Systematic Botany (2017), 42(4): pp. 680–693

DOI 10.1600/036364417X696456
Date of publication December 18, 2017

Systematics of New World *Maytenus* (Celastraceae) and a New Delimitation of the Genus

Leonardo Biral,[1,2,6] Mark P. Simmons,[3,6] Eric C. Smidt,[4] Luke R. Tembrock,[3] Mônica Bolson,[1] Robert H. Archer,[5] and Julio A. Lombardi[1]

[1]Departamento de Botânica, Instituto de Biociências de Rio Claro, Universidade Estadual Paulista – UNESP, Av. 24-A 1515 – Bela Vista, Caixa Postal 199, Rio Claro, São Paulo, Brazil
[2]Current address: Universidade Tecnológica Federal do Paraná – UTFPR, Prolongamento da Rua Cerejeira, s/n, Bairro São Luiz, 85892-000, Santa Helena, Paraná, Brazil
[3]Department of Biology, Colorado State University, Fort Collins, Colorado 80523-1878, U. S. A.
[4]Departamento de Botânica, Universidade Federal do Paraná – UFPR, Centro Politécnico, 81531-970, Caixa Postal 19031, Curitiba, Paraná, Brazil
[5]South African National Biodiversity Institute, National Herbarium, Private Bag X101, Pretoria, 0001, Republic of South Africa
[6]Authors for correspondence (leobiral@hotmail.com; psimmons@rams.colostate.edu)

Communicating Editor: Ricarda Riina

Abstract—*Maytenus* species are distributed in the New World from Argentina to the U. S. A. The genus delimitation has been controversial, especially in relation to the inclusion of *Gymnosporia*. *Maytenus* has been treated in a broad sense such that it was considered widely distributed in tropics and subtropics worldwide. Even in its current restricted circumscription, the genus remains paraphyletic with *Fraunhofera* and *Plenckia* nested within it. We increased taxon sampling relative to previous studies and sampled species representing the greatest morphological diversity from throughout the geographic distribution in order to confidently delimit monophyletic genera. The phylogeny was inferred using nuclear (ITS and 26S rDNA) and plastid (*matK* and *trnL-F*) gene regions together with morphological characters. The species currently recognized as *Maytenus* were resolved in three distinct clades. Delimitation of a single large genus, by including *Fraunhofera* and *Plenckia* within *Maytenus*, would result in a morphologically heterogeneous group. Instead we segregated *Maytenus* into two genera, re-established *Tricerma*, and maintain *Fraunhofera* and *Plenckia* as distinct genera. All of these genera are morphologically distinct from each other, primarily based on fruit characters. A total of 123 new combinations under the generic name *Monteverdia* are provided for species in the clade that does not contain the type of *Maytenus*.

Keywords—Celastroideae, *Fraunhofera*, *Monteverdia*, *Plenckia*, *Tricerma*, *Viposia*.

As circumscribed by McKenna et al. (2011), *Maytenus* Molina (Celastraceae) comprises ca. 140 species distributed from the southern United States (*Maytenus phyllanthoides* Benth.) to Tierra del Fuego, Argentina (*M. boaria* Molina, *M. disticha* (Hook. f.) Urb., and *M. magellanica* (Lam.) Hook. f.) (Biral et al. 2015). Within this area, the genus occurs in a broad diversity of vegetation types from sea level up to 3,900 m, as reported for *M. verticillata* (Ruiz & Pav.) DC. in the Andean mountains of Ecuador (Biral and Lombardi 2016). In addition to various types of tropical forests and savannas, some species are distributed in dry and wet chacos, deciduous and dry forests, swamps, rocky fields and outcrops, and paramos. The greatest species diversity is encountered in Brazil, with 49 species, including 36 endemics (BFG 2015).

The delimitation of *Maytenus* has been long debated particularly regarding the merger/segregation of species from *Gymnosporia* (Wight & Arn.) Hook. f. (Loesener 1942; Brenan 1953; Exell 1953; Ding Hou 1955, 1962; Sebsebe Demissew 1985; Jordaan and van Wyk 1999, 2003; McKenna et al. 2011) and, more recently, from *Fraunhofera* Mart. and *Plenckia* Reissek (Simmons et al. 2012; Groppo et al. 2014).

Loesener (1942) delimited *Gymnosporia* as Old World species with thorns and/or brachyblasts and fasciculate leaves, while similar plants that are unarmed with spiral or distichous (but not fasciculate) leaves were assigned to *Maytenus*. Loesener (1942) transferred several species from *Gymnosporia* to *Maytenus* based on these morphological distinctions (Sebsebe Demissew 1985). Brenan (1953) and Exell (1953) asserted that Loesener's (1942) proposal was artificial and opted to treat both genera in a broadly circumscribed *Maytenus*. Ding Hou (1955, p. 216) considered *Celastrus* L., *Gymnosporia*, and *Maytenus* to be closely related genera, but distinct by "several characters taken together and not any one single character." However, several character states are shared among the genera, and Ding Hou (1962) later changed his view about the differences between *Maytenus* and *Gymnosporia* by asserting that the characters he had previously considered were insufficient to separate them. Ding Hou (1962) retained *Celastrus* and *Maytenus* (including *Gymnosporia*) as different genera based on habit, degree of adnation of ovary and disc, and fruit structure. Sebsebe Demissew (1985) affirmed that Loesener's (1942) genera formed natural groupings, but asserted that they were not sufficiently distinct to be treated as separate genera. *Gymnosporia* was later re-established as a distinct genus by Jordaan and van Wyk (1999) based on the presence of thorns, brachyblasts, and the degree of aril coverage. We refer to the fleshy outgrowths on the seed surface as arils following Endress (1973), but based on the ontogenetic criterion applied by Zhang et al. (2011, 2014) these structures would be recognized as caruncles.

Phylogenetic analyses based on molecular and morphological data showed that the broadly circumscribed *Maytenus* is severely polyphyletic (Simmons et al. 2008; McKenna et al. 2011). Simmons et al. (2008) showed that *Maytenus* from the New and Old Worlds were independently derived from different lineages, with a third lineage representing the Austral-Pacific species. Therefore, *Maytenus* was redefined and the genus is now exclusive to the New World with the incorporation of *Moya* Griseb. and *Tricerma* Liebm. (i.e. *Maytenus* sensu McKenna et al. 2011). Species from the Old World previously included in *Maytenus* were transferred or recognized in the segregate genera *Denhamia* Meisn. and *Gymnosporia*, and the Neotropical *Gymnosporia* species are now treated as the genus *Haydenoxylon* M.P. Simmons (McKenna et al. 2011; Simmons and Barrie 2014). The African species of *Maytenus* remain the most challenging group with respect to species and generic delimitation (McKenna et al. 2011). New combinations for these African species are currently being drafted (R. H. Archer et al. in prep.).

Despite recognition of these segregate genera, New World *Maytenus* remains a polyphyletic group, and its delimitation needs to be revised in order to define natural genera and resolve the position of *Fraunhofera* and *Plenckia* (Simmons et al. 2012; Groppo et al. 2014). *Fraunhofera* and *Plenckia* were resolved as a clade nested within New World *Maytenus* by Simmons et al. (2012). Simmons et al. (2012) and Groppo et al. (2014) provided some comments about the relationship among these clades, but did not resolve the taxonomic problem.

As currently delimited, *Maytenus* (sensu McKenna et al. 2011) is characterized by having flattened or carinate young twigs; alternate leaves with crenate, spinose, or entire margins; fasciculate or cymose inflorescences that may be reduced to a single flower; a conspicuous intrastaminal disc with five (rarely four) flattened stamens inserted externally; and membranaceous or coriaceous capsules that open by two or three valves, with one to three (rarely four) seeds that are each enveloped entirely or partialy by a white, red, or yellowish aril. Two species are exceptions: *Maytenus megalocarpa* Groppo & Lombardi has considerably larger fruits that are tardily dehiscent, open by two upright valves, and contain four unusually large seeds, each of which is completely covered by a thick, fleshy aril (Groppo et al. 2014); and *Maytenus grisea* Lundell has distinctive inflated thin-walled capsules (Lundell 1972), which are more similar to fruits of *Haydenoxylon*, and might be misplaced within *Maytenus*. Because most *Maytenus* species have rather uniform reproductive structures, vegetative characters are often more important than reproductive characters for species identification (Steyermark 1988). Important species-identification characters include the presence of indumentum and lenticels, shape of young branches, thorns on branches, spinose leaf margins, and prominence of leaf venation.

Loesener (1942) proposed two *Maytenus* subgenera: *Maytenus* subg. *Pseudocelastrus* Loes., consisting of Australian species, and *Maytenus* subg. *Maytenus*, with the remaining species. He divided *Maytenus* subg. *Maytenus* into 15 sections, based mainly on vegetative characters. With the exception of *Maytenus* sect. *Oxyphylla*, which is defined as all species with spinose leaf margins, no other section from the New World is clearly diagnosed by a unique morphological character state. Therefore, Carvalho-Okano (1992) rejected some of these sections, placed *Maytenus* sects. *Coriifolia*, *Leptophylla*, *Microphylla*, *Pachyphylla*, and *Theoides* into *Maytenus* sect. *Maytenus*, and transferred *Maytenus macrophylla* Mart. from *Maytenus* sect. *Leptophylla* to *Maytenus* sect. *Oxyphylla*. However, both Loesener's (1942) and Carvalho-Okano's (1992) intrageneric classifications are polyphyletic based on McKenna et al.'s (2011) morphology- and molecular-based phylogeny. Spinose leaf margins appear to be a convergent character state given that *Maytenus* sect. *Oxyphylla* is polyphyletic (McKenna et al. 2011; Groppo et al. 2014).

The inclusion of *Fraunhofera* and *Plenckia* in *Maytenus* was initially suggested by Simmons et al. (2012) given that these two genera are nested within *Maytenus* in their inferred phylogeny. The clade *Fraunhofera* + *Plenckia* is well supported (96% parsimony jackknife [JK], 98% likelihood bootstrap [BS]), and synapomorphies include the presence of cupular or columnar nectar discs (Simmons et al. 2012) and indehiscent fruits (Groppo et al. 2014). In order to recognize only monophyletic groups, *Fraunhofera* and *Plenckia* must be synonymized with *Maytenus*, or *Maytenus* must be segregated into two genera with Lundell's (1971) *Tricerma* also being recognized as a distinct genus (Simmons et al. 2012). The nesting of *Fraunhofera* and *Plenckia* within *Maytenus* was unexpected because they are highly divergent from both *Maytenus* and each other with respect to their leaves, inflorescence types, and fruits. However, the close relationship of *Fraunhofera*, *Maytenus*, *Plenckia*, and *Tricerma* makes sense biogeographically given that these genera are all endemic to the New World.

Based on the results presented by McKenna et al. (2011) and Simmons et al. (2012), *Maytenus* consists of two distinct lineages: one of predominantly Brazilian, Mesoamerican, Amazonian, and Caribbean species (hereafter referred to as the tropical lineage), and the other of Andean and subtropical species from Argentina and Chile (with the exception of *M. boaria*, which also occurs at high elevations in Minas Gerais and Rio de Janeiro states of tropical Brazil; hereafter referred to as the Andean/subtropical lineage). The main morphological difference between these clades is fruits with a coriaceous (= ligneous) pericarp in the tropical lineage vs. fruits with a membranous pericarp in the Andean/subtropical lineage (Biral et al. 2015).

Lundell (1938, p. 285) described *Plenckia integerrima* Lundell as a new taxon based on its "abortive spine-like branches, small entire leaves, and the much reduced inflorescence," which are quite different from the three other described species of *Plenckia*. The other species (*P. bahiensis* Loes., *P. microcarpa* Reissek, and *P. populnea* Reissek) have larger and crenate leaves, highly branched cymes, and larger fruits. Lundell (1939) transferred *P. integerrima* to his new genus *Viposia* Lundell, and stated that this monotypic genus is related to *Plenckia* but distinguished from it by its red-mottled entire leaves and capsular fruits. Lundell (1939, p. 387) described the fruits of *Plenckia* as "samaroid" and the fruits of *Viposia* as flattened capsules, but "samaroid in appearance." However, Loesener (1942) later subsumed *Viposia* into *Plenckia*, as *Plenckia* subg. *Viposia*. The single species recognized by Lundell (1939) in *Viposia*, *V. integerrima* (Lundell) Lundell, is included in a phylogenetic analysis here for the first time in order to investigate the relationships among *Plenckia* s. s., *Viposia*, and *Maytenus*.

The purpose of this study is to finalize the delimitations of *Fraunhofera*, *Maytenus*, *Plenckia*, and *Tricerma* by recognizing monophyletic and morphologically distinct genera. To do so, we improved the species sampling applied in previous studies (Simmons et al. 2008; McKenna et al. 2011; Groppo et al. 2014; Biral et al. 2015) by adding species that encompass the morphological diversity (e.g. coriaceous and membranaceous fruit pericarps, capsules that open by two or three valves, and aril forms and colors) as well as species from geographic regions that had been previously poorly sampled, such as the Amazonian Basin. We also included additional specimens for species with remarkable morphological autapomorphies, such as *M. spinosa* (Griseb.) Lourteig & O'Donell, which had been segregated into the genus *Moya* Griseb. (Grisebach 1874), and *M. megalocarpa*, as well as highly polymorphic species such as *M. ilicifolia* Mart. ex Reissek and *M. floribunda* Reissek (two specimens of each species). We sampled characters from two nuclear gene regions (the internal transcribed spacers [ITS] of rDNA and 26S rDNA) and two plastid loci (maturase K [*matK*] and *trnL-F*). The sequence data were analyzed together with morphological characters, including 21 characters that were newly scored specifically for this study lineage.

