

A New Subgeneric Classification of *Rhipsalis* (Cactoideae, Cactaceae)

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Abstract—Most Cactaceae have succulent stems and inhabit dry or arid areas, but some are epiphytes of humid regions. *Rhipsalis* is the largest genus of epiphytic cacti. Species of *Rhipsalis* are notoriously difficult to identify, and the subgeneric classification of the genus has remained controversial. Between 1837 and 1995, eight different subgeneric classifications have been proposed for *Rhipsalis*. The most comprehensive taxonomic treatment of the genus recognized five subgenera, *Phyllarthrorhipsalis*, *Rhipsalis*, *Epallagonium*, *Calamorhipsalis*, and *Erythrorhipsalis*, characterized mainly by stem morphology. Here, molecular phylogenetic information combined with morphological data is used to re-evaluate the former subgeneric classifications proposed for the genus. Three monophyletic subgenera are recognized, *Rhipsalis*, *Calamorhipsalis* and *Erythrorhipsalis*, which are mainly characterized by floral traits. The changes proposed include expanding the circumscription of *Rhipsalis* by the inclusion of species previously included in *Phyllarthrorhipsalis* and *Epallagonium* and recognizing a broader *Calamorhipsalis*, also including species from subgenus *Epallagonium*. The circumscription of *Erythrorhipsalis* remains unchanged. For each subgenus a list of synonyms, a brief description and a list of species included are presented. A key for the identification of subgenera is also provided.

Keywords—Atlantic Forest, epiphytic cacti, Rhipsalideae.

Cactaceae includes 127 genera and 1,438 species distributed throughout the Neotropics, except for *Rhipsalis baccifera* (J. S. Muel.) Stearn, which also occurs in Africa and Asia (Hunt et al. 2006). The family is currently divided into four subfamilies: Pereskioideae, Opuntioideae, Cactoideae, and Maihuenioideae (Hunt et al. 2006). Pereskioideae includes the first two lineages to diverge in Cactaceae (Edwards et al. 2005). Species in this group are terrestrial and present regular persistent leaves. Opuntioideae species have stems flattened or cylindrical, glochids, seeds covered by a bony aril, and leaves deciduous and often cylindrical (Anderson 2001). Maihuenioideae is a small subfamily with two shrubby species of the genus *Maihuenia*, with cylindrical or globose succulent stems and small, cylindrical, persistent leaves (Anderson 2001). Cactoideae, the most diverse subfamily with nine tribes and the highest number of taxa, is characterized by absent or greatly reduced leaves (Anderson 2001). It presents the widest morphological variation in the family, including globular and columnar terrestrial species and cylindrical or winged lithophytic and epiphytic species (Barthlott and Hunt 1993).

Most Cactoideae have succulent stems and inhabit dry or arid areas, but some are epiphytes of humid regions. The tribes Hylocereeae and Rhipsalideae belong to subfamily Cactoideae and include most epiphytic cacti species (Hunt et al. 2006). Rhipsalideae is the largest taxon of epiphytic cacti. It encompasses four genera: *Hatiora* Britton & Rose, *Lepismium* Pfeiff., *Rhipsalis* Gaertn., and *Schlumbergera* Lem., of which *Rhipsalis* is the largest. A recent molecular phylogeny of Rhipsalideae supported the monophyly of *Rhipsalis* and *Lepismium* but indicated that *Hatiora* and *Schlumbergera* are paraphyletic as previously circumscribed (Calvente et al. 2011a). The majority of species belonging to this tribe are endemic to Brazil, and several species have restricted distribution ranges and are threatened due to habitat reduction.

The most recent and comprehensive taxonomic treatment of *Rhipsalis* included 33 species in five subgenera: *Calamorhipsalis* K. Schum., *Epallagonium* K. Schum., *Erythrorhipsalis* A. Berger, *Phyllarthrorhipsalis* Buxb., and *Rhipsalis* (Barthlott and Taylor 1995). The subgeneric classification of *Rhipsalis* proposed

by Barthlott and Taylor (1995) was also adopted in the most recent account of the Cactaceae, which recognized 35 species in *Rhipsalis* (Hunt et al. 2006). However, a recent molecular phylogeny of *Rhipsalis* (Calvente 2010; Calvente et al. 2011b) indicated that three subgenera are paraphyletic as previously circumscribed (*Rhipsalis*, *Calamorhipsalis*, and *Epallagonium*). Here, a new subgeneric classification for *Rhipsalis* is proposed based on morphological and molecular phylogenetic data (Calvente 2010; Calvente et al. 2011b). Only monophyletic subgenera, diagnosed by morphological characters, are recognized. The proposed changes mainly include expanding the circumscription of *Rhipsalis* subg. *Calamorhipsalis* by the inclusion of some species previously placed within *Rhipsalis* subg. *Epallagonium* and widening the circumscription of *Rhipsalis* subg. *Rhipsalis* by the inclusion of species previously comprised in *Rhipsalis* subg. *Phyllarthrorhipsalis* and *Rhipsalis* subg. *Epallagonium*. The circumscription of *Rhipsalis* subg. *Erythrorhipsalis* remains unchanged.

