Solanaceae

The **Solanaceae** (/ˌsplə'neɪsi.iː, -ˌaɪ/),[2] or the **nightshades**, are a family of flowering plants that ranges from annual and perennial herbs to vines, lianas, epiphytes, shrubs, and trees, and includes a number of agricultural crops, medicinal plants, spices, weeds, and ornamentals. Many members of the family contain potent alkaloids, and some are highly toxic, but many—including tomatoes, potatoes, eggplant, bell and chili peppers—are used as food. The family belongs to the order Solanales, in the asterid group and class Magnoliopsida (dicotyledons).[3] The Solanaceae consists of about 98 genera and some 2,700 species,[4] with a great diversity of habitats, morphology and ecology.

Fruits including tomatoes, tomatillos, eggplant, bell peppers and chili peppers, all of which are closely related members of the Solanaceae.

The name Solanaceae derives from the genus *Solanum*. The etymology of the Latin word is unclear. The name may come from a perceived resemblance of certain solanaceous flowers to the sun and its rays. At least one species of *Solanum* is known as the "sunberry". Alternatively, the name could originate from the Latin verb *solare*, meaning "to soothe", presumably referring to the soothing pharmacological properties of some of the psychoactive species of the family.

This family has a worldwide distribution, being present on all continents except Antarctica. The greatest diversity in species is found in South America and Central America. In 2017, scientists reported on their discovery and analysis of a fossil species belonging to the living genus *Physalis*, *Physalis infinemundi*, found in the Patagonian region of Argentina, dated to 52 million years ago. The finding has pushed back the earliest appearance of the plant family Solanaceae.[5]

The Solanaceae family includes a number of commonly collected or cultivated species. The most economically important genus of the family is *Solanum*, which contains the potato (*S. tuberosum*, in fact, another common name of the family is the "potato family"), the tomato (*S. lycopersicum*),

and the eggplant or aubergine (*S. melongena*). Another important genus, *Capsicum*, produces both chili peppers and bell peppers.

The genus *Physalis* produces the so-called groundcherries, as well as the tomatillo (*Physalis philadelphica*) and *Physalis peruviana* (Cape gooseberry). *Alkekengi officinarum* (Chinese Lantern) was previously included in the genus *Physalis* (as *Physalis alkekengi*), until molecular and genetic evidence placed it as the type species of a new genus.[6][7] The genus *Lycium* contains the boxthorns and the goji berry, *Lycium barbarum*. *Nicotiana* contains, among other species, tobacco. Some other important members of Solanaceae include a number of ornamental plants such as *Petunia*, *Browallia*, and *Lycianthes*, and sources of psychoactive alkaloids, *Datura*, *Mandragora* (mandrake), and *Atropa belladonna* (deadly nightshade). Certain species are widely known for their medicinal uses, their psychotropic effects, or for being poisonous.[8]

Most of the economically important genera are contained in the subfamily Solanoideae, with the exceptions of tobacco (*Nicotiana tabacum*, Nicotianoideae) and petunia (*Petunia* × *hybrida*, Petunioideae).

Many of the Solanaceae, such as tobacco and petunia, are used as model organisms in the investigation of fundamental biological questions at the cellular, molecular, and genetic levels.[9][10]

Etymology and pronunciation

The name "Solanaceae" (US: /ˌsoʊləˈneɪsi, -siˌaɪ, -siˌeɪ, -siˌiː/) comes to international scientific vocabulary from Neo-Latin, from *Solanum*, the type

Solanaceae

Temporal range: Early Eocene to Recent,

A flowering *Brugmansia suaveolens* from the US Botanic Garden

Scientific classification

Kingdom:	Plantae
Clade:	Tracheophytes
Clade:	Angiosperms
Clade:	Eudicots
Clade:	Asterids
Order:	Solanales
Family:	Solanaceae Juss.

Subfamilies[1]

Cestroideae
Goetzeoideae
Nicotianoideae
Petunioideae
Schizanthoideae
Schwenckioideae
Solanoideae

genus, + *-aceae*,[11] a standardized suffix for plant family names in modern taxonomy. The genus name comes from the Classical Latin word *solanum*, referring to nightshades (especially *Solanum nigrum*), "probably from sol, 'sun', + *-anum*, neuter of *-anus*."[11]

Description

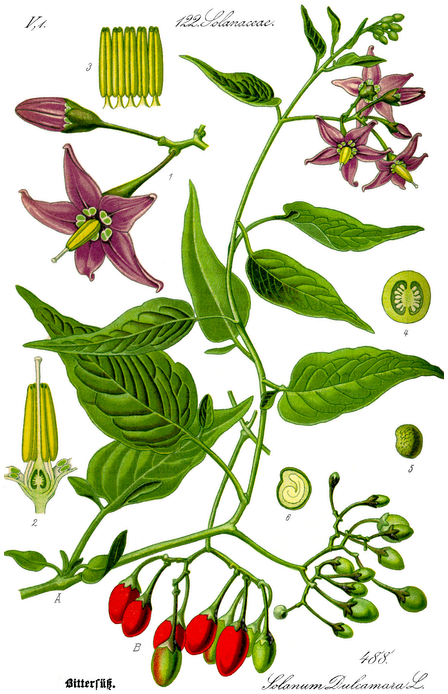
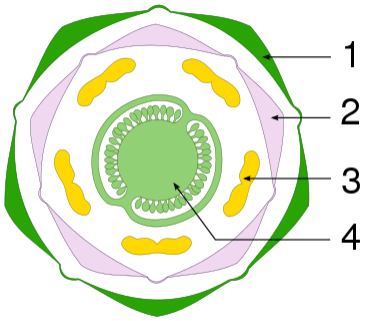


Illustration of *Solanum dulcamara*. 1. flower; 2. flower in longitudinal section, without the petals; 3. androecium; 4. ovary, in transverse section; 5. seed viewed from above; 6. seed in transverse section – note the curved embryo surrounding the endosperm; A. branch with leaves and flowers; B. stem with immature and mature fruit

Plants in the Solanaceae can take the form of herbs, shrubs, trees, vines and lianas, and sometimes epiphytes. They can be annuals, biennials, or perennials, upright or decumbent. Some have subterranean tubers. They do not have laticifers, nor latex, nor coloured saps. They can have a basal or terminal group of leaves or neither of these types. The leaves are generally alternate or alternate to opposed (that is, alternate at the base of the plant and opposed towards the inflorescence). The leaves can be herbaceous, leathery, or transformed into spines. The leaves are generally petiolate or subsessile, rarely sessile. They are frequently inodorous, but some are aromatic or fetid. The foliar lamina can be either simple or compound, and the latter can be either

pinnatifid or ternate. The leaves have reticulated venation and lack a basal meristem. The laminae are generally dorsiventral and lack secretory cavities. The stomata are generally confined to one of a leaf's two sides; they are rarely found on both sides.



