### A new tribal classification of Nyctaginaceae

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**Abstract** Recent phylogenetic work shows that existing tribal concepts within Nyctaginaceae are incompatible with the principle of recognizing monophyletic taxa. We review the history of supergeneric classification in Nyctaginaceae, clarify issues pertaining to priority of certain generic names, and discuss the application of the conserved family name to the tribe Nyctagineae. *Pisoniella* and *Phaeoptilum* are moved from tribe Nyctagineae to Pisonieae and Bougainvilleeae, respectively, while tribe Abronieae, containing *Abronia* and *Tripterocalyx*, is submerged into Nyctagineae. Two distinctive genera, *Caribea* and *Colignonia*, are assigned to their own tribes, recognizing both their uniqueness and the uncertainty of their phylogenetic relationships. Finally, subtribes are not recognized in tribe Nyctagineae. Updated descriptions are provided for each tribe and one new tribe, Caribeaeae Douglas & Spellenberg, is recognized. Plant habit and general geographic distribution seem to be at least as pertinent as the often-homoplasious morphological details which had been emphasized in previous classifications.

Keywords conserved names; nomenclature; Nyctaginaceae; phylogenetics; supergeneric taxonomy

### ■ INTRODUCTION

**Diversity, distribution, and morphology.** — The family Nyctaginaceae comprises 300-400 species of trees, shrubs, and herbs classified in approximately 30 genera (Mabberley, 1987; Bittrich & Kühn, 1993). Species in Nyctaginaceae are found in all warmer areas of the world, but the bulk of the diversity at the generic and specific levels occurs in two regions: the Neotropics, and arid western North America. In the Neotropics, the majority of species are shrubs or small trees found in the three large genera Neea, Guapira, and Pisonia. In addition, the familiar genus *Bougainvillea*, known primarily for the horticulturally important B. glabra, B. spectabilis and hybrids, is endemic to South America, and is especially diverse in Bolivia. Species of Colignonia are restricted to the Andean region. Diversity at the generic level is greater in the arid regions of North America where nearly half of the recognized genera in the family are present, the most diverse being the herbaceous and suffrutescent Abronia, Boerhavia, Mirabilis, and Acleisanthes. Commicarpus, with roughly 30 species in Africa and western Asia, is also found in North and South America with five endemic species.

The number of species in genera of Nyctaginaceae follows a classic "hollow curve" pattern of diversity (Willis, 1922). The few large genera differ in geographic distribution and are morphologically variable. There are many genera of low diversity, 14 of those being monotypic. While in some cases monotypic genera, or genera with very few species, represent minor offshoots of dubious distinction (for instance, three genera for four species in tribe Boldoeae), it is also apparent that many small genera are well differentiated from other members of the family. For example, the monotypic genus *Phaeoptilum* is a unique xeromorphic shrub with winged fruits. This endemic of southwestern Africa is the only genus not occurring in the Americas. Likewise, the monotypic genus *Grajalesia*, a poorly known forest species from Central America, possesses winged fruits quite unlike those of other trees in the family. Its fruits are more similar in general appearance to those of *Phaeoptilum* and the xerophytic herbs found in North America, *Tripterocalyx* and some *Acleisanthes*. *Okenia*, with one or two species, has unique geocarpous fruits.

Nyctaginaceae have provided considerable fodder at the suprageneric and infrageneric levels for several generations of taxonomists. At the species level, perceived intergradation across morphospecies, in combination with a proliferation of names, has led to much taxonomic confusion, e.g., Mirabilis, (Reed, 1969; Spellenberg, 2003a), and spicate species of Boerhavia (Kearney & Peebles, 1964; Reed, 1970; Spellenberg, 2002). Some of the differences in species concepts result from actual incomplete differentiation of populations, perhaps in response to recently changing environments as in geologically diverse western North America (Boerhavia, Abronia, Mirabi*lis*), and in response to changing taxonomic fashion with regard to species concepts (i.e., "lumping" and "splitting") over the past century (Weakley, 2005). In the arborescent tropical genera, comparatively poor preservation in herbarium specimens of many characters, combined with incomplete collections of these often-dioecious plants, has meant that species in the genera Neea, Guapira, and Pisonia remain poorly understood.

