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Nomenclatural changes and a new sectional classification in *Nicotiana* (Solanaceae)

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Recent studies using regions of the nuclear and plastid genomes have shown that T. H. Goodspeed's sectional groupings in *Nicotiana* are for the large part upheld. However, we have shown that in several cases sectional membership should be revised. Here we present a revised outline of the sections of *Nicotiana* with lists of their component species. Relationships of the sections as defined can be seen in accompanying figures. Two sectional names with priority over those in current use are introduced (*N.* sect. *Polydicliae* & sect. *Petunioides*) and one new section, *N.* sect. *Sylvestres*, is described here. Two species names are changed to those with priority over those adopted by Goodspeed in his monograph of the genus: *N. obtusifolia* for *N. trigonophylla* and *N. quadrivalvis* for *N. higelovii*. Synonymies are provided for each of these names. A short morphological description is provided for each section, along with a generalized distribution and a list of accepted species names.

KEYWORDS: classification, Nicotiana, phylogeny, Solanaceae, tobaccos



INTRODUCTION

Circumscription of the Linnaean genus Nicotiana, named for the French diplomat Jean Nicot, who is said to have brought seeds of tobacco from Portugal to France in the 16th century, has remained essentially the same through several centuries—the addition of new species merely serving to increase diversity rather than presenting problems of generic delimitation. The genus, with 76 naturally occurring species, is the sixth largest in the family Solanaceae (after Solanum L. with ca. 1500-2000, Lycianthes Hassl. with ca. 250, Cestrum L. with ca. 150, Physalis L. with ca. 90 and Lycium L. with more than 80 species; see Hunziker, 2001). Species of Nicotiana occur largely in the Americas and Australia, with a single species in Africa (Namibia; see Chase & al., 2003, table 1, for distributions of species); cultivated tobaccos (N. tabacum and N. rustica), however, have been spread worldwide by humans. Amphidiploid (allotetraploid) hybridization is common in the genus and appears to be unrelated to human intervention; both the tobaccos of commerce as well as several other species and species groups are amphidiploid hybrids (Goodspeed, 1954). The genus was last monographed by Goodspeed (1954) and 15 additional species have been described since then, mostly from Australia (see Chase & al., 2003: table 1). The addition of these new taxa and recent work on the phylogenetic relationships in the

genus means that a new sectional classification of the genus is necessary to stabilize nomenclature for future phylogenetic work and to reflect our current improved understanding of the composition of monophyletic species groups in *Nicotiana*. Several names currently in common use in floras and checklists also are in need of change, as earlier epithets have been suggested, but never taken up.



SPECIFIC EPITHETS

In his monograph *The Genus Nicotiana*, Goodspeed (1954) specifically alluded to species epithets with possible priority over those he adopted. Because Goodspeed was uncertain as to their application he chose not to apply the rules on priority. We have found that there are three species names that must now change to the older, validly published names or the provisions for conservation or rejection of names must be invoked. Two of these, N. obtusifolia for what was previously known as N. trigonophylla and N. quadrivalvis for what Goodspeed called N. bigelovii, apply to North American species of relatively restricted distribution and are currently being used in North American floras and other publications (Nee, 1993; Chase & al., 2003; USDA, NRCS, 2004). Nicotiana quadrivalvis is the cultivated native western North American tobacco collected by Lewis and Clark (among others), and this name is currently being widely used in the popular literature relating to the celebration of the bicentenary of their expedition (see for example, http://www.nationalgeographic.com/lewisandclark/ and http://www.lewis-clark.org/). Usage of both *N. obtusifolia* and *N. quadrivalvis* is becoming standard.

Goodspeed acknowledged that *N. obtusifolia* would be the correct name for *N. trigonophylla* should the types prove the same, but he rejected use of *N. quadrivalvis* on the following invalid grounds: "Although the designation *N. quadrivalvis* Pursh has priority over *N. bigelovii*, it is not reverted to since is was based on the 4-celled capsule, a character subsequently proven anomalous and unstable". Because of the relatively restricted distribution of these species and because the correct names have already been adopted in the works cited above, we see no reason for seeking to maintain the names adopted by Goodspeed (1954). The publication details of these two names and their synonyms are as follows; formal typifications are deferred to the monographic revision of *Nicotiana*:

- Nicotiana obtusifolia M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 12: 129. 1845. Syntypes: Mexico, Puebla, "regions cactiferes de Tehuacan, 5000 pieds de Ximapan, au nord de Mexico", Galeotti 1146, 1148 (BR).
- = *Nicotiana trigonophylla* Dunal in DC., Prodr. 13(1): 562. 1852.
- = *Nicotiana multiflora* Torr., Pacif. Railr. Rep. 5(2): 362. 1857.
- Nicotiana glandulosa Buckley, Proc. Acad. Nat. Sci. Philadelphia 6. 1893.
- Nicotiana trigonophylla var. pulla Nees ex Comes, Monogr. Nicotiana 49. 1899.

