

Phylogeny and circumscription of Sapindaceae revisited: molecular sequence data, morphology and biogeography support recognition of a new family, Xanthoceraceae

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Background and aims – Recent studies have adopted a broad definition of Sapindaceae that includes taxa traditionally placed in Aceraceae and Hippocastanaceae, achieving monophyly but yielding a family difficult to characterize and for which no obvious morphological synapomorphy exists. This expanded circumscription was necessitated by the finding that the monotypic, temperate Asian genus *Xanthoceras*, historically placed in Sapindaceae tribe Harpullieae, is basal within the group. Here we seek to clarify the relationships of *Xanthoceras* based on phylogenetic analyses using a dataset encompassing nearly $\frac{3}{4}$ of sapindaceous genera, comparing the results with information from morphology and biogeography, in particular with respect to the other taxa placed in Harpullieae. We then re-examine the appropriateness of maintaining the current broad, morphologically heterogeneous definition of Sapindaceae and explore the advantages of an alternative family circumscription.

Methods – Using 243 samples representing 104 of the 142 currently recognized genera of Sapindaceae s. lat. (including all in Harpullieae), sequence data were analyzed for nuclear (ITS) and plastid (*matK*, *rpoB*, *trnD-trnT*, *trnK-matK*, *trnL-trnF* and *trnS-trnG*) markers, adopting the methodology of a recent family-wide study, performing single-gene and total evidence analyses based on maximum likelihood (ML) and maximum parsimony (MP) criteria, and applying heuristic searches developed for large datasets, viz. a new strategy implemented in RAxML (for ML) and the parsimony ratchet (for MP). Bootstrap analyses were performed for each method to test for congruence between markers.

Key results – Our findings support earlier suggestions that Harpullieae are polyphyletic: *Xanthoceras* is confirmed as sister to all other sampled taxa of Sapindaceae s. lat.; the remaining members belong to three other clades within Sapindaceae s. lat., two of which correspond respectively to the groups traditionally treated as Aceraceae and Hippocastanaceae, together forming a clade sister to the largely tropical Sapindaceae s. str., which is monophyletic and morphologically coherent provided *Xanthoceras* is excluded.

Conclusion – To overcome the difficulties of a broadly circumscribed Sapindaceae, we resurrect the historically recognized temperate families Aceraceae and Hippocastanaceae, and describe a new family, Xanthoceraceae, thus adopting a monophyletic and easily characterized circumscription of Sapindaceae nearly identical to that used for over a century.

Key words – Aceraceae, Harpullieae, Hippocastanaceae, molecular phylogeny, new family, Sapindaceae, *Xanthoceras*, Xanthoceraceae.

INTRODUCTION

The systematics of the family Sapindaceae has challenged taxonomists for more than a century since its first comprehensive treatment was published by Radlkofer (1890, 1933). Until the late 1980s, Sapindaceae were widely treated as distinct from two closely related families, Hippocastanaceae and Aceraceae, based primarily on morphology and biogeography (Takhtajan 1987, Cronquist 1988, Dahlgren 1989). Several recent studies using pollen morphology (Müller & Leenhouts 1976), phytochemistry (Umadevi & Daniel 1991) and molecular sequence data (Gadek et al. 1996, Savolainen et al. 2000, APG II 2003, APG III 2009, Harrington et al. 2005, Buerki et al. 2009) have, however, led to the adoption of a broader concept in an effort to ensure monophyly, uniting these entities into a single family, Sapindaceae s. lat.

Sapindaceae s. lat. as currently circumscribed by Harrington et al. (2005), Thorne & Reveal (2007) and Buerki et al. (2009, 2010) comprise c. 1900 species and 142 genera distributed among four subfamilies: Dodonaeoideae Burnett, Hippocastanoideae Burnett, Sapindoideae Burnett and Xanthoceroideae Thorne & Reveal. Recently, Buerki et al. (2009) demonstrated the para-/polyphyly of all tribes as defined by Radlkofer (1933), with a single exception, Paullinieae Kunth. Although they sketched an informal system that recognizes a dozen monophyletic groups, they did not propose new tribal limits within the four subfamilies as many potentially important genera of Sapindaceae were not included in their study due to the lack of sequenceable material.

Historically, Radlkofer (1933) recognized fourteen tribes within Sapindaceae s. str., five in Dodonaeoideae and nine in Sapindoideae (see table 1 in Buerki et al. 2009 for details). Within Dodonaeoideae, however, he encountered difficulty assigning nine genera to the four previously described tribes, ultimately deciding to place them in a new tribe, Harpullieae Radlk. Within this heterogeneous assemblage, he recognized two informal groups according to the presence (*Delavaya* Franchet, *Ungnadia* Endl. and *Xanthoceras* Bunge) or absence (*Arfeuillea* Pierre, *Conchopetalum*, *Eurycorymbus* Hand.-Mazz., *Harpullia* Roxb., *Magonia* A.St.-Hil. and *Majidea* J.Kirk ex Oliv.) of a terminal leaflet. While revising Radlkofer's infra-familial system, largely on the basis of pollen and other morphological features, Müller & Leenhouts (1976) discussed the possible expansion of Harpullieae to include the three genera comprising Hippocastanaceae, viz. *Aesculus* L., *Billia* L. and *Handeliodendron* (these authors did not, however, comment on the taxonomic status of Aceraceae). In their revised classification, Müller & Leenhouts (1976) concluded that the connection between Hippocastanaceae and Harpullieae might involve two genera in particular, *Handeliodendron*, originally described in Sapindaceae (Rehder 1935), and *Delavaya*, which has always been placed in Sapindaceae. Müller & Leenhouts (1976) also regarded Harpullieae as a "heterogeneous assemblage", with several genera difficult to connect to the others. For example, they classified *Harpullia* pollen as both type-A and type-H and *Magonia* pollen as type-E, whereas other members of the tribe exclusively exhibit the more common type-A pollen (see Buerki et al. 2009 for more details on pollen morphology). Moreover, Harpullieae range from tropical (e.g. *Conchopetalum*, *Delavaya*, *Magonia*) to temperate (*Xanthoceras*) regions

and include both evergreen and deciduous species (Radlkofer 1933, Müller & Leenhouts 1976). Based on wood anatomy, Klaassen (1999) noted a difference between the temperate and tropical genera in the tribe, and among the tropical ones he indicated that *Delavaya* and *Ungnadia* stood out because their wood is similar to that of members of tribe Cupanieae Reichenb. (Sapindoideae). Buerki et al. (2009) found Harpullieae to be polyphyletic, with *Xanthoceras* occupying a basal position within Sapindaceae s. lat., *Arfeuillea*, *Eurycorymbus*, *Harpullia* and *Majidea* placed in Dodonaeoideae, *Delavaya* occupying a basal position within Sapindoideae, and *Conchopetalum* resolved in the *Macphersonia* group (Sapindoideae; Buerki et al. 2009) closely related to the newly described endemic Malagasy genus *Gereaaua* Buerki & Callm. (Buerki et al. 2010). A close relationship between *Delavaya* and *Ungnadia* was found in an earlier cladistic analysis based on morphology (Judd et al. 1994), which identified the presence of prolonged basal petal appendages and glabrous stamens as putative synapomorphies, again suggesting that Harpullieae were far from representing a natural assemblage.

In the present study we seek to (1) clarify the relationships of *Xanthoceras* within Sapindaceae s. lat. and in particular with respect to the other taxa traditionally and/or currently placed in Harpullieae, and (2) re-examine the appropriateness of maintaining the current broadly circumscribed but morphologically heterogeneous definition of Sapindaceae and explore the possible advantages of alternative family circumscriptions. Toward this end, we have significantly expanded the dataset of Buerki et al. (2009) to conduct a new set of phylogenetic analyses, comparing the results with information from morphology and biogeography.

MATERIAL AND METHODS

Sampling, sequence data and phylogenetic analyses

Species names, voucher information, and GenBank accession numbers for all sequences are provided in the appendix. The dataset presented in Buerki et al. (2009) was expanded to include a total of 243 samples encompassing more than 70% of the generic diversity in Sapindaceae s. lat. (104 of the currently recognized 142 genera; half of the 38 genera not included in this analysis are monospecific), representing an increase of ninety ingroup samples and nineteen genera. To assess the phylogenetic relationships of the taxa placed in tribe Harpullieae and in the traditionally recognized families Aceraceae and Hippocastanaceae, we sampled at least one species from each genus currently assigned to these groups by adding the following genera: *Magonia* and *Ungnadia* from Harpullieae, plus *Billia* and *Handeliodendron* from Hippocastanaceae (*Aesculus*, the third member of this family, was included in the analysis of Buerki et al. 2009, as were both genera of Aceraceae, *Acer* and *Dipteronia*). The outgroup sampling included one taxon each from Anacardiaceae (*Sorindeia* sp., used as the most external outgroup), Meliaceae (*Malleastrum* sp.) and Simaroubaceae (*Harrisonia abyssinica* Oliv.).

The DNA extraction, amplification and sequencing protocols used for the nuclear and plastid regions are provided in Buerki et al. (2009). The nuclear sequences include the whole ITS region (*ITS1*, 5.8S and *ITS2*) and plastid markers include

both coding (*matK* and *rpoB*) and non-coding regions (the *trnL* intron and the intergenic spacers *trnD-trnT*, *trnK-matK*, *trnL-trnF* and *trnS-trnG*).

