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A Review on Molecular Studies of Rattans, with Special Attention to the Genus *Calamus* (Arecaceae)

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Abstract: Rattans, spiny climbing palms belonging to the subfamily Calamoideae, are an ecologically and economically important group of palms. The taxonomic complexities such as, homoplasies, look-alike species, environmental plasticity and species complexes, impede the traditional identification and classification in this group. DNA barcoding and molecular phylogeny can lend a hand in better understanding systematics of these taxa. The slow rate of evolution of palm DNA restricts the use of plastid as well as nuclear gene regions in molecular systematics of palms. Recently, the introduction of low copy nuclear regions has facilitated to resolve these issues to some extent. Introduction of super barcodes as well as whole genome sequencing could act as a promising platform to strengthen the aspects of species discrimination in palms, in the near future. Molecular phylogeny teamed with biogeography can provide a wider insight into the distribution pattern of extant species as well as their origin of ancestral area. The deterioration of natural populations of rattans due to their extensive extraction has brought to the fore the importance of their conservation. Early sex determination of the dioecious plants using high-throughput molecular methods can lead to viable conservation programmes. Population genetic studies in this group will provide a better understanding the diverse genotypes existing within and among populations.

Key words: Species identification, DNA barcoding, phylogeny, sex determination, population genetics.

INTRODUCTION

Rattans are spiny, climbing palms with solid stems belonging to the subfamily Calamoideae, of family Arecaceae. There are around 600 species of rattans belonging to 13 genera, distributed in tropical and subtropical regions of the world. They are often regarded as 'green gold' owing to their economic values and unique properties such as strength, lightness, durability, appearance and flexibility (Mohan and Tandon, 1997). Thirteen genera under Calamoideae (*Calamus, Calospatha, Ceratolobus, Daemonorops, Eremospatha, Korthalsia, Laccosperma, Myrialepis, Oncocalamus, Plectocomia, Plectocomiopsis, Pogonotium* and *Retispatha*) are considered to be the commercially important rattans. Even though some species are shrubby non-climbers

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and seen as undergrowth in forest, they are included in rattan genera due to their reproductive features similar to other climbers. Sago palm, bertam and tree palms such as *Raphia* (Raffia) and *Metroxylon* (Sago palm) and shrub palms such as *Salacca* (Salak) (Uhl and Dransfield, 1987) belong to climbers. Species diversity is rich in Malaysia, Indonesia, Philippines, China, Bangladesh, Sri Lanka, Myanmar and India (Lalnuntluanga *et al.,* 2010).

Calamus is the largest genus of palms, characterized by spiny, acaulescent, erect or high climbing palms with solid stem. They can be clustering (clump-forming) or solitary with characterized fruits and necessary pre-adaptations to climbing habit (Dransfield, 1992). The genus *Calamus* is often regarded as "protean" (Uhl and Dransfield, 1987) because of the extreme morphological heterogeneity that it encompasses. This is predominantly an Asian genus and its distribution ranges from the Indian subcontinent and south China southwards and east through Malaysia and Indonesia to Fiji, Vanuatu and tropical and subtropical parts of eastern Australia. *C. deerratus*, only representative species of the genus in Africa exhibits morphological variations among populations.

They are extensively utilised for furniture making, handicrafts industries and making various sports items owing to their high strength, flexibility and durability of their elastic stem. In Southeast Asia, approximately half a million people are engaged directly in rattan trade (Uma Shaanker *et al.,* 2004) and global trade of canes approximates to US $ 4 billion per year (Arunachalam, 2012). They are also used in Ayurvedic systems of medicine for treatment of various diseases like cold, rabies, among others (Lakshmana, 1993). *Calamus* oil extracted from root is used for perfuming and flavouring liquors and tender shoots of *C. erectus, C. floribundus* and *C. latifolius* are edible (Singh *et al.,* 2004).

