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RESEARCH ARTICLE

# Phylogenetic position of the disjunct species *Musa ornata* (Musaceae): first approach to understand its distribution

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**Abstract** *Musa* L. commonly known as the banana group is one of the most important and oldest food crops of humankind. Among the wild relatives with ornamental interest in the genus, *Musa ornata* Roxb. shows a disjunct distribution between Asia and North America (Mexico). The wild occurrence of this species in Mexico has led to speculation about the evolutionary relationships with its Asian relatives. This study examined the phylogenetic relationships between intercontinental specimens of this species and, based on registered evidence, explored the more likely hypothesis about the origins of its distribution. The phylogeny of intercontinental specimens, along with other representatives of the same genus, was carried out using three molecular markers (ITS, *trnL-F,* and *atpB-rbcL*) and applying three phylogenetic reconstruction methods: maximum parsimony, maximum likelihood, and Bayesian inference. The genetic analysis of the combined dataset grouped together all the Mexican and most Asian specimens, but the monophyly of the species was not supported. The relationships suggest that Mexican populations may have originated from an Asian invasion. However, several studies and historical documents suggest the presence of *Musa* in America long before the arrival of Europeans. Based on its current distribution, phylogenetic evidence, and fossil record, this species' disjunct distribution could be explained in terms of an ancestral distribution range that encompassed America and Asia, followed by its subsequent restriction to the Old World and a secondary dispersal by humans. However, further studies are necessary to shed more light on the origins of this disjunct distribution.

**Keywords** Intercontinental disjunction · Musaceae · *Musa ornata* · Phylogeny · Tropical linage

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## Introduction

The disjunction between extant floras of Asia and North America has drawn scientific interest, as it offers an excellent opportunity to explore plant differentiation and allopatric speciation (Wen 2001; Donoghue and Smith 2004; Wen et al. 2010). Phylogenetic relationships between North American and Asian angiosperm species have been extensively

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studied (e.g. Zhou et al. 2006; Lo et al. 2009), particularly in disjunct temperate floras (Wen 1998; Manos and Donoghue 2001; Wen and Ickert-Bond 2009; Wen et al. 2010). By contrast, tropical intercontinental disjunctions remain poorly understood (Renner et al. 2001).

Different hypotheses have been used to elucidate how tropical lineages occupy disjunct geographic ranges. Vicariance has been proposed as an explanation of the wide distribution of lineages in the ancient Gondwana continent (Schönenberger and Conti 2003; Thorne 2004; De Queiroz 2005). According to Davis et al. (2002, 2004), the boreotropical migration hypothesis best explains the migration of some tropical lineages, with intercontinental disjunctions between the Old and the New World via the North Atlantic land bridges during the early Tertiary. Other studies suggest long-distance dispersal to new habitats as the origin of disjunct distributions (Davis and Shaw 2001; Cox and Moore 2005). It has also been noted that the intentional or incidental human dispersal of plants might have contributed to this type of distribution (Bullock et al. 2002; Blaum and Wichmann 2007). In this context, it has been suggested that humans are important dispersal vectors that have altered landscapes around the world (von der Lippe and Kowarik 2007).

Molecular data have been extensively employed to infer ancestral areas of disjunct plants (Wen 2000; Xiang and Soltis 2001). However, most studies of Asia-North America disjunctions in angiosperms have been carried out at the genus level or between groups of species. Therefore, there have been few studies on closely related or conspecific species (Li 1952; Wen 1999; Ze-Long et al. 2006), and even fewer of herbaceous plant species (Tiffney 1985a, b; Wen 1999; Nie et al. 2005).

*Musa* L. (Musaceae Juss.) is an herbaceous tropical genus, economically important as a crop, best known as the group of bananas (Li et al. 2010). The banana is the fourth most important food crop and the first fruit crop in the world (Wilson and Otsuki 2004). It is also an important source of income for many tropical countries that are home to the edible and ornamental species. Among the species in this genus, the wild banana *Musa ornata* Roxb. shows intercontinental disjunction between Asia and North America (Mexico; Fig. 1; Burgos-Hernández et al. 2013). Roxburgh (1814, 1824) originally described this species as native to Chittagong, Bangladesh. More recently, wild populations have been recorded in Andhra Pradesh and Harikhola, India (Häkkinen and Sharrock 2002). Interestingly, wild populations have also been recorded in tropical regions of Mexico, in important ecosystems such as tropical rain forests (Matuda 1950; Burgos-Hernández et al. 2013). The occurrence of wild populations of this species in conserved areas of Mexico has led to controversy about its apparent disjunct distribution.

Several hypotheses have been put forward to account for the occurrence of *M. ornata* in Mexico. Many believed that this species was first introduced to America by the Spanish and Portuguese, and became naturalized subsequently, as proposed for edible bananas (Daniells et al. 2001; Häkkinen and Sharrock 2002). However, several studies on plants and fossils from North and South America, along with documents by early explorers of Mexico, suggest the presence of *Musa* in America long before the arrival of the Europeans (e.g. Humboldt 1810; Berry 1925; Bassler 1926; Cheesman 1949; Acosta 1950; Jain 1965; Raven and Axelrod 1974; Manchester and Kress 1993). This evidence fueled controversy, as it suggested that edible bananas could have been domesticated in pre-Columbian times from endemic species.

Significant progress has been made recently on the phylogeny of the Musaceae family using sequenced data (Li et al. 2010; Liu et al. 2010; Bekele and Shigeta 2011; Novák et al. 2014). However, wild American specimens of *M. ornata* were not included in those studies. Therefore, the phylogenetic position of this species needs to be examined within a broader phylogenetic framework. Here, we describe the results from the first molecular phylogenetic analyses of intercontinental specimens of *M. ornata* in a comprehensive scheme, including its closest relatives. We compared and combined sequenced data generated in this study with data available in GenBank for the ribosomal internal transcribed spacer (ITS) and two plastid loci, the *atpB-rbcL* intergenic spacer and the *trnL-F* region. Then, we used a total-evidence phylogeny to address the following questions: (1) what are the phylogenetic relationships between Asian and Mexican specimens of *M. ornata*?; and, based on registered evidence, (2) which hypothesis better explains the disjunct distribution of *M. ornata*?

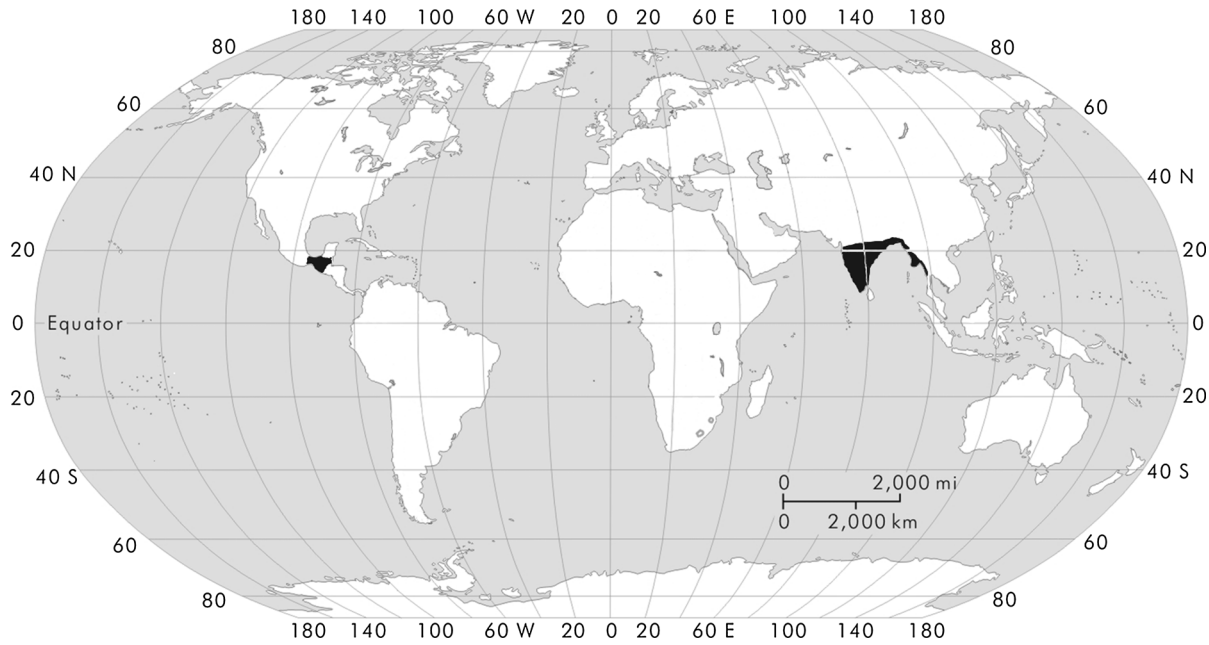



**Fig. 1** Intercontinental disjunct geographic distribution of *Musa ornata*

## Materials and methods

### Assembly of molecular data

Six Mexican individuals of *M. ornata* were selected for this study. They were chosen for their high levels of DNA polymorphism detected in a previous population-based study (Burgos-Hernández et al. 2013), and because they account for the entire distribution range of the species in Mexico: Atzalan (A), Misantla (M), Yecuatla (Y), and Hidalgotitlan (H), in the State of Veracruz; Jalapa de Díaz (O), in the State of Oaxaca; and Teapa (T), in Tabasco. Five Asian samples were also obtained from living collections at the University of Oxford Botanic Garden (OX), Botanic Garden of Helsinki (HE), Singapore Botanic Gardens (S), Fairchild Tropical Botanic Garden (F), and Missouri Botanical Garden (MB). For phylogenetic analyses, we included 62 additional sequences from GenBank. They correspond to four additional Asian specimens of *M. ornata*, 37 species with multiple specimens (53 accessions) representing the five recognized sections in the genus and four outgroup taxa (Tables 1, 2). The species of *Musa* included in the analyses comprise approximately 57% of the known species in this genus. The four outgroup taxa (*Heliconia caribaea, H. psittacorum, Ensete ventricosum* (two accessions), and *E. glaucum*) were chosen based on phylogenetic studies by Liu et al. (2009) and Li et al. (2010).