Single-gene, total evidence analyses and their corresponding bootstrap analyses were performed using the maximum parsimony (MP) and maximum likelihood (ML) criteria following the same procedure as in Buerki et al. (2009). Parsimony ratchet (Nixon 1999) was performed for each partition and for the combined data set using PAUPRat (Sikes & Lewis 2001). Ten independent searches were performed with 200 iterations and 15% of the parsimony informative characters perturbed. A strict consensus tree was constructed based on the shortest equally parsimonious trees. To assess support at each node, non parametric bootstrap analyses (Felsenstein 1985) were performed

using PAUP* (Swofford 2002) following the same procedure as in Buerki et al. (2009). Model selection for each partition was assessed using Modeltest v. 3.7 (Posada & Crandall 1998). ML analyses were performed using RAxML v. 7.0.0 (Stamatakis 2006, Stamatakis et al. 2008) with 1000 rapid bootstrap analyses followed by a search for the best-scoring tree in one single run. These analyses were done using the facilities made available by the CIPRES portal in San Diego, USA (<http://8ball.sdsc.edu:8888/cipres-web/home>).

Topological differences between single-gene phylogenetic trees were compared by taking into account the level of resolution obtained by each marker and its bootstrap support. Topological differences with bootstrap support (BS) less than 75% were not considered.

Table 1 – Characteristics of partitions used in the phylogenetic analyses of Sapindaceae s. lat.

IGS = intergenic spacer; MP = maximum parsimony; PI = potentially parsimony informative; CI = consistency index; RI = retention index; ¹for No. of sequences, the total number of samples for the combined analyses is indicated between brackets; ²for mean amount of phylogenetic information per sample: averaged by alignment size/variable sites number/PI sites number.

Phylogenetic information	Single-gene analysis								8 markers
	ITS	matK	rpoB	trnD-trnT IGS	trnK-matK IGS	trnL intron	trnL-trnF IGS	trnS-trnG IGS	
No. of ingroup sampled species/genera	156/89	159/89	174/96	94/69	119/74	169/97	165/93	74/52	214/104
No. sequences ¹	172	175	199	102	133	192	189	80	1242 (243)
Sequences: this study/Genbank	165/5	146/29	199/0	102/0	131/2	188/4	186/3	80/0	-
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	9657
No. constant characters (%)	584 (47.3%)	1062 (65.7%)	222 (61.1%)	965 (50.1%)	488 (52.4%)	454 (58.7%)	328 (49.6%)	1577 (73.1%)	5681 (58.8%)
No. variable characters (%)	653 (52.9%)	552 (34.2%)	141 (38.8%)	960 (49.9%)	443 (47.6%)	319 (41.2%)	333 (50.4%)	579 (26.8%)	3976 (41.2%)
No. potentially PI characters (%)	491 (39.8%)	392 (24.3%)	104 (28.7%)	505 (26.2%)	277 (29.8%)	194 (25.1%)	217 (32.8%)	227 (10.5%)	2404 (24.9%)
Mean amount of phylogenetic information per sample ²	-	-	-	-	-	-	-	-	16.4/39.7/9.9
No. trees retained	214	1967	2010	1975	1703	1500	667	1820	949
Tree length (steps)	4666	1185	281	1858	954	687	705	945	11526
Consistency Index (CI)	0.272	0.632	0.672	0.694	0.633	0.644	0.646	0.711	0.492
Retention Index (RI)	0.673	0.860	0.907	0.790	0.775	0.881	0.858	0.650	0.749

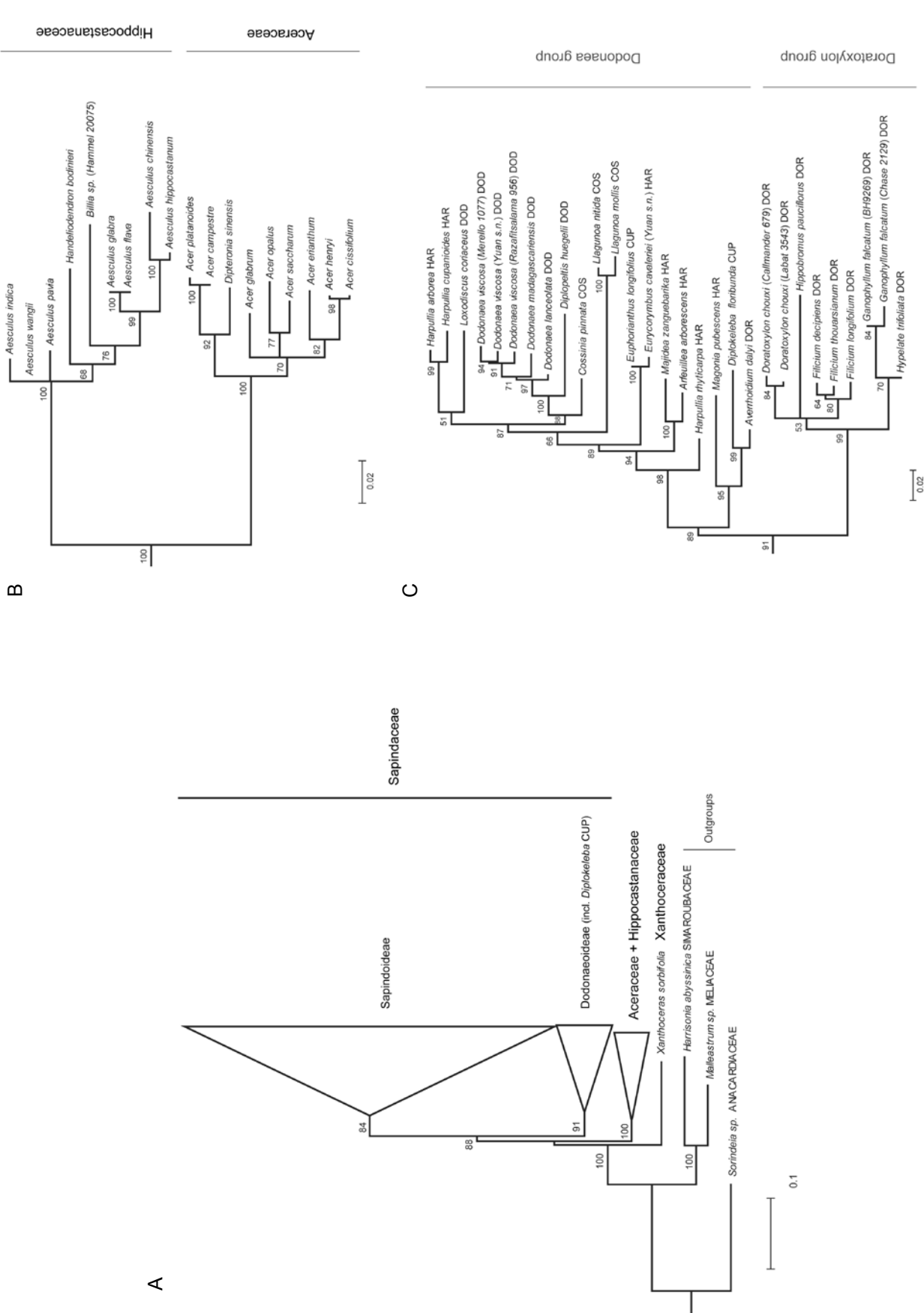


Figure 1 – A, best maximum likelihood phylogenetic tree for Sapindaceae s. lat.; B, relationships between and within Aceraceae and Hippocastanaceae; C, relationships within subfamily Dodonaeoideae. Bootstrap supports are indicated above branches. COS = Cossiniaceae; CUP = Cupaniaceae; DOR = Doratoxyleae; HAR = Harpulliaceae. The definition of the groups follows Buerki et al. (2009).

RESULTS

Alignment and phylogenetic analyses

The number of samples and statistics for each partition and the combined data set are summarized in table 2. The best-fit model for all partitions was the general time reversible (GTR) with an alpha parameter for the shape of the gamma distribution to account for among-site rate heterogeneity (GTR+G). The only exception was the ITS region, in which a proportion of invariable sites was added (GTR+G+I). The MP and ML single-gene phylogenies provided different levels of resolution, but no differences with a bootstrap support greater than 75% were identified when compared, so we combined them in a total evidence approach. Statistics (number of most parsimonious trees; tree length; and consistency and retention indices) for each analysis are reported in table 1.

For the combined analyses under the MP criterion, nine of the ten independent PAUPrat searches converged on a best score of 11526 steps and produced a total of 949 most parsimonious trees, which were used to compile a strict consensus (not shown); this consensus tree comprised several polytomies, especially near the tips. Under the ML criterion, the best-fit model for the combined matrix was GTR+G+I. This model was used to perform the single ML run search (log likelihood = -79995.7), followed by rapid bootstrap analyses.

When compared, analyses compiled under the MP and ML criteria yielded very similar topologies. Moreover, as no moderately to strongly supported differences were observed between the two phylogenetic trees, only the ML topology will be presented and discussed hereafter (figs 1 & 2).

Phylogenetic relationships

With the addition of the ninety ingroup samples used in the present analysis, including representatives of several genera of Sapindaceae s. lat. that had not previously been sequenced, the phylogenetic relationships revealed here are highly congruent with the informal system proposed by Buerki et al. (2009). Based on sampling that includes at least one representative of all genera traditionally placed in Sapindaceae tribe Harpullieae, Aceraceae and Hippocastanaceae, our results further confirm that *Xanthoceras sorbifolium* Bunge (previously assigned to Harpullieae by Radlkofer, 1933) is resolved as sister to the remaining sampled members of Sapindaceae s. lat. (however with a low BS; fig. 1A). Our results also indicate that the other genera of Harpullieae belong to three additional clades, one in subfam. Dodonaeoideae and two in subfam. Sapindoideae (figs 1 & 2), confirming the polyphyly of the tribe. Within Dodonaeoideae, five of the genera currently assigned to Harpullieae belong to the *Dodonaea* group, viz. *Arfeuillea*, *Eurycorymbus*, *Harpullia*, *Magonia* and *Majidea* (fig. 1C), and *Harpullia* itself appears to be polyphyletic, with the three species sampled occupying very different positions within the phylogeny (expanded sampling to include additional members of the genus are, however, needed to confirm this finding). Within Sapindoideae, two of the three remaining genera assigned to Harpullieae (*Delavaya* and *Ungnadia*) are placed in the *Delavaya* group, the

basal most lineage within the subfamily, and the third genus (*Conchopetalum*) belongs to the *Macphersonia* group (fig. 2).