Floral diagram of the potato (Solanum tuberosum), Legend: 1 = sepals 2 = petals 3 = stamens 4 = superior ovary

The flowers are generally hermaphrodites, although some are monoecious, andromonoecious, or dioecious species (such as some *Solanum* or *Symonanthus*). Pollination is entomophilous. The flowers can be solitary or grouped into terminal, cymose, or axillary inflorescences. The flowers are medium-sized, fragrant (*Nicotiana*), fetid (*Anthocercis*), or inodorous. The flowers are usually actinomorphic, slightly zygomorphic, or markedly zygomorphic (for example, in flowers with a bilabial corolla in *Schizanthus* species). The irregularities in symmetry can be due to the androecium, to the perianth, or both at the same time. In the great majority of species, the flowers have a differentiated perianth with a calyx and corolla (with five sepals and five petals, respectively) an androecium with five stamens and two carpels forming a gynoecium with a superior ovary[12] (they are therefore referred to as pentamers and tetracyclic). The stamens are epipetalous and are typically present in multiples of four or five, most commonly four or eight. They usually have a hypogynous disk. The calyx is gamosepalous (as the sepals are joined forming a tube), with the (4)5(6) segments equal, it has five lobes, with the lobes shorter than the tube, it is persistent and often accrescent. The corolla usually has five petals that are also joined forming a tube. Flower shapes are typically rotate (wheel-shaped, spreading in one plane, with a short tube) or tubular (elongated cylindrical tube), campanulated or funnel-shaped.

The androecium has (2)(4)5(6) free stamens within it opposite sepals (they alternate with the petals). They are usually fertile or, in some cases (for example in Salpiglossideae) they have staminodes. In the latter case, there is usually either one staminode (*Salpiglossis*) or three (*Schizanthus*). The anthers touch on their upper end forming a ring, or they are completely free, dorsifixed, or basifixed with poricide dehiscence or through small longitudinal cracks. The stamen's filament can be filiform or flat. The stamens can be inserted inside the coralline tube or

exserted. The plants demonstrate simultaneous microsporogenesis, the microspores are tetrad, tetrahedral, or isobilateral. The pollen grains are bicellular at the moment of dehiscence, usually open and angular.

The gynoecium is bicarpelar (rarely three- or five-locular) with a superior ovary and two locules, which may be secondarily divided by false septa, as is the case for Nicandreae and Datureae. The gynoecium is located in an oblique position relative to the flower's median plane. They have one style and one stigma; the latter is simple or bilobate. Each locule has one to 50 ovules that are anatropous or hemianatropous with axillar placentation. The development of the embryo sack can be the same as for *Polygonum* or *Allium* species. The embryo sack's nuclear poles become fused before fertilization. The three antipodes are usually ephemeral or persistent as in the case of *Atropa*. The fruit can be a berry as in the case of the tomato or wolfberry, or a dehiscent capsule as in *Datura*, or a drupe. The fruit has axial placentation. The capsules are normally septicidal or rarely loculicidal or valvate. The seeds are usually endospermic, oily (rarely starchy), and without obvious hairs. The seeds of most Solanaceae are round and flat, about 2–4 mm (0.079–0.157 in) in diameter. The embryo can be straight or curved, and has two cotyledons. Most species in the Solanaceae have 2n=24 chromosomes,[13] but the number may be a higher multiple of 12 due to polyploidy. Wild potatoes, of which there are about 200, are predominantly diploid (2 × 12 = 24 chromosomes), but triploid (3 × 12 = 36 chromosomes), tetraploid (4 × 12 = 48 chromosomes), pentaploid (5 × 12 = 60) and even hexaploid (6 × 12 = 72 chromosome) species or populations exist. The cultivated species *Solanum tuberosum* has 4 × 12 = 48 chromosomes. Some *Capsicum* species have 2 × 12 = 24 chromosomes, while others have 26 chromosomes.

Diversity of characteristics

Despite the previous description, the Solanaceae exhibit a large morphological variability, even in their reproductive characteristics. Examples of this diversity include:[14][15]

- The number of carpels that form the gynoecium

In general, the Solanaceae have a gynoecium (the female part of the flower) formed of two carpels. However, *Melananthus* has a monocarpelar gynoecium, there are three or four carpels in *Capsicum*, three to five in *Nicandra*, some species of *Jaborosa* and *Trianaea* and four carpels in *Iochroma umbellatum*.

- The number of locules in the ovary

The number of locules in the ovary is usually the same as the number of carpels. However, some species occur in which the numbers are not the same due to the existence of false septa (internal

walls that subdivide each locule), such as in *Datura* and some members of the Lycieae (the genera *Grabowskia* and *Vassobia*).

- Type of ovules and their number

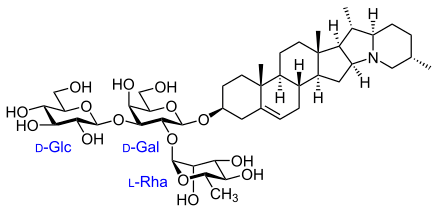
The ovules are generally inverted, folded sharply backwards (anatropous), but some genera have ovules that are rotated at right angles to their stalk (campilotropous) as in *Phrodus*, *Grabowskia* or *Vassobia*), or are partially inverted (hemitropous as in *Cestrum*, *Capsicum*, *Schizanthus* and *Lycium*). The number of ovules per locule also varies from a few (two pairs in each locule in *Grabowskia*, one pair in each locule in *Lycium*) and very occasionally only one ovule is in each locule as for example in *Melananthus*.