Taxonomic History—The first species of *Rhipsalis* was described as *Cassytha baccifera* J. S. Muell. However, *C. baccifera* was an illegitimate name at the generic level due to the previous publication of *Cassytha* L. within the Lauraceae (Linnaeus 1753). Gaertner (1788) subsequently described *Rhipsalis* and transferred *Cassytha baccifera* J. S. Muell. into *Rhipsalis* as *R. cassytha* (J. S. Muell.) Gaertner (originally in his publication as *R. cassutha*, but this is presumably a typographical error); he also recognized *R. cassytha* as the type of *Rhipsalis*. Even though Gaertner (1788) used the same type material of *Cassytha baccifera*, he adopted a different specific epithet, making *R. cassytha* (J. S. Muell.) Gaertner illegitimate. Stearn (1939) noticed this equivocal combination and published *Rhipsalis baccifera* (J. S. Muell.) Stearn; this is the correct type of *Rhipsalis*. It is also important to note that Adanson (1763) described the genus *Hariota* before the publication of *Cassytha baccifera* J. S. Muell. However, the problematic application of Adansonian uninomials (see Parkinson 1987, 1988) led to the conservation of *Rhipsalis* Gaertn. against *Hariota* Adans.

De Candolle (1828) presented the first comprehensive treatment of *Rhipsalis*, with seven species recognized without infrageneric classification (Table 1). *Rhipsalis* was subsequently

TABLE 1. History of the infrageneric classifications of *Rhipsalis*.

Author	Notes:
De Candolle 1828	Listed seven species for <i>Rhipsalis</i> without subdivisions
Pfeiffer 1837	Divided <i>Rhipsalis</i> (16 species) into four series based on stem shape (including species currently placed in <i>Lepismium</i>): <i>Alatae</i> (six species), <i>Angulosae</i> (three species), <i>Teretes</i> (five species) and <i>Articuliferae</i> (two species).
Salm-Dyck 1850	Divided <i>Rhipsalis</i> (19 species) into five series: <i>Alatae</i> (six species), <i>Angulosae</i> (four species), <i>Teretes</i> (five species), <i>Sarmentosae</i> (one species) and <i>Articuliferae</i> (three species, including one species previously positioned in <i>Hattoria</i>)
Schumann 1890	Divided <i>Rhipsalis</i> (36 species) into four series based on stem shape (including species currently placed in <i>Lepismium</i>): <i>Teretes</i> (11 species), <i>Angulatae</i> (nine species), <i>Alatae</i> (11 species, divided in <i>Perpetuae</i> and <i>Terminatae</i>) and <i>Sarmentosae</i> (one species). Four species were left as "incertae sedis."
Schumann 1899	Divided <i>Rhipsalis</i> (47 species, including <i>Lepismium</i> species) into eight subgenera based on stem and flower morphology: <i>Eurhripsalis</i> (18 species, including species mostly from previous <i>Teretes</i>), <i>Goniorhripsalis</i> (three species, previously included in <i>Angulatae</i>), <i>Ophiorhripsalis</i> (two species), <i>Phyllorhripsalis</i> (11 species, previous <i>Alatae</i>), <i>Acanthorhripsalis</i> (one species), <i>Calamorhripsalis</i> (six species with some species of <i>Teretes</i> and other from <i>Angulatae</i>), <i>Epallagonium</i> (one species, previously in <i>Angulatae</i>) <i>Lepismium</i> (five species).
Löfgren 1915, 1917	Described several Brazilian new species and provided a taxonomic treatment adopting the subgenera proposed by Schumann (1899) and two new genera: <i>Pfeiffera</i> and <i>Hariota</i> .
Britton and Rose 1923	Divided <i>Rhipsalis</i> (57 species) into 16 series (small groups of morphological similar species).
Buxbaum 1970	Recognized the tribe Hylocereeae, subtribe Rhipsalinae with three "linae": Pfeifferae, Schlumbergereae, and Rhipsales. Current <i>Rhipsalis</i> species are positioned in genera <i>Erythrorhripsalis</i> (Schlumbergereae) and <i>Rhipsalis</i> (Rhipsales). <i>Rhipsalis</i> is divided in four subgenera: <i>Goniorhripsalis</i> , <i>Phyllorhripsalis</i> (= <i>Perpetuae</i> , current <i>Lepismium</i> winged species), <i>Phyllarthrorhripsalis</i> (= <i>Terminatae</i> , current <i>Rhipsalis</i> winged species) and <i>Rhipsalis</i> . He further subdivided the subgenus <i>Rhipsalis</i> into four series: <i>Ophiorhripsalis</i> , <i>Mesembryanthoides</i> , <i>Cereusculii</i> , and <i>Rhipsalis</i> .
Barthlott 1987; Barthlott and Taylor 1995	Transferred species from <i>Rhipsalis</i> to <i>Lepismium</i> . Divided the remaining species of <i>Rhipsalis</i> (33 species) into five subgenera: <i>Rhipsalis</i> (six species), <i>Calamorhripsalis</i> (three species), <i>Epallagonium</i> (seven species), <i>Phyllarthrorhripsalis</i> (10 species), and <i>Erythrorhripsalis</i> (seven species).
Hunt et al. 2006	Followed the subgeneric classification of Barthlott and Taylor (1995) and recognized five subgenera: <i>Rhipsalis</i> , <i>Calamorhripsalis</i> , <i>Epallagonium</i> , <i>Phyllarthrorhripsalis</i> , and <i>Erythrorhripsalis</i> .