Nicotiana quadrivalvis Pursh, Fl. Amer. Sept. 1: 141. 1813. ≡ Amphipleis quadrivalvis (Pursh) Raf., Fl. Tellur. 3: 75. 1836. ≡ Dictyocalyx quadrivalvis (Pursh) Hook., Repert. Bot. Syst. 6: 572. 1846–1847. ≡ Polydiclis quadrivalvis (Pursh) Miers, Ann. Mag. Nat. Hist. ser. 2, 4: 362. 1849. ≡ Nicotiana bigelovii (Torrey) S. Watson var. quadrivalvis (Pursh) East, Bibliogr. Genet. 4: 250. 1928. Lectotype (designated by Goodspeed, 1954: 431): United States, South Dakota, "cultivated and spontaneous on the Missouri; principally among the Mandan and Ricara nations", 12 Oct 1804, Lewis & Clark s.n. (PH-1022091).

Nicotiana multivalvis Lindl., Bot. Reg. 13: tab. 1057. 1827. ≡ Dictyocalyx multivalvis (Lindl.) Hook. in Walp., Repert. Bot. Syst. 6: 572. 1846–1847. ≡ Polydiclis multivalvis (Lindley) Miers, Ann. Mag. Nat. Hist. ser. 2, 4: 362. 1849. ≡ Nicotiana quadrivalvis Pursh var. multivalvis

- (Lindl.) A. Gray, Syn. Fl. N. Amer. (ed. 2) 243. 1878. *Amphipleis foetida* Raf., Fl. Tellur. 3: 75. 1836.
- = Nicotiana plumbaginifolia Viv. var. bigelovii Torr., Pacif. Railr. Rep. 4(5): 127. 1857. ≡ Nicotiana bigelovii (Torr.) S. Watson, Botany Fortieth Parallel 276. 1871. ≡ Nicotiana quadrivalvis Pursh var. bigelovii (Torr.) DeWolf, Southwest. Naturalist 2: 179. 1957 [1958].

That *Nicotiana pusilla* L. might be the correct name for what was being called *N. plumbaginifolia* was specifically alluded to by Goodspeed (1954: 404), by DeWolf (1958: 179) in his review of Goodspeed's monograph and by Nee (1986: 131) in *Flora de Veracruz*. Careful typification of *N. pusilla* has confirmed that it applies to the species generally known as *N. plumbaginifolia*. However, because of the long-standing doubt as to the application of *N. pusilla* and the widespread use of *N. plumbaginifolia* for the most geographically widespread species of *Nicotiana* (occurring from the southern United States to Argentina), a formal proposal is being made to conserve *N. plumbaginifolia* over *N. pusilla* (Knapp, in prep.). For this reason we continue to use the familiar *N. plumbaginifolia* in this paper.

HISTORY OF SECTIONAL NOMEN-CLATURE

Linnaeus (1753) described four species of *Nicotiana* (*N. glutinosa*, *N. tabacum*, *N. rustica* and *N. paniculata*), all tropical American. Lehmann (1818) first treated the genus as a whole, and included 21 species, mentioning for the first time a "peculiar" species from "Nova Hollandiae" or Australia. He provided no infrageneric groupings in *Nicotiana* and included the genus *Petunia* Juss. in synonymy. Kunth, in his descriptions of the plants collected by Humboldt and Bonpland (Humboldt & al., 1818), divided the seven species of *Nicotiana* he treated into two unranked subdivisions; species with hypocrateriform flowers and obtuse corolla lobes and species with infundibuliform flowers and acute or acuminate corolla lobes.

George Don (1838) was the first to explicitly provide sectional names for the subdivisions of *Nicotiana*. He divided the genus into four sections, defined largely on flower shape and colour; "I Sect. *Tabacum*" with reddish funnel-shaped flowers, "II Sect. *Rustica*" with yellow flowers of a wide variety of shapes, "III Sect. *Petunioides*" with white salverform flowers and "IV Sect. *Polydiclia*" with white ventricose flowers and 4-valved capsules (see Table 1 for component species in Don's sections). He excluded *N. tomentosa* and *N. glutinosa*, treating the former as the sole species of

Lehmannia Spreng. and the latter as the sole species of his new genus Sairanthus.

In his comprehensive taxonomic treatment of the entire Solanaceae, Dunal (1852) divided *Nicotiana* into two groups, explicitly ranked as sections, based on capsular morphology; "Sectio I. *Didiclia*", those species with 2-valved capsules including most of the genus, and "Sectio II. *Polydiclia*", those species with multi-valved capsules, including only *N. quadrivalvis* and *N. multi-valvis*. Von Wettstein (1895) ignored Dunal's (1852) groupings and reverted to the use of Don's sections, *N.* sect. *Tabacum*, *Rustica* and *Petunioides*, including species from Don's *N.* sect. *Polydiclia* in his delimitation of *N.* sect. *Petunioides*.

