



Original Article

***Corchorus L.* and *Hibiscus L.*: Molecular Phylogeny Helps to Understand Their Relative Evolution and Dispersal Routes**

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ABSTRACT: Members of the genera *Corchorus L.* and *Hibiscus L.* are excellent sources of natural fibers and becoming much important in recent times due to an increasing concern to make the world greener. The aim of this study has been to describe the molecular phylogenetic relationships among the important members of these two genera as well as to know their relative dispersal throughout the world. Monophyly of *Corchorus L.* is evident from our study, whereas paraphyletic occurrences have been identified in case of *Hibiscus L.* Although *C. olitorius* is assumed to be originated from Africa and *C. capsularis* from Indian subcontinent, our study found both to be related through maternal inheritance. This prompted us to put forward a hypothesis with archeological support to explain the dispersal routes of migration of these two *Corchorus* species. Similar migratory occurrences may also be true for *Hibiscus L.*

KEYWORDS: *Corchorus L.*, *Hibiscus L.*, phylogenetic relationships, dispersal routes.

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INTRODUCTION

The herbaceous genus, *Corchorus* (jute) recently classified within the family Sparrmanniaceae,¹⁻³ consists of many species of large and small trees together with some shrubs.

The plant family Malvaceae to which the genera *Hibiscus* belongs consists of more than 100 genera which are distributed throughout the world with a primary abundance in the tropics⁴. *Corchorus* comprises a group (40-100 species) of annually grown dicotyledonous fiber-yielding plants cultivated in the tropics and sub-tropics⁵. The most widely cultivated species of this genus, *C. olitorius* and *C. capsularis*, produce the fiber, jute. In contrast, the genus *Hibiscus* has more than 300 tropical annual and perennial herbaceous plant species, including kenaf, (*H. cannabinus L.*) another important fiber producing crop.^{6,7} These plant fibers are non-abrasive, non-toxic

and biodegradable⁸ which makes them environment friendly and potential alternative for plastic fiber with a wide range of commercial applications⁹⁻¹¹.

Of these two genera, *Hibiscus L.* has been extensively studied from evolutionary perspective^{12,13} focusing either on geographical distribution or taxonomic position.^{11,14-16} On the other hand, very little effort has been made to know about the evolution of the members of the genus *Corchorus* and such studies if any have mostly been confined to the available accessions of the two cultivated species, *C. olitorius* and *C. capsularis*.¹⁷⁻²⁰

To investigate or validate one's evolutionary lineages and phylogenetic relationships, molecular data are considered more reliable than morphological information.^{21,22} Benor and co-workers²³ have carried out an internal transcribed spacer (ITS)-based phylogenetic analysis and concluded *Corchorus L.* to

be monophyletic. ITS region from nuclear rDNA includes ITS1 (18S-5.8S spacer), 5.8S region and ITS2 (5.8S-28S spacer)²⁴ and is mostly used to discriminate among species,²⁵ as it shows sufficient resolution at lower taxonomic levels.^{16,26,27} However, ITS-based phylogeny cannot rule out the possibility of partial homogenization in parental sequences.²⁸ Diploid hybrid species can even lose a part of parental ITS sequence through segregation.²⁹ One way to eliminate such chances is to compare ITS-based phylogeny with that of chloroplast DNA (cpDNA).³⁰ While the intergenic spacer (IGS) sequence in cpDNA (IGS1: *trnT*^{UGU}-*trnL*^{UAA} spacer; IGS2: *trnL*^{UAA} – *trnF*^{GAA} spacer) maintains an exclusive maternal inheritance in angiosperms,³⁰ the maturase K (*MatK*) gene (a protein-coding gene) in cpDNA exhibits relatively high proportion of transversions, a factor which helps in the reconstruction of angiosperm phylogeny.^{31,32} On the other hand, evolution of Xyloglucan endotransglucosylase/hydrolase (*XTH*) gene (encoded in the nuclear DNA), an ubiquitous regulatory enzyme of xyloglucan (XyG) assembly pathway³³ known for its highly conserved characteristic motif [DEIDFELFG]³⁴⁻³⁶ is likely to follow a relatively conserved evolutionary pattern to gain maximum selective advantages.³⁷ Such pattern could be really useful in explaining the issues with inheritance.

Present study aimed to elucidate the phylogenetic relationships among different species belonging to the genera *Corchorus L.* and *Hibiscus L.* using specific regions in cpDNA (MatK, IGS1 and IGS2), ITS sequences and XTH gene.