Materials and Methods

Taxon Sampling—A total of 75 taxa were sampled (Appendix 1; see also Simmons et al. 2008, 2012; McKenna et al. 2011; Groppo et al. 2014; Biral et al. 2015 for vouchers and GenBank accession numbers for taxa and sequences sampled from those studies). Fifty new specimens were included (Appendix 1). In order to explore the species complex formed by *Maytenus gonoclada* Mart., *M. robusta* Reissek, and *M. salicifolia* Reissek, we retained them as separate taxa following Carvalho-Okano and Leitão-Filho (2004) instead of treating them as a single species (Groppo 2009; Groppo and Erbert 2015). A nomenclatural update was made for one species sampled by McKenna et al. (2011), changing *M. elliptica* (Lam.) Krug & Urb. to *M. laevigata* (Vahl) Griseb. ex Eggers, because the former is a synonym of the latter. One new specimen that we sampled, *Maytenus* sp. (*Lombardi 7822*), could not be morphologically identified as any existing species, and probably represents an undescribed species. *Maytenus distichophylla* Mart. ex Reissek specimen *Lombardi 7212*, which was sampled by McKenna et al. (2011), was re-sequenced for the ITS region because of suspected (and later confirmed) contamination.

Morphological Characters—Initial morphological matrices were obtained from Simmons et al. (2008, 2012), McKenna et al. (2011), and Groppo et al. (2014). For the 75 taxa sampled in this study, 46 characters are parsimony informative (Appendix 2). The 21 new characters added for this study are (with the correspondent numbers in Appendix 2, included in parentheses): habit (1), type of transverse section of young twigs (4), lenticel presence on young twigs (5), indumentum presence on young twigs (6), kind of indumentum on young twigs (7), arrangement of leaves on branches (9), leaf position on twigs or branches (11), presence of leaf pubescence (12), leaf margin (13), distribution of spines on leaf margin (14), elevation of leaf margin (15), leaf consistency (16), elevation of secondary veins on adaxial face of leaves (17), elevation of secondary veins on abaxial side of leaves (18), position of secondary veins on leaves relative to the primary vein (19), wax presence on leaf surface (20), length of inflorescence peduncle relative to flower pedicel (23), distribution of flowers on the peduncle (24), capsular fruit shape (40), type of valves in dehiscent fruit (41), and pericarp consistency (42). All of these characters are used for species identification within *Maytenus*. Some character states represent autapomorphies, such as upright valves in dehiscent fruits for *M. megalocarpa*, whereas others are helpful to identify large groups, such as coriaceous pericarp, which we identified as a synapomorphy for a large clade. Other characters, such as habit, provide synapomorphies for small clades (shrublet, present only in the clade of *M. disticha* + *M. chubutensis* (Speg.) Lourteig, O'Donell & Sleumer). Finally, some of the characters used are helpful to identify species, but are highly homoplasious, such as the type of transverse section of young twigs. Characters were scored, to the degree possible, using reductive coding rather than composite coding (Wilkinson 1995; Simmons and Freudenstein 2002). The codings for the majority of morphological characters are described in detail by Simmons and Hedin (1999, pp. 746–751). All morphological characters, including both character and character-state definitions, are included as part of the simultaneous-analysis data matrix, which has been posted to the Dryad Digital Repository (Biral et al. 2017). The morphological characters were mapped on the strict consensus of all equally most parsimonious trees using WinClada ver. 1.00.08 (Nixon 2002).

Molecular Methods—Genomic DNA was extracted from herbarium specimens (authorized by curators of the HRCB, MO, and NY herbaria) and leaves preserved in silica gel using a combination of protocols from Couch and Fritz (1990; ascorbic acid and DIECA in the extraction buffer), De La Cruz et al. (1995; extraction and lysis buffers), and Alexander et al. (2007; for the column purification) that were merged by Tembrock et al. (2017). Alternatively, DNA was extracted from fresh leaves using 2 × CTAB protocols of Doyle and Doyle (1987) without the addition of RNAase A, and scaled to 2 mL tubes.

New sequences were generated for two plastid loci (*matK* and *trnL-F*) and two gene regions from the nuclear genome (ITS and 26S rDNA). Most gene regions were amplified using the following PCR protocol: an initial denaturation of 96°C preceding 10 cycles of denaturation (96°C for 45 s), annealing (50–53°C for 30 s), and extension (72°C for 2 min), followed by 25 cycles of denaturation (96°C for 20 s), annealing (50–53°C for 30 s), and extension (72°C for 2 min). Alternatively, PCR amplification of some fragments was performed using the following protocol: initial denaturation of 94°C (1 min) preceding 40 cycles of denaturation (94°C for 30 s), annealing (51°C for 40 s), and extension (72°C for 40 s), followed by a final extension (72°C for 5 min).

Most *matK* amplicons were produced using the primer combination *trnK*-710 (Johnson and Soltis 1995) and *matK*-8R (Steele and Vilgalys 1994). Alternatively, for some amplifications we used the primers 3F_KIM_f and 1R_KIM_r (Kim 2015). Some amplifications were separated into two reactions by using the primer combination *trnK*-710 (Johnson and Soltis 1995) and *matK*-R1 (Yokoyama et al. 2000) for the 5′ end, and *matK*-F1 (Yokoyama et al. 2000) and *matK*-8R (Steele and Vilgalys 1994) for the 3′ end. Amplifications of *trnL* were performed in one reaction using the primers 'c' and 'f' or in two reactions with the primers 'c' and 'd' for the 5′ end, and 'e' and 'f' for the 3′ end (Taberlet et al. 1991).

The ITS region (ITS1–5.8S – ITS2) was amplified using primers ITSA and ITSB (Blattner 1999), ITS1 and ITS4 (White et al. 1990; Rauscher et al. 2004), or ITS75 and ITS92 (Desfeux and Lejeune 1996). The 5′ end of the 26S rDNA region was generally amplified using primers 26S1 and 950rev. Alternatively, amplifications were done in two reactions using 26S1 with 641rev for the 5′ end, and 26S2 with 950rev for the 3′ end (Kuzoff et al. 1998). Amplified products were purified using Qiagen PCR Purification Kits or with polyethylene glycol (PEG 20%). Purified PCR products were sequenced by the University of Chicago Cancer Research Center DNA Sequencing Facility or Macrogen (Seoul, South Korea). The primers used for amplifications were also used for sequencing. All new sequences generated in this study have been deposited in GenBank as accession numbers KU892171 to KU892212 for the ITS region and KX231954 to KX232092 for the other regions (Appendix 1).

Data Analysis—We obtained preliminary nucleotide alignments for each gene region independently using MAFFT v. 6.5 (Katoh and Toh 2008b). The Q-INS-I algorithm, which considers inferred secondary structure of rDNA (Katoh and Toh 2008a), was used for alignments of ITS and 26S rDNA. The G-INS-I algorithm, the most accurate MAFFT algorithm for aligning loci other than rDNA, was used for the plastid gene regions. The 20 PAM nucleotide scoring matrix was used for the more divergent ITS and *trnL-F* regions, whereas the 1 PAM matrix was used for the other regions. The default gap opening penalty (1.53) was applied and the gap offset value was set to 0.1.

Manual adjustments were conducted after the MAFFT alignments in MacClade v. 4.03 (Maddison and Maddison 2001) using the procedure described by Simmons (2004b), following Zurawski and Clegg (1987). Some ambiguously aligned regions were detected where one or more sequences had a duplicate insertion (or the others had a deletion of one of two repeats) and the character-state distribution amongst the characters in the ambiguously-aligned region was the same for those sequences that have both repeats. In such cases the character-state distribution amongst the positions in question would be the same for either of the alternative alignments. These ambiguously-aligned regions were kept in the analysis following Davis et al. (1998). A total of 80 ambiguously-aligned positions were excluded from the analyses (26S rDNA: two positions from one region; ITS: 78 positions from six regions). Ambiguously-aligned nucleotides of individual sequences in regions that could not be unambiguously aligned with the remaining sequences were scored as ambiguous ("?").

Gap characters, whose inclusion often affect the inferred tree topology and increase branch-support values (Simmons et al. 2001), were scored manually using modified complex indel coding (Simmons and Ochoterena 2000; Müller 2006), including step matrices for gap characters 1136, 1138, and 1145 from the *trnL-F* region. A total of 46 parsimony-informative complex-indel-coding gap characters were scored from unambiguously aligned regions (26S rDNA: 8; ITS: 23; *matK*: 3; *trnL-F*: 12) for inclusion in the parsimony analyses.

As a means of data exploration, several alternative process partitions (Bull et al. 1993) of the characters were examined. Specifically, each of the four gene regions was analyzed independently from one another to resolve their respective gene trees. Putative coalescent genes (Hudson 1990; Doyle 1995) were then examined and their inferred trees compared to check for well supported, contradictory signals between partitions that may have been caused by lineage sorting, introgression, and/or unrecognized paralogy (Doyle 1992). As such, gene trees for rDNA gene regions and plastid loci were analyzed separately from each other to check for potential introgression of the plastid genome or rDNA (Doyle 1992; Wendel et al. 1995) or unrecognized paralogy problems with rDNA (Álvarez and Wendel 2003; Bailey et al. 2003). An analysis of all molecular characters was then conducted, followed by a simultaneous analysis of all molecular and morphological characters, which was used as the primary basis for phylogenetic inference and genus delimitation.

Equally weighted parsimony tree searches were conducted for each data matrix using 2,000 random addition tree-bisection-reconnection (TBR) searches in PAUP* v. 4.0b10 (Swofford 2001) with a maximum of ten trees held per search. Parsimony jackknife analyses (JK; Farris et al. 1996) were conducted using PAUP* with the removal probability set to approximately e^{-1} (36.7879%), and "jac" resampling emulated. One-thousand JK replicates were performed, each with 100 random-addition TBR searches and a maximum of ten trees held per search. All parsimony analyses were run while collapsing branches with a minimum possible optimized length of zero to increase tree-search efficiency (Davis et al. 2005) and reduce the potential for inflated jackknife values (Simmons and Freudenstein 2011). Trees were generated using TreeGraph 2.4.0–456 (Stöver and Müller 2010). Support values were mapped onto the parsimony strict consensus tree so as to help minimize frequency-within-replicates (Davis et al. 1998) and undersampling-within-replicates JK artifacts (Simmons and Freudenstein 2011).

Results

A simplified version of the simultaneous-analysis parsimony strict consensus tree inferred from all four gene regions and morphological characters, wherein multiple accessions of some taxa resolved as a clade are represented by single terminals, is presented in Fig. 1 with JK values ≥ 50% above each branch. The complete tree is presented in Fig. S1 as supplemental online material (Biral et al. 2017). Equivalent trees for each of the eight partitioned analyses are presented in Figs. S2–S9. The strict consensus tree with all morphological characters mapped onto it is presented in Fig. S10. Figures S1–S10 can be found on the Dryad Digital Repository (Biral et al. 2017). Data-matrix and tree statistics for all analyses are presented in Table 1.

Simultaneous Analyses—*Maytenus* species, as defined by McKenna et al. (2011), are resolved in three separate clades that are interspersed by a clade of *Fraunhofera* and *Plenckia* species. All four clades are unambiguously supported (100% JK). Five notable clades (Fig. 1) are described below.

The first notable clade is the Andean/subtropical lineage, which comprises all species sampled that have fruits with membranous pericarps that open by two or three valves, and includes the type species, *Maytenus boaria*. This clade is resolved with high support from all trees generated from different partitions, including those trees that have low resolution, such as the *matK* and *trnL-F* gene trees (Figs. S5, S6; 96% and 100% JK, respectively). Molecular synapomorphies include a 3-bp insertion at positions 235–237 of *trnL-F*, and a 2-bp insertion at positions 301–302 of ITS.

The second notable clade consists of the species that Lundell (1971) assigned to the genus *Tricerma*. This genus comprises those species recognized in *Maytenus* that have fleshy leaves that are spirally arranged, tricarpellate ovaries, one ovule per carpel, coriaceous fruits that open by three valves, and red arils that cover the seeds. The *Tricerma* clade was highly supported (100% JK for all trees, except 26S rDNA with 97% JK, Fig. S2), even in individual gene trees with low resolution. Molecular synapomorphies for this clade include a 2-bp insertion at positions 246–247 of ITS, and a 8-bp deletion at positions 1004–1011 of *trnL-F*.

The clade *Fraunhofera* + *Plenckia* is unambiguously supported (100% JK) as nested within *Maytenus* (sensu McKenna et al. 2011) and is well supported (98% JK) as sister to the clade of all *Maytenus* species that have fruits with coriaceous pericarp, open by two valves and have seeds with white arils. Groppo et al. (2014) indicated indehiscent fruits as a synapomorphy for the *Fraunhofera* + *Plenckia* clade, while Simmons et al. (2012) cited a cupular or columnar nectar disc. A molecular synapomorphy for this clade is an 8-bp deletion at positions 244–251 of *trnL-F*.

Plenckia integerrima and *P. populnea* are sister groups in a moderately supported (70% JK) clade. Synapomorphies for *Plenckia* include cymose inflorescences, samaroid fruits with one apical wing, and a 7-bp deletion at positions 363–369 of *trnL-F*.

The tropical lineage of *Maytenus* (labelled as *Monteverdia* A. Rich. in Fig. 1) is an unambiguously supported (100% JK) clade. Synapomorphies for this clade include fruits that have a coriaceous pericarp opening by two valves and a white aril that completely surrounds each seed.