Early 20th century work on the genetics of the genus (Splendore, 1906; Anastasia, 1912, 1920) used Don's sections as had von Wettstein (1895) — citing the putative parents of the amphidiploid N. tabacum as "rustica" and "petunioides", meaning species from those sections (sensu Don) respectively, not N. rustica or N. petunioides specifically. Setchell (1912) also used three of Don's sections, including in his N. sect. Petunioides those species segregated as N. sect. Polydiclia by Don. Genetic work done with members of the genus in the early to mid-20th century led both East (1928) and Kostoff (1930) to recognize a number of what were called "genetic centres"; Kostoff (1943) later called these same groups "sections", more or less the same as his earlier "genetic groups". These names were not validly published, because they were not accompanied by descriptions of any sort (see Article 41.2; Greuter & al., 2000).

Thomas H. Goodspeed worked extensively on the cytogenetics and taxonomy of the genus during the first half of the 20th century. His monograph (Goodspeed, 1954) has been the standard treatment for the last 50 years. He produced a taxonomic classification of the genus in which he elevated three of Don's sections (*N.* sect. *Tabacum*, *Rustica* and *Petunioides*) to subgeneric status, explicitly typifying them at the same time, and proposed a series of new sectional names for what he

recognised as related sets of species. He further refined this classification by segregating three groups of amphidiploids at the sectional rank; *N.* sect. *Nudicaules*, *Bigelovianae* and *Repandae*. Previously, Goodspeed (1945) had included *N. repanda* in *N.* sect. *Alatae* and *N. bigelovii* (*N. quadrivalvis*) and *N. nudicaulis* in his *N.* sect. *Acuminatae*.

Goodspeed's (1954) hypotheses as to species and higher-level relationships in the genus have not been questioned until recent work using molecular data clarified the origins of Nicotiana tabacum (e.g. Kenton & al., 1993; Lim & al., 2000) and other amphidiploid taxa (Chase & al., 2003). Phylogenetic work using both chloroplast (Aoki & Ito, 2000; Olmstead & Palmer, 1991; Clarkson, Knapp, Aoki, Garcia, Olmstead & Chase, in prep.) and nuclear (Komarnitsky & al., 1998a, b; Chase & al., 2003) data sets has been useful in resolving relationships of species Goodspeed (1954) considered problematic (i.e. N. glauca, N. glutinosa; see Chase & al., 2003). The results obtained from a variety of different analyses are in agreement as to the monophyletic groups in Nicotiana (see Fig. 1). The new sectional classification reflects these changes and those based on correct application of the Code (Greuter & al., 2000) with respect to priority.

SECTION

SECTIONAL CLASSIFICATION OF NICOTIANA

Only naturally occurring species of *Nicotiana* are included in this revised sectional classification, although we (and others) have included several artificial amphidiploids in molecular studies (e.g. *Nicotiana* × digluta, N. × didepta: see references above). We retain Goodspeed's sectional classification as the basic framework for this new classification, understanding that different ways of treating hybrids in phylogenetic classifications have been proposed. Goodspeed's sectional names have been so widely used in both the botanical

Table 1. Sectional classification of *Nicotiana* according to George Don (1838). Species names in **bold** are accepted names, the others are either synonyms of accepted names or are insufficiently known. For synonymy see Goodspeed (1954).

Section	Component species
"Sect. Tabacum"	N. tabacum L.; (many horticultural varieties); N. loxensis Kunth; N. fruticosa L.; N. macrophylla Spreng.;
	N. chinensis Lehm.; N. lancifolia Willd.; N. auriculata Bertero
"Sect. Rustica"	N. pusilla L.; N. undulata Ruiz & Pav.; N. paniculata L.; N. cerinthoides Lehm.; N. glauca Graham;
	N. langsdorffii Weinm.; N. rustica L.; N. humilis Link; N. pulmonaroides Kunth; N. andicola Kunth
"Sect. Petunioides"	N. suaveolens Lehm.; N. vincaeflora Lag.; N. longiflora Cav.; N. noctiflora Hook.; N. persica Lindl.;
	N. acuminata (Graham) Hook.; N. angustifolia Ruiz & Pav.; N. dilatata Link; N. plumbaginifolia Viv.;
	N. repanda Willd.; N. viscosa Lehm.; N. bonariensis Lehm.
"Sect. Polydiclia"	N. quadrivalvis Pursh; N. nana Lindl.; N. multivalvis Lindl.

