



Cross-species Transferability of Microsatellite Markers in Sesame Wild Relatives – A Promising Source of Markers for Molecular Applications

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Abstract

Sesamum indicum L., commonly known as sesame, is a diploid member of the family Pedaliaceae, cultivated widely across tropical regions for its oilseed. *Sesamum indicum* L. subsp. *malabaricum* (Burm.) Bedigian is the progenitor of the present day cultivated sesame, and domestication events were reported to have occurred in Indian sub-continent. With reference to sesame wild relatives, a few were endemic to Indian Sub-continent while majority of the wild relatives have their origin from African continent. Molecular markers are useful for assessing genetic diversity estimates, in marker assisted selection for breeding programs, and for efficient management of plant genetic resources. We have tested the cross-species transferability for 100 SSR markers from sesame to its wild relatives (10 species). Of these, 21 SSR markers were found to be cross-species transferable, and 15 of them had exhibited polymorphism. 15 polymorphic SSR markers produced a total of 68 alleles with an average number of 4.53 alleles per locus, and the amplicon size ranged between 140 bp and 300 bp. Higher expected heterozygosity ($H_e=0.61$), than observed heterozygosity (H_o), indicates their predominantly self-pollinated nature. However, the occurrence of heterozygosity underscores the presence of cross-pollination to some extent. Hence, this corroborates with the categorization of sesame as often-cross-pollinated crop. A UPGMA-based dendrogram was constructed which grouped the 14 accessions into two major clusters. Parallely, scanning electron microscopic image profiles for the seeds of these 10 sesame wild relatives were compared with the clustering pattern derived using SSR markers and found corroborative.

Keywords *Sesamum indicum* · Wild relatives · Genetic diversity · SSR markers · Cross-species transferability · Scanning electron microscopy

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Introduction

The family Pedaliaceae comprises 13 genera and 80 species, with majority of the species represented in the genus *Sesamum*, comprising 31 species, habituating arid and tropical regions (Purseglove 1968; Cronquist 1981; Mabberley 1997; Ihlenfeldt 2004; Manning and Magee 2018). This genus is distributed mainly in Africa, sporadically in Australia, the East Indies, and India (Namiki 1995). Sesame (*Sesamum indicum* L.) is one of the oldest oilseed crops grown widely in tropical climates (Amoo et al. 2017). Sesame seeds are an important source of oil (44–57%), proteins (18–25%), and carbohydrates (13.5%), and also have medicinal and nutritional value (Myint et al. 2020). Although a self-pollinated crop, the flower structure of sesame facilitates cross-pollination up to 65%, and hence it is classified as an often-cross-pollinated crop (Rashad et al. 1979). Besides high oil and

protein content, sesame seeds are also rich in antioxidants like sesamin and sesamol that makes it to be valued from health and nutrition perspective besides longer shelf-life (Liang et al. 2021).

Being an oilseed crop, the genetic gain and improvement is low when compared with cereal crops (Rangan et al. 2023). The availability of the sesame reference genome (Wang et al. 2016, 2022) and pan-genome assembly (Yu et al. 2019) had enhanced the utility of the genome-scale sequence information for sesame crop improvement. The sesame whole genome sequence has facilitated the generation of extensive molecular markers for its application in crop improvement. A total of 19,816 non-redundant Simple sequence repeats (SSR) markers were developed through genomic approaches (Uncu et al. 2015). From transcriptome data, a total of more than 7,000 EST-SSRs were reported in sesame (Wei et al. 2011, 2014a, b). SNPs, the most prevalent form of small-scale genetic variation in organisms have emerged as an essential tool for molecular genetic analysis. The first high-resolution SNP genetic map for sesame, with 13 linkage groups provided key data for super-scaffolded genome assembly (Zhang et al. 2016). The analysis through SNPs as a molecular marker is considered useful for investigating the genetic diversity of crop plants (Singh et al., 2022). Many methods exist to develop core collections, often using morphological data across various crops, but relying solely on morphological traits cannot fully capture the genetic diversity present in the entire germplasm (Hu et al. 2000). Core collections based on molecular data retained maximal genetic diversity with minimal number of accessions in sesame and had helped develop a genomics-assisted composite coreset for sesame from thousands of accessions (Ruperao et al. 2024, 2025). Once genotype based coreset is developed and made available, it can be augmented with other trait-specific phenotypic accessions to derive a composite coreset. This strategy will help reduce environmental bias. A few decades back, without next-generation sequencing (NGS) tools, coreset development entirely relied upon phenotypic data and to some extent the diversity pattern generated using a few SSR markers (Bisht et al. 1998, 2004).

Among various classes of molecular markers, SSRs were known to be one of the most valuable PCR-based DNA markers for a variety of applications because of their co-dominant nature, high abundance, stability, robustness, not influenced by environmental and epistatic interactions, and cross-species transferability to their nearest taxonomical entities (Koutita et al. 2005; Hirano et al. 2011; Thakur et al. 2015, 2017). In brief, SSRs are short repeats that are typically linked to a high frequency of length polymorphism. Due to its efficiency and abundance in plant genomes, SSR analysis has been used often to understand genetic diversity and relationships in several oilseed crop species (Teklu et

al. 2021; Maurya et al. 2025). SSR markers are widely used in genetic analysis, gene tagging, mapping, and marker-assisted breeding (Kumari et al. 2019).