Species as Non-Exclusive Lineages—Three species for which two specimens were sampled were not resolved as exclusive lineages within the tropical lineage of *Maytenus*. First, *M. distichophylla* 7212 is part of a lineage of Brazilian species from the Atlantic Rainforest (with the exception of *M. imbricata* Mart. ex Reissek, which grows on outcrops in central Brazil; Figs. 1, S2, S4, S9; simultaneous: 80% JK; 26S rDNA: < 50% JK; rDNA: 100% JK; molecular: 75% JK). On the other hand, *M. distichophylla* 8024 is weakly supported (Fig. 1; simultaneous: 58% JK) as sister to *M. floribunda* Reissek, which together are sister to a clade of Caribbean and Mesoamerican species (from *M. buxifolia* (A. Rich.) Griseb. to *M. laevigata*; Fig. 1; simultaneous: 90% JK).

Based on a suspected contamination after examining individual gene trees from McKenna et al. (2011) and Groppo et al. (2014), we re-sequenced the ITS region for the specimen *Maytenus distichophylla* 7212. The former sequence was resolved in a clade with the morphologically divergent *M. evonymoides* Reissek with high support (100% JK). But the re-sequenced *M. distichophylla* 7212 allele grouped with several species from the Brazilian Atlantic Rain Forest, which makes more sense biogeographically.

A second case of polyphyletic resolution of a species is *Maytenus obtusifolia*. *Maytenus obtusifolia* 1016 was alternatively resolved as sister to the clade of the Amazonian species *M. sprucei* Briq. and *Maytenus* sp. (Figs. 1, S4, S9; simultaneous: 64% JK, rDNA: 80% JK, molecular: 62% JK) or sister to *Maytenus* sp. (Fig. S3; ITS: 72% JK; *M. sprucei* was not sampled for ITS). In the remaining trees (Figs. S2, S5, S6, S7; 26S rDNA, *matK*, *trnL-F*, and plastid trees) *M. obtusifolia* 1016 is part of a polytomy or sister to a clade of several *Maytenus* species, but always with low support (< 50% JK). *Maytenus* aff. *obtusifolia* 7213 is resolved as sister to a large clade of Brazilian and Amazonian species in the simultaneous-analysis tree (Fig. 1; 74% JK). Only ITS and *trnL-F* regions were sampled for this specimen, which is part of a large polytomy with several other *Maytenus* species in these gene trees (Figs. S3, S6).

A third case is the species complex consisting of *Maytenus gonoclada*, *M. robusta*, and *M. salicifolia*, wherein *M. robusta* was resolved as paraphyletic (Fig. 1). *Maytenus robusta* 6902 is sister to *M. salicifolia* (Figs. 1, S6, S9; simultaneous: 99% JK, *trnL-F*: 93% JK, molecular: 99%) and this clade is sister to *M. robusta* 1085 (Figs. 1, S9; simultaneous: 98% JK, molecular: 92% JK). In the ITS and rDNA trees the three specimens form a polytomy (Figs. S3, S4; 89% JK and 88% JK, respectively). All other trees show low resolution, with *M. robusta* and *M. salicifolia* as part of large polytomies, with the exception of *matK* tree wherein *M. robusta* 1085 is in a polytomy with several species/clades that do not include *M. robusta* 6902 or *M. salicifolia* (Fig. S5; 65% JK).

Incongruence—Two notable cases of incongruence were detected when comparing alternative topologies. First, the two species of *Plenckia* are resolved as a clade in the simultaneous, 26S rDNA, and rDNA trees (Figs. 1, S2, S4; 70% JK, < 50% JK, and 71% JK, respectively). Alternatively, *P. integerrima* is sister to *Fraunhofera* in the molecular tree (Fig. S9; 66% JK), which in turn are sister to the unambiguously supported (100% JK)

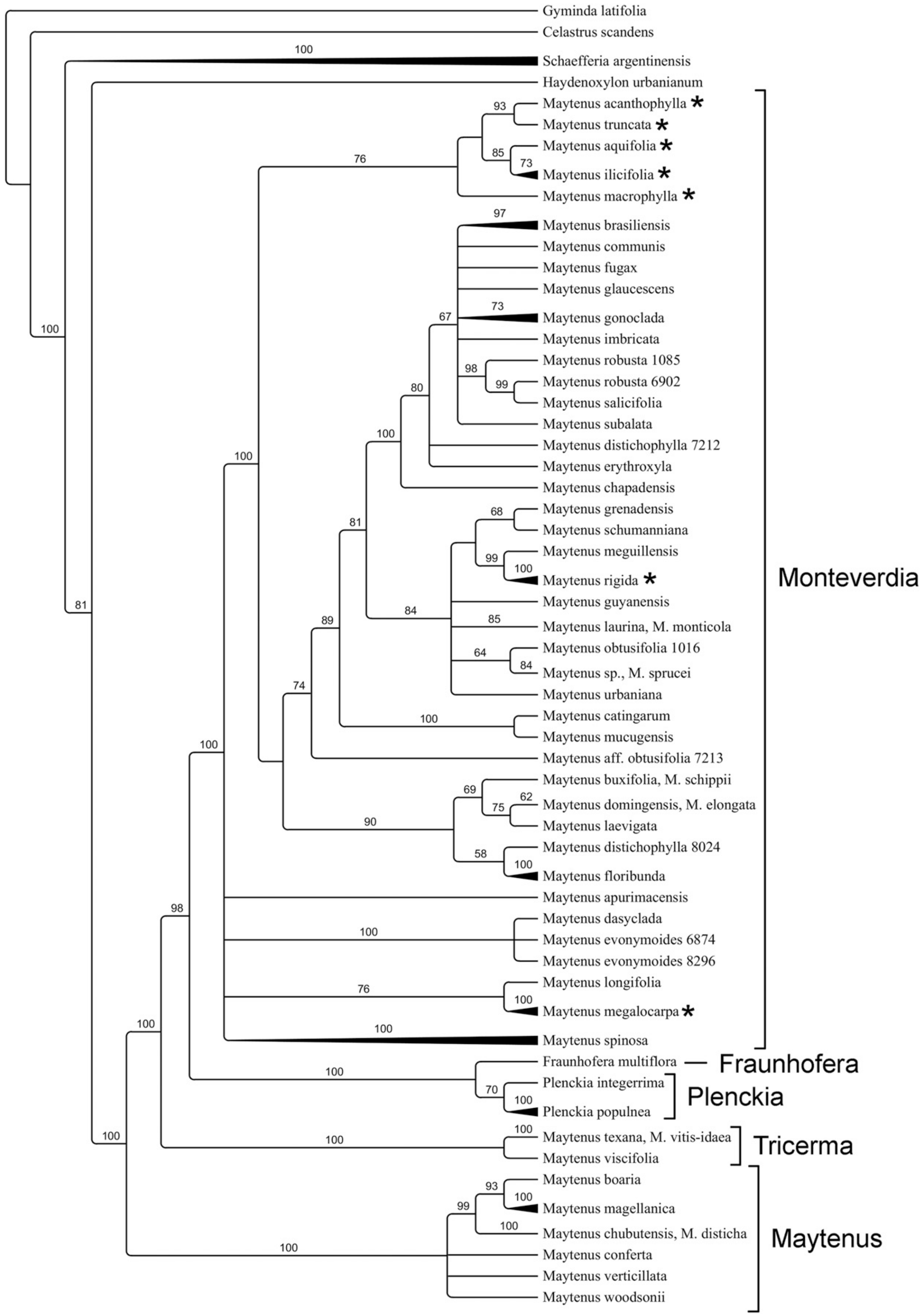

FIG. 1. Simplified simultaneous-analysis parsimony strict consensus tree [rDNA regions (ITS + 26S) and plastid regions (*matK* + *trnL-F*) + morphological data] with jackknife values ≥ 50% above each branch. Species represented by two or more specimens that form non-exclusive lineages have their respective collection number after the species name. Asterisks denote species with spinose leaves, which are members of *Maytenus* section *Oxyphylla* as defined by Carvalho-Okano (1992).

TABLE 1. Data-matrix and tree statistics for each of the gene-tree and phylogenetic analyses. CI = ensemble consistency index (Kluge and Farris 1969) on the most parsimonious tree(s) for the parsimony-informative characters. RI = ensemble retention index (Farris 1989). [1] The difference between the number of parsimony informative characters in the simultaneous analysis and the sum of characters from the molecular + morphology analyses is probably caused by including more than one accession of some species in the simultaneous analysis but not in the morphology-only analysis.

Matrix	# terminals	# characters analyzed	# of parsimony informative characters	% missing / inapplicable	Most parsimonious tree length	# of most parsimonious trees	Average jackknife support (%)	# of jackknife clades ≥ 50%	CI	RI
26S rDNA	71	960	70	7.7	232	44,500	78.9	21	0.34	0.67
ITS rDNA	74	746	260	16.6	847	88,710	90	39	0.49	0.80
rDNA (ITS, 26S)	75	1,706	330	12	1,109	79,000	89.4	44	0.49	0.81
matK	67	1,346	76	13	205	992,000	83.9	10	0.41	0.57
trnL-F	69	1,145	95	19.2	286	700	86.6	16	0.54	0.76
Plastid (*matK*, *trnL-F*)	73	2,491	171	15.9	498	13,700	93.4	8	0.37	0.49
Morphology only	75	46	33	14.9	169	4,100	76.7	3	0.15	0.19
All molecular	75	4,197	501	14.2	1,649	1,647	91.1	48	0.51	0.80
Simultaneous	75	4,243	537[1]	14.2	1,889	3,636	88.8	50	0.46	0.77

exclusive lineage of *P. populnea* specimens. Given that support for all of the alternative trees is low or moderate, we favor the simultaneous analysis, which includes the morphological synapomorphies for the genus, wherein *P. integerrima* is resolved as sister to *P. populnea*. On the other hand, we were unable to identify any morphological or indel synapomorphies uniting the clade *P. integerrima* + *Fraunhofera*.

Second, *Maytenus aquifolia* Mart. is alternatively resolved as nested within *M. ilicifolia* in the molecular tree (Fig. S9; 84% JK) or sister to an exclusive lineage of the two *M. ilicifolia* specimens in the simultaneous-analysis tree (Fig. 1; 85% JK). *Maytenus ilicifolia* 721 is sister to *M. aquifolia* in the *matK*, *trnL-F*, and plastid trees (Figs. S5, S6, S7; 63% JK, < 50% JK, and 80% JK, respectively). On the other hand, *M. ilicifolia* is an exclusive lineage in the 26S rDNA and rDNA trees (Figs. S2, S4; 52% JK and 73% JK, respectively). Given this conflict we are unable to determine whether or not *M. ilicifolia* is an exclusive lineage or if *M. aquifolia* is nested within it.

Discussion

Based on our results, which incorporate substantially greater taxon and morphological-character sampling for *Maytenus* relative to previous phylogenetic studies that sampled the genus (McKenna et al. 2011; Simmons et al. 2012; Groppo et al. 2014; Biral et al. 2015), *Maytenus*, as it has been delimited, consists of three distinct lineages that we are newly able to delimit using morphological characters. Given the phylogenetic and morphological distinctness of these lineages we separate *Maytenus* into two genera, re-establish Lundell's (1971) *Tricerma*, and retain *Fraunhofera* and *Plenckia* as distinct genera.

Maytenus Species With Membranaceous Pericarp—The clade consisting of *Maytenus boaria*, *M. chubutensis* (Speg.) Lourteig, O'Donell & Sleumer, *M. conferta* (Ruiz & Pav.) Reissek ex Loes., *M. disticha*, *M. magellanica*, *M. verticillata*, and *M. woodsonii* Lundell comprises all *Maytenus* species sampled that have capsular fruits with membranaceous pericarp that open by two or three reflexing valves. Lourteig and O'Donell (1955) reported yellowish arils for some Argentinean and Chilean species (*M. chubutensis, M. disticha, M. magellanica*) in this clade, but we have only observed red arils. The arils completely or partially cover the seeds within this lineage of 15–24 species. The species number is uncertain because of taxonomic problems in the delimitation of nine species. For example, *M. jamesonii* Briq., *M. pavonii* Briq. and *M. jelskii* Szyszyl. have not been clearly delimited morphologically from the closely related *M. verticillata*. Delimitation of these species is underway and new synonyms will likely be proposed soon. The clade consisting of species with membranaceous pericarp has a predominantly subtropical distribution or concentrated in high altitude areas in the tropics along the Andean mountains from Argentina to Venezuela. Just one species with membranaceous pericarp occurs outside of South America: *M. woodsonii*, which is distributed in the paramos of Costa Rica and Panama between 2,700 and 3,460 m above sea level (Biral et al. 2015). Because this clade contains the type of *Maytenus* (*M. boaria*), it must retain the generic name (Article 10; McNeill et al. 2012).

Tricerma—*Tricerma* is a lineage of just four species (or five, if *T. texanum* Lundell (Lundell) is treated as distinct from *T. phyllanthoides* (Benth.) Lundell; see Nesom [2009]) that is distributed from northwestern Argentina to the southern United States (Florida and Texas). The genus was described by Liebmann (1854) for those species with capsular fruits that open by three coriaceous valves. Loesener (1942) recognized *Tricerma*, but treated it as *Maytenus* section *Tricerma* (Liebm.) Loes. Lundell (1971, p. 158), like Liebmann (1854), recognized *Tricerma* at the generic level and transferred *Maytenus octogona* (L'Her) DC., *M. viscifolia* Griseb. and *M. vitis-idaea* Griseb. to *Tricerma* because they have "peculiar thick fleshy leaves, spirally arranged, and the 3-celled ovary with one ovule in each cell, and the 3-valved capsules." We sampled three *Tricerma* species that are resolved as an unambiguously supported lineage (Fig. 1) that is morphologically distinct. We suggest the resurrection of *Tricerma*, contra Lourteig and O'Donell (1955), McKenna et al. (2011), and Simmons et al. (2008), all of whom treated *Tricerma* as synonym of *Maytenus*. No new combinations are necessary for this taxonomic decision given that Lundell (1971) already proposed the relevant binomials. The genus may be recognized as those species that have the character states cited above by Lundell (1971) as well as coriaceous pericarp and a red aril covering completely the seeds (Table 2). Small (1928) presented a complete figure of *T. phyllanthoides* that demonstrates these traits.

