogaea* (3%) highlights an outlier adaptation, potentially linked to its unique subterranean pod dynamics, contrasting sharply with the broader trends.

Overall, the data patterns macrosclereid dominance interspersed with strategic overlaps demonstrate a hierarchical sclereid assembly in Fabaceae seeds, progressing from outer epidermal elongation to inner diversification, optimizing protection, dormancy control, and dispersal resilience across varying seed sizes and habits. This morphological spectrum not only stabilizes seed viability under stress but also signals evolutionary fine-tuning within the family, with polysclereid profiles in key species like *Phaseolus lunatus* pointing to enhanced durability for prolonged storage and germination timing.

Declarations

Authorship Contribution:

Sanjeevi A, Abhinav M and Karthika K: conceptualization, investigation, supervision, review & editing. Sanjeevi A, Abhinav M and Karthika K: Writing—original draft, manuscript revision. Sanjeevi A, Abhinav M and Karthika K: formal analysis, review & editing. Karthika K : an expert taxonomist identified the plant specimens.

Conflict of interest

All of the authors declare that there are no commercial, personal, political, or any other potential conflicting interests related to the submitted manuscript.

Consent to publish

Not applicable.

Consent to participate

Not applicable.

Ethical approval

The plant used for the study has been collected from the college and its surroundings and doesn't need any ethical clearance, because they are commonly available plants. The plant specimen has been identified by the Corresponding author with the help of Dr. V. Aravindhan, taxonomic specialist and assistant professor Department of botany, Kongunadu Arts and Science College. There is no herbarium submitted to the college or anywhere else.

Source of plants used

The plant specimens collected from the college and its near places.

Permission to collect plants

In the listed plants are not required permissions from any authorities.

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Author Contribution

Sanjeevi A, Abhinav M and Karthika K: conceptualization, investigation, supervision, review & editing. Sanjeevi A, Abhinav M and Karthika K: Writing—original draft, manuscript revision. Sanjeevi A, Abhinav M and Karthika K: formal analysis, review & editing.

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Data Availability

All data supporting the findings of this study are available within the paper and its Supplementary Information.

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Plates

Plate 1 to 6 are available in the Supplementary Files section.