In contrast, differences in classification at the generic level and above more likely result from the paucity of characters provided by the Nyctaginaceae flower with its simple and often reduced perianth, and the simple, single-carpel, uni-ovulate ovary. Given the apparent ease with which the perianth (and thus the anthocarp) is modified in response to pollination and dispersal pressures, characters of these organs are perhaps less conserved than are characters of the gynoecium wall in other families. We draw this inference from the fact that the accessory fruit characters (e.g., wings, ribs, glands) previously used in classifications display substantial homoplasy (Douglas & Manos, 2007). Thus, while ovary and fruit characteristics carry morphological information that is phylogenetically important in many families (e.g., Lawrence, 1951; Stebbins, 1974), artificial groupings have resulted when similar confidence has been extended to the characteristics of the anthocarps in Nyctaginaceae. Such artificial grouping was clearly demonstrated at the generic level, when three previously recognized genera, Acleisanthes s.str. (long perianth, vespertine, ribbed anthocarp), Ammocodon (= Selinocarpus) chenopodoides (short perianth, matutinal, winged anthocarp), and the remaining species of Selinocarpus (long perianth, vespertine, winged anthocarp) (see Fowler & Turner, 1977) each were found to be non-monophyletic separately, but instead to comprise multiple lineages embedded within a single clade (Levin, 2000). They are now all considered to belong within Acleisanthes (Levin, 2002). Similarly, changing concepts of the boundaries between groups at the generic level have resulted in very different taxonomies, e.g., Mirabilis (Standley, 1918; Spellenberg, 2003a), Boerhavia (Fosberg, 1978; Spellenberg, 2003b).

Supergeneric classifications. — The family was first recognized by Jussieu (1789). Early treatments of the family by Meisner (1841), Choisy (1849) and Bentham & Hooker (1880) established the outlines of a tribal classification by establishing Mirabileae Meisner, Pisonieae Meisner, Bougainvilleae Choisy, and Leucastereae Benth & Hook. Heimerl (1889) redrew the three tribes recognized by Bentham & Hooker. Standley (1918) recognized Heimerl's subtribes of tribe Mirabileae as tribes Abronieae, Bougainvilleae and Colignonieae. His publication of Abronieae and Colignonieae at tribal rank is valid by virtue of the inclusion of a dichotomous key to the tribes. Heimerl (1934) updated the tribal classification of Nyctaginaceae, recognizing five tribes. The tribe Pisonieae included genera that represented the majority of the tropical arborescent taxa, except the three genera in Leucastereae. The largest of Heimerl's tribes, Mirabileae, was further divided into four subtribes, one of which, Boerhaaviinae, contained most of the herbaceous and suffrutescent desert taxa. Bittrich & Kühn (1993) updated the treatment of the family and made several adjustments to Heimerl's 1934 treatment, including segregating from subtribe Boerhaaviinae a new subtribe, Nyctagininae, which represented genera with substantial bracts forming an involucre (Fig. 1).

The proper name for the tribe Boldoeae (Heimerl, 1889) has been confused in the literature for over 90 years. The tribe contains three genera that are similar to a degree that Standley included in Salpianthus Humb. & Bonpl. (1807) the genera Boldoa (commonly cited as Cav. ex Lag. 1816), and Cryptocarpus Kunth (1817) (Standley, 1918, 1931). When he combined these genera, he renamed the tribe Boldoeae as Salpiantheae. However, he apparently erred in determining the priority to be with Salpianthus. The original publication of the name Boldoa is as follows: Cavanilles, Hortus regius matritensis (1803: 8-9, tab. 7). This was later cited in Lagasca, Nova genera et species (1816: 10) (Heimerl, 1889). Both works include Latin descriptions of Boldoa and Boldoa purpurascens (likely explaining Standley's error) but the former also has an illustration of the species and clearly represents valid publication. Thus Boldoa has priority over Salpianthus if the four species in the group

were to be placed into a single genus, as Standley preferred. In his last treatment of the family, Heimerl (1934) maintained the three genera; naturally, he maintained Boldoeae. However, many treatments (e.g., Spellenberg, 2001) have followed Standley in treating *Boldoa* as a synonym of *Salpianthus*.