The inclusion of *Billia* and *Handelioidendron* in our analysis, along with additional species of *Acer* and *Aesculus*, strengthens support for the monophyly of both Aceraceae and Hippocastanaceae and confirms their sister relationship (fig. 1A & B). Our results suggest the possible paraphyly of *Acer* (with respect to *Dipteronia*) and of *Aesculus* (with respect to *Billia* and *Handelioidendron*), although this finding should be tested further with additional sampling. Support for the clade comprising Sapindaceae s. str. (i.e. Dodonaeoideae plus Sapindoideae) is likewise stronger in the present analysis (BS = 88) than in that of Buerki et al. (2009; BS = 69; fig. 1). Moreover, *Diplokeleba* N.E.Br., long regarded as a member of Sapindoideae (tribe Cupanieae), is instead placed within Dodonaeoideae (fig. 1C).

DISCUSSION

Polyphyly of Harpullieae

The results presented above clearly show that the tribe Harpullieae (as well as all other sapindaceous tribes with the exception of Paullinieae), as defined initially by Radlkofer (1890, 1933) and modified by Müller & Leenhouts (1976), is highly polyphyletic, with members placed in no fewer than four clades scattered among various parts of Sapindaceae s. lat. Harrington et al. (2005) and Buerki et al. (2009) argued that additional sampling (especially of Harpullieae) was required before taking a definitive stand regarding the phylogenetic and taxonomic status of *Xanthoceras*. Although we have now analyzed more than 70% of the genera and included all those that are putatively related to *Xanthoceras*, its precise phylogenetic position within Sapindaceae is not strongly supported (BS < 50; fig. 1A). However, both the MP and ML analyses presented here clearly point toward *Xanthoceras* comprising a basal lineage with Sapindaceae s. lat. (fig. 1A). Moreover, a study comparing the performance of supertree methods based on an identical dataset (Buerki et al. in press) produced the same result, with both the Matrix Representation with Parsimony and MinFlip supertree methods placing *Xanthoceras* as the most basally branching lineage. This phylogenetic pattern might be explained either by a higher rate of extinction in the lineage that now comprises only *Xanthoceras* than in the other lineages, or alternatively by a rapid diversification or radiation of these other lineages resulting in a loss of phylogenetic signal (Judd & Olmstead 2004). In the case of Sapindaceae s. lat., the former hypothesis seems more likely based on preliminary divergence time estimations that place the origin of the clade in the Late Cretaceous (c. 110 My), with divergence among the four lineages occurring between 90 and 80 My (Buerki et al. in prep.).

The pattern observed here, in which resolution between lineages remains problematic even after sequencing a large number of markers from a broad sampling of taxa, has been observed in many other angiosperm groups, especially among the rosids (Bello et al. 2009 and references within), such as Fabales, where the relationships among the currently accepted families remain unsolved. In order to clarify the situation within Sapindaceae s. lat. and provide a practical classifica-

Sapindoideae

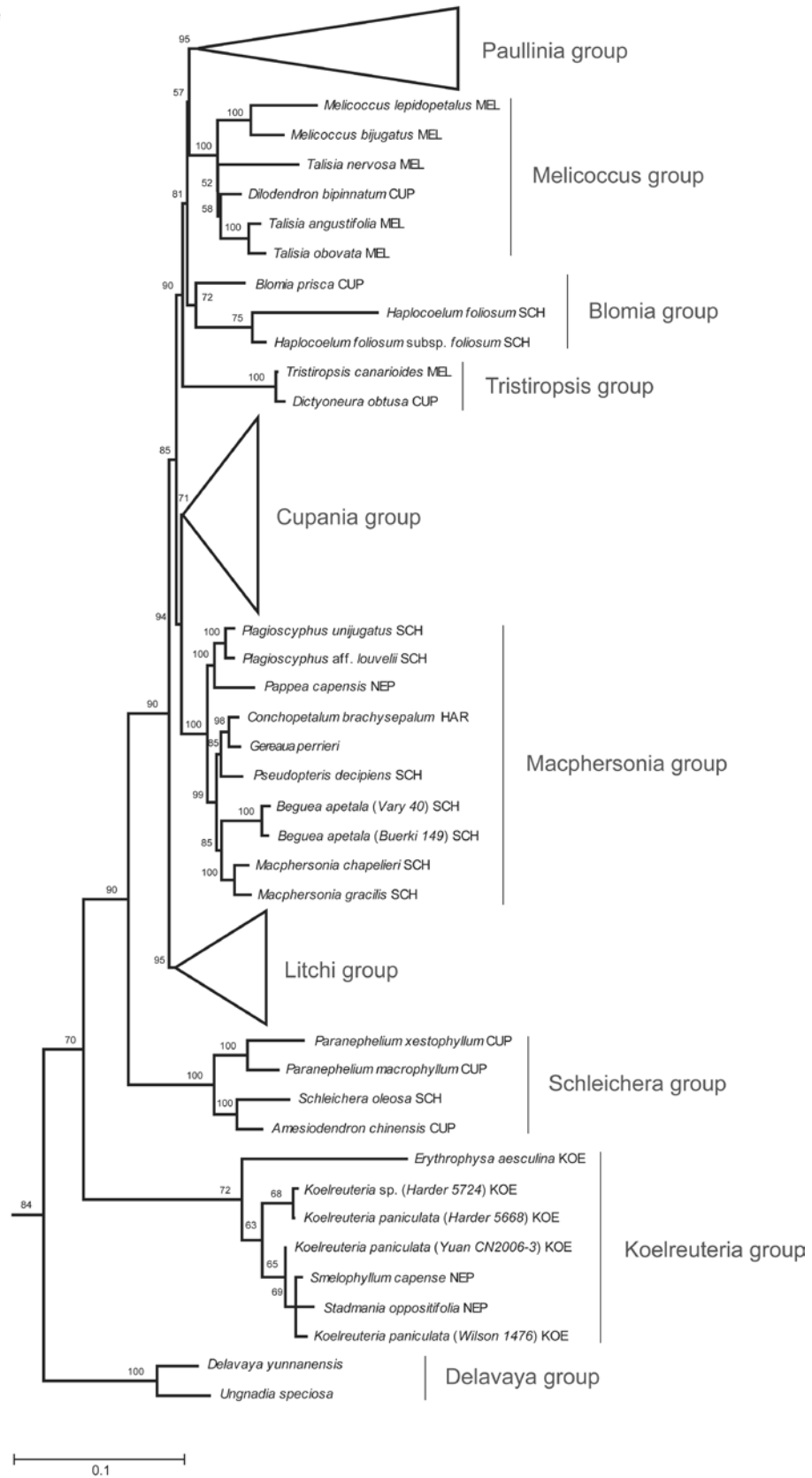


Figure 2 – Relationships within subfamily Sapindoideae. Bootstrap supports are indicated above branches. CUP = Cupanieae; KOE = Koelreuteriaceae; HAR = Harpullieae; MEL = Melicocceae; NEP = Nephelieae; SCH = Schleichereae. The definition of the groups follows Buerki et al. (2009).

tion that circumscribes easily recognizable groups, we suggest that other criteria should be considered in addition to monophyly. In addition to representing the most basal lineage within the family, *Xanthoceras* presents a unique and highly distinctive combination of morphological characters, including imparipinnate leaves (vs. paripinnate, evergreen leaves in most genera), large flowers with petals c. 1.5–2 cm long (vs. small flowers with petals < 1.5 cm long), 5-horn-like appendages protruding from the nectary disk (vs. no appendages protruding from the disk), 7–8 ovules per locule (vs. generally 1–2 ovules per locule) and > 15 seeds (vs. 1–3 seeds). Moreover, if *Xanthoceras* is included within Sapindaceae s. str., it stands out as the sole member with a north-temperate distribution, whereas all other genera occur in the tropics and/or subtropics.

The tropical Chinese genus *Delavaya*, traditionally assigned to Harpullieae, has been viewed by several authors (e.g. Müller & Leenhouts 1976, Cronquist 1988) as a “link” between Sapindaceae and Hippocastanaceae through the temperate genus *Handeliidendron*. The molecular analyses presented here failed to confirm this hypothesis (figs 1 & 2; see below). Instead, they indicate that *Handeliidendron* belongs to the Hippocastanaceae clade, a placement previously suggested by Forest et al. (2001) based on the presence of simple, opposite leaves, whereas *Delavaya* occupies a basal position within subfam. Sapindoideae along with *Ungnadia* from Texas and Florida, another genus originally assigned to Harpullieae (these two genera thus forming the *Delavaya* group; fig. 2). As indicated above, a close relationship between *Delavaya* and *Ungnadia* was previously suggested by Klaassen (1999) and Judd et al. (1994) based on wood anatomy and morphological cladistic analyses, respectively.

A majority (five out of nine) of the genera traditionally assigned to Harpullieae (viz., *Arfeuillea*, *Eurycorymbus*, *Harpullia*, *Magonia* and *Majidea*) belong to subfam. Dodonaeoideae, and in particular to the *Dodonaea* group, a finding that is consistent with Radlkofer’s (1890, 1933) original placement of Harpullieae. The basal most branch of the *Dodonaea* group includes the South American genus *Magonia* (fig. 1C), associated by Müller & Leenhouts (1976) with the temperate Asian *Xanthoceras* on the basis of their sharing seven or eight ovules per locule. The close relationship between *Averrhoidium*, *Diplokeleba* (previously assigned to Sapindoideae) and *Magonia* might be reflected in part by seed morphology; the first two genera are the only members of Sapindaceae to have winged seeds (Radlkofer 1933).