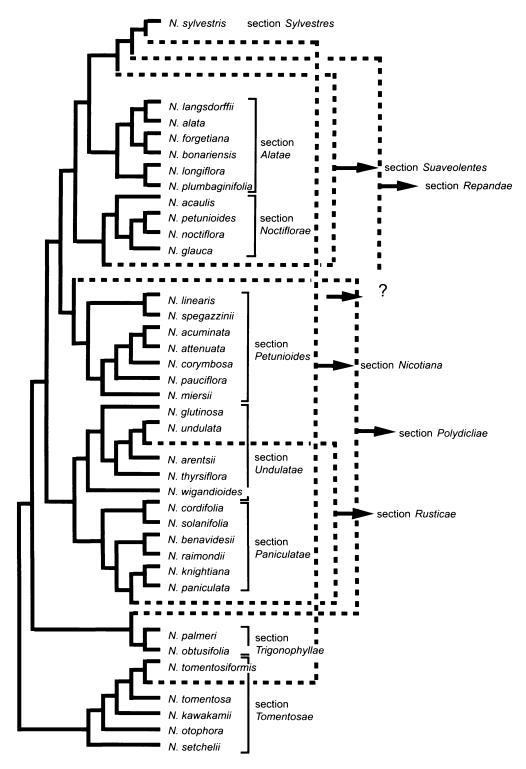


Fig. 1. Cladogram summary of our proposed classification of *Nicotiana* showing diploid species and their sectional classification. Sections of allotetraploid origin are indicated by dashed lines from both their parental lineages, except for *N.* sect. *Repandae* for which we currently know only one of the two parental lineages. More recent hybridization events are nested above those having occurred more distantly in the past (e.g., the reticulation that produced *N.* sect. *Nicotiana* overlays that of *N.* sect. *Suaveolentes*). We have indicated that one of the parental lineages of *N.* sect. *Repandae* and *Suaveolentes* was an ancestor of *N.* sylvestris, but it equally well could have been an ancestor common to both *N.* sylvestris and *N.* sect. *Alatae*. For additional information on methods and data sources, see Chase & al. (2003) and Clarkson & al. (in prep.). The allotetraploid *N. arentsii* is classified as a member of *N.* sect. *Undulatae* because its parents (*N. undulata* and *N. wigandioides*) are both members of that section.

and agronomic literature that a completely new classification would make relating new work to previous studies undesirably difficult.

Most of Goodspeed's sections are upheld by molecular analysis (see above and Fig. 1) but four diploid species are members of groups other than those in which Goodspeed placed them: N. glutinosa was treated by Goodspeed as a member of his N. sect. Tomentosae and N. thyrsiflora as the sole member of his N. sect. Thyrsiflorae, whereas here both are treated as members of N. sect. Undulatae. On account of its yellow flowers, Goodspeed (1954) considered N. glauca a member of N. sect. Paniculatae, although with reservations. Here we include it as a member of N. sect. Noctiflorae. Nicotiana sylvestris was treated as a member of N. sect. Alatae by Goodspeed, and although related to that group morphologically, it also shares morphological characters such as chromosome number with members of N. sect. Noctiflorae. The genome of Nicotiana sylvestris appears to have been involved in several allopolyploid events; it may be nearer to an ancestral Nicotiana genome than other extant species (see Chase & al., 2003). Nicotiana sylvestris is never well-supported (i.e., never more than 73% bootstrap support) as part of N. sect. Alatae or of N. sect. Noctiflorae in the strict sense in any of our analyses (Chase & al., 2003; Clarkson & al., in prep.; see Fig. 1); we here give it sectional status.

In this sectional classification we have placed all amphidiploid species in sections separate from their progenitor taxa because they represent fusion of two distinct genomes, and based on studies such as Kenton & al. (1993) we know that these genomic interactions create new traits and permit movement into new habitats. For example, N. sect. Suaveolentes (all allopolyploid) has extensively radiated in Australia and one species (sister to the Australian taxa) has persisted in Africa.

We have here defined an apparently paraphyletic *N*. sect. *Polydicliae* separate from *N*. sect. *Trigonophyllae* (see Fig. 1) due to their complex genomic origins. From both the ITS and plastid results (Chase & al., 2003; Clarkson & al., in prep.) it is apparent that two different polyploidization events at two times, involving the same parental species (putatively ancestral *N*. sect. *Trigonophyllae*-like and *N. sylvestris*-like; Chase & al., 2003, Clarkson & al., in prep.) have led to the evolution of *N. quadrivalvis* and *N. clevelandii*. We do not combine these two groups at present due to the amphidiploidy of *N. quadrivalvis* and *N. clevelandii*, and pending more detailed investigation of the allopolyploid origins of these taxa.