### DNA extraction, amplification and sequencing

DNA extraction was performed from 60 mg of dry leaf tissue with the DNeasy Plant Mini kit (Qiagen, Valencia, CA, USA) following the manufacturer's protocol. Based on previous phylogenetic studies in *Musa,* we sequenced one nuclear and two plastid regions (Liu et al. 2009; Gayral et al. 2010; Li et al. 2010; Bekele and Shigeta 2011; Hřibová et al. 2011). The nuclear region corresponded to the ribosomal internal transcribed spacer (ITS1 + 5.8S + ITS2); the plastid regions, to the *atpB-rbcL* intergenic spacer and the *trnL-F*. The ITS region was amplified and sequenced using primers ITS1 and ITS4 (White et al. 1990). All amplifications generated one single amplicon. Nonetheless, a BLAST (Altschul et al. 1990) was performed to confirm the identity of sequenced products. The *trnL-F* region (spanning *trnL* intron, the 3′ *trnL* exon, and intergenic spacer region) and the *atpB-rbcL* intergenic spacer were amplified and sequenced using primers Lc-Ff and SR2-rbcL respectively (Taberlet et al. 1991; Hoot et al. 1995).

**Table 1** Voucher information and GenBank accession numbers of the *Musa ornata* specimens that were sequenced

| Origin | Voucher | ITS | *trnL-F* | *atpB-rbcL* |
|---|---|---|---|---|
| Hidalgotitlán (H) | G. Castillo-Campos et al. *24,960* (XAL) | KR921958 | KR921974 | KR921948 |
| Misantla (M) | M. Burgos-Hernández et Barrientos *743* (XAL) | KR921954 | KR921970 | KR921944 |
| Yecuatla (Y) | M. Burgos-Hernández et Barrientos *744* (XAL) | KR921955 | KR921972 | KR921945 |
| Atzalan (A) | M. Burgos-Hernández et Barrientos *746* (XAL) | KR921953 | KR921969 | KR921943 |
| Jalapa de Días (O) | M. Burgos-Hernández et G. Castillo-Campos *172* (XAL) | KR921957 | KR921973 | KR921947 |
| Teapa (T) | M. Burgos-Hernández et G. Castillo-Campos *175* (XAL) | KR921956 | KR921971 | KR921946 |
| The University of Oxford Botanic Garden (OX) | | KR921959 | KR921964 | KR921950 |
| Botanic Garden of Helsinki, Finland (HE) | | KR921962 | KR921967 | KR921952 |
| Singapore Botanic Gardens (S) | | KR921961 | KR921965 | KR921951 |
| Fairchild Tropical Botanic Garden (F) | | KR921960 | KR921966 | KR921949 |
| Missouri Botanical Garden (MB) | | KR921963 | KR921968 | |

Voucher information is provided for Mexican specimens only

The polymerase chain reaction was carried out in 25 µL containing approximately 24 ng of genomic DNA, 5 µL Buffer 5× (20 mM Tris–HCl [pH 8.3], 100 mM KCl, 0.1 mM EDTA, 1 mM DTT, 0.5% Tween 20®, 0.5% NP-40, 50% glycerol), 1.5 mM $MgCl_2$, 0.2 mM dNTPs, 0.1 µM of each primer, 1.25 U Taq polymerase (Apex, 42-800B1), and 2.75 µL distilled water. Amplifications were carried out in an Eppendorf Mastercycler pro S thermocycler (Hamburg, Germany). PCR cycles included an initial 3 min denaturation cycle at 94 °C, followed by 35 cycles, each consisting of 1 min at 94 °C, 1 min at 52 °C, 2 min at 72 °C and a final extension step of 7 min at 72 °C. These conditions were used for all primers. Amplified products were purified prior to sequencing with the Wizard SV gel and PCR clean-up system kit (Promega, Madison, USA), following the manufacturer's protocol. Sequencing reactions were performed in both directions using Big Dye chemistry v3.1 (Applied Biosystems, Foster City, CA USA) and analyzed on an Applied Biosystems 310 capillary sequencer.

## Alignment and sequences analysis

The resulting sequences were edited with the software BioEdit version 7.2.5 (Hall 2013) and aligned using MAFFT version 7.110 (Katoh and Standley 2013) with default parameters, followed by a final adjustment by visual inspection. Sequence variation was obtained using DnaSP version 5.10 (Librado and Rozas 2009) and Arlequin version 3.5 (Excoffier and Lischer 2010). A $\chi^2$ test for base composition homogeneity across taxa was carried out in PAUP version 4.0 (Swofford 2003).

## Phylogenetic analyses

Phylogenetic analyses were performed separately for ITS and cpDNA, and in combination with maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI). The congruence of the phylogenetic signal of ITS and cpDNA datasets was assessed by visual comparison of the respective topologies. In addition, an incongruence length difference (ILD) test (Farris et al. 1995, implemented in PAUP as the partition-homogeneity test) between the ITS and cpDNA datasets was conducted. The partition homogeneity test revealed that the data partitions are not homogeneous ($P < 0.05$). However, it has been suggested that the ILD test should not be used as the only measure of data partition combinability (Yoder et al. 2001), since it is known to be susceptible to both type-I (false positives, Planet 2006) and type-II (false

**Table 2** Codes for sequences obtained from GenBank of the *Musa* species and outgroup used in this study

| Taxon | ITS | *trnL-F* | *atpB-rbcL* |
|---|---|---|---|
| *Australimusa* | | | |
| *M. maclayi* F. Muell. | FJ428068 | FJ428183 | FJ428032 |
| | FJ626373 | FJ621269 | |
| *M. peekelii* Lauterb. | FJ428070 | FJ428186 | FJ428030 |
| *M. textilis* Née | FJ428069 | FJ428187 | FJ428031 |
| | FJ626385 | FJ621281 | |
| *Callimusa* | | | |
| *M. barioensis* Häkkinen | FJ428067 | FJ428185 | FJ428027 |
| *M. beccarii* N.W. Simmonds | FJ428065 | FJ428189 | FJ428028 |
| | FJ626376 | FJ621272 | |
| *M. beccarii* N.W. Simmonds var. *hottana* Häkkinen | FJ428066 | FJ428190 | FJ428028 |
| *M. borneensis* Becc. | FJ626369 | FJ621265 | |
| *M. campestris* Becc. | FJ428076 | FJ428197 | FJ428025 |
| | FJ626377 | FJ621273 | |
| *M. coccinea* Andrews | FJ428062 | FJ428192 | FJ428035 |
| | FJ626371 | FJ621267 | |
| *M. gracilis* Holttum | FJ428075 | FJ428194 | FJ428022 |
| *M. hirta* Becc. | FJ428074 | FJ428199 | FJ428026 |
| *M. lutea* R. V. Valmayor, L. D. Danh et Häkkinen | FJ428064 | FJ428193 | FJ428034 |
| *M. monticola* M. Hotta ex Argent | FJ428073 | FJ428191 | FJ428049 |
| *M. paracoccinea* A. Z. Liu et D. Z. Li | FJ626375 | | |
| *M. salaccensis* Zoll. ex Backer | FJ428072 | FJ428196 | FJ428023 |
| | FJ626370 | FJ621266 | |
| *M. exotica* R. V. Valmayor | FJ428063 | FJ428023 | FJ428024 |
| *M. violascens* Ridl. | FJ428071 | FJ428195 | FJ428057 |
| *M. splendida* A. Chev. | FJ626386 | FJ621282 | |
| *Musa* | | | |
| *M. acuminata* Colla | FJ626387 | FJ621283 | |
| *M. acuminata* subsp. *banksii* (F.Muell.) N. W. Simmonds | FJ428097 | FJ428161 | FJ428053 |
| *M. acuminata* subsp. *burmannica* N. W. Simmonds | FJ428083 | FJ428169 | FJ428041 |
| *M. acuminata* subsp. *siamea* N. W. Simmonds | FJ428084 | FJ428175 | FJ428050 |
| *M. acuminata* subsp. *microcarpa* (Becc.) N. W. Simmonds | FJ428087 | FJ428174 | FJ428052 |
| *M. acuminata* subsp. *errans* (Blanco) R. V. Valmayor | FJ428094 | FJ428160 | FJ428051 |
| *M. acuminata* subsp. *zebrina* (Van Houtte ex Planch.) Nasution | FJ428089 | FJ428173 | FJ428054 |
| *M. balbisiana* Colla | FJ428102 | FJ428159 | FJ428060 |
| | FJ626383 | FJ621279 | |
| *M. basjoo* Siebold et Zucc. ex Iinuma | FJ428100 | FJ428188 | FJ428056 |
| | FJ626374 | FJ621270 | |
| *M. itinerans* Cheesman | FJ428098 | FJ428177 | FJ428059 |
| | FJ626380 | FJ621276 | |
| *M. nagensium* Prain | FJ428101 | FJ428158 | |
| | FJ626388 | FJ621284 | FJ428058 |
| *M. schizocarpa* N. W. Simmonds | FJ428088 | FJ428176 | FJ428042 |
| *M. tonkinensis* R. V. Valmayor, L. D. Danh et Häkkinen | FJ428099 | FJ428178 | FJ428176 |
| *M. yunnanensis* Häkkinen et H. Wang | FJ428095 | FJ428163 | FJ428043 |