Genetic diversity estimate is an important step to assess diversity at molecular level among the set of germplasm being handled. Also, the knowledge of the genetic variation between accessions conserved in a gene-bank has a direct impact on management of the collection as a whole and genetic variability detected by molecular methods has the advantage of generally being unaffected by the environmental factors (Lazaro and Aguinalalde, 2006). This will help identify the most diverse ones, genetically, that can be utilized for crop improvement. Additionally, the polymorphic markers and their information during diversity studies will help their utilization for molecular breeding approaches (Hasanbegovic et al. 2021). For sesame, various types of molecular markers were available i.e. random amplified polymorphic DNA (RAPD) (Bhat et al. 1999; Ercan et al. 2004), inter-simple sequence repeats (ISSR) (Kim et al. 2002), amplified fragment length polymorphism (AFLP) (Laurentin et al., 2006), sequence-related amplified polymorphisms (SRAP) (Zhang et al. 2010), genomic-SSR (Wei et al. 2014a, b; Dossa et al. 2016), and expressed sequence tag-SSR (EST-SSR) (Wang et al. 2012). Although EST-SSRs are helpful for genetic studies due to their presence in gene-rich areas of the genome, conversely, they also exhibit a relatively lesser polymorphism than the SSRs from non-genic regions of the genome (Cho et al. 2011). Genetic characterization of germplasm not only aids in its effective conservation but also reveals the degree of genetic relatedness among the set of accessions studied for (Bhat et al. 1999), leading to its utilization.

When there is no sequence information available for a species, cross-species transferability of SSRs is advantageous to study the genetic relatedness and molecular diversity in the species to which the markers were transferred. This is possible due to the conserved nature of SSRs with the nearest taxonomical entities with a synteny relationship (Wu et al. 2014; Uncu et al. 2015; Thakur et al. 2017; Biswas et al. 2020; Lopez-Roman et al., 2024).

The objective of the present study was to assess the cross-species transferability of 100 sesame SSR markers to the sesame wild relatives (14 accessions comprising 10 taxa), since there is no molecular or sequence information available for most of the wild species studied. The clustering pattern generated using the polymorphic SSRs (from among the cross-species transferred markers) were cross-compared with the seed surface's micro-morphological pattern derived using a scanning electron microscopic (SEM) profile. Macro- and micro-morphological seed surface patterns and seed coat sculpturing characteristics were an important aid for taxonomical studies (Sahai et al. 1997).

Materials and Methods

Plant Material and DNA Extraction

The seeds of the sesame wild relatives used in this study were: *Sesamum alatum* Thonn. (IC0641153), *S. angolense* Welw. (EC1076115), *S. angustifolium* (Oliv.) Engl. (EC1076120), *S. laciniatum* J.G. Klein ex Willd. (IC0648929), *S. latifolium* J.B. Gillett (EC1076125), *S. indicum* subsp. *malabaricum* Burm. (IC0557260), *S. mulayanum* N.C. Nair (IC0623407, though synonymized with *S. malabaricum* (Bedigian 2003), we retained the identity as per the passport information), *S. prostratum* Retz. (IC0641138), *S. radiatum* Schum. & Thonn. (IC0208663), *S. triphyllum* Welw. ex Asch. (EC1076132), and two natural hybrids of *S. mulayanum* (synonymized as *S. malabaricum* (Bedigian 2003) though we kept its identity as per the passport information to avoid conflicts) with *S. indicum* (IC0199445 and IC0643475). In addition, two sesame cultivars TMV-3 (IC129719) and Swetha (IC312565) were also used in this study. Fresh leaves from healthy plants of these 14 accessions (10 taxa) were collected and the DNA was isolated using ca. 300 mg of leaf tissue ground finely in a pestle and mortar using 3 mL of pre-heated (65 °C) 1X CTAB buffer using the protocol as described by Stewart and Via (1993). The genomic DNA obtained was dissolved in 100 µL of 1X TE buffer (10mM Tris, 1mM EDTA, pH 8.0) and stored at −20 °C until use. The quality and quantity of the genomic DNA were assessed using 0.8% agarose gel electrophoresis and a spectrophotometer (QIAxpert, Qiagen, Germany).

SSR Primers and PCR Conditions

For SSR analysis, 100 sesame SSR primers as reported earlier (Dixit et al. 2005; Wang et al. 2014; Dossa et al. 2016) were synthesized and used in our experiments (details were provided in the supplementary information, Table S1). These 100 primers were screened for cross-species transferability using the genomic DNA extracted from the 14 accessions. Polymerase Chain Reaction (PCR) with these SSR primers were performed in a total volume of 10 µL containing 5 µL EmeraldAmp Max PCR Master Mix (2X Premix, Takara Inc.), 1.0 µL of template DNA (ca. 200 ng), 0.5 µL each of forward and reverse primer (each at 0.5 µM final concentration), and was made to a final volume of 10 µL using molecular grade sterilized distilled water. The PCR amplification was carried out using a Biometra TAdvanced thermocycler with the following parameters: Initial denaturation at 94 °C for 5 min; 35 cycles of denaturation (94 °C for 15 s), annealing (57 °C for 30 s), and extension (72 °C for 30 s). The amplification cycles were completed with a final extension at 72 °C for 5 min and program was set to hold at

4 °C till the products were taken forward for the downstream applications.

Agarose Gel Electrophoresis (AGE)

Amplified PCR products were resolved on a 2.5% agarose gel prepared using 1X TAE buffer along with a lane containing 50 bp marker (GeneDiReX) for scoring the allelic variations. The electrophoresis unit was run at 120 V using 1X TAE buffer to resolve the DNA fragments on the gel. The ethidium bromide stained gels were documented using a gel documentation system (G: Box, Syngene).

Scoring and Statistical Analysis

The allelic polymorphism was scored using the documented gel images for the 15 SSR primers that had exhibited polymorphism. The relative size of the amplified products was determined and scored in a co-dominant fashion with reference to the 50 bp ladder profile. The scored data was subjected to diversity analysis using GenAlEx v6.5 (Peakall and Smouse 2012). Genetic diversity parameters, such as number of alleles per locus (N_a), number of effective alleles per locus (N_e), Shannon's information index (I), observed (H_o) and expected (H_e) heterozygosity, unbiased expected heterozygosity (uH_e) and fixation index (F) were determined. Pair-wise genetic distance among the accessions studied was calculated using the Nei's Genetic Distance (Nei 1972) option within the GenAlEx tool and a genetic distance matrix was obtained. Unweighted pair group method with arithmetic mean (UPGMA) based dendrogram was constructed using this distance matrix in MEGA v.11.0.13 software (Tamura et al. 2021). Bootstrapping for the derived dendrogram was performed with 999 replicates using PoppR v2.9.6 package in RStudio (Kamvar et al. 2024).

