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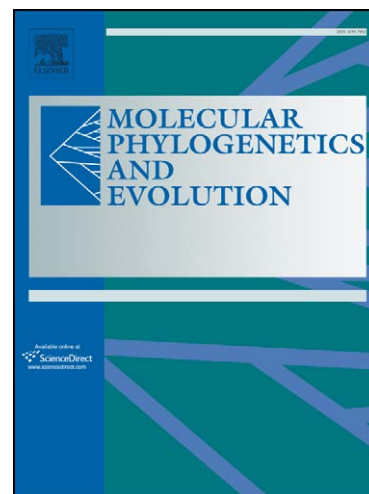
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1 **Plastid and nuclear DNA markers reveal intricate relationships at subfamilial and tribal**
2 **levels in the soapberry family (Sapindaceae)**

3

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25

26 **Abstract**

27 The economically important soapberry family (Sapindaceae) comprises about 1900
28 species mainly found in the tropical regions of the world, with only a few genera being
29 restricted to temperate areas. The infrafamilial classification of the Sapindaceae and its
30 relationships to the closely related Aceraceae and Hippocastanaceae – which have now
31 been included in an expanded definition of Sapindaceae (i.e., subfamily Hippocastanoideae)
32 – have been debated for decades. Here we present a phylogenetic analysis of Sapindaceae
33 based on eight DNA sequence regions from the plastid and nuclear genomes and including
34 85 of the 141 genera defined within the family. Our study comprises 997 new sequences of
35 Sapindaceae from 152 specimens. Despite presenting 18.6% of missing data our complete
36 data set produced a topology fully congruent with the one obtained from a subset without
37 missing data, but including fewer markers. The use of additional information therefore led to
38 a consistent result in the relative position of clades and allowed the definition of a new
39 phylogenetic hypothesis. Our results confirm a high level of paraphyly and polyphyly at the
40 subfamilial and tribal levels and even contest the monophyletic status of several genera. Our
41 study confirms that the Chinese monotypic genus *Xanthoceras* is sister to the rest of the
42 family, in which subfamily Hippocastanoideae is sister to a clade comprising subfamilies
43 Dodonaeoideae and Sapindoideae. On the basis of the strong support demonstrated in
44 Sapindoideae, Dodonaeoideae and Hippocastanoideae as well as in 14 subclades, we
45 propose and discuss informal groupings as basis for a new classification of Sapindaceae.

46

47 **Key words:** Aceraceae; classification; Hippocastanaceae; molecular phylogeny; paraphyly;
48 polyphyly; Sapindaceae; *Xanthoceras*.

49

50

51 1. Introduction

52 The soapberry family (Sapindaceae: Sapindales) comprising c. 1900 species
53 (Acevedo-Rodríguez, pers. comm.), has a predominantly pantropical distribution with the
54 occurrence of some taxa in temperate areas (e.g., *Acer*, *Aesculus*, *Atalaya*, *Diplopeltis*,
55 *Dodonaea*). Sapindaceae include many economically important species used for their fruits
56 [e.g., guarana (*Paullinia cupana*), litchi (*Litchi chinensis*), longan (*Dimocarpus longan*),
57 pitomba (*Talisia esculenta*) and rambutan (*Nephelium lappaceum*)], wood [e.g., buckeyes
58 (*Aesculus*)] or as ornamentals (*Koelreuteria*, *Unghadia*).

59 The circumscription of the family as well as the relationships among subfamilial
60 entities have been widely challenged since the very first worldwide treatment of Sapindaceae
61 sensu stricto (s.s.) (including subfamilies Sapindoideae and Dodonaeoideae) proposed by
62 Radlkofer (1890, 1933; for a review see Harrington et al., 2005). For instance, several
63 genera within the Sapindoideae (e.g., *Tinopsis* and *Plagioscyphus* from Madagascar;
64 Capuron, 1969) were shown to be morphologically transitional between tribes described by
65 Radlkofer (1933), which prevented the recognition of unequivocal tribes. Within Sapindaceae
66 s.s. the higher taxonomic entities (subfamilies and tribes) were originally defined by
67 Radlkofer (1933) based on the number and type of ovules per locule, the fruit morphology,
68 the presence or not of an arillode, the leaf type and the cotyledon shape. On the basis of
69 macromorphological and palynological characters, Müller and Leenhouts (1976) revised the
70 classification of Radlkofer (1933). They recognized eight major pollen types (A to H) and
71 several subtypes (e.g., type-A1), mainly based on their shape and characteristics of the
72 aperture (Fig. 1). The pollen grains in Sapindaceae are triporate [the diporate type-D pollen
73 of *Lophostigma* recognized by Müller and Leenhouts (1976) was wrongly identified; see
74 Acevedo-Rodríguez (1993a)]. Spherical pollen shape occurs in the majority of species (e.g.,
75 types A, B and H), whereas a triangular (type-C) or oblate (type-A1) shape is more restricted.
76 The colpi may be absent (e.g., type-G) or parasyncolporate (e.g., type-A) to syncolporate
77 (e.g., type-B) (Fig. 1). Based on those characters Müller and Leenhouts (1976) rearranged
78 the nine tribes of Sapindoideae recognized by Radlkofer (1933) into three taxonomically

79 unranked groups characterized by their distribution, the presence or absence of an arillode
80 surrounding the seed and the pollen types [i.e., group A comprised Sapindeae,
81 Lepisantheae (incl. Aphanieae) and Melicocceae; group B comprised Schleichereae,
82 Nephelieae and Cupanieae; group C comprised Paullinieae and Thouinieae]. They did not,
83 however, modify the classification within the Dodonaeoideae and maintained the five tribes
84 described by Radlkofer (i.e., Cossinieae, Dodonaeae, Doratoxyleae, Harpullieae and
85 Koelreuterieae; 1933). Furthermore, Müller and Leenhouts (1976) kept the predominantly
86 temperate families Aceraceae and Hippocastanaceae separate from the rest of
87 Sapindaceae. The circumscription of Sapindaceae has been debated ever since. Takhtajan
88 (1987), Cronquist (1988) and Dahlgren (1989) maintained Aceraceae and Hippocastanaceae
89 separate from Sapindaceae, whereas broader concepts of the family have been adopted by
90 several workers (e.g., Umadevi and Daniel, 1991; Judd et al., 1994; Gadek et al., 1996;
91 Savolainen et al., 2000; Thorne, 2000, 2007; APGII, 2003).

92 Building on a large-scale molecular phylogenetic analysis of Sapindales (Gadek et al.,
93 1996), Harrington et al. (2005) published the first molecular phylogeny of Sapindaceae sensu
94 lato (s.l.) (including Aceraceae and Hippocastanaceae) inferred from the plastid genes *rbcl*
95 and *matK*. Their phylogeny recognized the subdivision of Sapindaceae s.l. into four
96 supported lineages, a monotypic Xanthoceroideae, Hippocastanoideae (including
97 Aceraceae, Hippocastanaceae and *Handeliodendron*), a more narrowly defined
98 Dodonaeoideae and Sapindoideae (including *Koelreuteria* and *Ungnadia*). Relationships
99 between these four lineages remained weakly supported. Confirming previous works based
100 on morphological features, Harrington et al. (2005) highlighted the paraphyletic or
101 polyphyletic nature of several tribes described by Radlkofer (1933).

102 According to the new assessment of the Sapindaceae s.l. proposed by Thorne (2007;
103 mainly based on Harrington et al., 2005) and a broad review of currently described taxa, it is
104 now widely accepted that the c. 1900 species of this cosmopolitan family are divided into 141
105 genera (see Table 1; Acevedo-Rodríguez, pers. comm.). Even if Harrington et al. (2005)
106 covered worldwide representatives of Sapindaceae s.l., the sampling (64 of the 141 genera,

107 i.e., 45.4%) and the number of markers were not sufficient to assess the relationships among
108 and within the major lineages of the family with confidence. In this study we provide a new
109 assessment of the phylogenetic relationships within Sapindaceae s.l. based on 60.3% of the
110 generic diversity (85 of the 141 genera) and including the previously unsampled tribe
111 Cossinieae. The analysis is based on a combination of one nuclear (ITS region; *ITS1*, *5.8S*,
112 *ITS2*) and seven plastid (coding *matK* and *rpoB*; non coding *trnL* intron and intergenic
113 spacers *trnD-trnT*, *trnK-matK*, *trnL-trnF* and *trnS-trnG*) markers. Coding plastid regions have
114 proven to be useful in addressing phylogenetic relationships at higher taxonomic levels (e.g.,
115 Clayton et al., 2007; Muellner et al., 2006, 2007; Harrington et al., 2005), whereas noncoding
116 regions (introns and intergenic spacers) were shown to be more useful at lower taxonomic
117 ranks (Baldwin, 1992; Soltis and Soltis, 1998). The combination of several markers from both
118 nuclear and plastid genomes as well as coding and non coding regions are expected to
119 improve the resolution of phylogenetic relationships within the family. In this study, our
120 objectives are (1) to examine the relationships between the traditionally defined Aceraceae
121 and Hippocastanaceae with the rest of Sapindaceae, (2) to evaluate the tribal concepts of
122 Radlkofer (1933) and Müller and Leenhouts (1976), (3) to examine phylogenetic relationships
123 among taxa in light of characters traditionally used to define the higher level groupings in
124 Sapindaceae s.l. (e.g., number of ovules per locule, pollen morphology, leaf type and
125 presence/absence of an arillode) and (4) to propose a new preliminary infrafamilial
126 classification for Sapindaceae s.l.

127 In addition of being a challenging family at the taxonomic level, the amplification of
128 molecular markers in Sapindaceae s.l. is made difficult by several mutations occurring in
129 flanking regions of widely used plastid and nuclear regions such as *matK* (Harrington et al.,
130 2005) and ITS (Edwards and Gadek, 2001). Those mutations complicate the compilation of
131 multilocus data sets without missing data. Maximizing taxa and markers representation to
132 provide a reliable phylogenetic hypothesis inferred from nuclear and plastid genomes is
133 required to propose a new classification for family Sapindaceae. This was achieved by
134 analysing two data sets based on the same taxa, but including different levels of missing

135 data (i.e., different number of markers). While the inclusion of missing data was widely
136 recognized as a major drawback in phylogenetic analyses during the early 90's (e.g.,
137 Huelsenbeck, 1991; Wiens and Reeder, 1995), recent simulations (Wiens, 1998, 2003, 2006)
138 and empirical analyses (Bapste et al., 2002 ; Driskell et al., 2004; Philippe et al., 2004) have
139 shown that taxa comprising high levels of missing data could be accurately placed in
140 phylogenies. Moreover, adding incomplete taxa to a phylogenetic analysis was even shown
141 to improve the accuracy of a given topology, e.g. by subdividing misleading long branches
142 (Wiens, 2005). However, there is a strong heterogeneity in the ability of the different
143 phylogenetic algorithms for managing data sets with substantial levels of missing data
144 (Wiens, 2006), with maximum parsimony performing poorly compared to model-based
145 algorithms such as maximum likelihood and Bayesian inference (Wiens, 2005, 2006).

146

147 **2. Material and Methods**

148 *2.1. Taxon sampling*

149 Species names, voucher information, and GenBank accession numbers for all
150 sequences are provided in the Appendix. The sampling strategy was designed to encompass
151 the majority of subfamilies, tribes and genera of the family as recognized by the existing
152 classifications of Radlkofer (1933), Müller and Leenhouts (1976) and Thorne (2007). Ingroup
153 sampling comprised 152 specimens representing 60.3% of the generic diversity (85 of the
154 141 genera; 28 of the 57 missing genera in this analysis are monospecific; Table 1). The
155 outgroup included Anacardiaceae (*Sorindeia* sp.; defined as outgroup in all analyses;
156 Savolainen et al., 2000 and Muellner et al., 2007) and Simaroubaceae (*Harrisonia*
157 *abyssinica*). Silica-gel dried samples (Chase and Hills, 1991) were collected in the field by
158 the authors and complemented with materials from the DNA banks of the Missouri Botanical
159 Garden (St. Louis, U.S.A.), the Royal Botanic Gardens, Kew (London, U.K.) and the James
160 Cook University (Cairns, Australia).

161

162 *2.2. DNA sequencing*

163 Samples from the collections of the Missouri Botanical Garden and field collected
164 samples were extracted in the laboratory of Evolutionary Botany at the University of
165 Neuchâtel (Switzerland) using the QIAGEN DNeasy plant kit (Qiagen, Hilden, Germany) and
166 following the manufacturer's protocol. Samples from the collections of the Royal Botanic
167 Gardens, Kew, were extracted using the 2X cetyltrimethylammonium bromide (CTAB)
168 procedure of Doyle and Doyle (1987) with minor modifications (see Muellner et al., 2005)
169 followed by additional purification using a caesium chloride/ethidium bromide gradient (1.55
170 g/ml) and a dialysis procedure. The samples from James Cook University (Cairns, Australia)
171 were extracted with the CTAB procedure of Doyle and Doyle (1987).

172 Seven plastid DNA regions and one nuclear ribosomal DNA region were amplified.
173 Primers for the plastid regions are those described in Edwards and Gadek (2001) for *matK*
174 (specific primer for the Dodonaeoideae were designed by Harrington et al., 2005) and the
175 *trnK-matK* intergenic spacer (IGS), the DNA barcoding project
176 (<http://www.kew.org/barcoding/update.html>) for *rpoB*, Demesure et al. (1995) for the *trnD-*
177 *trnT* IGS, Taberlet et al. (1991) for *trnL* intron and *trnL-trnF* IGS, and Hamilton (1995) for
178 *trnS-trnG* IGS. Primers for the ITS region are described in White et al. (1990) and additional
179 primers were designed by Edwards and Gadek (2001) for Sapindaceae s.l.

180 Amplification of selected regions were achieved in a 25 µl reaction mixture containing
181 5 µl 5X PCR buffer, 1.5 µl 25mM MgCl₂, 0.5 µl 10mM dNTPs, 0.5 µl 10mM primers, 0.2 µl
182 GoTaq polymerase (5u/µl) (Promega, Madison, WI, USA), and 14.5 µl ddH₂O. The
183 amplification of the *matK* region was improved by the addition of 4% DMSO in the total
184 volume of the PCR mix. PCR was performed in a Biometra ® T3 thermocycler. Initial
185 denaturation was programmed for 2 min at 95°C, followed by 35 cycles at 95°C for 45 s,
186 50°C for 45 s, 72°C for 1 min, plus a final extension of 10 min at 72°C. PCR products were
187 purified using the QIAquick PCR purification kit (Qiagen, Hilden, Germany) and fluorescent
188 sequencing was performed by Macrogen, Inc. (Seoul, South Korea) with the same primers
189 used for PCR amplification.

190

191 *2.3. Alignment*

192 The program Sequencher version 4.1 (Gene Codes Corp., Ann Arbor, Michigan,
193 USA) was used to assemble complementary strands and verify software base-calling. The
194 eight regions were initially aligned individually with ClustalX (Thompson et al., 1997), and
195 thereafter manually adjusted with the program Bioedit (Hall, 1999) using the similarity
196 criterion (Morrison, 2006). The program Concatenate (Alexis Criscuolo,
197 <http://www.lirmm.fr/~criscuolo/>) was used to construct two combined matrices, differing in the
198 number of markers considered and in the level of missing data (see below).

199

200 *2.4. Phylogenetic analyses*201 *2.4.1. Single-gene analyses*

202 Individual phylogenetic analyses and their corresponding bootstrap analyses were
203 performed using the maximum likelihood (ML) and maximum parsimony (MP) criteria. Each
204 partition and the combined data sets were analyzed using parsimony ratchet (Nixon, 1999)
205 as implemented in PAUPrat (Sikes and Lewis, 2001). Based on recommendations by Nixon
206 (1999), ten independent searches were performed with 200 iterations and 15% of the
207 parsimony informative characters perturbed. The shortest equally most parsimonious trees
208 were combined to produce a strict consensus tree. To assess the support at each node, non
209 parametric bootstrap analyses (Felsenstein, 1985) were performed using PAUP* version
210 4.0b10 (Swofford, 2002) with 1000 replicates, SPR branch swapping, simple sequence
211 addition, MULTREES and holding 10 trees per replicate. We used SPR branch swapping
212 because it has been shown to be twice as fast as TBR and results in support percentages
213 that are not significantly different (Salamin et al., 2003).