- The type of fruit

The fruits of the great majority of the Solanaceae are berries or capsules (including pyxidia) and less often drupes. Berries are common in the subfamilies Cestroideae, Solanoideae (with the exception of *Datura*, *Oryctus*, *Grabowskia* and the tribe Hyoscyameae) and the tribe Juanulloideae (with the exception of *Markea*). Capsules are characteristic of the subfamilies Cestroideae (with the exception of *Cestrum*) and Schizanthoideae, the tribes Salpiglossoideae and Anthocercidoideae, and the genus *Datura*. The tribe Hyoscyameae has pyxidia. Drupes are typical of the Lycieae tribe and in Iochrominae.[16]

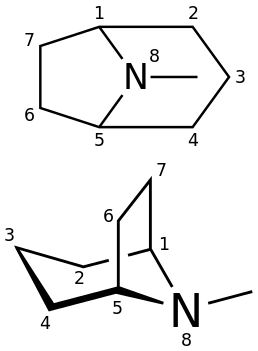
Alkaloids

Alkaloids are nitrogenous organic substances produced by plants as a secondary metabolite and which have an intense physiological action on animals even at low doses. Solanaceae are known for having a diverse range of alkaloids. To humans, these alkaloids can be desirable, toxic, or both. The tropanes are the most well-known of the alkaloids found in the Solanaceae. The plants that contain these substances have been used for centuries as poisons. However, despite being recognized as poisons, many of these substances have invaluable pharmaceutical properties. Many species contain a variety of alkaloids that can be more or less active or poisonous, such as scopolamine, atropine, hyoscyamine, and nicotine. They are found in plants such as henbane (*Hyoscyamus albus*), belladonna (*Atropa belladonna*), jimson weed (*Datura stramonium*), mandrake (*Mandragora autumnalis*), tobacco, and others. Some of the main types of alkaloids are:



Chemical structure of solanine

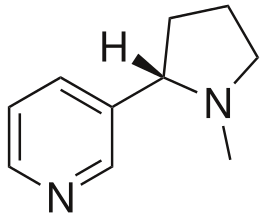
- Solanine: A toxic glycoalkaloid with a bitter taste, it has the formula $C_{45}H_{73}NO_{15}$. It is formed by the alkaloid solanidine with a carbohydrate side chain. It is found in leaves, fruit, and tubers of various Solanaceae such as the potato and tomato. Its production is thought to be an adaptive defence strategy against herbivores. Substance intoxication from solanine is characterized by gastrointestinal disorders (diarrhoea, vomiting, abdominal pain) and neurological disorders (hallucinations and headache). The median lethal dose is between 2 and 5 mg/kg of body weight. Symptoms manifest 8 to 12 hours after ingestion. The amount of these glycoalkaloids in potatoes, for example, varies significantly depending on environmental conditions during their cultivation, the length of storage, and the variety. The average glycoalkaloid concentration is 0.075 mg/g of potato.[17] Solanine has occasionally been responsible for poisonings in people who ate berries from species such as *Solanum nigrum* or *Solanum dulcamara*, or green potatoes.[18][19]



Chemical structure of the tropanes.

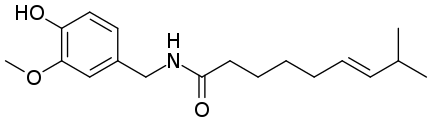
- Tropanes: The term "tropane" comes from a genus in which they are found, *Atropa* (the belladonna genus). *Atropa* is named after the Greek Fate, Atropos, who cut the thread of life. This nomenclature reflects its toxicity and lethality. They are bicyclic organic nitrogen compounds (IUPAC nomenclature: 8-methyl-8-azabicyclo[3.2.1]octane), with the chemical formula of $C_8H_{15}N$. These alkaloids include, among others, atropine, cocaine, scopolamine, and hyoscyamine. They are found in various species, such as mandrake (*Mandragora officinarum* and M. autumnalis), black henbane or stinking nightshade (*Hyoscyamus niger*), belladonna (*Atropa belladonna*), jimson weed or devil's snare (*Datura stramonium*) and *Brugmansia* , as well as many others in the family Solanaceae.[20] Pharmacologically, they are the most powerful known anticholinergics in existence, meaning they inhibit the neurological signals transmitted by the endogenous neurotransmitter, acetylcholine. More commonly, they can halt many types of allergic reactions. Symptoms of overdose may include dry mouth, dilated pupils, ataxia, urinary retention, hallucinations, convulsions, coma, and death. Atropine, a commonly used ophthalmological agent, dilates the pupils and thus facilitates examination of the interior of the eye. In fact, juice from the berries of *A. belladonna* were used by Italian courtesans during the Renaissance to exaggerate the size of their eyes by causing the dilation of their pupils ("bella

donna" means "pretty woman" in Italian). Despite the extreme toxicity of the tropanes, they are useful drugs when administered in extremely small dosages. They can reverse cholinergic poisoning, which can be caused by overexposure to organophosphate insecticides and chemical warfare agents such as sarin and VX. Scopolamine (found in *Hyoscyamus muticus* and *Scopolia carniolica*), is used as an antiemetic against motion sickness or for people suffering from nausea as a result of receiving chemotherapy.[21][22] Scopolamine and hyoscyamine are the most widely used tropane alkaloids in pharmacology and medicine due to their effects on the parasympathetic nervous system. Atropine has a stimulant effect on the central nervous system and heart, whereas scopolamine has a sedative effect. These alkaloids cannot be substituted by any other class of compounds, so they are still in demand. This is one of the reasons for the development of an active field of research into the metabolism of the alkaloids, the enzymes involved, and the genes that produce them. Hyoscyamine 6-β-hydroxylase, for example, catalyses the hydroxylation of hyoscyamine that leads to the production of scopolamine at the end of the tropane's biosynthetic pathway. This enzyme has been isolated and the corresponding gene cloned from three species: *H. niger*, *A. belladonna* and *B. candida*.[23][24][25]



Chemical structure of nicotine.