subdivided into four series (*Alatae*, *Angulosae*, *Teretes*, and *Articuliferae*), characterized by the shape and disposition of the stems (Pfeiffer 1837). A modified version of this subgeneric classification was adopted by Salm-Dyck (1850), who also recognized *Sarmentosae* in addition to *Alatae*, *Angulosae*, *Teretes*, and *Articuliferae*. Schumann (1890) maintained the same subgeneric division of *Rhipsalis* in series but divided *Alatae* into *Perpetuae* and *Terminatae* according to G. A. Lindberg (cited in Schumann 1890), and did not recognize *Articuliferae* (species of *Articuliferae* were transferred to series *Teretes* and to genus *Hariota*).

Schumann (1899) was the first author to divide the genus into subgenera and to use flower morphology as another key diagnostic feature of infrageneric taxa of *Rhipsalis*. He described eight subgenera (*Eurhripsalis* K. Schum., *Goniorhripsalis* K. Schum., *Ophiorhripsalis* K. Schum., *Phyllorhripsalis* K. Schum., *Acanthorhripsalis* K. Schum., *Calamorhripsalis* K. Schum., *Epallagonium* K. Schum., and *Lepismium* K. Schum.) and placed all species with immersed pericarpel (the term pericarpel refers to the lower part of the cactus flower including the ovary, which is embedded in stem tissue; Taylor and Zappi 2004), within *Calamorhripsalis*, *Epallagonium*, and *Lepismium*. Löfgren (1915, 1917) subsequently accepted the eight subgenera proposed by Schumann (1899), but widened the circumscription of *Rhipsalis* to include two additional subgenera (*Pfeiffera* Loefgr. and *Hariota* Loefgr.), both including species currently placed within genera *Rhipsalis*, *Hattoria*, and *Pfeiffera*. Britton and Rose (1923) did not follow the classifications proposed by Schumann (1899) or Löfgren (1915, 1917) and divided *Rhipsalis* into 16 new series. They included *Rhipsalis* in the subtribe Rhipsalidanae together with the newly described genera *Erythrorhripsalis* Berger (currently positioned within *Rhipsalis* subg. *Erythrorhripsalis*), *Rhipsalidopsis* Britton & Rose (currently positioned within *Schlumbergera*) and the genera *Pfeiffera* Salm-Dyck, *Acanthorhripsalis* (K. Schum.) Britton & Rose,

Pseudorhripsalis Britton & Rose, *Lepismium* Pfeiff. and *Hattoria* Britton & Rose.

More recently, Buxbaum (1970) recognized the subtribe Rhipsalinae with three "linae" (Pfeifferae: genera *Pfeiffera* and *Acanthorhripsalis*; Schlumbergereae: genera *Erythrorhripsalis*, *Hattoria*, *Rhipsalidopsis*, *Schlumbergera*, and *Zygocactus* K. Schum.; and Rhipsales: genera *Rhipsalis* and *Lepismium*) and divided *Rhipsalis* into four subgenera: *Goniorhripsalis*, *Phyllorhripsalis* (= *Perpetuae*, current *Lepismium* winged species), *Phyllarthrorhripsalis* Buxb. (= *Terminatae*, current *Rhipsalis* winged species) and *Rhipsalis*. In addition, Buxbaum (1970) subdivided the subgenus *Rhipsalis* in four series: *Ophiorhripsalis*, *Mesembryanthoides*, *Cereusculii*, and *Rhipsalis*. Most species currently placed in the genus *Rhipsalis* were included in *Erythrorhripsalis* (Schlumbergereae) and in *Rhipsalis* (Rhipsales) itself under Buxbaum's classification.

The classifications of Barthlott (1987) and Barthlott and Taylor (1995) transferred almost all species of *Rhipsalis* with basitonic (branching primarily from the base of the segment) and mesotonic (branching primarily from the middle part of the segment) branching and indeterminate growth to the genus *Lepismium*, recognizing *Rhipsalis* in a narrower sense. This classification also recognized five subgenera within *Rhipsalis* (*Rhipsalis*, *Calamorhripsalis*, *Epallagonium*, *Phyllarthrorhripsalis*, and *Erythrorhripsalis*), mainly characterized by stem shape and some flower characters. The latest treatment of Cactaceae (Hunt et al. 2006) recognized four genera (*Hattoria*, *Lepismium*, *Rhipsalis*, and *Schlumbergera*) within tribe Rhipsalideae, although several species previously assigned to *Lepismium* were transferred to *Pfeiffera*. In this classification Hunt et al. (2006) divided *Rhipsalis* into the same five subgenera proposed by Barthlott (1987) and Barthlott and Taylor (1995). Calvente et al. (2011a) reconstructed a molecular phylogeny for Rhipsalideae recognizing *Lepismium* and *Rhipsalis* as monophyletic (as circumscribed by Hunt et al. 2006). In this same

work Calvente et al. (2011a) found *Hatiora* and *Schlumbergera* paraphyletic, transferring the species previously positioned in *Hatiora* subg. *Rhipsalidopsis* to *Schlumbergera*.