Scanning Electron Microscopic (SEM) Seed Profiling of the Taxa Studied

Five representative air-dried seed samples from each of the taxa studied were used for SEM analysis' sample preparation. The seed samples were placed (horizontally and vertically) on a double-sided adhesive tape (copper or carbon, conducting both sides) mounted on an Aluminium stub in such a way that we obtain both dorsal (including 500X magnification) and side view. The stub with samples mounted on the adhesive tape were sputter-coated with Au-Pd (Gold-Palladium, at 60:40 ratio) for 180 s at 18 mA using a Gold sputter coater. Hence Au-Pd coated samples were examined under SEM (Carl Zeiss EVO 50) at an accelerating voltage up to 20 kV. These images were used to study and

describe the surface characteristics in wild sesame seeds. The descriptions for micromorphological characters were based on previous descriptive features (Song et al. 2005; Fawzi 2011; Gabr 2014, 2018).

Results

Comparison of Heterozygosity Parameters Between Accessions using 15 Polymorphic SSR Markers/ Cross-species Transferability of Sesame SSR Markers to its Wild Relatives

Of the 100 sesame SSR markers (Dixit et al. 2005; Wang et al. 2014; Dossa et al. 2016) tested for their cross-species transferability, 21 were found to be transferable, and of which, 15 were found to be polymorphic among the set of 14 accessions (10 taxa) studied. These polymorphic SSRs produced a total of 68 alleles with an average number of 4.533 alleles per locus, and the amplicon size ranged between 140 bp and 300 bp (Table 1). The average allele frequency per locus was found to be 4.53. Locus Si38, Si46 and Si97 exhibited the maximum (6) number of alleles (Na) as shown in Fig. 1; Table 1. The number of effective alleles (Ne) ranged from 1.5 (Si9) to 4.4 (Si46) with an average of 2.85 effective alleles per locus. The maximum observed heterozygosity (Ho) was 0.61 (Si46) with an average of 0.12 per locus. The maximum expected heterozygosity was 0.775 (Si46) with an average of 0.61 per locus (Table 1). The Unbiased expected heterozygosity (uHe) value was 0.81 (Si55) while the average was 0.63. The fixation index

(F) ranged from 0.2 (Si46) to 1.0 (Si8, Si9, Si38, Si42, Si66) with an average of 0.82. Shannon's information index was 1.6 (Si46) with an average of 1.18 (Table 1). Percentage transferability was recorded as percentage of amplification of the SSR markers amplified in the 14 accessions studied. The transferability rate in our study was assessed and found to be 21%.

Clustering Pattern Between the Taxa Studied using SSR Markers

To understand the clustering behavior with reference to the polymorphic SSRs studied, an UPGMA-based dendrogram was constructed using the genetic distance matrix derived from the SSR scoring data. The resulting tree grouped these 14 accessions into two major clusters. Cluster 1 included 10 accessions, while the rest were grouped into Cluster 2. Within cluster 1, wild species *S. mulayanum* (synonymized as *S. malabaricum* (Bedigian 2003) and *S. indicum* subsp. *malabaricum* were clustered together (Fig. 2). The two putative natural hybrids resulting from the cross of *S. mulayanum* (synonymized as *S. malabaricum* (Bedigian 2003) with cultivated *S. indicum* formed a separate sub-cluster within the major cluster. Additionally, *S. prostratum* and *S. laciniatum*, the two closely related taxa with $2n=4x=32$ were found to cluster together. Other wild species, such as *S. radiatum* and *S. latifolium*, were also included in this major cluster. Cluster 2 consisted of 4 wild accessions viz., *S. alatum*, *S. triphyllum*, *S. angustifolium*, and *S. angolense*. Of these, the former two and the latter two formed sub-clusters.

Table 1 Comparison of Heterozygosity parameters between accessions using 15 polymorphic SSR markers among the 100 SSRs tested for

Locus	N	Na	Ne	I	Ho	He	uHe	F
Si2	14	4.000	2.481	1.058	0.143	0.597	0.619	0.761
Si8	14	3.000	1.782	0.759	0.000	0.439	0.455	1.000
Si9	14	3.000	1.556	0.656	0.000	0.357	0.370	1.000
Si18	11	3.000	2.847	1.070	0.091	0.649	0.680	0.860
Si38	14	6.000	3.769	1.537	0.000	0.735	0.762	1.000
Si40	14	5.000	3.596	1.410	0.071	0.722	0.749	0.901
Si42	14	4.000	1.849	0.895	0.000	0.459	0.476	1.000
Si46	13	6.000	4.447	1.605	0.615	0.775	0.806	0.206
Si54	14	4.000	1.990	0.938	0.214	0.497	0.516	0.569
Si55	11	5.000	4.400	1.539	0.091	0.773	0.810	0.882
Si66	13	4.000	2.522	1.091	0.000	0.604	0.628	1.000
Si67	11	5.000	2.814	1.295	0.182	0.645	0.675	0.718
Si72	13	5.000	2.268	1.085	0.077	0.559	0.582	0.862
Si74	12	5.000	3.000	1.314	0.167	0.667	0.696	0.750
Si97	14	6.000	3.500	1.489	0.143	0.714	0.741	0.800
Mean	13.067	4.533	2.855	1.183	0.120	0.613	0.638	0.821
SE	0.316	0.274	0.238	0.077	0.040	0.033	0.035	0.055

Na- no. of different alleles, Ne- no. of effective alleles = $1/(\sum p_i^2)$, I- Shannon's information index = $-1 \cdot \sum (p_i \cdot \ln(p_i))$, Ho- observed heterozygosity = no. of Hets/N, He- expected heterozygosity = $1 - \sum p_i^2$, uHe- Unbiased expected heterozygosity = $(2N/(2N-1)) \cdot He$, F- fixation index = $(He - Ho)/He = 1 - (Ho/He)$

