The Transfer of the Genus *Lytocaryum* to *Syagrus*

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In this paper we formally transfer all four known species of *Lytocaryum* to the genus *Syagrus* based on recent molecular analyses that show it as a monophyletic group either nested within *Syagrus*, making *Syagrus* paraphyletic or sister to it. Because of these conflicting results between gene and species trees and the imperfect morphological character distinctions used to maintain these two genera, we have decided that *Lytocaryum* should be subsumed taxonomically within *Syagrus*. The new combination *Sygrus itapebiensis* is made.

Noblick and Lorenzi (2010a) reviewed the genus *Lytocaryum* in detail and a new species, *L. itapebiense*, was described. The objective of this paper is to justify the transfer of *Lytocaryum* to *Syagrus*. Placing *Lytocaryum* and *Syagrus* into the same genus is not a new concept. Early-discovered species of *Lytocaryum* were originally placed together with many current *Syagrus* species in the genus *Cocos*, i.e. *C. insignis* and *C. weddelliana* (Drude 1881, Hooker 1884, Wendland 1871). Transferring *Lytocaryum* into *Syagrus* is also not a new concept. Beccari (1916) did just that when he created two new names in *Syagrus, S. insignis*

and *S. weddelliana*. Even Burret (1937) did the same when he described *Syagrus hoehnei*. It was Toledo (1944) and Burret and Potzal (1956) who respectively created the genera *Lytocaryum* and *Microcoelum*, with the only difference being in the nature of their endosperm. However, because the only differences were in endosperm, *Microcoelum* was then synonymized into *Lytocaryum* by Uhl and Dransfield (1987). After several failed attempts to publish a revision of *Syagrus*, Glassman (1987) was forced by the strong popular botanical opinion at the time to reverse his earlier unpopular idea of sinking most of the

segregate genera including Lytocaryum and Microcoelum into the genus Syagrus (Glassman 1965). In the 1965 publication, Glassman had denigrated the importance of the splitting exocarp and mesocarp (Fig. 1) in *Microcoelum* and Lytocaryum as a weak characteristic for generic distinction. Although he conceded the presence of a thin, fragile endocarp as a character of these two genera, he still questioned whether these two characteristics (splitting exocarp and mesocarp and fragile endocarp) were sufficient for generic distinction, Thus, Glassman (1965) synonymized Lytocaryum and Microcoelum into Syagrus along with several other segregate genera, including Arecastrum, Arykuryroba, Barbosa, and Chrysallidosperma. All of these segregate genera have presently been accepted as synonyms of Syagrus except for Lytocaryum (Uhl & Dransfield 1987, Dransfield et al. 2005, 2008).

Imperfect Morphological Evidence

There is no one character found in *Lytocaryum* that is also not more or less already present in *Syagrus*, except perhaps for the fine abaxial leaflet tomentum. Dransfield et al. (2008) used the following characters in their dichotomous key to maintain *Lytocaryum* generically distinct from *Syagrus*:

Leaflets densely white or pale brown tomentose abaxially.

Leaflets very narrow, close, and regularly arranged.

Epicarp and mesocarp splitting regularly and longitudinally from the apex to the base into three sections at maturity, exposing the thin endocarp (Fig. 1).

Anthers versatile.

Leaflets with densely white or pale brown tomentose abaxially. While many Syagrus species have a heavy waxy bloom abaxially, there are no species with fine tomentose hairs on the abaxial side of the leaflet laminae. Many Syagrus do have ramenta on the abaxial vein (sometimes even profusely so), but no fine tomentum on the abaxial leaflet blade. Nevertheless, this is a weak character on which to base a genus. Take for example the former genus *Polyandrococos* and *Allagoptera*. Polyandrococos not only has tomentum abaxially, while Allagoptera is glabrous, but it is also caulescent and has an entirely different leaflet anatomy. Polyandrococos is a proven sister to the Allagoptera clade both with molecular (Hahn 2002, Gunn 2004) and morphological data (Noblick et al. 2013), but nevertheless the genus was synonymized (Dransfield et al. 2005, 2008). Therefore, Dransfield et al. (2005, 2008) apparently concluded that the presence of tomentum on the abaxial side of leaflets was not a good character on which to base a genus.