Even though palms have numerous observable morphological characteristics such as leaf, stem, inflorescence and fruit structures for identification, in depth studies in taxonomy were difficult due to their spiny nature and the absence of flowers and fruits most of the year (Uhl *et al*., 1995). Lack of sufficient herbarium specimens also creates an obstacle for comparison of species (Sreekumar *et al.,* 2006). Several taxonomic complexities like homoplasies, look-alike species, environmental plasticity and species complexes, encountered within this group make their species identification using morphological characters alone, more complicated (Boer, 1968; Sreekumar and Henderson, 2014). The presence of homoplasy in several morphological characters often creates difficulties in resolving the taxonomic complexities existing in the family (Uhl *et al*., 1995). Even though, phylogenetic studies have been reported in palms (Barfod *et al*., 1999; Pintoud, 1999; Henderson, 2002) morphological data alone are not adequate to resolve phylogenetic relationships (Uhl, 1995; Baker *et al*., 1999; Baker *et al*., 2000a; Lewis *et al*., 2000).

Extensive extraction, loss of habitats and other anthropogenic factors have led to the deterioration of natural populations of rattans, further accentuated by dioecy and premature harvest of rattans. The sex of species cannot be determined morphologically till the reproductive maturity age of five or more years are attained and rarity of flowering further hastens the issue in rattans. A number of endemic rattan species are already threatened and are on the verge of becoming endangered (Lakshmana, 1995; Lyngdoh *et al.,* 2005). A few studies have addressed the population genetic consequences of habitat fragmentation in many rattan species (Wickneswari and Boyle, 2000; Ravikanth *et al.,* 2001; Lyngdoh *et al.,* 2005).

Species identification using molecular tools

A clear understanding of species delimitation is important for the stable taxonomic classification of rattans which can be utilised for their conservation and sustainable development. A widespread species may be referred to, by many names because its range encompasses a number of language groups. Similarly, for multi-purpose species names also exist based on the different uses of plant or various stages of development from juvenile to adult. Commonly, blanket names for "cane" are given to a wide range of species. However, it is essential to know the commercially important species for meaningful inventories of commercially important taxa and assessment of silvicultural potential of each species (Dransfield, 2001). Molecular techniques were employed to sort out the existing taxonomic problems in rattans and found to be an important tool for rattan classification with high level of precision (Baker *et al.,* 2000b; Sreekumar *et al*., 2005).

DNA barcoding was reported as an efficient supplementary tool for the identification of palms. The successful species identification by using combination of three barcodes – *mat*K*, rbc*L and nrITS2 were reported in tribe Caryoteae (subfamily Coryphoideae (Jeanson *et al.,* 2011). *psb*A-*trn*H was found as potential barcode for identification of *Phoenix dactylifera* L. cultivars (Al-Qurainy *et al*., 2011) and *Calamus* species from China (Yang *et al*., 2012). The *psb*Z-*trnf*M (CAU) region was reported as a suitable barcode for identification of *Phoenix* (Ballardini *et al.,* 2013). The inefficiency of single nuclear genic region for species discrimination was reported in *Daemonorops* (Umapathy *et al*., 2015). Even though barcoding studies using plastid regions has been reported in palms, reliability of these barcode regions in rattans needs to be ascertained due to its slow evolutionary rate.

The availability of standardized universal primers, makes shorter DNA sequences-mini-barcodes, a more suitable option for DNA barcode analysis through inexpensive and comprehensive large-scale species identification (Hajibabaei and McKenna, 2012). While for closely related species, whole-plastid-based barcodes, super barcodes offer great potential in species discrimination (Li *et al*., 2015). Continuing advances in sequencing technologies, may uphold whole genome sequencing and super barcodes as most preferred choice for palm identification in near future.

Molecular Phylogeny

Palms belonging to commelinid clade of monocotyledons are monophyletic in origin (Asmussen *et al*., 2006; Chase *et al*., 2006). Even though phylogenetic studies based on morphology has been reported in palms (Barford, 1999; Pintoud, 1999; Henderson, 1999), homoplasies and taxonomic complexities limited their interpretation to resolve phylogenetic relationships (Uhl, 1995; Baker *et al*., 2000; Lewis *et al*., 2000). Initially restriction fragment length polymorphism (RFLP) data have been used for reconstructing molecular phylogeny of the Palm family (Uhl *et al*., 1995).