214 Model selection for each partition was assessed using Modeltest version 3.7 (Posada
215 and Crandall, 1998) and the Akaike information criterion (Akaike, 1973). ML analyses were
216 performed using RAxML version 7.0.0 (Stamatakis, 2006; Stamatakis et al., 2008) with a
217 1000 rapid bootstrap analyses followed by the search of the best-scoring ML tree in one

218 single run. This analysis was done using the facilities offered by the CIPRES portal in San-
219 Diego, U.S.A. (<http://8ball.sdsc.edu:8888/cipres-web/home>).

220 In this study, nodes with bootstrap supports (BS) below 50% are considered not
221 supported, 50-74% are considered weakly supported, 75-89% are moderately supported and
222 90-100% are strongly supported. Topological differences between single-gene phylogenetic
223 trees were compared using TreeJuxtaposer (Munzner et al., 2003), taking into account the
224 level of resolution of each marker and their bootstrap supports. In this study, topological
225 differences having a bootstrap support inferior to 75% were not considered.

226

227 2.4.2. Combined analyses

228 The impact of missing data on combined MP and ML phylogenetic analyses was
229 tested based on two different combined matrices. The first matrix (hereafter named “4
230 markers” data set) was composed of specimens for which sequence information was
231 available for the nuclear ribosomal ITS region and for three of the seven plastid regions
232 (*rpoB*, *trnL* intron and *trnL-trnF* IGS). In this combined matrix, the four remaining plastid
233 markers were not included in order to have a complete matrix without missing data. The
234 second combined matrix (hereafter named “4+4 markers” data set) comprised the same set
235 of taxa as the “4 markers” data set, but also included the other four plastid markers (*matK*,
236 *trnD-trnT* IGS, *trnK-matK* IGS and *trnS-trnG* IGS). This data set was designed to evaluate
237 the effect of additional information on the resolution and support of topologies in comparison
238 to the “4 markers” analyses. Taxa for which no sequences were available for a given marker
239 were coded as missing data for the corresponding cells in the combined matrix (sensu Wiens
240 and Reeder, 1995).

241 Total evidence trees (sensu Kluge, 1989) were determined using both ML and MP
242 criteria on the two data sets using the same settings as in the single-gene analyses. Non
243 parametric bootstrap analyses were performed for the data sets following the same settings
244 as for the single-gene analyses. Before computing total evidence trees, an incongruence

245 length difference (ILD) test (Farris et al., 1994) was performed as implemented in PAUP*
246 version 4.0b10 (Swofford, 2002) with 100 replicates.

247

248 2.5. Topological congruence and impact of missing data on combined analyses

249 Based on analyses of the combined matrices (i.e., “4 markers” and “4+4 markers”
250 data sets), the impact of of missing data on MP and ML phylogenetic analyses was
251 investigated (i) by assessing topological distances among trees obtained using different data
252 sets and algorithms and (ii) by comparing taxa groupings (and clade supports) in each
253 topology. The explicitly agree distance (Estabrook et al., 1985; Estabrook, 1992; EA
254 distance) was calculated to evaluate the extent to which total evidence trees were compatible
255 with each other. The EA distance quantifies the differences between trees of the same size
256 (i.e., comprising the same number of terminal taxa). It evaluates the proportion of triplets that
257 are resolved identically in two trees (see Wilkinson et al., 2005). EA distances were
258 calculated using DARWIN 5 (Perrier et al., 2003). The congruence of topological groupings in
259 analyses obtained from different data sets and algorithms was evaluated using
260 TreeJuxtaposer (Munzner et al., 2003) and bootstrap supports of each main clade were
261 compared.

262

263 3. Results

264 3.1. Alignment

265 The number of sequences included in each single-gene partition varied from 69 in
266 *trnS-trnG* IGS to 154 in *rpoB*, *trnL* intron and *trnL-trnF* IGS (Table 2). For the ITS region, all
267 specimens were sequenced, except the outgroup species *Sorindeia* sp. (i.e., 153 sequences
268 were produced). All sequences used to reconstruct the phylogenetic tree of Sapindaceae s.l.
269 were produced for this study. The alignment length ranged from 363 bp in *rpoB* to 2156 bp in
270 *trnS-trnG* IGS (Table 2). The ITS region had the highest number of variable characters
271 (51.4%), whereas *trnS-trnG* IGS had the lowest (23.8%), even less than the coding regions
272 *matK* and *rpoB* (29.1% and 37.2%, respectively). The same trend was recorded for the

273 percentage of potentially parsimony-informative characters (37.8% for the ITS region and
274 9.0% for the *trnS-trnG* IGS; Table 2).

275 The combined data sets consisted respectively of 615 sequences (154 specimens; no
276 missing data in ingroup taxa) for the “4 markers” data set, and 997 sequences (154
277 specimens; 18.6 % missing data) for the “4+4 markers” data set (Table 2). The alignment
278 length of the two data sets was respectively 3031 bp (“4 markers”) and 9657 bp (“4+4
279 markers”). The “4 markers” data set had a highest percentage of variable characters (44.7%)
280 than the “4+4 markers” data set (37.0%). The same observations were recorded for the
281 percentage of potentially parsimony-informative characters (30.3% for the “4 markers” and
282 21.2% for the “4+4 markers” data sets; Table 2). However, when considering the total
283 amount of phylogenetic information averaged by the number of taxa, the “4 markers” data set
284 shown a value more than twice higher than did the “4+4 markers” data set (Table 2).

285

286 3.2. Phylogenetic analyses

287 3.2.1. Single-gene analyses

288 The best-fit model for all partitions was the general time reversible (GTR) with an
289 alpha parameter for the shape of the gamma distribution to account for among-site rate
290 heterogeneity (Yang, 1993). The only exception was for the ITS region for which a proportion
291 of invariable sites was added. Although the MP and ML single-gene analyses provided
292 topologies with different levels of resolution within Sapindaceae s.l. (e.g., the MP trees were
293 usually not resolved in several parts of the tree), no moderately to strongly supported
294 differences (> 75%) were observed between single-gene trees. In addition, the ILD test was
295 not significant ($P=0.9$) and indicated that the eight data sets were congruent. Those results
296 allowed the combination of the partitions in a total evidence approach. Statistics (number of
297 most parsimonious trees; tree length; consistency and retention indices) for each analysis
298 are reported in Table 2.

299

300 3.2.2. Combined analyses

301 The most parsimonious trees for the two combined analyses under the MP criterion
302 were respectively 5889 (“4 markers” data set) and 9843 (“4+4 markers” data set) steps.
303 Under the ML criterion, the best-fit model for the combined matrices was GTR with a
304 proportion of invariable sites and an alpha parameter for the shape of the gamma distribution
305 to account for among-site rate heterogeneity (Yang, 1993). This model was used to perform
306 the ML search (log likelihoods were -34322.2 for the “4 markers” data set and -69253.8 for
307 the “4+4 markers” data set) followed by rapid bootstrap analyses.

308

309 3.3. Topological congruence and impact of missing data on combined analyses

310 The congruence (expressed by 1 - EA distance) between total evidence trees
311 compiled under the ML criterion was higher (98% of common triplets between total evidence
312 trees based on “4 markers” and “4+4 markers” data sets) than between total evidence trees
313 obtained under MP criterion (90% of common triplets between total evidence trees based on
314 “4 markers” and “4+4 markers” data sets) (Table 3). The MP “4 markers” total evidence tree
315 exhibits the highest EA distances with the other total evidence trees (Table 3).

316 Each of the four total evidence analyses showed support for the monophyly of
317 Sapindaceae s.l. as defined by Thorne (2007) including Aceraceae and Hippocastanaceae
318 (Table 4). No matter which data set or algorithm were considered, the family was subdivided
319 into three moderately to strongly-supported lineages and a fourth lineage only consisting of
320 *Xanthoceras sorbifolia*, with the following relationships: (*Xanthoceras sorbifolia*, (clade A,
321 (clade B, clade C))) (Table 4; Fig. 2). Despite strong support for each clade, the sister
322 position of the monotypic *Xanthoceras* was not supported in any analyses (see clade A +
323 clade B + clade C in Table 4). This lineage corresponded to subfamily Xanthoceroideae as
324 described by Thorne (2007). Clade A corresponded to subfamily Hippocastanoideae
325 (including the previous recognized families Aceraceae and Hippocastanaceae) as described
326 by Harrington et al. (2005) and Thorne (2007). Clade B corresponded to subfamily
327 Dodonaeoideae as described by Harrington et al. (2005) and Thorne (2007) with the addition
328 of *Euphorianthus* (Cupanieae; Sapindoideae). Clade C corresponded to subfamily

329 Sapindoideae (Thorne, 2007; Harrington et al., 2005) plus one representative from
330 Dodonaeoideae, *Conchopetalum*, included in tribe Harpullieae. Clade C was moderately to
331 strongly supported as monophyletic and divided into ten groups, but not in the MP “4
332 markers” total evidence tree (only one exception: clade V nested in clade VI; Table 4). The
333 bootstrap supports of each clade obtained under the ML algorithm are consistent in both data
334 sets (Table 4), whereas support slightly increases in MP analyses, in parallel to an increase
335 in missing data (Table 4).

336 The “4 markers” and “4+4 markers” topologies recognized all the classical tribes
337 (except the Paullinieae) as paraphyletic or polyphyletic. However, phylogenetic status of
338 tribes Cossinieae and Koelreuterieae were not tested because only one genus per tribe was
339 considered. In total 5 of the 67 non-monotypic sampled genera (7.5%) are paraphyletic or
340 polyphyletic (*Cupaniopsis*, *Guioa*, *Haplocoelum*, *Matayba*, *Sarcotoechia*). However, the
341 phylogenetic status of some of these genera needs to be treated with caution because of
342 weak bootstrap supports and limited sampling (e.g., *Guioa*).

343

344 4. Discussion

345 4.1. Congruence of topologies with and without missing data

346 Our results indicate a high level of congruence among topologies obtained using data
347 sets with and without missing data and based on different algorithms. Considering the “4
348 markers” data set (without missing data), MP and ML algorithms however produced slightly
349 different topologies regarding clades C-V and C-VI (i.e., in the MP “4 markers” tree clade C-
350 VI is paraphyletic with the inclusion of the clade C-V, whereas all other topologies considered
351 this clade as monophyletic; Table 4). This could be explained mostly by the small amount of
352 phylogenetic information in the “4 markers” data set that prevent the MP algorithm to find a
353 proper solution (averaged over the number of terminal taxa; Table 2). Although the addition
354 of 4 markers to the data set generated 18.6% of missing data (27.3% of missing nucleotides)
355 in the “4+4 markers” data set, the added information doubled the mean amount of potentially
356 parsimonious-informative characters per terminal taxa and increased the bootstrap support

357 for several nodes in the total evidence trees (Tables 2, 4). Since our results highlight a high
358 congruence level among topologies obtained with different data sets and algorithms, only the
359 ML total evidence tree inferred from the “4+4 markers” data set will be discussed in order to
360 maximize phylogenetic information (Figs. 2-6).

361

362 4.2. Phylogenetic relationships

363 Our results support (1) the paraphyly of the currently defined Dodonaeoideae and
364 Sapindoideae as defined by Thorne (2007); (2) the polyphyly of all tribes (tribes Cossinieae
365 and Koelreuterieae are not considered because only one genus per tribe was sampled) with
366 the possible exception of Paullinieae – whose monophyletic status shall be evaluated by the
367 inclusion of three missing genera *Houssayanthus*, *Lophostigma* and *Thinouia* in future
368 analyses – and (3) the paraphyly or polyphyly of 5 of the 67 non-monotypic sampled genera
369 (7.5%) included in this study (Table 1).

370 In light of these results, a new infrafamilial classification for Sapindaceae s.l. is
371 required. However, we recommend caution in formally proposing new tribes until (i) non-
372 molecular synapomorphies supporting putative new tribal delimitations are identified and (ii)
373 the inclusion of missing genera in future phylogenetic analyses. In order to provide efficient
374 guidelines for a new classification of the family, the phylogenetic framework obtained here is
375 discussed according to several key morphological characters such as leaf type (including
376 phyllotaxy), wood anatomy, number of ovules per locule, fruit type and pollen (Fig. 1), as well
377 as geographical distribution. Hereafter, the definition of Dodonaeoideae and Sapindoideae
378 will be expanded to include *Euphorianthus* in the former and *Conchopetalum* in the latter.

379 Xanthoceroideae and Hippocastanoideae occur mostly in temperate regions [except
380 *Billia* (not included here), which occurs from Mexico to tropical South America], whereas
381 Dodonaeoideae have a temperate (e.g., south of Australia) and tropical pattern of
382 distribution. On the other hand, Sapindoideae have mainly radiated in tropical regions. Within
383 Sapindaceae s.l., a trend towards the reduction of the number of ovule per locule is
384 observed: from six to eight (Xanthoceroideae) to two (Hippocastanoideae and most of the

385 Dodonaeoideae) and finally one (Sapindoideae except *Conchopetalum*). All four subfamilies
386 recognized by Thorne (2007) are discussed separately below.

387

388 4.3. Subfamily Xanthoceroideae (Fig. 2)

389 The phylogenetic position of the monotypic Chinese *Xanthoceras* in relation to the
390 other three main lineages of Sapindaceae remains unsupported (BS<50) (Fig. 2; Table 4).
391 Nevertheless, this species was moderately supported as the earliest-diverging lineage in
392 Sapindaceae s.l. in earlier studies (*matK*, *rbcL*, Harrington et al. 2005; *rbcL*, Savolainen et al.
393 2000; 18S rDNA, *atpB*, *rbcL*, Soltis et al. 2000). In the first molecular phylogeny of
394 Sapindaceae s.l., Harrington et al. (2005) argued that an increased sampling of other
395 monotypic Southeast Asian genera of Harpullieae (e.g., *Arfeuillea*, *Delavaya*, *Eurycorymbus*)
396 and Koelreuterieae (*Sinoradlkofera*) might help break up possible long-branch attraction and
397 stabilize the position of this taxon. However, our study shows that even when considering
398 60.3% of the generic diversity and including *Arfeuillea*, *Delavaya* and *Eurycorymbus*, the
399 phylogenetic position of this genus remains unchanged. This small shrub is characterized by
400 unusual features in Sapindaceae such as deciduous imparipinnate leaves (vs. deciduous
401 simple leaves or sempervirent imparipinnate or paripinnate leaves in other Sapindaceae), six
402 to eight fertile ovules per locule (generally 1 or 2 ovules per locule in the rest of the family)
403 and the presence of orange horn-like appendages protruding from the disk (absent in other
404 genera). Moreover, this species exhibits a type-A pollen which was expected to be ancestral
405 in Sapindaceae by Müller and Leenhouts (1976) (Fig. 1). However, this pollen type is
406 widespread across the taxa sampled in our phylogeny and is consequently of limited
407 systematic utility.

408

409 4.4. Subfamily Hippocastanoideae (Clade A; Figs. 2)

410 The inclusion of Aceraceae and Hippocastanaceae in Sapindaceae has been
411 debated for decades (e.g., Radlkofer, 1933; Müller and Leenhouts, 1976; Umadevi and
412 Daniel, 1991; Judd et al., 1994) and both are currently included in Sapindaceae by the

413 Angiosperm Phylogeny Group (APGII, 2003). However, the final decision regarding the
414 taxonomic level of this well-supported clade (BS 100; Fig. 2) is somewhat dependant on the
415 placement of *Xanthoceras sorbifolia*. Although *Billia* and *Handeliiodendron*, thought to be
416 close relative of *Aesculus* (Xiang et al., 1998; Forest et al., 2001), were not sampled here,
417 the analysis confirms the definition of Hippocastanoideae as previously suggested by Judd et
418 al. (1994) and Harrington et al. (2005). This temperate clade is characterized by deciduous
419 opposite simple leaves (generally palmatilobate), two ovules per locule and a type-A pollen
420 (Biesboer, 1975; Müller and Leenhouts, 1976; Fig. 1).

