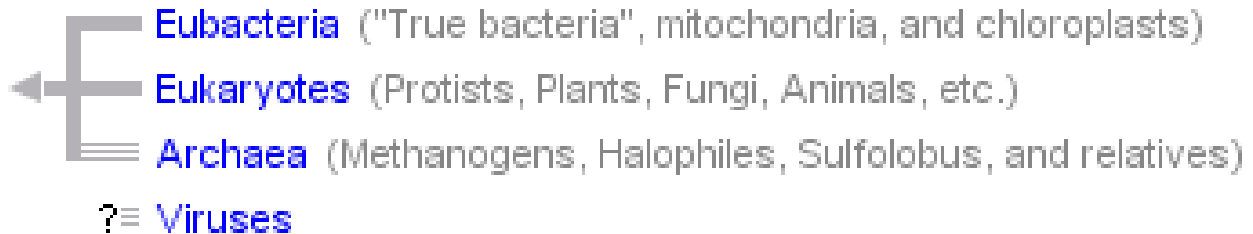


# Taxonomy *Asteraceae*

The rooting of the Tree of Life, and the relationships of the major lineages, are controversial. The monophyly of Archaea is uncertain, and recent evidence for ancient lateral transfers of genes indicates that a highly complex model is needed to adequately represent the phylogenetic relationships among the major lineages of Life.

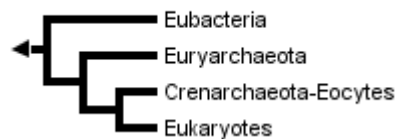


Two alternative views on the relationship of the major lineages (omitting viruses) are shown below:

- The "archaea tree" :



- The "eocyte tree":



*Archaea* C.r. Woese *et al.*, 1990 (singular *archaeon*). They are a domain or kingdom of single-celled microorganisms. These microbes are prokaryotes, meaning they have no cell nucleus or any other membrane-bound organelles in their cells.

*Archaea* were initially classified as bacteria, receiving the name archaeobacteria (in Kingdom *Monera*), but this classification is outdated. Archaeal cells have unique properties separating them from the other two domains of life: *Bacteria* and *Eukaryota*. The *Archaea* are further divided into four recognized *phyla*. Classification is difficult because the majority have not been studied in the laboratory and have only been detected by analysis of their nucleic acids in samples from their environment.

*Archaea* and *bacteria* are similar in size and shape, although a few archaea have very strange shapes, such as the flat and square-shaped cells of *Haloquadratum walsbyi*. Despite this visual similarity to *bacteria*, *archaea* possess genes and several metabolic pathways that are more closely related to those of eukaryotes, notably the enzymes involved in transcription and translation. Other aspects of archaeal biochemistry are unique, such as their reliance on ether lipids in their cell membranes. *Archaea* use more energy sources than eukaryotes: these range from organic compounds such as sugars, to ammonia, metal ions or even hydrogen gas. Salt-tolerant archaea (the *Haloarchaea*) use sunlight as an energy source, and other species of archaea fix carbon; however, unlike plants and cyanobacteria, no known species of archaea does both. *Archaea* reproduce asexually by binary fission, fragmentation, or budding; unlike bacteria and eukaryotes, no known species forms spores.

*Archaea* were initially viewed as extremophiles living in harsh environments, such as hot springs and salt lakes, but they have since been found in a broad range of habitats, including soils, oceans, marshlands and the human colon and navel. *Archaea* are particularly numerous in the oceans, and

the archaea in plankton may be one of the most abundant groups of organisms on the planet. *Archaea* are a major part of Earth's life and may play roles in both the carbon cycle and the nitrogen cycle. No clear examples of archaeal pathogens or parasites are known, but they are often mutualists or commensals. One example is the methanogens that inhabit the human gut and the ruminant gut, where their vast numbers aid digestion. Methanogens are used in biogas production and sewage treatment, and enzymes from extremophile archaea that can endure high temperatures and organic solvents are exploited in biotechnology.

*Eocyta Lake et al.* 1984. The “eocyte hypothesis” is a biological classification that indicates eukaryotes evolved from the prokaryotic *Crenarchaeota* (formerly known as eocytes), a *phylum* within the archaea. This hypothesis was originally proposed by James A. Lake and colleagues in 1984 based on the discovery that the shapes of ribosomes in the *Crenarchaeota* and eukaryotes are more similar to each other than to either bacteria or the second major kingdom of *archaea*, the *Euryarchaeota*.

The “eocyte hypothesis” gained considerable attention after its introduction due to the interest in determining the origin of the eukaryotic cell. This hypothesis has primarily been in contrast with the three-domain system, which was introduced by Carl Woese in 1977. Additional evidence supporting the eocyte hypothesis was published in the 1980s, but despite fairly equivocal evidence, support waned for the eocyte hypothesis in favor of the three-domain system.

With advancements in genomics, the “eocyte hypothesis” experienced a revival beginning in the mid-2000s. As more archaeal genomes were sequenced, numerous genes coding for eukaryotic traits have been discovered in various *archaeal phyla*, seemingly providing support for the “eocyte hypothesis”. In addition to a *Crenarchaeal* origin of eukaryotes, some studies have suggested that eukaryotes may have originated in the *Thaumarchaeota*.

## *Eukaryotes* (Chatton, 1925) Whittaker & Margulis, 1978

### **Other Names for *Eukaryotes***

*Eukarya*, *Eukaryota*, Organisms with nucleated cells.

### **Introduction**

Even if you do not know the word ‘eukaryote’, you are already familiar with what they are, because you and nearly all other life forms that you experience with your unaided eyes are eukaryotes. The vast majority of eukaryotes that we knowingly interact with each day, mainly land plants and animals, are large – macroscopic – organisms, usually consisting of trillions of individual cells. Even using our rather limited senses, we can immediately tell that macroscopic eukaryotes represent enormous diversity on many different levels. However, the true diversity of eukaryotes is far greater than ordinary experiences would lead you to appreciate; most of the many millions of eukaryotic species on Earth are hidden from view, because most eukaryotic life forms are microscopic. The diversity of these microbial eukaryotes must be discovered and explored with powerful equipment and techniques such as electron microscopy and molecular biology.

Eukaryotes (also referred to as the *Eukaryota* or the *Eukarya*) comprise one of the three recognized domains of cellular life, the other two being the *Archaea* (or *Archaeobacteria*) and the *Eubacteria* (or *Bacteria*). *Eukaryotes* are distinguished from *Archaea* and *Eubacteria* in many different ways, but most importantly, the cells of eukaryotes display a much greater degree of structural organization and complexity. Archaeal and eubacterial cells generally lack internal structural organization (with a few notable exceptions, like the cyanobacteria). Eukaryotic cells, by contrast, share several complex structural characteristics. Most of these are parts of two interrelated systems: the cytoskeletal system and a system of membrane-delimited compartments. The cytoskeleton is an elaborate and highly organized internal scaffolding of proteins, such as actin-based microfilaments and tubulin-based microtubules. It also includes several molecular motors, such as kinesins and dyneins that provide the dynamic forces necessary for import and export mechanisms and many

different modes of cell locomotion. Internal membrane-delimited compartments include mitochondria and plastids as well as different elements of the endomembrane system: the endoplasmic reticulum, Golgi bodies, vacuoles, and the nuclear envelope. The word 'eu-karyote' literally means 'true kernel', in reference to the sequestering of the genome into the membrane-bounded compartment called the nucleus.

With these basic building blocks, eukaryotes have evolved an amazing array of structural and behavioral characters. One of the most significant innovations is the ability to engulf and internalize particles and other cells, a process called endocytosis or phagocytosis (literally meaning 'cell eating'). This mode of nutrition opened up many new predatory niches that ultimately facilitated the formation of permanent associations between very different life forms via endosymbiosis. Endosymbiotic associations have provided eukaryotes with much of their central metabolism, which has remained relatively conserved throughout the group's history. Overall, *Archaea* and *Eubacteria* show tremendous diversity in their metabolic capacities, but fairly limited morphological and behavioral diversity; conversely, eukaryotes share relatively similar (albeit sloppy) metabolic machinery but have undergone tremendous evolutionary diversification in morphology and behavior.

### **Characteristics**

The known diversity of morphological characters in eukaryotes is simply staggering and can be attributed to the vast multitude of possible solutions to basic biological problems, such as nutrition/feeding, locomotion, defense, refuge, mate selection and reproduction.

*Eukaryotes* are built from one or more internally differentiated cells comprised of intricate subcellular systems.

Several single-celled lineages, for instance, have reached the utmost degree of morphological complexity within the confines of a single enveloping cell membrane (e.g. parabasalids, ciliates, dinoflagellates), while others have reached the lower limits of morphological complexity by becoming extremely streamlined (e.g. *picophytoeukaryotes*, yeasts).

Moreover, some multicellular eukaryotes have struck the upper physical limits of overall body size (e.g. dinosaurs, elephants, and whales), while others are miniaturized to the point of being smaller than single-celled counterparts in the same ecosystem (e.g. gastrotrichs, tardigrades, rotifers and nematodes).

Regardless of major differences in body size and morphological peculiarities, eukaryotes share many characteristics in common.

Many of these characteristics are homologous for the entire group, whether comparing a blue whale to an amoeba or a human to a giant redwood tree.