The pattern of evolution among the cultivated species of *Corchorus* has always been a matter of discrepancy^{23,38} while many disagree on the monophyly of the genus *Hibiscus*, since some paraphyletic occurrences have been reported.^{6,15} To help clarifying such issues we have analyzed sequences of specific regions of ITS, MatK and XTH genes as well as their combined data (cpDNA-regions and all genes studied here)^{39,40} and put forward a hypothesis with support from data of several archeological studies, documented human history^{41,42} and long-distance dispersal (LDD) of plants.^{43,44}

MATERIALS AND METHODS

DNA isolation from plant material

Eight *Corchorus L.* species and six *Hibiscus L.* species (Table 4) were used in this study. Seeds of were collected from Bangladesh Jute Research Institute (BJRI). Genomic DNA was isolated from 4-5 days old seedlings following a protocol described by Haque and co-workers.⁴⁵ Chloroplast DNA was isolated from 30-40 day old plant leaves according to a protocol of Triboush and colleagues.⁴⁶

Table 1: Primer list and thermal cycles used in the study.

DNA Type	Region Name	Primer Name	Primer Sequence	Thermal Cycle	Amplified Product Size
rDNA	Inter-transcribed Spacer (ITS)	18S for	5'-TGGGGATAGATCATT GCAATTGTTGGTC-3'	95°C – 5 minutes 95°C – 40 seconds 50°C – 1 minute 72°C – 1 minute 72°C – 7 minutes 4°C – Hold	} 35 cycles ~950 bp
		28S rev	5'-TCCYGGTTCGCTCGCC GTTACTA-3'(Y = A/T)		
cpDNA (Non-coding)	Intergenic Spacer 1 (IGS1) (<i>trnT-trnL</i>)	Chl1 F	5'-CATTACAAATGCGAT GCTCT-3'	95°C – 5 minutes 95°C – 50 seconds 56°C – 1 minute 72°C – 90 seconds 72°C – 5 minutes 4°C – Hold	} 35 cycles ~1000 bp
		Chl1 R	5'-TCTACCGATTTTCGCCA TATC-3'		
cpDNA (Non-coding)	Intergenic Spacer 2 (IGS2) (<i>trnL-trnF</i>)	Chl3 For	5'-ATTGAACTGGTGACA CGAG-3'	95°C – 5 minutes 95°C – 40 seconds 58°C – 50seconds 72°C – 1 minute 72°C – 5 minutes 4°C – Hold	} 35 cycles ~630 bp (<i>Corchorus L.</i>) ~470 bp (<i>Hibiscus L.</i>)
		Chl3 Rev	5'-AGTCCCATTCTACATG TCAATATCG-3'		
cpDNA (Coding)	Maturase K (<i>MatK</i>)	MatK F1	5'-GAGGAATTCAAGTA TATTTAGAAC-3'	95°C – 5 minutes 95°C – 50 seconds 58°C – 50 seconds 72°C – 1 minute 72°C – 5 minutes 4°C – Hold	} 35 cycles ~570 bp
		MatK R1	5'-ATGTTGATCGTAAATG AGAAGATTG-3'		
Nuclear gDNA (Coding)	Endoxyloglucan Transferase (<i>XTH</i>)	EXGT 3'- end For	5'-GCAGCCGACACTTGT ATGGT-3'	95°C – 5 minutes 95°C – 1 minute 58°C – 40 seconds 72°C – 50 seconds 72°C – 5 minutes 4°C – Hold	} 35 cycles ~550 bp
		EXGT 3'- end Rev	5'-GATTTGTCGGTGCAAT AAT-3'		

Table 2. GenBank accession numbers (with source vouchers) specific for different regions.

Taxon	Voucher	Accession Numbers for Specific Regions				
		ITS	IGS1	IGS2	MatK	XTH
<i>C. olerorius</i>	1419	FJ161701	JQ609257	JQ625351	JQ693588	JQ693581
<i>C. fascicularis</i>	1473	FJ527600	FJ624205	JQ625345	JQ693589	JQ693579
<i>C. aestuans</i>	3951	FJ527605	JQ609256	JQ625348	JQ693590	JQ693576
<i>C. pseudo-olerorius</i>	4155	FJ527602	-	JQ625352	JQ693591	-
<i>C. siliquosus</i>	1475	FJ527604	FJ624202	JQ625349	JQ693592	JQ693577
<i>C. tridens</i>	3714	FJ527603	FJ624201	JQ625346	JQ693593	JQ693580
<i>C. trilocularis</i>	3700	FJ527601	FJ624200	JQ625347	JQ693594	JQ693582
<i>C. capsularis</i>	210143	FJ527599	JQ609258	JQ625350	JQ693595	JQ693578
<i>H. sabdariffa</i> var. <i>sabdariffa</i>	1720	FJ527608	FJ624203	JQ625356	JQ693596	JQ693585
<i>H. cannabinus</i>	1653	FJ527607	JQ609259	JQ625353	JQ693597	JQ693584
<i>H. suratensis</i>	CGR_1750	FJ527609	JQ609262	JQ625358	JQ693598	-
<i>H. acetosella</i>	4293	FJ621494	JQ609260	JQ625357	JQ693599	JQ693583
<i>H. radiates</i>	4993	FJ527606	JQ609261	JQ625354	JQ693600	JQ693587
<i>H. sabdariffa</i> var. <i>altissima</i>	4203	JQ609255	FJ624204	JQ625355	JQ693601	JQ693586

Table 3. Properties of the data matrices generated based on the sequence analysis.