421

422 4.5. Subfamily Dodonaeoideae (Clade B; Figs. 2, 3)

423 The improved sampling for subfamily Dodonaeoideae (i.e., the addition of genera
424 *Arfeuillea*, *Averrhoidium*, *Doratoxylon*, *Euphorianthus*, *Eurycorymbus*, *Llagunoa* and *Majidea*)
425 allows the recognition of two moderately to well-supported clades (Fig. 3; Table 4). This
426 topology was partially recovered by Harrington et al. (2005), but the addition of new taxa
427 allow their delimitation based on fruit morphology: clade I (*Doratoxylon* group) occurs from
428 Africa, Madagascar to Australasia and is characterized by indehiscent berry-like fruits,
429 whereas clade II (*Dodonaea* group) is distributed in South America, Madagascar, Australasia
430 and the Pacific islands (*Dodonaea viscosa* had a worldwide distribution) and comprises
431 species with dehiscent fruits. In addition to the widespread type-A pollen occurring in both
432 clades, specialized pollen types characterizing specific taxa occur in clade II [i.e., type-F
433 (*Diplopeltis huegii*) and type-H (*Harpullia cupanoides*)] (George and Erdtman, 1969; Müller
434 and Leenhouts, 1976; Fig. 1). Clades I and II have generally two ovules per locule; however
435 a reduction to one ovule per locule occurs independently in the two clades (*Filicium* in clade I
436 and *Euphorianthus* in clade II). Moreover, a few species of *Harpullia* (clade II), such as *H.*
437 *arborea*, have 1-2 ovules per locule (Adema et al., 1994).

438

439 4.6. Subfamily Sapindoideae (clade C; Figs. 2, 4-6)

440 4.6.1. Early-diverging lineages (Fig. 4)

441 Subfamily Sapindoideae is by far the most diverse lineage in terms of species. Based
442 on our analyses, we propose to divide it into ten groups that are discussed in light of their
443 morphological features, geographical distribution and compared to tree topologies obtained
444 by Harrington et al. (2005) (Figs. 4-6). The *Delavaya* group is the first lineage to diverge in
445 Sapindoideae (clade I). Only the Chinese monotypic genus *Delavaya* is included in the
446 present study. Results from Harrington et al. (2005) highlighted the Mexican and Texan
447 genus *Ungnadia* (from which nuclear sequences were unavailable) as the most basal lineage
448 in Sapindoideae. Combined plastid analyses (S. Buerki, unpubl. data) revealed a close-
449 relationship between those two genera as suggested by Judd et al. (1994; based on
450 morphological characters); however this relationship must be further examined using nuclear
451 sequences. The *Delavaya* group is characterized by elongated petal base appendages and
452 glabrous stamens (Judd et al., 1994) and the wood anatomy within the group is identical to
453 the Cupanieae (Klaassen, 1999). The *Koelreuteria* group (clade II; BS 100), here comprising
454 only *Koelreuteria*, is distributed in southern China and western Pacific. The study of
455 Harrington et al. (2005) revealed a close-relationship between this genus and *Smellophyllum*
456 and *Stadmania*, distributed in East-Africa, Madagascar and the Mascarene archipelago.
457 When a broad definition is considered, the *Koelreuteria* group shows both ancestral (type-A
458 pollen; Müller and Leenhouts, 1976; Fig. 1) and derived characters (one ovule per locule in
459 *Smellophyllum* and *Stadmania*) and is characterized by the presence of trichomes on the
460 anther. Since these two lineages show a disjunct distribution and transitional character
461 states, they might be relicts of early diversification events in the subfamily (caused by long
462 distance dispersals for example). The *Schleichera* group, which is partially recovered by
463 Harrington et al. (2005), here with the inclusion of *Amesiodendron* (Cupanieae), is a well-
464 supported (BS 100) tropical Asian clade (clade III; Fig. 4). This clade is characterized by a
465 Cupanieae-like wood anatomy (Klaassen, 1999) and type-B pollen (Müller and Leenhouts,
466 1976; Fig. 1).

467

468 4.6.2. *The Litchi group (Figs. 4, 5)*

469 This clade (clade IV; BS 98; Fig. 4) is divided into two well-supported groups (*a* and *b*;
470 Fig. 5). Clade *a* (BS 100) partially corresponds to the *Dimocarpus* group proposed by Müller
471 and Leenhouts (1976; traditionally comprising *Cubilia*, *Dimocarpus*, *Litchi*, *Nephelium*,
472 *Pometia* and *Xerospermum*) and a heterogeneous group comprising mostly African genera
473 as well as the Indian and Australian *Lepidopetalum*. Our study also confirms the close
474 relationships of *Pometia* (characterized by type-C1 pollen; Müller and Leenhouts, 1976; van
475 der Ham, 1990; Fig. 1) with the other member of the *Dimocarpus* group as expected by
476 Müller and Leenhouts (1976). The Lepsiantheae-type wood anatomy of *Eriocoelum*
477 (Cupanieae; Klaassen, 1999) confirms its relationships with the other genera of
478 Lepsiantheae from this clade. A more comprehensive analysis of this clade is currently being
479 undertaken (S. Buerki, unpubl. data).

480 Clade *b* (BS 100) partially corresponds to group A of Müller and Leenhouts (1976)
481 with the addition of *Pseudima* (Cupanieae). The inclusion of the South American *Pseudima* is
482 supported by type-A pollen (Müller and Leenhouts, 1976; Fig. 1) and similar wood anatomy
483 shared with other Sapindeae (Klaassen, 1999). Our results highlight the close affinities of
484 *Lepisanthes*, *Sapindus* and *Atalaya*, but the understanding of relationships within this group
485 will require additional data. The monophyly of the African-Malagasy *Deinbollia* is supported
486 by molecular analyses and type-A1 pollen (Müller and Leenhouts, 1976; Fig. 1).

487

488 4.6.3. The *Macphersonia* group (Fig. 4)

489 Our study reveals for the first time relationships between southeast African and
490 Malagasy genera (BS 100; Fig. 4). Two strongly supported clades were formed by South
491 African *Pappea capensis* and Malagasy *Plagioscyphus* (BS 100) and Malagasy *Beguea*,
492 *Conchopetalum* and *Haplocoelum perrieri*, as well as east African and Malagasy
493 *Macphersonia* (BS 100). *Pappea* was previously thought to be related to other Nephelieae
494 (*Alectryon*, *Podonephelium*, *Smelophyllum* and *Stadmania*) by Müller and Leenhouts (1976),
495 and placed without support as sister to Paullinieae and Thouinieae by Harrington et al.
496 (2005). The position of *Conchopetalum*, characterized by inflated fruits without arillode, in the

497 traditional core Malagasy Schleichereae, defined by indehiscent fruits and a fleshy arillode
498 surrounding the seed, was an unexpected result (Capuron, 1969). This clade is
499 characterized by actinomorphic flowers, one ovule per locule (except two in *Conchopetalum*)
500 and is distributed throughout Madagascar and southeast Africa.

501

502 4.6.4. The *Cupania* group (Figs. 4, 6)

503 The Australasian and Malagasy/South American clade VI (BS 75; Fig. 4) encloses the
504 majority of Cupanieae genera (23 of the 32 sampled genera) and is divided into two main
505 groups (Figs. 4, 6). In the Australasian clade *a* (BS 100), the monophyly of *Elattostachys* is
506 well supported and the expected close relationship between the New Caledonian
507 *Podonephelium* and Australasian and Pacific *Alectryon* is confirmed by this phylogenetic
508 analysis and the shared type-A pollen (Müller and Leenhouts, 1976; Fig. 1). Only one non
509 Cupanieae taxon belongs to clade *b* (BS 100): *Tinopsis apiculata* (Schleichereae). The
510 Malagasy *Tinopsis* was first described as part of the Cupanieae (Radlkofer, 1933) and later
511 transferred to the Schleichereae based on the indehiscence of the fruit and the presence of a
512 fleshy arillode (Capuron, 1969). However, no floral or vegetative characters have been
513 identified to discriminate this genus from the Malagasy Cupanieae genera *Tina* and *Neotina*.
514 This study confirms the close relationships between these genera and supports Radlkofer's
515 (1933) hypothesis. This example and others encountered in clades II and V provide strong
516 arguments supporting the convergent evolution of fruit morphology and consequently its
517 limited systematic utility. The plasticity of fruit types has been demonstrated in several
518 phylogenetic studies performed on a wide range of taxa (e.g., van Welzen, 1990; Adema,
519 1991; Muellner et al., 2003). The *Cupania* group is characterized by type-B pollen (except
520 *Alectryon* and *Podonephelium* which have type-A pollen; Müller and Leenhouts, 1976; Fig.
521 1). In general, taxa within clade *b* present low genetic distances among them while having
522 long terminal branches (especially the Australasian representatives such as *Cupaniopsis*,
523 *Gongrodiscus* and *Toechima*).

524

525 4.6.5. *The Paullinia group and allies (Tristiropsis, Blomia and Melicoccus groups) (Figs. 4)*

526 Although strongly supported in general (except for the *Blomia* group; Table 4), the
527 relationships between these four groups remain unclear (Fig. 4). The monophyly of the
528 Australasian clade VII and the Mexico/East African clade VIII are weakly to well-supported
529 (BS 100 and BS 61, respectively; Fig. 4). To date, no morphological characters have been
530 identified that circumscribe these lineages. The monophyly of the South American clade IX is
531 well supported (BS 100; Fig. 4) and confirms the suggested affinities between *Melicoccus*
532 and *Talisia* argued by Acevedo-Rodríguez (2003) based on morphology and pollen
533 characters.

534 The pantropical clade X (Figs. 4) is strongly supported (BS 100) and corresponds
535 both to the Nomophyllae group defined by Radlkofer (1933) and to the group C proposed by
536 Müller and Leenhouts (1976) containing Paullinieae and Thouinieae. Although no
537 representatives of genus *Allophylus* (Thouinieae) were included here, our study confirms the
538 results of the morphological cladistic analyses of the two tribes conducted by Acevedo-
539 Rodríguez (1993b) and the molecular analyses of Harrington et al. (2005), which show a
540 monophyletic Paullinieae nested in a paraphyletic Thouinieae. Our analysis indicates that the
541 enigmatic species *Sapindus oligophyllus* has affinities with genera in this clade (Fig. 7). The
542 generic position of this taxon has puzzled taxonomists for decades. It was first described as
543 a member of *Aphania* and subsequently transferred in *Sapindopsis*, *Howethoa*, *Sapindus*
544 (see Rauschert, 1982 for review) and recently merged, although informally, in *Lepisanthes* by
545 Xia and Gadek (2007). The increase of sampling and the inclusion of *Allophylus* species
546 might help to circumscribe the position of this taxon. Type-A pollen and the tree life-form are
547 shared by the most basal lineages in this clade (*Athyana weinmannifolia*, *Diatenopteryx*
548 *sorbifolia* and *Bridgesia incisifolia*; Acevedo-Rodríguez, 1993b; Figs. 1, 7), whereas the other
549 taxa have a highly specialized pollen type (type-C2-3; Müller and Leenhouts, 1976; Fig. 1)
550 and a tendency towards liana habit. Species with subtype-C pollen do not form a
551 monophyletic group and consequently this character is of limited systematic value (e.g., type-
552 C3 is encountered in *Thouinia* and *Paullinia*; Müller and Leenhouts, 1976; Acevedo-

553 Rodriguez, 1993b; Figs. 1, 4). Clade X is characterized by zygomorphic flowers, petals with a
554 prominent scale, an unilateral disk and imparipinnate leaves. The liana habit and the
555 development of tendrils and stipules constitute synapomorphies for Paullinieae (Fig. 4).

556

557 4.7. Informal tribal groupings within Sapindaceae

558 The phylogenetic analysis inferred from eight nuclear and plastid regions provides a
559 robust assessment of the relationships within Sapindaceae s.l. (although the relationships
560 between the subfamilies remain weakly supported) (Fig. 2). Nevertheless, the tribal
561 delimitations as currently defined (and based largely on fruit morphology) must be revised
562 because of the plasticity of fruit characters in this group. When Richardson et al. (2000a, b)
563 assessed the tribal classification of Rhamnaceae (also defined by fruit morphology), they
564 encountered the same taxonomic difficulty and proposed a new classification based on
565 molecular data in combination with morphological characters. We follow a similar approach
566 and propose here an informal grouping that could serve as basis for a formal reclassification
567 of Sapindaceae s.l. based on molecular and morphological data. The family is subdivided
568 into four subfamilies (as recognized by Thorne, 2007) and 14 groups: Xanthoceroideae,
569 Hippocastanoideae (two groups); Dodonaeoideae (two groups) and Sapindoideae (10
570 groups) (Figs. 2-4). The groups within subfamilies might represent circumscriptions for the
571 definition of future tribes.

572

573 Subfamily Xanthoceroideae

574 It includes the monotypic Chinese *Xanthoceras sorbifolia*, this deciduous shrub is
575 characterized by alternate imparipinnate leaves, 6-8 ovules per locule and orange horn-like
576 appendages protruding from the disk (Fig. 2).

577

578 Subfamily Hippocastanoideae

579 Temperate deciduous shrubs and trees (except *Billia* found from Mexico to tropical South
580 America) with simple generally palmatilobate opposite leaves and 2 ovules per locule (Fig.

581 2). Although our sampling is limited for this subfamily, results from other studies (Judd et al.,
582 1996; Harrington et al., 2005; S. Buerki, unpubl. data) allows us to suggest two groups within
583 subfamily Hippocastanoideae, corresponding to the formerly recognized families Aceraceae
584 and Hippocastanaceae (Fig. 4):

585

- 586 - *Acer* group (*Acer* and *Dipteronia*): leaves palmately lobed to 3-foliolate or imparipinnate, or
587 entire; actinomorphic unisexual or bisexual flowers and samara;
- 588 - *Aesculus* group (*Aesculus*, *Billia* and *Handeliiodendron*): leaves palmately divided into 3-5
589 leaflets; zygomorphic andromonoecious flowers and dehiscent fruit with one seed.

590

591 Subfamily Dodonaeoideae

592 This subfamily is expanded to include *Euphorianthus*, formerly placed in Sapindoideae.
593 The Dodonaeoideae as defined by Radlkofer (1890, 1933) are characterized by the presence
594 of two or rarely more apotropous and upright ovules per locule, or rarely one ovule that is
595 epitropous and pendulous. However, this does not hold anymore because of the inclusion of
596 the above mentioned genus of Sapindoideae showing one campylotropous ovule per locule.
597 This subfamily is divided into two groups (Fig. 3):

598

- 599 - *Doratoxylon* group (*Doratoxyleae*, without *Averrhoidium*): indehiscent berry-like fruits;
- 600 - *Dodonaea* group (*Cossinieae*, *Dodonaeae*, *Arfeuillea*, *Averrhoidium*, *Eurycorymbus*,
601 *Euphorianthus*, *Harpullia* and *Majidea*): dehiscent fruits.