Finally, the results of the phylogenetic analyses presented in this study are in agreement with the findings of Buerki et al. (2009) with regard to the position of the last genus traditionally assigned to Harpullieae, the Malagasy endemic *Conchopetalum*, which is confirmed to belong to the *Macphersonia* group (Sapindoideae; fig. 2; see Buerki et al. in press for more details). Relationships between this taxon and other members of Sapindaceae are discussed in Buerki et al. (2009).

Harpullieae have traditionally been considered to represent a “link” between Aceraceae, Hippocastanaceae and Sapindaceae, but as mentioned above, the molecular analyses presented here fail to confirm this hypothesis (figs 1 & 2). Our analyses do not support the long-held view that Apera-

ceae and Sapindaceae are closely related (Radlkofer 1890, 1933, Müller & Leenhouts 1976, Umadevi & Daniel 1991). Instead, they show that the two genera currently placed in Aceraceae form a strongly supported group, and that they are more closely related to Hippocastanaceae than to the clade comprising Sapindaceae s. str. (fig. 1B), as earlier suggested by Harrington et al. (2005), Thorne & Reveal (2007) and Buerki et al. (2009).

The present analyses further confirm that (i) Sapindaceae s. lat. constitute a monophyletic entity that is supported by molecular (but not morphological) synapomorphies; (ii) the three traditionally recognized families Aceraceae, Hippocastanaceae and Sapindaceae, as circumscribed by Radlkofer (1933), are each monophyletic and moderately to strongly supported, provided that *Xanthoceras* is excluded from Sapindaceae; and (iii) *Xanthoceras sorbifolium* is sister to the clade comprising these three families (fig. 1A). The concept of a broadly defined Sapindaceae that includes Aceraceae, Hippocastanaceae and *Xanthoceras*, recently adopted by the Angiosperm Phylogeny Group (APG II 2003) and followed by Harrington et al. (2005), Buerki et al. (2009) and APG III (2009), is consistent with the phylogenetic relationships revealed in earlier studies and confirmed here. However, this broad circumscription of Sapindaceae presents several conceptual problems. First, no clear morphological synapomorphies have been identified for Sapindaceae s. lat. (Harrington et al. 2005, Thorne & Reveal 2007, Buerki et al. 2009) and the high level of heterogeneity that results from the inclusion of *Xanthoceras* and the taxa traditionally placed in Aceraceae and Hippocastanaceae makes it difficult to characterize the family. Second, treating Sapindaceae broadly reduces these easily identified and widely recognized families to synonymy, changing the long-established family assignment of several well known, emblematic and widely cultivated genera, most notably *Acer* and *Aesculus*.

Classification

Two alternative approaches are available to address the family level circumscription of the taxa currently placed in Sapindaceae s. lat.: (i) retain the broad definition recently proposed by the Angiosperm Phylogeny Group (APG II 2003, APG III 2009) or (ii) resurrect the temperate families Aceraceae and Hippocastanaceae, restrict Sapindaceae s. str. slightly by excluding *Xanthoceras*, and describe a new family to accommodate this genus. Both interpretations are consistent with the primary principle of classification as defined by Backlund & Bremer (1998), which requires the monophyly of taxonomic entities. However, the second approach is clearly preferable when two other principles proposed by these authors are taken into consideration, maximizing ease of identification and maintaining nomenclatural stability. While an argument could be made that it is preferable to avoid adding a new name at the family rank (Stevens 1997), in the present case we believe that this is significantly outweighed by the clear advantages of maintaining Aceraceae, Hippocastanaceae and Sapindaceae (excluding *Xanthoceras*) as the morphologically and biogeographically coherent entities that have been recognized for well over a century. In order to render Sapindaceae

Key to distinguish Xanthoceraceae from closely related families

1. Leaves alternate, compound (rarely unifoliate in some *Allophylus* and *Dodonaea* species, both Sapindaceae).....2
 - 1'. Leaves opposite, simple or compound.....3
 2. Flower large, petals c. 2 cm long; disc with 5-horn-like appendages; ovules 7 or 8 per locule, all fertile; seeds > 15 per fruit; leaves imparipinnately compound, plants deciduous; temperate regions of eastern Asia, from inner Mongolia across China to Korea.....**Xanthoceraceae**
 - 2'. Flower small, petals < 1.5 cm long; disc lacking horn-like appendages; ovules 1 or 2 per locule (7 or 8 in the South American genus *Magonia*), fertile ovule generally 1 per locule; seeds 1 to 3 per fruit; leaves paripinnately compound (rarely imparipinnate, unifoliate or simple), plants evergreen; tropical to subtropical regions.....**Sapindaceae**
 3. Flower actinomorphic, leaves palmately lobed or pinnately compound; fruit a schizocarpic fruits with 1-seeded samaroid mericarps.....**Aceraceae**
 - 3'. Flower zygomorphic, leaves palmately compound; fruit a 3-carpellate, usually 1-seeded capsule.....**Hippocastanaceae**
-

s. str. monophyletic, we therefore propose to place *Xanthoceras* in a new monotypic family, Xanthoceraceae.

Taxonomy

Xanthoceraceae Buerki, Callm. & Lowry **fam. nov.** ≡ Sapindaceae subfam. Xanthoceroideae Thorne & Reveal (Thorne & Reveal 2007: 119).

Haec familia ab Aceraceis Hippocastanaceis et Sapindaceis flore grandi (petalis c. 2 cm longis) appendicibus 5 corniformibus e disco nectarifero exsertis, ovulis (omnibus fertilibus) in quoque loculo 6 ad 8 atque seminibus exarillatis plus quam 15 distinguitur. – Type: *Xanthoceras sorbifolium* Bunge (von Bunge 1833: 85).

Shrubs or small trees, andromonoecious. Leaves imparipinnately compound; leaflets serrate; bracts ovate, large. Flowers in dense racemes 15–20 cm long, staminate and perfect flowers borne in separate inflorescences, all actinomorphic. Sepals 5, oblong, imbricate. Petals 5, large, c. 2 cm long, broadly obovate, shortly clawed at base, scale absent. Disk 5-lobed, lobes alternate to petals, apex with five suberect, obtuse, abaxial horn-like appendage. Stamens 8, not exserted; anthers ellipsoid, gland-tipped. Ovary ellipsoid, 3-locular; ovules 7 or 8 per locule, in 2 lines, all fertile; style terminal, erect; stigma papillate. Fruit a globose to pyriform capsule, 3-ridged, pericarp very thick, dehiscent loculicidally into 3 schizocarps. Seeds numerous (> 15), compressed-globose, arillode absent. $2n = 30$.

Included genus: *Xanthoceras* Bunge.

Distribution and habitat – *Xanthoceras sorbifolium* is widespread in north temperate China, where it grows on hills and slopes in Gansu, Hebei, Henan, Nei Mongol, Ningxia, Shaanxi, Shandong and Shanxi provinces; it is also found in Korea (Xia & Gadek 2007).

Etymology – Von Bunge (1833) published the name *Xanthoceras* in reference to the unique yellow horn-like appendages found on the floral disc in the sole member of this genus, *X. sorbifolium*, and coined a common name in English, yel-

lowhorn. In Chinese *Xanthoceras* is referred to as *wen guan guo* (Xia & Gadek 2007).

Ethnobotany – *Xanthoceras* is used as a folk medicine in China for treating various diseases (Chan & Mak 2006) as well as enuresis in children (Chan et al. 2008). Its seeds are sweet and are prized as a food. Acylated triterpene saponins were recently isolated from the husk of *X. sorbifolium* (Chan et al. 2008) and exhibited cytotoxicity towards several human cancer cell lines (Chan & Mak 2006).

Notes – The new family Xanthoceraceae can be distinguished from Aceraceae, Hippocastanaceae and Sapindaceae (as circumscribed here) by a number of morphological features, as summarized in the key presented above.

SUPPLEMENTARY DATA

Supplementary data are available at *Plant Ecology and evolution*, Supplementary Data Site (<http://www.ingentaconnect.com/content/botbel/plecevo/supp-data>), and consist of a tabular version of the appendix (pdf format).

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Appendix – Voucher information and GenBank accession numbers for taxa used in the phylogenetic analysis of Sapindaceae s. lat. (including outgroups). For each taxon, voucher information (between brackets) is listed in the following order: the phyloger collector and collection number, institution where the voucher was deposited, country. Accession numbers are listed in the following order: ITS, matK, rpoB, trnD-trnT, trnK-matK, trnL, trnL-F, trnS-trnG. Hyphens indicate that no data are available. The entire table is available as an electronic appendix (see Supplementary Data).