Another issue that has never been satisfactorily addressed concerns the proper name for the tribe containing the type of the family name Nyctaginaceae. Nyctago, the generic name upon which the family name is based (Art. 10.6 of the ICBN, McNeill & al., 2006) is a superfluous and illegitimate name to be typified by the type of Mirabilis. Nowicke (1970) noted that Article 19 of the *Code* required that Heimerl's (1934) tribe Mirabileae, subtribe Boerhaaviinae be changed to tribe Nyctagineae, subtribe Nyctagininae, establishing these names by reference to Heimerl (1934). However, she referred to Mirabileae in two subsequent publications on pollen morphology (Nowicke, 1975; Nowicke & Skvarla, 1979). Bogle (1974) discussed a conflict that existed in the 1966 and 1972 Codes that pertained to families with conserved names, noting that both Heimerl's and Nowicke's names could be considered correct, depending on whether one emphasized the requirement that subfamilial taxa conform to the "correct" name of an included genus, or the requirement that the names of such groups be based on the same stem as the next higher taxon. Article 19.3 was revised in the Sydney Code (Voss & al., 1983) so that such a taxon was to be based on the "type of the adopted, legitimate name of the family to which it is assigned, but without citation of an author's name". This wording is maintained in the Vienna *Code* Article 19.4 except that the proscription of author citations in tribal and subtribal names disappeared with the Tokyo Code (Greuter & al., 1988). In this case, Nyctago nom. illeg. is the type genus. Article 19.5 further clarifies this issue by stating that subfamilial names based on illegitimate generic names are legitimate if they are also the base of a conserved family name, meaning that the proper name of the tribe that includes Mirabilis is Nyctagineae. Bittrich & Kühn (1993), like Nowicke (1970), recognized the bulk of the genera in Heimerl's (1934) tribe Mirabileae as tribe Nyctagineae, citing no author as per the final clause in Art. 19.3 then in effect. In fact, the first use of this tribal name was by Horaninov (1847: 105-107), whose tribe Nyctagineae was equivalent to the modern Nyctaginaceae and was one of four tribes in a broadly conceived "Allioniaceae", along with Plumbagineae, Staticeae, and Plantagineae. If a subtribe including Mirabilis were recognized (which we will not do) its proper name would be Nyctagininae Nowicke.

### TAXONOMIC IMPLICATIONS OF MOLECULAR STUDIES

The first molecular phylogenetic study of Nyctaginaceae (Levin, 2000) explicitly focused on some members of tribe Nyctagineae. Due to sampling limitations and poor backbone resolution, the only result pertinent to higher-level classification was the suggestion that *Boerhavia* and *Allionia* were relatively closely related, calling into question the separation of subtribes Boerhaviinae and Nyctagininae. A recent phylogenetic study

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Mirabileae-Boerhaavieae	Mirabileae-Boerhaaviinae	Nyctagineae-Boerhaviinae	Nyctagineae	Commicarpus 🗕	
Mirabileae-Boerhaavieae	Mirabileae-Boerhaaviinae	Nyctagineae-Nyctagininae	Nyctagineae	Mirabilis 🗕	
Mirabileae-Abronieae	Mirabileae-Abroniinae	Abronieae	Nyctagineae	Tripterocalyx 🗕	<u></u> L
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Pisonieae	Pisonieae	Nyctagineae-Colignoniinae	Pisonieae	Pisoniella 🗕	
Mirabileae-Bougainvillaeeae	Mirabileae-Bougainvilleinae	Bougainvilleeae	Bougainvilleeae	Bougainvillea 🗕	- I II
		Bougainvilleeae	Bougainvilleeae	Belemia 🗕	JP 1L
	Mirabileae-Phaeoptilinae	Nyctagineae-Phaeoptilinae	Bougainvilleeae	Phaeoptilum 🗕	r
Mirabileae-Boldoeae	Colignonieae	Nyctagineae-Colignoniinae	Colignonieae	Colignonia 🗕	
Mirabileae-Boldoeae	Boldoeae	Boldoeae	Boldoeae	Salpianthus 🗕	⊦
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Leucastereae	Leucastereae	Leucastereae	Leucastereae	Andradea 🗕	
Mirabileae-Boldoeae	Leucastereae	Leucastereae	Leucastereae	Reichenbachia 🗕	
		Nyctagineae-Boerhaviinae	Caribeeae	Caribea 🗕	
Mirabileae-Boldoeae	Boldoeae	Boldoeae	Boldoeae	Boldoa	
Leucastereae	Boldoeae	Boldoeae	Boldoeae	Cryptocarpus	
		Pisonieae	Pisonieae	Graialesia	
Pisonieae	Pisoniese	Pisonieae	Pisonieae	Cenhalotomandra	
i isoffiede	1 isofileae	Pisonieae	Pisoniege	Neeonsis	
	Mirabiloao Roorbaaviinaa	Nyetaginana Nyetagininan	Nyotaginaga	Cusationia	
		Typeragineae-typeragininae	nyclagineae	Cuscaliania	