602

603 Subfamily Sapindoideae

604 The subfamily Sapindoideae should be expanded to include *Conchopetalum*, formerly
605 placed into the Dodonaeoideae. This subfamily as defined by Radlkofer (1933) are
606 characterized by a single apotropous and upright or ascending ovule per locule; however the
607 inclusion of several genera with two ovules per locule [*Conchopetalum* (this study),
608 *Delavaya*, *Koelreuteria* and *Ungnadia*; Harrington et al., 2005; Thorne, 2007; this study]

609 renders this key-character obsolete. Based on our phylogenetic analysis, ten groups are now
610 recognized (Fig. 4):

611

- 612 - *Delavaya* group (*Delavaya* and *Ungnadia*): two ovules per locule; type-A pollen;
613 elongated basal petals appendages; glabrous stamens and Cupanieae wood anatomy.
- 614 - *Koelreuteria* group (*Koelreuteria*, *Smelophyllum* and *Stadmania*): type-A pollen and
615 trichomes on anthers.
- 616 - *Schleichera* group (*Amesiodendron*, *Paranephelium* and *Schleichera*): type-B pollen and
617 Cupanieae-type IV wood anatomy.
- 618 - *Litchi* group [Lepisantheae, Nephelieae (without *Alectryon*, *Pappea*, *Podonephelium*,
619 *Stadmania*, *Smelophyllum*), Sapindeae (without *Sapindus oligophyllus*), *Blighia*,
620 *Eriocoelum*, *Haplocoelopsis*, *Laccodiscus*, *Lecaniodiscus*, *Lepidopetalum* and
621 *Pseudima*]): to date, no morphological characters characterizing this group have been
622 identified.
- 623 - *Macphersonia* group (*Beguea*, *Conchopetalum*, *Haplocoelum perrieri*, *Macphersonia*,
624 *Pappea*, and *Plagioscyphus*): actinomorphic flowers and one ovule per locule (except two
625 in *Conchopetalum*).
- 626 - *Cupania* group (Cupanieae [without *Amesiodendron*, *Blighia*, *Blomia*, *Dictyoneura*,
627 *Eriocoelum*, *Haplocoelopsis*, *Laccodiscus*, *Lepidopetalum*, *Pseudima*], *Alectryon*,
628 *Podonephelium* and *Tinopsis*): type-B pollen (except *Alectryon* and *Podonephelium*,
629 which demonstrate type-A pollen).
- 630 - *Tristiropsis* group (*Dictyoneura* and *Tristiropsis*): to date, no morphological characters
631 characterizing this group have been identified.
- 632 - *Blomia* group (*Blomia* and *Haplocoelum foliosum*): to date, no morphological characters
633 characterizing this group have been identified.
- 634 - *Melicoccus* group (*Talisia* and *Melicoccus*): pollen type-A and Melicocceae wood
635 anatomy.

636 - *Paullinia* group (Paullinieae, Thouinieae and *Sapindus oligophyllus*): imparipinnate
637 leaves; zygomorphic flowers; petals with a prominent scale and a unilateral disk.

638

639 4.8. Conclusions

640 This study based on eight nuclear and plastid regions and 60.3% of the generic
641 diversity of the Sapindaceae s.l. (152 samples and 139 species) (1) provides strong support
642 for the monophyly of the family when *Xanthoceras sorbifolia*, Aceraceae and
643 Hippocastanaceae are included (although relationships among subfamilies are still weakly
644 supported), (2) highlights a high degree of paraphyly and polyphyly at subfamilial and tribal
645 level, especially in Sapindaceae s.s. (subfamilies Dodonaeoideae and Sapindoideae) and (3)
646 proposes a new informal classification for infrafamilial arrangements. Increased sampling,
647 filled sequence gaps and the compilation of an extensive morphological matrix are now
648 required to establish strong synapomorphies for each phylogenetic clade. A particular
649 attention might be given to inflorescence types (and breeding systems) and floral morphology
650 (e.g., shape and type of petal scale, type of disk, number of carpels, pubescence on the
651 anthers, toxicity of the arillode). This might lead to a new formal infrafamilial classification for
652 Sapindaceae s.l., based on the patterns highlighted in this study.

653

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669

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938 **Figures legends**

939 **Fig. 1.** Schematic representation of pollen types in Sapindaceae following Müller and
940 Leenhouts (1976). See text for explanations regarding the morphological differentiation
941 between pollen types.

942

943 **Fig. 2.** Best maximum likelihood phylogenetic tree for Sapindaceae s.l. inferred from eight
944 nuclear and plastid nucleotide sequences. Bootstrap supports are indicated above branches.
945 The revised infrafamilial classification based on molecular and morphological characters is
946 indicated in grey. Abbreviations: Cossinieae (COS); Cupanieae (CUP); Dodonaeae (DOD);
947 Doratoxyleae (DOR); Koelreuterieae (KOE); Harpullieae (HAR); Lepisantheae (LEP);
948 Meliocceae (MEL); Nephelieae (NEP); Paullinieae (PAU); Sapindeae (SAP); Schleichereae
949 (SCH) and Thouinieae (THO).

950

951 **Fig. 3.** Relationships within subfamilies Hippocastanoideae (clade A) and Dodonaeoideae
952 (clade B). Bootstrap supports are indicated above branches. The revised infrafamilial
953 classification based on molecular and morphological characters is indicated in grey. See Fig.
954 2 for abbreviations of tribes.

955

956 **Fig. 4.** Relationships within subfamily Sapindoideae (clade C). Bootstrap supports are
957 indicated above branches. The revised infrafamilial classification based on molecular and
958 morphological characters is in grey. See Fig. 2 for abbreviations of tribes.

959

960 **Fig. 5.** Phylogenetic relationships within the *Litchi* group (clade C-IV; see Fig. 4). Bootstrap
961 supports are indicated above branches. See Fig. 2 for abbreviations of tribes.

962

963 **Fig. 6.** Phylogenetic relationships within the *Cupania* group (clade C-VI; see Fig. 4).
964 Bootstrap supports are indicated above branches. See Fig. 2 for abbreviations of tribes.

965

Table 1. Infraclassification of Sapindaceae sensu lato (Thorne, 2007). Information on number of taxa, habit and distribution of genera were taken from literature (Radlkofer, 1933; Acevedo-Rodríguez, 1993, 2003; Adema et al., 1994; Ferrucci 1991, 1998; Davies, 1997; Davies and Verdcourt, 1998; Klaassen, 1999; Thomas and Harris, 1999; Xia and Gadek, 2007; Mabberley, 2008). Abbreviations are as follows: s = shrub, st = small tree, t = tree and l = liana. Genera sampled for the phylogenetic analysis of Sapindaceae are indicated in bold and genera found to be either paraphyletic or polyphyletic are identified by an asterisk (*).

Sapindaceae Jussieu

104/141 genera, 205/1886 species

Dodonaeoideae Burnett

Cossinieae Bl. (Cos)

2/2 genera, 3/7 species

Dodonaeae Kunth (Dod)

3/5 genera, 5/78 species

Doratoxyleae Radlk. (Dor)

6/9 genera, 8/22 species

Genera	Author	Taxa	Habit	Distribution
<i>Cossinia</i>	Comm. ex Lam.	4	s-st	Mascarenes, New Caledonia, E Australia, Fiji
<i>Llagunoa</i>	Ruíz & Pavón	3	s-st	W tropical South America
<i>Diplopeltis</i>	Endl.	5	s-t	NW Australia
<i>Distichostemon</i>	F. Muell.	6	s	Australia
<i>Dodonea</i>	Miller	c. 65	s-st	Mainly in Australia, Malesia, New Guinea, Caribbean and Madagascar
<i>Hirania</i>	Thulin	1	s	Somalia
<i>Loxodiscus</i>	Hook. f.	1	s	New Caledonia
<i>Averrhoidium</i>	Baillon	2	t	South America
<i>Doratoxylon</i>	Thou. ex Hook. f.	5	st-t	Madagascar and Mascarenes Islands
<i>Euchorium</i>	Eckman & Radlk.	1	t	Cuba
<i>Exothea</i>	Macfad.	3	t	West Indies, Central America and Florida
<i>Filicium</i>	Thw ex Hook. f.	3	s-st	E Africa, Madagascar and SE India
<i>Ganophyllum</i>	Blume	2	t	W and C Africa, Andamans and Nicobars to NE Australia and Solomon Islands to Malesia
<i>Hippobromus</i>	Ecklon & Zeyher	1	t	South Africa

Table 1. Continued

Dodonaeoideae Burnett**Harpullieae Radlk. (Har)**

6/6 genera, 8/34 species

Genera	Author	Taxa	Habit	Distribution
<i>Hypelate</i>	P. Browne	1	s-st	West Indies and Florida
<i>Zanha</i>	Hiern	4	t	Tropical Africa and Madagascar
<i>Arfeuillea</i>	Pierre ex Radlk.	1	t	SE Asia
<i>Conchopetalum</i>	Radlk.	2	st-t	Madagascar
<i>Eurycorymbus</i>	Handel-Mazzetti	1	t	China
<i>Harpullia</i>	Roxb.	26	s-st	India, SE China, Malesia to Australia, New Caledonia and Pacific Islands
<i>Magonia</i>	A. St. Hil.	1	t	South America
<i>Majidea</i>	J. Kirk ex Oliver	3	t	Tropical Africa and Madagascar
Hippocastanoideae Burnett				
5/5 genera, 18/129 species				
<i>Acer</i>	L.	111	s-t	N temperate & tropical mountains
<i>Aesculus</i>	L.	13	t	SE Europe, India, E Asia and N America
<i>Billia</i>	Peyr.	2	s-t	S Mexico to Tropical South America
<i>Dipteronia</i>	Oliver	2	s-st	C & S China
<i>Handeliodendron</i>	Rehder	1	s-t	China - deciduous
Sapindoideae Burnett				
Cupanieae Reichenb. (Cup)				
36/48 genera, 79/462 species				
<i>Amesiodendron</i>	Hu	1	t	China, Indo-China and Malesia
<i>Aporrhiza</i>	Radlk.	6	t	Tropical Africa
<i>Arytera</i>	Blume	c. 28	s-t	Indo-Malesia to E Australia and Pacific
<i>Blighia</i>	Koenig	4	t	Tropical Africa
<i>Blighiopsis</i>	Van der Vecken	1	t	Tropical Africa
<i>Blomia</i>	Miranda	1	t	Mexico
<i>Chesmocarpon</i>	Adema	4	s-st	Australia and Papua New Guinea
<i>Cupania</i>	L.	c. 45	s-t	Tropical America
<i>Cupaniopsis</i>*	Radlk.	60	s-st	Malesia, New Guinea, N-E Australia, Pacific islands, New Caledonia
<i>Dictyoneura</i>	Blume	3	s-st	Malesia
<i>Dilodendron</i>	Radlk.	1	t	South America
<i>Diploglottis</i>	Hook.f.	12	t	NE Australia and Papua New Guinea
<i>Diplokeleba</i>	N.E. Br.	2	st	South America
<i>Elattostachys</i>	(Blume) Radlk.	c. 20	s-t	Malesia to Australia, W Pacific
<i>Eriocoelum</i>	Hook.f.	c. 10	t	Tropical Africa

Table 1. Continued

Sapindoideae Burnett
Cupanieae Reichenb. (Cup)

Genera	Author	Taxa	Habit	Distribution
<i>Euphorianthus</i>	Radlk.	1	t	E Malesia
<i>Gloeocarpus</i>	Radlk.	1	t	Philippines
<i>Gongrodiscus</i>	Radlk.	3	s-t	New Caledonia
<i>Gongrospermum</i>	Radlk.	1	t	Philippines
<i>Guioa</i> *	Cav.	65	s-t	SE Asia, Malesia to E Australia; Pacific and New Caledonia
<i>Haplocoelopsis</i>	F.G. Davies	1	s-t	E Africa
<i>Jagera</i>	Blume	2	t	New Guinea and Australia
<i>Laccodiscus</i>	Radlk.	4	s-st	W Africa
<i>Lepiderema</i>	Radlk.	8	t	Australia and New Guinea
<i>Lepidopetalum</i>	Blume	7	s-t	India, NE Australia and Solomon Islands
<i>Lynchodiscus</i>	Radlk.	6	t	W Tropical Africa
<i>Matayba</i> *	Aublet.	c. 56	s-t	Tropical America
<i>Mischarytera</i>	(Radlk.) H.Turner	3	t	Australia, Papua New Guinea
<i>Mischocarpus</i>	Blume	15	s-t	SE Asia, Malesia to Australia
<i>Molinaea</i>	Comm. ex. Juss.	9	s-t	Madagascar, Mascarenes
<i>Neotina</i>	Capuron	2	t	Madagascar
<i>Paranephelium</i>	Miq.	4	s-t	SE Asia and W Malesia
<i>Pavieasia</i>	Pierre	3	t	S China, N Vietnam
<i>Pentascyphus</i>	Radlk.	1	t	Guyana
<i>Phyllotrichum</i>	Thorel ex Lecompte	1	t	SE Asia
<i>Pseudima</i>	Radlk.	3	t	South America
<i>Rhysotoechia</i>	Radlk.	14	s-t	Australia, New Guinea, Malesia
<i>Sarcopteryx</i>	Radlk.	12	s-t	Malesia, New Guinea and E Australia
<i>Sarcotoechia</i> *	Radlk.	11	t	NE Australia and New Guinea
<i>Scyphonychium</i>	Radlk.	1	t	NE Brazil
<i>Sisyrolepis</i>	Radlk.	1	s-st	Thailand
<i>Storthocalyx</i>	Radlk.	4	s	New Caledonia
<i>Synima</i>	Radlk.	2	t	Australia and SE New Guinea
<i>Tina</i>	Roem. & Schult.	6	s-st	Madagascar
<i>Toechima</i>	Radlk.	7	t	Australia and New Guinea
<i>Trigonachras</i>	Radlk.	8	t	Malesia
<i>Tripterodendron</i>	Radlk.	1	t	Brazil
<i>Vouarana</i>	Aublet.	1	t	NE South America

Table 1. Continued

Sapindoideae Burnett
Koelreuterieae Radlk. (Koe)

2/4 genera, 2/15 species

Genera	Author	Taxa	Habit	Distribution
<i>Erythrophysa</i>	E. Mey ex Arnott	9	s	Africa and Madagascar
<i>Koelreuteria</i>	Laxmann	3	t	S China, Japan
<i>Sinoradlkofera</i>	F.G. Mey	2	st	China and N Vietnam
<i>Stocksia</i>	Benth.	1	s	E Iran, Afghanistan
Lepisantheae Radlk. (Lep)				
4/10 genera, 7/97 species				
<i>Chonopetalum</i>	Radlk.	1	t	Tropical W Africa
<i>Chytranthus</i>	Hook f.	c. 30	st	Africa
<i>Glenniea</i>	Hook.f.	8	t	Tropical Africa, Madagascar, Sri Lanka, Malesia
<i>Lepisanthes</i>	Blume	24	s-t	Tropical Africa, Madagascar, S-SE Asia, Malesia and NW Australia
<i>Namataea</i>	D.W. Thomas & D.J. Harris	1	st	Cameroon
<i>Pancovia</i>	Willd.	c. 13	st	Tropical Africa
<i>Placodiscus</i>	Radlk.	c. 15	t	Tropical W Africa
<i>Pseudopancovia</i>	Pellegrin	1	t	Tropical W Africa
<i>Radlkofera</i>	Gilg.	1	s-st	Tropical Africa
<i>Zollingeria</i>	Kurz	3	t	SE Asia and Malesia
Melicocceae Blume (Mel)				
5/5 genera, 8/67 species				
<i>Castanospora</i>	F. Muell.	1	t	NE Australia
<i>Melicoccus</i>	P. Browne	10	t	Tropical America
<i>Talisia</i>	Aublet	52	s-t	Tropical America
<i>Tristira</i>	Radlk.	1	t	Malesia
<i>Tristiropsis</i>	Radlk.	3	t	Pacific Ocean, Australia, Solomon Islands and Malesia
Nephelieae Radlk. (Nep)				
11/12 genera, 15/77 species				
<i>Alectryon</i>	Gaertn.	c. 30	s-st	E Malesia, Australia, New Zealand, New Caledonia, to Hawaii
<i>Cubilia</i>	Blume	1	t	Malesia
<i>Dimocarpus</i>	Lour.	6	s-t	S and SE Asia and Australia
<i>Litchi</i>	Sonn.	1	t	Tropical China to W Malesia
<i>Nephelium</i>	L.	22	t	SE Asia and Malesia
<i>Otonephelium</i>	Radlk.	1	t	India

Table 1. Continued

Sapindoideae Burnett
Nephelieae Radlk. (Nep)

Paullinieae Kunth (Pau)

4/7 genera, 15/466 species

Sapindeae DC (Sap)

3/7 genera, 12/89 species

Schleichereae Radlk. (Sch)