### **Unifying Features of Eukaryotes**

Below is a list of important features that are likely to have been present in the common ancestor of eukaryotes. Some of these features are still universally found in all eukaryotic diversity, while others have been lost or drastically transformed in some lineages, but are nevertheless ancestral to those groups.

- Cytoskeleton consisting of tubulin-based microtubules and actin-based microfilaments, and ancestrally including motile cell extensions called 'flagella' or 'cilia' that contain an axoneme of 9 peripheral microtubular doublets and 2 central microtubules.  
An endomembrane system that consists of endoplasmic reticulum, Golgi bodies, vacuoles, lysosomes, peroxisomes, and the nuclear envelope.
- Primary genome of each cell consisting of multiple linear chromosomes contained within a membrane-bound nucleus. Following replication of the genome the chromosomes are segregated by the process of mitosis. Cells in many species can have more than one nucleus.
- Mitochondria - organelles with diverse functions, usually including aerobic respiration, iron sulfur cluster assembly, and synthesis and breakdown of small molecules such as lipids and amino acids.

Mitochondria are bounded by two membranes, and usually contain a small genome. They are the descendents of an alpha-proteobacterial endosymbiont.

- Translation machinery in the form of 80S ribosomes, each consisting of four molecules of RNA complexed with many proteins, and partitioned in a small (40S) and a large (60S) subunit.

### **Other Common Characteristics of Eukaryotes**

- A number of other characteristics are common to many eukaryotes and not to prokaryotes, but these are not ancestral to all eukaryotes, and many have evolved several times independently.
- Multicellularity and tissue formation (e.g. green algae, land plants, red algae, brown algae, animals and fungi).
- Secreted hard parts (e.g. mollusk shells, plant cell walls, ecdysozoan cuticles, coccoliths, vertebrate endoskeletons, chrysophyte scales, polychaete tubes, diatom frustules, brachiopod shells, cnidarian corallites, euglenophyte loricas, poriferan spicules, echinoderm ossicles, foraminiferan and radiozoan tests).
- Extrusive organelles that function in defense, prey capture or parasitic invasion (e.g. ejectisomes of cryptomonads; trichocysts of alveolates; polar tubes of microsporidian fungi, gun cells of oomycetes; nematocysts of cnidarians, myxozoans and some dinoflagellates).
- Plastids, including chloroplasts and their homologues. Referring to plastids as homoplasies is a qualified statement, since the vast majority of plastids do ultimately stem from a common primary endosymbiosis with a cyanobacterium (the one possible exception being the ‘chromophore’ of the euglyphid amoeba *Paulinella*), but their subsequent spread via secondary and tertiary endosymbioses has led to a complicated distribution on the tree of eukaryotes

### **Role of Endosymbiosis in Eukaryotic Evolution**

In addition to providing a significant nutritional mode, the advent of endocytosis in an ancestor of living eukaryotes also enabled a completely new way to generate cellular change and complexity: endosymbiosis.

Put simply, endosymbiosis is the process by which one cell is taken up by another and retained internally, such that the two cells live together and integrate at some level, sometimes permanently. Endosymbiotic interactions have been common in eukaryotic evolution, and many such partnerships persist today.

In two cases, however, endosymbiotic events had far-reaching effects on the evolution of life: these are the origins of mitochondria and plastids (chloroplasts).

Mitochondria are generally known as the energy-generating powerhouses of eukaryotic cells, where oxidative phosphorylation and electron transport metabolism takes place. They are also involved in several other jobs such as oxidation of fatty acids, amino acid metabolism, and assembly of iron-sulfur clusters.

They are bounded by two membranes, the innermost of which is generally highly infolded to form ‘cristae’ that take characteristic shapes, either flat, tubes, or paddle-shapes.

The presence of mitochondria is an ancestral trait in eukaryotes, although in certain anaerobes and microaerophiles they have radically reduced or transformed functions: in some cases they are not involved in energy production at all (e.g., the ‘mitosomes’ of microsporidia, diplomonads, and archaemoebae, or ‘hydrogenosomes’ of parabasalia, some ciliates, and some chytrid fungi). Mitochondria can be traced back to a single endosymbiosis of an alpha-proteobacterium.

Plastids are the photosynthetic organelles of plants and algae. “Plastid” (Figure 1) is a general term for all such organelles, including chloroplasts (in the green lineage), rhodoplasts (in the red lineage), leucoplasts (colourless plastids), etc.



Figure 1 . Plastids. There are many different types of plastids, characterised by different pigments, structures, and envelopes: the blue-green coloured primary "chromophores" that were independently acquired by *Paulinella chromatophora*, the red coloured primary plastids of the red alga *Porphyridium*, the brown colored secondary plastids of *Mallomonas insignis* the green-colored secondary plastids of the euglenid *Phacus*, and a TEM view of secondary green plastid of the euglenid *Eutreptia pertyi*

Plastids have diverse functions in addition to photosynthesis, including the biosynthesis of amino acids, fatty acids and isoprenoids.

As in the case of mitochondria, plastids in many lineages have been radically reduced or transformed, primarily through the loss of photosynthesis (e.g., the 'apicoplast' of Apicomplexa, and the relict plastids of many parasitic algae and plants. Plastids can also be traced back to a single endosymbiosis event involving a cyanobacterium and the ancestor of the *Archaeplastida*.

However, unlike mitochondria, plastids then spread to other eukaryotic lineages by secondary and tertiary endosymbiotic events. In these events, one eukaryotic cell took up another eukaryote that already contained a plastid (an alga), and this second, endosymbiotic eukaryote was then reduced and integrated. In most cases all that remains of this alga is the plastid surrounded by the remains of the endosymbiont's plasma membrane.

However, in cryptomonads and chlorarachniophytes a tiny relict of the algal nucleus called a "nucleomorph" is also retained, the study of which helped elucidate the complex evolutionary history of plastids. Other endosymbiotic relationships based on photosynthesis are also known, but typically these are not integrated to the extent that they are generally accepted to be 'organelles' rather than 'endosymbionts'. One possible exception is the euglyphid amoeba *Paulinella chromatophora*, where a cyanobacterium similar to *Synechococcus* or *Prochlorococcus* has been integrated to an extent approaching that of canonical plastids.

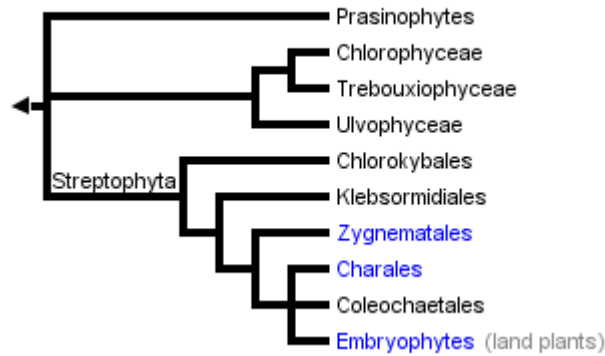
## Green plants

### Other Names for Green plants

*Plantae* Haeckel, 1866; plants; *Viridiplantae* Cavalier-Smith, 1981.

Green plants include all organisms commonly known as green algae and land plants, including liverworts, mosses, ferns and other nonseed plants, and seed plant.

Green plants as defined here includes a broad assemblage of photosynthetic organisms that all contain chlorophylls a and b, store their photosynthetic products as starch inside the double-membrane-bounded chloroplasts in which it is produced, and have cell walls made of cellulose. In this group are several thousand species of what are classically considered green algae, plus several hundred thousand land plants.

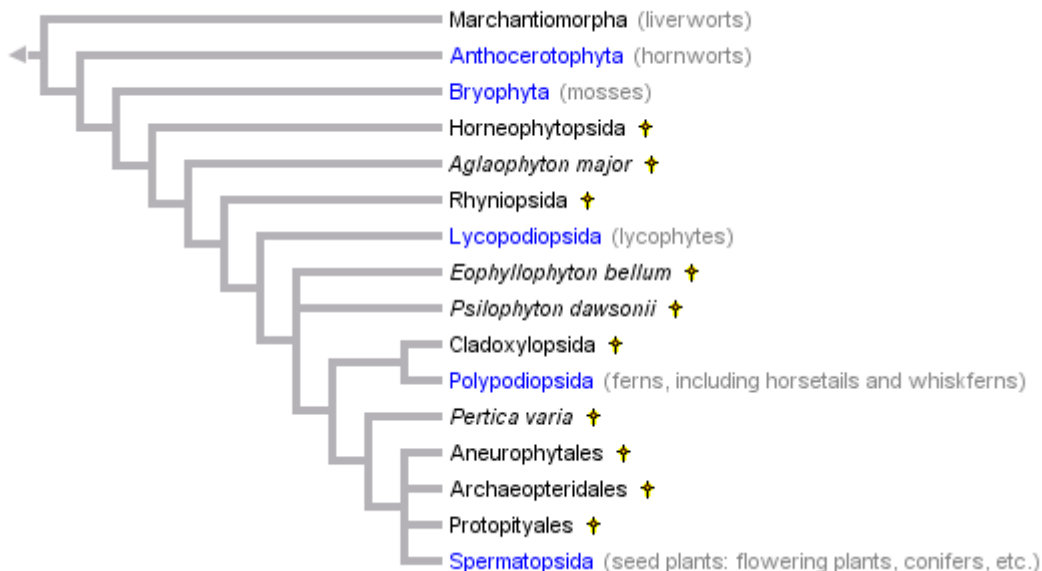


***Embryophyta*** Endlicher, 1836, emend. Lewis & McCourt, 2004

*Cormophyta* Endlicher, 1836

Vernacular Names: Land Plants

The *Embryophyta*, or *Metaphyta*, are the most familiar subkingdom of green plants that form vegetation on earth. The embryophytes include hornworts, liverworts, mosses, ferns and their allies, gymnosperms and flowering plants, but exclude the green algae. The *Embryophyta* are informally called land plants because they live primarily in terrestrial habitats, while the related green algae are primarily aquatic. All are complex multicellular eukaryotes with specialized reproductive organs. The name derives from their innovative characteristic of nurturing the young embryo sporophyte during the early stages of its multicellular development within the tissues of the parent gametophyte. With very few exceptions, embryophytes obtain their energy by photosynthesis, that is by using the energy of sunlight to synthesize their food from carbon dioxide and water.