Fraunhofera + Plenckia—The clade of *Fraunhofera* + *Plenckia* is unambiguously supported as nested within the currently recognized *Maytenus* (Fig. 1), as previously asserted by Simmons et al. (2012). *Fraunhofera* is a monotypic genus endemic to the Brazilian semi-arid vegetation ("caatinga," in forest formations), and has been recorded from just three states in northeastern Brazil (BFG 2015). The genus is identified by having sessile and pubescent leaves, axillary and terminal racemose inflorescences with strigose peduncles, and by the fruit type (Table 2), which has been described as drupes (Simmons 2004a) or indehiscent capsules (Groppo et al. 2014). Simmons (2004a) identified the fruits as drupes, but indicated doubt because only immature fruits were known to him. Groppo et al. (2014) recognized the fruits as indehiscent capsules based on Lorenzi (2009). The uncertainty about fruit type in *Fraunhofera* is probably because specimens of the genus are scarce in botanical collections; most of the specimens that we have examined only have flowers. We prefer to wait and examine more specimens before definitively describing the fruit type.

Plenckia includes four recognized species, all endemic to South America. Three of these species are distributed in savanna habitats of central Brazil, Bolivia, and Paraguay, whereas *P. integerrima* occurs in xeric scrub vegetation ("matorrales") in Bolivia and northwestern Argentina. *Plenckia populnea*, *P. microcarpa,* and *P. bahiensis* are morphologically very similar described taxa and probably represent a single biological species. But *P. integerrima* is quite distinct morphologically. The leaves of *P. integerrima* are subsessile, lanceolate, smaller, and have entire margins; the inflorescences are lax and few-flowered (usually 1–5 flowers per inflorescence); and the fruits are considerably smaller. In contrast, other *Plenckia* species usually have long reddish petioles, ovate leaves with crenate margins, multi-flowered inflorescences (~20 flowers or commonly more), and markedly larger fruits. The genus may be recognized as those species with cymose inflorescences and samaroid fruits that have one apical wing (Table 2).

Lundell (1939) transferred *Plenckia integerrima* to his new monotypic genus *Viposia*, arguing that *Plenckia* fruits are samaroid and *Viposia* fruits are capsules with samaroid appearance. However, we have seen no difference between *Viposia* and *Plenckia* fruits aside from variations in size and number per inflorescence. Loesener (1942) treated *Viposia* as a synonym of *Plenckia*, including it as a subgenus. We agree that *Viposia* is a synonym of *Plenckia*, an opinion also shared by Lourteig and O'Donell (1955) and Simmons (2004a).

The clade of *Fraunhofera* + *Plenckia* consists of species with flowers that have two carpels and two ovules per carpel. Simmons et al. (2012) suggested cupular or columnar nectar discs as a synapomorphy for this clade, but we have observed the ovary in many specimens, especially those deposited in HRCB, and this trait is actually variable. The cupular/columnar disc seems to be result of ovarian growth after fertilization, wherein the ovary elongates both itself and the disc. In young flowers the disc is flat, as in *Maytenus* (sensu McKenna et al. 2011) and *Fraunhofera*. Groppo et al. (2014) suggested indehiscent fruits as a synapomorphy for the *Fraunhofera* + *Plenckia* clade. Although they are indehiscent, the fruits of the two genera are quite different. Illustrations for the main morphological traits of *Fraunhofera* and *Plenckia* are included in Reissek (1861).

Maytenus Species With Coriaceous Pericarp—All species in this clade have fruits with coriaceous pericarp that open by two reflexed valves (with the exception of *M. megalocarpa*, which has upright valves) and a white aril that completely covers the seeds. The ovary is bilocular with two ovules per locule, as in *Fraunhofera*, *Plenckia*, and some *Maytenus* species from the Andean/subtropical lineage. This clade comprises many species with broad distributions in the Neotropics.

Maytenus section *Oxyphylla*, comprising those species with spiny leaves, is polyphyletic and consists of three distinct lineages, thereby corroborating the preliminary results from McKenna et al. (2011) and Groppo et al. (2014). Five of the seven species from this section are in a moderately supported (76% JK; Fig. 1) clade, but the resolution of *M. megalocarpa* and *M. rigida* Mart. indicates that spiny leaves have been convergently derived. Except for *Tricerma*, which we recognize at the generic level, all other New World *Maytenus* sections have already been recognized as polyphyletic (McKenna et al. 2011).

TABLE 2. Number of species, distribution, and primary distinguishing morphological traits for the genera recognized in this study.

Genus	Species #	Distribution	Main morphological characters
Maytenus	15–24	Subtropical South America, Andes from Argentina to Venezuela, paramos in Costa Rica and Panama	Chartaceous or coriaceous leaves, rarely fleshy, that are spirally or distichously arranged; axillary fasciculate or cymose inflorescences, sometimes reduced to an individual flower; flowers with two or three carpels, one or two ovules per carpel; capsular fruits with membranaceous pericarp that open by two or three reflexing valves; red or yellowish arils that completely or partially cover the seeds
Tricerma	4 or 5	Northwestern Argentina, Bolivia, Peru, Ecuador (including Galapagos Islands), Mexico, Cuba, Bahamas, Florida and Texas	Thick and fleshy leaves that are spirally arranged; axillary fasciculate inflorescences; flowers with three carpels, one ovule per carpel; capsular fruits with coriaceous pericarp that open by three reflexing valves; red arils that completely cover the seeds
Plenckia	4	Central Brazil, Paraguay and Bolivia (in savannas)	Chartaceous leaves that are distichously arranged; axillary cymose inflorescences; flowers with two carpels, two ovules per carpel; samaroid fruits with one apical wing; aril absent
Fraunhofera	1	Drylands of northeastern Brazil	Membranaceous or chartaceous leaves that are distichously arranged; axillary and terminal racemose inflorescences; flowers with two carpels, two ovules per carpel; fruits indehiscent capsules (or drupes?); aril absent
Monteverdia	~120	Widely distributed in the Neotropics	Membranaceous, chartaceous or coriaceous leaves that are spirally or distichously arranged; axillary fasciculate or cymose inflorescences that are sometimes reduced to an individual flower; flowers with two carpels, two ovules per carpel; capsular fruits with coriaceous pericarp that open by two reflexing or (rarely) upright valves; white arils that completely cover the seeds

Grisebach (1874) described the genus *Moya* and considered it to be closely related to *Gymnosporia* because of the presence of spines (actually thorns) and fasciculate leaves on brachyblasts, an unusual trait in Neotropical Celastraceae but common among African *Gymnosporia* species. Lourteig and O'Donell (1955) subsumed *Moya* into *Maytenus* given that both genera have atrophied ovules in functionally male flowers. *Moya* was confirmed as a synonym of *Maytenus* by Simmons et al. (2008) and McKenna et al. (2011). In our more comprehensive inferred phylogeny, *Moya*, represented by two accessions of *M. spinosa*, is unambiguously supported (100% JK; Fig. 1) as a member of the tropical *Maytenus* clade. *Moya boliviana* (Loes.) Loes. was recognized as a species by Loesener (1942), but Lourteig and O'Donell (1955) synonymized it with *Maytenus scutioides* (Griseb.) Lourteig & O'Donell. Yet *Moya scutioides* Griseb. was transferred to *Maytenus* by Lourteig and O'Donell (1955) and considered as a synonym of *Maytenus spinosa* by Biral (2014).

Maytenus distichophylla appears to be a polyphyletic taxon (Fig. 1), such that this binomial has been applied to more than one biological species. The specimen *Lombardi 7212* is from the Atlantic Rainforest in Bahia state, Brazil, and has the typical morphological features for the species, including lenticels on the young branches, plicate and pruinose leaves, and fasciculate inflorescences. It is part of a polytomy with *M. erythroxyla* Reissek (a very similar species morphologically) and a clade of nine other species from the Atlantic Rainforest. On the other hand, specimen *Lombardi 8024* is sister to *M. floribunda*, a widespread species in South America (Biral et al. 2015), and together they are sister to a clade of primarily Caribbean species. Interestingly, *Lombardi 8024* was collected in Fernando de Noronha, a volcanic archipelago located about 350 km off the northeastern Brazilian coast in the Atlantic Ocean (Rocha et al. 2009). Further taxonomic studies are necessary to determine the relationship between this specimen from Fernando de Noronha and the Caribbean species.

Maytenus obtusifolia also appears to be a polyphyletic species (Fig. 1). This species occurs predominantly in the coastal forests ("restinga") and ombrophyllous forests along the Brazilian coastline, with some plants growing in mangrove areas of the Amazonian region. The specimen *Biral 1016*, from the Atlantic Rainforest in Espírito Santo state (eastern Brazil), is part of a clade with *Maytenus* sp. and *M. sprucei* Briq., both Amazonian species, that is part of a polytomy with several other species, most of which are also from the Amazonian Basin. However, specimen *Lombardi 7213* is resolved as sister to a large clade of Brazilian and Amazonian species. *Lombardi 7213* has some unusual morphological traits relative to more typical specimens of *M. obtusifolia*, such as more highly branched inflorescences with shorter peduncles, and was identified with doubt (*M.* aff. *obtusifolia*) in McKenna et al. (2011). The divergent resolution of these two specimens of *M. obtusifolia* is not a complete surprise given that *M.* aff. *obtusifolia* probably represents a new species that is distantly related to *M. obtusifolia*. Specimens identified as *M. obtusifolia* from Bahia and Sergipe states that may also belong to this new taxon are being examined.

According to Carvalho-Okano and Leitão-Filho (2004, p. 17), *Maytenus robusta* is distinguishable from *M. salicifolia* and *M. gonoclada* by having "pruinose leaves, lax inflorescences, peduncles longer than 0.4 cm and pyriform fruits vs. glabrous leaves, dense inflorescences, peduncles shorter than 0.3 cm and orbicular fruits." Carvalho-Okano and Leitão-Filho (2004) also differentiated *M. gonoclada* from *M. salicifolia* by the former having quadrangular branches and chartaceous leaves (vs. cylindrical or flattened branches and membranaceous leaves in *M. salicifolia*). However, when numerous specimens are examined, the differentiation of these species based on these characters is tenuous given the overlap of traits, especially fruit shape. Given this overlap of morphological traits, Groppo (2009) synonymized *M. robusta* with *M. gonoclada*, and later synonymized *M. salicifolia* with *M. gonoclada* as well (Groppo and Erbert 2015). Based on our phylogenetic analysis (Fig. 1), *M. robusta* is an exclusive lineage only if *M. salicifolia* is included. However, *M. gonoclada* (represented by two accessions, which have been merged in Fig. 1) is distinct from the clade *M. robusta* + *M. salicifolia*, though it may be sister given that both clades are part of a large polytomy. Our results indicate that *M. robusta* (with *M. salicifolia*) and *M. gonoclada* may be recognized as distinct species, although the morphological differences between these taxa are not completely clear. *Maytenus robusta* occurs in semideciduous and ombrophyllous forests from Santa Catarina to Bahia states in Brazil, and has predominantly flattened young twigs, chartaceous leaves, and larger leaves and inflorescences than *M. gonoclada*. On the other hand, *M. gonoclada* is more common in cerrado, gallery forest, and rock-outcrop vegetation in central Brazil, and has predominantly carinate young twigs, coriaceous leaves, and smaller leaves and inflorescences than *M. robusta*. However, these traits are insufficient to differentiate these species because of intermediate individuals.

Genus Delimitation—New World *Maytenus*, as currently defined by McKenna et al. (2011), consists of three divergent lineages, each of which is morphologically distinct. These three divergent lineages are interspersed with *Fraunhofera* and *Plenckia*. We split *Maytenus* into two genera, resurrect *Tricerma* and maintain *Plenckia* and *Fraunhofera* as separate genera so as to delimit monophyletic genera that are morphologically distinct. *Maytenus* species in the tropical lineage are transferred to *Monteverdia.* No new combinations are required other than those proposed in *Monteverdia*. The main morphological traits used to distinguish these five genera are presented in Table 2.

Richard (1845) described the genus *Monteverdia* based on a single species, *M. buxifolia*, from Cuba. Richard (1845) distinguished *Monteverdia* from *Celastrus*, *Euonymus*, and *Myginda* based on its coriaceous and indehiscent fruits with arils that completely cover the seeds. Given that the specimens from Richard's herbarium, which has since been deposited at P, only have immature fruits, his inference that they are indehiscent is mistaken. Grisebach (1866) treated *Monteverdia* as a synonym of *Maytenus* given their similar fruits and arils. He treated *Monteverdia* provisionally as a *Maytenus* section, but did not publish the section validly. This section also included *Maytenus cochlearifolia* Griseb., *M. elaeidendroides* Griseb. and *M lineata* C. Wright ex Griseb., all of which are endemic to Cuba. Following Grisebach's (1866) treatment, *Monteverdia* has consistently been treated as a synonym of *Maytenus* (e.g. Loesener 1942; Carvalho-Okano 1992; Mory 2010; Biral 2016). Given that neither *Maytenus* nor *Monteverdia* have well resolved or well supported internal resolution, we do not propose any subgenera or sections.