Name of the Data Matrices	Number of Taxa	Total Number of Characters	Number of Conserved Characters	Number of Variable Characters	Number of Parsimony-Informative Characters
ITS	57	1037	355	672	571
XTH	16	648	278	368	266
MatK	53	607	507	99	68
cpDNA-combined (IGS1, IGS2 and MatK)	172	2893	1501	1220	882
All-combined (IGS1, IGS2, ITS, XTH and MatK)	202	4578	2134	2260	1719

DNA sequence retrieval

Thermal cycles for PCR, primer sequences and sizes of amplified products are given in Table 1. The amplified products were checked by agarose gel electrophoresis⁴⁷ and then purified using MinElute Gel Extraction Kit (QIAGEN Ltd.).⁴⁸ Purified PCR products were sequenced by a commercial service provider, 1st Base (Selangor Darul Ehsan, Malaysia) and contigs were assembled using CAP3 sequence assembly program.⁴⁹ All DNA sequences derived from the contigs were verified using BLASTn⁵⁰ and deposited in GenBank (See Table 2). Sequence data of species from Malvaceae and Sparrmanniaceae families belonging to genera other than *Corchorus L.* and *Hibiscus L.* were obtained from the NCBI GenBank. (See Supplementary file 1).

Phylogenetic analysis based on sequence data

Multiple sequence alignments were performed with CLUSTALW2.⁵¹ A region specific data matrix was built based on sequence alignment. To generate combined sequence alignment of multiple regions, SeaView4.4.0^{52,53} was used. Two combined data matrices were built in this study; cpDNA-combined

and all-combined. Final data matrices of the latter analyses were built using MEGA version 6.³⁴ Maximum Likelihood (ML) method was applied for phylogenetic analysis following the Tamura-Nei model.⁵⁴ Percentage of replicate trees in which the associated taxa cluster together in the bootstrap⁵⁵ test (1000 replicates) are shown next to the branches (Figure 1-5).

RESULTS

The properties of data matrices subjected to phylogenetic analysis are reported in Table 3. The majority-rule consensus trees using Maximum Likelihood (ML) methods (1000 bootstrap replicates) are illustrated in Figures 1 to 5. Several other genera of both Malvaceae and Sparrmanniaceae family were used to test the monophyly of genera *Corchorus* and *Hibiscus*. All the trees were re-rooted to *Corchorus spp.* and most trees were found to segregate both the genera into two different well-resolved primary clades (Figure 1-5). However IGS1 region of *C. pseudo-olerorius*, XTH region of *C. pseudo-olerorius* and *H. suratensis* could not be amplified with the designed sets of primers.