The evolutionary origins of the embryophytes are discussed further below, but they are believed to have evolved from within a group of complex green algae during the Paleozoic era (which started around 540 million years ago). Charales or the stoneworts may be the best living illustration of that developmental step. Embryophytes are primarily adapted for life on land, although some are secondarily aquatic. Accordingly, they are often called land plants or terrestrial plants.

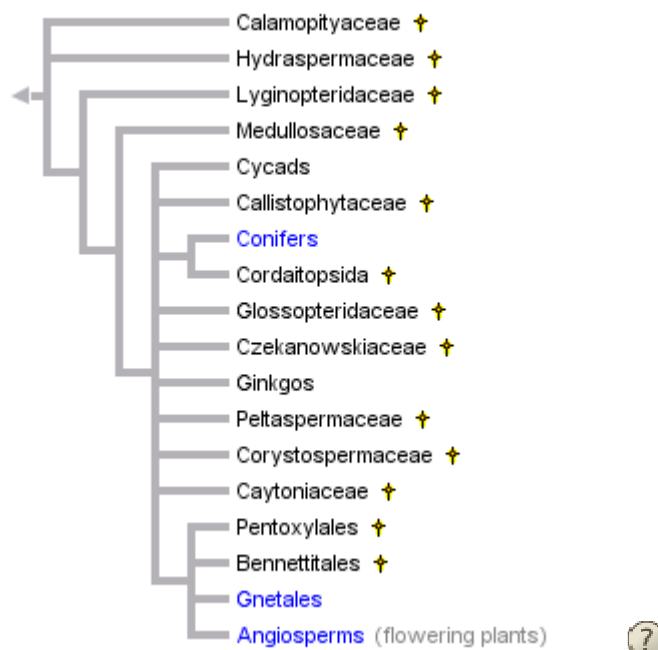
On a microscopic level, the cells of embryophytes are broadly similar to those of green algae, but differ in that in cell division the daughter nuclei are separated by a phragmoplast. They are eukaryotic, with a cell wall composed of cellulose and plastids surrounded by two membranes. The latter include chloroplasts, which conduct photosynthesis and store food in the form of starch, and are characteristically pigmented with chlorophylls a and b, generally giving them a bright green color. Embryophyte cells also generally have an enlarged central vacuole enclosed by a vacuolar membrane or tonoplast, which maintains cell turgor and keeps the plant rigid.

In common with all groups of multicellular algae they have a life cycle which involves 'alternation of generations'. A multicellular generation with a single set of chromosomes – the haploid gametophyte – produces sperm and eggs which fuse and grow into a multicellular generation with twice the number of chromosomes – the diploid sporophyte. The mature sporophyte produces haploid spores which grow into a gametophyte, thus completing the cycle. Embryophytes have two features related to their reproductive cycles which distinguish them from all other plant lineages. Firstly, their gametophytes produce sperm and eggs in multicellular structures (called 'antheridia' and 'archegonia', and fertilization of the ovum takes place within the archegonium rather than in the external environment. Secondly, and most importantly, the initial stage of development of the fertilized egg (the zygote) into a diploid multicellular sporophyte, take place within the archegonium where it is both protected and provided with nutrition. This second feature is the origin of the term 'embryophyte' – the fertilized egg develops into a protected embryo, rather than dispersing as a single cell. In the bryophytes the sporophyte remains dependent on the gametophyte, while in all other embryophytes the sporophyte generation is dominant and capable of independent existence.

Embryophytes also differ from algae by having metamers. Metamers are repeated units of development, in which each unit derives from a single cell, but the resulting product tissue or part is largely the same for each cell. The whole organism is thus constructed from similar, repeating parts or metamers.

## *Spermatopsida*

Seed plants



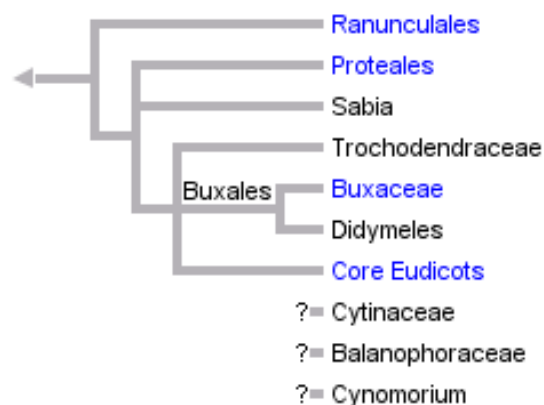


## Angiosperms Flowering Plants



Relationships after Qiu *et al.* (1999, 2000), P. Soltis *et al.* (1999), D. E. Soltis *et al.* (2000), Zanis *et al.* (2002) and Hilu *et al.* (2003).

## Eudicots James A. Doyle and Carol L. Hotton, 1991 Tricolpates



Relationships after Savolainen *et al.* 2000 and Hilu *et al.* (2003).

The eudicots, *Eudicotidae* or eudicotyledons are a monophyletic clade of flowering plants that had been called tricolpates or non-magnoliid dicots by previous authors. The botanical terms were introduced in 1991 by evolutionary botanist James A. Doyle and paleobotanist Carol L. Hotton to emphasize the later evolutionary divergence of tricolpate dicots from earlier, less specialized, dicots. The close relationships among flowering plants with tricolpate pollen grains was initially seen in morphological studies of shared derived characters. These plants have a distinct trait in their pollen grains of exhibiting three colpi or grooves paralleling the polar axis. Later molecular evidence confirmed the genetic basis for the evolutionary relationships among flowering plants with tricolpate pollen grains and dicotyledonous traits. The term means "true dicotyledons", as it contains the majority of plants that have been considered dicots and have characteristics of the dicots. The term "eudicots" has subsequently been widely adopted in botany to refer to one of the two largest clades of angiosperms (constituting over 70% of the angiosperm species), monocots being the other. The remaining angiosperms are sometimes referred to as basal angiosperms or paleodicots, but these terms have not been widely or consistently adopted, as they do not refer to a monophyletic group.

The other name for the eudicots is tricolpates, a name which refers to the grooved structure of the pollen. Members of the group have tricolpate pollen, or forms derived from it. These pollens have three or more pores set in furrows called colpi. In contrast, most of the other seed plants (that is the

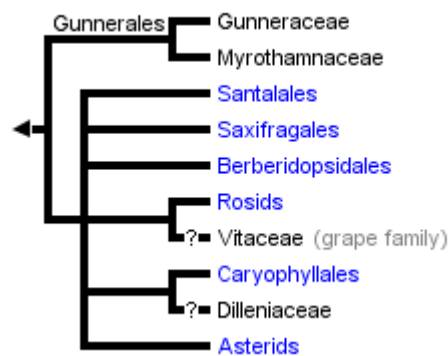


gymnosperms, the monocots and the paleodicots) produce monosulcate pollen, with a single pore set in a differently oriented groove called the sulcus. The name "tricolpates" is preferred by some botanists to avoid confusion with the dicots, a nonmonophyletic group.

Numerous familiar plants are eudicots, including many common food plants, trees, and ornamentals. Some common and familiar eudicots include members of the sunflower family such as the common dandelion, the forget-me-not, cabbage and other members of its family, apple, buttercup, maple, and macadamia. Most leafy trees of midlatitudes also belong to eudicots, with notable exceptions being magnolias and tulip trees which belong to magnoliids, and *Ginkgo biloba*, which is not an angiosperm.

The name "eudicots" (plural) is used in the APG system, of 1998, and APG II system, of 2003, for classification of angiosperms. It is applied to a clade, a monophyletic group, which includes most of the (former) dicots.

## Core Eudicots Core Tricolpates



Relationships after Savolainen *et al.* (2000b) and D. Soltis *et al.* (2003).

The core eudicots are an extremely large, diverse assemblage of flowering plants, with an enormous range of variation in habit, morphology, chemistry, geographic distributions, and other attributes. Based on analyses of morphology, classical systematists did not previously recognize the core eudicot group. Instead, the circumscription of the core eudicots as a clade was based on the very strong support obtained in analyses of DNA data sets.