Ingroup: *Acer campestre* L. (s.n., -, Spain) -, AJ438796, -, -, AJ438796, -, -, -, *Acer cissifolium* (Siebold & Zucc.) K.Koch (-, -, -) AF241483, -, -, -, -, -, *Acer erianthum* Schwer. (Chase 19983, K, China) EU720501, -, EU720843, EU720980, -, EU721271, EU721459, -, *Acer glabrum* Torr. (Morris Arb. 93-277B, MO, -) -, -, -, -, -, DQ978532, DQ978532, -, *Acer henryi* Pax (-, -, -) AF401141, -, -, -, -, -, *Acer opalus* Mill. (Grimm GG01305, -, -) AM238317, -, -, -, -, -, *Acer platanoides* L. (-, -, -) -, AJ438788, -, -, AJ438788, -, -, -, *Acer saccharum* Marshall (Chase 106, K, Cult. source, Orange Co.) EU720502, -, EU720844, -, -, EU721272, EU721460, -, *Aesculus chinensis* Bunge (Xiang 305, -, -) -, AY724267, -, -, -, -, -, *Aesculus flava* Sol. (98-48, -, -) -, AY968670, -, -, -, -, -, *Aesculus glabra* Willd. (J.C. Raulston Acen. No. 960612, -, -) -, AY968671, -, -, -, -, -, *Aesculus hippocastanum* L. (living collection 6911289263, -, -) -, AY724266, -, -, -, -, -, *Aesculus indica* (Wall. ex Cambess.) Hook. (Chase 19987, K, India) EU927392, -, EU720845, EU720981, -, EU721273, EU721461, -, *Aesculus pavia* Castigl. (Chase 503, K, -) -, -, EU720846, EU720982, -, EU721274, EU721462, -, *Aesculus wangii* Hu (-, -, -) -, -, -, -, -, AF411085, AF411085, -, *Alectryon connatus* Radlk. (Chase 2047, K, Australia) EU720415, EU720577, EU720732, EU720928, EU721025, EU721169, EU721357, EU721534; *Alectryon coriaceus* Radlk. (Edwards KE59, JCT, Australia) -, EU720599, EU720756, -, EU721039, EU721192, EU721380, EU721548; *Alectryon excelsum* Gaertn. (-, -, -) EF635451, -, -, -, -, -, *Allophyllus arboreus* Choux (Rakotavao 2812, MO, Madagascar) EU720508, -, EU720852, -, -, -, -, *Allophyllus arboreus* Choux (Rakotavao 3131, MO, Madagascar) EU720531, EU720681, EU720879, -, EU721118, -, -, -, *Allophyllus cobbe* (L.) Rauesch (Callmander 462, MO, Madagascar) EU720517, -, EU720861, -, -, -, -, *Allophyllus longipes* Radlk. (-, -, -) -, -, -, -, -, AY207572, AY207572, -, *Allophyllus natalensis* De Winter (Edwards KE227, JCT, South Africa) -, AY724268, -, -, -, -, *Allophyllus* sp. (Edwards KE273, JCT, Tanzania) -, AY724269, -, -, -, -, *Allophyllus trichodesmus* Radlk. (Rakotavao 2897, MO, Madagascar) EU720511, -, EU720855, -, -, -, -, *Allophyllus trichodesmus* Radlk. (Ravelonarivo 1619, MO, Madagascar) EU720516, -, EU720860, -, -, -, -, *Amesiodendron chinensis* (Mert.) Hu (Yuan s.n., NEU, China) EU720403, -, EU720718, EU720917, -, EU721155, EU721344, EU721525; *Arfeuillea arborescens* Pierre (Chase 2122, K, Bogor, BG) EU720461, EU720629, EU720793, EU720962, EU721067, EU721229, EU721417, -, *Arytera divaricata* F.Muell. (Edwards KE010, JCT, Australia) -, AY724271, -, -, -, -, *Arytera littoralis* Blume (Yuan s.n., NEU, China) EU720405, EU720566, EU720720, EU720919, EU721018, EU721157, EU721346, EU721527; *Arytera littoralis* Blume (Chase 2123, K, Bogor, BG) EU720462, EU720630, EU720794, EU720963, EU721068, EU721230, EU721418, -, *Arytera microphylla* (Benth.) Radlk. (Edwards KE60, JCT, Australia) -, AY724270, -, -, -, -, *Atalaya alata* (Sim) H.Forbes (Edwards KE228, JCT, South Africa) EU720425, EU720593, EU720748, EU720939, EU721036, EU721184, EU721372, EU721543; *Atalaya angustifolia* S.T.Reynolds (West 5349, ANH, Australia) -, EU720569, EU720723, -, -, EU721160, EU721348, -, *Atalaya capense* R.A.Dyer (Edwards KE509, JCT, South Africa) EU720429, -, EU720752, -, -, EU721188, EU721376, -, *Atalaya salicifolia* (DC.) Blume (Edwards KE58, JCT, Australia) -, AY724272, -, -, -, *Athya weinmannifolia* (Griseb.) Radlk. (Pennington 17581, MO, Peru) EU720487, EU720649, EU720824, EU720975, EU721086, EU721257, EU721445, EU721576; *Averrhoidium dalyi* Acev.-Rodr. & Ferrucci (Weckerle 00/03/18-1/1, Z, Peru) EU720495, -, EU720836, -, -, EU721268, EU721456, -, *Beguea apetala* Capuron (Buerki 149, NEU, Madagascar) EU720491, EU720652, EU720828, EU720978, EU721089, EU721261, EU721449, -, *Beguea apetala* Capuron (Vary 40, MO, Madagascar) EU720512, EU720663, EU720856, -, EU721100, EU721281, EU721469, -, *Billia* sp. (Hammel 20075, -, -) -, AY724275, -, -, -, -, *Blighia sapida* K.D.Koenig (Edwards KE86, JCT, West Africa) EU720416, EU720578, EU720733, EU720929, EU721026, EU721170, EU721358, EU721535; *Blighia unijugata* Baker (Edwards KE274, JCT, Tanzania) -, AY724276, -, -, -, -, *Blomia prisca* (Standl.) Lundell (Acevedo 12242, US, Mexico, Yucatán) EU720444, EU720611, EU720772, -, EU721050, EU721208, EU721396, -, *Bridgesia incisifolia* Bertero ex Cambess. (Killip & Pisano 39778, K, Chile) EU720476, EU720645, EU720811, EU720973, EU721082, EU721247, EU721435, -, *Cardiospermum grandiflorum* Sw. (Edwards KE207, JCT, -) -, EU720588, EU720743, EU720935, -, EU721179, EU721367, -, *Cardiospermum microcarpum* Kunth (Yuan s.n., NEU, China) -, -, EU720712, EU720911, -, EU721149, EU721338, -, *Cardiospermum* sp. (Yuan s.n., NEU, China) EU720399, -, EU720713, EU720912, -, EU721150, EU721339, -, *Castanospora alphanidii* (F.Muell.) F.Muell. (Edwards KE88, JCT, Australia) -, AY724279, -, -, -, -, *Chytranthus carneus* Radlk. (Chase 2868, RBG, -) EU720477, EU720646, EU720812, EU720974, EU721083, EU721248, EU721436, EU721575; *Chytranthus prieurianus* Baill. (Edwards KE272, JCT, Tanzania) -, AY724280, -, -, -, -, *Conchopetalum brachysepalum* Capuron (Rabarimanarivo 8, MO, Madagascar) EU720530, EU720680, EU720877, -, EU721117, EU721299, EU721487, EU721586; *Cossinia pinnata* Comm. ex Lam. (Lorence 4510, MO, Mauritius) -, -, EU720820, -, -, EU721253, EU721441, -, *Cubilia cubili* (Blanco) Adelb. (Chase 2125, K, Bogor, BG) EU720463, EU720631, EU720795, EU720964, EU721069, EU721231, EU721419, EU721567; *Cupania dentata* DC. (Acevedo 12241, US, Mexico, Yucatán) EU720523, EU720670, EU720867, EU720988, EU721107, EU721289, EU721477, EU721581; *Cupania guatemalensis* (Turcz.) Radlk. (Davidse 35743, MO, Belize) -, EU720678, EU720875, EU720993, EU721115, EU721297, EU721485, -, *Cupania hirsuta* Radlk. (Acevedo 1101, US, French Guiana) EU720521, EU720668, EU720865, -, EU721105, EU721287, EU721475, -, *Cupania rubiginosa* (Poir.) Radlk. (Mori 8868, MO, French Guiana) EU720481, -, EU720817, -, -, EU721251, EU721439, -, *Cupania scrobiculata* Rich. (Acevedo 11100, US, French Guiana) EU720524, EU720671, EU720868, EU720989, EU721108, EU721290, EU721478, -, *Cupaniopsis anacardioides* Radlk. (Chase 217, K, Australia) EU720438, EU720605, EU720763, EU720946, EU721045, EU721199, EU721387, EU721552; *Cupaniopsis flagelliformis* (Bailey) Radlk. (Edwards KE42, JCT, Australia) EU720432, EU720598, EU720755, EU720942, -, EU721191, EU721379, EU721547; *Cupaniopsis fruticosa* Radlk. (Munzinger 564, MO, New Caledonia) EU720533, -, EU720881, -, EU721119, EU721302, EU721490, -, *Cupaniopsis* sp. (Munzinger 710, MO, New Caledonia) EU720532, -, EU720880, EU720996, -, EU721301, EU721489, EU721587; *Cupaniopsis* sp. (Munzinger 1103, MO, New Caledonia) EU720507, EU720660, EU720851, -, EU721097, EU721278, EU721466, -, *Deinbollia borbonica* Scheff. (Edwards KE197, JCT, Tanzania) EU720412, EU720574, EU720729, -, -, EU721166, EU721354, EU721532; *Deinbollia macrocarpa* Capuron (Antilahimena 4293, MO, Madagascar) -, EU720626, EU720790, -, EU721064, EU721226, EU721414, EU721565; *Deinbollia macrocarpa* Capuron (H. Razafindraibe 118, MO, Madagascar) EU720535, EU720683, EU720883, -, EU721121, EU721304, EU721492, EU721589; *Deinbollia macrocarpa* Capuron (Buerki 144, NEU, Madagascar) EU720503, EU720656, EU720847, -, EU721093, EU721275, EU721463, -, *Deinbollia oblongifolia* (E.Mey. ex Arn.) Radlk. (Edwards KE233, JCT, South Africa) EU720427, EU720595, EU720750, -, -, EU721186, EU721374, EU721545; *Deinbollia pervillei* (Blume) Radlk. (Phillipson 5919, MO, Madagascar) EU720395, EU720560, EU720708, -, EU721012, EU721145, EU721334, -, *Deinbollia pervillei* (Blume) Radlk. (Callmander 688, MO, Madagascar) EU720514, -, EU720858, -, -, EU721283, EU721471, -, *Delavaya yunnanensis* Franch. (Forrest 20682, MO, China, Yunnan) EU720484, -, EU720821, -, -, EU721254, EU721442, -, *Diatenopterix sorbifolia* Radlk. (Zardini 43371, MO, Paraguay) EU720534, EU720682, EU720882, -, EU721120, EU721303, EU721491, EU721588; *Diatenopterix sorbifolia* Radlk. (Tressens 3504, K, Argentina) -, -, EU720810, -, -, EU721246, EU721434, -, *Dictyoneura obtusa* Blume (Edwards KE142, JCT, Australia) EU720428, -, EU720751, -, -, EU721187, EU721375, -, *Dilodendron bipinnatum* Radlk. (Acevedo 11129, US, Bolivia) -, EU720677, EU720874, -, EU721114, EU721296, EU721484, EU721584; *Dimocarpus australianus* Leenh. (Edwards KE34, JCT, Australia) EU720433, -, EU720757, -, -, EU721381, -, *Dimocarpus longan* Lour. (Yuan s.n., NEU, China) -, EU720563, EU720714, EU720913, EU721015, EU721151, EU721340, EU721521; *Dimocarpus longan* Lour. (Edwards KE502, JCT, Asia) -, EU720590, EU720745, -, -, EU721181, EU721369, -, *Dimocarpus longan* Lour. (-, -, Thailand) EF532337, -, -, -, -, *Dimocarpus longan* Lour. (Chase 1351, K, Bogor, BG) -, EU720615, EU720777, EU720953, EU721053, EU721213, EU721401, EU721559; *Diploglottis campbelli* Cheel (Chase 2048, K, Australian, BG) EU720457, EU720624, EU720788, EU720960, EU721062, EU721224, EU721412, -, *Diploglottis diphyllostegia* (F.Muell.) Radlk. (Edwards KE001, JCT, Australia) -, AY724287, -, -, -, -, *Mischarytera* sp. (Edwards KE159, JCT, Australia) EU720417, EU720579, EU720734, EU720930, EU721027, EU721171, EU721359, -, *Diploglottis smithii*