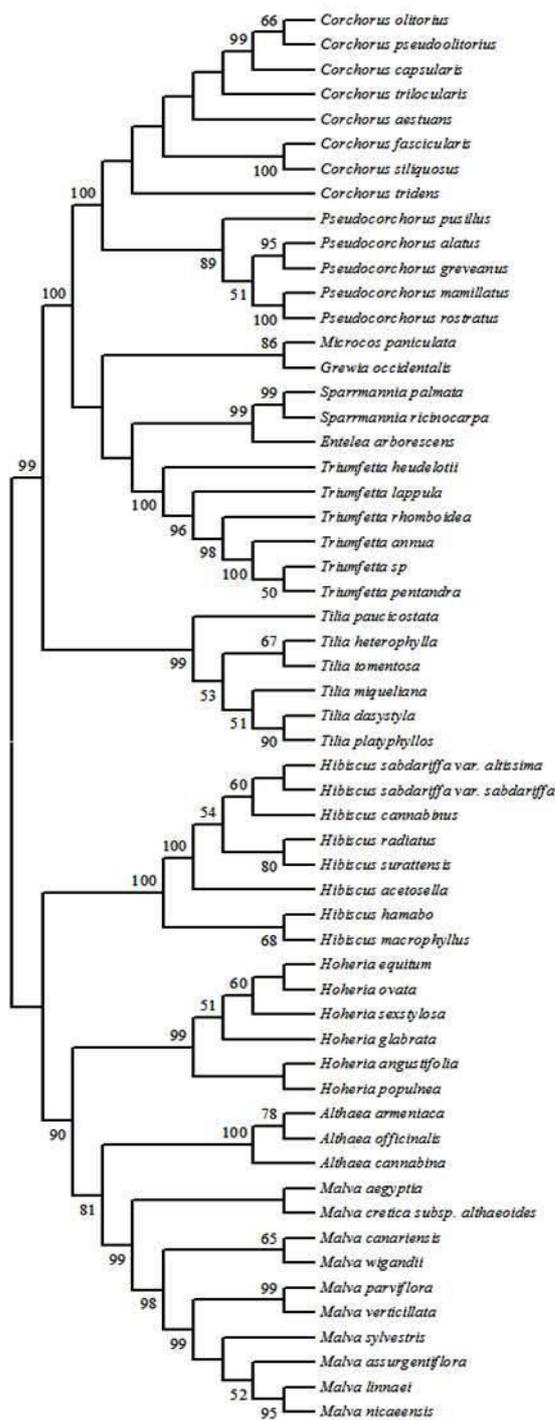


Figure 1. The majority rule bootstrap consensus tree inferred from 1000 replicates based on ITS data matrix by Maximum Likelihood (ML) method.

ML tree from ITS data matrix

The ML analysis of ITS sequence data matrix resulted in a bootstrap consensus tree with the log likelihood of -10007.40 [SBL (Sum of Branch Length) = 2.86729418; consensus cut-off value = 50] (Figure 1). This analysis showed well defined clades for genera *Corchorus* and *Hibiscus* with strong bootstrap support and no outgroup member (Figure 1). The genus *Hibiscus* was found to have two sub-clades; one containing *H. macrophyllus* and *H. hamabo* with 68%

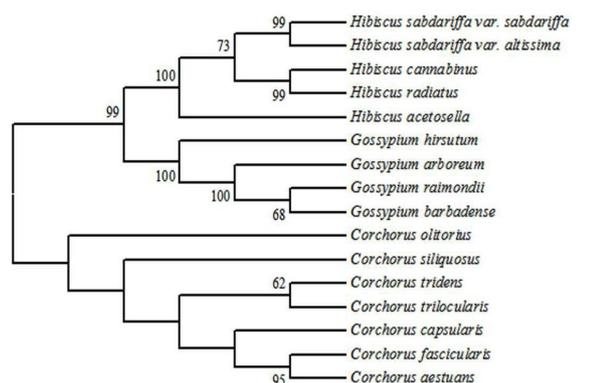


Figure 2. The majority rule bootstrap consensus tree inferred from 1000 replicates based on XTH data matrix analyzed by Maximum Likelihood (ML) method.

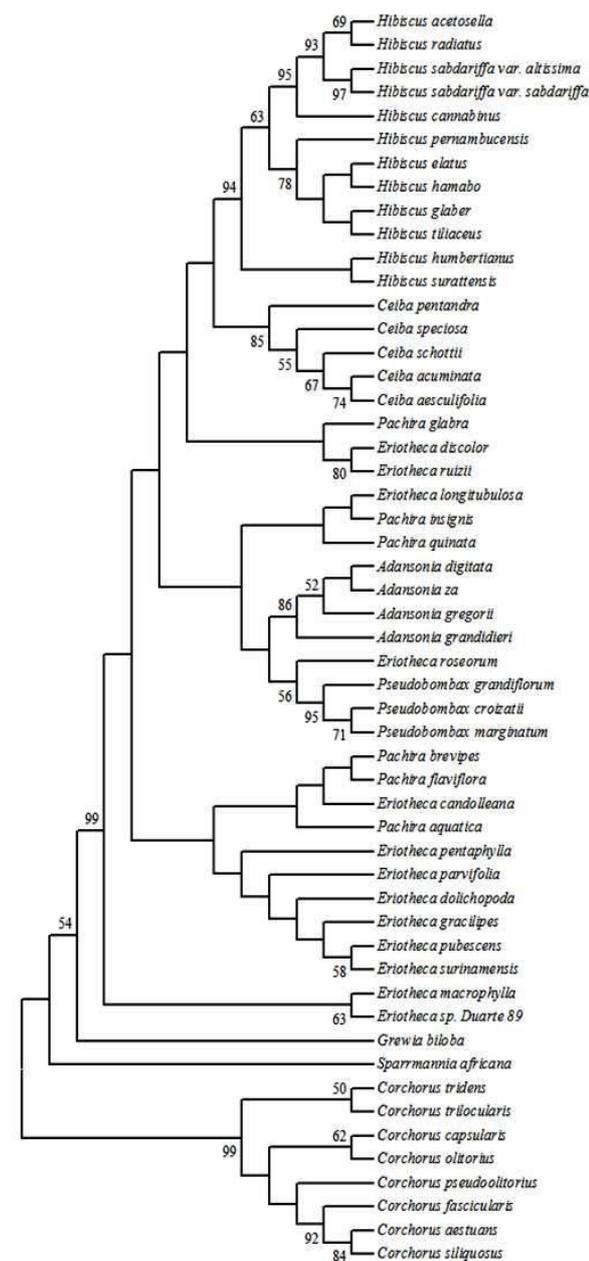


Figure 3. The majority rule bootstrap consensus tree inferred from 1000 replicates based on MatK data matrix analyzed by Maximum Likelihood (ML) method.

bootstrap support, while the other members from section Furcaria⁵⁶ were placed in another well resolved subclade (bootstrap 100%). Although with less bootstrap significance, a single terminal clade was found for two varieties of *H. sabdariffa*. This agrees well with their taxonomy (<50% bootstrap). *H. suratensis* and *H. raditus* were also in the same terminal clade with 80% bootstrap. Subclades of *Corchorus spp.* on the other hand, were not so well-resolved (bootstrap value <50%), except for the terminal clade of *C. fascicularis* and *C. siliquosus* (bootstrap 100%).