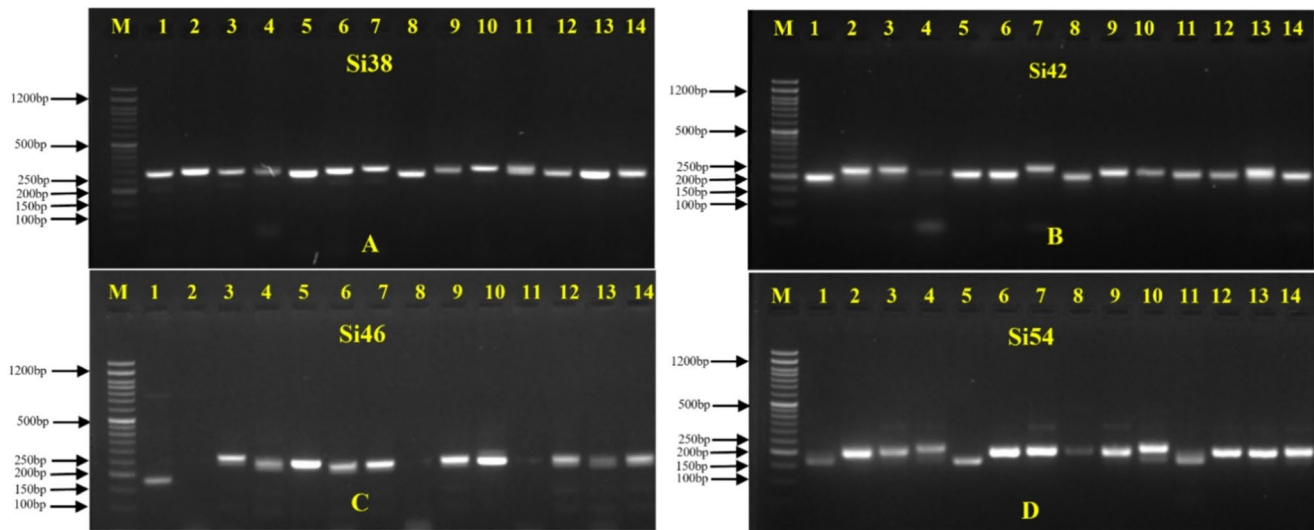


Fig. 1 PCR amplification profiles of the SSR primers for 14 samples. (A) for primer Si38; (B) for primer Si42; (C) for primer Si46; and (D) for primer Si54

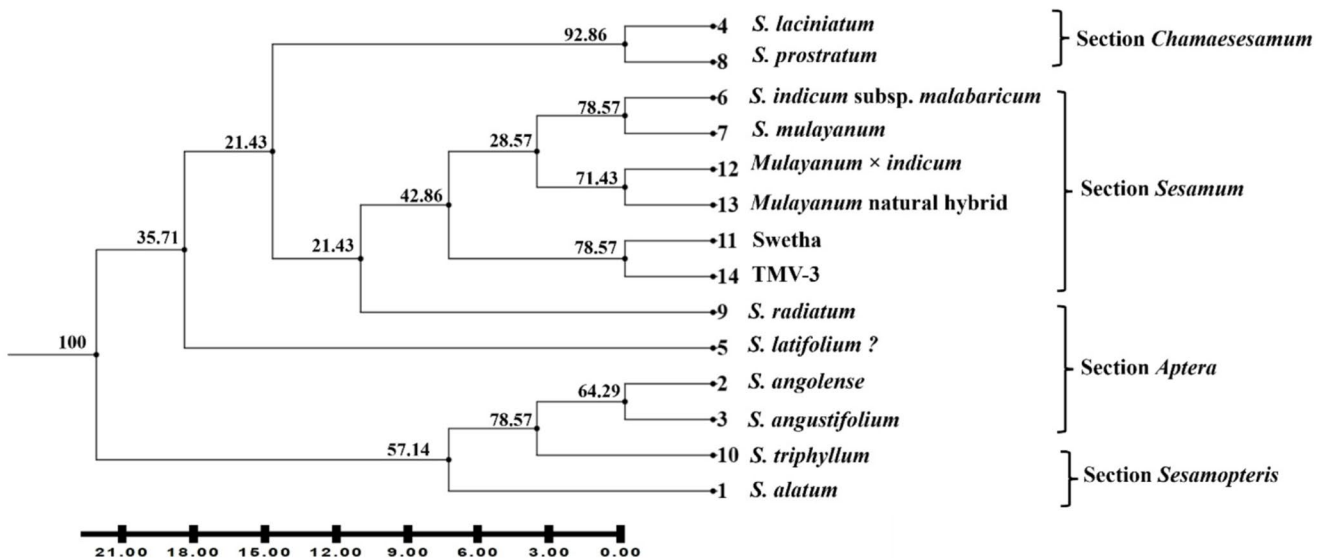


Fig. 2 UPGMA dendrogram derived based on the genetic distance matrix calculated using SSR dataset for 14 sesame accessions studied. Though *S. mulayanum* was synonymized with *S. malabaricum* (Bedigian 2003), we have retained the identity as per the passport informa-

tion. The tree is drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic tree. Bootstrapping was performed using bootstrap value of 999

The genetic distance matrix was generated using GenAlEx 6.5 (Peakall and Smouse 2012). The maximum genetic distance of 55 was found between *S. alatum* and *S. prostratum* (Fig. 2). Based on the clustering pattern, *S. alatum* was found to cluster with *S. triphyllum*, while *S. prostratum*, clustered with *S. laciniatum*. The accessions of *S. indicum* subsp. *malabaricum* and *S. mulayanum* (synonymized as *S. malabaricum* (Bedigian 2003) had exhibited the least genetic distance of 12 (Fig. 2). In the second cluster (Fig. 2), *S. angustifolium* and *S. angolense* clustered together.