Obtaining well resolved phylogenetic trees at species level in the family is a challenge due to notoriously slow rate of molecular evolution, convergent evolution among some morphological characters, difficulties in outgroup choice and character polarisation (Hahn, 2002b). The slow rate of evolution in plastid regions as well as mitochondrial regions is a major hitch for comparative research in these taxa (Eyre-Walker and Gaut, 1997; Baker *et al*., 2000a). Chloroplast DNA was observed to have 5 to 13 fold slow rate of evolution (Wilson *et al*., 1990). *rbc*L has 5 times and *Adh* has 2.5 times slower evolutionary rate in palms when compared with that of grasses (Gaut *et al*., 1992; 1996). Phylogenetic relationship of 22 genera of Calamoideae using *rps16* intron was studied and supported the slower evolutionary rates of chloroplast regions (Baker *et al*., 1999). The slow evolutionary rate of chloroplast, mitochondrial and nuclear gene regions was found within this genus (Gaut *et al*., 1992; Eyre-Walker and Gaut, 1997). In spite of its low evolutionary rate, plastids has been successfully used to resolve relationship at lower taxonomic levels in palms (Asmussen *et al.,* 2000; Cuenca and Asmussen-Lange, 2007; Baker *et al.,* 2009). Molecular phylogenetic studies in palms were limited in the past due to the lack of appropriate primers (Baker and Couvreur, 2012), later on such studies have been increasing (Meerow *et al*., 2009; Barfod *et al*., 2010; Roncal *et al*., 2013).

Nuclear (5Snr DNA, 5S spacers) and plastid (*trn*L-F*, rps16* intron, *atp*B*, rbc*L*)* regions have been included in palm phylogenetics (Barrow, 1996; Asmussen 1999a & b; Baker 1999a; 2000 a & b; Asmussen and Chase 2001; Hahn, 2002a). Monophyletic origin of Palmae was well supported in phylogenetic studies using chloroplast regions (Chase *et al*., 1993;1995). Relationship based on morphological and chloroplast DNA suggested monophyly of Coryphoideae, Calamoideae and Phytelephantoideae (Uhl, 1995). Monophyly of tribe *Genomeae* was reported using *rps16* intron (Asmussen *et al*.,1999b) as well as *rbc*L and *trn*L-F intergenic spacer region (Asmussen and Chase, 2001). Chloroplast DNA introns and *rps16* data were adopted to reveal monophyly in Calyptrogyne, Calyptronome, *Pholidostachys* and *Welfia* (Asmussen *et al*., 1999a). Faye *et al*. (2014) studied 100 primers covering 50 % of plastid genome and *atp*H-*atp*I, *psb*A-*trn*H*, psb*Z-*trnf*M *rps3-rpL* regions were selected to prove monophyly of subtribe Ancystrophyllinae. However phylogenetic relationships among genera, Laccospermae, Ermospathae, Oncocalamoideae remain unresolved. This study

supported the efficiency of these four plastid markers in phylogeny (Faye *et al*., 2014). *rps16* intron showed low levels of variation and only suitable for family level phylogeny, substantiated previous studies that the chloroplast genome of palms is highly conserved (Wilson *et al*., 1990; Gaut *et al*., 1996; Baker *et al.,* 2000a). Domenech *et al*. (2014) reported the poor utility of plastid sequences in phylogenetic studies of Archontophoenicinae. Plastid regions *rps 16* along with *trn*L-*trn*F were reported to resolve phylogeny in palms, which changed the systematic position of palm species *Iriartea,* tribe Caryoteae and major clade comprising four subfamilies, Coryphoideae, Ceroxyloideae, Arecoideae and Phytelephantoideae (Asmussen *et al*., 2000). Even though poor performance of *trn*L-*trn*F conserved region for phylogenetic utility among species or closely related genera in Palmae has been reported, this spacer region revealed better relationship in higher taxonomic groups. Even at infrageneric level, very few studies have been reported using chloroplast regions to resolve phylogenetic relationship (Cuenca and Asmussen-Lange, 2007; Couvreur *et al*., 2011). Several studies reported the usefulness of plastid markers in combination with nuclear markers to resolve phylogenetic relationship (Lewis and Doyle, 2001; Roncal, 2013).