S.T.Reynolds (BG838, BBG, Australia) -, AY724288, -, -, -, -, -, -, -, -, *Diplokeleba floribunda* N.E.Br. (Acevedo 11130, US, Bolivia, St Cruz) -, -, EU720773, EU720950, -, EU721209, EU721397, -, *Diplopeltis huegelii* Endl. (Chase 2192, K, Australia) EU720473, EU720642, EU720807, EU720971, EU721079, EU721243, EU721431, -, *Dipterionia sinensis* Oliv. (Chase 502, RBG, -) EU720445, EU720612, EU720774, -, -, EU721210, EU721398, -, *Dodonaea lanceolata* F.Muell. (Edwards KE120, JCT, Australia) -, AY724290, -, -, -, -, -, -, -, *Dodonaea madagascariensis* Radlk. (Bocksberger GB028, NEU, Madagascar) EU720518, -, EU720862, EU720984, -, EU721284, EU721472, -, *Dodonaea viscosa* Jacq. (Razafitsalama 956, MO, Madagascar) EU720519, EU720666, EU720863, EU720985, EU721103, EU721285, EU721473, -, *Dodonaea viscosa* Jacq. (Merello 1077, MO, Peru) EU720536, EU720684, EU720884, EU720997, EU721122, EU721305, EU721493, -, *Dodonaea viscosa* Jacq. (Yuan s.n., NEU, China) EU720406, EU720567, EU720721, EU720920, EU721019, EU721158, EU721347, -, *Doratoxylon chouxii* Capuron (Labat JNL3543, P, Madagascar) EU720394, EU720559, EU720707, EU720908, EU721011, EU721144, EU721333, -, *Doratoxylon chouxii* Capuron (Callmander 679, MO, Madagascar) EU720513, EU720664, EU720857, -, EU721101, EU721282, EU721470, -, *Elatostachys apetala* Radlk. (Munzinger 692, MO, New Caledonia) EU720537, EU720685, EU720885, EU720998, EU721123, EU721306, EU721494, EU721590; *Elatostachys apetala* Radlk. (McPherson 18184, MO, New Caledonia) EU720538, EU720686, EU720886, EU720999, EU721124, EU721307, EU721495, EU721591; *Elatostachys megalantha* S.T.Reynolds (Irvine IRV507, CSIRO, Atherton) -, EU720609, EU720768, -, EU721048, EU721204, EU721392, -, *Elatostachys microcarpa* S.T.Reynolds (Edwards KE98, JCT, Australia) EU720409, EU720571, EU720726, -, -, EU721163, EU721351, -, *Elatostachys nervosa* (F.Muell.) Radlk. (Chase 2022, K, Australian, BG) EU720455, EU720622, EU720786, EU720959, EU721060, EU721222, EU721410, EU721563; *Elatostachys* sp. (Lowry 5650A, MO, New Caledonia) EU720529, EU720679, EU720876, EU720994, EU721116, EU721298, EU721486, EU721585; *Eriocoleum kerstingii* Gilg ex Engl. (Merello 1586, MO, Ghana) EU720539, EU720687, EU720887, EU721000, EU721125, EU721308, EU721496, EU721592; *Eriocoleum mespermum* Radlk. (Bradley 1025, MO, Gabon) EU720540, EU720688, EU720888, EU721001, EU721126, EU721309, EU721497, EU721593; *Erythrophylla aesculana* Baill. (Randrianasolo 625, MO, Madagascar) -, -, -, -, -, EU721329, -, -, *Euphorianthus longifolius* Radlk. (Chase 2126, K, Bogor, BG) EU720464, -, EU720796, -, -, EU721232, EU721420, -, *Eurycorymbus cavalerieri* (H.Lév.) Rehder & Hand.-Mazz. (Yuan s.n., NEU, China) EU720404, EU720565, EU720719, EU720918, EU721017, EU721156, EU721345, EU721526; *Filicium decipiens* (Wight & Arn.) Thwaites (Chase 2128, K, Bogor, BG) EU720466, EU720633, EU720798, -, -, EU721234, EU721422, -, *Filicium longifolium* (H.Perrier) Capuron (Rabentanandro 1113, MO, Madagascar) EU720541, -, EU720889, -, -, EU721310, EU721498, -, *Filicium thouarsianum* (A.DC.) Capuron (Antilahimena 5021, MO, Madagascar) EU720493, -, EU720832, -, -, EU721265, EU721453, -, *Ganophyllum falcatum* Blume (Chase 2129, K, Bogor, BG) EU720467, EU720634, EU720799, -, EU721071, EU721235, EU721423, -, *Ganophyllum falcatum* Blume (BH9269, CSIRO, Australia) -, -, -, -, -, EU721330, -, -, *Glennia pervillei* (Baill.) Leenh. (Andriamihajarivo 1053, MO, Madagascar) EU720490, EU720651, EU720827, EU720977, EU721088, EU721260, EU721448, -, *Glennia pervillei* (Baill.) Leenh. (Andriamihajarivo 1025, MO, Madagascar) -, EU720653, EU720829, -, EU721090, EU721262, EU721450, -, *Gongrodiscus bilocularis* H.Turner (Munzinger 749, MO, New Caledonia) EU720542, EU720689, EU720890, -, EU721127, EU721311, EU721499, -, *Guindilia trinervis* Gilles ex Hook. (Chase 802, K, Chile) -, EU720613, EU720775, EU720951, EU721051, EU721211, EU721399, EU721557; *Guioa acutifolia* Radlk. (Edwards KE14, JCT, Australia) -, AY724297, -, -, -, -, -, -, *Guioa glauca* Radlk. (McPherson 18230, MO, New Caledonia) EU720545, EU720692, EU720893, -, EU721130, EU721315, EU721503, -, *Guioa lasoneura* Radlk. (BG1888, BBG, Australia) -, AY724298, -, -, -, -, -, -, *Guioa microsepala* Radlk. (Munzinger 744, MO, New Caledonia) EU720546, EU720693, EU720894, -, EU721131, EU721316, EU721504, EU721596; *Guioa semiglaucula* (F.Muell.) Radlk. (Chase 2058, K, Australia, BG) EU720458, EU720625, EU720789, -, EU721063, EU721225, EU721413, -, *Guioa villosa* Radlk. (McPherson 18040, MO, New Caledonia) EU720544, EU720691, EU720892, EU721003, EU721129, EU721314, EU721502, EU721595; *Guioa* sp. (Munzinger 945, MO, New Caledonia) EU720505, EU720658, EU720849, -, EU721095, EU721277, EU721465, -, *Handeliendron bodinieri* (H.Lév.) Rehder (*QYXiang* 302 / *C. Ming* 050923, -, -), AY724299, -, -, -, EF186776, -, -, *Haplocoelopsis africana* F.G.Davies (Edwards KE276, JCT, Tanzania) EU720441, EU720608, EU720767, EU720949, -, EU721203, EU721391, EU721555; *Haplocoelum foliosum* (Hiern) Bullock (Friis 1894, MO, Ethiopia) EU720479, -, EU720815, -, -, EU721250, EU721438, -, *Haplocoelum foliosum* subsp. *foliosum* (Hiern) Bullock (Edwards KE195, JCT, Tanzania) EU720410, EU720572, EU720727, EU720924, -, EU721164, EU721352, EU721530; *Haplocoelum gallaense* (Engl.) Radlk. (Edwards KE501, JCT, South Africa) -, EU720583, -, -, -, -, -, *Haplocoelum perrieri* Capuron (Rakotomalaza 1165, MO, Madagascar) EU720396, -, EU720709, EU720909, -, EU721146, EU721335, EU721519; *Harpullia arborea* (Blanco) Radlk. (Chase 1353, K, Bogor, BG) EU720448, -, EU720779, -, -, EU721215, EU721403, -, *Harpullia cupanioides* Roxb. (-, -, -) AY2075669, -, -, -, -, -, -, *Harpullia rhyticarpa* C.White & Francis (Edwards KE003, JCT, -), AY724303, -, -, -, -, -, -, *Hippobromus pauciflorus* Radlk. (Edwards KE229, JCT, -), AY724305, -, -, -, -, -, *Hypelate trifoliata* Sw. (R. Rankin HAJ72057, K, -) -, -, -, -, -, -, *Jagera javanica* (Blume) Blume ex Kalkman (Chase 2130, K, Bogor, BG) EU720468, EU720635, EU720800, -, EU721072, EU721236, EU721424, EU721569; *Jagera javanica* subsp. *australiana* Leenh. (Edwards KE178, JCT, Australia) EU720442, -, EU720769, -, -, EU721205, EU721393, EU721556; *Jagera pseudorhus* var. *pseudorhus* f. *pilosiuscula* Radlk. (Edwards KE41, JCT, Australia) -, EU720606, EU720764, EU720947, EU721046, EU721200, EU721388, EU721553; *Koelreuteria paniculata* Laxm. (Harder 5668, MO, Vietnam) EU720548, EU720695, EU720896, -, EU721133, EU721318, EU721506, -, *Koelreuteria paniculata* Laxm. (Yuan CN2006-3, NEU, China) EU720397, EU720561, EU720710, -, EU721013, EU721147, EU721336, EU721520; *Koelreuteria paniculata* Laxm. (Wilson 1476, RBG, -), AY724308, -, -, -, -, -, -, *Koelreuteria* sp. (Harder 5724, MO, Vietnam) EU720547, EU720694, EU720895, EU721004, EU721132, EU721317, EU721505, -, *Laccodiscus klaineanus* Pierre ex Engl. (Walters 1269, MO, Gabon) EU720549, EU720696, EU720897, -, EU721134, EU721319, EU721507, -, *Lecaniodiscus fraxinifolius* Baker (Edwards KE194, JCT, Tanzania) EU720418, EU720580, EU720735, EU720931, EU721028, EU721172, EU721360, EU721536; *Lepiderema hirsuta* S.T.Reynolds (Edwards KE36, JCT, Australia) EU720435, EU720601, EU720759, -, EU721041, EU721195, EU721383, EU721549; *Lepiderema pulchella* Radlk. (Chase 2020, K, Australian, BG) EU720454, -, EU720785, EU720958, -, EU721221, EU721409, -, *Lepidopetalum fructoglabrum* Welzen (Edwards KE139, JCT, Australia) EU720408, -, EU720724, EU720922, -, EU721161, EU721349, EU721528; *Lepisanthes alata* (Blume) Leenh. (Chase 1355, K, Bogor, BG) EU720450, EU720618, EU720781, -, EU721056, EU721217, EU721405, -, *Lepisanthes feruginea* (Radlk.) Leenh. (Chase 1354, K, Bogor, BG) EU720449, EU720617, EU720780, -, EU721055, EU721216, EU721404, -, *Lepisanthes rubiginosa* (Roxb.) Leenh. (Chase 1350, K, Bogor, BG) EU720446, EU720614, EU720776, EU720952, EU721052, EU721212, EU721400, EU721558; *Lepisanthes senegalensis* (Poir.) Leenh. (Callmander 627, MO, Madagascar) EU720492, EU720654, EU720830, EU720979, EU721091, EU721263, EU721451, EU721577; *Litchi chinensis* Sonn. (Yuan s.n., NEU, China) EU720400, EU720564, EU720715, EU720914, EU721016, EU721152, EU721341, EU721522; *Llagunoa mollis* Kunth (*Jaramilloleja* 3199, MO, Colombia) EU720482, -, EU720818, -, -, EU721252, EU721440, -, *Llagunoa nitida* Ruiz & Pav. (Pennington 17552, MO, Peru) EU720486, -, EU720823, -, -, EU721256, EU721444, -, *Loxodiscus coriaceus* Hook.f. (Bradford 1136, MO, New Caledonia) EU720488, -, EU720825, -, -, EU721258, EU721446, -, *Macphersonia chapelierii* (Baill.) Capuron (Buerki 138, NEU, Madagascar) EU720459, EU720627, EU720791, EU720961, EU721065, EU721227, EU721415, EU721566; *Macphersonia gracilis* O.Hoffm. (Rabentanandro 1081, MO, Madagascar) EU720550, EU720697, EU720898, EU721005, EU721135, EU721320, EU721508, EU721597; *Magonia pubescens* A.St.-Hil. (Mori 16966, MO, Brazil) EU720483, -, EU720819, -, -, -, -, -, *Majidea zanguebarika* Kirk ex Oliv. (TH275, MO, Madagascar) EU720552, -, EU720900, EU721006, -, EU721322, EU721510, -, *Matayba apetala* Radlk. (Acevedo 11929, US, Jamaica) EU720526, EU720674, EU720871, -, EU721111, EU721293, EU721481, EU721583; *Matayba* cf. *opaca* Radlk. (Acevedo 11118, US, French Guiana) EU720522, EU720669, EU720866, EU720987, EU721106, EU721288, EU721476, EU721580; *Matayba domingensis* (DC.) Radlk. (Taylor 11819, MO, Caribbean) EU720551, EU720698, EU720899, -, EU721136, EU721321, EU721509, EU721598; *Matayba elaeagnoides* Radlk. (Zardini 43278, MO, Paraguay) EU720553, EU720699, EU720901, -, EU721137, EU721323, EU721511, -, *Matayba guianensis* Aubl. (Acevedo 12342, US, French Guiana) EU720527, EU720675, EU720872, -, EU721112, EU721294, EU721482, -, *Matayba laevigata* Radlk. (Acevedo 12357, US, French Guiana) EU720528, EU720676, EU720873, EU720992, EU721113, EU721295, EU721483, -, *Melicoccus bijugatus* Jacq. (Acevedo s.n., US, Puerto Rico) EU927391, EU720610, EU720771, -, EU721049, EU721207, EU721395, -, *Melicoccus lepidopetalus*