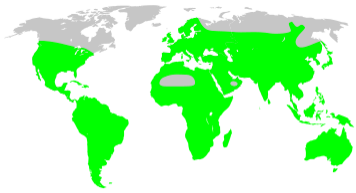
- Nicotine: Nicotine (IUPAC nomenclature (*S*)-3-(1-methylpyrrolidin-2-yl) pyridine) is a pyrrolidine alkaloid produced in large quantities in the tobacco plant (*Nicotiana tabacum*). Edible Solanaceae such as eggplants, tomatoes, potatoes, and peppers also contain nicotine, but at concentrations 100,000 to 1,000,000 times less than tobacco.[26][27] Nicotine's function in a plant is to act as a defense against herbivores, as it is a very effective neurotoxin, in particular against insects. In fact, nicotine has been used for many years as an insecticide, though its use is currently being replaced by synthetic molecules derived from its structure. At low concentrations, nicotine acts as a stimulant in mammals, which causes the dependency in smokers. Like the tropanes, it acts on cholinergic neurons, but with the opposite effect (it is an agonist as opposed to an antagonist). It has a higher specificity for nicotinic acetylcholine receptors than other ACh proteins.



Chemical structure of capsaicin

- Capsaicin: Capsaicin (IUPAC nomenclature 8-methyl-*N*-vanillyl-*trans*-6-nonenamide) is structurally different from nicotine and the tropanes. It is found in species of the genus *Capsicum*, which includes chilis and habaneros and it is the active ingredient that determines the Scoville rating of these spices. The compound is not noticeably toxic to humans. However, it stimulates specific pain receptors in the majority of mammals, specifically those related to the perception of heat in the oral mucosa and other epithelial tissues. When capsaicin comes into contact with these mucosae, it causes a burning sensation little different from a burn caused by fire. Capsaicin affects only mammals, not birds. Pepper seeds can survive the digestive tracts of birds; their fruit becomes brightly coloured once its seeds are mature enough to germinate, thereby attracting the attention of birds that then distribute the seeds. Capsaicin extract is used to make pepper spray, a useful deterrent against aggressive mammals.

Distribution



Map showing the distribution of the Solanaceae throughout the world (light green areas)

Even though members of the Solanaceae are found on all continents except Antarctica, the greatest variety of species are found in Central America and South America. Centers of diversity also occur in Australia and Africa. Solanaceae occupy a great number of different ecosystems, from deserts to rainforests, and are often found in the secondary vegetation that colonizes disturbed areas. In general, plants in this family are of tropical and temperate distribution.

Plant host

The potato tuber moth (*Phthorimaea operculella*) is an oligophagous insect that prefers to feed on plants of the family Solanaceae, especially the potato plant (*Solanum tuberosum*). Female *P. operculella* use the leaves to lay their eggs and the hatched larvae will eat away at the mesophyll

of the leaf. After feeding on the foliage, the larvae will then delve down and feed on the tubers and roots of the plant.[28]

Taxonomy

The following taxonomic synopsis of the Solanaceae, including subfamilies, tribes and genera, is based on the most recent molecular phylogenetics studies of the family:[3][4][29][30]

Cestroideae (Browallioideae)

Cestrum elegans, (subfamily : Cestroideae), a shrub used as an ornamental.

Browallia americana

Streptosolen jamesonii, Cultivated plant, Chelsea Physic Garden London UK.

Flower of *Salpiglossis sinuata*, Botanischer Garten Jena, Germany

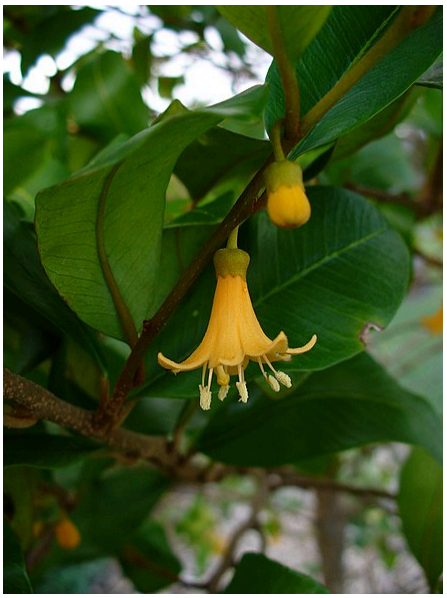
This subfamily is characterised by the presence of pericyclic fibres, an androecium with four or five stamens, frequently didynamous. The basic chromosome numbers are highly variable, from x=7 to x=13. The subfamily consists of eight genera (divided into three tribes) and about 195 species distributed throughout the Americas. The genus *Cestrum* is the most important, as it contains 175 of the 195 species in the subfamily. The *Cestreae* tribe is unusual because it includes taxa with long chromosomes (from 7.21 to 11.511 µm in length), when the rest of the family generally possesses short chromosomes (for example between 1.5 and 3.52 µm in the Nicotianoideae)

- Browallieae Hunz.
  - *Browallia* L., genus with six species distributed throughout the Neotropical realm to Arizona in the United States

- *Streptosolen* Miers, monotypic genus native to the Andes

- Cestreae tribe Don, three genera of woody plants, generally shrubs
  - *Cestrum* L., some 175 species distributed throughout the Neotropical realm
  - *Sessea* Ruiz & Pav., 19 species from the Andes
  - *Vestia* Willd., monotypic genus from Chile
- Salpiglossideae tribe (Benth.) Hunz.
  - *Reyesia* Gay, four species, three confined to northern Chile and one in both northern Chile and northern Argentina.
  - *Salpiglossis* Ruiz & Pav., three species, two originating from southern South America and one from Mexico

Goetzeoideae



Goetzea elegans (subfamily *Goetzeoideae*) in bud and flower, South Miami, Florida United States.