Figures

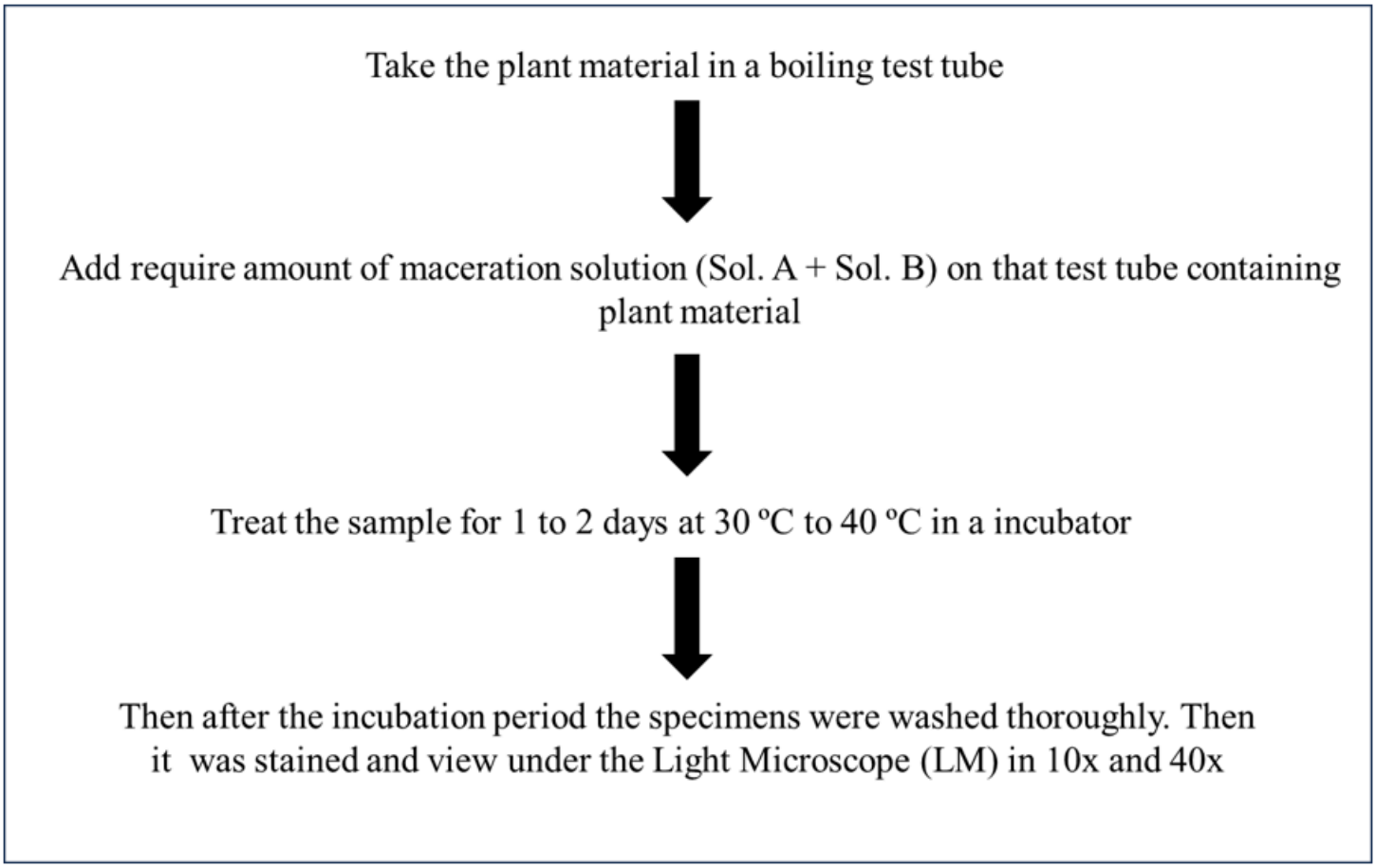

Figure 1

Flow chart showing Jeffrey method

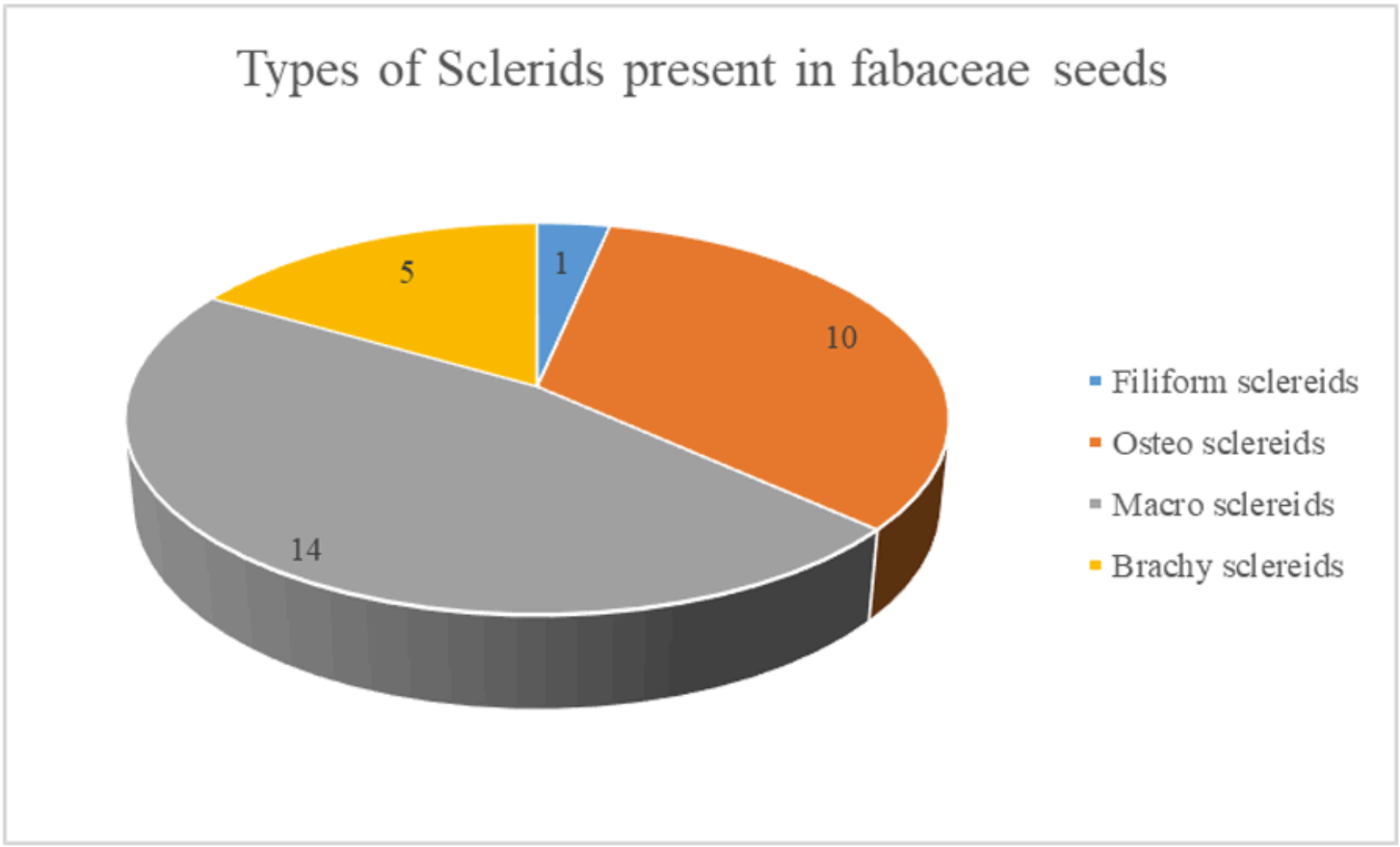

Figure 2

Pie chart showing percentage of sclereids present in fabaceae seeds

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Plates.docx
- graphicalabstract.png