The alternative generic-delimitation option is to treat all ingroup species as members of a single genus, *Maytenus*. This option would be simpler and more uniform nomenclaturally because it would require just three new combinations and new names for *Fraunhofera multiflora* and *Plenckia microcarpa* (because *M. multiflora* Reissek and *M. microcarpa* Facw. & Rendle have already been proposed), instead of requiring 123 new combinations. But this alternative approach would delimit a large genus with no diagnostic morphological traits that includes five fruit types, presence or absence of an aril, and three different aril colors.

TAXONOMIC TREATMENT

We propose 123 new combinations within *Monteverdia* for *Maytenus* species that have capsular fruits with coriaceous pericarp that open by two valves and have white arils that completely cover the seeds. Doubtfully distinct species, such as *Maytenus grisea*, as well as those ruled out (i.e. doubtful species, excluded taxa, and untreated species) from taxonomic works (Carvalho-Okano and Leitão-Filho 2004; Biral 2016), are not transferred to *Monteverdia* at this time. We formally treat *Moya* as a synonym of *Monteverdia*.

MONTEVERDIA A. Rich., Hist. Phys. Cuba, Pl. Vasc. 346. 1845.—TYPE: *Monteverdia buxifolia* A. Rich., Hist. Phys. Cuba, Pl. Vasc. 347, t. XXXVI. 1845.

Moya Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 111. 1874.—TYPE: *Moya spinosa* Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 111, t. 1, f. 3a-e. 1874.

Monteverdia acanthophylla (Reissek) Biral, comb. nov. *Maytenus acanthophylla* Reissek, Fl. Bras. 11: 6. 1861.

Monteverdia aggostini (Steyerm.) Biral, comb. nov. *Maytenus aggostinii* Steyerm., Ernstia 23: 24. 1984.

Monteverdia amazonica (Mart. ex Reissek) Biral, comb. nov. *Maytenus amazonica* Mart. ex Reissek, Fl. Bras. 11: 25. 1861.

Monteverdia apiculata (Steyerm.) Biral, comb. nov. *Maytenus apiculata* Steyerm., Fieldiana, Bot. 28: 334. 1952.

Monteverdia apurimacensis (Loes.) Biral, comb. nov. *Maytenus apurimacensis* Loes., Bot. Jahrb. Syst. 50(Beibl. 111): 8. 1913.

Monteverdia aquifolia (Mart.) Biral, comb. nov. *Maytenus aquifolia* Mart., Flora 24(Beibl.): 91. 1841.

Monteverdia ardisiifolia (Reissek) Biral, comb. nov. *Maytenus ardisiifolia* Reissek, Fl. Bras. 11: 26. 1861.

Monteverdia basidentata (Reissek) Biral, comb. nov. *Maytenus basidentata* Reissek, Fl. Bras. 11: 7. 1861.

Monteverdia belizensis (Standl) Biral, comb. nov. *Maytenus belizensis* Standl., Publ. Carnegie Inst. Wash. 461: 69. 1935.

Monteverdia brasiliensis (Mart.) Biral, comb. nov. *Maytenus brasiliensis* Mart., Flora 24(Beibl.): 87. 1841.

Monteverdia cassineformis (Reissek) Biral, comb. nov. *Maytenus cassineformis* Reissek, Fl. Bras. 11: 15. 1861.

Monteverdia cassinoides (Poir.) Biral, comb. nov. *Rhamnus cassinoides* Poir., Encycl.4: 474. 1798; *Maytenus cassinoides* (Poir.) Urb., Symb. Antill. 5: 67. 1904.

Monteverdia catingarum (Reissek) Biral, comb. nov. *Maytenus catingarum* Reissek, Fl. Bras. 11: 26. 1861.

Monteverdia cestrifolia (Reissek) Biral, comb. nov. *Maytenus cestrifolia* Reissek, Fl. Bras. 11: 24. 1861.

Monteverdia chapadensis (R. M. Carvalho-Okano ex Biral & Groppo) Biral, comb. nov. *Maytenus chapadensis* R. M. Carvalho-Okano ex Biral & Groppo, Brittonia 66: 330. 2014.

Monteverdia chiapensis (Lundell) Biral, comb. nov. *Maytenus chiapensis* Lundell, Wrightia 1: 156. 1946.

Monteverdia claredonensis (Britton) Biral, comb. nov. *Maytenus claredonensis* Britton, Bull. Torrey Bot. Club. 39: 8. 1912.

Monteverdia communis (Reissek) Biral, comb. nov. *Maytenus communis* Reissek, Fl. Bras. 11: 22. 1861.

Monteverdia comocladiiformis (Reissek) Biral, comb. nov. *Maytenus comocladiiformis* Reissek, Fl. Bras. 11: 8. 1861.

Monteverdia corei (Lundell) Biral, comb. nov. *Maytenus corei* Lundell, Wrightia 4: 136. 1970.

Monteverdia crassipes (Urb.) Biral, comb. nov. *Maytenus crassipes* Urb., Symb. Antill. 5: 404. 1908.

Monteverdia cuzcoina (Loes.) Biral, comb. nov. *Maytenus cuzcoina* Loes., Bot. Jahrb. Syst. 37: 574. 1906.

Monteverdia cymosa (Krug & Urb.) Biral, comb. nov. *Maytenus cymosa* Krug & Urb., Symb. Antill. 5: 61. 1904.

Monteverdia dasyclada (Mart.) Biral, comb. nov. *Maytenus dasyclada* Mart., Flora 24(Beibl.): 89. 1841.

Monteverdia distichophylla (Mart. ex Reissek) Biral, comb. nov. *Maytenus distichophylla* Mart. ex Reissek, Fl. Bras. 11: 17. 1861.

Monteverdia domingensis (Krug & Urb.) Biral, comb. nov. *Maytenus domingensis* Krug & Urb., Symb. Antill. 5: 56. 1904.

Monteverdia duqueana (Cuatrec.) Biral, comb. nov. *Maytenus duqueana* Reissek, Brittonia 11: 163. 1959.

Monteverdia ebenifolia (Reissek) Biral, comb. nov. *Maytenus ebenifolia* Reissek, Fl. Bras. 11: 18. 1861.

Monteverdia eggersii (Loes.) Biral, comb. nov. *Maytenus eggersii* Reissek, Bot. Jahrb. Syst. 20: 39. 1895.

Monteverdia elaeodendroides (Griseb.) Biral, comb. nov. *Maytenus elaeodendroides* Griseb., Cat. Pl. Cub. 54. 1866.

Monteverdia elongata (Urb.) Biral, comb. nov. *Maytenus elliptica* (Lam.) Krug & Urb. var. *elongata* Urb., Symb. Antill. 5: 66. 1904; *Maytenus elongata* (Urb.) Britton, Sci. Surv. Porto Rico & Virgin Island 5: 516. 1924.

Monteverdia erythroxyla (Reissek) Biral, comb. nov. *Maytenus erythroxyla* Reissek, Fl. Bras. 11: 21. 1861.

Monteverdia evonymoides (Reissek) Biral, comb. nov. *Maytenus evonymoides* Reissek, Fl. Bras. 11: 11. 1861.

Monteverdia ficiformis (Reissek) Biral, comb. nov. *Maytenus ficiformis* Reissek, Fl. Bras. 11: 20. 1861.

Monteverdia flagellata (Rusby) Biral, comb. nov. *Maytenus flagellata* Rusby, Mem. Torrey Bot. Club 6: 20. 1896.

Monteverdia floribunda (Reissek) Biral, comb. nov. *Maytenus floribunda* Reissek, Fl. Bras. 11: 16. 1861.

Monteverdia fugax (Biral & Lombardi) Biral, comb. nov. *Maytenus fugax* Biral & Lombardi, Phytotaxa 261: 99. 2016.

Monteverdia glaucescens (Reissek) Biral, comb. nov. *Maytenus glaucescens* Reissek, Fl. Bras. 11: 10. 1861.

Monteverdia gonoclada (Mart.) Biral, comb. nov. *Maytenus gonoclada* Mart., Flora 24(Beibl.): 89. 1841.

Monteverdia grenadensis (Urb.) Biral, comb. nov. *Maytenus grenadensis* Urb., Symb. Antill. 5: 63. 1904.

Monteverdia haitiensis (Urb.) Biral, comb. nov. *Maytenus haitiensis* Urb., Ark. Bot. 22A: 67. 1928.

Monteverdia harrisii (Krug & Urb.) Biral, comb. nov. *Maytenus harrisii* Krug & Urb., Notizbl. Königl Bot. Gart. Berlin 1: 78. 1895.

Monteverdia horrida (Reissek) Biral, comb. nov. *Maytenus horrida* Reissek, Fl. Bras. 11: 5. 1861.

Monteverdia hotteana (Urb.) Biral, comb. nov. *Maytenus hotteana* Urb., Ark. Bot. 22A: 67. 1928.

Monteverdia huberi (Steyerm.) Biral, comb. nov. *Maytenus huberi* Steyerm., Ann. Missouri Bot. Gard. 75: 1063. 1988.

Monteverdia insculpta (Steyerm.) Biral, comb. nov. *Maytenus insculpta* Steyerm., Ann. Missouri Bot. Gard. 75: 1063. 1988.

Monteverdia ilicifolia (Mart. ex Reissek) Biral, comb. nov. *Maytenus ilicifolia* Mart. ex Reissek, Fl. Bras. 11: 8. 1861.

Monteverdia imbricata (Mart. ex Reissek) Biral, comb. nov. *Maytenus imbricata* Mart. ex Reissek, Fl. Bras. 11: 16. 1861.

Monteverdia jamaicensis (Krug & Urb.) Biral, comb. nov. *Maytenus jamaicensis* Krug & Urb., Notizbl. Königl Bot. Gart. Berlin 1: 78. 1895.

Monteverdia jefeana (Lundell) Biral, comb. nov. *Maytenus jefeana* Lundell, Phytologia 53: 414. 1983.

Monteverdia kanukuensis (A. C. Sm.) Biral, comb. nov. *Maytenus kanukuensis* A. C. Sm., Lloydia 2: 189. 1939.

Monteverdia karstenii (Reissek) Biral, comb. nov. *Maytenus karstenii* Reissek, Fl. Bras. 11: 19. 1861.

Monteverdia krukovii (A. C. Sm.) Biral, comb. nov. *Maytenus krukovii* A. C. Sm., J. Arnold Arbor. 20: 294. 1939.

Monteverdia laevigata (Vahl) Biral, comb. nov. *Rhamnus laevigata* Vahl, Symb. Bot. 3: 41. 1794; *Ceanothus laevigata* (Vahl) DC., Prodr. 2: 30. 1825. *Maytenus laevigata* (Vahl) Griseb. ex Eggers, Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 3: 109. 1876.

Monteverdia laevis (Reissek) Biral, comb. nov. *Maytenus laevis* Reissek, Fl. Bras. 11: 27. 1861.

Monteverdia laurina (Briq.) Biral, comb. nov. *Maytenus laurina* Briq., Annuaire Conserv. Jard. Bot. Genève 20: 362. 1919.

Monteverdia lineata (C. Wright ex Griseb.) Biral, comb. nov. *Maytenus lineata* C. Wright ex Griseb., Cat. Pl. Cub. 54. 1866.

Monteverdia littoralis (R. M. Carvalho-Okano) Biral, comb. nov. *Maytenus littoralis* R. M. Carvalho-Okano, Hoehnea 32: 467. 2005.

Monteverdia loeseneri (Urb.) Biral, comb. nov. *Maytenus loeseneri* Urb., Symb. Antill. 5: 56. 1904.

Monteverdia longifolia (Reissek ex Loes.) Biral, comb. nov. *Maytenus longifolia* Reissek ex Loes., Bot. Jahrb. Syst. 15(Beibl): 9. 1893.

Monteverdia longistipitata (Steyerm.) Biral, comb. nov. *Maytenus longistipitata* Steyerm., Ann. Missouri Bot. Gard. 75: 1064. 1988.

Monteverdia lucayana (Britton) Biral, comb. nov. *Maytenus lucayana* Britton, Bull. New York Gard. 4: 140. 1906.

Monteverdia macrocarpa (Ruiz & Pav.) Biral, comb. nov. *Celastrus macrocarpa* Ruiz & Pav., Fl. Peruv. 3: 8. 1802; *Haenkea macrocarpa* (Ruiz & Pav.) Steud., Nomencl. Bot. 1: 170, 387. 1821. *Maytenus macrocarpa* (Ruiz & Pav.) Briq., Annuaire Conserv. Jard. Bot. Genève 20: 361. 1919.

Monteverdia macrophylla (Reissek) Biral, comb. nov. *Maytenus macrophylla* Mart., Flora 24(Beibl.): 95. 1841.

Monteverdia maestrensis (Urb.) Biral, comb. nov. *Maytenus maestrensis* Urb., Repert. Spec. Nov. Regni Veg. 21: 215. 1925.

Monteverdia manabiensis (Loes.) Biral, comb. nov. *Maytenus manabiensis* Loes., Repert. Spec. Nov. Regni Veg. 1: 161. 1905.

Monteverdia matudae (Lundell) Biral, comb. nov. *Maytenus matudae* Lundell, Lilloa 4: 383. 1939.

Monteverdia megalocarpa (Groppo & Lombardi) Biral, comb. nov. *Maytenus megalocarpa* Groppo & Lombardi, Syst. Bot. 39: 480. 2014.

Monteverdia meguillensis (Rusby) Biral, comb. nov. *Maytenus meguillensis* Rusby, Mem. New York Bot. Gard. 7: 289. 1927.

Monteverdia microcarpa (Fawc. & Rendle) Biral, comb. nov. *Maytenus microcarpa* Fawc. & Rendle, J. Bot. 59: 19. 1921.

Monteverdia microphylla (Urb., Ekman & Loes.) Biral, comb. nov. *Maytenus microcarpa* Urb., Ekman & Loes., Repert. Spec. Nov. Regni Veg. 33: 182. 1933.