**Fig. 1.** Incongruence of historically influential classification schemes for Nyctaginaceae with respect to the phylogenetic hypothesis of Douglas & Manos (2007) and the new classification proposed here. All branches in the phylogenetic tree were supported at least >70% in parsimony or likelihood bootstrap or >95 bayesian posterior probability; otherwise they were collapsed. Hyphenated names correspond to tribe-subtribe; names in bold represent changes from Bittrich & Kühn (1993); genera unconnected to the tree were not included in the 2007 analysis.

of Nyctaginaceae that included nearly all currently accepted genera (Douglas & Manos, 2007) found that all previous classifications of Nyctaginaceae at the tribal level are incongruent with the evolutionary relationships among the genera demonstrated by molecular evidence (Fig. 1). With respect to the most recent (Bittrich & Kühn, 1993), the tribe Nyctagineae is not monophyletic due the basal position of the genus *Acleisanthes* (tribe Nyctagineae subtribe Boerhaviinae, now including *Selinocarpus* and *Ammocodon*; Levin, 2002) with respect to a clade that contains *Abronia* and *Tripterocalyx* (tribe Abronieae) and the remaining members of tribe Nyctagineae subtribes Nyctagininae and Boerhaviinae. The inclusion in tribe Nyctagineae of the distantly related *Phaeoptilum* and *Colignonia* (as the monogeneric subtribes Phaeoptilinae and Colignoniinae, respectively) is incompatible with a monophyletic tribe. The distinction between the subtribes Boerhaviinae and Nyctagininae is artificial due to the highly homoplasious distribution of involucral bracts in the North American xerophytic clade (Douglas & Manos, 2007). Finally, *Caribea* was included in subtribe Boerhaviinae, but a preliminary result based on a fragmentary *ndhF* sequence indicated that this poorly known taxon is probably more closely related to *Bougainvillea* or *Pisoniella* than to any members of the Nyctagineae. Now that the relationships among the genera of the family are better understood, a formal reclassification of the family into monophyletic tribes is warranted. We propose the following classification, which accomplishes the goal of recognizing monophyletic groups, is conservative with respect to previous classifications, and which accommodates remaining phylogenetic uncertainty with the recognition of two monogeneric tribes: (1) The tribe Colignonieae Standl. (1918) is recognized, containing the genus *Colignonia*. The ambiguity in the exact placement of this distinctive genus in the molecular phylogeny of the family (Douglas & Manos, 2007) means that our recognition of the tribe Colignonieae is likely to remain stable even if phylogenetic resolution is improved. Furthermore, the genus *Pisoniella* will be recognized in Pisonieae, as it had been in every classification until Bittrich & Kühn (1993) moved it into tribe Nyctagineae, subtribe Colignoniinae. The molecular results place *Pisoniella* sister, with high support, to the other genera in Pisonieae.

(2) Similarly, the genus *Caribea* is removed from tribe Nyctagineae and placed in a distinct tribe, Caribeaeae. This distinctive Cuban endemic is known only from the type collection (*Alain & Lopez P. 7013*, Cuba, Oriente, 1959. Holotype at LS, isotype at NY!). The present phylogenetic uncertainty (Douglas & Manos, 2007) refutes the present classification without clearly suggesting a justifiable alternative placement. This, in combination with the unique morphology of the genus (Alain, 1960), leads us to conclude that tribal status will be stable in the face of new evidence if and when this genus is rediscovered and can be studied in more detail.