Nuclear regions provided a good source of phylogenetic information at low taxonomic levels since they appear to evolve more rapidly than those from plastid genome and have advantage of being potentially an independent source of evidence that can be compared with existing phylogenies (Gaut *et al*., 1996; Eyre-Walker and Gaut, 1997). The nuclear internal transcribed spacer (nrITS) region is showing higher level of polymorphism in Calamoideae due to concerted evolution which leads to higher level of homoplasy, suggesting that phylogenies derived from ITS may not be reliable (Baker *et al*., 1999). Higher level of within-individual polymorphism was identified in ITS region, indicating that concerted evolution is not effectively homogenizing ITS repeats. However these regions appear to have limited value in palm phylogenetics because of lack of homogeneity among repeats within individual palm genomics (Baker *et al*., 2000a & b). Phylogenetic analyses using morphological and molecular data supported monophyly of subfamily Calamoideae as well as subtribe Calaminae (Uhl *et al*., 1995; Baker *et al*., 1999a; Asmussen *et al.,* 2000; Tomlinson and Fisher, 2000).

Non-coding regions of highly repeated nuclear ribosomal DNA cistrons (copies of ITS regions of 18S-5.8-26S) are also utilized in plant phylogeny, but their resolution in palm phylogeny has been problematic due to their high degree of polymorphism within palms and relationships among paralogues can be difficult to interpret at species level. 5S nr DNA region were used to resolve phylogeny of palm subtribe Calaminae, but paralogous of 5S copies were present showing complex and indecipherable relationships in tribe Areaceae and Genomeae leading the interpretation more difficult (Baker *et al*., 2000b).

Since chloroplast and nuclear DNA have limited applications in palm systematics, the researchers searched for a new region like low copy number genes. Low copy nuclear regions provide robust evidences for relationships at intermediate and lower taxonomic level due to faster rate of evolution. The distinction of orthologous loci, complications related to concerted evolution or recombination among paralogous loci and intragenic polymorphism are challenges while using low copy nuclear gene (Small *et al*., 2004). Despite these obstacles, low copy nuclear genes represent the largest source of molecular data in palm phylogenetics (Mort and Crawford, 2004; Trenel, 2007). Palm phylogenetics indicated the utility of low copy nuclear regions, PRK (phosphoribulokinase), RPB2 (RNA polymerase II) and MS (malate synthase*)* to resolve complexities at lower taxonomic levels i.e. Borasseae (Bayton, 2005), Geonomeae (Roncal *et al.,* 2005), Ptychospermatinae (Zona *et al.,* 2011), Hyophorbe (Lewis and Martinez, 2000), Areceae (Lewis and Doyle, 2002), Chamaedorea (Thomas *et al*., 2006), Arecinae (Loo *et al.,* 2006), Heterospathe and Rhopaloblaste (Norup, 2006).

Malate Synthase (MS) sequences are reported to be variable in palms and potentially contain more phylogenetic information (Lewis and Doyle, 2001). Lack of resolution among major lineages within family using chloroplast and MS region may be due to rapid evolutionary radiation, without sufficient time for mutations to accumulate along internal branches (Lewis and Doyle, 2001). Single copy genes such as waxy (granule-bound starch synthase) (Mason-Gamer *et al.,* 1998), pistillata (Bailey and Doyle, 1999) and chloroplast expressed glutamine synthetase (Emshwiller and Doyle, 1999) have proven to be particularly useful as phylogenetic markers in palm families. PRK, gene encoding Calvin cycle enzyme phosphoribulokinase has been shown to be sufficiently variable to examine low level relationships within palms (Lewis and Martiner, 2000; Lewis and Doyle, 2002; Gunn *et al*., 2004; Roncal, 2005; Thomas *et al*., 2006). Non-coding intron RPB2 was found informative in exploring low level relationship in Arecoideae (Roncal *et al*., 2005). PRK and RPB2 produced well resolved phylogeny in Arecoid palms (Baker *et al.,* 2011). Roncal *et al.* (2005) developed palm specific primers for intron 23 of RPB2 for phylogenetic studies of palms and revealed monophyly of Genomeae. Monophyly of subtribe Ptychospermatinae was supported using RPB2 and PRK low copy nuclear regions (Zona *et al*., 2009). These regions are also supported resurrection and expanded circumscription of genus *Ponapea* as well as non-monophyly of genera *Drymophlew, Ponapea* and *Velicha.* Phylogenetic hypotheses suggested the divergence of Ptychospermeae into six major clades with repeated radiation into Australia and Western Pacific. The divergence studies also suggested the presence of newly discovered *Adonidia,* confirmed as sister species to *Adonidia merillis* likely to be the result of long distance dispersal (Zona *et al*., 2009). Molecular phylogenetic analysis of Arecaeae (Asmussen and Chase, 2001; Lewis and Doyle, 2002) confirmed the placement of Genomeae in subfamily Arecoideae (Uhl and Dransfield, 1987).