We have combined Goodspeed's N. sect. Repandae and Nudicaules here as N. sect. Repandae, as both plastid and nuclear datasets indicate they share the same two parental taxa and are thus a monophyletic group (Chase

& al., 2003; Clarkson & al., in prep.). Goodspeed classified these taxa in two sections based on floral morphology. The diurnal flowering and short-tubular corolla of *N. nudicaulis* are markedly different to the long-tubular vespertine corollas of *N. repanda*, *N. stocktonii* and *N. nesophila*. Molecular data indicate a *N. sylvestris*-type progenitor as one parent and a *N. obtusifolia*-type ancestor as the other (based on nuclear glutamine synthetase data, Clarkson & al., unpubl.).

The orthography of sectional names has been changed in accordance with Article 21 of the Code (Greuter & al., 2000), and the group containing the generitype (see Jarvis & al., 1993) must, following Article 22, be called Nicotiana sect. Nicotiana. Even though Goodspeed (1945, 1954) did not use sectional names that clearly had priority (e.g., those of G. Don), the names of only a few sections in the genus will need to change. The correct name for Goodspeed's N. sect. Acuminatae is N. sect. Petunioides, and the correct name for his N. sect. Bigelovianae is N. sect. Polydicliae. For the most part, Goodspeed explicitly designated types for his sectional names and typified Don's sectional names as synonyms of his own subgenera. Those sectional names without explicit type designations are lectotypified here.

We have not included in the sectional synonymy genera based upon component species (e.g., Lehmannia tomentosa (Ruiz & Pav.) Spreng. [N. tomentosa], Sairanthus glutinosus (L.) G. Don [N. glutinosa], Polydiclia Miers [N. quadrivalvis] and the many genera that are synonyms of N. tabacum); for the most part these generic names have not been lectotypified, and we leave this task for a full monographic treatment of the genus Nicotiana. Species-level synonymy follows Goodspeed (1954) and Purdie & al. (1982). Species not included in any of our molecular analyses have been assigned to sections on the basis of overall morphology; these are indicated with an asterisk (*) before the species name. For detailed species distributions and chromosome numbers see Goodspeed (1954) and Chase & al. (2003). Sections are listed here alphabetically; their relationships can be seen in Fig. 1.

Nicotiana L., Sp. Pl. 180. 1753. Lectotype (designated by Setchell, 1912: 6): *Nicotiana tabacum* L.

Nicotiana sect. *Alatae* Goodsp., Univ. Calif. Publ. Bot. 18: 339 (1945). – Type: *N. alata* Link & Otto.

Rosette-forming herbs; leaves sessile, variously pubescent, usually viscid, few leaves on upper stems, those present clasping and markedly smaller than the basal rosette; corolla zygomorphic, salverform, green, white or pink to red, the tube with an abrupt dilation at the throat, the lobes acute or rounded (*N. langsdorffii*);

flowering usually vespertine with flowers wilting in day, occasionally (*N. langsdorffii*) diurnal. Chromosome number: n = 9, 10. Mexico-Uruguay. Included species: *Nicotiana alata* Link & Otto; **Nicotiana azambujae* L. B. Smith & Downs; *Nicotiana bonariensis* Lehm. (Fig. 2A); *Nicotiana forgetiana* Hemsl.; *Nicotiana langsdorffii* Weinm.; *Nicotiana longiflora* Cav.; **Nicotiana mutabilis* Stehmann & Samir; *Nicotiana plumbaginifolia* Viv.

Nicotiana sect. Nicotiana. ≡ Nicotiana sect. Tabacum G. Don, Gen. Syst. 4: 462 (1838). – Lectotype (designated by Goodspeed, 1945): N. tabacum L. ≡ Nicotiana sect. Didiclia Dunal in DC., Prodr. 13: 557. 1852. – Lectotype (designated here): N. tabacum L.

"Nicotiana sect. Genuinae" Goodsp., Univ. Calif. Publ. Bot. 18: 338 (1945), non rite publ. (Art. 22.2).

Stout, thick-stemmed herbs or single-stemmed shrubs; leaves large, sessile or broadly wing-petioled, viscid-tomentose; corolla nearly regular, salverform, usually pinkish, but ranging from white to red, the tube broadly inflated, the lobes acute; flowering diurnal. Chromosome number: n = 24. Andes, naturalized worldwide. Included species: *Nicotiana tabacum* L. (Fig. 2B)

Nicotiana sect. *Noctiflorae* Goodsp., Univ. Calif. Publ. Bot. 18: 340 (1945). – Type: *N. noctiflora* Hook.

Annual or perennial herbs or small trees; leaves sessile or petiolate, finely puberulent to viscid, usually with a whitish cast, the margins often erose or crisped; corolla regular, tubular to salverform, red, yellow or white, the tube straight or apically dilated, the lobes usually rounded; flowering diurnal or vespertine. Chromosome number: n = 12. S. South America. Included species: Nicotiana acaulis Speg.; *Nicotiana ameghinoi Speg.; Nicotiana glauca Graham (Fig. 2C); Nicotiana noctiflora Hook. (Fig. 2D); *Nicotiana paa Mart. Crov.; Nicotiana petuniodes (Griseb.) Millán.