A New Subgeneric Classification of *Rhipsalis*—The molecular phylogeny of Rhipsalideae (Calvente et al. 2011a) supports the segregation of *Lepismium* from *Rhipsalis* and a narrower circumscription of *Rhipsalis* as proposed by Barthlott (1987),

Barthlott and Taylor (1995) and Hunt et al. (2006). In these classifications *Rhipsalis* includes only species with stem segments longer than seven cm and small, actinomorphic, translucent flowers with flower tubes absent or never exceeding the pericarpel. However, recent molecular phylogenetic analyses (Calvente et al. 2011b) using *psbA-trnH*, *trnQ-rps16*, *rpl32-trnL*, ITS and *MS* (Fig. 1) do not support an infrageneric division of

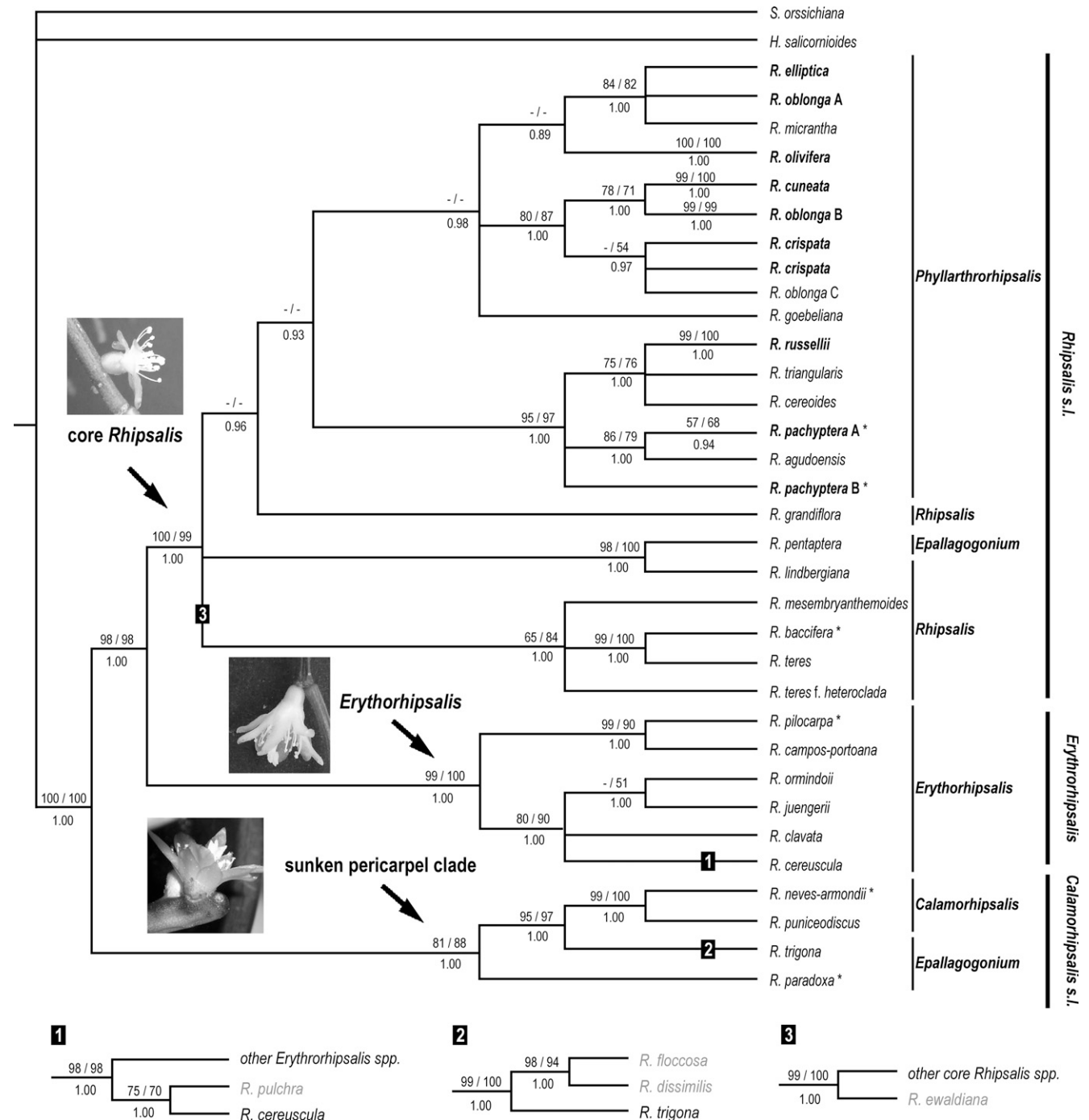


FIG. 1. Majority rule consensus tree of *Rhipsalis* derived from the Bayesian analysis of cpDNA (*psbA-trnH*, *trnQ-rps16*, *rpl32-trnL*), ITS and *MS*. Maximum parsimony bootstrap and maximum likelihood bootstrap are indicated above branches and Bayesian posterior probabilities are indicated below branches. Species for which multiple specimens were sampled are highlighted in bold; monophyletic species are represented by a single terminal (additional specimens were trimmed); non-monophyletic species are indicated with letters A, B or C following species names. *Rhipsalis* subgenera according to Hunt et al. (2006) are indicated to the right of the tree, in the first column, with subgenera type species indicated by an asterisk following species names. Clades 1, 2, 3 in the lowest part of the figure were recovered from the analysis of ITS + cpDNA data set and reconstruct the position of species (in grey) not included in the cpDNA, ITS and *MS* data set. Modified from Calvente (2010) and Calvente et al. (2011b).

Rhipsalis based on stem shape. Instead, these analyses suggest a subdivision of the genus in three main lineages that are characterized mainly by flower traits (Fig. 1): (1) *Rhipsalis* s. l. ("core *Rhipsalis*"); (2) *Erythrorhipsalis*; and (3) *Calamorhipsalis* s. l. (= "sunken pericarpel" clade). Although stem shape is a variable character in the genus, it is not consistent in the subgeneric level and appears to be more useful in species level taxonomy.

The previous circumscription of *Erythrorhipsalis* (Barthlott 1987; Barthlott and Taylor 1995; Hunt et al. 2006) is corroborated by the molecular phylogenetic data (Bayesian posterior probability = 1.00, maximum parsimony bootstrap = 0.99, maximum likelihood bootstrap = 1.00). Species belonging to *Erythrorhipsalis* have pendent flowers, which can be campanulate and either lateral or terminal; or rotate and, in this case, always terminal. The four remaining subgenera (*Rhipsalis*, *Calamorhipsalis*, *Epallagonium*, and *Phyllarthrorhipsalis*) are either paraphyletic or not strongly supported (bootstrap values < 0.75, posterior probability values < 0.95).