ML tree from XTH data matrice

The ML analysis with XTH data matrice resulted in a bootstrap consensus tree with log likelihood of -3256.01 [SBL = 1.16892516; consensus cut-off value = 50] (Figure 2). The XTH inference showed no paraphyly for *Corchorus L.* which was in agreement with the ITS data. Root clade for *Hibiscus spp.* was also evident (bootstrap 100%), suggesting monophyletic properties. No close relationships were observed between *C. oltorius* and *C. capsularis*. However, *C. fascicularis* and *C. aestuans* were placed in proximal positions with 95% bootstrap support. Unlike ITS data, terminal clade of two varieties of *H. sabdariffa* was found to be well-resolved here (99% bootstrap), as well as the terminal clade of *H. cannabinus* and *H. radiatus* (99% bootstrap).

ML tree from MatK data matrice

The ML analysis with MatK data matrice resulted in a bootstrap consensus tree with log likelihood of -1675.97 [SBL = 0.21567191; consensus cut-off value = 50] (Figure 3). Inferred ML tree separated both the genera, *Corchorus* and *Hibiscus* into well resolved primary clades. Members of the genus *Hibiscus* segregated into multiple subclades. Except for *H. suratensis*, other members of section Furcaria (*H. cannabinus*, *H. acetosella*, *H. radiates* and *H. sabdariffa*) were placed together in a subclade. However, *H. cannabinus* was found to have >90% bootstrap support for its separation from the others. In case of *Corchorus spp.*, one subclade included *C. oltorius* and *C. capsularis* (62% bootstrap), while another contained *C. tridens* and *C. trilocularis* (50% bootstrap). A trio, including *C. fascicularis*, *C. siliquosus* and *C. aestuans* were placed in another subclade (92% bootstrap).

ML trees from combined data matrices

The ML analysis of cpDNA-combined (IGS1, IGS2 and MatK) and all-combined (ITS, IGS1, IGS2, MatK and XTH) data matrices resulted in bootstrap consensus trees with the log likelihood of -14740.69 [SBL = 1.88269404; consensus cut-off-value = 50] (Figure 4) and -29627.59 [SBL (Sum of Branch Length) = 4.64032122; consensus cut-off value = 50] (Figure 5) respectively. Both ML trees confirmed the monophyly of *Corchorus L.* with good bootstrap support. However, the inferences were not the same

for *Hibiscus L.*, as combined-cpDNA tree (Figure 4) gave two different clades for the genus, while its members were placed in different clades in the all-combined tree (Figure 5).

DISCUSSION

Over time, analyses of different coding and non-coding genomic regions have been made to better interpret evolutionary relationships. In order to determine maternal ancestry, several chloroplast regions/genes have also been taken into consideration.^{16,47,57,58} However, reaching a conclusion becomes complicated if there is disagreement in the phylogenetic inferences from different genomic regions. In such cases, combined phylogenetic approaches are more informative,^{59,60} since it can minimize the specific regional and functional effects on phylogenetic inferences.

A significant part of this study was made to know more about the origins of both the genera, as the issue is still a matter of controversy.^{61,62} To test the monophyly of members of the genera *Corchorus* and *Hibiscus*, several other genera members of their respective families, Sparrmanniaceae and Malvaceae were included as controls. However, for the species of the two genera included in this study sequences of all 5 regions (ITS, IGS1, IGS2, MatK and XTH) were not available in the database. Therefore, based on sequence availability, different regions were analyzed using different genera of both the families to understand the phylogenetic relationship within the members of genera *Corchorus* and *Hibiscus*.

This study sought to answer only the above issues and not to propose any taxonomic classification. Therefore, a rational approach was implemented for inclusion of species from genera *Corchorus* and *Hibiscus* based on their economic importance and diversity in worldwide distribution (Table 4). The *Corchorus* species included in this study are widely distributed in the African and Indian tropics.^{61,63} Although the first three species (9, 10, 11 in Table 4) of the genus *Hibiscus* are reported to have originated in Africa,⁷ controversies are still there regarding their routes of dispersal.⁶² A similar disagreement also prevails for the two cultivated species (*C. oltorius* and *C. capsularis*) of *Corchorus*.³⁸

Evolutionary divergence or distance estimation test results^{64,65} speculated the species of the genus *Corchorus* to be more divergent than *Hibiscus L.* (Suppl. 3, 5-6). This could explain the strong species-speciation⁶⁶ between the members and why inter-specific hybridization among the *Corchorus* species has never been successful.^{38,61}

All the inferred ML trees from different data matrices (Figures 1-5) strongly support the monophyly of *Corchorus*, agreeing with earlier reports.^{17,23} Moreover, such inferences also support the new classification of *Corchous spp.*,³ as the different

Table 4. List of the species of genera *Corchorus* and *Hibiscus* included in the study and the reason for their inclusion.