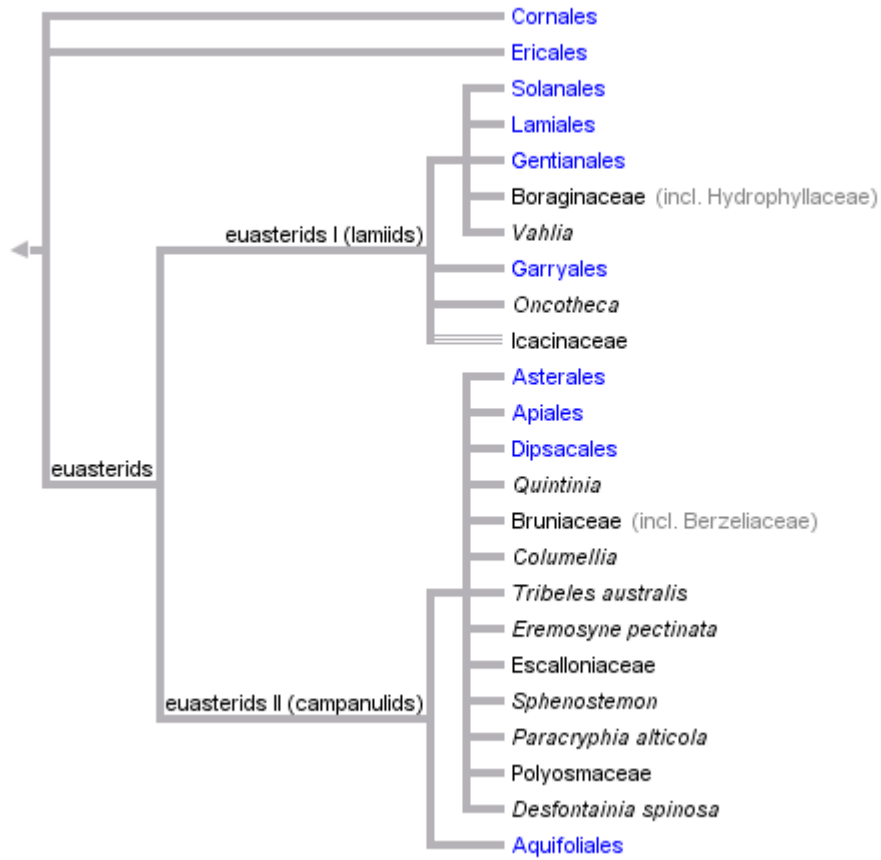
### Characteristics

Although the core eudicot group was not originally identified based on morphological evidence, subsequent research has identified several key events that correspond fairly closely to the origin of the core eudicots, including the evolution of flowers organized in a predictable manner with a stable number of parts (e.g., flowers with parts in fives or multiples of five, a clear differentiation of sepals and petals, twice the number of stamens as petals, and a gynoecium of three to five typically fused (at least partially) carpels, production of ellagic and gallic acids, and perhaps the duplication of several floral organ identity genes including homologs of the *Arabidopsis* genes, *Apetala3* and *Apetala1*.

### Asterids

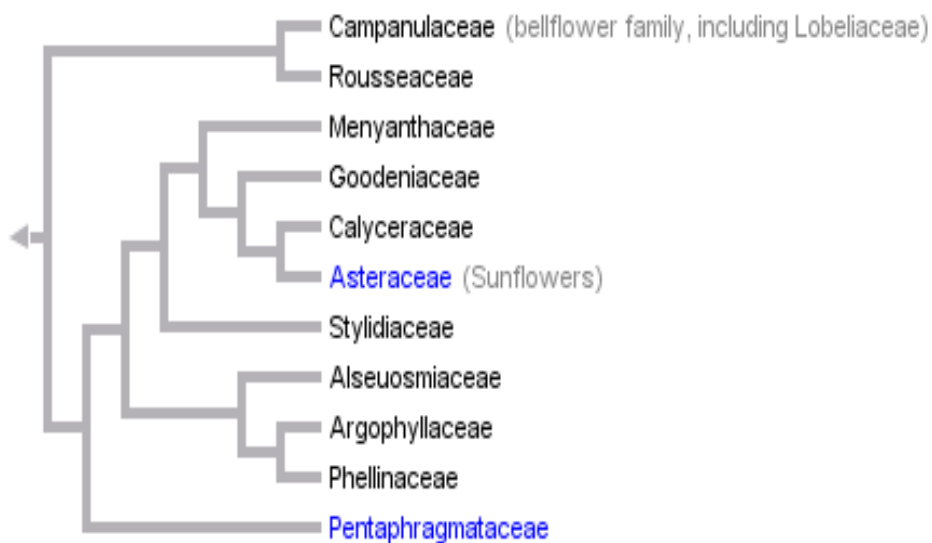
For the classification of flowering plants, the name asterids denotes a clade (a monophyletic group). Most of the taxa belonging to this clade had been referred to the *Asteridae* in the Cronquist system (1981) and to the *Sympetalae* in earlier systems. The name asterids (not necessarily capitalised) resembles the earlier botanical name but is intended to be the name of a clade rather than a formal

ranked name, in the sense of the ICBN. This clade is one of the two most speciose groups of eudicots, the other being the rosids.



Relationships after Albach *et al.* (2001), Olmstead *et al.* (2000), Savolainen (2000), and Hilu *et al.* (2003).

### *Asterales* Lindl., 1833



Tree adapted from Tank and Donoghue (2010)

*Asterales* is an order of dicotyledonous flowering plants that includes the large family *Asteraceae* (or *Compositae*) known for composite flowers made of florets, and ten families related to the *Asteraceae*.

The order is a cosmopolite (plants found throughout most of the world including desert and frigid zones), and includes mostly herbaceous species, although a small number of trees (such as the giant *Lobelia* and the giant *Senecio*) and shrubs are also present.

*Asterales* are organisms that seem to have evolved from one common ancestor.

*Asterales* share characteristics on morphological and biochemical levels.

Synapomorphies (a character that is shared by two or more groups through evolutionary development) include the presence in the plants of oligosaccharide inulin, a nutrient storage molecule used instead of starch; and unique stamen morphology.

The stamens are usually found around the style, either aggregated densely or fused into a tube, probably an adaptation in association with the plunger (brush; or secondary) pollination that is common among the families of the order, wherein pollen is collected and stored on the length of the pistil.

### **Evolution**

Although most extant species of *Asteraceae* are herbaceous, the examination of the basal members in the family suggests that the common ancestor of the family was an arborescent plant, a tree or shrub, perhaps adapted to dry conditions, radiating from South America.

Less can be said about the *Asterales* themselves with certainty, although since several families in *Asterales* contain trees, the ancestral member is most likely to have been a tree or shrub.

Because all clades are represented in the southern hemisphere but many not in the northern hemisphere, it is natural to conjecture that there is a common southern origin to them. *Asterales* are angiosperms, flowering plants that appeared about 140 million years ago.

The *Asterales* order probably originated in the Cretaceous (145 – 66 Mya) on the supercontinent Gondwana which broke up from 184 – 80 Mya, forming the area that is now Australia, South America, Africa, India and Antarctica.

*Asterales* contain about 14% of eudicot diversity.

From an analysis of relationships and diversities within the *Asterales* and with their superorders, estimates of the age of the beginning of the *Asterales* have been made, which range from 116 Mya to 82Mya.

However few fossils have been found, of the *Menyanthaceae-Asteraceae* clade in the Oligocene, about 29 Mya.

Fossil evidence of the *Asterales* is rare and belongs to rather recent epochs, so the precise estimation of the order's age is quite difficult.

An Oligocene (34 – 23 Mya) pollen is known for *Asteraceae* and *Goodeniaceae*, and seeds from Oligocene and Miocene (23 – 5.3 Mya) are known for *Menyanthaceae* and *Campanulaceae* respectively.

### **Biogeography**

The core *Asterales* are *Stylidiaceae* (six genera), APA clade (*Alseuosmiaceae*, *Phellinaceae* and *Argophyllaceae* (7 genera) and MGCA clade (*Menyanthaceae*, *Goodeniaceae*, *Calyceraceae* - total 20 genera), and *Asteraceae* (1,600 genera). Other *Asterales* are *Rousseaceae* (four genera), *Campanulaceae* (84 genera) and *Pentaphragmataceae* (one genus).

All *Asterales* families are represented in the Southern Hemisphere; however, *Asteraceae* and *Campanulaceae* are cosmopolitan and *Menyanthaceae* nearly so.

### **Economic importance**

The *Asterales*, by dint of being a super-set of the family *Asteraceae*, include some species grown for food, including the sunflower (*Helianthus annuus*), lettuce (*Lactuca sativa*) and chicory (*Cichorium*). Many spices and medicinal herbs are also present.

*Asterales* are common plants and have many known uses. For example, *Pyrethrum* (refers to several Old World plants of the genus *Chrysanthemum*) is a natural insecticide with minimal environmental impact. Wormwood, a genus that includes the sagebrush, is used as a source of flavouring for absinthe, a bitter classical liquor of European origin. Of horticultural importance are many of the *Asteraceae* (e. g. *chrysanthemum*) and *Campanulaceae*.