Leaflets that are very narrow, close, and regularly arranged. Middle leaflet width in Lytocaryum can vary from 0.5–2.0 cm, with L. hoehnei having the widest leaflets. Narrow leaflets with a regular leaflet arrangement are also found in Syagrus, especially among the acaulescent ones. The combination of narrow and regularly spaced leaflets is not as common in Syagrus; yet, S. graminifolia, S. lilliputiana, S. procumbens and S. pleiocladoides have both very narrow (0.4–1.5 cm) and regularly arranged leaflets.

The epicarp and mesocarp splitting from apex to base. In the most recently discovered Lyto*caryum* species (Noblick & Lorenzi 2010a), we observed that the newest species belonging to this clade, L. itapebiense, does not have a splitting exocarp and mesocarp and yet it has all of the other morphological characters that have been used to delineate the genus (narrow, regularly spaced leaflets and abaxially tomentose leaflets, versatile anthers). The molecular analyses of several WRKY loci also place it solidly in the Lytocaryum clade with strong support (Meerow et al. 2009, 2014). There are four other *Syagrus* species the fruit of which split at least at their tips, often exposing their endocarp (Fig. 2). All of these are rock-loving palms from the Serra do Mar region of Brazil (Rio de Janeiro, Espirito Santo, southern Bahia) and include S. picrophylla Barb.Rodr., S. lorenzoniorum Noblick & Lorenzi, S. kellyana Noblick & Lorenzi, and S. ruschiana (Bondar) Glassman (Lorenzi et al. 2010, Noblick & Lorenzi 2010b).

Anthers versatile. Under the Lytocaryum/Syagrus couplet, Dransfield et al. (2008) admitted that some Syagrus species (even if only rarely) do also have versatile anthers.

Dransfield et al. (2008) also mentioned a thin, rather fragile endocarp, which Glassman (1965) reported as well. Although the presence of a thin fragile endocarp is mostly true, even some of the newly discovered acaulescent *Syagrus* species have thin endocarps as well. Therefore, it would appear that nearly all of the morphological characters for maintaining the genus *Lytocaryum* distinct from *Syagrus* are imperfect.



1. Mature Lytocaryum weddellianum (= Syagrus weddelliana) fruits showing the longitudinally splitting epicarps and exposed endocarps.

Molecular Evidence

The close relationship of Lytocaryum and Syagrus inferred by previous studies with plastid (Hahn 2002) and nuclear (Gunn 2004) sequences, morphology (Dransfield et al. 2008, Uhl et al. 1987), and combinations of molecular and morphological characters (Baker et al. 2009) was further corroborated by Meerow et al. (2009, 2014). Meerow and colleagues used the highly resolute WRKY gene family, first across 72 samples of the subtribe Attaleinae (Meerow et al. 2009) and later across the entire tribe Cocoseae (Meerow et al. 2014). The former 2009 study resolved Lytocaryum embedded within Syagrus. In Meerow et al. (2014), Lytocaryum, previously nested in Syagrus, was now positioned by combined maximum parsimony with the software program PAUP ver. 4.0b10 (Swofford 2002) and maximum likelihood (ML) using TREEFINDER (Jobb 2011) as sister to Syagrus with high support; but Bayesian analysis (BEAST v.1.8.0; Heled & Drummond 2010, Drummond et al. 2012) maintained Lytocaryum embedded within Syagrus. Lytocaryum was also embedded within Syagrus in four parsimony (shortest) consensus gene trees for the loci WRKY12,