**Table 2** continued

| Taxon | ITS | *trnL-F* | *atpB-rbcL* |
|---|---|---|---|
| *M. beccarii* N. W. Simmonds | FJ626376 | FJ621272 | |
| *M. formosana* (Warb.) Hayata (is a synonym of *M. itinerans* var. *formosana* (Warb.) Häkkinen et C. L. Yeh) | FJ626379 | FJ621275 | |
| *Rhodochlamys* | | | |
| *M. aurantiaca* G. Mann ex Baker | FJ428090 | FJ428162 | FJ428037 |
| *M. laterita* Cheesman | FJ428082 | FJ428157 | FJ428033 |
| | FJ626372 | FJ621268 | |
| *M. mannii* H. Wendl. ex Baker | FJ428091 | FJ428166 | FJ428040 |
| | FJ626389 | FJ621285 | |
| *M. ornata* Roxb. | FJ428096 | FJ428164 | FJ428038 |
| | FJ626382 | FJ621278 | |
| | HQ331356 | FJ626382 | |
| | HQ331350 | GQ374832 | |
| *M. rosea* Baker | FJ428080 | FJ428171 | FJ428045 |
| | FJ626367 | FJ621263 | |
| *M. rubinea* Hakkinen et C. H. Teo | FJ428093 | FJ428163 | FJ428048 |
| *M. rubra* Wall. ex Kurz | FJ428081 | FJ428172 | FJ428046 |
| | FJ626381 | FJ621277 | |
| *M. siamensis* Häkkinen et Rich. H. Wallace | FJ428086 | FJ428168 | FJ428047 |
| *M. velutina* H. Wendl. et Drude | FJ428092 | FJ428165 | FJ428039 |
| | FJ626368 | FJ621264 | |
| *M. sanguinea* Hook.f. | FJ626378 | FJ621274 | |
| *Ingentimusa* | | | |
| *M. ingens* N. W. Simmonds | FJ428077 | FJ428184 | FJ428036 |
| *Ensete* Bruce ex Horan. | | | |
| *E. glaucum* (Roxb.) Cheesman | FJ428103 | FJ428154 | FJ428019 |
| | FJ626398 | FJ621294 | |
| *E. ventricosum* (Welw.) Cheesman | FJ428078 | FJ428156 | FJ428020 |
| | FJ626392 | FJ621288 | |
| *E. superbum* (Roxb.) Cheesman | FJ626395 | FJ621291 | |
| | FJ626395 | FJ621291 | |
| *Heliconia* L. | | | |
| *H. caribaea* Lam. | FJ428106 | FJ428179 | FJ428018 |
| *H. psittacorum* Sessé et Moc. | FJ428105 | FJ428180 | FJ428016 |

negatives, Ramírez 2006) errors. Moreover, since no strongly supported conflicting topologies were found among molecular data partitions and the separate data (cpDNA and ITS) showed a poorer resolution, we concatenate the datasets for further analyses and presentation in this study.

Parsimony analyses were performed with the NONA ratchet algorithm implemented in WinClada-Asado (Goloboff 1994; Goloboff et al. 2000; Nixon 1999) with 1000 iterations and retaining 100 trees per iteration. Gaps were recorded as missing. The shortest trees were saved, and a strict consensus tree was produced. Statistical branch support was determined by means of the jackknife (JK) analysis, running 1000 replicates with 50% character deletion (Lanyon 1985).

Bayesian analyses implementing the Markov Chain Monte Carlo (MCMC) technique were conducted using MrBayes version 3.2.2 (Huelsenbeck and

Ronquist 2001; Ronquist and Huelsenbeck 2003). A general time-reversible model (rates = gamma, nst = 6) was used. Four MCMC chains—one cold and three heated—were performed. Each MCMC analysis was run for three million generations, starting from different random points in the parameter space, with a discarded burn-in of 25% (75,000 initial trees) and sampled every 100th generation. Nodes with posterior probabilities (PP) ≥50% were retained in the majority-rule consensus tree.

An ML analysis was performed using the software GARLI version 0.951 (Zwickl 2006). In order to reduce total runtimes, model parameters were fixed according to the values obtained with the jModelTest version 0.1.1 and selected with Akaike's criterion (Guindon and Gascuel 2003; Felsenstein 2005; Posada 2008). The models used were TIM3 + I + G for ITS, TPM2uf + G for cpDNA and GTR + I + G for total evidence. Searches consisted of ten replicates to guarantee that results were consistent and reproducible. Branch support for ML was determined simultaneously with 100 non-parametric bootstrap (BS) iterations in each of the ten replicates.

## Results

### Sequences analysis

The length of the ITS sequences generated in this study ranged from 600 to 682 bp, similar to those recorded by Liu et al. (2009) and Sulistyaningsih et al. (2014). The length for sequences downloaded from GenBank from other *Musa* species ranged from 599 to 697 bp. After the alignment, the ITS sequence data matrix consisted of 774 nucleotides; from these, 214 were polymorphic (27.6%). The aligned sequences showed low insertion and deletion ratios among them (7.7%). The GC content for ITS1 and ITS2 was 64.8%. This value is similar to the one reported for other wild species of *Musa,* with values from 54.13 to 79.97%, and is within the expected range for angiosperms (41–77%; Baldwin et al. 1995; Hřibová et al. 2011; Sulistyaningsih et al. 2014). The 5.8S rDNA sequence region showed a GC content of 57% and is similar for other banana species (49.68–57.48%). The highly conserved region 5.8S rRNA comprises from position 266 to 470 and corresponds to 26.3% of the sequence. The rest (73.7%) corresponds to ITS1 and ITS2 regions. Similar proportions of nucleotides (28.9% for 5.8 S and 71.1% for ITS1 and ITS2) have been reported for other wild banana species (Sulistyaningsih et al. 2014). Lengths for ITS1 (265 bp) and ITS2 (275 bp) in our sequences closely resemble the ranges reported previously for *Musa* and other angiosperms (Baldwin et al. 1995; Hřibová et al. 2011; Sulistyaningsih et al. 2014).

The length of the chloroplast DNA dataset was 2179 bp; from these, 596 were polymorphic (27.3%). The aligned sequences showed low insertion and deletion ratios among them (8.6%). Overall, the GC content was 31.2%. The length of the *trnL-F* sequences in *Musa* ranged from 810 to 987, and of *atpB-rbcL,* from 735 to 812. The *trnL-F* region spans from positions 1 to 1202 and corresponds to 54.9% of the sequences. The rest (45.1%) corresponds to the *atpB-rbcL* region. GC content (28.1%) in the *atpB-rbcL* and (32.5%) *trnL-F* spacers agrees with levels observed in other flowering plants (Manen and Natali 1995; Bakker et al. 2000). Soltis et al. (2000) demonstrated that data from these two genes could be pooled and are useful for phylogenetic reconstruction in angiosperms. Finally, the $\chi^2$ test used to detect heterogeneity in base composition indicates that there was no significant variation in the AT/GC content between species for individual genes (ITS: $\chi^2 = 102.04$, df = 246, $P = 1.000$; *trnL-F*: $\chi^2 = 21.72$, df = 216, $P = 1.000$; *atpB-rbcL*: $\chi^2 = 19.25$, df = 216, $P = 1.000$).

### Phylogenetic analysis of ITS

The ITS dataset consisted of 774 characters, 349 (45%) of which were constant and 266 (34%) were parsimony-informative. The MP analysis resulted in 915 most-parsimonious trees of 875 steps (consistency index excluding uninformative characters CI = 0.67, and retention index RI = 0.84).