8/12 genera, 12/55 species

Genera	Author	Taxa	Habit	Distribution
<i>Pappea</i>	Eckl. & Zeyh.	1	s-t	Tropical E to S Africa
<i>Podonephelium</i>	Baillon	4	s-t	New Caledonia
<i>Pometia</i>	Forst. & Forst.	2	t	Malesia and Pacific Islands
<i>Smelophyllum</i>	Radlk.	1	t	South Africa
<i>Stadmania</i>	Lam.	6	t	Tropical E Africa, S Africa, Madagascar and Mascarenes Islands
<i>Xerospermum</i>	Blume	2	s-st	Indochinese Peninsula and Malesia
<i>Cardiospermum</i>	L.	c. 12	l	Tropical and subtropical America; 1 sp. extending to Africa
<i>Houssayanthus</i>	Hunz.	3	s-l	South America
<i>Lophostigma</i>	Radlk.	2	l	South America
<i>Paullinia</i>	L.	c. 200	l	Tropical America and one pantropical sp.
<i>Serjania</i>	Miller	c. 226	l	Tropical America
<i>Thinouia</i>	Triana & Planchon	9	l	Tropical America
<i>Urvillea</i>	Kunth	14	l	Tropical America
<i>Atalaya</i>	Blume	12	st	Australia, New Guinea and S Africa
<i>Deinbollia</i>	Schumach. & Thonn.	c. 40	t	Tropical Africa and Madagascar
<i>Hornea</i>	Baker	1	s-t	Mauritius
<i>Porocystis</i>	Radlk.	2	s-t	Tropical South America
<i>Sapindus</i>	L.	13	t	Tropical to warm temperate regions
<i>Thouinidium</i>	Radlk.	7	s-t	Mexico and West Indies
<i>Toulicia</i>	Aublet	14	t	South America
<i>Beguea</i>	Capuron	1	t	Madagascar
<i>Bizonula</i>	Pellegrin	1	t	Tropical Africa
<i>Camptolepis</i>	Radlk.	4	t	E Africa and Madagascar
<i>Chouxia</i>	Capuron	6	s-st	Madagascar
<i>Haplocoelum*</i>	Radlk.	c. 6	st-t	Tropical Africa and Madagascar
<i>Lecaniodiscus</i>	Planch. ex Benth.	3	st	Tropical Africa
<i>Macphersonia</i>	Blume	8	s-t	Tropical E Africa and Madagascar
<i>Plagioscyphus</i>	Radlk.	10	st-t	Madagascar
<i>Pseudopteris</i>	Baill.	3	s	Madagascar

Table 1. Continued

	Genera	Author	Taxa	Habit	Distribution
Sapindoideae Burnett Schleichereae Radlk. (Sch)	<i>Schleichera</i>	Willd.	1	t	Tropical SE Asia to Indo-China and Malesia
	<i>Tinopsis</i>	Radlk.	11	t	Madagascar
	<i>Tsingya</i>	Capuron	1	t	Madagascar
Thouinieae Bl. (Tho) 6/6 genera, 10/285 species	<i>Allophylus</i>	L.	c. 250	s-st-l	Pantropical
	<i>Athyana</i>	(Griseb.) Radlk.	1	t	South America
	<i>Bridgesia</i>	Bertero ex Cambess.	1	s-st	Chile
	<i>Diatenopteryx</i>	Radlk.	2	t	South America
	<i>Guindilia</i>	Hook & Arn.	3	s	South America
	<i>Thouinia</i>	Poit.	28	l	Mexico and West Indies
Sapindoideae unplaced taxa 2/2 genera, 2/2 species	<i>Delavaya</i>	Franchet	1	s-st	SW China and N Vietnam
	<i>Ungnadia</i>	Endl.	1	s-st	S North America
Xanthoceroideae Thorne & Reveal 1/1 genera, 1/1 species	<i>Xanthoceras</i>	Bunge	1	s-st	N-NE China and Korea

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Table 2

Table 2. Characteristics of partitions used in the phylogenetic analyses of the Sapindaceae s.l.. See text for explanations regarding the compilation of combined data sets (i.e. “4 markers” and “4+4 markers”). IGS, intergenic spacer; the asterisk (*) indicates markers included in the combined “4 markers” phylogenetic analysis. MP, maximum parsimony.

Phylogenetic information	Single-gene analysis								Combined analyses	
	<i>ITS</i> *	<i>matK</i>	<i>rpoB</i> *	<i>trnD-trnT</i> IGS	<i>trnK-matK</i> IGS	<i>trnL</i> intron*	<i>trnL-trnF</i> IGS*	<i>trnS-trnG</i> IGS	4 markers*	4*+4 markers
No. of ingroup sampled species/genera	139/84	110/69	139/84	79/62	100/63	139/84	139/84	67/47	139/84	139/84
No. sequences incl. outgroup (in brackets, total number of samples for the combined analyses)	153	119	154	85	109	154	154	69	615 (154)	997 (154)
Sequence length range	650-705	1074-1242	357-363	1086-1425	705-753	510-522	380-430	1311-1365	-	-
Alignment length	1234	1614	363	1925	931	773	661	2156	3031	9657
Missing data (percentage of ingroup sequences; in brackets percentage of nucleotides for the combined analyses)	0	21.7	0	44.1	28.3	0	0	54.6	0 (0)	18.6 (27.3)
No. constant characters (%)	599 (48.5)	1144 (70.9)	228 (62.8)	1096 (56.9)	530 (56.9)	489 (63.3)	359 (54.3)	1643 (76.2)	1675 (55.3)	6088 (63.0)
No. variable characters (%)	635 (51.4)	470 (29.1)	135 (37.2)	829 (43.1)	401 (43.1)	284 (36.7)	302 (45.7)	513 (23.8)	1356 (44.7)	3569 (37.0)
No. potentially parsimony-informative (PI) characters (%)	467 (37.8)	295 (18.3)	95 (26.2)	405 (21.0)	230 (24.7)	166 (21.5)	190 (28.7)	195 (9.0)	918 (30.3)	2043 (21.2)
Mean amount of phylogenetic information per sample (averaged by variable sites number/PI sites number)	-	-	-	-	-	-	-	-	8.8/6.0	23.2/13.3
No. trees retained (MP)	525	1991	1997	2001	1786	1707	1023	1190	1138	1010
Tree length (MP ; step)	4365	837	246	1447	790	578	576	798	5889	9843
Consistency Index (MP)	0.282	0.701	0.707	0.731	0.675	0.681	0.680	0.741	0.372	0.504
Retention Index (MP)	0.640	0.849	0.899	0.811	0.790	0.879	0.861	0.665	0.698	0.726

Table 3. Level of topological agreement (based on EA distances) between total evidence trees inferred from the “4 markers” and “4+4 markers” data sets. See text for explanations regarding the compilation of these data sets. MP, maximum parsimony; ML, maximum likelihood.

	1	2	3	4
1- ML "4 markers"	-			
2- MP "4 markers"	0.177	-		
3- ML "4+4 markers"	0.021	0.189	-	
4- MP "4+4 markers"	0.028	0.173	0.027	-

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Table 4

Table 4. Summary of the bootstrap support for each clade recovered in the four total evidence trees (two data sets and two algorithms). Bootstrap supports for clade C-I are not indicated because this lineage is only composed by *Delavaya yunnanensis*. Note: Although monophyletic, clade C-V is nested into clade C-VI, the latter is not recovered by the MP analysis based on the “4 markers” data set. MP, maximum parsimony; ML, maximum likelihood.

	ML		MP	
	4 markers	4+4 markers	4 markers	4+4 markers
Combined data sets				
Sapindaceae s.l.	94	91	97	97
Clade A + Clade B + Clade C	65	58	60	57
Clade A	100	100	99	99
Clade B	94	91	99	99
B-I	100	100	100	100
B-II	88	77	86	86
Clade C	92	87	96	98
C-II	100	100	100	100
C-III	100	100	100	100
C-IV	77	98	<50	65
C-IV-a	73	100	73	100
C-IV-b	100	100	<50	83
C-V	100	100	99	100
C-VI	60	75	-	<50
C-VI-a	69	89	<50	65
C-VI-b	65	83	<50	58
C-VII	100	100	100	100
C-VIII	60	61	50	70
C-IX	100	100	99	100
C-X	100	100	93	100

Appendix

Appendix. Voucher information and GenBank accession numbers for taxa used in the phylogenetic analysis of family Sapindaceae s.l. (including outgroups). Abbreviations: ANH = Andong National University, South Korea; BBG = Bogor Botanic Garden, India, living collections; CSIRO = CSIRO Arboretum, Australia; G = Conservatoire et Jardin Botanique de la ville de Genève, Switzerland; JCT = James Cook University of Northern Queensland, Australia; K = Royal Botanic Gardens, Kew, U.K.; NEU = Neuchâtel, Switzerland; MO = Missouri Botanical Garden, U.S.A.; P = Muséum d'Histoire Naturelle, France; RBG = Royal Botanic Gardens, Kew, U.K., living collections; US = Smithsonian Institution, U.S.A and Z = University of Zürich, Switzerland.

Genera	species	Author	Voucher	Herbarium	Country	GenBank accession number							
						ITS	matK	rpoB	trnD-trnT	trnK-matK	trnL	trnL-F	trnS-trnG
Ingroup													
<i>Acer</i>	<i>erianthum</i>	Schwer.	<i>Chase 19983</i>	K	China	EU720501	-	EU720843	EU720980	-	EU721271	EU721459	-
<i>Acer</i>	<i>saccharum</i>	Marshall	<i>Chase 106</i>	K	Cult. source, Orange Co.	EU720502	-	EU720844	-	-	EU721272	EU721460	-
<i>Aesculus</i>	<i>indica</i>	(Wall. ex Cambess.) Hook.	<i>Chase 19987</i>	K	India	EU927392	-	EU720845	EU720981	-	EU721273	EU721461	-
<i>Alectryon</i>	<i>connatus</i>	Radlk.	<i>Chase 2047</i>	K	Australia	EU720415	EU720577	EU720732	EU720928	EU721025	EU721169	EU721357	EU721534
<i>Amesiodendron</i>	<i>chinensis</i>	(Merr.) Hu	<i>Yuan s.n.</i>	NEU	China	EU720403	-	EU720718	EU720917	-	EU721155	EU721344	EU721525
<i>Arfeuillea</i>	<i>arborescens</i>	Pierre	<i>Chase 2122</i>	K	Bogor, BG	EU720461	EU720629	EU720793	EU720962	EU721067	EU721229	EU721417	-
<i>Arytera</i>	<i>littoralis</i>	Blume	<i>Yuan s.n.</i>	NEU	China	EU720405	EU720566	EU720720	EU720919	EU721018	EU721157	EU721346	EU721527
<i>Arytera</i>	<i>littoralis</i>	Blume	<i>Chase 2123</i>	K	Bogor, BG	EU720462	EU720630	EU720794	EU720963	EU721068	EU721230	EU721418	-
			<i>Edwards KE228</i>	JCT	South Africa								
<i>Atalaya</i>	<i>alata</i>	(Sim) H. Forbes	<i>Edwards KE 509</i>	JCT	South Africa	EU720425	EU720593	EU720748	EU720939	EU721036	EU721184	EU721372	EU721543
<i>Atalaya</i>	<i>capense</i>	R.A. Dyer				EU720429	-	EU720752	-	-	EU721188	EU721376	-
<i>Athyana</i>	<i>weinmannifolia</i>	(Griseb.) Radlk.	<i>Pennington 17581</i>	MO	Peru	EU720487	EU720649	EU720824	EU720975	EU721086	EU721257	EU721445	EU721576
<i>Averrhoidium</i>	<i>dalyi</i>	Acev.-Rodr. & Ferrucci	<i>Weckerle 00/03/18-1/1</i>	Z	Peru	EU720495	-	EU720836	-	-	EU721268	EU721456	-
<i>Beguea</i>	<i>apetala</i>	Capuron	<i>Buerki 149</i>	NEU	Madagascar	EU720491	EU720652	EU720828	EU720978	EU721089	EU721261	EU721449	-
<i>Beguea</i>	<i>apetala</i>	Capuron	<i>Vary 40</i>	MO	Madagascar	EU720512	EU720663	EU720856	-	EU721100	EU721281	EU721469	-
			<i>Edwards KE86</i>	JCT	West Africa								
<i>Blighia</i>	<i>sapida</i>	K.D. Koenig				EU720416	EU720578	EU720733	EU720929	EU721026	EU721170	EU721358	EU721535
<i>Blomia</i>	<i>prisca</i>	(Standl.) Lundell	<i>Acevedo 12242</i>	US	Mexico, Yucatan	EU720444	EU720611	EU720772	-	EU721050	EU721208	EU721396	-
<i>Bridgesia</i>	<i>incisifolia</i>	Bertero ex Cambess.	<i>Killip & Pisano 39778</i>	K	Chile	EU720476	EU720645	EU720811	EU720973	EU721082	EU721247	EU721435	-
<i>Cardiospermum</i>	sp.		<i>Yuan s.n.</i>	NEU	China	EU720399	-	EU720713	EU720912	-	EU721150	EU721339	-
<i>Chytranthus</i>	<i>carneus</i>	Radlk.	<i>Chase 2868</i>	RBG	-	EU720477	EU720646	EU720812	EU720974	EU721083	EU721248	EU721436	EU721575
<i>Conchopetalum</i>	<i>brachysepalum</i>	Capuron	<i>Rabarimanarivo 8</i>	MO	Madagascar	EU720530	EU720680	EU720877	-	EU721117	EU721299	EU721487	EU721586
<i>Cubilia</i>	<i>cubili</i>	(Blanco) Adelb.	<i>Chase 2125</i>	K	Bogor, BG	EU720463	EU720631	EU720795	EU720964	EU721069	EU721231	EU721419	EU721567