Monteverdia monticola (Sandwith) Biral, comb. nov. *Maytenus monticola* Sandwith, Fl. Trinidad & Tobago 1: 174. 1930.

Monteverdia mucugensis (R. M. Carvalho-Okano ex Biral & Groppo) Biral, comb. nov. *Maytenus mucugensis* R. M. Carvalho-Okano ex Biral & Groppo, Brittonia 66: 332. 2014.

Monteverdia myrsinoides (Reissek) Biral, comb. nov. *Maytenus myrsinoides* Reissek, Fl. Bras. 11: 21. 1861.

Monteverdia neblinae (Steyerm.) Biral, comb. nov. *Maytenus neblinae* Steyerm., Ann. Missouri Bot. Gard. 75: 1064. 1988.

Monteverdia nitida (Mart.) Biral, comb. nov. *Maytenus nitida* Mart., Flora 24(Beibl.): 91. 1841.

Monteverdia oblongata (Reissek) Biral, comb. nov. *Maytenus oblongata* Reissek, Fl. Bras. 11: 25. 1861.

Monteverdia obtusifolia (Mart.) Biral, comb. nov. *Maytenus obtusifolia* Reissek, Flora 24(Beibl.): 88. 1841.

Monteverdia ocoensis (M. M. Mejía & Zanoni) Biral, comb. nov. *Maytenus ocoensis* M. M. Mejía & Zanoni, Moscosoa 4: 112. 1986.

Monteverdia opaca (Reissek) Biral, comb. nov. *Maytenus opaca* Reissek, Fl. Bras. 11: 28. 1861.

Monteverdia patens (Reissek) Biral, comb. nov. *Maytenus patens* Reissek, Fl. Bras. 11: 13. 1861.

Monteverdia peruana (Loes.) Biral, comb. nov. *Maytenus alaternoides* Reissek var. *peruana* Loes., Bot. Jahrb. Syst. 37: 574. 1906; *Maytenus peruana* (Loes.) Liesner, Monogr. Syst. Bot. Missouri Bot. Gard. 127: 1271. 2014.

Monteverdia pittieriana (Steyerm.) Biral, comb. nov. *Maytenus pittieriana* Steyerm., Fieldina, Bot. 28: 338. 1952.

Monteverdia planifolia (A. C. Sm.) Biral, comb. nov. *Maytenus planifolia* A. C. Sm., Lloydia 2: 189. 1939.

Monteverdia ponceana (Britton) Biral, comb. nov. *Maytenus ponceana* Britton, Bull. Torrey Bot. Club 51: 10. 1924.

Monteverdia pruinosa (Reissek) Biral, comb. nov. *Maytenus pruinosa* Reissek, Fl. Bras. 11: 20. 1861.

Monteverdia psammophila (Biral & Lombardi) Biral, comb. nov. *Maytenus* Biral & Lombardi, Harvard Pap. Bot. 18: 129. 2013.

Monteverdia purpusii (Lundell) Biral, comb. nov. *Maytenus purpusii* Lundell, Amer. Midl. Naturalist 20: 238. 1938.

Monteverdia pustulata (Steyerm.) Biral, comb. nov. *Maytenus pustulata* Steyerm., Ann. Missouri Bot. Gard. 75: 1084. 1988.

Monteverdia quadrangulata (Schrad.) Biral, comb. nov. *Celastrus quadrangulata* Schrad., Goett. Gel. Anz. 1: 716. 1821; *Maytenus quadrangulata* (Schrad) Loes., Nat. Pflanzenfam 2: 142. 1942.

Monteverdia radlkoferiana (Loes.) Biral, comb. nov. *Maytenus radlkoferiana* Loes., Bot. Jahrb. Syst. 15(Beibl.): 7. 1893.

Monteverdia recondita (Hammel) Biral, comb. nov. *Maytenus recondita* Hammel, Novon 7: 150. 1997.

Monteverdia reflexa (Urb.) Biral, comb. nov. *Maytenus reflexa* Urb., Symb. Antill. 5: 64. 1904.

Monteverdia retusa (Poir.) Biral, comb. nov. *Celastrus retusa* Poir., Encycl. Suppl. 2: 146. 1811; *Maytenus retusa* (Poir.) Briq., Annuaire. Conserv. Jard. Bot. Genève 20: 351. 1919.

Monteverdia revoluta (Alain) Biral, comb. nov. *Maytenus revoluta* Alain, Contr. Ocas. Mus. His. Nat. Col. "De La Salle" 12: 5. 1953.

Monteverdia revoluta (Alain) Biral var. ***bissei*** Mory, comb. nov. *Maytenus revoluta* Alain var. *bissei* Mory, Feddes Repert. 96: 549. 1985.

Monteverdia revoluta (Alain) Biral var. ***jaucoensis*** Mory, comb. nov. *Maytenus revoluta* Alain var. *jaucoensis* Mory, Feddes Repert. 96: 549. 1985.

Monteverdia revoluta (Alain) Biral var. ***macrophylla*** Mory, comb. nov. *Maytenus revoluta* Alain var. *macrophylla* Mory, Feddes Repert. 96: 550. 1985.

Monteverdia rigida (Mart.) Biral, comb. nov. *Maytenus rigida* Mart., Flora 24(Beibl.): 90. 1841.

Monteverdia robusta (Reissek) Biral, comb. nov. *Maytenus robusta* Reissek, Fl. Bras. 11: 15. 1861.

Monteverdia rupestris (Pirani & R. M. Carvalho-Okano) Biral, comb. nov. *Maytenus robusta* Pirani & R. M. Carvalho-Okano, Novon 9: 95. 1999.

Monteverdia samydiformis (Reissek) Biral, comb. nov. *Maytenus samydiformis* Reissek, Fl. Bras. 11: 11. 1861.

Monteverdia sapotiformis (Reissek) Biral, comb. nov. *Maytenus sapotiformis* Reissek, Fl. Bras. 11: 27. 1861.

Monteverdia saxicola (Britton & Wilson) Biral, comb. nov. *Maytenus saxicola* Britton & Wilson, Bull. Torrey Bot. Club 50: 41. 1923.

Monteverdia schippii (Lundell) Biral, comb. nov. *Maytenus schippii* Lundell, Phytologia 1: 305. 1939.

Monteverdia schumanniana (Loes.) Biral, comb. nov. *Maytenus schumanniana* Loes., Notizbl. Bot. Gart. Berlin-Dahlen 13: 218. 1938.

Monteverdia segoviarum (Standl. & L. O. Williams) Biral, comb. nov. *Maytenus segoviarum* Standl. & L. O. Williams, Ceiba 1: 85. 1950.

Monteverdia serpentini (Borhidi & O. Muñiz) Biral, comb. nov. *Maytenus buxifolia* (A. Rich) Griseb. var. *serpentini* Borhidi & O. Muñiz, Acta Bot. Acad. Sci. Hung. 17: 14. 1971; *Maytenus serpentini* (Borhidi & O. Muñiz) Borhidi & O. Muñiz, Bot. Közlem 62: 25. 1975.

Monteverdia sieberiana (Krug & Urb.) Biral, comb. nov. *Maytenus sieberiana* Krug & Urb., Symb. Antill. 5: 60. 1904.

Monteverdia splendens (Urb.) Biral, comb. nov. *Maytenus splendens* Urb., Symb. Antill. 9: 68. 1923.

Monteverdia spinosa (Griseb.) Biral, comb. nov. *Moya spinosa* Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 111. 1874; *Gymnosporia spinosa* (Griseb.) Loes. ex Hicken, Bol. Soc. Physis 1: 30. 1912. *Maytenus spinosa* (Griseb.) Lourteig & O'Donell, Natura 1: 188. 1955.

Monteverdia sprucei (Briq.) Biral, comb. nov. *Maytenus sprucei* Briq., Annuaire Cons. Jard. Bot. Genève 20: 363. 1911.

Monteverdia stipitata (Lundell) Biral, comb. nov. *Maytenus stipitata* Lundell, Phytologia 56: 139. 1984.

Monteverdia subalata (Reissek) Biral, comb. nov. *Maytenus subalata* Reissek, Fl. Bras. 11: 12. 1861.

Monteverdia tetragona (Griseb.) Biral, comb. nov. *Maytenus tetragona* Griseb., Fl. Brit. W. I. 709. 1864.

Monteverdia tikalensis (Lundell) Biral, comb. nov. *Maytenus tikalensis* Lundell, Wrightia 4: 90. 1968.

Monteverdia truncata (Nees) Biral, comb. nov. *Ilex truncata* Nees, Flora 4: 301. 1821; *Maytenus truncata* (Nees) Reissek, Fl. Bras. 11: 5. 1861.

Monteverdia urbaniana (Loes.) Biral, comb. nov. *Maytenus urbaniana* Loes., Bot. Jahrb. Syst. 15(Beibl.): 10. 1893.

Monteverdia urbanii (Alain) Biral, comb. nov. *Maytenus urbanii* Alain, Sida 20: 1645. 2003.

Monteverdia urquiolae (Mory) Biral, comb. nov. *Maytenus urquiolae* Mory, Feddes Repert. 104: 432. 1993.

Monteverdia versluysii (Bold.) Biral, comb. nov. *Maytenus versluysii* Bold., Fl. Dutch W. Ind. Is. 2: 58. 1914.

Monteverdia virens (Urb.) Biral, comb. nov. *Maytenus virens* Urb., Symb. Antill. 5: 60. 1904.

Monteverdia wendtii (Lundell) Biral, comb. nov. *Maytenus wendtii* Phytologia 51: 28. 1984.

KEY TO THE GENERA OF CELASTRACEAE DERIVED FROM NEW WORLD *MAYTENUS* LINEAGES

1\. Indehiscent fruits, aril absent 2
    2\. Glabrous leaves, axillary cymose inflorescences, pedicellate flowers, fruits samaroid .... *Plenckia* Reissek
    2\. Pubescent leaves, axillary and terminal racemose inflorescences, sessile flowers, fruits capsular .... *Fraunhofera* Mart.
1\. Dehiscent fruits, aril present 3
    3\. Flowers 4- or 5-merous, membranaceous pericarp, red or yellowish aril that completely or partially covers the seeds .... *Maytenus* Molina
    3\. Flowers 5-merous, coriaceous pericarp, red or white aril that completely covers the seeds 4
        4\. Leaves fleshy, ovary 3-carpellate, one ovule per carpel, fruits open by three valves, red aril .... *Tricerma* Liebm.
        4\. Multiple leaf types (membranaceous, chartaceous or coriaceous), very rarely fleshy, ovary 2-carpellate, two ovules per carpel, fruits open by two valves, white aril .... *Monteverdia* A. Rich.

ACKNOWLEDGMENTS. We thank two anonymous reviewers and the editors for several helpful suggestions with which to improve the manuscript; the curators of MO and NY for permission to take samples from their collections for DNA extraction; Ricardo Paupitz for informatic support; Fred Barrie for the help with nomenclatural changes; Mariana Saka for the specimen of *Maytenus macrophylla*; Fabíula M. Arantes and Vítor de Andrade Kamimura for help editing the figures; the Fundação de Amparo à Pesquisa do Estado de São Paulo – FAPESP for fellowship grants to L. B. (#2011/21879-5 and #2014/22093-3) and to J. A. L. (#2010/17400-3); and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for fellowship grants to J. A. L. (#307997/2013-8) and E.C.S. (#311001/2014-9), as well as for a research grant to J. A. L. (MCT/CNPq/MEC/CAPES/PROTAX no 562240/2010-1).

LITERATURE CITED

Alexander, P. J., G. Rajanikanth, C. D. Bacon, and C. D. Bailey. 2007. Recovery of plant DNA using a reciprocating saw and silica-based columns. *Molecular Ecology Notes* 7: 5–9.

Álvarez, I. and J. F. Wendel. 2003. Ribosomal ITS sequences and plant phylogenetic inference. *Molecular Phylogenetics and Evolution* 29: 417–434.

Bailey, C. D., T. G. Carr, S. A. Harris, and C. E. Hughes. 2003. Characterization of angiosperm nrDNA polymorphism, paralogy, and pseudogenes. *Molecular Phylogenetics and Evolution* 29: 435–455.

BFG – The Brazil Flora Group. 2015. Growing knowledge: An overview of seed plant diversity in Brazil. *Rodriguésia* 66: 1085–1113.

Biral, L. 2014. Novidades taxonômicas em *Maytenus* (Celastraceae) para a flora da Argentina. *Bonplandia* 23: 43–49.

Biral, L. 2016. *Sistemática e filogenia de* Maytenus *Molina (Celastraceae) na região neotropical*. Ph.D. thesis. Rio Claro, São Paulo: Universidade Estadual Paulista "Júlio de Mesquita Filho".

Biral, L. and J. A. Lombardi. 2016. New synonyms and lectotypifications in the genus *Maytenus* (Celastroideae, Celastraceae) and a new name for the illegitimate *Maytenus nemorosa* from Brazil. *Phytotaxa* 261: 97–100.

Biral, L., E. C. Smidt, M. Bolson, and J. A. Lombardi. 2015. A new species of *Maytenus* (Celastraceae) from the Brazilian Atlantic Forest, with evidence of molecular phylogeny, and two new synonyms for *Maytenus floribunda*. *Phytotaxa* 231: 53–62.

Biral, L., M. P. Simmons, E. C. Smidt, L. R. Tembrock, M. Bolson, R. H. Archer, and J. A. Lombardi. 2017. Data from: Systematics of New World *Maytenus* (Celastraceae) and a new delimitation of the genus. Dryad Digital Repository. http://doi.org/10.5061/dryad.dn78f.