Espadaea amoena (subfamily *Goetzeoideae*).

This subfamily is characterized by the presence of drupes as fruit and seeds with curved embryos and large fleshy cotyledons. The basic chromosome number is x=13. It includes four genera and five species distributed throughout the Greater Antilles. Some authors suggest their molecular data indicate the monotypic genera *Tsoala* Bosser & D'Arcy should be included in this subfamily, endemic to Madagascar, and *Metternichia* to the southeast of Brazil. Goetzeaceae Airy Shaw is considered as a synonym of this subfamily.[31]

- *Coeloneurum* Radlk., monotypic genus endemic to Hispaniola
- *Espadaea* Rchb., monotypic, from Cuba
- *Goetzea* Wydler, includes two species from the Antilles
- *Henoonia* Griseb., monotypic, originating in Cuba

Nicotianoideae

Tobacco inflorescence, *Nicotiana tabacum*

- Anthocercideae G.Don: This tribe, endemic to Australia, contains 31 species in seven genera. Molecular phylogenetic studies of the tribe indicate it is the sister of *Nicotiana,* and the genera *Anthocercis, Anthotroche, Grammosolen*, and *Symonanthus* are monophyletic. Some characteristics are also thought to be derived from within the tribe, such as the unilocular stamens with semicircular opercula, bracteolate flowers, and berries as fruit.[32]
  - *Anthocercis* Labill., 10 species, Australia
  - *Anthotroche* Endl., four species, Australia
  - *Crenidium* Haegi, monotypic genus, Australia
  - *Cyphanthera* Miers, 9 species, Australia

- *Duboisia* R.Br., four species, Australia
- *Grammosolen* Haegi, two species, Australia
- *Symonanthus* Haegi, two species, Australia

- Nicotianeae tribe Dum.
  - *Nicotiana* L., genus widely distributed, with 52 American species, 23 Australian, and one African

Petunioideae

Brunfelsia pauciflora subfamily Petunioideae

Nierembergia frutescens subfamily Petunioideae

Petunia exserta

Molecular phylogenetics indicates that Petunioideae is the sister clade of the subfamilies with chromosome number x=12 (Solanoideae and Nicotianoideae). They contain calistegins, alkaloids similar to the tropanes. The androecium is formed of four stamens (rarely five), usually with two different lengths. The basic chromosome number of this subfamily can be x=7, 8, 9 or 11. It consists of 13 genera and some 160 species distributed throughout Central and South America. Molecular data suggest the genera originated in Patagonia. *Benthamiella*, *Combera*, and *Pantacantha* form a clade that can be categorized as a tribe (Benthamielleae) that should be in the subfamily Goetzeoideae.

- *Benthamiella* Speg., 12 species native to Patagonia
- *Bouchetia* Dunal, three neotropical species
- *Brunfelsia* L., around 45 species from the neotropics
- *Calibrachoa* Cerv. ex La Llave & Lex., consists of 32 species from the neotropics. The morphological data suggest this genus should be included within the *Petunia*. However, the molecular and cytogenetic data indicate both should be kept separate. In fact, *Calibrachoa* has a basic chromosome number x=9, while that of *Petunia* is x=7.[33][34]
- *Combera* Sandw., two species from Patagonia
- *Fabiana* Ruiz & Pav., 15 species native to the Andes
- *Hunzikeria* D'Arcy, three species from the southwest United States and Mexico
- *Leptoglossis* Benth., seven species from western South America
- *Nierembergia* Ruiz & Pav., 21 species from South America

- *Pantacantha* Speg., monospecific genus from Patagonia
- *Petunia* (Juss.) Wijsman, 18 species from South America
- *Plowmania* Hunz. & Subils, monotypic genus from Mexico and Guatemala

Schizanthoideae

Zygomorphic flowers, with bilabiate corolla of *Schizanthus pinnatus*, a schizanthoidea ornamental

The Schizanthoideae include annual and biennial plants with tropane alkaloids, without pericyclic fibres, with characteristic hair and pollen grains. The flowers are zygomorphic. The androecium has two stamens and three staminodes, anther dehiscence is explosive. In terms of fruit type, the Schizanthoidae retain the plesiomorphic fruit form of the family Solanaceae, capsules, which rely on an anemochorous, abiotic form of dispersal. This is present in Schizanthoidae due both to the genetic constraints of early divergence (see below) as well as Schizanthus evolution and presence in open habitats.[35] The embryo is curved. The basic chromosome number is x=10. *Schizanthus* is a somewhat atypical genus among the Solanaceae due to its strongly zygomorphic flowers and basic chromosome number. Morphological and molecular data suggest *Schizanthus* is a sister genus to the other Solanaceae and diverged early from the rest, probably in the late Cretaceous or in the early Cenozoic, 50 million years ago.[29][30] The great diversity of flower types within *Schizanthus* has been the product of the species' adaptation to the different types of pollinators that existed in the Mediterranean, high alpine, and desert ecosystems then present in Chile and adjacent areas of Argentina.[36]

- *Schizanthus* Ruiz & Pav., 12 species originating from Chile.

Schwenckioideae

Annual plants with pericyclic fibres, their flowers are zygomorphic, the androecium has four didynamous stamens or three staminodes; the embryo is straight and short. The basic chromosome number is x=12. It includes four genera and some 30 species distributed throughout South America.