GenBank accession number

Genera	species	Author	Voucher	Herbarium	Country	ITS	Genera	species	Author	Voucher	Herbarium	Country	ITS
<i>Cupania</i>	<i>dentata</i>	DC.	<i>Acevedo 12241</i>	US	Mexico, Yucatan	EU720523	EU720670	EU720867	EU720988	EU721107	EU721289	EU721477	EU721581
<i>Cupania</i>	<i>hirsuta</i>	Radlk.	<i>Acevedo 1101</i>	US	French Guiana	EU720521	EU720668	EU720865	-	EU721105	EU721287	EU721475	-
<i>Cupania</i>	<i>rubiginosa</i>	(Poir.) Radlk.	<i>Mori 8868</i>	MO	French Guiana	EU720481	-	EU720817	-	-	EU721251	EU721439	-
<i>Cupania</i>	<i>scrobiculata</i>	Rich.	<i>Acevedo 11100</i> <i>Chase 217</i>	US	French Guiana Australia	EU720524	EU720671	EU720868	EU720989	EU721108	EU721290	EU721478	-
<i>Cupaniopsis</i>	<i>anacardioides</i>	Radlk.	<i>Edwards KE42</i>	K JCT	Australia	EU720438	EU720605	EU720763	EU720946	EU721045	EU721199	EU721387	EU721552
<i>Cupaniopsis</i>	<i>flagelliformis</i>	(Bailey) Radlk.				EU720432	EU720598	EU720755	EU720942	-	EU721191	EU721379	EU721547
<i>Cupaniopsis</i>	<i>fruticosa</i>	Radlk.	<i>Munzinger 564</i>	MO	New Caledonia	EU720533	-	EU720881	-	EU721119	EU721302	EU721490	-
<i>Cupaniopsis</i>	sp.		<i>Munzinger 710</i>	MO	New Caledonia	EU720532	-	EU720880	EU720996	-	EU721301	EU721489	EU721587
<i>Cupaniopsis</i>	sp.		<i>Munzinger 1103</i> <i>Edwards KE197</i>	MO JCT	New Caledonia Tanzania	EU720507	EU720660	EU720851	-	EU721097	EU721278	EU721466	-
<i>Deinbollia</i>	<i>borbonica</i>	Scheff.				EU720412	EU720574	EU720729	-	-	EU721166	EU721354	EU721532
<i>Deinbollia</i>	<i>macrocarpa</i>	Capuron	<i>H. Razafindraibe 118</i>	MO	Madagascar	EU720535	EU720683	EU720883	-	EU721121	EU721304	EU721492	EU721589
<i>Deinbollia</i>	<i>macrocarpa</i>	Capuron	<i>Buerki 144</i> <i>Edwards KE233</i>	NEU JCT	Madagascar South Africa	EU720503	EU720656	EU720847	-	EU721093	EU721275	EU721463	-
<i>Deinbollia</i>	<i>oblongifolia</i>	(E. Mey. ex Arn.) Radlk.				EU720427	EU720595	EU720750	-	-	EU721186	EU721374	EU721545
<i>Deinbollia</i>	<i>pervillei</i>	(Blume) Radlk.	<i>Phillipson 5919</i>	MO	Madagascar	EU720395	EU720560	EU720708	-	EU721012	EU721145	EU721334	-
<i>Deinbollia</i>	<i>pervillei</i>	(Blume) Radlk.	<i>Callmander 688</i>	MO	Madagascar	EU720514	-	EU720858	-	-	EU721283	EU721471	-
<i>Delavaya</i>	<i>yunnanensis</i>	Franch.	<i>Forrest 20682</i>	MO	China, Yunnan	EU720484	-	EU720821	-	-	EU721254	EU721442	-
<i>Diatenopteryx</i>	<i>sorbifolia</i>	Radlk.	<i>Zardini 43371</i> <i>Edwards KE142</i>	MO JCT	Paraguay Australia	EU720534	EU720682	EU720882	-	EU721120	EU721303	EU721491	EU721588
<i>Dictyoneura</i>	<i>obtusa</i>	Blume	<i>Edwards KE34</i>	JCT	Australia	EU720428	-	EU720751	-	-	EU721187	EU721375	-
<i>Dimocarpus</i>	<i>australianus</i>	Leenh.				EU720433	-	EU720757	-	-	EU721193	EU721381	-
<i>Diploglottis</i>	<i>campbelli</i>	Cheel	<i>Chase 2048</i>	K	Australian, BG	EU720457	EU720624	EU720788	EU720960	EU721062	EU721224	EU721412	-
<i>Diplopeltis</i>	<i>huegelii</i>	Endl.	<i>Chase 2192</i>	K	Australia	EU720473	EU720642	EU720807	EU720971	EU721079	EU721243	EU721431	-
<i>Dipteronia</i>	<i>sinensis</i>	Oliv.	<i>Chase 502</i>	RBG	-	EU720445	EU720612	EU720774	-	-	EU721210	EU721398	-
<i>Dodonaea</i>	<i>madagascariensis</i>	Radlk.	<i>Bocksberger GB028</i> <i>Razafitsalama 956</i>	NEU	Madagascar	EU720518	-	EU720862	EU720984	-	EU721284	EU721472	-
<i>Dodonaea</i>	<i>viscosa</i>	Jacq.		MO	Madagascar	EU720519	EU720666	EU720863	EU720985	EU721103	EU721285	EU721473	-

GenBank accession number

Genera	species	Author	Voucher	Herbarium	Country	ITS	Genera	species	Author	Voucher	Herbarium	Country	ITS
<i>Dodonaea</i>	<i>viscosa</i>	Jacq.	<i>Merello 1077</i>	MO	Peru	EU720536	EU720684	EU720884	EU720997	EU721122	EU721305	EU721493	-
<i>Dodonaea</i>	<i>viscosa</i>	Jacq.	<i>Yuan s.n.</i>	NEU	China	EU720406	EU720567	EU720721	EU720920	EU721019	EU721158	EU721347	-
<i>Doratoxylon</i>	<i>chouxii</i>	Capuron	<i>Labat JNL3543</i>	P	Madagascar	EU720394	EU720559	EU720707	EU720908	EU721011	EU721144	EU721333	-
<i>Doratoxylon</i>	<i>chouxii</i>	Capuron	<i>Callmander 679</i>	MO	Madagascar	EU720513	EU720664	EU720857	-	EU721101	EU721282	EU721470	-
<i>Elattostachys</i>	<i>apetala</i>	Radlk.	<i>Munzinger 692</i>	MO	New Caledonia	EU720537	EU720685	EU720885	EU720998	EU721123	EU721306	EU721494	EU721590
<i>Elattostachys</i>	<i>apetala</i>	Radlk.	<i>McPherson 18184</i>	MO	New Caledonia	EU720538	EU720686	EU720886	EU720999	EU721124	EU721307	EU721495	EU721591
<i>Elattostachys</i>	<i>microcarpa</i>	S.T. Reynolds	<i>Edwards KE98</i>	JCT	Australia	EU720409	EU720571	EU720726	-	-	EU721163	EU721351	-
<i>Elattostachys</i>	<i>nervosa</i>	(F. Muell.) Radlk.	<i>Chase 2022</i>	K	Australian, BG	EU720455	EU720622	EU720786	EU720959	EU721060	EU721222	EU721410	EU721563
<i>Elattostachys</i>	sp.		<i>Lowry 5650A</i>	MO	New Caledonia	EU720529	EU720679	EU720876	EU720994	EU721116	EU721298	EU721486	EU721585
<i>Eriocoelum</i>	<i>kerstingii</i>	Gilg ex Engl.	<i>Merello 1586</i>	MO	Ghana	EU720539	EU720687	EU720887	EU721000	EU721125	EU721308	EU721496	EU721592
<i>Eriocoelum</i>	<i>microspermum</i>	Radlk.	<i>Bradley 1025</i>	MO	Gabon	EU720540	EU720688	EU720888	EU721001	EU721126	EU721309	EU721497	EU721593
<i>Euphorianthus</i>	<i>longifolius</i>	Radlk.	<i>Chase 2126</i>	K	Bogor, BG	EU720464	-	EU720796	-	-	EU721232	EU721420	-
<i>Eurycorymbus</i>	<i>cavalerieri</i>	(H. Lév.) Rehder & Hand.-Mazz.	<i>Yuan s.n.</i>	NEU	China	EU720404	EU720565	EU720719	EU720918	EU721017	EU721156	EU721345	EU721526
<i>Filicium</i>	<i>decipiens</i>	(Wight & Arn.) Thwaites	<i>Chase 2128</i>	K	Bogor, BG	EU720466	EU720633	EU720798	-	-	EU721234	EU721422	-
<i>Filicium</i>	<i>longifolium</i>	(H. Perrier) Capuron	<i>Rabenantonadro 1113</i>	MO	Madagascar	EU720541	-	EU720889	-	-	EU721310	EU721498	-
<i>Filicium</i>	<i>thouarsianum</i>	(A. DC.) Capuron	<i>Antilahimena 5021</i>	MO	Madagascar	EU720493	-	EU720832	-	-	EU721265	EU721453	-
<i>Ganophyllum</i>	<i>falcatum</i>	Blume	<i>Chase 2129</i>	K	Bogor, BG	EU720467	EU720634	EU720799	-	EU721071	EU721235	EU721423	-
<i>Glenniea</i>	<i>pervillei</i>	(Baill.) Leenh.	<i>Andriamihajarivo 1053</i>	MO	Madagascar	EU720490	EU720651	EU720827	EU720977	EU721088	EU721260	EU721448	-
<i>Gongrodiscus</i>	<i>bilocularis</i>	H.Turner	<i>Munzinger 749</i>	MO	New Caledonia	EU720542	EU720689	EU720890	-	EU721127	EU721311	EU721499	-
<i>Guioa</i>	<i>glauca</i>	Radlk.	<i>McPherson 18230</i>	MO	New Caledonia	EU720545	EU720692	EU720893	-	EU721130	EU721315	EU721503	-
<i>Guioa</i>	<i>microsepala</i>	Radlk.	<i>Munzinger 744</i>	MO	New Caledonia	EU720546	EU720693	EU720894	-	EU721131	EU721316	EU721504	EU721596
<i>Guioa</i>	<i>semiglauca</i>	(F. Muell.) Radlk.	<i>Chase 2058</i>	K	Australian, BG	EU720458	EU720625	EU720789	-	EU721063	EU721225	EU721413	-
<i>Guioa</i>	<i>villosa</i>	Radlk.	<i>McPherson 18040</i>	MO	New Caledonia	EU720544	EU720691	EU720892	EU721003	EU721129	EU721314	EU721502	EU721595

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Genera	species	Author	Voucher	Herbarium	Country	ITS	Genera	species	Author	Voucher	Herbarium	Country	ITS
<i>Guioa</i>	sp.		<i>Munzinger 945 Edwards KE276</i>	MO JCT	New Caledonia Tanzania	EU720505	EU720658	EU720849	-	EU721095	EU721277	EU721465	-
<i>Haplocoelopsis</i>	<i>africana</i>	F.G. Davies				EU720441	EU720608	EU720767	EU720949	-	EU721203	EU721391	EU721555
<i>Haplocoelum</i>	<i>foliosum</i>	(Hiern) Bullock	<i>Friis 1894 Edwards KE195</i>	MO JCT	Ethiopia Tanzania	EU720479	-	EU720815	-	-	EU721250	EU721438	-
<i>Haplocoelum</i>	<i>foliosum</i> subsp. <i>foliosum</i>	(Hiern) Bullock				EU720410	EU720572	EU720727	EU720924	-	EU721164	EU721352	EU721530
<i>Haplocoelum</i>	<i>perrieri</i>	Capuron	<i>Rakotomalaza 1165</i>	MO	Madagascar	EU720396	-	EU720709	EU720909	-	EU721146	EU721335	EU721519
<i>Harpullia</i>	<i>arborea</i>	(Blanco) Radlk.	<i>Chase 1353</i>	K	Bogor, BG	EU720448	-	EU720779	-	-	EU721215	EU721403	-
<i>Jagera</i>	<i>javanica</i>	(Blume) Blume ex Kalkman	<i>Chase 2130 Edwards KE178</i>	K JCT	Bogor, BG Australia	EU720468	EU720635	EU720800	-	EU721072	EU721236	EU721424	EU721569
<i>Jagera</i>	<i>javanica</i> subsp. <i>australiana</i>	Leenh.				EU720442	-	EU720769	-	-	EU721205	EU721393	EU721556
<i>Koelreuteria</i>	<i>paniculata</i>	Laxm.	<i>Harder 5668</i>	MO	Vietnam	EU720548	EU720695	EU720896	-	EU721133	EU721318	EU721506	-
<i>Koelreuteria</i>	<i>paniculata</i>	Laxm.	<i>Yuan CN2006-3</i>	NEU	China	EU720397	EU720561	EU720710	-	EU721013	EU721147	EU721336	EU721520
<i>Koelreuteria</i>	sp.		<i>Harder 5724</i>	MO	Vietnam	EU720547	EU720694	EU720895	EU721004	EU721132	EU721317	EU721505	-
<i>Laccodiscus</i>	<i>klaineanus</i>	Pierre ex Engl.	<i>Walters 1269 Edwards KE194</i>	MO JCT	Gabon Tanzania	EU720549	EU720696	EU720897	-	EU721134	EU721319	EU721507	-
<i>Lecaniodiscus</i>	<i>fraxinifolius</i>	Baker	<i>Edwards KE36</i>	JCT	Australia	EU720418	EU720580	EU720735	EU720931	EU721028	EU721172	EU721360	EU721536
<i>Lepiderema</i>	<i>hirsuta</i>	S.T. Reynolds				EU720435	EU720601	EU720759	-	EU721041	EU721195	EU721383	EU721549
<i>Lepiderema</i>	<i>pulchella</i>	Radlk.	<i>Chase 2020</i>	K JCT	Australian, BG	EU720454	-	EU720785	EU720958	-	EU721221	EU721409	-
<i>Lepidopetalum</i>	<i>fructoglabrum</i>	Welzen	<i>Edwards KE139</i>		Australia	EU720408	-	EU720724	EU720922	-	EU721161	EU721349	EU721528
<i>Lepisanthes</i>	<i>alata</i>	(Blume) Leenh.	<i>Chase 1355</i>	K	Bogor, BG	EU720450	EU720618	EU720781	-	EU721056	EU721217	EU721405	-
<i>Lepisanthes</i>	<i>feruginea</i>	(Radlk.) Leenh.	<i>Chase 1354</i>	K	Bogor, BG	EU720449	EU720617	EU720780	-	EU721055	EU721216	EU721404	-
<i>Lepisanthes</i>	<i>rubiginosa</i>	(Roxb.) Leenh.	<i>Chase 1350</i>	K	Bogor, BG	EU720446	EU720614	EU720776	EU720952	EU721052	EU721212	EU721400	EU721558
<i>Lepisanthes</i>	<i>senegalensis</i>	(Poir.) Leenh.	<i>Callmander 627</i>	MO	Madagascar	EU720492	EU720654	EU720830	EU720979	EU721091	EU721263	EU721451	EU721577
<i>Litchi</i>	<i>chinensis</i>	Sonn.	<i>Yuan s.n.</i>	NEU	China	EU720400	EU720564	EU720715	EU720914	EU721016	EU721152	EU721341	EU721522
<i>Llagunoa</i>	<i>mollis</i>	Kunth	<i>Jaramilloleija 3199</i>	MO	Colombia	EU720482	-	EU720818	-	-	EU721252	EU721440	-
<i>Llagunoa</i>	<i>nitida</i>	Ruiz & Pav.	<i>Pennington 17552</i>	MO	Peru	EU720486	-	EU720823	-	-	EU721256	EU721444	-
<i>Loxodiscus</i>	<i>coriaceus</i>	Hook. f.	<i>Bradford 1136</i>	MO	New Caledonia	EU720488	-	EU720825	-	-	EU721258	EU721446	-

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<i>Macphersonia</i>	<i>chapelierii</i>	(Baill.) Capuron	<i>Buerki 138</i>	NEU	Madagascar	EU720459	EU720627	EU720791	EU720961	EU721065	EU721227	EU721415	EU721566
<i>Macphersonia</i>	<i>gracilis</i>	O. Hoffm.	<i>Rabenantoandro 1081</i>	MO	Madagascar	EU720550	EU720697	EU720898	EU721005	EU721135	EU721320	EU721508	EU721597
<i>Majidea</i>	<i>zanguebarika</i>	Kirk ex Oliv.	<i>TH275</i>	MO	Madagascar	EU720552	-	EU720900	EU721006	-	EU721322	EU721510	-
<i>Matayba</i>	<i>apetala</i>	Radlk.	<i>Acevedo 11929</i>	US	Jamaica	EU720526	EU720674	EU720871	-	EU721111	EU721293	EU721481	EU721583
<i>Matayba</i>	cf. <i>opaca</i>	Radlk.	<i>Acevedo 11118</i>	US	French Guiana	EU720522	EU720669	EU720866	EU720987	EU721106	EU721288	EU721476	EU721580
<i>Matayba</i>	<i>domingensis</i>	(DC.) Radlk.	<i>Taylor 11819</i>	MO	Caribbean	EU720551	EU720698	EU720899	-	EU721136	EU721321	EU721509	EU721598
<i>Matayba</i>	<i>elaeagnoides</i>	Radlk.	<i>Zardini 43278</i>	MO	Paraguay	EU720553	EU720699	EU720901	-	EU721137	EU721323	EU721511	-
<i>Matayba</i>	<i>guianensis</i>	Aubl.	<i>Acevedo 12342</i>	US	French Guiana	EU720527	EU720675	EU720872	-	EU721112	EU721294	EU721482	-
<i>Matayba</i>	<i>laevigata</i>	Radlk.	<i>Acevedo 12357</i>	US	French Guiana	EU720528	EU720676	EU720873	EU720992	EU721113	EU721295	EU721483	-
<i>Melicoccus</i>	<i>bijugatus</i>	Jacq.	<i>Acevedo s.n.</i>	US	Puerto Rico	EU927391	EU720610	EU720771	-	EU721049	EU721207	EU721395	-
<i>Melicoccus</i>	<i>lepidopetalus</i>	Radlk.	<i>Acevedo 11128</i> <i>Edwards KE159</i>	US JCT	Bolivia Australia	EU720443	-	EU720770	-	-	EU721206	EU721394	-
<i>Mischarytera</i>	sp.	-	<i>Edwards KE30</i>	JCT	Australia	EU720417	EU720579	EU720734	EU720930	EU721027	EU721171	EU721359	-
<i>Mischocarpus</i>	<i>exangulatus</i>	(F. Muell.) Radlk.	<i>Edwards KE37</i>	JCT	Australia	EU720434	EU720600	EU720758	EU720943	EU721040	EU721194	EU721382	-
<i>Mischocarpus</i>	<i>grandissimus</i>	Radlk.				EU720437	EU720604	EU720762	EU720945	EU721044	EU721198	EU721386	EU721551
<i>Mischocarpus</i>	<i>pentapetalus</i>	(Rox.) Radlk.	<i>Chase 2133</i>	K	Bogor, BG	EU720470	EU720637	EU720802	EU720966	EU721074	EU721238	EU721426	EU721571
<i>Mischocarpus</i>	<i>pyriformis</i>	(F. Muell.) Radlk.	<i>Chase 2059</i> <i>Rabenantoandro 1448</i>	K	Australian, BG	EU720460	EU720628	EU720792	-	EU721066	EU721228	EU721416	-
<i>Molinaea</i>	<i>petiolaris</i>	Radlk.	<i>Antilahimena 4301</i>	MO	Madagascar	EU720554	EU720700	EU720902	EU721007	EU721138	EU721324	EU721512	-
<i>Molinaea</i>	sp. nov.		<i>H. Razafindraibe 119</i>	MO	Madagascar	EU720510	EU720662	EU720854	EU720983	EU721099	EU721280	EU721468	EU721578
<i>Neotina</i>	<i>coursii</i>	Capuron		MO	Madagascar	EU720543	EU720690	EU720891	EU721002	EU721128	EU721313	EU721501	EU721594
<i>Nephelium</i>	<i>lappaceum</i> (=N. <i>chryseum</i>)	L.	<i>Yuan s.n.</i> <i>Edwards KE231</i>	NEU JCT	China Tanzania	EU720401	-	EU720716	EU720915	-	EU721153	EU721342	EU721523
<i>Pancovia</i>	<i>golungensis</i>	(Hiern) Exell & Mendonça	<i>Edwards KE232</i>	JCT	South Africa	EU720411	EU720573	EU720728	EU720925	EU721022	EU721165	EU721353	EU721531
<i>Pappea</i>	<i>capensis</i>	Eckl. & Zeyh.				EU720424	EU720592	EU720747	EU720938	EU721035	EU721183	EU721371	EU721542
<i>Paranephelium</i>	<i>macrophyllum</i>	King	<i>Chase 1356</i>	K	Bogor, BG	EU720451	EU720619	EU720782	EU720955	EU721057	EU721218	EU721406	-