Scanning Electron-microscopy (SEM) Analysis of the Seeds for the Taxa Studied

The seed micromorphological characters for ten *Sesamum* species were summarized in Table 2 and their representative SEM profiles were given in Figs. 3, 4 and 5. The width and length of the dorsal side of the seed varied from 0.8 (*S. angustifolium*) to 2 (*S. indicum*) mm and 1.4 (*S. angustifolium*) to 3.7 (*S. mulayanum* x *S. indicum*, natural hybrid) mm, respectively (Table 2). Seed shape for most of the species was broadly ovate to oblong; while the surface texture

Table 2 Measurement of seed length and breadth along with description of seed surface characteristics of the studied taxa based on SEM analysis (refer Figs. 3, 4 and 5). Species identity retained as per the passport information to avoid the conflict in accession identify though *S. mulayanum* was synonymized with *S. malabaricum* (Bedigian 2003)

S.No.	Species	Dorsal view		Side view		Shape	Description
		Width (mm)	Length (mm)	Width (mm)	Length (mm)		
1	<i>S. indicum</i> ssp. <i>indicum</i> (IC536811)	2.036	3.326	0.606	2.752	ovoid and tear-drop shaped	Laevigate type (faintly reticulate, colliculate cells)
2	<i>S. indicum</i> ssp. <i>malabaricum</i> (IC557260)	1.705	2.4	0.6357	2.2	Broadly ovate-oblong	Finely reticulate, slightly colliculate, foveolate cells
3	<i>S. angustifolium</i> (EC1076120)	0.8682	1.4	0.3667	1.3	Ovate	Deeply Reticulate and rugose
4	<i>S. indicum</i> ssp. <i>mulayanum</i> (IC623407)	1.747	2.8	0.74804	2.3	Broadly ovate-oblong	Coarsely reticulate, foveolate-reticulate cells
5	<i>S. radiatum</i> (IC208663)	1.900	2.8	0.4972	2.5	Ovate to globose	Tuberculate-reticulate, colliculate cells
6	<i>S. latifolium</i> (EC1076125)	1.995	2.6	0.5853	2.5	Elongate	Rugose-Reticulate with thick walls
7	<i>S. alatum</i> (IC0641153)	1.182	2.322	0.6075	2.2	Oval-oblong with wings at sides	Strongly rugose-reticulate, tuberculate-colliculate cells
8	<i>S. laciniatum</i> (IC0648929)	1.538	2.600	0.5298	2.996	Ovate	Foveolate-reticulate with rugose sub-type, smooth ridges
9	<i>S. triphyllum</i> (EC1076132)	1.294	3.1	0.8839	2.7 2.3	Oblong, Wing-like at ends (base and tip).	Reticulate-tuberculate, foveolate-tuberculate cells
10	<i>S. prostratum</i> (IC0641138)	1.541	2.8	0.4293	2.9	Ovate with angular edge	Colliculate-reticulate (deeply pitted, foveate), colliculate-foveolate cells
11	<i>S. angolense</i> (EC1076115)	1.569	2.0	0.4697	2.0	Broadly ovate	Rugose-reticulate or colliculate, tuberculate-reticulate cells
12	<i>S. mulayanum</i> × <i>indicum</i> (IC199445)	2.075	3.711	0.705	2.858	Ovate	coarsely reticulate (Colliculate-rugose), colliculate cells

characteristics were generally laevigate or reticulately rugose to colliculate and foveate types (Table 2; Figs. 3, 4 and 5).

Discussion

SSR Marker Variability/transferability Across Sesame Wild Species

The present study evaluated the heterozygosity parameters and transferability of SSR markers to the sesame wild relatives using the SSRs reported in cultivated sesame (Dixit et al. 2005; Wang et al. 2014; Dossa et al. 2016). We observed that the average allele frequency per locus of 4.53 is marginally higher, due to multiple taxa, than those reported by Asekova et al. (2018) using 23 SSRs among 129 Korean sesame genotypes. Dixit et al. (2005); Wei et al. (2014a, b) reported average values of 4.6 and 5.46 alleles per microsatellite locus respectively. The maximum observed heterozygosity (H_o) was 0.61 (Si46) with an average of 0.12 per locus. The maximum expected heterozygosity (H_e) value was 0.775 (Si46) with an average of 0.61 per locus (Table 1). The mean expected heterozygosity value of 0.61 was found to be higher than observed heterozygosity in the present study,

suggesting that self-pollination is the major factor, while occurrence of heterozygosity underscores the occurrence of cross-pollination as well. Hence, this corroborates with the categorization of sesame as often-cross-pollinated crop. Our results were found to be in corroboration with the report of Wei et al. (2014a, b); where the average H_e (0.68) was more than H_o (0.24) from a set of 31 diverse sesame accessions from 12 countries.

Cross-species transferability, from the nearest taxonomically related species, is advantageous when there is no sequence/marker information available (Luro et al. 2008). It is a cost-effective approach as compared to developing new SSR markers for a particular species wherein the related taxa possess the required information. In case of pulse crops, the transferability was reported to be more than 90% within *Vigna* genus (Saini et al. 2023), while across genera it was roughly 20% only (Gupta et al. 2013), though self-pollinated. In case of oilseed crops, transferability was found to be roughly 15% across genera (*Helianthus* to *Carthamus*) as reported by García-Moreno et al., (2008) while within genera (*Brassica juncea* cultivars), a high transferability rate of 84.8% was reported (Thakur et al. 2015). The transferability rate in our study was assessed and found to be 21% which is lower when compared to other self or often-cross-pollinated crop species. The average rate of transfer for SSR markers from