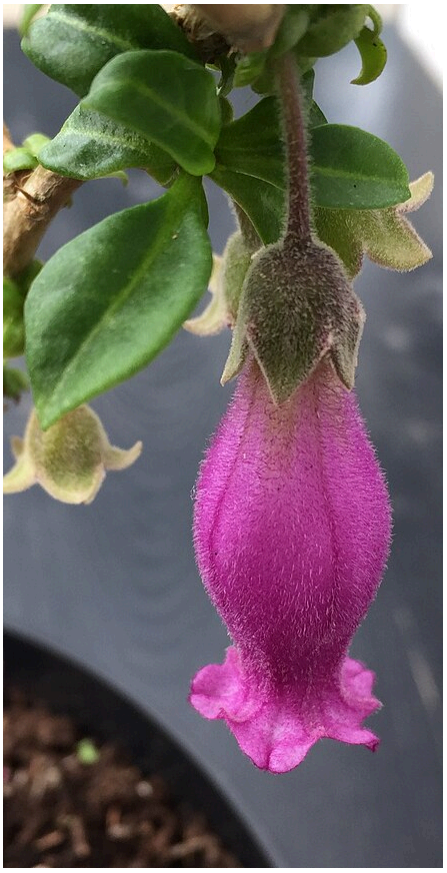
- *Heteranthia* Nees & Mart., one species from Brazil
- *Melananthus* Walp., five species from Brazil, Cuba, and Guatemala
- *Protoschwenckia* Soler , monotypic genus from Bolivia and Brazil, some molecular phylogenetic studies have suggested this genus has an uncertain taxonomic position within the subfamily
- *Schwenckia* L., 22 species distributed throughout the neotropical regions of America

Solanoideae

Capsicum frutescens cultivar "tabasco", a solanoidea

Atropa belladonna (Deadly Nightshade) flower

Black Henbane (*Hyoscyamus niger*)



Latua pubiflora subfamily Solanoideae

Nicandra physalodes flower

Solandra maxima flower

In the fruit of *Physalis peruviana* (Cape gooseberry), the persistent calyx surrounds the fruit.

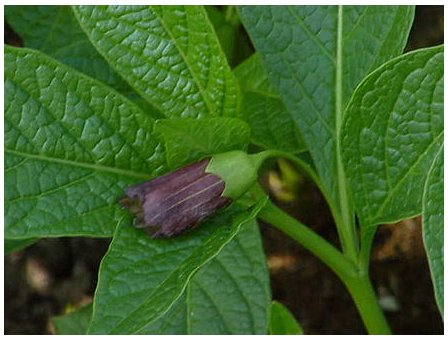
Eriolarynx australis (known formerly as *Iochroma australe*) flower, cultivated plant, UBC Botanical Garden, British Columbia.

Jaltomata procumbens flower

Solanum bonariense flower

Flower of *Solanum betaceum* (*Cyphomandra betacea*)

Acnistus arborescens flower



Scopolia carniolica flower

- Capsiceae Dumort
  - *Capsicum* L. includes 40 accepted neotropical species[37]
  - *Lycianthes* (Dunal) Hassler, some 200 species distributed throughout America and Asia
- Datureae G.Don, two genera are perfectly differentiated at both the morphological and molecular levels, *Brugmansia* includes tree species, while *Datura* contains herbs or shrubs, the latter genus can be divided into three sections: *Stramonium*, *Dutra* and *Ceratocaulis*.[38] The

monotypic genus Trompettia has recently been created to accommodate the Bolivian shrub formerly known as *Iochroma cardenasianum* - now known to belong to Datureae and not Physaleae as previously thought.[39]

- *Brugmansia* Persoon, six species from the Andes
- *Datura* L., 12 neotropical species
- *Trompettia* J.Dupin, Single species from Andean Bolivia

- Hyoscyameae Endl.
  - *Anisodus* Link, four species from China, India and the Himalayas
  - *Archihyoscyamus* A.M.Lu, single species from Turkey and Iran.
  - *Atropa* L., four Euro-Asiatic species[37]
  - *Atropanthe* Pascher, monotypic genus from China
  - *Hyoscyamus* L., 10 accepted species[37] distributed from the Mediterranean to China
  - *Physochlaina* G.Don, 6 accepted Euro-Asiatic species[37]
  - *Przewalskia* Maxim., 2 species from China
  - *Scopolia* Jacq., disjunct distribution with two European species and two from East Asia.
- Jaboroseae Miers
  - *Jaborosa* Juss., genus that includes 23 species from South America.
- Solandreae Miers
  - Subtribe Juanulloinae consists 10 genera of trees and epiphytic shrubs with a neotropical distribution .[40] Some of these genera (*Dyssochroma*, *Merinthopodium* and *Trianaea*) show a clear dependency on various species of bats both for pollination and dispersion of seeds.[41]
    - *Dyssochroma* Miers, two species from the south of Brazil
    - *Hawkesiophyton* Hunz. two species from South America
    - *Juanulloa* Ruiz & Pav., 11 species from South and Central America
    - *Markea* Rich., 9 species from South and Central America
    - *Merinthopodium* J. Donn. Sm. three species originating from South America
    - *Poortmannia* Drake, one species, from Colombia, Ecuador and Peru (South America)
    - *Schultesianthus* Hunz., eight neotropical species
    - *Trianaea* Planch. & Linden, six South American species

- Subtribe Solandrinae, a monotypical subtribe, differs from Juanulloinae in that its embryos have incumbent cotyledons and semi-inferior ovaries.[40]
- *Solandra* Sw., 10 species from the neotropical regions of America

- Lycieae Hunz. has three genera of woody plants, which grow in arid or semiarid climates. The cosmopolitan genus *Lycium* is the oldest in the tribe and it has the greatest morphological variability.[42] Molecular phylogenetic studies suggest both *Grabowskia* and *Phrodus* should be included in the *Lycium*,[43] and this genus, along with *Nolana* and *Sclerophylax*, form a clade (Lyciina), which currently lacks a taxonomic category.[31] The red fleshy berries dispersed by birds are the main type of fruit in *Lycium*. The different types of fruit in this genus have evolved from the type of berry just mentioned to a drupe with a reduced number of seeds.[44]
  - *Grabowskia* Schltdl., three species from South America
  - *Lycium* L., 83 cosmopolitan species
  - *Phrodus* Miers, two species endemic to the north of Chile
- Mandragoreae (Wettst.) Hunz. & Barboza tribe does not have a defined systematic position according to molecular phylogenetic studies.[31]
  - *Mandragora* L., two species from Eurasia
- Nicandreae Wettst. is a tribe with two South American genera. Molecular phylogenetic studies indicate the genera are not interrelated nor are they related with other genera of the family, so their taxonomic position is uncertain.[31]
  - *Exodeconus* Raf., six species from western South America
  - *Nicandra* Adans, one species distributed throughout neotropical regions
- Nolaneae Rchb. are mostly herbs and small shrubs with succulent leaves, they have very beautiful flowers that range from white to various shades of blue, their fruit is schizocarpal, giving rise to various nuts.
  - *Nolana* L., 89 species distributed throughout western South America
- Physaleae Miers, is a large tribe that is the sister of Capsiceae.
  - Subtribe Iochrominae (Miers) Hunz., a clade within the Physaleae tribe. contains 37 species, mainly distributed in the Andes, assigned to six genera. The members of this subtribe are characterized by being woody shrubs or small trees with attractive tubular or rotated flowers. They also possess great floral diversity, containing every type is present in the family. Their flowers can be red, orange, yellow, green, blue, purple, or white. The corolla can be tubular to rotated, with a variation of up to eight times in the length of the tube between the various species.[45]