Radlk. (*Acevedo* 11128, US, Bolivia) EU720443, -, EU720770, -, -, EU721206, EU721394, -; *Mischarytera lautereriana* (F.M.Bailey) H.Turner (*Edwards* KE1302, JCT, Australia) -, -, EU720742, -, -, -, -, -; *Mischarytera macrobotrys* (Merr. & L.M.Perry) H.Turner (BH6631, CSIRO, Australia) -, AY724313, -, -, -, -, -, -; *Mischarytera* sp. (*Edwards* KE159, JCT, Australia) EU720417, EU720579, EU720734, EU720930, EU721027, EU721171, EU721359, -; *Mischocarpus exangulatus* (F.Muell.) Radlk. (*Edwards* KE30, JCT, Australia) EU720434, EU720600, EU720758, EU720943, EU721040, EU721194, EU721382, -; *Mischocarpus grandissimus* Radlk. (*Edwards* KE37, JCT, Australia) EU720437, EU720604, EU720762, EU720945, EU721044, EU721198, EU721386, EU721551; *Mischocarpus pentapetalus* (Roxb.) Radlk. (*Chase* 2133, K, Bogor, BG) EU720470, EU720637, EU720802, EU720966, EU721074, EU721238, EU721426, EU721571; *Mischocarpus pyriformis* (F.Muell.) Radlk. (*Chase* 2059, K, Australian, BG) EU720460, EU720628, EU720792, -, EU721066, EU721228, EU721416, -; *Molinia petiolaris* Radlk. (*Rabenantandro* 1448, MO, Madagascar) EU720554, EU720700, EU720902, EU721007, EU721138, EU721324, EU721512, -; *Molinia* sp. nov. (*Antilahimena* 4301, MO, Madagascar) EU720510, EU720662, EU720854, EU720983, EU721099, EU721280, EU721468, EU721578; *Neotina coursii* Capuron (*H. Razafindraibe* 119, MO, Madagascar) EU720543, EU720690, EU720891, EU721002, EU721128, EU721313, EU721501, EU721594; *Nephelium lappaceum* L. (*Edwards* KE222, JCT, Asia) -, EU720584, EU720738, EU720932, EU721030, EU721175, EU721363, EU721537; *Nephelium lappaceum* L. (*Yuan* s.n., NEU, China) EU720401, -, EU720716, EU720915, -, EU721153, EU721342, EU721523; *Nephelium mutabile* Blume (*Chase* 2134, K, Bogor, BG) -, AY724316, -, -, -, -, -, -; *Pancovia golungensis* (Hiern) Exell & Mendonça (*Edwards* KE231, JCT, Tanzania) EU720411, EU720573, EU720728, EU720925, EU721022, EU721165, EU721353, EU721531; *Pappea capensis* Eckl. & Zeyh. (*Edwards* KE232, JCT, South Africa) EU720424, EU720592, EU720747, EU720938, EU721035, EU721183, EU721371, EU721542; *Paranephelium macrophyllum* King (*Chase* 1356, K, Bogor, BG) EU720451, EU720619, EU720782, EU720955, EU721057, EU721218, EU721406, -; *Paranephelium xestophyllum* Miq. (*Edwards* KE503, JCT, Asia) EU720421, EU720582, EU720737, -, EU721029, EU721174, EU721362, -; *Paullinia alata* subsp. *alata* G.Don (*Weckerle* 00/03/09-2/1, Z, Peru) -, -, EU720834, -, -, -, -, -; *Paullinia elegans* Cambess. (*Weckerle* 00/05/27-1/1, Z, Peru) -, -, EU720835, -, -, EU721267, EU721455, -; *Paullinia eriocarpa* Triana & Planch. (*Weckerle* 00/06/13-1/5, Z, Peru) EU720497, -, EU720839, -, -, -, -, -; *Paullinia faginea* (Triana & Planch.) Radlk. (*Weckerle* 00/05/27-1/5, Z, Peru) -, -, EU720837, -, -, -, -, -; *Paullinia faginea* (Triana & Planch.) Radlk. (*Weckerle* 00/06/13-1/3, Z, Peru) EU720496, -, EU720838, -, -, -, -, -; *Paullinia pachycarpa* Benth. (*Weckerle* 01/01/26-1/1, Z, Peru) EU720500, -, EU720842, -, -, -, -, -; *Paullinia pinnata* L. (*Edwards* KE199, JCT, Tanzania) EU720413, EU720575, EU720730, EU720926, EU721023, EU721167, EU721355, -; *Paullinia subauriculata* Radlk. (*Weckerle* 00/03/19-1/1, Z, Peru) EU720494, -, EU720833, -, -, EU721266, EU721454, -; *Plagioscyphus* aff. *louvelii* Danguy & Choux (*Lowry* 6034, MO, Madagascar) EU720555, EU720701, EU720903, EU721008, EU721139, EU721325, EU721513, EU721599; *Plagioscyphus unijugatus* Capuron (*Buerki* 145, NEU, Madagascar) EU720475, EU720644, EU720809, EU720972, EU721081, EU721245, EU721433, EU721574; *Podonephelium homei* Radlk. (*McPherson* 18156, MO, New Caledonia) -, -, -, -, -, EU721312, EU721500, -; *Podonephelium homei* Radlk. (*Pillon* 156, MO, New Caledonia) EU720489, EU720650, EU720826, EU720976, EU721087, EU721259, EU721447, -; *Pometia pinnata* J.R.Forst. & G.Forst. (*Chase* 2135, K, Bogor, BG) EU720471, EU720638, EU720803, EU720967, EU721075, EU721239, EU721427, EU721572; *Pometia pinnata* J.R.Forst. & G.Forst. (*Yuan* s.n., NEU, China) EU720402, -, EU720717, EU720916, -, EU721154, EU721343, EU721524; *Pseudima* sp. (*McPherson* 15867, MO, Panama) EU720556, EU720702, EU720904, EU721009, EU721140, EU721326, EU721514, EU721600; *Pseudopteris decipiens* Baill. (*Kakazomanjary* 12529-SF, MO, Madagascar) EU720480, -, EU720816, -, -, -, -, -; *Rhysotoechia mortoniana* (F.Muell.) Radlk. (*Edwards* KE117, JCT, Australia) EU720414, EU720576, EU720731, EU720927, EU721024, EU721168, EU721356, EU721533; *Rhysotoechia robertsonii* (F.Muell.) Radlk. (*Edwards* KE277, JCT, Australia) -, EU720570, EU720725, EU720923, EU721021, EU721162, EU721350, EU721529; *Sapindus oligophyllus* Merr. & Chun (*Yuan* s.n., NEU, China) EU720407, EU720568, EU720722, EU720921, EU721020, EU721159, -, -, -; *Sapindus saponaria* L. (*Chase* 2136, K, Bogor, BG) -, EU720639, EU720804, EU720968, EU721076, EU721240, EU721428, -; *Sapindus trifoliatus* L. (*Edwards* KE504, JCT, Asia) -, EU720586, EU720740, EU720934, EU721032, EU721177, EU721365, EU721538; *Sarcopteryx