(3) The monotypic genus *Phaeoptilum* is transferred to the Bougainvilleeae. This transfer, in combination with proposed changes 1 and 2, will remove from tribe Nyctagineae those genera that are demonstrably not closely related to the clade, which comprises the bulk of tribe Nyctagineae sensu Bittrich & Kühn (1993). We note that Heimerl (1901) mentioned several similarities between *Phaeoptilum spinosum* and *Bougainvillea patagonica* (= *B. spinosa*), especially in a particular short hair type, and leaf form and arrangement, and for a time placed the two genera in the same subtribe (Heimerl, 1897). Like Leucastereae, this tribe is essentially native to the southern hemisphere.

(4) The tribe Abronieae Standl. (1918) is no longer recognized. The two genera within it, *Abronia* and *Triperocalyx*, are now in the tribe Nyctagineae. These two genera are clearly related based on morphological similarity and molecular evidence, and they are distinctive within the family based on characters of pollen morphology, stigma shape, inflorescence architecture, fruit morphology, and embryo shape. This concentration of unique apomorphic characters makes this clade a poor fit with any other tribe, which is why it has often been recognized as distinct. The molecular evidence clearly indicates that it is derived from within the North American xerophytic clade.

(5) We do not recognize any subtribes within tribe Nyctagineae. The close relationship of *Nyctaginia* to *Anulocaulis* (previously in separate subtribes) and low support values for the relationships between *Allionia*, *Commicarpus*, and *Mirablis*, preclude any justifiable grouping of these genera into subtribes. Nevertheless, the Nyctagineae now represents a coherent group of mostly herbaceous genera based the North American xerophytic clade.

Four additional recognized genera were not sampled for the phylogenetic study; without evidence to justify alternative assignments, we propose no changes in the tribal assignment of these genera. It should be noted that the winged fruits of *Grajalesia*, an arborescent species from Mexico and Central America, bear at least superficial similarity to those of *Phaeoptilum*, but at present we lack any convincing evidence to suggest its placement elsewhere, or its removal from, the Pisonieae. Based on general morphological similarity, the other unsampled genera, *Neeopsis*, *Cephalotomandra*, and *Cuscatlania*, seem likely to remain within the tribes where they are currently placed.

Descriptions of the tribes follow below. Characters of the tribes are gleaned from the literature, and where possible from specimens when such were available. Genera included, their size, and general geographic distribution are noted.

# Tribe 1. Leucastereae Benth. & Hook. f., Gen. Pl. 3: 3. 1880 ('Leucasterae').

Trees or scandent shrubs, unarmed. Leaves alternate, petiolate, elliptic to lanceolate, with scurfy stellate hairs or scales; base symmetric to slightly asymmetric; margin entire. Inflorescences of axillary paniculate cymes or racemes; bracts minute, triangular, at base of pedicel or absent. Flowers perfect, rotate; perianth contracted in the middle or tubular throughout, tomentose or not, accrescent, 3–5-lobed, the lobes spreading or reflexed. Stamens 2 or 3 (12–20), connate at base, included. Pollen 3-colpate, 20–35  $\mu$ m, exine reticulate or spinulose. Style linear or thickened, or essentially absent; stigma lateral, crested, or sulcate. Anthocarp with 12 ribs or anthocarp usually absent. Embryo hooked. *Andradea* (1 sp., E Brazil); *Ramisia* (1 sp., SE Brazil); *Reichenbachia* (2 spp., trop. South Amer.); *Leucaster* (1 sp., SE Brazil).

Tribe 2. Boldoeae Heimerl in Engler & Prantl, Nat. Pflanzenfam. 3(1b): 21, 31. 1889.