Blattner, F. R. 1999. Direct amplification of the entire ITS region from poorly preserved plant material using recombinant PCR. *BioTechniques* 27: 1180–1186.

Brenan, J. P. M. 1953. Plants collected by the Vernay Nyasaland expedition of 1946. *Memoirs of the New York Botanical Garden* 8: 191–256.

Bull, J. J., J. P. Huelsenbeck, C. W. Cunningham, D. L. Swofford, and P. J. Waddell. 1993. Partitioning and combining data in phylogenetic analysis. *Systematic Biology* 42: 384–397.

Carvalho-Okano, R. M. 1992. *Estudos taxonomicos do genero* Maytenus *Mol. emend. Mol. (Celastraceae) no Brasil extra-amazônico*. Ph.D. thesis. Campinas, São Paulo: Universidade Estadual de Campinas.

Carvalho-Okano, R. M. and H. F. Leitão-Filho. 2004. O gênero *Maytenus* Mol. emend. Mol. (Celastraceae) no Brasil extra-amazônico. Pp. 11–51 in *Conservação e uso sustentável de plantas medicinais e aromáticas: Maytenus spp., espinheira-santa*, eds. M. S. Reis and S. R. Silva. Brasília: Ibama.

Couch, J. A. and P. J. Fritz. 1990. Isolation of DNA from plants high in polyphenolics. *Plant Molecular Biology Reporter* 8: 8–12.

Davis, J. I., K. C. Nixon, and D. P. Little. 2005. The limits of conventional cladistic analysis. Pp. 119–147 in *Parsimony, phylogeny, and genomics*, ed. V. A. Albert. Oxford: Oxford University Press.

Davis, J. I., M. P. Simmons, D. W. Stevenson, and J. F. Wendel. 1998. Data decisiveness, data quality, and incongruence in phylogenetic analysis: an example from the monocotyledons using mitochondrial *atpA* sequences. *Systematic Biology* 47: 282–310.

De La Cruz, M., R. Whitkus, and L. Mota-Bravo. 1995. Tropical tree DNA isolation and amplification. *Molecular Ecology* 4: 787–789.

Desfeux, C. and B. Lejeune. 1996. Systematics of Euromediterranean *Silene* (Caryophyllaceae): Evidence from a phylogenetic analysis using ITS sequences. *Comptes Rendus de l'Académie des Sciences. Série III, Sciences de la Vie* 319: 351–358.

Ding Hou. 1955. A revision of the genus *Celastrus*. *Annals of the Missouri Botanical Garden* 42: 215–302.

Ding Hou. 1962. Celastraceae I. *Flora Malesiana, ser. 1* 6: 227–291.

Doyle, J. J. 1992. Gene trees and species trees: molecular systematics as one-character taxonomy. *Systematic Botany* 17: 144–163.

Doyle, J. J. 1995. The irrelevance of allele tree topologies for species delimitation, and a non-topological alternative. *Systematic Botany* 20: 574–588.

Doyle, J. J. and J. L. Doyle. 1987. A rapid DNA isolation procedure for small amounts of leaf tissue. *Phytochemical Bulletin* 19: 810–815.

Endress, P. K. 1973. Arils and aril-like structures in woody Ranales. *The New Phytologist* 72: 1159–1171.

Exell, A. W. 1953. Tropical African plants: XXIII: Celastraceae. *Kew Bulletin* 23: 103–104.

Farris, J. S. 1989. The retention index and the rescaled consistency index. *Cladistics* 5: 417–419.

Farris, J. S., V. A. Albert, M. Källersjö, D. Lipscomb, and A. G. Kluge. 1996. Parsimony jackknifing outperforms neighbor-joining. *Cladistics* 12: 99–124.

Grisebach, A. 1866. Catalogus Plantarum Cubensium exhibens collectionem Wrightianam aliasque minores ex insula Cuba missas. Lipsiae: Guilielmun Engelmann.

Grisebach, A. 1874. Plantae Lorentzianae. Bearbeitung der ersten und zweiten Sammlung argentinischer Pflanzen des Professor Lorentz zu Cordoba. *Abhandlungen der Königlichen Gesellschaft der Wissenschaften zu Göttingen* 11: 49–283.

Groppo, M. 2009. Celastraceae. Pp. 49–57 in *Flora fanerogâmica da Ilha do Cardoso* vol. 14, eds. M. M. F. R. Melo, F. Barros, S. A. C. Chiea, M. Kirizawa, S. L. Jund-Mendaçolli, and M. G. S. Wanderley. São Paulo: Instituto de Botânica.

Groppo, M. and C. Erbert. 2015. Flora da Serra do Cipó, Minas Gerais: Celastraceae. *Boletim de Botânica da Universidade de São Paulo* 33: 15–27.

Groppo, M., M. P. Simmons, J. Cappa, L. Biral, and J. A. Lombardi. 2014. A new species of *Maytenus* (Celastraceae) with fleshy fruits from eastern Brazil, with notes on the delimitation of *Maytenus*. *Systematic Botany* 39: 478–484.

Hudson, R. R. 1990. Gene genealogies and the coalescent process. *Oxford Surveys in Evolutionary Biology* 7: 1–44.

Johnson, L. A. and D. E. Soltis. 1995. Phylogenetic inference in Saxifragaceae s. s. and *Gilia* (Polemoniaceae) using *matK* sequences. *Annals of the Missouri Botanical Garden* 82: 149–175.

Jordaan, M. and A. E. van Wyk. 1999. Systematic studies in the subfamily Celastroideae (Celastraceae) in southern Africa: Reinstatement of the genus *Gymnosporia*. *South African Journal of Botany* 65: 177–181.

Jordaan, M. and A. E. van Wyk. 2003. Reinstatement of *Gymnosporia* (Celastraceae): Implications for the Flora Malesiana region. *Telopea* 10: 155–167.

Katoh, K. and H. Toh. 2008a. Improved accuracy of multiple ncRNA alignment by incorporating structural information into a MAFFT based framework. *BMC Bioinformatics* 9: 212.

Katoh, K. and H. Toh. 2008b. Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics* 9: 286–298.

Kim, K.-J. 2015. *Consortium for the barcode of life: Plant working group*. Washington D. C.: National Museum of Natural History. http://www.barcoding.si.edu/plant_working_group.html/ (last accessed 28 May 2015).

Kluge, A. G. and J. S. Farris. 1969. Quantitative phyletics and the evolution of Anurans. *Systematic Zoology* 18: 1–32.

Kuzoff, R. K., J. A. Sweere, D. E. Soltis, P. S. Soltis, and E. A. Zimmer. 1998. The phylogenetic potential of entire 26S rDNA sequences in plants. *Molecular Biology and Evolution* 15: 251–263.

Liebmann, F. M. 1854. Novorum plantarum mexicanarum generum Decas. *Videnskabelige Meddelelser fra den naturhistoriske Forening i Kjoebenhavn* 1853: 90–107.

Loesener, T. 1942. Celastraceae. Pp. 87–197 in *Die Natürlichen Pflanzenfamilien* vol. 20b, eds. A. Engler, H. Harms, and J. Mattfeld. Berlin: Duncker and Humblot.

Lorenzi, H. 2009. *Árvores Brasileiras* vol. 3. Nova Odessa: Instituto Plantarum de Estudos da Flora Ltda.

Lourteig, A. and C. A. O'Donell. 1955. Las Celastrales de Argentina y Chile. *Natura* 1: 181–233.

Lundell, C. L. 1938. Two new species of *Plenckia*. *Phytologia* 1: 284–286.

Lundell, C. L. 1939. Studies in American Celastraceae. II. Notes on genera and species from Mexico and South America. *Lilloa* 4: 377–387.

Lundell, C. L. 1971. Studies of American plants III. *Wrightia* 4: 153–170.

Lundell, C. L. 1972. Studies of American plants V. *Wrightia* 5: 1–9.

Maddison, D. R. and W. P. Maddison. 2001. MacClade: Analysis of phylogeny and character evolution version 4.03. Sunderland: Sinauer Associates.

McKenna, M. J., M. P. Simmons, C. D. Bacon, and J. A. Lombardi. 2011. Delimitation of the segregation genera of *Maytenus*. *Systematic Botany* 36: 922–933.

McNeill, J., F. R. Barrie, W. R. Buck, V. Demoulin, W. Greuter, D. L. Hawksworth, P. S. Herendeen, S. Knapp, K. Marhold, J. Prado, W. F. Prud'homme van Reine, G. F. Smith, J. H. Wiersema, and N. J. Turland. 2012. International code of botanical nomenclature (Melbourne code) adopted by the Eighteenth International Botanical Congress, Melbourne, Australia, July 2011. *Regnum Vegetabile* 154. Koeltz Scientific Books: Königstein.

Mory, B. 2010. Celastraceae. Pp. 3–80 in *Flora de la República de Cuba, Série A, Plantas Vasculares. Fascículo 16*, eds. W. Greuter and R. Rankin Rodríguez. Ruggell: Editorial Gantner.

Müller, K. 2006. Incorporating information from length-mutational events into phylogenetics analysis. *Molecular Phylogenetics and Evolution* 38: 667–676.

Nesom, G. L. 2009. Notes on the taxonomy of *Maytenus phyllanthoides* (Celastraceae). *Phytologia* 9: 64–68.

Nixon, K. C. 2002. WinClada version 1.00.08. Ithaca: published by the author.

Rauscher, J. T., J. J. Doyle, and A. H. D. Brown. 2004. Multiple origins and nrDNA internal transcribed spacer homeologue evolution in the *Glycine tomentella* (Leguminosae) allopolyploid complex. *Genetics* 166: 987–998.

Reissek, S. 1861. Celastrineae, Ilicineae, Rhamneae. Pp. 1–34 in *Flora Brasiliensis* vol. 11(1), eds. K. F. P. Martius and A. G. Eichler. Lipsiae: Frid Fleischer.

Richard, A. 1845. Botanique. Plantes Vasculaires. In: de la Sagra, R. (ed.) *Histoire Physique, Politique et Naturelle L'ile de Cuba*, t. 10. Arthus Bertrand, Paris.

Rocha, C. F. D., D. Vrcibradic, V. A. Menezes, and C. V. Ariani. 2009. Ecology and natural history of the easternmost native lizard species in South America, *Trachylepis atlantica* (Scincidae), from the Fernando de Noronha Archipelago, Brazil. *Journal of Herpetology* 43: 450–459.

Sebsebe Demissew. 1985. The genus *Maytenus* (Celastraceae) in NE tropical Africa and tropical Arabia. *Acta Universitatis Upsaliensis. Symbolae Botanicae Upsaliensis* 25: 1–98.

Simmons, M. P. 2004a. Celastraceae. Pp. 29–64 in *The families and genera of flowering plants. VI. Flowering plants. Dicotyledons. Celastrales, Oxalidales, Rosales, Cornales, Ericales*, ed. K. Kubitzki. Berlin: Springer.

Simmons, M. P. 2004b. Independence of alignment and tree search. *Molecular Phylogenetics and Evolution* 31: 874–879.

Simmons, M. P. and F. R. Barrie. 2014. *Haydenoxylon*, a replacement name for *Haydenia* (Celastraceae). *Novon* 23: 224–225.

Simmons, M. P. and J. V. Freudenstein. 2002. Artifacts of coding amino acids and other composite characters for phylogenetic analysis. *Cladistics* 18: 354–365.

Simmons, M. P. and J. V. Freudenstein. 2011. Spurious 99% bootstrap and jackknife support for unsupported clades. *Molecular Phylogenetics and Evolution* 61: 177–191.

Simmons, M. P. and J. P. Hedin. 1999. Relationships and morphological character change among genera of Celastraceae sensu lato (including Hippocrateaceae). *Annals of the Missouri Botanical Garden* 86: 723–757.

Simmons, M. P. and H. Ochoterena. 2000. Gaps as characters in sequence based phylogenetic analyses. *Systematic Biology* 49: 369–381.

Simmons, M. P., H. Ochoterena, and T. G. Carr. 2001. Incorporation, relative homoplasy, and effect of gap characters in sequence-based phylogenetic analyses. *Systematic Biology* 50: 454–462.

Simmons, M. P., J. J. Cappa, R. H. Archer, A. J. Ford, D. Eichstedt, and C. C. Clevinger. 2008. Phylogeny of the Celastreae (Celastraceae) and the relationships of *Catha edulis* (qat) inferred from morphological characters and nuclear and plastid genes. *Molecular Phylogenetics and Evolution* 48: 745–757.

Simmons, M. P., C. D. Bacon, J. J. Cappa, and M. J. McKenna. 2012. Phylogeny of Celastraceae subfamilies Cassinoideae and Tripterygioideae inferred from morphological characters and nuclear and plastid loci. *Systematic Botany* 37: 456–467.

Small, J. K. 1928. *Maytenus phyllanthoides. Addisonia: Colored Illustrations and Popular Descriptions of Plants* 13: 39–40. Pl. 436.

Steele, K. P. and R. Vilgalys. 1994. Phylogenetic analyses of Polemoniaceae using nucleotide sequences of the plastid gene *matK*. *Systematic Botany* 19: 126–142.

Steyermark, J. A. 1988. Flora of Venezuelan Guayana V. *Annals of the Missouri Botanical Garden* 75: 1058–1086.

Stöver, B. C. and K. F. Müller. 2010. TreeGraph 2: Combining and visualizing evidence from different phylogenetic analyses. *BMC Bioinformatics* 11: 7.

Swofford, D. L. 2001. PAUP*: Phylogenetic analysis using parsimony (*and other methods). Sunderland: Sinauer Associates.

Taberlet, P., L. Gielly, G. Pautou, and J. Bouvet. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* 17: 1105–1109.