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<i>Paranephelium</i>	<i>xestophyllum</i>	Miq.	Edwards KE503	JCT	Asia	EU720420	EU720582	EU720737	-	EU721029	EU721174	EU721362	-
<i>Paullinia</i>	<i>pinnata</i>	L.	Edwards KE199	JCT	Tanzania	EU720413	EU720575	EU720730	EU720926	EU721023	EU721167	EU721355	-
<i>Paullinia</i>	<i>subauriculata</i>	Radlk.	Weckerle 00/03/19-1/1	Z	Peru	EU720494	-	EU720833	-	-	EU721266	EU721454	-
<i>Plagioscyphus</i>	<i>aff. louvelii</i>	Danguy & Choux	Lowry 6034	MO	Madagascar	EU720555	EU720701	EU720903	EU721008	EU721139	EU721325	EU721513	EU721599
<i>Plagioscyphus</i>	<i>unijugatus</i>	Capuron	Buerki 145	NEU	Madagascar	EU720475	EU720644	EU720809	EU720972	EU721081	EU721245	EU721433	EU721574
<i>Podonephelium</i>	<i>homei</i>	Radlk.	Pillon 156	MO	New Caledonia	EU720489	EU720650	EU720826	EU720976	EU721087	EU721259	EU721447	-
<i>Pometia</i>	<i>pinnata</i>	J.R. Forst. & G. Forst.	Chase 2135	K	Bogor, BG	EU720471	EU720638	EU720803	EU720967	EU721075	EU721239	EU721427	EU721572
<i>Pometia</i>	<i>pinnata</i>	J.R. Forst. & G. Forst.	Yuan s.n.	NEU	China	EU720402	-	EU720717	EU720916	-	EU721154	EU721343	EU721524
<i>Pseudima</i>	sp.		McPherson 15867	MO	Panama	EU720556	EU720702	EU720904	EU721009	EU721140	EU721326	EU721514	EU721600
<i>Rhysotoechia</i>	<i>mortoniana</i> <i>oligophyllus</i> (=Aphania <i>oligophylla</i>)	(F. Muell.) Radlk.	Edwards KE117	JCT	Australia	EU720414	EU720576	EU720731	EU720927	EU721024	EU721168	EU721356	EU721533
<i>Sapindus</i>		Merr. & Chun	Yuan s.n. Irvine IRV1810	NEU CSIRO	China Australia	EU720407	EU720568	EU720722	EU720921	EU721020	EU721159	EU721159	-
<i>Sarcopteryx</i>	<i>martyana</i>	(F. Muell.) Radlk.	Gray BG1137	CSIRO	Australia	EU720426	EU720594	EU720749	EU720940	EU721037	EU721185	EU721373	EU721544
<i>Sarcopteryx</i>	<i>reticulata</i>	S.T. Reynolds	Edwards KE49	JCT	Australia	EU720421	EU720587	EU720741	-	EU721033	EU721178	EU721366	EU721539
<i>Sarcopteryx</i>	sp.	-	Edwards KE31	JCT	Australia	EU720439	EU720607	EU720765	EU720948	EU721047	EU721201	EU721389	EU721554
<i>Sarcotoechia</i>	<i>serrata</i>	S.T. Reynolds	Edwards KE102	JCT	Australia	EU720436	EU720603	EU720761	EU720944	EU721043	EU721197	EU721385	EU721550
<i>Sarcotoechia</i>	<i>villosa</i>	S.T. Reynolds	Chase 2137	K	Bogor, BG	EU720419	EU720581	EU720736	-	-	EU721173	EU721361	-
<i>Schleichera</i>	<i>oleosa</i>	(Lour.) Oken	Weckerle 00/07/02-1/4	Z	Peru	EU720423	EU720591	EU720746	EU720937	-	EU721182	EU721370	EU721541
<i>Serjania</i>	<i>altissima</i>	(Poepp.) Radlk.	Chase 2138	K	Bogor, BG	EU720498	-	EU720840	-	-	EU721269	EU721457	-
<i>Serjania</i>	<i>communis</i>	Cambess.	Merello 1058	MO	Peru	EU720472	EU720640	EU720805	EU720969	EU721077	EU721241	EU721429	-
<i>Serjania</i>	<i>glabrata</i>	Kunth		MO	Peru	EU720557	EU720703	EU720905	EU721010	EU721141	EU721327	EU721515	-
<i>Storthocalyx</i>	sp.		Munzinger 960 Edwards KE19	MO JCT	New Caledonia Australia	EU720504	EU720657	EU720848	-	EU721094	EU721276	EU721464	-
<i>Synima</i>	<i>macrophylla</i>	S.T. Reynolds				EU720430	EU720596	EU720753	EU720941	-	EU721189	EU721377	EU721546
<i>Talisia</i>	<i>angustifolia</i>	Radlk.	Zardini 43668	MO	Paraguay	EU720558	EU720705	EU720907	-	EU721143	EU721328	EU721516	-
<i>Talisia</i>	<i>nervosa</i>	Radlk.	Pennington 628	MO	-	EU720474	EU720643	EU720808	-	EU721080	EU721244	EU721432	-
<i>Talisia</i>	<i>obovata</i>	A.C. Sm.	R.Lombello 13	MO	Brazil	EU720485	EU720648	EU720822	-	EU721085	EU721255	EU721443	-

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							Genera	species	Author	Voucher	Herbarium	Country	ITS
<i>Thouinia</i>	<i>acuminata</i>	S. Watson	<i>Liston 633-2</i>	MO	Mexico, Jalisco	EU720478	EU720647	EU720814	-	EU721084	EU721249	EU721437	-
<i>Tina</i>	<i>isaloensis</i>	Drake	<i>Ranirison PR827</i>	G	Madagascar	EU720520	EU720667	EU720864	EU720986	EU721104	EU721286	EU721474	EU721579
<i>Tina</i>	<i>striata</i>	Radlk.	<i>Vary 45</i>	MO	Madagascar	EU720509	EU720661	EU720853	-	EU721098	EU721279	EU721467	-
<i>Tinopsis</i>	<i>apiculata</i>	Radlk.	<i>Buerki 131</i> <i>Edwards KE20</i>	NEU JCT	Madagascar Australia	EU720422	EU720589	EU720744	EU720936	EU721034	EU721180	EU721368	EU721540
<i>Toechima</i>	<i>erythrocarpum</i>	(F. Muell.) Radlk.				EU720431	EU720597	EU720754	-	EU721038	EU721190	EU721378	-
<i>Toechima</i>	<i>plurinerve</i>	Radlk.	<i>Chase 1357</i>	K	Bogor, BG	EU720452	EU720620	EU720783	EU720956	EU721058	EU721219	EU721407	EU721561
<i>Toechima</i>	<i>tenax</i>	(Cunn. ex Benth.) Radlk.	<i>Chase 2046</i>	K	Australian, BG	EU720456	EU720623	EU720787	-	EU721061	EU721223	EU721411	EU721564
<i>Toechima</i>	<i>tenax</i>	(Cunn. ex Benth.) Radlk.	<i>Chase 2132</i>	K	Bogor, BG	EU720469	EU720636	EU720801	EU720965	EU721073	EU721237	EU721425	EU721570
<i>Tristiropsis</i>	<i>acutangula</i>	Radlk.	<i>Chase 1358</i> <i>Weckerle</i> <i>00/07/05-1/1</i>	K Z	Bogor, BG Peru	EU720453	EU720621	EU720784	EU720957	EU721059	EU721220	EU721408	EU721562
<i>Urvillea</i>	<i>ulmaceae</i>	Kunth				EU720499	EU720655	EU720841	-	EU721092	EU721270	EU721458	-
<i>Vouarana</i>	<i>guianensis</i>	Aubl.	<i>Lucas 109</i>	MO	French Guiana	EU720525	EU720673	EU720870	EU720991	EU721110	EU721292	EU721480	EU721582
<i>Xanthoceras</i>	<i>sorbifolium</i>	Bunge	<i>Yuan CN2006</i>	NEU	China	EU720398	EU720562	EU720711	EU720910	EU721014	EU721148	EU721337	-
Outroup													
<i>Sorindeia</i>	sp.		<i>Buerki 137</i> <i>Edwards KE510</i>	NEU JCT	Madagascar Tanzania	-	-	EU720831	-	-	EU721264	EU721452	-
<i>Harrisonia</i>	<i>abyssinica</i>	Oliv.				EU720440	-	EU720766	-	-	EU721202	EU721390	-