The ML and BI analyses (not shown) produced topologies similar to that of the strict consensus of MP trees (Fig. 2a), in which the in-group formed a monophyletic group with weak support (<50%). Two major clades were recovered within the genus *Musa*. The first one (clade I, Fig. 2a) included mostly specimens from sections *Rhodochlamys* and *Musa* (BS = 87, JK = 97), except for *M. campestris*, *M. salaccensis* and, *M. textilis*, which belong to other sections nested in this clade. The second clade (clade

II, Fig. 2a) included specimens from sections *Callimusa*, *Ingentimusa*, and *Australimusa* (BS = 68, PP = 0.99, JK = 85), with relationships ranging from moderate to well resolved.

Most *M. ornata* specimens (both Asian and Mexican) were placed in a poorly resolved subclade, with support values of BS = 95 and JK = 98. Meanwhile, *M. balbisiana* and *M. textilis* formed a sister group with a robust support (BS = 92, PP = 1.00, JK = 95), with the MB Asian representative of *M. ornata* as the sister taxon with the highest support (BS = 95, PP = 1.00, JK = 96). Two additional subclades containing *M. ornata* specimens were recovered in this analysis. One of them was strongly supported, with values of BS = 94, PP = 1.00, and JK = 83, and included two specimens of *M. ornata* and one of *M. velutina.* The remaining *M. ornata* specimens remained unresolved.

## Phylogenetic analysis of cpDNA

The cpDNA data set consisted of 2179 characters, 1527 (70%) of which were constant and 185 (8.5%) were parsimony-informative. The MP analysis

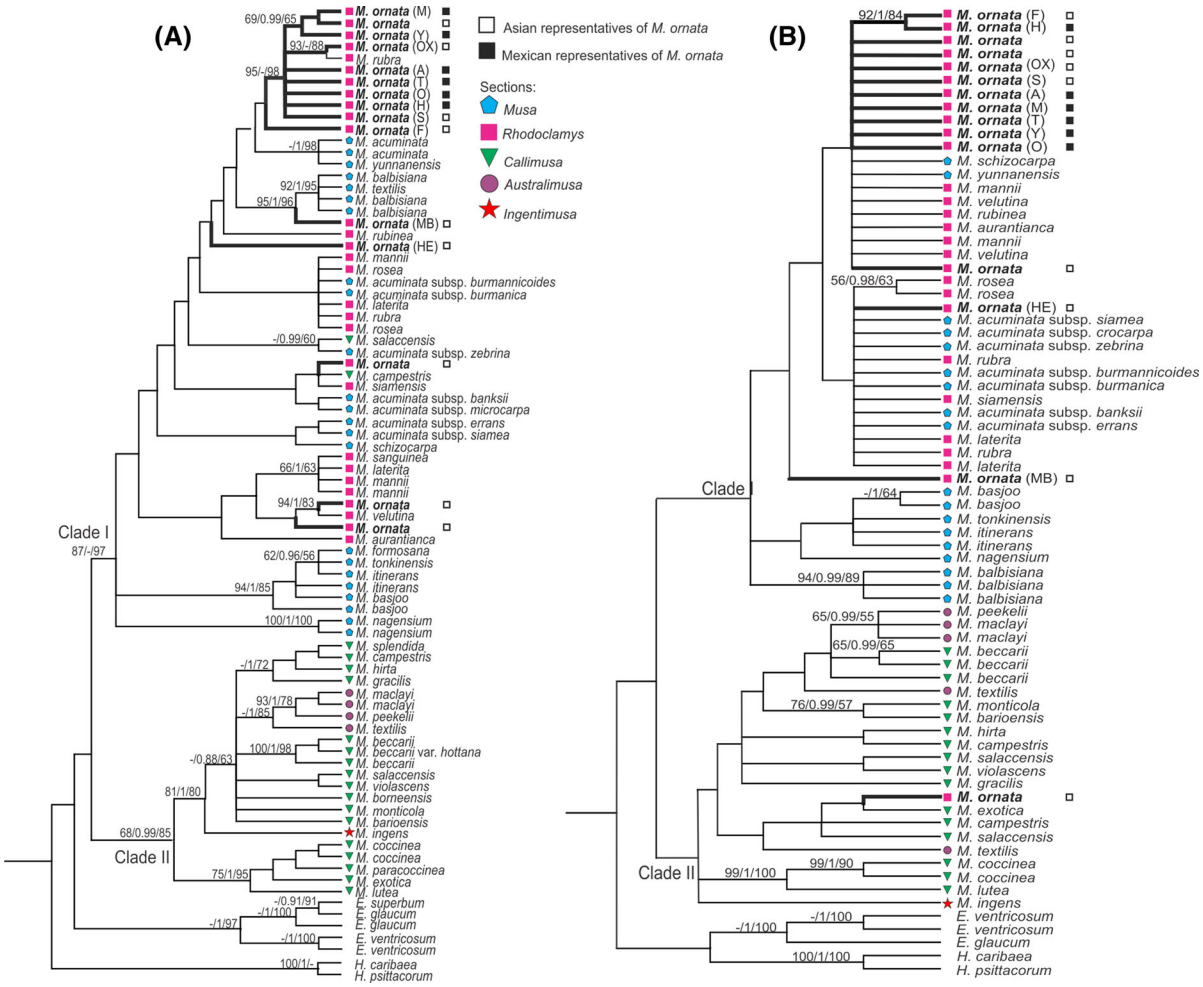



**Fig. 2** Strict consensus tree of *Musa* inferred from **a** nuclear ITS (tree length = 875 steps, CI = 0.67 and RI = 0.84) and **b** combined plastid (*trnL-F* and *atpB-rbcL*; tree length = 856 steps, CI = 0.83 and RI = 0.82). The bootstrap values (BS; *left*), posterior probabilities (PP; *center*) and, jackknife values (JK; *right*) are labeled above the branches. Only support values above 60% and with at least two statistical supports are shown; a *dash* denotes no support values. Representatives of genera *Heliconia* and *Ensete* were used as outgroup. *A* Atzalan, *F* Fairchild Tropical Botanic Garden, *H* Hidalgotitlan, *HE* Botanic Garden of Helsinki, *M* Misantla, *MB* Missouri Botanical Garden, *O* Jalapa de Díaz, *OX* University of Oxford Botanic Garden, *T* Teapa, *S* Singapore Botanic Gardens, *Y* Yecuatla

resulted in 2035 most-parsimonious trees of length 856 (consistency index excluding uninformative characters CI = 0.83, and retention index RI = 0.82). In general, the topology of the cpDNA tree is very similar to the one based on the ITS dataset (Fig. 2a, b). As in the ITS tree, *Musa* was resolved as a monophyletic group with two clades (clades I and II, Fig. 2b), but these were unsupported.

*Musa ornata* was not monophyletic, only specimens F and H were clustered together in an unresolved clade with support values of BS = 92, PP = 1.00, JK = 84. The major discrepancy between the cpDNA and ITS trees was the position of specimen F of *M. ornata*. In cpDNA trees, the relationship between F and H (Asian and Mexican specimens, respectively) was highly supported, whereas with the ITS data, specimen F was a sister to the *M. ornata* subclade (BS = 95, JK = 98) in all cases.

### Phylogenetic analysis of concatenated sequence data

We generated sequence data for eleven *M. ornata* specimens; six Mexican (A, M, Y, H, T, O) and five Asian (S, MB, OX, F, HE; Table 1), and four additional Asian specimens were recovered from GenBank (Table 2). The concatenated dataset of these species plus the data retrieved from GenBank consisted of 3034 characters for 73 specimens, 2236 (74%) of which were constant and 462 (15%) were informative for the MP analysis. This analysis produced 27,876 equally parsimonious trees with a tree length of 1313, a consistency index (CI) excluding uninformative characters of 0.49, and a retention index (RI) of 0.77.

The GTR + I + G substitution model obtained under Akaike's information criterion (AIC) resulted in the following nucleotide frequencies and substitution rate: "Lset base = (0.3120 0.1903 0.1957) nst = 6 rmat = (0.7370 1.8905 0.7684 0.9649 2.5650) rates = gamma shape = 0.6570 ncat = 4 pinvar = 0.4590″. Analyses with these fixed model parameters resulted in a log likelihood (–ln) score of 14,181.2431.