- *Acnistus* Schott, one species distributed throughout the neotropics
- *Dunalia* Kunth., five species from the Andes
- *Eriolarynx* Hunz., three species from Argentina and Bolivia
- *Iochroma* Benth., 24 species from the Andes
- *Saracha* Ruiz & Pav., two species from the Andes.
- *Vassobia* Rusby, two South American species

- Physalinae (Miers) Hunz. , a monophyletic subtribe, contains 10 genera and includes herbs or woody shrubs with yellow, white, or purple solitary axillary flowers pollinated by bees. Once pollination occurs, the corolla falls and the calyx expands until it entirely covers the boll that is developing (the calyx is called accrescent). In many species, the calyx turns yellow or orange on maturity. The berries contain many greenish to yellow-orange seeds, often with red or purple highlights.[46]
  - *Alkekengi* Mill., monotypic genus; a Far East species formerly included in genus *Physalis* (*Physalis alkekengi* L.).
  - *Brachistus* Miers, three species from Mexico and Central America.
  - *Chamaesaracha* (A.Gray) Benth. & Hook., has 10 species from Mexico and Central America.
  - *Darcyanthus*, genus with just 1 species originating in Bolivia and Peru.
  - *Leucophysalis* Rydberg, includes 3 species from the south west of the United States and Mexico.
  - *Margaranthus* Schlecht., with 1 species from Mexico.
  - *Oryctes* S. Watson, monotypic genus from the south west of the United States.
  - *Physalis* L., the largest genus of the subtribe, with 85 species distributed through the tropical regions of the Americas and with 1 species in China.
  - *Quincula* Raf. with just 1 species from the south west of the United States and from Mexico.
  - *Trozelia* Raf. with 2 species from Ecuador and Peru.
  - *Tzeltalia*, genus segregated from *Physalis*, with 2 species distributed throughout Mexico and Guatemala.
  - *Witheringia* L' Heritier, genus with 15 species from neotropical regions.

- Subtribe Salpichroinae, this is a subtribe of Physaleae that includes 16 American species distributed in 1 genera:
  - *Nectouxia* Kunth., monotypic genus that is endemic to Mexico.
  - *Salpichroa* Miers, genus with 15 species from the Andes and other regions of South America.
- Subtribe Withaninae, is a subtribe of Physaleae with a broad distribution, including 9 genera:
  - *Archiphysalis* Kuang, with 3 species from China and Japan.
  - *Athenaea* Sendtn., which includes 7 species from Brazil.
  - *Aureliana* Sendtn., with 5 species from South America.
  - *Cuatresia* Hunz., with 11 neotropical species. Molecular studies indicate that this genus, along with *Deprea* and *Larnax* has an uncertain taxonomic position.[31]
  - *Deprea* Raf., with 6 neotropical species.
  - *Discopodium* Hochst. with 2 species in tropical Africa.
  - *Larnax* Miers, many taxonomists consider it to be a synonym for *Deprea*, contains 22 species native to the Andes.
  - *Mellissia* Hook. f., monotypic genus from Saint Helena with the common name Saint Helena boxwood (genus recently subsumed in *Withania*)
  - *Nothocestrum* A.Gray with 4 species from Hawaii.
  - *Physaliastrum* Makino, with 10 Asiatic species (genus recently subsumed in *Withania*).
  - *Tubocapsicum* (Wettst.) Makino, with just one species endemic to China.
  - *Withania* Pauq., with 10 species native to the Canary Islands, Africa and Nepal.
- Tribe Solaneae. The genera *Cyphomandra* Sendtn., *Normania* Lowe, *Triguera* Cav. and *Lycopersicum* Mill have been transferred to *Solanum*. The subtribe is therefore composed of two genera:[31]
  - *Jaltomata* Schltdl., which contains 50 neotropical species.
  - *Solanum* L., the largest genus in the family and one of the broadest of the angiosperms, with 1,328 species distributed across the whole world.

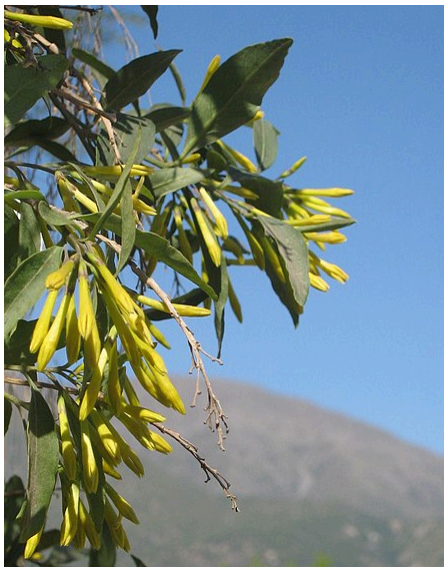
Incertae sedis

Sclerophylax kurtzii.

The following genera have not yet been placed in any of the recognized subfamilies within the solanaceas (*incertae sedis*).