The "core *Rhipsalis*" clade (Bayesian posterior probability = 1.00, maximum parsimony bootstrap = 1.00, maximum likelihood bootstrap = 0.99) includes all species previously included in *Rhipsalis* subg. *Phyllarthrorhipsalis* and *Rhipsalis* subg. *Rhipsalis*, plus *R. pentaptera* (subg. *Epallagonium*). While *Rhipsalis* subg. *Phyllarthrorhipsalis* is monophyletic with low support (Bayesian posterior probability = 0.93, maximum likelihood and parsimony bootstrap < 0.5), *Rhipsalis* subg. *Rhipsalis* is paraphyletic if *Phyllarthrorhipsalis* is maintained (Fig. 1). One possibility would be to recognize smaller clades in the "core *Rhipsalis*" clade as subgenera and to maintain *Phyllarthrorhipsalis* even though it is weakly supported. However, this choice is not practical because the subgeneric distinction would be confusing in the genus as overall morphology is not consistent in these smaller clades (see detailed discussion below regarding the proposed classification of Korotkova et al. 2011). In the other hand, all species from the "core *Rhipsalis*" clade present a clear morphological characterization if maintained together, as they all have patent rotate lateral flowers with pericarpel not immersed in the areole. Therefore, we propose to recognize a broader and well defined morphologically subgenus *Rhipsalis* composed of all "core *Rhipsalis*" species.

The "sunken pericarpel" clade (Bayesian posterior probability = 1.00, maximum parsimony bootstrap = 0.81, maximum likelihood bootstrap = 0.88) includes all species previously placed within subgenera *Calamorhipsalis* and *Epallagonium*, except for *R. pentaptera*. Previously included within subg. *Epallagonium*, *R. pentaptera* emerges within the "core *Rhipsalis*" clade in the molecular phylogeny, what is corroborated by the flower morphology. *Rhipsalis pentaptera* presents patent rotate flowers with the pericarpel not immersed in the stem, matching perfectly the flower morphology found in the remaining species of the "core *Rhipsalis*" clade. The patent rotate lateral flowers and a pericarpel deeply immersed in the stem, on the other hand, characterize all species belonging to the "sunken pericarpel" clade. All species from the "sunken pericarpel" clade are here included in a broader subgenus *Calamorhipsalis*.