Despite the large number of species in order *Asterales*, they do not compare in economic benefit for mankind to the *Poales* or to the *Fabaceae*. Furthermore, [www.invasive.org](http://www.invasive.org) notes 838 invasive plant species in the *Asterales*, all members of the *Asteraceae*.

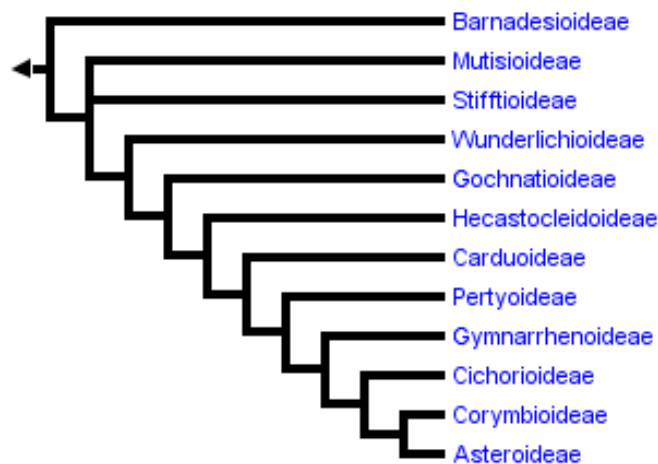
### *Asteraceae* Martynov, 1820

Sunflowers, daisies

Other Names:

*Compositae* Giseke, 1792

Vernacular names: sunflowers, daisies



The *Asteraceae* Martynov, 1820 (*Compositae* Giseke, 1792, alternate name) with its approximately 1,620 genera and more than 23,600 species is the largest family of flowering plants. The family is distributed worldwide except for Antarctica but is especially diverse in the tropical and subtropical regions of North America, the Andes, eastern Brazil, southern Africa, the Mediterranean region, central Asia, and southwestern China. The majority of *Asteraceae* species are herbaceous, yet an important component of the family is constituted by shrubs or even trees occurring primarily in the tropical regions of North and South America, Africa and Madagascar and on isolated islands in the Atlantic and Pacific Oceans. Many species of sunflowers are ruderal and especially abundant in disturbed areas, but a significant number of them, especially in mountainous tropical regions, are narrow endemics. Because of the relentless habitat transformation precipitated by human expansion in montane tropical regions, a number of these species are consequently in danger of extinction. The family contains several species that are important sources of cooking oils, sweetening agents, and tea infusions. Members of several genera of the family are well-known for their horticultural value and popular in gardens across the world and include zinnias, marigolds, dahlias, and chrysanthemums. The commercial sunflower genus *Helianthus* has been used as a model in the study of hybridization and its role in speciation.

#### **Characteristics**

The family is characterized by having a capitulum or head, an inferior, unilocular ovary with one ovule, and with few exceptions fused anthers surrounding the style. The capitulum (capitula plural) is a specialized indeterminate inflorescence that can contain 1 to hundreds of individual flowers (florets). The flowering sequence in the capitulum is nearly always from the outside to the center, that is, centripetal. The florets sit on the disc or receptacle, an expanded shoot that can be flat,

concave, convex, or rarely columnar. The disc and florets are surrounded by bracts or leaf-like structures called phyllaries and collectively forming an involucre. The phyllaries can be arranged in one row and be of equivalent length or can be unequal in length. Most sunflowers have involucre with several series of phyllaries. In these sunflowers the phyllaries can be subequal with all phyllaries of equivalent length or imbricate. Involucre composed of imbricate phyllaries are the most common condition in the family and exemplified by the artichoke (*Cynara cardunculus*) in which multiple series of phyllaries overlap each other. In some species the outermost phyllaries sometimes resemble leaves. The receptacle can be naked or sometimes have bract-like structures called paleae, scales or hairs surrounding each floret. The involucre can have different shapes ranging from tubular to hemispheric.

Radiate capitulum composed of two types of florets enclosed by the involucre.

There are six types of corollas present in the *Asteraceae* two of which are actinomorphic and the other four are zygomorphic. Actinomorphic corollas are composed of five equivalent lobes and normally termed disc corollas (as they occupy most of the disc area). They have five lobes and when viewed from above, the reflexed lobes of the actinomorphic corolla resemble a five point star. Disc corollas may have fewer lobes with four being the most common departure, although corollas with three lobes are also seen. Tubular corollas are narrow actinomorphic corollas, mostly lacking stamens. Zygomorphic corollas are mostly confined to the first row of florets in the capitulum, although some species may have several rows of zygomorphic corollas. Bilabiate corollas are generally present only in several genera belonging to the earliest divergences of the family. The bilabiate corolla has a 3+2 arrangement of lobes with the 3-lobe lamina facing towards the outside and the 2-lobe lamina to the center of the capitulum. Sometimes the 2 lobes are separate and coiled. The pseudobilabiate corolla has a 4+1 arrangement. The ray floret is present in several tribes of the subfamilies *Cichorioideae* and *Asteroideae* and consists of a lamina that terminates in 2-3 lobes. Some members of tribe *Arctotideae* have a ray floret that terminates in 4 lobes. Ligulate corollas have 5 lobes.

The capitula of sunflowers can contain florets with corollas of the same morphology or a combination of two or sometimes three types of corollas. In discoid capitula all florets have actinomorphic corollas and can be either bisexual and fertile or functionally staminate or pistillate. In radiate capitula the peripheral florets are ray florets and these can be pistillate or styliiferous and sterile or neuter (no style present). Radiant capitula are discoid capitula with peripheral corollas having lobes variously expanded. In ligulate or liguliflorous capitula all the florets are bisexual and have ligulate corollas; this capitulum type is only found in members of tribe Cichorieae. Disciform capitula have florets with actinomorphic corollas with peripheral florets having tubular corollas. These peripheral corollas are pistillate. Homogamous capitula have florets exhibiting similar sexual forms whereas heterogamous capitula have florets with two or more sexual forms.

Most sunflower florets have five anthers corresponding to the number of lobes in the corolla. The anthers are positioned along the sinuses of the corolla lobes (alternate to the lobes). The anther filaments are free from the corolla just above the tube and the two thecae (pollen sacs) of each stamen are connate with the thecae of adjacent stamens producing a tube that surrounds the style. Pollen is shed to the interior of this tube (introrse dehiscence). The connective, the tissue connecting the two anther thecae of each anther, may continue beyond the anther thecae and produce an appendage. Some sunflowers do not have appendages (e.g., many *Asteroideae*: *Eupatorieae*). The anther collar is located at the end of the filament just below the connective and is an area of sclerified cells involved in the mechanical aspects of pollen presentation in sunflowers. The anther collar is progressively shorter on the adaxial side facing the style. If the thecae extend below the point of insertion between the filament and connective, the anther is calcarate; if not, the anther is ecalcarate. Anthers can have tails, sometimes very elaborate with branched projections. Calcarate and caudate (tailed) anthers are common among the basal lineages of the family whereas ecalcarate anthers are more common in the *Asteroideae*.

The styles of sunflowers have two stigmatic branches or arms. They may be smooth (glabrous) or pubescent with trichomes confined mostly to the distal end of the style and the abaxial surfaces of the style branches. In fertile florets, the adaxial surface of the style branch has stigmatic (fertile) papillae. In some groups the stigmatic papillae are continuous throughout the style branches, whereas in others the stigmatic papillae are confined to the margins of the style branches. As the floret matures, the style grows through the tube formed by the fused anthers pushing the pollen up. This secondary pollen presentation mechanism ensures pollen is available to insects visiting the capitulum on a daily basis as new florets open. The pollination biology of sunflowers has not been extensively studied but an excellent summary of the available literature is provided by Lane (1996). Sunflowers produce dry, indehiscent fruits termed cypselae (achenes in many publications). A few species have fleshy fruits reminiscent of a drupe (*Chrysanthemoides*, *Tilesia*). Most species have a pappus on the distal end of the cypselae. This structure is derived from the calyx of the floret (Carlquist, 1976). The pappus aids in dispersal or defense against herbivory (Stuessy and Garver, 1996).

### **Taxonomy**

The initial classification of the family was produced by Cassini who grouped genera into tribes. His tribal concepts have been refined by taxonomists subsequently and are still the main category above the genus level used to classify sunflowers. The grouping of these tribes into subfamilies is a relatively recent academic pursuit in *Asteraceae* systematics that began with Carlquist (1976) and Wagenitz (1976) defining the concepts of subfamilies *Cichorioideae* and *Asteroideae*. The morphological characteristics used to circumscribe these two groups are mostly based on discontinuities in corolla, anther, and style morphology. According to Bremer (1994), the *Asteroideae* are characterized (with some exceptions) by having true ray florets, disc corollas with short lobes, cavate pollen, stigmatic surfaces of style branches separated into two marginal lines sometimes confluent at apices, and a distinctive secondary chemistry. These morphological characteristics are rarely seen in *Cichorioideae*.