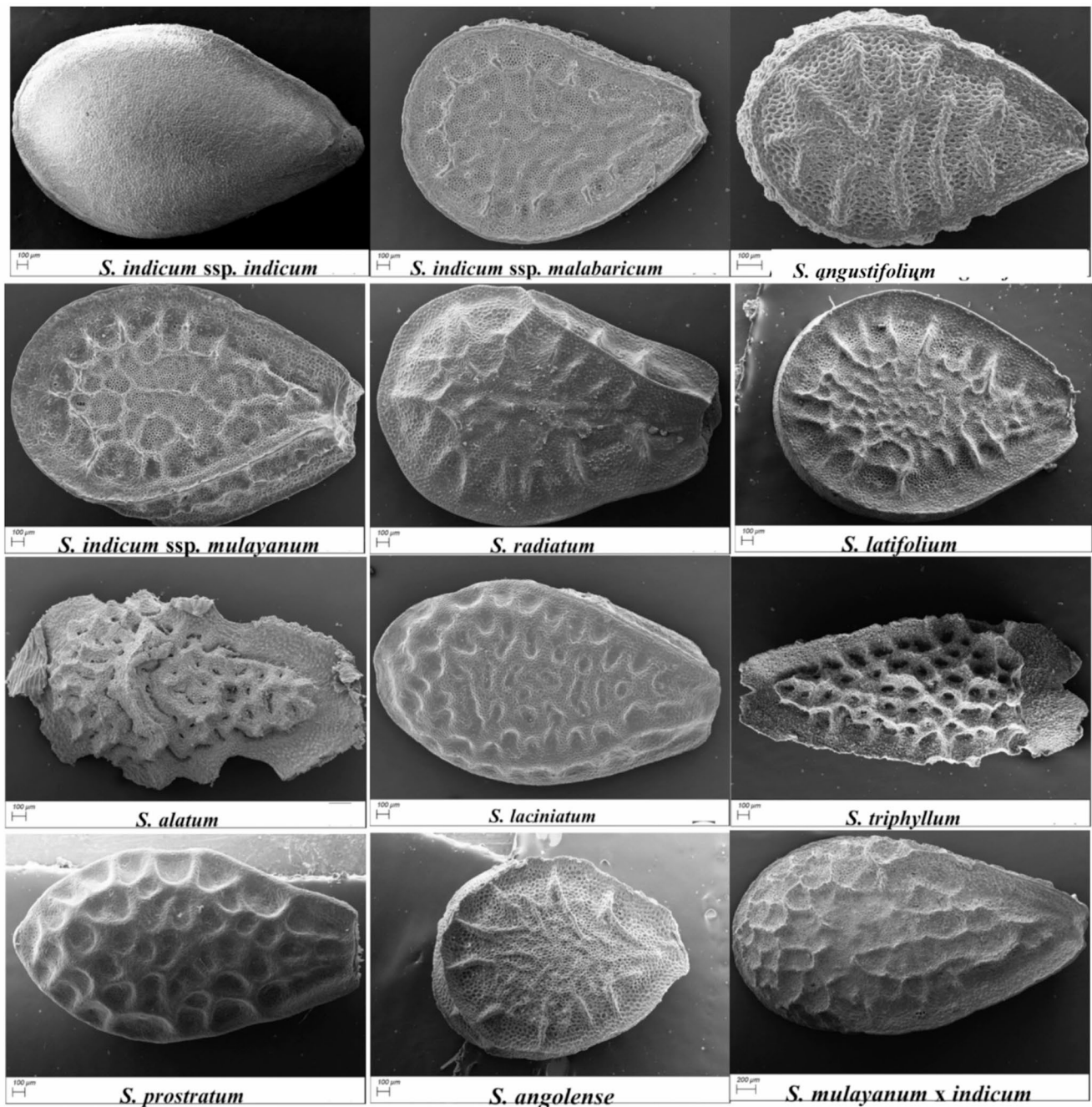


Fig. 3 Electron micrographs of the seeds of *Sesamum* spp. (dorsal view)

four major cereal crops (Wheat, Rice, Maize, Sorghum) to other grass taxa was in the range of 55–57% (Wang et al. 2005). These values were notably higher than those in the legume family (8–31%) (Wang et al. 2004). These reports highlight a broad range of cross-species transferability depending on their breeding system and the degree of closeness between the taxa involved in transfer process, besides taxonomical hierarchy.

Comparison of the Clustering Pattern and the SEM Image Profiles Between the Taxa Studied using SSR Markers

The resulting tree grouped the 14 accessions into two major clusters, with Cluster 1 comprising 10 accessions and the remaining grouped into Cluster 2. Within cluster 1, under the section *Sesamum* wild species *S. mulayanum* and *S. indicum* subsp. *malabaricum* were clustered together (Fig. 2) indicating their degree of relatedness and thereby validating