WRKY16, WRKY19 and WRKY21 (Supplementary Information Figs. S3-S6, respectively, in Meerow et al. 2014). Meerow et al. (2014) also did three different species tree analyses. Species tree analyses attempt to resolve the most likely phylogeny (evolutionary tree) for the group under study, treating each of the individual gene trees separately (rather than combining them into one super matrix). These methodologies grew out of the realization that each gene history may not conform exactly to the "true" species phylogeny. This can be due to several factors: hybridization, gene duplication and loss, or what is called incomplete lineage sorting or deep coalescence (Maddison 1997, Maddison & Knowles 2006, Degnan & Rosenberg 2009, Edwards 2009, Knowles 2009, Anderson et al. 2012). In the latter, gene sequences diverge before speciation takes place. The species trees from all three analyses positioned Lytocaryum as sister to Syagrus.

Conclusion

Whether *Lytocaryum* is indeed sister to *Syagrus* is clearly controversial. Again, it is necessary to look at the six MP consensus gene trees,



2. Mature *Syagrus ruschiana* fruits showing the epicarps beginning to split longitudinally.

four of which render Syagrus paraphyletic by embedding Lytocaryum within it (Meerow et al. 2014, Supplementary Information Figs. S3–6). It is only when all six loci are combined that a sister relationship emerges (Fig. 1 in Meerow et al. 2014). Yet this is also supported by all three of the species trees (Fig. 3A-C in Meerow et al. 2014). The question that perhaps should be asked, then, is whether there is much merit maintaining *Lytocaryum* as a genus distinct from Syagrus, regardless of which resolution is the "true" one. Our conclusion is that there is no merit in maintaining Lytocaryum as a distinct genus. Not only is the morphological support imperfect, but the molecular evidence is inconclusive as well, even though we are inclined to accept the genus as a sister to Syagrus. The question of whether the Lytocaryum clade is a sister to Syagrus or embedded within Syagrus becomes a moot point by simply synonymizing Lytocaryum species into Syagrus as did Glassman (1965) nearly 50 years ago.

Taxonomic Treatment

Syagrus Mart., Palm. fam. 18. 1824. Type: S. cocoides Mart.

Langsdorffia Raddi, Mem. Mat. Fis. Soc. Ital. Sci. 18(2): 345. 1820 (non Mart., 1818).

Type: *L. pseudococos* Raddi (=*Syagrus pseudococos* (Raddi) Glassman).

Platenia H.Karst., Linnaea 28: 250. 1856. Type: *P. chiragua* H. Karst. (*=Syagrus chiragua* (H. Karst.) H. Wendl.) (see Bernal & Galeano 1989).

Glaziova Mart. ex Drude, in Mart., Fl. bras. 3(2): 295. 1881. Lectotype: *G. martiana Glaz.* ex Drude (illegitimate name) (= *Lytocaryum weddellianum* [H. Wendl.] Toledo) (see H.E. Moore 1963) (=*Syagrus weddelliana* [H. Wendl.] Becc.).

Barbosa Becc., Malpighia 1: 349, 352. 1887. Type: *B. pseudococos* (Raddi) Becc. (*Langsdorffia pseudococos* Raddi) (=*Syagrus pseudococos* (Raddi) Glassman).

Rhyticocos Becc., Malpighia 1: 350, 353. 1887. Type: *R. amara* (Jacq.) Becc. (*Cocos amara* Jacq.) (=*Syagrus amara* (Jacq.) Mart.).

Arikuryroba Barb.Rodr., Pl. jard. Rio de Janeiro 1:5. 1891. Type: *A. capanemae* Barb. Rodr. *=A. schizophylla* (Mart.) L.H. Bailey (*Cocos schizophylla* Mart.). *=Syagrus schizophylla* (Mart.) Glassman).

Arikury Becc., Agric. Colon. 10: 445. 1916. Superfluous substitute name.

Arecastrum (Drude) Becc., Agric. Colon. 10: 446. 1916. Cocos subgenus Arecastrum Drude in Mart., Fl. bras. 3 (2): 402. 1881. Type: A. romanzoffianum (Cham.) Becc. (Cocos romanzoffiana Cham.) (=Syagrus romanzoffiana (Cham.) Glassman).