Figure 1

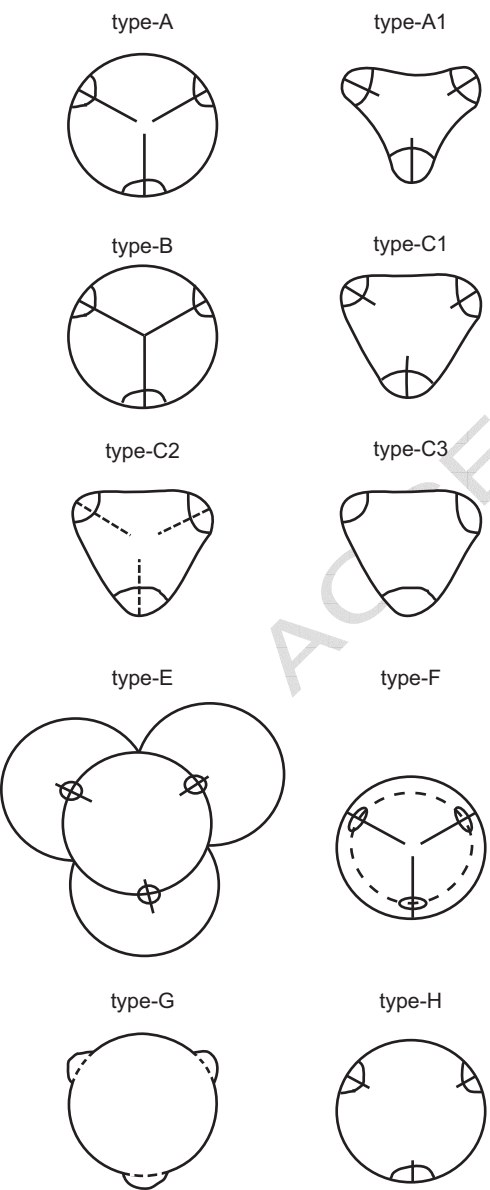


Figure 2

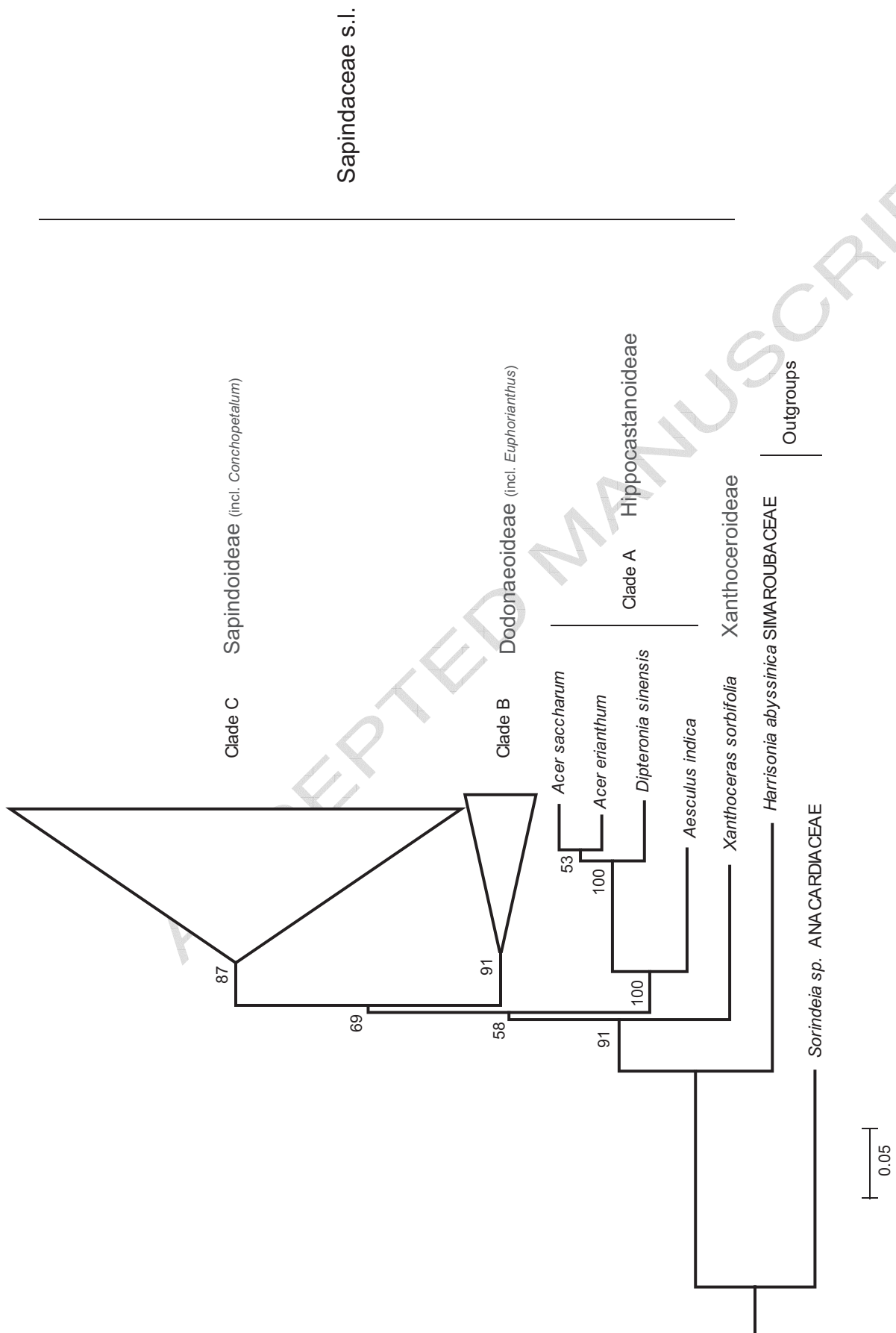
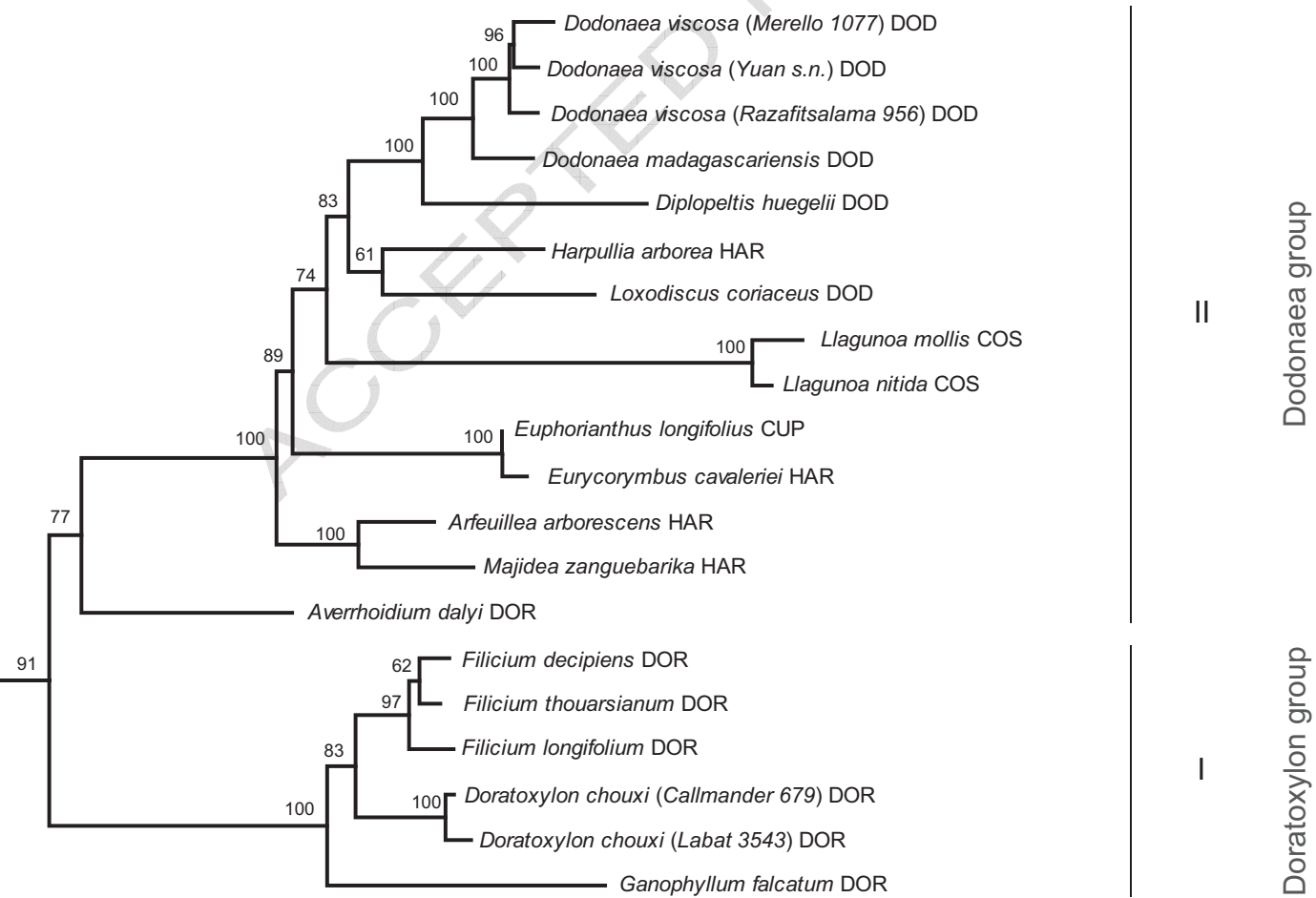


Figure 3

Clade B

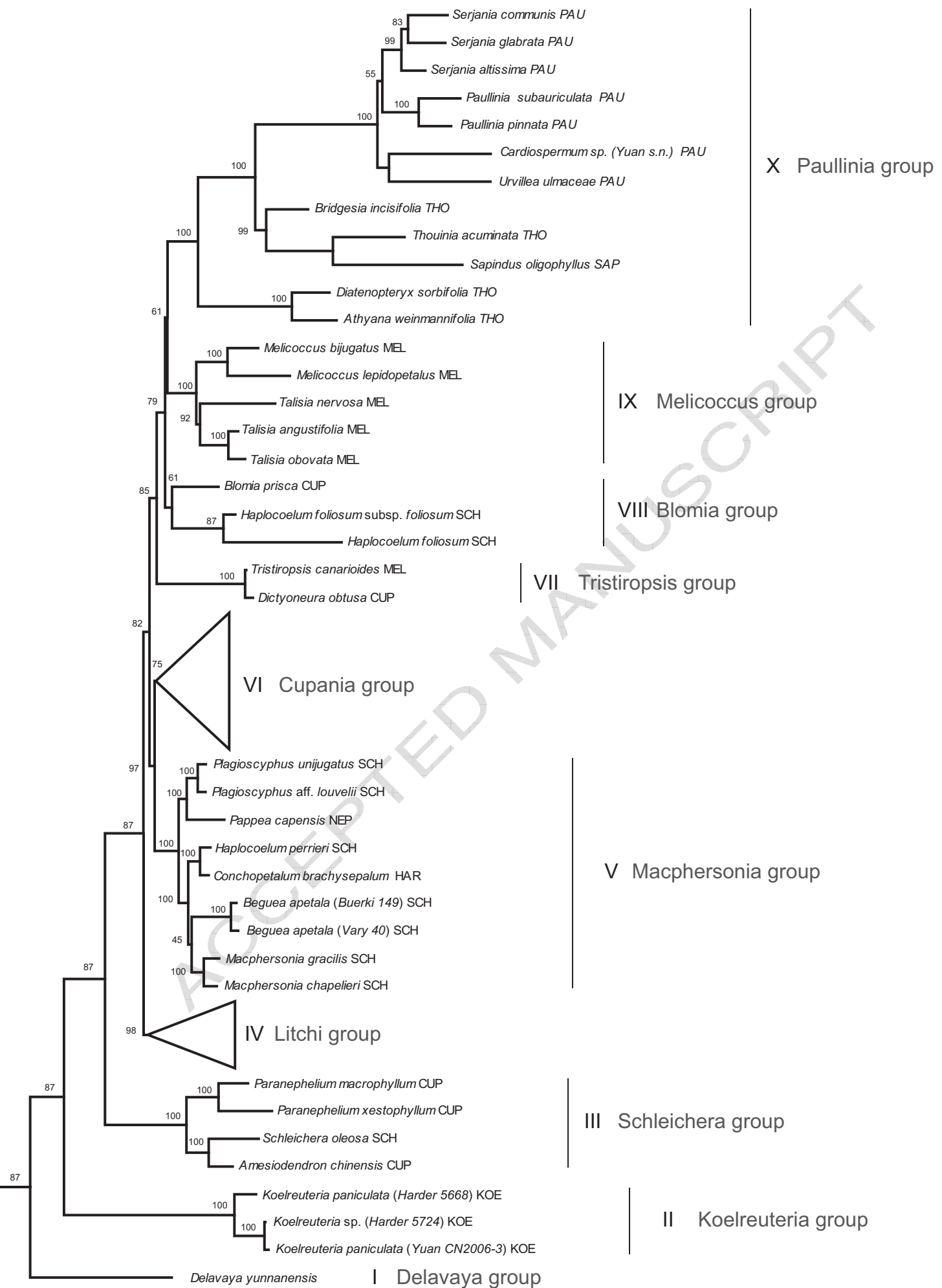


II
Dodonaea group

I
Doratoxylon group

0.02

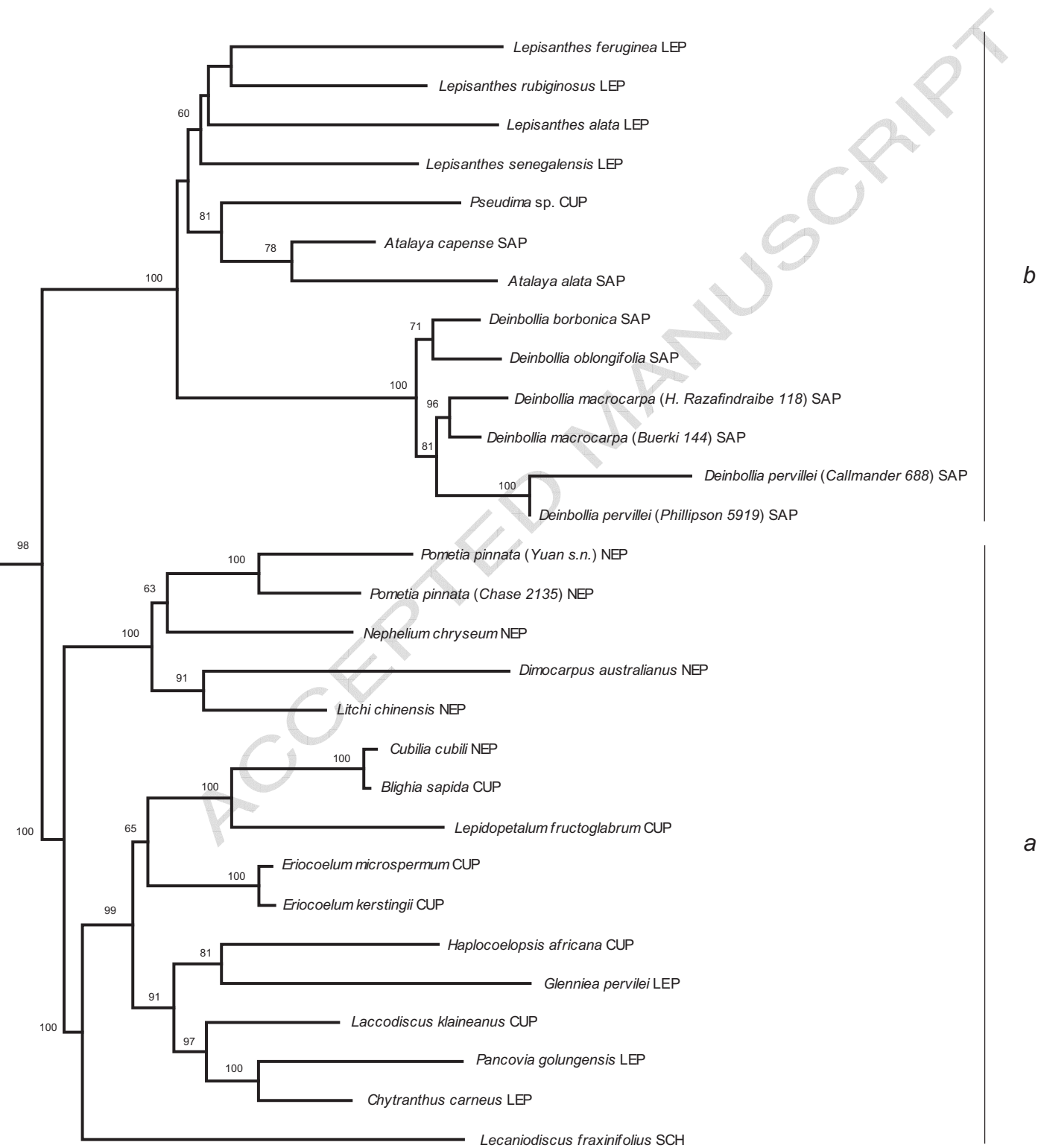
Figure 4
Clade C



0.02

Figure 5

Clade C-IV

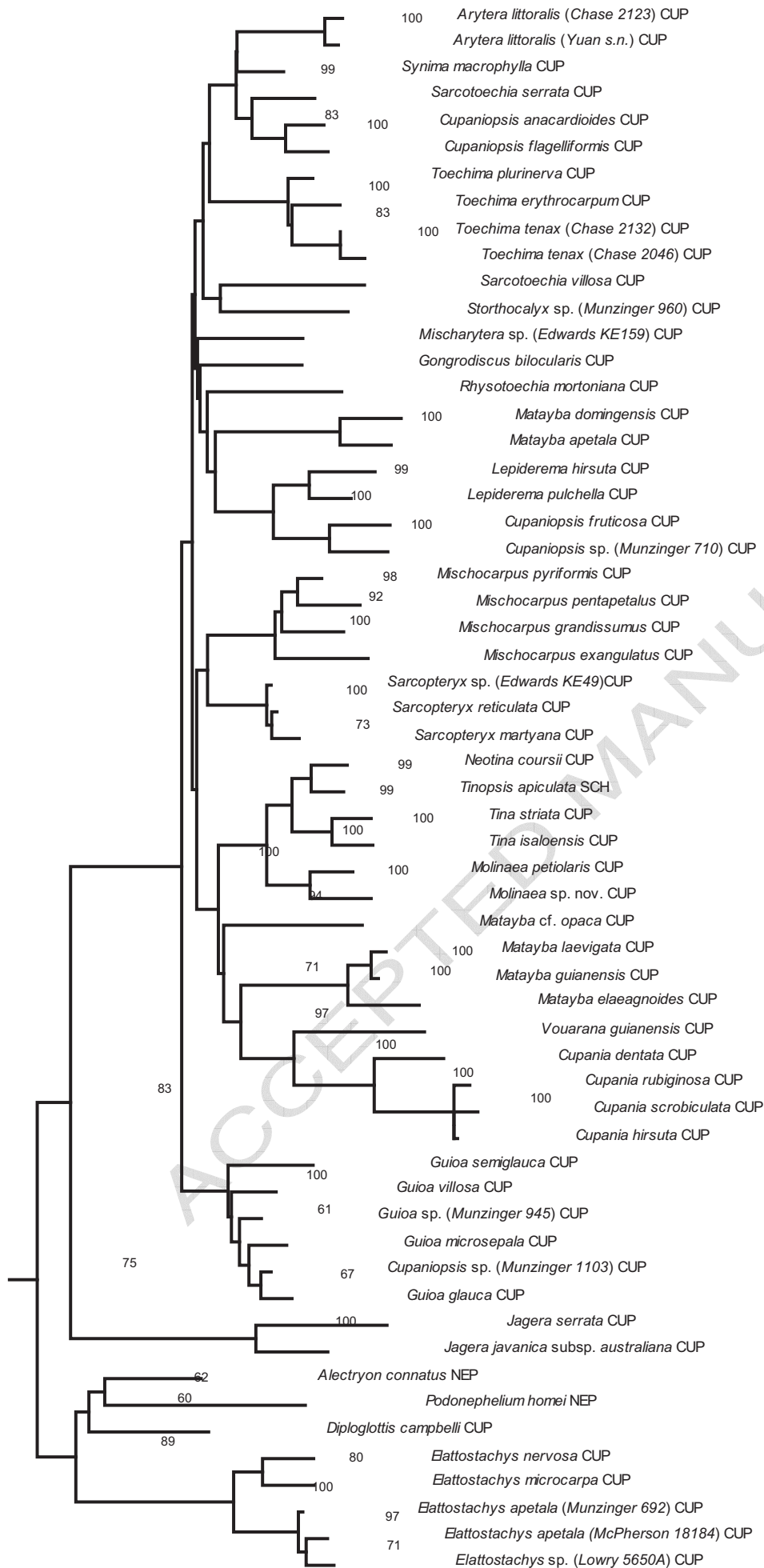


b

a

0.01

Figure 6 Clade C-VI



b

a

0.01