Plants suffrutescent or herbaceous, often subshrubs, unarmed. Roots unknown. Leaves alternate, petiolate, thickish, elliptic to rhomboid, tomentose or not, viscid, hairs straight or hooked; bases symmetric or nearly so; margin entire. Inflorescences congested axillary or terminal paniculate cymes of glomerules or racemes, bostryches (Bittrich & Kühn, 1993), bracts absent. Flowers perfect, rotate, 3–5-lobed, 2–5 mm, tubular to campanulate, not contracted above the ovary, pubescent. Stamens 3–5, exserted, filaments free. Pollen tricolpate, 20–46 µm, exine spinulose. Style short, linear-filiform, stigma delicate, fimbriate. Anthocarp globose or subglobose, coriaceous. Embryo curved. *Boldoa* (2–3 spp., Mexico); *Cryptocarpus* (1 sp., S Mexico, Centr. Amer., NW South Amer.); *Salpianthus* (1 sp., Mexico, Cent. Amer., N South Amer.).

# Tribe 3. Colignonieae Standl. in Britton, N. Amer. Fl. 21: 195. 1918.

Lianas or scandent shrubs, unarmed. Roots tuberous or fibrous, also adventitious. Leaves opposite or whorled, shortpetiolate, deltoid, ovate, or elliptic, glabrous, puberulous, or rufo-pilose, trichomes 3–4-celled; base truncate; margin entire. Inflorescence a cymose, umbel-like condensed dichasium; bracts white, green, or reddish, broadly lanceolate to obovate. Flowers perfect, rotate; perianth lobes 3(–4)–5, campanulate or spreading, connate only at base. Stamens 5, exserted, episepalous, basally connate; filaments flattened, nectariferous; anthers subglobose. Pollen 12-pantoporate, 17–30  $\mu$ m, exine spinulose. Ovary stalked, style clavate, stigma penicillate. Anthocarp present, winged or angled. Embryo curved. *Colignonia* (6 spp., Andean South Amer.).

### Tribe 4. Bougainvilleeae Choisy in Candolle, Prodr. 13: 427, 436. 1849. ('Bougainvilleae')

Trees, or shrubs, sometimes scandent, perennial, occasionally with spines. Leaves alternate, opposite, or fasciculate on short branches, petiolate or nearly sessile, ovate, orbicular, to linear-lanceolate, succulent to membranous, glabrous or pubescent; base symmetric or nearly so, margin entire. Inflorescence cymose or racemose or flowers solitary, bracts absent or 3, often showy, the flowers often borne on costae of bracts. Flowers perfect or imperfect (plants then possibly polygamous, Stannard, 1988), rotate, tubular or salverform. Stamens 5–12, often connate at base, included or didymous with longer stamens exserted. Pollen tricolpate with reticulate exine or pantocolpate. Style short, filiform or stout, stigma linear to penicilliate or multifid. Anthocarp fusiform and 5-ribbed or with 4 translucent, scarious wings. Embryo curved. Belemia (1 sp., E Brazil); Bougainvillea (14–18 spp., Centr. & trop. South Amer.); Phaeoptilum (1 sp., SW Africa).

### Tribe 5. Pisonieae Meisn., Pl. Vasc. Gen. 10: Tab. Diagn. 318, Comm. 230. 1841.

Trees, shrubs, or scandent shrubs, unarmed or with paired axillary spines. Leaves alternate, opposite, whorled, or verticillate, sometimes anisophyllous, petiolate, lanceolate, elliptic to (ob)ovate, membranous to coriaceous or fleshy, glabrous to glandular puberulent; base symmetric; margins entire. Inflorescences axillary and terminal paniculate cymes, corymbs, or glomerules; bracts 2-3 beneath each flower, persistent or cauducous. Flowers perfect or imperfect, or polygamous, campanulate, urceolate, rotate-salverform, or tubular, the limb 5-lobed. Stamens (2-)5-10(-many), exserted or included, connate at base, adnate to base of pistil in perfect flowers, filaments unequal, Pollen generally tricolpate-spinulose. Style exserted, stigma penicillate or pappilose. Anthocarps oblong, clavate, or ellipsoid, 5-ribbed, coriaceous and glandular-sticky, or globose, fleshy and glabrous. Embryo straight. Cephalotomandra (1-3 spp., Colombia); (Grajalesia (1 sp., Mexico); Guapira (ca. 70 spp., trop. Amer.); Neea (ca. 80 spp., trop. Amer.); Neeopsis (1 sp., Guatemala); Pisonia (ca. 40 spp., pantropical, but especially diverse in the Americas and SE Asia); Pisoniella (1 sp., Mexico, Centr. & S South Amer.).