With the incorporation of results from molecular phylogenetic studies the classification of the *Asteraceae* has changed relatively quickly, mainly through the recognition of monophyletic groups traditionally included in *Cichorioideae*. With the work of Jansen and Palmer (1987), Bremer (1994) recognized three subfamilies (*Asteroideae*, *Barnadesioideae*, and *Cichorioideae*) and 17 tribes. Thorne and Reveal (2007) recognized the same subfamily groups using the possibly earlier name *Carduoideae* for the *Cichorioideae*. They expanded the number of tribes to 25, recognizing the three new tribes identified by molecular analysis named in Baldwin et al. (2002) but maintained a polyphyletic Heliantheae. Jeffrey (2007) accepted the tribal groupings of Panero and Funk (2002), ultimately recognizing 24 tribes and grouping them into five subfamilies. He recognized a monophyletic *Barnadesioideae*, a monophyletic *Asteroideae*, and split the grade of clades between these two groups: *Cichorioideae* or *Carduoideae* into 3 subfamilies: *Mutisioideae*, *Carduoideae*, and *Cichorioideae*, each shown to be polyphyletic. As the capacity to expand both taxon and character sampling in molecular studies has grown, providing more resolution and certainty in phylogenetic analyses, more major lineages of the family have been identified. Increased sampling, particularly sampling of taxa considered anomalous in the family (uncertain tribal position, Bremer, 1994), resulted in the discovery that the genera *Corymbium*, *Gymnarrhena*, and *Hecastocleis* represent monotypic lineages sister to major clades and provided evidence for more lineages than previously recognized. The classification of Panero and Funk (2008), shown in the tree above, recognizes 12 strictly monophyletic subfamilies.

The classification of the *Asteraceae* is dominated by the large subfamily *Asteroideae* that contains more than 70% of the species of the family. The three main lineages within *Asteroideae* found by molecular studies have been recognized at the supertribe level recently as *Asterodae*, *Helianthodae*, and *Senecionodae*. Other large subfamilies include *Carduoideae* and *Cichorioideae* each with more than 2000 species. All other subfamilies each contain less than 1000 species with *Gymnarrhenoideae* and *Hecastocleidoideae* containing only one species each.

## Discussion of Phylogenetic Relationships

The phylogenetic tree shown on this and subsequent pages is drawn after that reported in Panero and Funk (2008) based on analyses of combined sequence data from multiple chloroplast loci including the genes *matK*, *ndhD*, *ndhI*, *ndhF*, *rbcL*, *rpoB*, *exon1* of *rpoC1*, and the intron and intergenic spacer regions of the *trnL-trnF*.

Each of the major clades of *Asteraceae* (subfamilial and tribal clades) was inferred in both Maximum Parsimony and Bayesian phylogenetic analyses with significant measures of clade support (bootstrap and posterior probability respectively). Relationships among these clades were also resolved with significant statistical support and were robust to method with the exception of the relationships of *Stifftioideae* and *Wunderlichioideae*. The phylogeny of Panero and Funk (2008) represents the best resolved and statistically supported hypothesis of evolutionary relationships among the major clades of the family currently available. Preliminary results from their study (Panero and Funk, 2008) have been used previously as the backbone phylogeny for the construction of a metatree of the family (Funk et al., 2009). The nomenclature used here is consistent with that of NCBI Genbank.

Relationships among the deepest branches of the *Asteraceae* tree of life have primarily been elucidated through investigations of the chloroplast genome. Comparative nucleotide confirmed the original discovery based on restriction fragment polymorphisms (RFLPs) that *Barnadesioideae*, lacking the 22 kb inversion present in all other sunflowers is sister to all other *Asteraceae*.

A *Cichorioideae* clade sister to *Asteroideae* was recovered with weak bootstrap support in the *ndhF* study and identified with strong support (bootstrap and posterior probability) in the multi-locus chloroplast study of Panero and Funk (2008).

The multi-locus study also recovered strong statistical support for the *Mutisioideae*, *Stifftioideae*, *Gochnatioideae*, *Hecastocleidoideae*, *Carduoideae*, *Pertyoideae*, *Gymnarrhenioideae*, and *Corymbioideae* clades. All family-wide molecular phylogenetic studies to date have shown support for a monophyletic *Asteroideae*.

Evidence from the nuclear genetic compartment, an analysis of the nuclear ribosomal internal transcribed spacer (nrITS) region, is congruent with chloroplast results in the relationships of *Barnadesioideae* and *Mutisioideae* to other *Asteraceae*, in the monophyly of the *Asteroideae*, and in the sister relationship of *Athroismeae* and *Heliantheae* s.l.

Relationships of other major clades of *Asteraceae* recovered from the nrITS study (strict consensus tree) are not congruent with chloroplast results. However, these may conservatively be viewed as equivocal because of low statistical support (bootstrap proportions).

The phylogenetic tree presented here primarily reflects the evolutionary history of the chloroplast genome.

*Asteraceae* provide some of the best documented examples of hybrid evolution in plants, but the full extent of reticulation in the evolutionary history of sunflowers is not yet known, nor how closely this genome phylogeny corresponds to the organismal phylogeny of sunflowers.

## Fossil Record

The fossil record of *Asteraceae* is for the most part composed of pollen deposits and fruits. Few pollen records exist for the Eocene but the pollen of *Asteraceae* becomes increasingly common in samples dated to the Oligocene/Miocene.

These data show the increasing importance of the family in most biomes of the world from the mid to late Oligocene to present.

Pollen samples from Paleocene-Eocene deposits in southwestern Africa have been attributed to Mutisieae or to a Dicoma-like taxon and recently dated to the mid-Eocene. *Asteraceae* pollen dated to the Eocene has also been found in Egypt, China and North America.

Fossil pollen records have been used recently to shed light on the time of origin of *Asteraceae*. Dated and properly identified, pollen deposits can be used to place a minimum age for the origin of a particular clade.



Using the rate of mutation of the gene *rbcL* and a fossil calibration, Bremer and Gustafsson (1997) concluded the family to have originated at least 38 Ma.

A similar approach using the *ndhF* and *rbcL* genes was used to date the origin of molecular rearrangements in the chloroplast genome of the *Asteraceae*. Their study concluded that the family originated in the mid Eocene (42-47 Ma).

### Economically Important Sunflowers

Several species of sunflowers are of economic importance.

Below is a list of species that have a widespread use in society (Table 1).

Many more species of *Asteraceae* of narrow distribution, especially in tropical regions, are used locally for various medicinal and food purposes. The economic importance of many species of sunflowers is yet to be fully explored.

Table 1 - List of species that have a widespread use such as oil, food, ornamental, medicinal and industrial.

Species	Taxonomy	Common Name	Country
<i>Guizotia abyssinica</i> (L. f.) Cass.	Asteroideae: <i>Millerieae</i>	Niger seed oil	Northeast tropical Africa
<i>Carthamus tinctorius</i> L.	Asteroideae: <i>Heliantheae</i>	Safflower oil	North America
<i>Helianthus annuus</i> L.	Asteroideae: <i>Heliantheae</i>	Sunflower oil	North America
<i>Cynara cardunculus</i> L.	Carduoideae: <i>Cynareae</i>	Artichoke	Eurasia
<i>Cichorium endivia</i> L.	Cichorioideae: <i>Cichorieae</i>	Endive	Europe
<i>Helianthus tuberosus</i> L.	Asteroideae: <i>Heliantheae</i>	Jerusalem artichoke	North America
<i>Lactuca sativa</i> L.	Cichorioideae: <i>Cichorieae</i>	Lettuce	cultivar of Asian species
<i>Tagetes lucida</i> Cav.	Asteroideae: <i>Tageteae</i>	Mexican tarragon	Mexico
<i>Cichorium intybus</i> L.	Cichorioideae: <i>Cichorieae</i>	Radicchio	Europe
<i>Tragopogon porrifolius</i> L.	Cichorioideae: <i>Cichorieae</i>	Salsifi	Europe
<i>Helianthus annuus</i> L.	Asteroideae: <i>Heliantheae</i>	Sunflower seeds	North America
<i>Artemisia dracunculus</i> L.	Asteroideae: <i>Anthemideae</i>	Tarragon	Eurasia
<i>Rudbeckia hirta</i> L.	Asteroideae: <i>Heliantheae</i>	Black-Eyed Susans	USA, Canada
<i>Chrysanthemum</i> several species	Asteroideae: <i>Anthemideae</i>	Chrysanthemums	Asia
<i>Dahlia coccinea</i> Cav.	Asteroideae: <i>Coreopsideae</i>	Dahlias	Mexico
<i>Echinacea purpurea</i> (L.) Moench	Asteroideae: <i>Heliantheae</i>	Purple Coneflower	North America
<i>Echinacea paradoxa</i> , (Norton) Britton	Asteroideae: <i>Heliantheae</i>	Yellow Coneflower	North America
<i>Tagetes erecta</i> L.	Asteroideae: <i>Tageteae</i>	Marigolds	Mexico, Central America
<i>Santolina</i> spp	Asteroideae: <i>Anthemideae</i>	Santolinas	Europe
<i>Zinnia angustifolia</i> Kunth	Asteroideae: <i>Heliantheae</i>	Zinnias	Mexico, South America
<i>Zinnia peruviana</i> (L.) L.	Asteroideae: <i>Heliantheae</i>	Zinnias	Mexico, South America
<i>Zinnia violacea</i> Cav.	Asteroideae: <i>Heliantheae</i>	Zinnias	Mexico, South America
<i>Artemisia annua</i> L.	Asteroideae: <i>Anthemideae</i>	Anti-malarial	eastern Asia
<i>Matricaria recutita</i> L.	Asteroideae: <i>Anthemideae</i>	Chamomile tea	Europe
<i>Echinacea purpurea</i> (L.) Moench	Asteroideae: <i>Heliantheae</i>	Echinacea tea	North America
<i>Artemisia absinthium</i> L.	Asteroideae: <i>Anthemideae</i>	Absinthe (beverage)	Europe
<i>Pyrethrum tanacetum</i> Bernh.	Asteroideae: <i>Anthemideae</i>	Insecticides (pyrethrins	Eurasia
<i>Pyrethrum vulgare</i> (L.) Boissier	Asteroideae: <i>Anthemideae</i>	and cinerins)	Eurasia
<i>Tagetes erecta</i> L.	Asteroideae: <i>Tageteae</i>	Orange dye	Mexico
<i>Tagetes patula</i> L.	Asteroideae: <i>Tageteae</i>	Orange dye	Mexico
<i>Carthamus tinctorius</i> L.	Cichorioideae: <i>Cichorieae</i>	Orange dye	central Asia
<i>Parthenium argentatum</i> A. Gray	Asteroideae: <i>Heliantheae</i>	Rubber, Guayule	North America
<i>Stevia rebaudiana</i> (Bertoni) Bertoni	Asteroideae: <i>Eupatorieae</i>	Sweetener	South America