Korotkova et al. (2011) recently published a phylogenetic hypothesis for Rhipsalideae based strictly on chloroplast markers (*trnK* intron, *matK*, *rbcL*, *rps3-rpl16*, *rpl16* intron, *psbA-trnH*, and *trnQ-rps16*). Their results indicate a slightly different scenario with a different positioning of *Rhipsalis*

paradoxa, which is more closely related to "core *Rhipsalis*" than to the "sunken pericarpel clade." Calvente et al. (2011a) also found *R. paradoxa* more related to "core *Rhipsalis*," however with low support (bootstrap = 0.51, posterior probability = 0.8). We believe that the addition of *MS* sequences for all species together with a more complete sampling of chloroplast regions (especially including *rpl32-trnL*, which offered better resolution of relationships among these species) were responsible for the change in this relationship and for the better resolution and support shown in Calvente et al. (2011b) for these clades. The same must be the reason for the conflicting positioning of *R. paradoxa* shown by Korotkova et al. (2011) and Calvente et al. (2011b), since Korotkova et al. (2011) did not include *MS* and *rpl32-trnL* sequences in their work. Korotkova et al. (2011) also briefly proposed a different subgeneric division for *Rhipsalis* based on their phylogenetic inference, in which *Rhipsalis* is divided in six subgenera. However, these authors do not present a consistent and explicit diagnosis for each of these subgenera or a key for their identification. In addition to *Erythrorhipsalis* (as circumscribed here) and *Calamorhipsalis* (as circumscribed here but excluding *R. paradoxa*), they recognize a separate subgenus for *Rhipsalis paradoxa* (*Epallagonium*). Korotkova et al. (2011) characterize *Calamorhipsalis* (excluding *R. paradoxa*) as having species with terete stem segments and woolly sunken areoles but include *R. trigona*, which has trigonous stems, while they exclude all other *Rhipsalis* with terete stems (ca. 14 *Rhipsalis* species) as well as *R. paradoxa*, which has woolly sunken areoles. The separation of *R. paradoxa* from *Calamorhipsalis* is not supported by our results or by our analysis of morphology.

Furthermore Korotkova et al. (2011) subdivide "core *Rhipsalis*" into subgenus *Rhipsalis* (as previously circumscribed but excluding *R. grandiflora*, *R. lindbergiana*, and *R. ewaldiana* and including *R. sulcata* and *R. shaferi*, which was previously considered a subspecies of *R. baccifera*), *Phyllarthrorhipsalis* (including *R. grandiflora*, *R. ewaldiana*, and *R. pittieri*, which was previously considered a subspecies of *R. floccosa*), and *Goniorhipsalis* (including *R. lindbergiana*, *R. pentaptera*, and *R. pacheco-leonis*).

Korotkova et al. (2011) did not provide a formal description for the subgenus *Rhipsalis* as circumscribed in their work, nevertheless they stated that the "typical" form of this subgenus is characterized by strictly acrotonical branching (that also occur in most species of the entire genus *Rhipsalis*), terete stems (that also occur in ca. 14 *Rhipsalis* species, as well as in the excluded *R. grandiflora*, *R. lindbergiana*, and *R. shaferi*) and the presence of "indeterminate basal extension shoots" (which also occur in almost all species of *Rhipsalis* subg. *Erythrorhipsalis*). Calvente et al. (2011b) did find a clade composed of *R. baccifera*, *R. teres*, and *R. mesembryanthemoides* inside "core *Rhipsalis*" clade (Fig. 1), but they did not include *R. sulcata* (this species was described from cultivated material and is only available in private collections; despite efforts, it was not possible to obtain material for DNA sequencing) and *R. shaferi* as a separate taxon as they did not explore infra-specific classifications in their work (in previous classifications *R. shaferi* was considered a subspecies of *R. baccifera*). Even so this clade would not make a good taxon at the subgeneric level, because it is not characterized by distinctive synapomorphies. As discussed above, it is preferential to consider a wider *Rhipsalis* subgenus *Rhipsalis* that also includes this clade.

Phyllarthrorhopsis as originally described contained only species with flattened or winged stems (Buxbaum 1970), and the use of this diagnostic character for this subgenus was followed in further classifications of *Rhopsis*. Korotkova et al. (2011) maintained the species with flattened or winged stems in this group but also included *R. grandiflora*, *R. ewaldiana*, and *R. pittieri* (which was previously considered a subspecies of *R. floccosa*) in *Phyllarthrorhopsis*, all having terete stems (*R. ewaldiana* also has angled stem segments). Nevertheless, these authors recognize that this new proposed circumscription of *Phyllarthrorhopsis* is not supported by any morphological character. The placement of *R. pittieri* in this clade as indicated by Korotkova et al. (2011) is surprising, as it also has sunken areoles and resembles *R. floccosa*. Therefore a more detailed study should be conducted with this species, including nuclear DNA markers and different specimens from distinct wild populations to confirm this position and the relationship with *R. floccosa*. In this work it is proposed to maintain the previous classification of this taxon as *R. floccosa* subsp. *pittieri* (Britton & Rose) Barthlott & N. P. Taylor and, therefore, it follows the inclusion of *R. floccosa* and all of its infra-specific taxa and is assigned under *Rhopsis* subg. *Calamorhopsis*. Calvente et al. (2011b) also found *R. grandiflora* more related to *Phyllarthrorhopsis* clade (Fig. 1) than to the other "core *Rhopsis*" species and *R. ewaldiana* related to "core *Rhopsis*," however, here they are positioned in a wider *Rhopsis* subg. *Rhopsis* including *Phyllarthrorhopsis* and the remaining smaller clades of "core *Rhopsis*" to make the classification more practical.