Nicotiana sect. *Paniculatae* Goodsp., Univ. Calif. Publ. Bot. 18: 336 (1945). – Type: *N. paniculata* L.

Stout herbs or small trees; leaves petiolate, usually with short downy pubescence; corolla tubular, regular, greenish or yellow, the tube straight, the lobes small, rounded; flowering diurnal. Chromosome number: n = 12. W. South America. Included species. Nicotiana benavidesii Goodsp.; Nicotiana cordifolia Phil.; *Nicotiana cutleri D'Arcy; Nicotiana knightiana Goodsp.; Nicotiana paniculata L. (Fig. 2E); Nicotiana raimondii J. F. Macbr.; Nicotiana solanifolia Walp.

Nicotiana sect. Petunioides G. Don, Gen. Hist. 4: 465 (1838). – Lectotype (designated by Goodspeed, 1945): N. acuminata (Graham) Hook. ≡ Nicotiana

sect. *Acuminatae* Goodsp., Univ. Calif. Publ. Bot. 18: 341 (1945).

Annual herbs, occasionally somewhat woody at the base; leaves petiolate or winged-petiolate on upper stems, viscid-pubescent; corolla regular or slightly zygomorphic, salverform, white, the outer surface of the tube greenish or purplish, the lobes acute; flowering verspertine, the flowers not wilting markedly diurnally. Chromosome number: n = 12. S.W. United States and S. South America. Included species: *Nicotiana acuminata* (Graham) Hook.; *Nicotiana attenuata* Torrey ex S. Watson (Fig. 2F); *Nicotiana corymbosa* J. Rémy; *Nicotiana linearis* Phil. (Fig. 2G); **Nicotiana longibracteata* Phil.; *Nicotiana miersii* J. Rémy; *Nicotiana pauciflora* J. Rémy; **Nicotiana spegazzinii* Millán.

- Nicotiana sect. Polydicliae G. Don, Gen. Hist. 4: 467 (1838). Lectotype (designated here): Nicotiana quadrivalvis Pursh.
- = *Nicotiana* sect. *Bigelovianae* Goodsp., Chronica Botanica 16: 446 (1954). Lectotype (designated by Goodspeed, 1954): *N. bigelovii* (Torrey) S. Watson (synonym of *N. quadrivalvis* Pursh).

Annual herbs, sometimes rosette-forming; leaves short-petiolate, the cauline leaves often sessile, sparsely pubescent, usually somewhat viscid; corolla regular, salverform, white, the tube straight, the lobes acute; flowering vespertine. Chromosome number: n = 24. S.W. United States and Mexico. Included species: *Nicotiana clevelandii* A. Gray (Fig. 2H); *Nicotiana quadrivalvis* Pursh

Nicotiana sect. *Repandae* Goodsp., Chronica Botanica 16: 405 (1954). – Type: *N. repanda* Willd.

 Nicotiana sect. Nudicaules Goodsp., Chronica Botanica 16: 454 (1954). – Type: N. nudicaulis S. Watson.

Rosette-forming herbs; leaves long petiolate or wing-petioled in rosette, finely pubescent, the upper cauline leaves short-petioled or pandurate and clasping; corolla regular or somewhat zygomorphic, tubular-salverform or salverform, white, the tube sometimes very narrow (*N. repanda*, *N. stocktonii*, *N. nesophila*), the lobes acute or rounded; flowering diurnal (*N. nudicaulis*) or vespertine. Chromosome number: n = 24. S.W. United States and N. Mexico. Included species. *Nicotiana nesophila* I. M. Johnston (Fig. 3A); *Nicotiana nudicaulis* S. Watson (Fig. 3B); *Nicotiana repanda* Willd.; *Nicotiana stocktonii* Brandegee.

Nicotiana sect. Rusticae G. Don, Gen. Hist. 4: 464 (1838). – Type: N. rustica L.

Stout herbs; leaves petiolate, densely pubescent, viscid; corolla tubular, regular or slightly zygomorphic,