Phylogenetic utility of sequence of WRKY transcription factors, AGA1 (Agamous 1) and PHYB (Phytochrome B) genes were also analysed to determine palm phylogenetics (Meerow *et al*., 2009; Ludena *et al*., 2011). Exploration of these low copy nuclear regions will give a new insight to phylogeny of rattan genera.

Limited studies have been reported in molecular phylogeny of genus *Calamus*. The highly speciose genus *Calamus* was found to be non-monophyletic using 5S nr region with all five remaining genera (*Calospatha, Retispatha, Daemonorops, Ceratolobus* and *Pogonotium*) of subtribe Calameae being embedded within it (Baker *et al*., 2000b). Later on *Daemonorops, Ceratolobus, Calospatha, Pogonotium* and *Retispatha* were subsumed into genus *Calamus* (Baker, 2015). This leads to the inclusion of more species in the largest palm genus at over 370 species to around 520. The 5S non-transcribed spacer is too divergent across most taxa but proved to be useful at lower taxonomic levels. Subfamily Calamoideae, based on molecular phylogeny and fossils, is assumed to have diverged from other palms at crown node of family in Eurasia, expanding into Africa prior to divergence of its crown node (80 mya). Tribe Eugeissoneae was the first to be diverged from remaining Calamoideae in Eurasia and later, tribes Calameae and Lepidocaryeae, diverged from each other and former dispersed in Eurasia and latter in Africa (Baker *et al*., 2011). The dispersal of different genera from its inferred ancestral area to its present distribution is unclear and need to be explored.

Sex Determination

Sex of dioecious palm genera is generally determined from floral characteristics, which may not be possible throughout the year owing to seasonal flowering and fruiting (between the months of April and June) in rattans. Development of gender specific markers and early sexing of seedlings in genus *Calamus* can facilitate and ensure viable populations for *ex situ* conservation purposes. Screening of plants at seedling stage can be facilitated by PCR-based DNA markers. Kumar and Arumuganathan (1997) have determined nuclear DNA content of 42 species of rattan. Very few rattans have been investigated cytologically to determine chromosome numbers, diploid numbers vary from 22–24 (Rao and Rao, 1998). The genome size varied between 1.8 and 10.5 pg DNA per 2C nucleus. On the other hand, low frequency of sex-linked bands indicated DNA segments involved in sex determination are very small and probably represent a single gene or very few genes (Hormaza *et al*., 1994). A male specific random amplified polymorphic DNA (RAPD) molecular marker with approximately 500 bp length was generated for sex determination of *C. simplicifolius* (Yang *et al.,* 2005). SCAR marker generated for identification of male individual of *C. simplicifolius* was attempted in other two species, *C. tetradactylus* and *Daemonorops margaritae*, but failed to get amplification (Li *et al*., 2010). ISSR4_600 is a putative sex-linked marker for *C. tenuis*, first attempt to include ISSR markers for gender determination (Sarmah and

Sarma, 2011).

The introduction of high-throughput techniques like genotyping-by-sequencing (GBS) and restriction site associated DNA sequencing (RAD-Seq) can accelerate the early sexing procedures in rattans. These techniques help to avoid repetitive regions of genomes by choosing appropriate restriction enzymes, and lower copy regions can be targeted with higher efficiency (Gore *et al*., 2007). These have been successfully used to detect sex linked SNPs in *Pistacia vera* (Kofkas *et al*., 2015), *Loliumperenne* (Pfender *et al*., 2011; Hegarty *et al*., 2013), eggplant (Barchi *et al*., 2011), grape (Wang *et al*., 2012), globe artichoke (Scaglione *et al*., 2012), *Hippoglossus hippoglossus* (Palaiokostas *et al*., 2013). The use of GBS and RAD-Seq in rattans, for sex determination is recommended.