TAXONOMIC TREATMENT

Below an alternative new subgeneric classification of *Rhopsis* that only recognizes monophyletic subgenera characterized by morphological features is presented. The changes proposed mainly include expanding the circumscription of subgenus *Rhopsis* by the inclusion of species previously included in *Phyllarthrorhopsis* and *Epallagonium* and the recognition of a broader *Calamorhopsis* (also includes species from subg. *Epallagonium*). The circumscription of *Erythrorhopsis* remains unchanged.

RHIPSALIS Gaertn., Fruct. Sem. pl. 1: 137. 1788, nom. cons.
Hariota Adans., Fam. Pl. 2: 243. 1763. *Cassytha* J. S. Muell.,

Gard. Dict., ed. 8. 1768, non L., 1753.—TYPE: *Rhopsis baccifera* (J. S. Muell.) Stearn.

1. RHIPSALIS subg. RHIPSALIS

Rhopsis subg. *Phyllarthrorhopsis*, Buxb. in Krainz, Kakteen 44–45: 1970, syn. nov.—TYPE: *Rhopsis pachyptera* Pfeiff.

Rhopsis subg. *Goniorhopsis* K. Schum., Gesamtbeschr. Kakt.: 615. 1898, syn. nov.—TYPE: *Rhopsis pentaptera* A. Dietr.

Stem segments cylindrical or 2–6 winged. Flowers patent, rotate, lateral or sublateral, rarely also apical in stem segments; pericarpel not immersed in the areole.

Species Included—*R. agudoensis* N. P. Taylor, *R. baccifera* (Mill.) Stearn, *R. cereoides* (Backeb. & Voll) Backeb., *R. crispata* (Haw.) Pfeiff., *R. crispimarginata* Loefgr., *R. cuneata* Britton & Rose, *R. elliptica* G. Lindb. ex K. Schum., *R. ewaldiana* Barthlott & N. P. Taylor, *R. goebeliana* Backeb., *R. grandiflora* Haw., *R. hileiabaiana* (N. P. Taylor & Barthlott) N. Korotkova & Barthlott, *R. lindbergiana* K. Schum., *R. mesembryanthemoides* Haw., *R. micrantha* (Kunth) DC., *R. oblonga* Loefgr., *R. olivifera* N. P. Taylor & Zappi, *R. pachyptera* Pfeiff., *R. pentaptera* A. Dietr., *R. russellii* Britton & Rose, *R. shaferi* Britton & Rose, *R. sulcata* F. A. C. Weber, *R. teres* (Vell.) Steud., *R. triangularis* Werderm.

2. RHIPSALIS subg. ERYTHRORHIPSALIS A. Berger, Monatsschr. Kakteenk. 30: 4. 1920.—TYPE: *Rhopsis pilocarpa* Loefgr.

Stem segments cylindrical to clavate. Flowers pendent; campanulate, apical or lateral in stem segments or rotate and strictly apical in stem segments; pericarpel not immersed in the areole.

Species Included—*R. aurea* M. F. Freitas & J. M. A. Braga, *R. burchellii* Britton & Rose, *R. campos-portoana* Loefgr., *R. clavata* F. A. C. Weber, *R. juengeri* Barthlott & N. P. Taylor, *R. ormindoi* N. P. Taylor & Zappi, *R. pulchra* Loefgr., *R. cereuscula* Haw., *R. pilocarpa* Loefgr.

3. RHIPSALIS subg. CALAMORHIPSALIS K. Schum., Gesamtbeschr. Kakt.: 615. 1898.—TYPE: *Rhopsis neves-armondii* K. Schum.

Rhopsis subg. *Epallagonium* K. Schum., Gesamtbeschr. Kakt.: 615. 1898, syn. nov.—TYPE: *Rhopsis paradoxa* (Salm-Dyck ex Pfeiff.) Salm-Dyck.

Stem segments cylindrical, with well-developed podaria, angled or with narrow wings, not continuous in stem segments. Flowers patent, rotate, lateral or sublateral in stem segments; pericarpel conspicuously immersed in the areole.

Species Included—*R. dissimilis* (G. Lindb.) K. Schum., *R. floccosa* Salm-Dyck ex Pfeiff., *R. hoelleri* Barthlott & N. P. Taylor, *R. neves-armondii* K. Schum., *R. pacheco-leonis* Loefgr., *R. paradoxa* (Salm-Dyck ex Pfeiff.) Salm-Dyck, *R. puniceodiscus* G. Lindb., *R. trigona* Pfeiff.