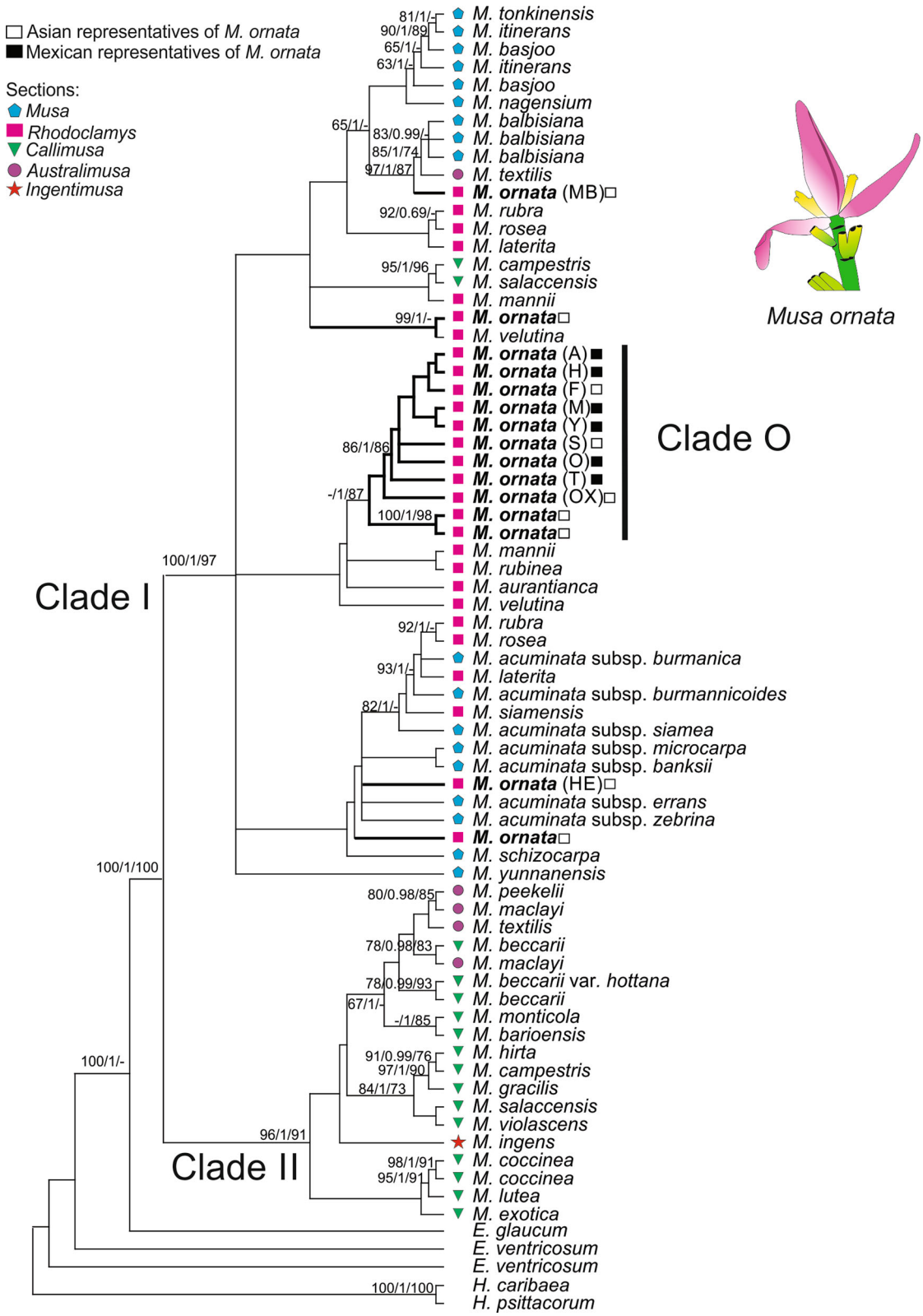
A significant congruence was observed between the majority consensus tree derived from the BI analysis (Fig. 3) and MP and ML analyses (Online Resource 1), with only minor differences in the placement of some specimens. Consequently, from this point onwards only the BI tree is described with the corresponding bootstrap (BS), posterior probabilities (PP), and jackknife (JK) support values (Fig. 3).

The monophyly of the genus *Musa* was strongly supported (BS = 100, PP = 1.00, JK = 100). Within the genus, two inclusive well-supported monophyletic groups were differentiated: clade I (BS = 100, PP = 1.00, JK = 97) comprised taxa from sections *Musa* and *Rhodochlamys*; exceptions were two species from the section *Callimusa* (*M. campestris* and *M. salaccensis*) and one from *Australimusa* (*M. textilis*, Fig. 3), which were also included in this clade. Several strongly supported subclades were included in clade I, but their backbone relationships were largely unresolved. Clade II (BS = 96, PP = 1.00, JK = 91) contained species of sections *Australimusa*, *Callimusa*, and *Ingentimusa* (Fig. 3), and basal branches were better resolved than those in clade I.

The relationships inferred between *M. ornata* specimens were similar with the three different phylogenetic reconstruction methods used (Online Resource 1). Most *M. ornata* specimens were clustered together in a subclade (clade O) within clade I, with support values of PP = 1.00 and JK = 87. Three Asian specimens were positioned at the most basal nodes within this clade. However, the monophyly of this species was not supported, since the analyses placed four Asian specimens outside clade O. The MB specimen was resolved as sister of a strongly supported (BS = 97, PP = 1.00, JK = 87) subclade comprising all the specimens of *M. balbisiana* (section *Musa*) and one of *M. textilis* (section *Australimusa*) in a polytomy. The position of the other three *M. ornata* specimens was unresolved in a large polytomy within clade I. Meanwhile, the Mexican specimens of *M. ornata* (A, M, Y, H, T, and O) formed a non-monophyletic group, being included in clade O together with two Asian specimens.

## Discussion

The molecular phylogeny reported here (Fig. 3) is consistent with results from previous molecular phylogenetic studies using both nrITS and plastid sequence data (Gawel et al. 1992; Wong et al. 2002; Nwakanma et al. 2003; Liu et al. 2009; Li et al. 2010; Bekele and Shigeta 2011). Our results support the hypothesis proposed by Wong et al. (2003) and, more


Asian representatives of M. ornata
Mexican representatives of M. ornata
Sections:
Musa
Rhodoclamys
Callimusa
Australimusa
Ingentimusa
M. tonkinensis
M. itinerans
M. basjoo
M. itinerans
M. basjoo
M. nagensium
M. balbisiana
M. balbisiana
M. balbisiana
M. textilis
M. ornata (MB)
M. rubra
M. rosea
M. laterita
M. campestris
M. salaccensis
M. mannii
M. ornata
M. velutina
M. ornata (A)
M. ornata (H)
M. ornata (F)
M. ornata (M)
M. ornata (Y)
M. ornata (S)
M. ornata (O)
M. ornata (T)
M. ornata (OX)
M. ornata
M. ornata
Clade O
M. mannii
M. rubinea
M. aurantianca
M. velutina
M. rubra
M. rosea
M. acuminata subsp. burmanica
M. laterita
M. acuminata subsp. burmannicoides
M. siamensis
M. acuminata subsp. siamea
M. acuminata subsp. microcarpa
M. acuminata subsp. banksii
M. ornata (HE)
M. acuminata subsp. errans
M. acuminata subsp. zebrina
M. ornata
M. schizocarpa
M. yunnanensis
M. peekelii
M. maclayi
M. textilis
M. beccarii
M. maclayi
M. beccarii var. hottana
M. beccarii
M. monticola
M. barioensis
M. hirta
M. campestris
M. gracilis
M. salaccensis
M. violascens
M. ingens
M. coccinea
M. coccinea
M. lutea
M. exotica
E. glaucum
E. ventricosum
E. ventricosum
H. caribaea
H. psittacorum
Clade I
Clade II
81/1/-
90/1/89
65/1/-
63/1/-
65/1/-
83/0.99/-
85/1/74
97/1/87
92/0.69/-
95/1/96
99/1/-
86/1/86
-/1/87
100/1/98
100/1/97
92/1/-
93/1/-
82/1/-
100/1/100
80/0.98/85
78/0.98/83
78/0.99/93
67/1/-
-/1/85
100/1/-
91/0.99/76
97/1/90
84/1/73
96/1/91
98/1/91
95/1/91
100/1/100
Musa ornata

◀**Fig. 3** Bayesian Inference tree of *Musa*, based on combined plastid (*trnL-F* and *atpB-rbcL*) and ITS dataset. The bootstrap values (BS; *left*), posterior probabilities (PP; *center*) and, jackknife values (JK; *right*) are labeled above the branches. Only support values above 60% and with at least two statistical supports are shown; a *dash* denotes no support values. Representatives of genera *Heliconia* and *Ensete* were used as outgroup. *A* Atzalan, *F* Fairchild Tropical Botanic Garden, *H* Hidalgotitlan, *HE* Botanic Garden of Helsinki, *M* Misantla, *MB* Missouri Botanical Garden, *O* Jalapa de Díaz, *OX* University of Oxford Botanic Garden, *T* Teapa, *S* Singapore Botanic Gardens, *Y* Yecuatla

recently, by Häkkinen (2013) of only two sections within the genus *Musa*: *Musa* (*Eumusa-Rhodochlamys*) and *Callimusa* (*Callimusa-Australimusa*). The poorly resolved topology of clade I contrast with the clades resolved in previous studies of this genus using the same markers (Liu et al. 2009; Li et al. 2010; Bekele and Shigeta 2011). However, it is important to note that those studies focused on elucidating the phylogenetic relationships within the genus and, thus, encompassed less than 50% of the species of *Musa* and used only one specimen from each one. In this study, we examined 57% of the species in the genus and, for most of them, at least two representatives were included and, for *M. ornata*, a total of 15 specimens were included in our analyses, with the aim of knowing their phylogenetic position. These differences in taxon sampling may explain in part the variation in resolution observed. The question whether it is better to add more taxa has been one of the biggest controversies in systematics. Several studies have shown that adding taxa can lead to more accurate phylogeny estimation (Poe 2003; Sorenson et al. 2003) while others indicate that under some conditions adding taxa decrease phylogenetic accuracy (e.g. Wiens and Tiu 2012). Nonetheless, increasing taxon sampling can test the robustness of the phylogenetic hypothesis when it is included only a few representatives and can emerge new or different relationships. For example, although the objective of this work was not focused in the wild ancestor of edible bananas, highlights the fact that *M. acuminata* is polyphyletic. Also, the close relationship between *M. laterita* and *M. acuminata* described by Wong et al. (2002) and Liu et al. (2009) where a few specimens of *Musa* were used is not supported in our phylogenetic hypothesis. Thereby, including more taxa has questioned some relationships described in previous studies. Therefore, further taxonomic and molecular systematic work in this genus is still needed, since several species show taxonomic issues, as has been documented in several studies (Kress et al. 2001; Liu et al. 2002; Wong et al. 2002; Liu et al. 2009; Li et al. 2010; Christelová et al. 2011; Häkkinen 2013).