Legend:

Oil	Food	Ornamentals	Medicinal	Industrial
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*Carduoideae* Cass. ex Sweet, 1826



*Carduoideae* is the thistle subfamily of the *Asteraceae*, or sunflower family, of flowering plants. It comprises a number of tribes in various circumscriptions of the family, in addition to the *Cynareae*. Takhtajan, according to Reveal, includes ten tribes in addition to the *Cynareae*: the *Arctotideae*, the *Barnadesieae*, the *Carlineae*, the *Cichorieae*, the *Echinopseae*, the *Eremothamneae*, the *Gundelieae*, the *Liabeae*, the *Mutisieae*, and the *Vernonieae*. Of these eleven, Thorne agrees with seven in his 8 tribe taxonomy of the *Carduoideae*, placing the *Cardueae* (*Cynareae*), plus *Arctotideae*, *Cichorieae*, *Eremothamneae*, *Liabeae*, *Mutisieae*, and *Vernonieae* tribes in the subfamily, plus the *Tarchonantheae*. The Panero and Funk classification of 2002 (a molecular phylogenetic classification based upon chloroplast genes) places just three tribes in the subfamily: the *Cynareae*, plus the *Dicomeae* (created by Panero and Funk's paper, consisting of *Dicoma*, *Erythrocephalum*, *Gladiopappus*, *Macleodium*, *Cloiselia*, *Pasaccardoa*, and *Pleiotaxis*), and the *Tarchonantheae* (*Tarchonanthus* plus *Brachylaena*). The genus *Oldenburgia* may be within this subfamily but the data on this is inconclusive. The Takhtajan system divides the *Asteraceae* into only two subfamilies, the *Asteroideae* in addition to the *Carduoideae*, while Thorne adds the basal, monophyletic subfamily, the *Barnadesioideae*. The recent phylogeny of Panero and Funk divides the *Asteraceae* into 11 subfamilies.

Below are given two classical representatives of the clade *Carduoideae*: *Carduus tenuiflorus* and *Oldenburgia grandis*. The first, is known variously as slender-flower thistle, sheep thistle, shore thistle, slender thistle, winged plumeless thistle, winged slender thistle, and winged thistle is a species of thistle. It is native to Europe and North Africa. It is well-known on other continents, where it is an introduced species and noxious weed. The second is a shrub or small, gnarled tree in the family *Asteraceae*. It occurs in the mountains around Grahamstown in South Africa. It grows to a height of about 5m on sandstone outcrops. It has thick corky bark and large leaves clustered at the ends of branches. The leaves are dark green and leathery, reminiscent of loquat leaves, but generally a good deal larger. The emergent leaves are densely and completely felted with white hair. Most of the felt is lost as the leaf matures, but some persists on under-surfaces. Flowers are purple and in large heads about 12 cm in diameter. The flowerheads are solitary and terminal. It is threatened by habitat loss.



*Carduus tenuiflorus* Curtis 1793



*Oldenburgia grandis* (Thunb.) Baill. 1882

*Cynareae* Lam. & DC., 1806 or *Cardueae* Cass., 1819



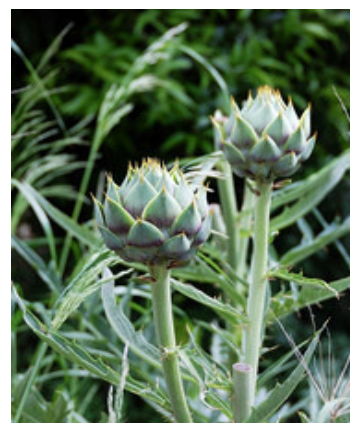
*Cynareae* or *Cardueae* are a tribe of flowering plants in the daisy family (*Asteraceae*). Most of them are commonly known as thistles; four of the best known genera are *Carduus*, *Cynara* (containing the widely eaten artichoke), *Cirsium*, and *Onopordum*.

They are annual, biennial or perennial herbs. Many species are thorny on leaves, stems or involucre, and some have laticifers or resin conduits. Almost 80 genera with 2,500 species are assigned to this tribe, native of tempered regions of Europe and Asia (specially of the Mediterranean region and Minor Asia), some of Australia and tropical Africa; only three genera have native species of America.

*Cardueae* is a synonym for *Cynareae*, but the name *Cynareae* was published almost a decade earlier and so has precedence.

Some authors have divided the plants traditionally held to be in this tribe into three tribes: *Cynareae* in the narrow sense, *Carlineae*, and *Echinopeae*. However, other authors have retained the traditional broader classification.

Below are given three classical representatives of the clade *Cynareae*: *Echinops sphaerocephalus* L., 1753; *Carlina biebersteinii* Bernh. ex Horn. 1819 and *Cynara cardunculus* L., 1753.



*Echinops sphaerocephalus* L., 1753    *Carlina biebersteinii* Bernh. ex Horn. 1819    *Cynara cardunculus* L., 1753

*Echinops sphaerocephalus* is a glandular, woolly perennial herbaceous plant with an average height of 50–100 centimetres (20–39 in), occasionally reaching two meters.

Its erect branching, gray, slightly wrinkled and hairy stems bear the occasional large, soft, sharply toothed, sharp-lobed pointed green leaves. They are sticky hairy above, and white woolly below.

Atop each stem is an almost perfectly spherical inflorescence up to 6 cm in diameter, packed with white or blue-gray disc florets. It flowers from June until September.

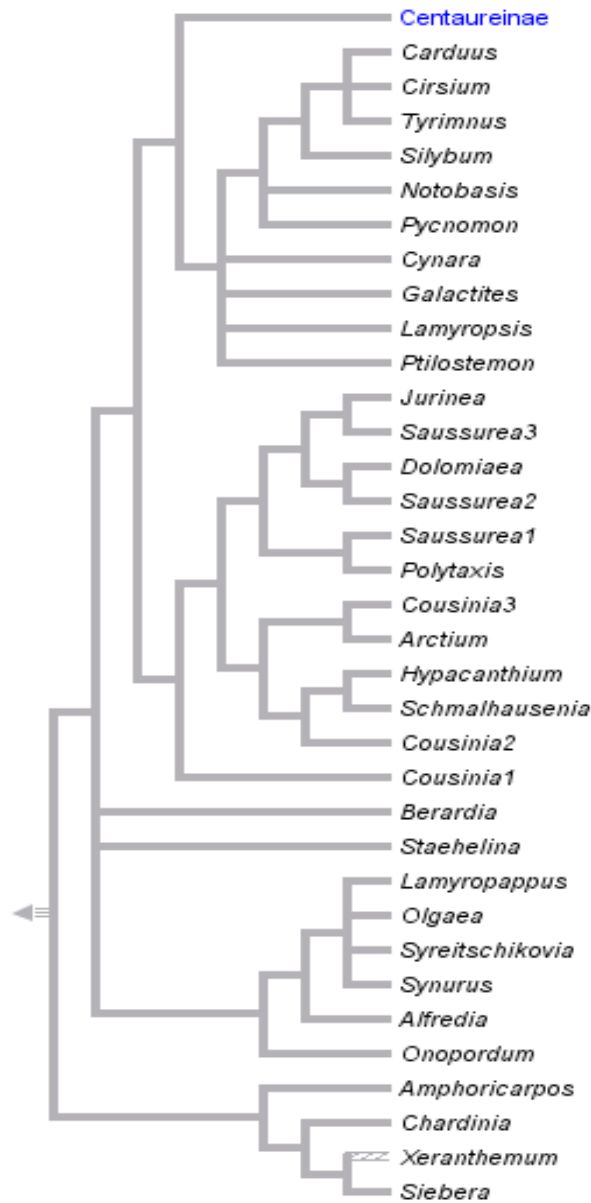
The flowers are pollinated by insects (usually bees, wasps and butterflies) (entomogamy) and are hermaphrodite (self fertilization or autogamy). The fruits are hairy cylindrical achenes about 7 to 8 mm long. They ripen from September through October. The seeds are dispersed by wind (anemochory).