Tembrock, L. R., M. P. Simmons, C. M. Richards, P. A. Reeves, A. Reilley, M. A. Curto, H. Meimberg, G. Ngugi, S. Demissew, A. W. Al Khulaidi, M. Althobhani, S. Simpson, and D. M. Varisco. 2017. Phylogeography of the wild and cultivated stimulant plant qat (*Catha edulis*, Celastraceae) in areas of historic cultivation. *American Journal of Botany* 104: 538–549.

Wendel, J. F., A. Schnabel, and T. Seelanan. 1995. Bidirectional interlocus concerted evolution following allopolyploid speciation in cotton (*Gossypium*). *Proceedings of the National Academy of Sciences USA* 92: 280–284.

White, T. J., T. Bruns, S. Lee, and J. Taylor. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315–322 in *PCR protocols: A guide to methods and applications*, eds. M. Innis, D. Gelfand, J. Sninsky, and T. White. San Diego: Academic Press.

Wilkinson, M. 1995. A comparison of two methods of character construction. *Cladistics* 11: 297–308.

Yokoyama, J., M. Suzuki, K. Iwatsuki, and M. Hasebe. 2000. Molecular phylogeny of *Coriaria*, with special emphasis on the disjunct distribution. *Molecular Phylogenetics and Evolution* 14: 11–19.

Zhang, X., Z. Zhang, and T. Stützel. 2011. Aril development in Celastraceae. *Feddes Repertorium* 122: 445–455.

Zhang, X., Z. Zhang, and T. Stützel. 2014. Ontogeny on the ovule and seed wing in *Catha edulis* (Vahl) Endl. (Celastraceae). *Flora – Morphology, Distribution. Functional Ecology of Plants* 209: 179–184.

Zurawski, G. and M. T. Clegg. 1987. Evolution of higher-plant chloroplast DNA-encoded genes: implications for structure-function and phylogenetic studies. *Annual Review of Plant Physiology* 38: 391–418.

Appendix 1. List of taxa sampled with taxonomic authorities, voucher information and GenBank accession numbers for new sequences (ITS rDNA, 26S rDNA, *matK*, *trnL-F*) generated for this study.

Maytenus acanthophylla Reissek—*L. Biral 1072*, Brazil (HRCB); KU892171, KX231994, KX231954, KX232036. ***M. apurimacensis*** Loes.—*M. Merello 1078*, Peru (MO); KU892172, KX231995, KX231955, KX232037. ***M. brasiliensis*** Mart.—*L. Biral 804*, Brazil (HRCB); KU892173, KX231996, KX231956, KX232038. ***M. brasiliensis*** Mart.—*L. Biral 805*, Brazil (HRCB); KU892174, KX231997, KX231957, KX232039. ***M. catingarum*** Reissek—*L. Biral 746*, Brazil (HRCB); KU892175, KX231998, KX231958, KX232040. ***M. chapadensis*** R. M. Carvalho-Okano ex Biral & Groppo—*L. Biral 826*, Brazil (HRCB); KU892176, KX231999, KX231959, KX232041. ***M. chubutensis*** (Speg.) Lourteig, O'Donell & Sleumer—*R.H. Fortunato 5774*, Argentina (MO); KU892177, KX232000, KX231960, KX232062 (*trnL* intron), KX232078 (*trnL* spacer). ***M. communis*** Reissek—*J.A. Lombardi 8567*, Brazil (HRCB); KU892178, KX232001, KX231961, KX232042. ***M. conferta*** (Ruiz & Pav.) Reissek ex Loes.—*S.G. Beck 28853*, Bolivia (HRCB); KU892179, KX232002, KX231962, KX232063 (*trnL* intron), KX232079 (*trnL* spacer). ***M. dasyclada*** Mart.—*L. Biral 896*, cult. Brazil (HRCB); KU892180, KX232003, KX231963, KX232043. ***M. distichophylla*** Mart. ex Reissek—*J.A. Lombardi 8024*, Brazil (HRCB); KU892181, KX232004, KX231964, KX232064 (*trnL* intron), KX232080 (*trnL* spacer). ***M. erythroxyla*** Reissek—*J. Jardim 5905*, Brazil (HRCB); KU892182, KX232005, KX231965, KX232065 (*trnL* intron), KX232081 (*trnL* spacer). ***M. evonymoides*** Reissek—*J.A. Lombardi 8296*, Brazil (HRCB); KU892183, KX232006, KX231966, KX232066 (*trnL* intron), KX232082 (*trnL* spacer). ***M. floribunda*** Reissek—*L. Biral 835*, Brazil (HRCB); KU892184, KX232007, KX231967, KX232044. ***M. fugax*** Biral & Lombardi—*L. Biral 810*, Brazil (HRCB); —,—,—, KX232052. ***M. glaucescens*** Reissek—*L. Biral 876*, Brazil (HRCB); KU892185, KX232008, KX231968, KX232045. ***M. gonoclada*** Mart.—*J.A. Lombardi 9123* (HRCB); KU892186, KX232009, KX231969, KX232046. ***M. gonoclada*** Mart.—*J.A. Lombardi 9150*, Brazil (HRCB); KU892187, KX232010, KX231970, KX232067 (*trnL* intron), KX232083 (*trnL* spacer). ***M. guyanensis*** Klotzsch ex Reissek—*E. Prata 229*, Brazil (HRCB); KU892188, KX232011,—, KX232068 (*trnL* intron), KX232084 (*trnL* spacer). ***M. ilicifolia*** Mart. ex Reissek—*L. Biral 721*, Brazil (HRCB); KU892189, KX232012, KX231971, KX232047. ***M. imbricata*** Mart. ex Reissek—*L. Biral 1083*, Brazil (HRCB); KU892190, KX232013, KX231972, KX232048. ***M. laurina*** Briq.—*E. Prata 591*, Brazil (HRCB); KU892191, KX232014, KX231973, KX232069 (*trnL* intron). ***M. longifolia*** Reissek ex Loes.—*L. Biral 809*, Brazil (HRCB); KU892192, KX232015, KX231974, KX232049. ***M. macrophylla*** Mart.—*M.N. Saka 279*, Brazil (HRCB); KU892193, KX232016, KX231975, KX232050. ***M. megalocarpa*** Groppo & Lombardi—*L. Biral 1084*, Brazil (HRCB); KU892194, KX232017, KX231976, KX232070 (*trnL* intron), KX232085 (*trnL* spacer). ***M. meguillensis*** Rusby—*S. G. Beck 25113*, Bolivia (HRCB); KU892195, KX232018,—, KX232071 (*trnL* intron), KX232086 (*trnL* spacer). ***M. monticola*** Sandwith—*K. Lee 56*, Trinidad and Tobago (NY); KU892196, KX232019, KX231977, KX232072 (*trnL* intron), KX232087 (*trnL* spacer). ***M. mucugensis*** R. M. Carvalho-Okano ex Biral & Groppo—*L. Biral 749*, Brazil (HRCB); KU892197, KX232020, KX231978, KX232051. ***M. obtusifolia*** Mart.—*L. Biral 1016*, Brazil (CVRD); KU892198, KX232021, KX231979, KX232053. ***M. rigida*** Mart.—*L. Biral 752*, Brazil (HRCB); KU892199, KX232022, KX231980, KX232054. ***M. robusta*** Reissek—*L. Biral 1085*, Brazil (HRCB); KU892200, KX232023, KX231981, KX232055. ***M. schippii*** Lundell—*E. Velasco-Sinaca 582*, Mexico (NY); KU892201, KX232024, KX231982, KX232073 (*trnL* intron), KX232088 (*trnL* spacer). ***M. schumanniana*** Loes.—*L. Biral 803*, Brazil (HRCB); KU892202, KX232025, KX231983, KX232056. ***Maytenus* sp.**—*J.A. Lombardi 7822*, Brazil (HRCB); KU892203, KX232026, KX231984, KX232057. ***M. sprucei*** Briq.—*E. Prata 721*, Brazil (HRCB); —, KX232028, KX231986, KX232074 (*trnL* intron), KX232089 (*trnL* spacer). ***M. spinosa*** (Griseb.) Lourteig & O'Donell—*R. Michel 4111*, Bolivia (MO); KU892204, KX232027, KX231985, KX232075 (*trnL* intron), KX232090 (*trnL* spacer). ***M. subalata*** Reissek—*L. Biral 884*, Brazil (HRCB); KU892205, KX232029, KX231987,—. ***M. truncata*** (Nees) Reissek—*L. Biral 1078*, Brazil (HRCB); KU892206,—, KX231988, KX232058. ***M. urbaniana*** Loes.—*L. Biral 1063*, Brazil (HRCB); KU892207, KX232030, KX231989, KX232059. ***M. viscifolia*** Griseb.—*S.G. Beck 33020*, Argentina (HRCB); KU892208, KX232031,—,—. ***M. vitis-idaea*** Griseb.—*S.G. Beck 9746*, Bolivia (HRCB); KU892209, KX232032, KX231990, KX232076 (*trnL* intron), KX232090 (*trnL* spacer). ***Plenckia integerrima*** Lundell—*G. Torrico 290*, Bolivia (HRCB); KU892210, KX232033, KX231991, KX232077 (*trnL* intron), KX232092 (*trnL* spacer). ***P. populnea*** Reissek—*L. Biral 828*, Brazil (HRCB); KU892211, KX232034, KX231992, KX232060. ***Schaefferia argentinensis*** Speg.—*L. Biral 799*, Brazil (HRCB); KU892212, KX232035, KX231993, KX232061.

APPENDIX 2. List of morphological characters included in the simultaneous analysis.

1) habit: 0 = shrublet, 1 = shrub, 2 = tree, 3 = liana; 2) thorn presence: 0 = absent, 1 = present; 3) young twigs arrangement: 0 = whorled, 1 = distichous; 4) type of transverse section of young twigs: 0 = flattened, 1 = carinate, 2 = sub-winged or winged; 5) lenticel presence on young twigs: 0 = absent, 1 = present; 6) indumentum presence on young twigs: 0 = absent, 1 = present; 7) kind of indumentum on young twigs: 0 = tomentose, 1 = puberulent, 2 = strigose; 8) phyllotaxy on vegetative shoots: 0 = alternate, 1 = opposite or whorled; 9) arrangement of leaves on branches: 0 = distichous, 1 = spiral; 10) leaf position along the branches: 0 = more or less evenly spaced throughout the branches, 1 = more or less evenly spaced throughout the branches, but some leaves concentrated at the apex of the branches, 2 = fascicled on short branches; 11) leaf position on twigs or branches: 0 = spreading, 1 = ascending or imbricated; 12) presence of leaf pubescence: 0 = absent, 1 = present; 13) leaf margin: 0 = entire, 1 =crenate/dentate, 2 = spinose; 14) distribution of spines on leaf margin: 0 = regular, 1 = irregular, concentrated on base, 2 = irregular, concentrated on apex; 15) elevation of leaf margin: 0 = flat, 1 = revolute; 16) leaf consistency: 0 = membranaceous, 1 = chartaceous, 2 = coriaceous, 3 = fleshy; 17) elevation of secondary veins on adaxial face of leaves: 0 = immersed, 1 = flat, 2 = raised, 3 = inconspicuous; 18) elevation of secondary veins on abaxial side of leaves; 0 = flat, 1 = raised, 2 = inconspicuous; 19) position of secondary veins on leaves relative to the primary vein: 0 = spreading, 1 = ascending; 20) wax presence on leaf surface: 0 = absent, 1 = present; 21) inflorescence position: 0 = entirely axillary, 1 = at least some inflorescences terminal, 2 = cauline; 22) inflorescence type: 0 = cymose, 1 = thyrsoid to racemose, 2 = umbel, 3 = fasciculate, 4 = flowers solitary; 23) length of inflorescence peduncle relative to flower pedicel length: 0 = 1–11 mm long × 1–7 mm long, 1 = 13–36 mm long × 3–10 mm long; 24) distribution of flowers on the peduncle: 0 = along the peduncle, 1 = concentrated only at the apex; 25) flower sexuality: 0 = unisexual, 1 = bisexual; 26) plants with unisexual-flowers: 0 = dioecious, 1 = monoecious; 27) perianth merosity: 0 = 4-merous, 1 = 5-merous; 28) disc division: 0 = continuous, 1 = discontinuous; 29) disc shape: 0 = cupular or columnar, 1 = annular, flat, or margins upturned; 30) filament insertion relative to disc: 0 = at outer disc margin on top of disc, 1 = inside inner edge of disc; 31) anther attachment: 0 = basifixed, 1 = dorsifixed; 32) anther versatility: 0 = fixed, 1 = versatile; 33) ovary pubescence: 0 = glabrous, 1 = puberulent; 34) carpel number: 0 = two, 1 = three; 35) ovary septa walls for axile placentation: 0 = complete, 1 = incomplete; 36) ovule number per locule: 0 = one, 1 = two or four; 37) axile ovule attachment: 0 = 'basal to axile, erect to horizontal', 1 = pendulous; 38) fruit type: 0 = dehiscent, 1 = indehiscent; 39) indehiscent fruit type: 0 = drupe, 1 = samaroid; 40) capsular fruit shape: 0 = obovoid to spheroid, 1 = tetragonal; 41) type of valves in dehiscent fruit: 0 = reflexed, 1 = upright; 42) pericarp consistency: 0 = membranaceus, 1 = coriaceous; 43) aril presence: 0 = present, 1 = absent; 44) aril position on seed: 0 = entirely enveloping seed, 1 = partly enveloping seed; 45) presence of crystals in leaf epidermal cells: 0 = absent, 1 = present; 46) type of stomata: 0 = cyclocytic, 1 = laterocytic, 2 = anisocytic.