The higher resolution and statistical support figures obtained with ITS topologies suggest that this region provides more informative signals, with 34% informative characters, relative to the cpDNA, which only had 8.5%. However, none of the single locus analysis recovered most specimens of *M. ornata* in a single clade, as the total evidence analysis. These results show a better resolving power when data is combined. Several studies show that all available tests of incongruence are too coarse to be useful and that the best way to detect true incongruence is by examining the results (Seelanan et al. 1997; Soltis et al. 2000). Other studies have shown that conflicting signals from individual gene sequences are resolved when sequence data are combined (Rokas et al. 2003). In general, the resulting topologies (Figs. 2a, b) for the two regions were congruent.

The results obtained from the combined datasets revealed that *M. balbisiana* (section *Musa*) specimens formed a polytomy within clade I, which also included one specimen of *M. textilis* (section *Australimusa*), denoting a close relationship between them. This relationship had been previously reported, with strong support, in molecular studies of *Musa* (Gawel and Jarret 1991; Nwakanma et al. 2003; Liu et al. 2009). Likewise, a numerical taxonomic analysis of morphological data carried out by Simmonds and Weatherup (1990) placed section *Australimusa* close to *M. balbisiana*. The relatively close genetic relationship between these two species may be due to a naturally occurring hybridization between them (Simmonds 1962). Meanwhile, the strong support of the relationship of *M. ornata* and the subclade of *M. balbisiana* suggest the probability of a misidentification of MB specimen. It is well-known that species determination within *Musa* is difficult. Therefore, taxonomic misidentifications could be an explication of some conflicts of our results. In consequence, further taxonomic and molecular review is still needed within the collections.

Results from the combined analysis showed the six Mexican representatives of *M. ornata* were nested together with two Asian specimens in a strongly supported clade (clade O, Fig. 3). This relationship

suggests that Mexican populations of *M. ornata* may have originated from an Asian invasion, probably more than once, a scenario that has been proposed for edible bananas as well. Previous archaeological and linguistic studies have indicated that cultivated bananas were initially domesticated by farmers in Southeast Asia about 7000 years ago and were subsequently introduced to other regions of the world by transmigrants and travelers (Sykora 1990). There is a historical record showing that the Portuguese introduced bananas to America, bringing them from West Africa to the Canary Islands and then to Hispaniola in 1516 (De Candolle 1886). However, there are studies on plants from America and documents of early explorers of Mexico that suggest the presence of *Musa* in the Americas long before the arrival of the Portuguese and the Spaniards (e.g., Humboldt 1810; Bassler 1926; Cheesman 1949; Acosta 1950; Raven and Axelrod 1974; Manchester and Kress 1993).

The current distribution range of *Musa* makes it reasonable to hypothesize that this genus evolved and diversified in tropical Asia (Liu et al. 2009), as proposed in other studies (Daniells et al. 2001; Häkkinen and Sharrock 2002; Janssens et al. 2016). However, the distribution of *M. ornata* and the fossil evidence jointly point to alternative scenarios about the origin and diversification of the Musaceae. In 1993, Manchester and Kress reported the presence of *Ensete* (Musaceae) in the North American Tertiary; one year later, Rodriguez de la Rosa and Cevallos-Ferriz (1994) reported zingiberalean fruits from Coahuila, Mexico. Additionally, the genus *Spirematospermum* Chandler has a closer affinity with Musaceae (Rodriguez de la Rosa and Cevallos-Ferris 1994), particularity *Spirematospermum chandlereae* Friis, with fossil record in North America (Friis 1988; Fischer et al. 2009; Friis et al. 2011). These findings are important, first, because such fossils were found in a continent where apparently there are no wild living species of *Musa*. Second, because these were the first unequivocal fossil records of any genus of the Musaceae. By contrast, the only fossil record of *Musa* in Asia (described by Jain 1963, 1965 from India) had an unknown affinity to existing *Musa* species (Liu et al. 2009), and the reexamination of the material by Manchester and Kress (1993) demonstrated that such "fossil" was, in fact, a non-biological concretion. This evidence has led botanists to reconsider the origin of the bananas.

Notwithstanding some studies suggest that the family originated in Southeast Asia (Kress and Specht 2006; Janssens et al. 2016), but other analyses in Zingiberales indicated an Australian origin, with several major radiations occurring in Africa and Neotropical America (Deng et al. 2016). The Southeast Asia origin is in fact, incongruent with the Australian origin. Moreover, a weakness in these studies is that none included American specimens of *Musa,* which restricts their analysis. Consequently, more efforts are needed to shed light on the banana origin. Other studies have addressed the origins of different plant groups from the New World that currently also occur in the Old World. Such is the case of the family Berberidaceae, which is distributed in both Mexico and Asia. For some time this group was believed to have originated in the Old World; however, recent studies suggest that North America may have been an important diversification and radiation area for at least some members of this family (Ramírez and Cevallos-Ferris 2000). The same scenario has been proposed for other plant species (Lavin and Luckow 1993; Lavin et al. 2000; Renner et al. 2001; Davis et al. 2002) and apparently also in the opposite direction, from the Old to the New World (Doyle and Le Thomas 1997; Chanderbali et al. 2001).

Although Musaceae is commonly considered to have originated in the Old World, fossil data indicate an early history in America. However, it is not known whether wild members of the family were already present in America before the anthropic introduction of edible bananas. Assuming that *Musa* was already established in Asia in the Tertiary (although biogeographic and paleobotanical evidence is lacking), then the picture that emerges is that the family Musaceae has a pantropical distribution (Manchester and Kress 1993). Given this scenario and considering the present-day distribution of *M. ornata*, the phylogenetic relationships and the fossil record is still open the possibility that *M. ornata* ancestrally inhabited both continents—America and Asia—probably with a subsequent restriction to the Old World and a secondary dispersal by an anthropic introduction to the New World. However, the underlying causes of *M. ornata*'s current distribution are still difficult to determine with certainty. Historical biogeography data and paleobotanical studies are needed to shed more light on the origins of the disjunct distribution of *M. ornata*: this, in turn, can yield further insights on

the origin of this species and the banana group, which might turn out to be different from the explanation currently accepted.

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**Compliance with ethical standards**

**Conflict of interest** The authors declare that they have no conflict of interest.

## References

Acosta J (1950) Historia natural y moral de las Indias. Biblioteca de Autores Españoles, Madrid

Altschul FS, Gish W, Miller W, Myers WM, Lipman JD (1990) Basic local alignment search tool. J Mol Biol 215:403–410

Bakker FT, Culham A, Gomez-Martinez R, Carvalho J, Compton J, Dawtrey R, Gibby M (2000) Patterns of nucleotide substitution in angiosperm cpDNA *trnL* (UAA)—*trnF* (GAA) regions. Mol Biol Evol 17:1146–1155

Baldwin BG, Sanderson JM, Porter MJ, Wojciechowski MF, Campbell SC, Donoghue JM (1995) The ITS region of nuclear ribosomal DNA: a valuable source of evidence on angiosperm phylogeny. Ann Mo Bot Gard 82:247–277

Bassler H (1926) *Musa* in tropical America. J New York Bot Gard 27:49–54

Bekele E, Shigeta M (2011) Phylogenetic relationships between *Ensete* and *Musa* species as revealed by the *trnT-trnF* region of cpDNA. Genet Resour Crop Evol 58:259–269

Berry EW (1925) A banana in the tertiary of Colombia. Am J Sci 10:530–537

Blaum N, Wichmann MC (2007) Short-term transformation of matrix into hospitable habitat facilitates gene flow and mitigates fragmentation. J Anim Ecol 76:1116–1127

Bullock JM, Kenward RE, Hails RS (2002) Dispersal ecology. Blackwell Science, Oxford