Serial	Species	Reasons	Reference
1, 2	<i>C. oleritorius</i> and <i>C. capsularis</i>	Two most cultivated species	(Mahapatra et al. 1998)
3	<i>C. aestuans</i>	The most dominating wild species in the Indian sub-continent.	(Sinha et al. 2011)
4	<i>C. fascicularis</i>	One of the dominating wild species in both the Indian sub-continent and Africa.	(Sinha et al. 2011)
5	<i>C. siliquosus</i>	Wild in American continent.	(Sinha et al. 2011)
6	<i>C. tridens</i>	Wild and widely distributed in Africa.	(Burkill 1995)
7	<i>C. pseudo-oleritorius</i>	Immune to fungal attack.	(Sinha et al. 2011)
8	<i>C. trilocularis</i>	Show strong resistance to fungal attack.	(Sinha et al. 2011)
9, 10	<i>H. cannabinus</i> and <i>H. sabda riffa</i> var. <i>altissima</i>	Two most cultivated species.	(Pursejlove 1976)
11	<i>H. acetosella</i>	Highly resistant to root-knot nematode (<i>Meloidogyne spp.</i>) disease, whereas the cultivated species are susceptible to it.	(Menzel and Wilson 1961)
12	<i>H. sabdariffavar.sabdariffa</i>	Susceptible to root-knot nematode and not highly productive.	(Lawton 2004)
13, 14	<i>H. radiatus</i> and <i>H. surattensis</i>	Wild and native to the Asian and African tropics.	(Lawton 2004)

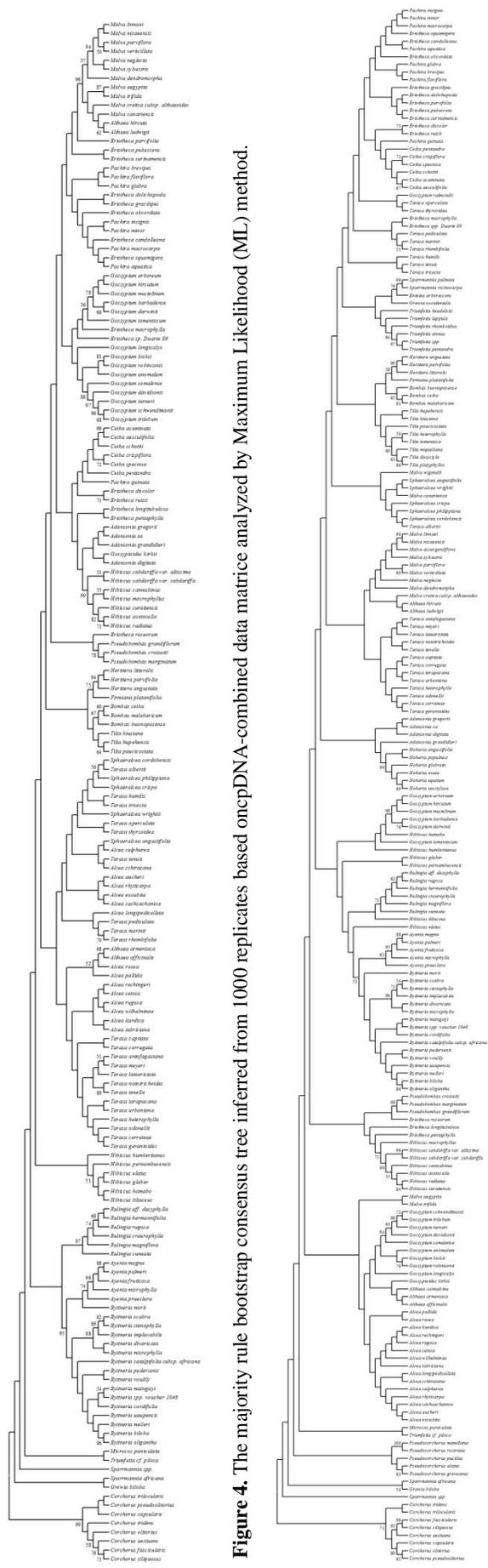


Figure 4. The majority rule bootstrap consensus tree inferred from 1000 replicates based on cpDNA-combined data matrix analyzed by Maximum Likelihood (ML) method.