Lytocaryum Toledo, Arq. Bot. Estado São Paulo ser. 2. 2(1): 6. 1944. Type: *L. hoehnei* (Burret) Toledo (*=Syagrus hoehnei* Burret).

Microcoelum Burret & Potztal, Willdenowia 1: 387. 1956. Lectotype: M. martianum (Glaz. ex Drude) Burret & Potztal (Glaziova martiana Glaz. ex Drude [illegitimate name], =Syagrus weddelliana [H. Wendl.] Becc. [Cocos weddellianum H. Wendl., Lytocaryum weddellianum (H. Wendl.) Toledo, M. weddellianum (H. Wendl.) H.E. Moore]).

Chrysallidosperma H.E. Moore, Principes 7: 109. 1963. Type: *C. smithii* H.E. Moore (= *Syagrus smithii* (H.E. Moore) Glassman).

Syagrus hoehnei Burret, Notizbl. Bot. Gart. Berlin-Dahlem 13: 678. 1937.

Lytocaryum hoehnei (Burret) Toledo, Arq. Bot. Estado São Paulo, n.s., f.m., 2: 7. 1944.

Syagrus insignis (Rob.) Becc., Agric. Colon. 10: 467. 1916.

**Glaziova insignis* Rob., Gard. Chron., n.s., 1: 665. 1874.

Cocos insignis (Rob.) Mart. ex Hook. f., Rep. Roy. Bot. Gard. Kew 1882: 72, 74. 1884.

Calappa insignis (Rob.) Kuntze, Revis. Gen. Pl. 2: 982. 1891.

Lytocaryum insigne (Rob.) Toledo, Arq. Bot. Estado São Paulo, n.s., f.m., 2: 8. 1944.

Microcoelum insigne (Rob.) Burret & Potztal, Willdenowia 1: 388. 1956.

Syagrus itapebiensis (Noblick & Lorenzi) Noblick & Meerow, **comb. nov.**

**Lytocaryum itapebiense* Noblick & Lorenzi, Palms 54: 13. 2010.

Syagrus weddelliana (H. Wendl.) Becc., Agric. Colon. 10: 468. 1916.

**Cocos weddelliana* H. Wendl., Florist & Pomol. 1871: 114. 1871.

Lytocaryum weddellianum (H. Wendl.) Toledo, Arq. Bot. Estado São Paulo, n.s., f.m., 2: 8. 1944.

Microcoelum weddellianum (H. Wendl.) H.E. Moore, Gentes Herb. 9: 267. 1963.

Glaziova elegantissima H. Wendl., Florist & Pomol. 1871: 116. 1871.

Cocos elegantissima (H. Wendl.) Schaedtler, Hamburger Garten-Blumenzeitung 31: 158. 1875.

Glaziova martiana Glaz. ex Drude in Mart., Fl. bras. 3(2): 397. 1881.

Calappa elegantina Kuntze, Revis. Gen. Pl. 2: 982. 1891.

Cocos pynaertii auct., Gard. Chron., ser. 3, 9: 683. 1891.

Cocos weddelliana var. pinaertii G. Nicholson & Mottet, Dict. Prat. Hort. 5: 754. 1899.

Syagrus weddelliana var. *cinereus* Becc., Agric. Colon. 10: 471. 1916.

Syagrus weddelliana var. *pinaertii* Becc., Agric. Colon. 10: 468. 1916.

Lytocaryum weddellianum var. *cinereum* (Becc.) A.D. Hawkes, Arch. Bot. São Paulo, n.s., 2: 190. 1952.

Lytocaryum weddellianum var. *pinaertii* (G. Nicholson & Mottet) A.D. Hawkes, Arch. Bot. São Paulo, n.s., 2: 190. 1952.

Microcoelum martianum (Glaz. ex Drude) Burret & Potztal, Willdenowia 1: 388. 1956.

* indicates the basionym

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