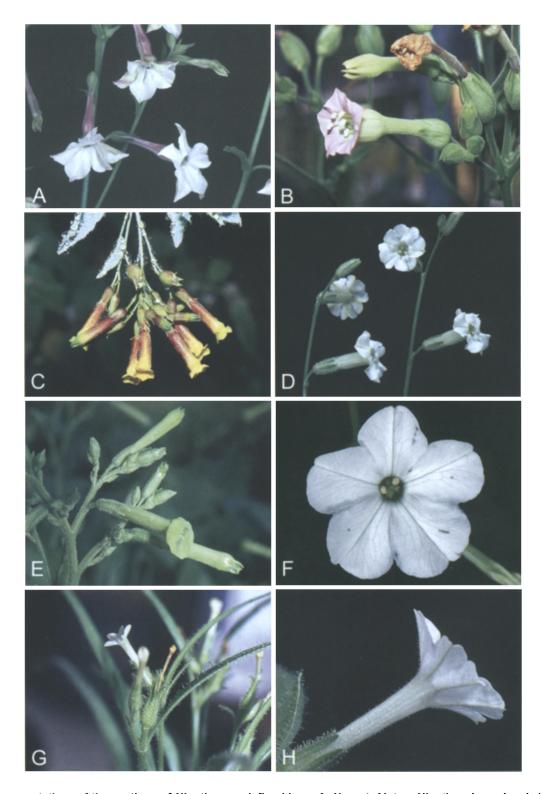


Fig. 2. Representatives of the sections of *Nicotiana* as defined here. A, *N.* sect. Alatae: *Nicotiana bonariensis* (cult. RBG Kew;); B, *N.* sect. *Nicotiana*: *Nicotiana tabacum* (cult. University of Nijmegen; acc. A04750053); C, *N.* sect. *Noctiflorae*: *N. glauca* (Bolivia; *Nee & al. 51725*); D, *N.* sect. *Noctiflorae*: *N. petunioides* (cult. RBG Kew); E, *N.* sect. *Petunioides*: *N. attenuata* (cult. RBG Kew); G, *N.* sect. *Petunioides*: *N. linearis* (cult. University of Nijmegen; acc. 964750099); H, *N.* sect. *Polydicliae*: *N. clevelandii* (cult. RBG Kew). All cultivated material is vouchered; locations of these specimens can be found in Chase & al. (2003) and Clarkson & al. (in prep.).

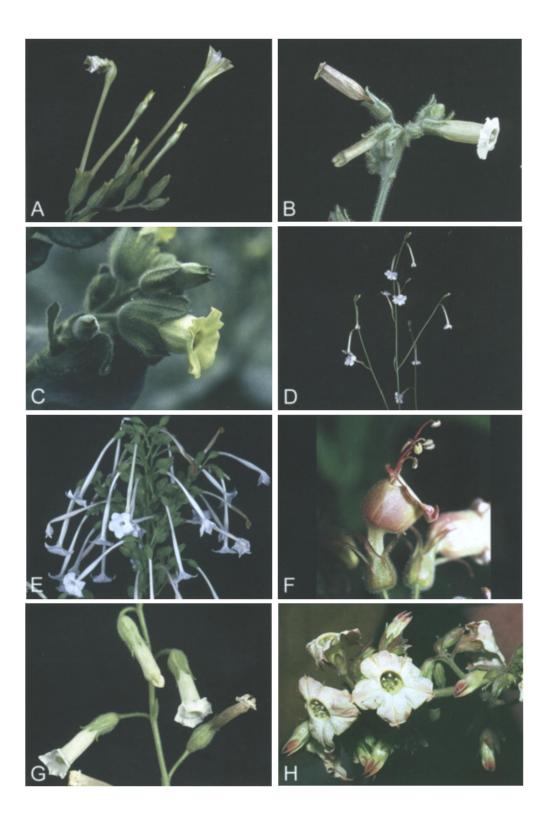


Fig. 3. Representatives of the sections of *Nicotiana* as defined here, continued. A, *N.* sect. *Repandae*: *N. nesophila* (cult. RBG Kew); B, *N.* sect. *Repandae*: *N. nudicaulis* (cult. RBG Kew); C, *N.* sect. *Rusticae*: *N. rustica* (cult. RBG Kew); D, *N.* sect. *Suaveolentes*: *N. suaveolens* (cult. RBG Kew); E, *N.* sect. *Sylvestres*: *N. sylvestris* (cult. RBG Kew); F, *N.* sect. *Tomentosae*: *N. otophora* (Bolivia; Nee & al. 51727); G, N. sect. *Trigonophyllae*: N. palmeri (cult. RBG Kew); H, N. sect. *Undulatae*: N. wigandioides (Bolivia; Nee & al. 51764). All cultivated material is vouchered; locations of these specimens can be found in Chase & al. (2003) and Clarkson & al. (in prep.).

greenish or yellow, the tube straight, short, the lobes acute; flowering diurnal. Chromosome number: n = 24. Andes, naturalized worldwide. Included species: *Nicotiana rustica* L. (Fig. 3C).

Nicotiana sect. *Suaveolentes* Goodsp., Univ. Calif. Publ. Bot. 18: 342 (1945). – Type: *N. suaveolens* Lehm.