KEY TO THE SUBGENERA OF RHIPSALIS

1. Pericarpel immersed in the areole *Rhopsis* subg. *Calamorhopsis*
1. Pericarpel not immersed in the areole 2
 2. Stems cylindrical or clavate; flowers pendent, campanulate (and lateral or apical in stem segments) or rotate (and exclusively apical in stem segments) *Rhopsis* subg. *Erythrorhopsis*
 2. Stems cylindrical or winged; flowers patent, rotate and lateral in stem segments (rarely apical but in this case lateral flowers are also present) *Rhopsis* subg. *Rhopsis*

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LITERATURE CITED

Adanson, M. 1763. *Familles des Plantes*. Paris: Vincent.
Anderson, E. F. 2001. *The cactus family*. Portland: Timber Press.
Barthlott, W. 1987. New names in Rhipsalidinae (Cactaceae). *Bradleya* 5: 97–100.

Barthlott, W. and D. R. Hunt. 1993. Cactaceae. Pp. 161–196 in *The families and genera of vascular plants*, eds. K. Kubitzki, J. G. Rohwer, and V. Bittrich. Berlin: Springer-Verlag.
Barthlott, W. and N. P. Taylor. 1995. Notes towards a monograph of Rhipsalideae (Cactaceae). *Bradleya* 13: 43–79.
Britton, N. L. and J. N. Rose. 1923. *The Cactaceae: descriptions and illustrations of plants of the cactus family*. Volume 4. Washington: The Carnegie Institution of Washington.
Buxbaum, F. 1970. Das phylogenetische System der Cactaceae. Pp. 1–5 in *Die Kakteen*, ed. H. Krainz. Stuttgart: Kosmos-Verlag, Franckh'sche verlagshandlung.
Calvente, A. 2010. *Filogenia molecular, evolução e sistemática de Rhopsis*. Ph. D. dissertation, São Paulo: Universidade de São Paulo.

- Calvente, A., D. C. Zappi, F. Forest, and L. G. Lohmann. 2011a. Molecular phylogeny of tribe Rhipsalideae (Cactaceae) and taxonomic implications for *Schlumbergera* and *Hatiora*. *Molecular Phylogenetics and Evolution* 58: 456–468.
- Calvente, A., D. C. Zappi, F. Forest, and L. G. Lohmann. 2011b. Molecular phylogeny, evolution and biogeography of South American epiphytic cacti. *International Journal of Plant Sciences* 172: 902–914.
- De Candolle, A. P. 1828. *Prodromus Systematis Naturalis Regni Vegetabilis* P. III. Parisiis: Sumptibus Sociorum Treuttel et Würtz.
- Edwards, E. J., R. Nyffeler, and M. J. Donoghue. 2005. Basal cactus phylogeny: implications of *Pereskia* (Cactaceae) paraphyly for the transition to the cactus life form. *American Journal of Botany* 92: 1177–1188.
- Gaertner, J. 1788. *De Fructibus et Seminibus Plantarum* Stutgardiae: Typis Academiae Carolinae.
- Hunt, D., N. Taylor, and G. Charles. 2006. *The new cactus lexicon*. Milborne Port: dh books.
- Korotkova, N., T. Borsch, D. Quandt, N. P. Taylor, K. F. Muller, and W. Barthlott. 2011. What does it take to resolve relationships and to identify species with molecular markers? An example from the epiphytic Rhipsalideae (Cactaceae). *American Journal of Botany* 98: 1549–1572.
- Linnaeus, C. 1753. *Species Plantarum*. 1. ed. Holmiae: Impensis Laurentii Salvii.
- Löfgren, A. 1915. O Gênero *Rhipsalis*. *Archivos do Jardim Botânico do Rio de Janeiro* 1: 59–104.
- Löfgren, A. 1917. Novas Contribuições para o Gênero *Rhipsalis*. *Archivos do Jardim Botânico do Rio de Janeiro* 2: 34–45.
- Parkinson, P. G. 1987. Adanson's generic names for seed plants: Status of listed nomina rejicienda. *Taxon* 36: 745–753.
- Parkinson, P. G. 1988. Adansonian nomina rejicienda et nomina conservanda proposita, 1983–1986. *Taxon* 37: 148–151.
- Pfeiffer, L. 1837. *Enumeratio Diagnostica Cactearum*. Berolini: Sumtibus Ludovici Oehmigke.
- Salm-Dyck, J. 1850. *Cactae in Horto Dyckensi cultae*. Bonnae: Henry & Cohen.
- Schumann, K. M. 1890. Cactaceae. Pp. 266–300 in *Flora Brasiliensis* 4 (2), ed. C. F. P. V. Martius. Lipsiae: Frid. Fleischer.
- Schumann, K. M. 1899. *Gesamtbeschreibung der Kakteen*. Berlin: J. Neumann-Neudamm.
- Stearn, W. T. 1939. Plantae succulentae in Horto Alenconio, H. A. Durval. A facsimile with introduction by W. T. Stearn. *Cactus and Succulent Journal of Great Britain* 7: 107.
- Taylor, N. P. and D. C. Zappi. 2004. *Cacti of eastern Brazil*. Richmond: The Royal Botanic Garden, Kew.