Figure 5. The majority rule bootstrap consensus tree inferred from 1000 replicates based on mtDNA-combined data matrix analyzed by Maximum Likelihood (ML) method.

genera of Sparrmanniaceae family were found to be placed close to each other than those from Malvaceae (Figure 1, 3, 4, 5). On the other hand, the combined-cpDNA ML tree (Figure 4) did not infer monophyly between all the members of genus *Hibiscus* here, as two separate clades were found for them. Moreover, the all-combined tree (Figure 5) showed presence of several *Hibiscus spp.* in clades of genera other than their own. Such occurrences could be considered as a major paraphyletic occurrence for this genus.

Strong kinship between *H. acetosella* and *H. radiatus* were found from the cp-combined inferences (Figure 4) as well as the MatK inference (Figure 3), while other regions showed no such relationship. This is most likely due to same maternal ancestry. On the other hand, *H. radiatus* was found close to *H. suratensis* (84% bootstrap support) in all-combined inferences (Figure 5) and *H. Cannabinus* in XTH inferences, (Figure 2). These kinships are credible as there are reports that speculate *H. radiatus* to be a hybrid of *H. cannabinus* and *H. suratensis*.^{67,68} On another matter, XTH regions seem to be bearing the semblances of long-lost ancestry, which is always crucial for phylogenetic analyses.

Although ITS-ML tree (Figure 1) supports monophyly of the genus *Hibiscus*, segregation of the species under section *Azanza* (*H. macrophyllus* and *H. hamabo*) within the genus⁵⁶ from sect. *Furcaria* (other *Hibiscus spp.*) is in full accordance with their taxonomy (100% Bootstrap). Same seclusion can also be noticed from MatK-ML tree (Figure 3). Almost without any bootstrap support (5%), identical inference showed *H. suratensis* to be in the same terminal clade with the *Azanza* species. Two varieties of *H. sabdariffa* found in close proximity in all ML trees, agrees well with their taxonomic positions.

In case of *Corchorus L.*, close proximal position of *C. fascicularis* with *C. siliquosus* inferred by both ITS (100% bootstrap) (Figure 1) and the all-combined trees (Figure 5), was of interest as they are native to two distant continents.^{23,61} On the other hand, XTH inference (Figure 2) showed a kinship between *C. fascicularis* and *C. aestuans* (99% bootstrap). MatK inference (Figure 3) also hypothesizes all three to be related to each other (>60% bootstrap), suggesting a close maternal ancestry. Since *C. siliquosus* is a wild American species and the other two are native to Africa, a possible migratory event could have been involved here.

Neither the ITS nor the XTH tree (Figure 2) inferred any significant phylogenetic kinship between the two cultivated species of *Corchorus* (*C. olitorius* and *C. capsularis*), supporting previous reports.⁶⁹⁻⁷¹ However, MatK tree inferences strongly oppose such conclusion (Figure 3), as it suggests a significant relationship (62% bootstrap) between *C. olitorius* and *C. capsularis*. This implies a closely related maternal ancestry -a possibility raised in earlier studies.^{23,38} Nonetheless, such likelihood still lacks credence, as little semblance is found in the morphologies of *C. capsularis* and *C. olitorius*.⁷¹ Moreover, the former is considered native to India³⁸ while the latter is indigenous in Africa.¹⁷ Such ambiguity can be resolved if the possibility of a migratory event is taken into consideration. As the African tropics is considered the center of origin for the genus *Corchorus*,⁷² it can be hypothesized that both *C. olitorius* and *C. capsularis* have their origins in Africa, but the latter migrated to the Indian sub-continent and eventually evolved to such a form that it now bears little semblance to the genomic DNA or morphology of the former.