Rosette-forming herbs, occasionally without a marked basal rosette; leaves sessile or wing-petiolate, viscid-pubescent; corolla slightly zygomorphic or regular, salverform, white, the tube straight or apically dilated, the lobes rounded; flowering vespertine or the flowers not opening and plants cleistogamous. Chromosome number: n = 16, 18, 19, 20, 21, 22. Australia, New Caledonia, Namibia. Included species. Nicotiana africana Merxm.; Nicotiana amplexicaulis N. T. Burb.; Nicotiana benthamiana Domin; *Nicotiana burbidgeae Symon; Nicotiana cavicola N. T. Burb.; Nicotiana debneyi Domin; Nicotiana excelsior (J. M. Black) J. M. Black; Nicotiana exigua H.-M. Wheeler; Nicotiana fragrans Hooker; Nicotiana goodspeedii H.-M. Wheeler; Nicotiana gossei Domin; Nicotiana hesperis N. T. Burb.; *Nicotiana heterantha Kenneally & Symon; Nicotiana ingulba J. M. Black; Nicotiana maritima H.-M. Wheeler; Nicotiana megalosiphon Van Huerck & Müll. Arg.; Nicotiana occidentalis H.-M. Wheeler; Nicotiana rosulata (S. Moore) Domin; Nicotiana rotundifolia Lindl.; Nicotiana simulans N. T. Burb.; *Nicotiana stenocarpa H.-M. Wheeler; Nicotiana suaveolens Lehm. (Fig. 3D); *Nicotiana truncata D. E. Symon; Nicotiana umbratica N. T. Burb.; Nicotiana velutina H.-M. Wheeler; *Nicotiana wuttkei Clarkson & Symon.

Nicotiana sect. *Sylvestres* S. Knapp, sect. nov. – Type: *N. sylvestris* Speg. & Comes.

Herbae robustae vel arbores parvae, foliis grandibus sessilibus vel alatipetiolatis vel auriculatis, inflorescentia congesta, floribus regularibus albis hypocrateriformibus tubo corollae longissimo ventricoso vel fusiformi lobis acutis, vesperi florentes.

Robust herbs or small treelets; leaves large, forming a basal rosette when the plant is young, sessile, wingpetioled or auriculate, viscid-tomentose; corolla regular, salverform, white, the tube very long and ventricosespindleform in the upper half, the lobes acute; flowering vespertine. Chromosome number: n = 12. Andes, Bolivia to Argentina. Included species: *Nicotiana sylvestris* Speg. & Comes (Fig. 3E).

Nicotiana sect. Tomentosae Goodsp., Univ. Calif. Publ. Bot. 18: 338 (1945). – Type: N. tomentosa Ruiz & Pav.

Stout, soft-wooded shrubs or small trees; leaves large, wing-petioled, densely pubescent, usually some-

what viscid; corolla zygomorphic, campanulate-salverform, red to pinkish to dirty-white, the tube curved, the lobes acute or slightly rounded; flowering diurnal or partially nocturnal, the flowers not withering at daybreak. Chromosome number: n = 12. Andes, Peru to Argentina. Included species. *Nicotiana kawakamii* Y. Ohashi; *Nicotiana otophora* Griseb. (Fig. 3F); *Nicotiana setchellii* Goodsp.; *Nicotiana tomentosa* Ruiz & Pav.; *Nicotiana tomentosiformis* Goodsp.

Nicotiana sect. *Trigonophyllae* Goodsp., Univ. Calif. Publ. Bot. 18: 339 (1945). – Type: *N. trigonophylla* Dunal (synonym of *N. obtusifolia* M. Martens & Galeotti).

Annual or partially perennial herbs; leaves sessile, spathulate, viscid-tomentose, the upper cauline leaves clasping the stem; corolla regular, tubular-salverform, greenish-white; flowering diurnal. Chromosome number: n = 12. S.W. United States and Mexico. Included species. *Nicotiana obtusifolia* M. Martens & Galeotti (Fig. 3G); *Nicotiana palmeri* A. Gray.

Nicotiana sect. Undulatae Goodsp., Univ. Calif. Publ. Bot. 18: 339 (1945). – Type: N. undulata Ruiz & Pav.

 Nicotiana sect. Thrysiflorae Goodsp., Univ. Calif. Publ. Bot. 18: 337 (1945). Type: N. thrysiflora Bitter ex Goodsp.

Herbs to soft-wooded small trees; leaves almost sessile to petiolate, pubescent, usually viscid; corolla zygomorphic or almost regular, salverform, yellow to pink or white, the tube straight or curved, the lobes acute; flowering diurnal. Chromosome number: n = 12. Andes, Ecuador to Bolivia. Included species. *Nicotiana arentsii* Goodsp.; *Nicotiana glutinosa* L.; *Nicotiana thrysiflora* Bitter ex Goodsp.; *Nicotiana undulata* Ruiz & Pav.; *Nicotiana wigandioides* Koch & Fintelm. (Fig. 3H).

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