- *Duckeodendron* Kuhlmannb, monotypic genus from the Amazon rainforest.
- *Pauia* Deb. & Dutta, monotypic genus from Assam and Arunachal Pradesh in N.E.India

Genera and distribution of species



Flowers and foliage of *Cestrum parqui*.

Metternichia principis

The Solanaceae contain 98 genera and some 2,700 species. Despite this immense richness of species, they are not uniformly distributed between the genera. The eight most important genera contain more than 60% of the species, as shown in the table below. *Solanum* – the genus that typifies the family - includes nearly 50% of the total species of the solanaceas.

Genera	Approximate number of species
Solanum	1,330
Lycianthes	200
Cestrum	150
Nolana	89
Physalis	85
Lycium	85
Nicotiana	76
Brunfelsia	45
Estimated number of species in the family	2,700

Economic importance

Pink, double-flowered *Brugmansia* cultivar

Triple-flowered *Datura metel* 'Fastuosa': ancient cultivar created from *Datura innoxia* by Pre-Columbian horticulturalists in the Greater Antilles

Petunia × atkinsiana, a herbaceous annual commonly cultivated as a summer bedding plant

The family Solanaceae contains such important food species as the potato (*Solanum tuberosum*), the tomato (*Solanum lycopersicum*), the pepper (*Capsicum annuum*) and the aubergine or eggplant (*Solanum melongena*). *Nicotiana tabacum,* originally from South America, is now cultivated throughout the world to produce tobacco. Many solanaceas are important weeds in various parts of the world. Their importance lies in the fact that they can host pathogens or diseases of the cultivated plants, therefore their presence increases the loss of yield or the quality of the harvested product. An example of this can be seen with *Acnistus arborescens* and *Browalia americana* that host thrips, which cause damage to associated cultivated plants,[47] and certain species of *Datura* that play host to various types of virus that are later transmitted to cultivated solanaceas.[48] Some species of weeds such as, *Solanum mauritianum* in South Africa represent such serious ecological and economic problems that studies are being carried out with the objective of developing a biological control through the use of insects.[49]

A wide variety of plant species and their cultivars belonging to the Solanaceae are grown as ornamental trees, shrubs, annuals and herbaceous perennials[50] Examples include *Brugmansia x candida* ("Angel's Trumpet") grown for its large pendulous trumpet-shaped flowers, or *Brunfelsia latifolia*, whose flowers are very fragrant and change colour from violet to white over a period of 3 days. Other shrub species that are grown for their attractive flowers are *Lycianthes rantonnetii* (Blue Potato Bush or Paraguay Nightshade) with violet-blue flowers and *Nicotiana glauca* ("Tree Tobacco") Other solanaceous species and genera that are grown as ornamentals are the petunia *(Petunia × hybrida)*, *Lycium, Solanum, Cestrum, Calibrachoa × hybrida* and *Solandra*. There is even a hybrid between *Petunia* and *Calibrachoa* (which constitutes a new nothogenus called *× Petchoa* G. Boker & J. Shaw) that is being sold as an ornamental.[51] Many other species, in particular those that produce alkaloids, are used in pharmacology and medicine *(Nicotiana, Hyoscyamus*, and *Datura*).[8]

Solanaceae and the genome

Many of the species belonging to this family, among them tobacco and the tomato, are model organisms that are used for research into fundamental biological questions. One of the aspects of the solanaceas' genomics is an international project that is trying to understand how the same collection of genes and proteins can give rise to a group of organisms that are so morphologically and ecologically different. The first objective of this project was to sequence the genome of the tomato. In order to achieve this each of the 12 chromosomes of the tomato's haploid genome was assigned to different sequencing centres in different countries. So chromosomes 1 and 10 were sequenced in the United States, 3 and 11 in China, 2 in Korea, 4 in Britain, 5 in India, 7 in France, 8 in Japan, 9 in Spain and 12 in Italy. The sequencing of the mitochondrial genome was carried out in Argentina and the chloroplast genome was sequenced in the European Union.[52][53]

See also

- List of plants poisonous to equines

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External links

- Sol Genomics Network (http://solgenomics.net)
- Solanaceae Network - pictures of plants (https://web.archive.org/web/20050307011715/http://solanaceae.net/index.php)
- Solanaceae Source (http://www.solanaceaesource.org/) - A worldwide taxonomic monograph of all species in the genus Solanum.

- Solanaceae of Chile, by Chileflora (http://www.chileflora.com/Florachilena/FloraEnglish/PIC_FAMILIES_SIMPLE_138.php)
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- Family Solanaceae (http://flowersinisrael.com/FamSolanaceae.html) Archived (https://web.archive.org/web/20130618052644/http://flowersinisrael.com/FamSolanaceae.html) 2013-06-18 at the Wayback Machine Flowers in Israel
- *SOL Genomics Network*, Universidad de Cornell (http://www.sgn.cornell.edu)
- Imagines de various species of Solanaceae (https://web.archive.org/web/20050307011715/http://solanaceae.net/index.php)
- Solanaceae de Chile, by Chileflora (http://www.chileflora.com/Florachilena/FloraSpanish/PIC_FAMILIES_SIMPLE_138.php)
- Chilli: La especia del Nuevo Mundo (http://www.ejournal.unam.mx/cns/no69/CNS06908.pdf) Archived (https://web.archive.org/web/20121114184110/http://www.ejournal.unam.mx/cns/no69/CNS06908.pdf) 2012-11-14 at the Wayback Machine (Article in Spanish by Germán Octavio López Riquelme regarding the biology, nutrition, culture and medical aspects of Chile.
- Solanaceae Resources on the Web (http://solgenomics.net/community/links/related_sites.pl)
- Jäpelt RB, Jakobsen J (2013) Vitamin D in plants: a review of occurrence, analysis, and biosynthesis. Front Plant Sci 4, No. 136 -- Note the reference to higher cholesterol levels (and consequent Vitamin D3 levels) in family *Solanaceae* (http://www.frontiersin.org/Journal/Abstract.aspx?s=907&name=plant_physiology&ART_DOI=10.3389/fpls.2013.00136)