#### Tribe 6. Nyctagineae Horan., Char. Ess. Fam.: 106. 1847.

Woody or suffrutescent subshrubs, or annual or perennial herbs, sometimes scandent, unarmed, in some with bands of viscid exudate on internodes. Roots slender and fleshy to tuberous or spongy-woody taproots, rarely rhizomatous. Leaves opposite, frequently anisophyllous, sessile or petiolate, membranous to fleshy, linear, cordate, ovate, or orbicular, glabrous or pubescent, often glandular; base symmetric to asymmetric; margins entire, crenate, undulate or sinuate, glandular pubescent to glabrous. Inflorescences terminal or axillary spikes, cymes, umbels or flowers solitary. Involucres of 3-20 connate or free bracts, or 1-2 often minute, persistent or cauducous bracts subtending individual flowers or terminal cymes; bracts oblong, linear, acuminate, or lanceolate, green or scarious. Flowers actinomorphic or slightly to strongly zygomorphic, campanulate to tubular to salverform, constricted above the ovary (4-)5-lobed (in some cleistogamous flowers often present, these quite reduced). Stamens (1-)2-5(-18), included or exserted, united at base and sometimes inserted on perianth tube. Pollen 100-200 µm, pantoporate with spinulose exine, or tricolpate with reticulate exine. Style included or exserted, filiform, stigma linear, capitate, or peltate. Anthocarp globose, turbinate, clavate, obpyramidal to fusiform, radially symmetric (gibbous in Cyphomeris, cymbiform with 2 rows of teeth in Allionia), coriaceous (spongy and geocarpous in Okenia), 3-10 costate, often with membranaceous wings or viscid glands; sulci smooth, pappilose, or rugose. Embryo hooked. Abronia (ca. 20 spp., W and C North Amer.); Acleisanthes (17 spp., SW and SC North Amer., with 1 sp. in NE Africa); Allionia (1-2 spp., Americas); Anulocaulis (5 spp., SC and SW North Amer.); Boerhavia (ca. 40 spp., worldwide in tropical and subtropical regions, annuals especially diverse in SW North Amer.); Commicarpus (30-35 spp., nearly worldwide in tropical and subtropical regions, especially diverse in Africa and W Asia); Cyphomeris (2 spp., SC North Amer.); Mirabilis (ca. 60 spp., Americas and 1 sp. in SC Asia); Nyctaginia (1 sp., SC North Amer.); Okenia (1-2 spp., Mexico, Centr. America); Tripterocalyx (4 spp., SW North Amer.).

## Tribe 7. Caribeeae Douglas & Spellenb., tr. nov. – Type: *Caribea* Alain in Candollea 17: 113. 1960.

Fruticulus perennis valde abbreviatus, depressus; caules numerosi, in base lignescentes, dense foliosi, striate, glandulosi. Folia opposita. Flores 3–5-bracteolati, solitarrii, terminales. Perianthium infundibulare, tubo supra ovarium constricto, limbo 5-lobato. Stamina 2, filamentis capillaribus ad basim perianthii adnati. Ovarium globoso-oblongum, stylus filiformis, exsertus, stigmate capitato. Anthocarpium globosooblongum, laeve (adapted from Alain, 1960).

Tufted, compact mat-forming, taprooted perennial. Leaves petiolate, opposite, forming a stipuliform sheath at base, oblanceolate, fleshy or succulent, glabrous, margin entire. Inflorescence terminal, flowers solitary, subtended by an involucre of 3–5 free narrow bracts. Perianth constricted above the ovary, distil portion nearly urceolate, with 5 shallow lobes. Stamens 2, exserted, filiments adenate to perianth base. Style filiform, exserted, stigma capitate. Anthocarp subglobose, smooth. Embryo unknown. *Caribea* (1 sp., Cuba).

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