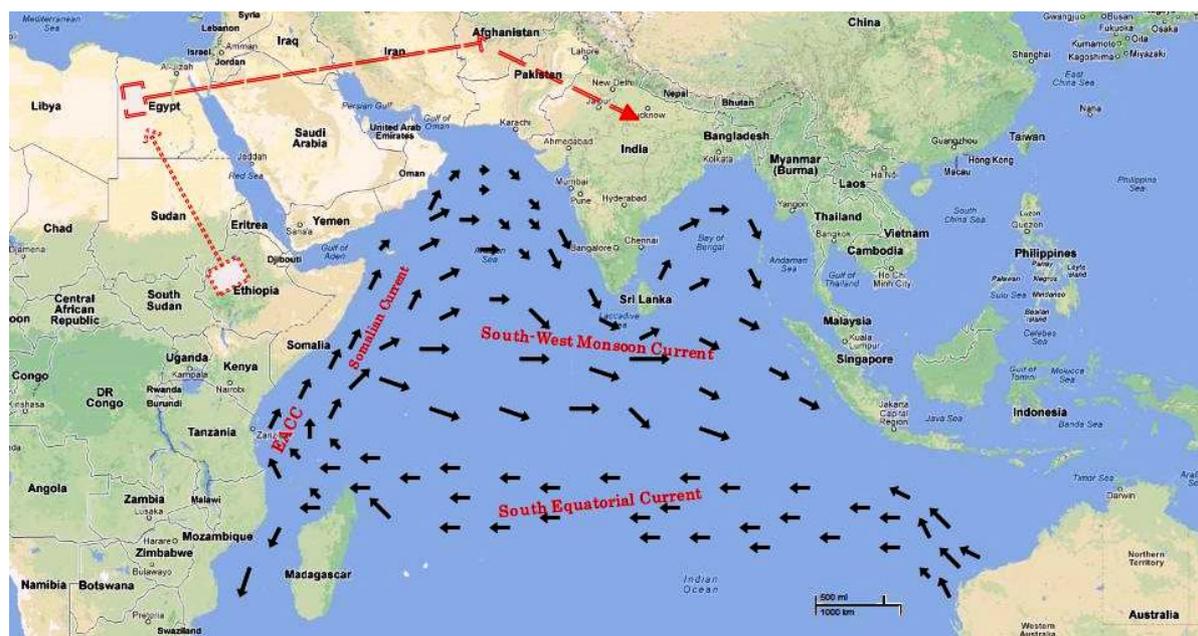


Figure 6. Two possible migratory routes for *Corchorus L.* one from East Africa to Indian subcontinent via the Egyptian trade route and the other along the coasts of East Africa to India carried by East-African Coastal current (EACC), Somalian and South-West Monsoon currents (Ocean currents are drawn according to the description by Iversen et al. (Iversen et al. 1984)).

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Migrations have played important roles in such ancestral events and there are several reports of relocation of different *Hibiscus* species from their origins to distant places^{56,73} generally through Long Distance Dispersal (LDD).⁴⁴ No such theory has been proposed for *Corchorus L.* However, Benor¹⁷ anticipated a dispersal route from East Africa to Asia through the ancient Mediterranean-Indian trade route.

Based on our results and archeological records, we propose a more coherent hypothesis for the dispersal and evolution of *Corchorus spp.* Besides Egypt, ancient trade relation between East Africa (Ethiopia) and India dates back only to the mid-first century AD, known as *Periplus Maris Erythraei* (Periplus of the Erythraean Sea).⁷⁴ In contrast, there are evidences of the presence of jute clothes (generally made with fiber of *C. olitorius* and *C. capsularis*) in the Indus civilization dating back to 2200-1900 BC.⁴² This suggests for the existence of jute in India even before ancient trade relations between India and east Africa.

A trade route, called *lapis lazuli* between Egypt to Harappa, Lothal in northwestern India existed in the third millennium BC⁷⁵ and another route joining Egypt and Ethiopia was present in the fourth millennium BC.^{41,76} Because of high concentration of *Corchorus spp.*¹⁷ in eastern Africa, the region can be considered a hub for this fiber crop. It is likely that seeds were brought to India from Ethiopia or other East African region by Egyptian traders between the 3rd and 4th millennium.

Such LDD (Long Distance Dispersal) events of seeds could have also been driven by migratory animals like birds, extreme meteorological phenomena (huge explosions dispersing everything in their path), wind or ocean currents.⁴⁴ Floatable seeds, seedpods and rafts transporting seedpods are known to cross hundreds of kilometers through the ocean currents.⁴⁴ Records suggest that seeds of 78% of plants in the volcanic island, Surtsey (35 km from Iceland) reached there through ocean currents.^{44,77}

In case of *Corchorus L.*, our results indicate significant kinship in maternal ancestry and possible migratory events from East Africa to India. Therefore, another potential dispersal route through ocean currents could be hypothesized for *Corchorus spp.* Seeds or seed pods from east Africa could have migrated through the currents of the Indian Ocean flowing along with the East African coastal, Somalian and South-West monsoon currents before reaching India (Figure 6). This hypothesis of LDD via the

currents of Indian Ocean could also be true for the dispersal of those *Hibiscus* species which are described to have an East African origin.⁶⁷

CONCLUSION

Analyses of four different regions of the nuclear and chloroplast genomes support monophyly of the genus *Corchorus L.* In contrast, paraphyletic occurrences were observed for *Hibiscus L.* in combined-ML analyses, which agree well with several previous reports.^{11,16}

Two commonly cultivated species of the genus *Corchorus* namely *C. olitorius* and *C. capsularis*, can be inferred as descendants of the same or closely related maternal ancestor in Africa. *C. capsularis* could have come much earlier to India than *C. olitorius* via two possible routes, ancient Egyptian trade route or Indian Ocean currents.

Resemblance in cpDNA analyses among three wild *Corchorus spp.*; *C. fascicularis*, *C. aestuans* and *C. siliquosus* also suggest closeness in their maternal ancestry, suggesting another possible ancestral migratory event. However, such assumptions can only be established with proper paleontological evidences, which eventually will help to precisely describe their origins.

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