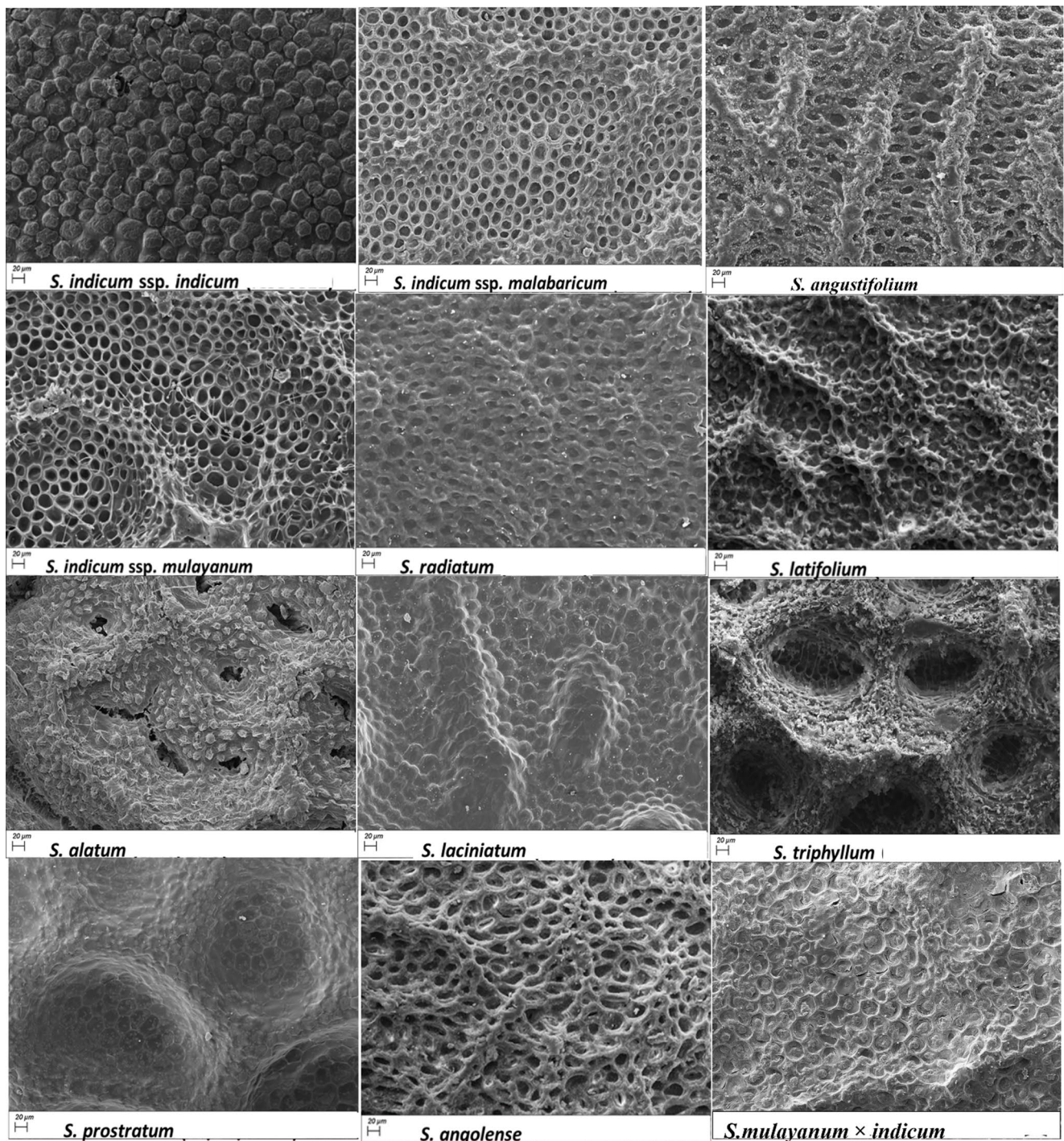


Fig. 4 Electron micrographs of the seeds of *Sesamum* spp. (dorsal view, at higher magnification, 500x)

the synonymization of *S. mulayanum* with *S. indicum* subsp. *malabaricum* by Bedigian (2003). The overlapping distribution pattern across the geographical ranges of these taxa likely facilitated gene flow between them, in their natural habitat (Pradheep et al. 2021). Both these taxa exhibited the chromosome number, $2n=2x=26$ (Ihlenfeldt 2004). The two natural hybrids resulting from the cross of *S. mulayanum*

(synonymized as *S. malabaricum* (Bedigian 2003) with cultivated *S. indicum* formed a separate sub-cluster within the major cluster. Additionally, *S. prostratum* and *S. laciniatum*, the two closely related taxa with $2n=4x=32$ were found to be clustered together under the section *Chamaesamum*. Other wild species, such as *S. radiatum* and *S. latifolium*, were also included in this major cluster. Cluster 2 consisted

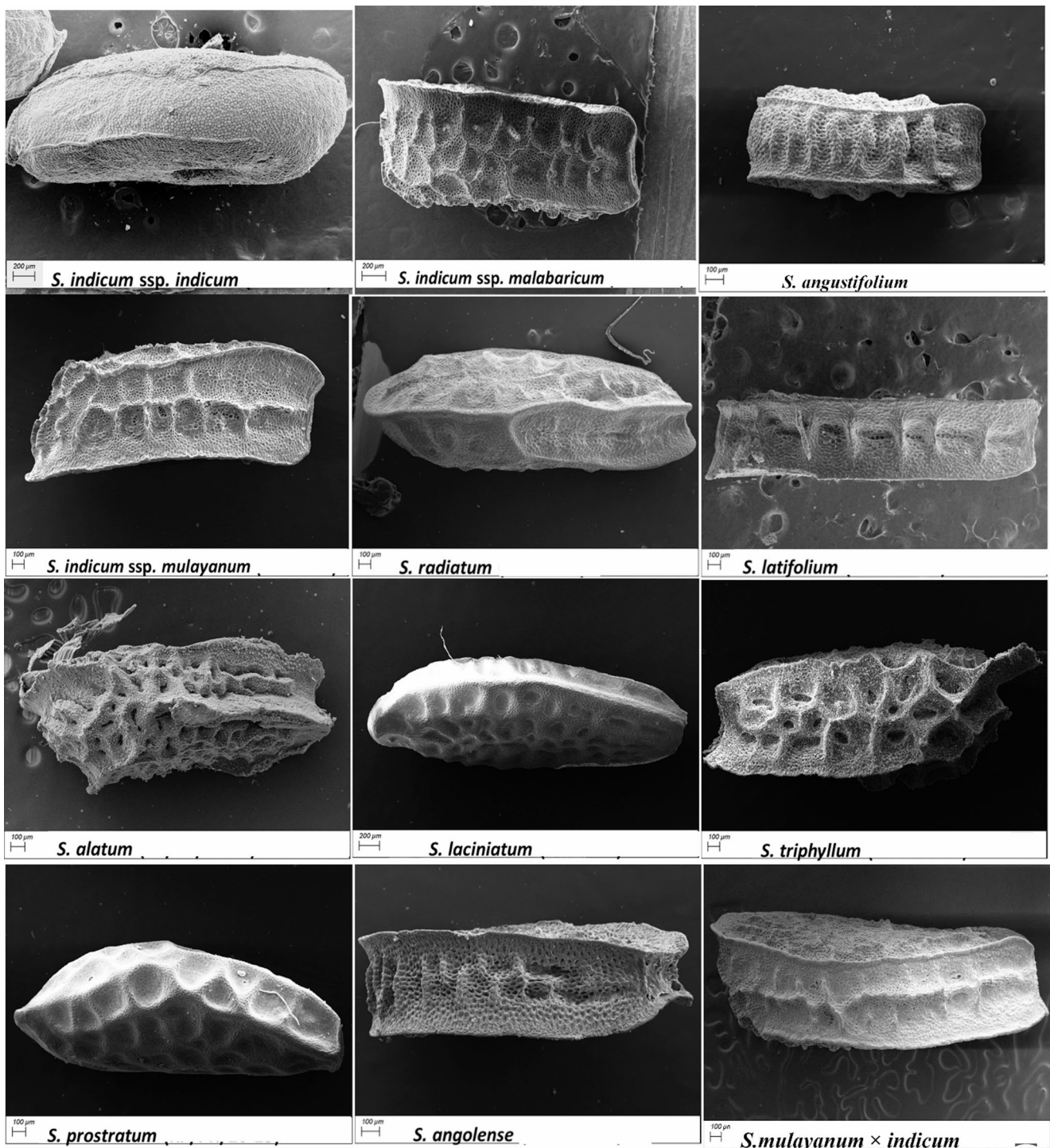


Fig. 5 Electron micrographs of the seeds of *Sesamum* spp. (side view)