Population genetic structuring

Genetic diversity within populations is affected by key factors such as geographic distribution and mode of seed dispersal (Hamrick *et al*., 1991). Provenance and progeny trials have been carried out on *C. subinermis*, *C. manan* and some other species in Sabah (Lee, 1999). Bon (1997) investigated genetic variability in *C. subinermis* and demonstrated considerable variability in wild populations of this species in Sabah in relation to their geographic distribution. The proportion of polymorphic loci amplified in *C. thwaitesii* was 85 %. The high percentage of polymorphism has been reported in other rattans such as *C. metzianus* (Sreekumar, 2005). The high level of polymorphism is an indicative of increasing level of outcrossing between populations and among individuals consequent high level of genetic variability (Karron, 1991). The highest genetic diversity using RAPD markers was observed in *C. thwaitesii* accessions of Goa region, recommended as 'hot spot' of genetic variation and an important reservoir of potentially useful genes required to provide high priority for management strategies and conservation (Sreekumar and Renuka, 2006). Four biodiversity hotspot sites of north-eastern Himalayas of India, for conserving *C. flagellum* was identified using molecular markers (Lyngdoh *et al*., 2005). The species and genotype specific RAPD markers were developed for *Calamus* (Sarmah *et al.,* 2007) and suggested the conversion of RAPD markers into SCAR markers for further validation Arunachalam (2012). *C. thwaitesii* populations in different types of locations, *viz*. protected areas, buffer zones, and peripheral areas in the Western Ghats were analysed using ISSR markers, and found that protected areas, conserve genetic resources of rattans better than the other types of locations, indicating the vulnerability of rattans (Ramesha *et al*., 2007).

One of the major constraints in population genetic studies of rattans is the lack of availability of precise molecular markers. Among available genetic markers, Simple Sequence Repeats (SSRs) or microsatellites are the co-dominant, locus-specific, ubiquitous, experimentally reproducible, multiple allele markers with high amount of polymorphism (Selkoe and Toonen, 2006; Zhang *et al*., 2014; Harris-Shultz *et al*.,

2014; Chen and Okie, 2015; Kumbhar *et al.,* 2015; Mason, 2015). SSR markers have been particularly useful to distinguish closely related genotypes owing to their high degree of variability making them ideal for population genetics (Smith and Devey, 1994). The coconut microsatellite markers were successfully used to reveal the molecular differentiation of the four rattan genera by cross-species amplification, and suggested possibility of widespread use of microsatellites across species and genera (Rao *et al.,* 2007).

SSR markers were employed to analyze genetic diversity and population structure of other palms such as *Pheonix dactylifera* (Billotte *et al*., 2004; Elshibli and Korpelainen, 2008)*, Elaeis guineensis* (Billotte *et al*., 2001), *Cocos nucifera* (Perera *et al*., 2000; Teulat *et al*., 2000; Meerow *et al*., 2003). In rattans, SSR markers were used in *C. thwaitesii* (Kurian *et al*., 2013) and *C. simplicifolius* (Li *et al*., 2013). Cross species amplification of SSR markers in four genera of rattans such as *Korthalsia, Daemonorops, Zalacca a*nd *Calamus* were also reported (Rao *et al*., 2007). The intraspecific variability of rattans remains a poorly known area of research, much in need of further study.

CONCLUSION

Rattans*,* the spiny climbing palm of subfamily Calamoideae (Arecaceae) is beset with problems of environmental plasticity, homoplasies, look-alike species and species complexes which lead to difficulties in species identification and classification. Species discrimination and phylogeny analyses using molecular data have gone through many hurdles due to slow evolutionary rate in palm genome. Limitations of nuclear and chloroplast regions lead to the utilization of low copy nuclear regions. The vast data generated exploiting new genomic methods like whole genome sequencing, super barcodes etc. may be required to generate more robust phylogeny and comprehensive species resolution of rattan genera. This also aids in understanding the biogeography and distribution patterns of rattans. As the existing methods in early sex determination lack reproducibility, high-throughput molecular methods need to be adopted. A better understanding of the population genetic structure can be used a strong foundation for deriving meaningful conservation strategies in rattans.

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