Burgos-Hernández M, González D, Castillo-Campos G (2013) Genetic diversity and population genetic structure of wild banana *Musa ornata* (Musaceae) in Mexico. Plant Syst Evol 299:1899–1910

Chanderbali AS, van der Werff H, Renner SS (2001) Phylogeny and historical biogeography of Lauraceae: evidence from the chloroplast and nuclear genomes. Ann Mo Bot Gard 88:104–134

Cheesman EE (1949) Classification of the bananas: critical notes on species: *Musa ornata*. Kew Bull 4:24–28

Christelová P, Valárik M, Hřibová E, De Langhe E, Doležel J (2011) A multi gene sequence-based phylogeny of the Musaceae (banana) family. BMC Evol Biol 11:103. doi:10.1186/1471-2148-11-103

Cox CB, Moore PD (2005) Biogeography: an ecological and evolutionary approach. Blackwell Publishing, Oxford

Daniells J, Jenny C, Karamura D, Tomekpe K (2001) *Musa*logue: a catalogue of *Musa* germplasm. Diversity in the genus *Musa*. International Network for the Improvement of Banana and Plantain, Montpellier

Davis MB, Shaw RG (2001) Range shifts and adaptive responses to quaternary climate change. Science 292:673–679

Davis CC, Bell CD, Mathews S, Donoghue MJ (2002) Laurasian migration explains Gondwanan disjunctions: evidence from Malpighiaceae. PNAS 99:6833–6837

Davis CC, Fritsch PW, Bell CD, Mathews S (2004) High-latitude tertiary migrations of an exclusively tropical clade: evidence from Malpighiaceae. Int J Plant Sci 165:107–121

De Candolle A (1886) Origin of cultivated plants. D. Appleton, New York

De Queiroz A (2005) The resurrection of oceanic dispersal in historical biogeography. Trends Ecol Evol 20:68–73

Deng J, Gao G, Zhang Y, He F, Luo X, Zhang F, Liao X, Shafique AK, Yang R (2016) Phylogenetic and ancestral area reconstruction of Zingiberales from plastid genomes. Biochem Syst Ecol 66:123–128

Donoghue MJ, Smith SA (2004) Patterns in the assembly of temperate forests around the Northern Hemisphere. Philos T Roy Soc B 359:1633–1644

Doyle JA, Le Thomas A (1997) Phylogeny and geographic history of Annonaceae. Geogr Phys Quatern 51:353–361

Excoffier L, Lischer H (2010) Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. Mol Ecol Resour 10:564–567

Farris JS, Källersjö M, Kluge AG, Bult C (1995) Testing significance of incongruence. Cladistics 10:315–319

Felsenstein J (2005) PHYLIP (Phylogeny Inference Package). Department of Genome Sciences, University of Washington, Seattle

Fischer TC, Butzmann R, Meller B, Rattei T, Newman M, Hölscher D (2009) The morphology, systematic position and inferred biology of *Spirematospermum*—an extinct genus of Zingiberales. Rev Palaeobot Palyno 157:391–426

Friis EM (1988) *Spirematospermum chandlerae* sp. nov., an extinct species of Zingiberaceae from the North American Cretaceous. Tert Res 9:7–12

Friis EM, Crane PR, Pedersen KR (2011) Early flowers and angiosperm evolution. Cambridge Univ Press, Cambridge

Gawel NJ, Jarret RL (1991) Chloroplast DNA restriction fragment length polymorphisims in *Musa* species. Theor Appl Genet 81:783–786

Gawel NJ, Jarret RL, Whittemore AP (1992) Restriction fragment length polymorphism (RFLP)-based phylogenetic analysis of *Musa*. Theor Appl Genet 84:286–290

Gayral P, Blondin L, Guidolin O, Carreel F, Hippolyte I, Perrier X, Iskra-Caruana M-L (2010) Evolution of endogenous sequences of *Banana Streak Virus*: what can we learn from banana (*Musa* sp.) evolution? J Virol 84:7346–7359

Goloboff PA (1994) NONA: A Tree Searching Program. program and documentation. Fundacion e Instituto Miguel Lillo, Tucuman. http://www.cladistics.com. Accessed 15 June 2015

Goloboff PA, Farris JS, Nixon K (2000) TNT tree analysis using new technology. Beta Test Version v. 0.1, computer program. http://www.zmuc.dk/public/phylogeny/TNT. Accessed 15 June 2015

Guindon S, Gascuel O (2003) A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. Syst Biol 52:696–704

Häkkinen M (2013) Reappraisal of sectional taxonomy in *Musa* (Musaceae). Taxon 4:809–813

Häkkinen M, Sharrock S (2002) Diversity in the genus *Musa*—focus on Rhodochlamys. In: International Network for the Improvement of Banana and Plantain (ed) INIBAP Annual Report 2001. INIBAP, Montpellier, pp 16–23

Hall T (2013) BioEdit. Biological sequence alignment editor for Win95/98/NT/2 K/XP/7. http://www.mbio.ncsu.edu/BioEdit/bioedit.html. Accessed 01 Jan 2016

Hoot SB, Culham A, Crane PR (1995) The utility of *atpB* gene sequences in resolving phylogenetic relationships: comparison with *rbcL* and 18S ribosomal DNA sequences in the Lardizabalaceae. Ann Mo Bot Gard 82:194–207

Hřibová E, Čížková J, Christelová P, Taudien S, De Langhe E, Doležel J (2011) The ITS1-5.8S-ITS2 sequence region in the Musaceae: structure, diversity and use in molecular phylogeny. PLoS One 6:e17863. doi:10.1371/journal.pone.0017863

Huelsenbeck J, Ronquist F (2001) MrBayes: bayesian inference of phylogeny. Bioinformatics 17:754–755

Humboldt A (1810) Ensayo político sobre el reino de la nueva España. Porrúa, Mexico

Jain RK (1963) Studies in Musaceae—1. *Musa cardiosperma* sp. nov., a fossil banana fruit from the Deccan Intertrappean Series, India. Palaeobotanist 12:45–54

Jain RK (1965) Studies in Musaceae–III. Fossil records of Musaceae and the origin of bananas. Proc Indian Acad Sci (Plant Sci) 6:170–179

Janssens BS, Vandelook F, De Langhe E, Verstraete B, Smets E, Vandenhouwe I, Swennen R (2016) Evolutionary dynamics and biogeography of Musaceae reveal a correlation between the diversification of the banana family and the geological and climatic history of Southeast Asia. New Phytol. doi:10.1111/nph.13856

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol Biol Evol 30:772–780

Kress WJ, Specht CD (2006) The evolutionary and biogeographic origin and diversification of the tropical monocot order Zingiberales. Aliso 22:621–632

Kress WJ, Prince ML, Hahn JW, Zimmer AE (2001) Unraveling the evolutionary radiation of the families of the Zingiberales using morphological and molecular evidence. Syst Biol 50:926–944

Lanyon SM (1985) Detecting internal inconsistencies in distance data. Syst Zool 34:397–403

Lavin M, Luckow M (1993) Origins and relationships of tropical North America in the context of the boreotropics hypothesis. Am J Bot 80:1–14

Lavin M, Thulin M, Labat J-N, Pennington RT (2000) Africa, the odd man out: molecular biogeography of dalbergioid legumes (Fabaceae) suggests otherwise. Syst Bot 25:449–467

Li HL (1952) Floristic relationships between eastern Asia and eastern North America. T Am Philos Soc 42:371–429

Li L, Häkkinen M, Hao G, Lu Y, Ge X-J (2010) Molecular phylogeny and systematics of the banana family (Musaceae) inferred from multiple nuclear and chloroplast DNA fragments, with a special reference to the genus *Musa*. Mol Phyloget Evol 57:1–10. doi:10.1016/j.ympev.2010.06.021

Librado P, Rozas J (2009) DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. Bioinformatics 25:1451–1452

Liu A-Z, Kress WJ, De-Zhu L (2010) Phylogenetic analyses of the banana family (Musaceae) based on nuclear ribosomal (ITS) and chloroplast (trnl-F) evidence. Taxon 59:20–28

Liu A-Z, Li DZ, Wang H, Kress WJ (2002) Ornithophilous and Chiropterophilous pollination in *Musa itinerans* (Musaceae), a pioneer species in tropical rain forests of Yunnan, southwestern China. Biotropica 34:254–260

Liu A-Z, Kress WJ, De-Zhu L (2009) Phylogenetic analyses of the banana family (Musaceae) based on nuclear ribosomal (ITS) and chloroplast (*trnl-F*) evidence. Taxon 59:20–28

Lo EYY, Stefanovic S, Christensen KI, Dickinson TA (2009) Evidence for genetic association between East Asian and western North American *Crataegus* L. (Rosaceae) and rapid divergence of the western North American lineages based on multiple DNA sequences. Mol Phyloget Evol 51:157–168

Manchester SR, Kress WJ (1993) Fossil Bananas (Musaceae): *Ensete oregonense* sp. nov. from the Eocene of western North America and its phytogeographic. Am J Bot 80:1264–1272