martyana* (F.Muell.) Radlk. (*Irvine* IRV1810, CSIRO, Australia) EU720426, EU720594, EU720749, EU720940, EU721037, EU721185, EU721373, EU721544; *Sarcopteryx reticulata* S.T.Reynolds (*Gray* BG1137, CSIRO, Australia) EU720421, EU720587, EU720741, -, EU721033, EU721178, EU721366, EU721539; *Sarcopteryx* sp. (*Edwards* KE49, JCT, Australia) EU720439, EU720607, EU720765, EU720948, EU721047, EU721201, EU721389, EU721554; *Sarcotoechia serrata* S.T.Reynolds (*Edwards* KE31, JCT, Australia) EU720436, EU720603, EU720761, EU720944, EU721043, EU721197, EU721385, EU721550; *Sarcotoechia villosa* S.T.Reynolds (*Edwards* KE102, JCT, Australia) EU720419, EU720581, EU720736, -, -, EU721173, EU721361, -; *Schleichera oleosa* (Lour.) Oken (*Chase* 2137, K, Bogor, BG) EU720423, EU720591, EU720746, EU720937, -, EU721182, EU721370, EU721541; *Scyphonichium* cf. *multiflorum* (Mart.) Radlk. (*Acevedo* 11102, US, French Guiana) -, EU720672, EU720869, EU720990, EU721109, EU721291, EU721479, -; *Serjania altissima* (Poepp.) Radlk. (*Weckerle* 00/07/02-1/4, Z, Peru) EU720498, -, EU720840, -, -, EU721269, EU721457, -; *Serjania communis* Cambess. (*Chase* 2138, K, Bogor, BG) EU720472, EU720640, EU720805, EU720969, EU721077, EU721241, EU721429, -; *Serjania glabrata* Kunth (*Merello* 1058, MO, Peru) EU720557, EU720703, EU720905, EU721010, EU721141, EU721327, EU721515, -; *Serjania mexicana* (L.) Willd. (*Davidse* 35748, MO, Belize) -, EU720704, EU720906, -, EU721142, -, -, -, -; *Serjania triquetra* Radlk. (-, -, -) AY207571, -, -, -, -, -, -; *Smelophyllum capense* Radlk. (*Edwards* KE506, JCT, South Africa) -, AY724330, -, -, -, -, -, -; *Stadmannia oppositifolia* (Lam.) Poir. (*Edwards* KE505, JCT, Madagascar) -, AY724331, -, -, -, -, -, -; *Storthocalyx leioneurus* Radlk. (*Munzinger* 1100, MO, New Caledonia) EU720506, EU720659, EU720850, -, EU721096, -, -, -; *Storthocalyx* sp. (*Munzinger* 960, MO, New Caledonia) EU720504, EU720657, EU720848, -, EU721094, EU721276, EU721464, -; *Synima cordieri* (F.Muell.) Radlk. (*Edwards* KE29, JCT, Australia) -, EU720602, EU720760, -, EU721042, EU721196, EU721384, -; *Synima macrophylla* S.T.Reynolds (*Edwards* KE19, JCT, Australia) EU720430, EU720596, EU720753, EU720941, -, EU721189, EU721377, EU721546; *Talisia angustifolia* Radlk. (*Zardini* 43668, MO, Paraguay) EU720558, EU720705, EU720907, -, EU721143, EU721328, EU721516, -; *Talisia nervosa* Radlk. (*Pennington* 628, MO, -) EU720474, EU720643, EU720808, -, EU721080, EU721244, EU721432, -; *Talisia obovata* A.C.Sm. (*R. Lombello* 13, MO, Brazil) EU720485, EU720648, EU720822, -, EU721085, EU721255, EU721443, -; *Thouinia acuminata* S.Watson (*Liston* 633-2, MO, Mexico, Jalisco) EU720478, EU720647, EU720814, -, EU721084, EU721249, EU721437, -; *Tina isaloensis* Drake (*Ranirison* PR827, G, Madagascar) EU720520, EU720667, EU720864, EU720986, EU721104, EU721286, EU721474, EU721579; *Tina striata* Radlk. (*Vary* 45, MO, Madagascar) EU720509, EU720661, EU720853, -, EU721098, EU721279, EU721467, -; *Tinopsis apiculata* Radlk. (*Buerki* 131, NEU, Madagascar) EU720422, EU720589, EU720744, EU720936, EU721034, EU721180, EU721368, EU721540; *Toechima daemelianum* Radlk. (JC66, CSIRO, Australia) -, AY724334, -, -, -, -, -, -; *Toechima erythrocarpum* (F.Muell.) Radlk. (*Edwards* KE20, JCT, Australia) EU720431, EU720597, EU720754, -, EU721038, EU721190, EU721378, -; *Toechima plurinerve* Radlk. (*Chase* 1357, K, Bogor, BG) EU720452, EU720620, EU720783, EU720956, EU721058, EU721219, EU721407, EU721561; *Toechima tenax* (Cunn. ex Benth.) Radlk. (*Chase* 2046, K, Australian, BG) EU720456, EU720623, EU720787, -, EU721061, EU721223, EU721411, EU721564; *Toechima tenax* (Cunn. ex Benth.) Radlk. (*Chase* 2132, K, Bogor, BG) EU720469, EU720636, EU720801, EU720965, EU721073, EU721237, EU721425, EU721570; *Tristira triptera* (Blanco) Radlk. (*Chase* 2139, K, Asia) -, EU720585, EU720739, EU720933, EU721031, EU721176, EU721364, -; *Tristiropsis acutangula* Radlk. (*Chase* 1358, K, Bogor, BG) EU720453, EU720621, EU720784, EU720957, EU721059, EU721220, EU721408, EU721562; *Ungnadia speciosa* Endl. (*Chase* 2854, RBG, -) -, EU720706, -, -, -, EU721332, EU721518, -; *Urvillea ulmaceae* Kunth (*Weckerle* 00/07/05-1/1, Z, Peru) EU720499, EU720655, EU720841, -, EU721092, EU721270, EU721458, -; *Vouaranea guianensis* Aubl. (*Lucas* 109, MO, French Guiana) EU720525, EU720673, EU720870, EU720991, EU721110, EU721292, EU721480, EU721582; *Xanthocera sorbifolius* Bunge (*Yuan* CN2006, NEU, China) EU720398, EU720562, EU720711, EU720910, EU721014, EU721148, EU721337, -; *Xerospermum noronhianum* (Blume) Blume (*Chase* 2130, K, Bogor, BG) -, EU720641, EU720806, EU720970, EU721078, EU721242, EU721430, EU721573; **Outgroups:** *Sorindeia* sp. (*Buerki* 137, NEU, Madagascar) -, -, EU720831, -, -, EU721264, EU721452, -; *Harrisonia abyssinica* Oliv. (*Edwards* KE510, JCT, Tanzania) EU720440, -, EU720766, -, -, EU721202, EU721390, -; *Malleastrum* sp. (*Rakotovo* 2609, MO, Madagascar) -, -, EU720878, EU720995, -, EU721300, EU721488, -.