of 4 wild accessions viz., *S. alatum*, *S. triphyllum* under the section *Sesamopteris*; while *S. angustifolium*, and *S. angolense* fall under the section *Aptera*. Of these, the former two and the latter two formed sub-clusters. The latter two have the chromosome number of $2n=4x=32$; while the former two have $2n=2x=26$ chromosomes (Subramanian 2003).

The maximum genetic distance was found between *S. alatum* and *S. prostratum* (Fig. 2). Both species had different geographical distribution. *S. alatum* is known to be widely distributed in tropical Africa, occurring in dry regions from Senegal to South Africa (Bedigian 2010). *S. prostratum* is a species endemic to Indian sub-continent (India and Sri

Lanka) and is distributed along the Eastern coastal regions of Tamil Nadu, Puducherry and Andhra Pradesh (Rangan et al. 2022; Wadugodapitiya et al. 2013). Based on the clustering pattern, *S. alatum* was found to cluster with *S. triphyllum*. Both were known to be diploid with chromosome number $2n=2x=26$ (Ihlenfeldt 2004). The SEM images of both species, *S. alatum* and *S. triphyllum* exhibited wing-like structures at both the apex and base; besides, they also exhibited deeper pits on seed surface, found to be unique for these two species among the taxa studied (Fig. 3). The wings were suborbicular, and the seed testa exhibited honeycomb-like pits, prominently visible over the reticulated seed surface (Figs. 4 and 5). Similarly, *S. prostratum* Retz., clustered together with *S. laciniatum*; and both were tetraploid species with chromosome number of $2n=4x=32$ (Ihlenfeldt 2004). SEM examination for these two taxa had revealed an ovate shape with an angular edge in case of *S. prostratum*. (Fig. 3). The micro-texturing or secondary sculpturing included reticulated-foveate pattern, and additionally with a rugose sub-type pattern for *S. laciniatum* (Fig. 4). The reticulate pattern comprises a network of ridges and depressions, creating a honeycomb-like appearance, further emphasizing the structural similarities between these taxa (Pradheep et al. 2021). Pits are large and deep in *S. prostratum* and hence their number is few when compared to *S. laciniatum* (Fig. 3). This distinct characteristic feature also supports in treating them as independent taxa (Rangan et al. 2022, 2024). These findings were in close correlation with the micromorphological features as revealed through their seed surface SEM profiling (Figs. 3 and 4).

The accessions *S. indicum* subsp. *malabaricum* and *S. mulayanum* had exhibited the least genetic distance (Fig. 2). This also supports the earlier taxonomical work (Bedigian 2003) that had synonymized these two taxa. The seed surface details of *S. mulayanum* showed a reticulate ornamentation while that of *S. malabaricum* showed a fine reticulate foveate pattern (Figs. 3 and 4). The seed surface appears to be rough and uneven, with a network of fine ridges and grooves (Fig. 5). Additionally, *S. radiatum* and *S. latifolium* from cluster 1 also had exhibited a similar pattern. SEM analysis of the seeds of these two species had revealed a broadly ovate shape, with a characteristic reticulately rugose texture on its surface (Fig. 3). Although *S. latifolium* has not been taxonomically ranked under any section, our studies suggest this species to be a member under the section *Aptera* (Fig. 2). This clue from molecular studies will aid detailed taxonomical and molecular studies for its appropriate taxonomical ranking.

In the second cluster (Fig. 2), *S. angustifolium* and *S. angolense* were found to be clustered together. The seeds of *S. angustifolium* were ovate to sub-ellipsoid in shape, with a reticulated rugose surface and undulated margins. Similarly,

the seeds of *S. angolense* were broadly ovate and exhibited a reticulated-foveate pattern with a rugose surface (Figs. 3 and 4). The SEM images also revealed that the clustering pattern derived through SSR marker studies is in line with the variations observed in their seed micromorphological features (Fig. 3).

The clustering pattern obtained in the dendrogram revealed a similar pattern in line with the taxonomical relationship (Manning and Magee 2018; Pradheep et al. 2021). The same is reflected in the SEM profiles for the seeds of these taxa, as SEM with high resolution images, help us to know the unknown surface structural features besides macromorphological features (Heywood 1969, 1971). The molecular markers are helpful in understanding the tree of life at various hierarchical levels and supplement morphological data for taxonomic studies.

Conclusion

The present study assessed the cross-species transferability of SSR markers from the cultivated sesame to its wild relatives. Of 100 SSR markers tested for, 21% were found to be transferable, and 15 were found to be polymorphic. These transferred and polymorphic SSRs markers will be of potential use for population genetics and molecular diversity experiments in sesame wild relatives, where there is no molecular or sequence information is available. Besides, these markers will also be helpful in hybridity testing while experimenting for wide-hybridization experiments to develop derivatives with desirable traits that can be successfully introgressed in cultivars for sesame improvement. Studies on seed surface micromorphological features have revealed that their textural pattern is in coherence with the taxonomical relationship. A comparison between the SSR derived clustering pattern and the SEM image profiles for the taxa studied were found to be correlative and thereby supporting the potential use of SSRs to supplement the morphological features involving taxonomical studies.

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Data Availability The data pertaining to this manuscript is provided as supplementary information.

Declarations

Ethical standards Not applicable.

Competing interests The authors declare no competing interests.

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