Manen J-F, Natali A (1995) Comparison of the evolution of Ribulose-1, 5-Biphosphate Carboxylase (*rbcL*) and *atpB-rbcL* noncoding spacer sequences in a recent plant group, the tribe Rubiaeae (Rubiaceae). J Mol Evol 41:920–927

Manos PS, Donoghue MJ (2001) Progress in northern Hemisphere phytogeography. Int J Plant Sci 162:1–2. doi:10.1086/324421

Matuda E (1950) Descripción de Musa mexicana. Madroño 10:166–169

Nie Z-L, Wen J, Sun H, Bartholomew B (2005) Monophyly of *Kelloggia* Torrey ex Benth. (Rubiaceae) and evolution of its intercontinental disjunction between western North America and eastern Asia. Am J Bot 92:642–652

Nixon KC (1999) The parsimony ratchet a new method for rapid parsimony analysis. Cladistics 15:407–414

Novák P, Hřibová E, Neumann P, Koblížková A, Doležel J, Macas J (2014) Genome-wide analysis of repeat diversity across the family Musaceae. PLoS One 9:e98918. doi:10.1371/journal.pone.0098918

Nwakanma DC, Pillay M, Okoli BE, Tenkouano A (2003) Sectional relationships in the genus *Musa* L. inferred from the PCR-RFLP of organelle DNA sequences. Theor Appl Genet 107:850–856

Planet PJ (2006) Tree disagreement: measuring and testing incongruence in phylogenies. J Biomed Inform 39:86–102

Poe S (2003) Evaluation of the strategy of long-branch subdivision to improve the accuracy of phylogenetic methods. Syst Biol 52:423–428

Posada D (2008) jModelTest: phylogenetic Model Average. Mol Biol Evol 25:1253–1256

Ramírez MJ (2006) Further problems with the incongruence length difference test: ''hypercongruence'' effect and multiple comparisons. Cladistics 22:289–295

Ramírez JL, Cevallos-Ferris SRS (2000) Leaves of Berberidaceae (*Berberis* and *Mahonia*) from Oligocene sediments, near Tepexi de Rodríguez, Puebla. Rev Palaeobot Palyno 110:247–257

Raven PH, Axelrod DI (1974) Angiosperm biogeography and past continental movements. Ann Mo Bot Gard 61:539–673

Renner SS, Clausing G, Meyer K (2001) Historical biogeography of Melastomataceae: the roles of Tertiary migration and long distance dispersal. Am J Bot 7:1290–1300

Rodríguez de la Rosa AR, Cevallos-Ferriz SRS (1994) Upper Cretaceous Zingiberalean fruits with in situ seeds from southeastern Coahuila, Mexico. Int J Plant Sci 155:786–805

Rokas A, Williams BL, King N, Carroll SB (2003) Genome-scale approaches to resolving incongruence in molecular phylogenies. Nature 425:798–804

Ronquist F, Hueselbeck JP (2003) Mr Bayes 3: Bayesian phylogenetic inference under mix models. Bioinformatics 19:1572–1574

Roxburgh W (1814) *Musa ornata*. Hortus Bengal, Mission Press, Serampore, Calcultta

Roxburgh W (1824) *Musa ornata*. In: Carey W (ed) Flora Indica, vol 2. Mission Press, Serampore, pp 488–491

Schönenberger J, Conti E (2003) Molecular phylogeny and floral evolution of Penaeaceae, Oliniaceae, Rhynchocalycaceae, and Alzateaceae (Myrtales). Am J Bot 90:293–309

Seelanan T, Schnabel A, Wendel FJ (1997) Congruence and consensus in the cotton tubre (Malvaceae). ASPT 22:259–290

Simmonds NW (1962) The evolution of bananas. Longmans, London

Simmonds NW, Weatherup STC (1990) Numerical taxonomy of the wild bananas (*Musa*). New Phytol 115:567–571

Soltis DE, Soltis PS, Chase MW, Mort ME, Albach DC, Zanis M, Savolainen V, Hahn WH, Hoot SB, Fay MF, Axtell M, Swensen SM, Prince LM, Kress WJ, Nixon KC, Farris JS (2000) Angiosperm phylogeny inferred from 18S rDNA, *rbcL*, and *atpB* sequences. Bot J Linn Soc 133:381–461

Sorenson DE, Oneal E, García-Moreno J, Mindell PD (2003) More taxa, more characters: the hoatzin problem is still unresoved. Mol Biol Evol 20:1484–1499. doi:10.1093/molbev/msg157

Sulistyaningsih DL, Megia R, Widjaja AE (2014) Phylogenetical study of wild banana species (*Musa* L.) in Sulawesi inferred from internal transcribed spacer region of nuclear ribosomal DNA sequences. Biotropia 21:13–24

Swofford DL (2003) PAUP* Phylogenetic analysis using parsimony version 4.0b10. Sinauer Associates, Sunderland. http://paup.sc.fsu.edu. Accessed May 2015

Sykora KV (1990) History of the impact of man on the distribution of plant species. In: Di Castri F, Hansen AJ, Debussche M (eds) Biological invasions in Europe and the Mediterranean basin. Kluwer Academic Publishers. Dordrecht, pp 37–50. doi:10.1007/978-94-009-1876-4

Taberlet P, Gielly L, Pautou G, Bouvet J (1991) Universal primers for amplification of three non-coding regions of chloroplast DNA. Plant Mol Biol 17:1105–1109

Thorne R (2004) Tropical plant disjunctions: a personal reflection. Int J Plant Sci 165(4 suppl):137–138

Tiffney BH (1985a) Perspectives on the origin of the floristic similarity between eastern Asia and eastern North America. J Arnold Arbor 66:73–94

Tiffney BH (1985b) The eocene north Atlantic land BRIDGE and its importance in Tertiary and modern phytogeography of the Northern Hemisphere. J Arnold Arbor 66:243–273

von der Lippe M, Kowarik I (2007) Long-distance dispersal of plants by vehicles as a driver of plant invasions. Conserv Biol 21:986–996

Wen J (1998) Evolution of the Eastern Asian and Eastern North American disjunct pattern: insights from phylogenetic studies. Korean J Pl Taxon 28:63–81

Wen J (1999) Evolution of eastern Asian and eastern North American disjunct distributions in flowering plants. Ann Rev Ecol Syst 30:421–455

Wen J (2000) Internal transcribed spacer phylogeny of the Asian and eastern North American disjunct *Aralia* sect. *Dimorphanthus* (Araliaceae) and its biogeographic implications. Int J Plant Sci 161:959–966

Wen J (2001) Evolution of eastern Asian-North American biogeographic disjunctions: a few additional issues. Int J Plant Sci 162:117–122

Wen J, Ickert-Bond SM (2009) Evolution of the Madrean–Tethyan disjunctions and the North and South American amphitropical disjunctions in plants. J Syst Evol 47:331–348

Wen J, Ickert-Bond SM, Nie ZL, Li R (2010) Timing and modes of evolution of eastern Asian—North American biogeographic disjunctions in seed plants. In: Long M, Gu H, Zhou Z (eds) Darwin's heritage today: proceedings of the Darwin 200. Beijing international conference, Higher Education Press, Beijing, China, pp 252–269

White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds) PCR Protocols: a guide to methods and applications. Academic Press, San Diego, pp 315–322

Wiens JJ, Tiu J (2012) Highly incomplete taxa can rescue phylogenetic analyses from the negative impacts of limited taxon sampling. PLoS One 7:e42925. doi:10.1371/journal.pone.0042925

Wilson SJ, Otsuki T (2004) To spray or not to spray: pesticides, banana exports, and food safety. Food Policy 29:131–146

Wong C, Kiew R, Argent G, Ohn S, Lee S, Gan Y (2002) Assessment of the validity of the sections in *Musa* (Musaceae) using AFLP. Ann Bot Lond 90:231–238

Wong C, Argent G, Kiew R, Ohn S, Gan Y (2003) The genetic relations of *Musa* species from Mount Jaya, New Guinea, and a reappraisal of the sections *Musa* (Musaceae). Gard Bull (Singapore) 55:97–111

Xiang QY, Soltis DE (2001) Dispersal–vicariance analyses of intercontinental disjuncts: historical biogeographical implications for angiosperms in the Northern Hemisphere. Int J Plant Sci 162:29–39

Yoder AD, Irwin JA, Payseur BA (2001) Failure of the ILD to determine data combinability for slow loris phylogeny. Syst Biol 50:408–424

Ze-Long N, Sun H, Beardsley M, Olmstead GR, Wen J (2006) Evolution of biogeographic disjunction between eastern Asia and eastern North America in *Phryma* (Phrymaceae). Am J Bot 93:1343–1356

Zhou S, Renner SS, Wen J (2006) Molecular phylogeny and intra- and intercontinental biogeography of Calycanthaceae. Mol Phylogenet Evol 39:1–15. doi:10.1016/j.ympev.2006.01.015

Zwickl DJ (2006) Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. Dissertation, University of Texas