*Carlina biebersteinii* is a purple-flowered herb found in Europe, Russia, Kazakhstan and in the Xinjiang region of China.

*Cynara cardunculus*, called cardoon, artichoke thistle, cardone, cardoni, carduni or cardu, is a thistle-like. It is a naturally occurring species that is sometimes considered to include the globe

artichoke, and has many cultivated forms. It is native to the western and central Mediterranean region, where it was domesticated in ancient times.

*Carduinae* (Cass.) Dumort., 1827



The name of this *clade* was taken from the genus *Carduus* whose name in Latin means "thistle" which in turn could be derived from a Greek word whose meaning is closer to our word "shave"; but further research would be derived from a different root, always Greek, "ardis" (= "tip of the arrow"), alluding of course to the thorns of the thistle plant.

The scientific name of this *clade* has been defined for the first time by Count Alexandre Henri Gabriel de Cassini (1781-1832), French botanist and naturalist, published in the *Journal de Physique, de Chimie et d'Histoire Naturelle des Arts*, 88: 155 of 1819, then perfected by the botanist, naturalist and Belgian political Barthélemy Charles Joseph Dumortier (Tournai, April 3, 1797-9 June, 1878) in 1827.



We report such as representatives of this group the following species: *Cirsium vulgare* Ten., 1836, *Cynara alba* Boiss., 1838.



*Cirsium vulgare* (Savi) Ten., 1836



*Cynara alba* Boiss., 1838

*Cirsium vulgare* (common name Spear Thistle) is a species of the genus *Cirsium*, native throughout most of Europe (north to 66°N, locally 68°N), western Asia (east to the Yenisei Valley), and northwestern Africa (Atlas Mountains). It is also naturalised in North America and Australia and is as an invasive weed in some areas. It is the national flower of Scotland.

It is a tall biennial or short-lived monocarpic thistle, forming a rosette of leaves and a taproot up to 70 cm long in the first year, and a flowering stem 1–1.5 m tall in the second (rarely third or fourth) year. The stem is winged, with numerous longitudinal spine-tipped wings along its full length. The leaves are stoutly spined, grey-green, deeply lobed; the basal leaves up to 15–25 cm long, with smaller leaves on the upper part of the flower stem; the leaf lobes are spear-shaped (from which the English name derives). The inflorescence is 2.5–5 cm diameter, pink-purple, with all the florets of similar form (no division into disc and ray florets). The seeds are 5 mm long, with a downy pappus, which assists in wind dispersal. As in other species of *Cirsium* (but unlike species in the related genus *Carduus*), the pappus hairs are feathery with fine side hairs.

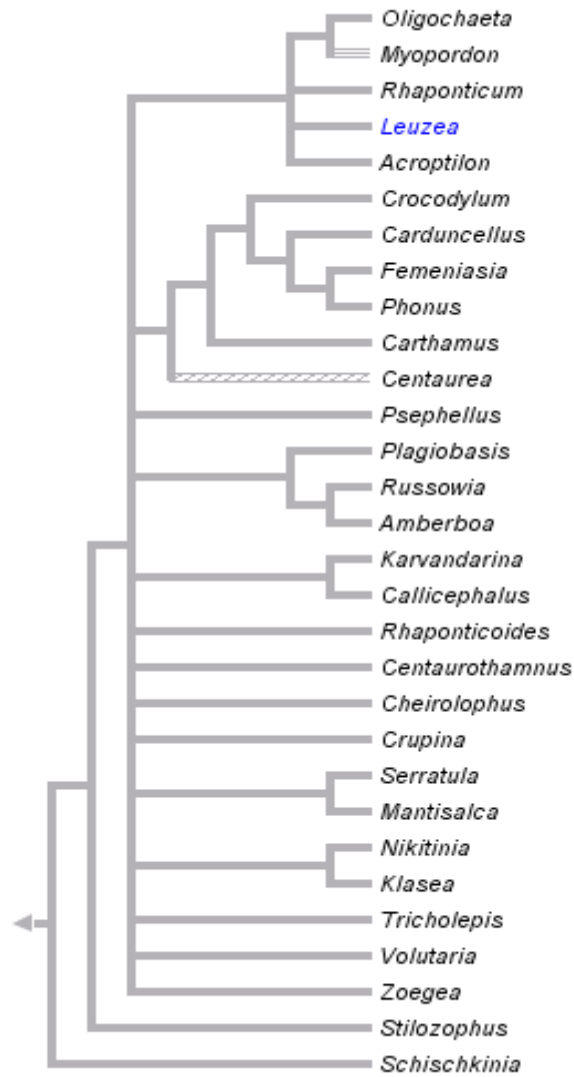
### ***Centaureinae*** (Cass.) Dumort., 1827

According to some authors this group could be monophyletic along with the neighboring clade of the *Carduinae*. The various phylogenetic studies made so far have not yet clarified this taxonomy. Here the two subtribes are still treated separately.

The *Centaureinae* include 32 genera divided into 7 groups with about 620 species. This division is based on studies of the morphology of pollen on the analysis of DNA sequences is still informal and probably susceptible to revisions. Several taxa do not fall clearly into any group, and remain isolated.

The cladogram below indicated show the phylogenetic position of the various groups. Some groups are not monophyletic, while others have an uncertain position or not supported sufficiently.

The genera of the "basal" clade *Centaureinae* can be divided into two parts. The first part includes three genera annual (*Schischkinia*, *Stizolophus* and *Zoegea*) Cladistic analyzes that are "sister group" to the rest of the *Centaureinae*. It is unclear whether their position is determined by a real relationship "sister group" or is caused artificially by their habitus year. [7] The second part is substantially isolated from the rest of the subtribe. The reconstruction of the similarities and relationships between these genera is very difficult and problematic. Some studies have included *Serratula* in this group, others consider it as a specific subgroup with two other genera (*Klasea* and *Nikitinia*). The description of a new genus *Archiserratula* may belong to this group. The distribution is mainly concentrated between Mediterranean Europe and Central Asia. The group includes 9 genera with about 158 species.



The genera listed representative are: *Carthamus lanatus* L., 1753, *Centaurea americana* Spreng, 1826, *Serratula tinctoria* L., 1753.



*Carthamus lanatus* L., 1753

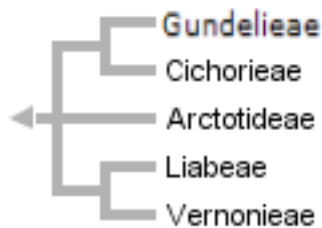


*Centaurea americana* Spreng, 1826



*Serratula tinctoria* L., 1753

*Cichorioideae* (Juss.) Chevall. (1828)



Familiar members of *Cichorioideae* include lettuce, dandelions, and *Gazania* species. The subfamily comprises about 240 genera and about 2,900 species. It is heterogeneous and hard to characterize except with molecular characters.

The subfamily as understood in 1998 turned out to be paraphyletic, based on studies of DNA sequences, so a number of clade were moved to new clades. Names for the new clades were published in 2002. In 2004, 2007, and 2008, molecular phylogenetic studies further clarified relationships within *Cichorioideae*.

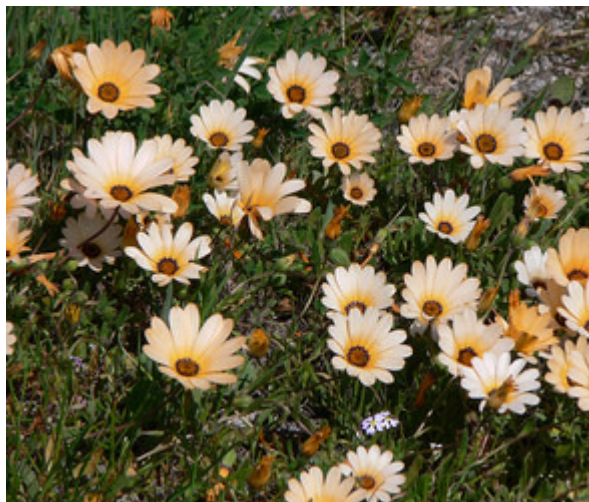
Major works on *Asteraceae* were published in 2007 and 2009. These were the only comprehensive treatments of the family since 1994. In the 2007 book, *Gundelia* and *Warionia* were segregated from the *Cichorieae* to form the *Gundelieae*. *Eremothamnus*, *Hoplophyllum*, *Heterolepis*, and *Platycarpha* were placed incertae sedis in *Arctotideae*, while *Distephanus*, *Trichospira*, *Moquinia*, and *Pseudostiffia* were placed in the clade *Vernonieae*. Some of this classification was not supported by phylogenetic studies that came out later. For example, the *Arctotideae* was only weakly supported as monophyletic, but its two clades, *Arctotidinae* and *Gorteriinae*, were strongly supported.

In the 2009 book, the *Gundelieae* were sunk into the *Cichorieae*. The new clade *Platycarpheae* was recognized, as well as the *Eremothamneae* and *Moquinieae*. *Heterolepis* was placed in the *Arctotideae*, at least provisionally. *Distephanus* was not placed in the *Moquinieae* or the *Vernonieae*, but is closely related to them. *Trichospira* was placed in the *Vernonieae*, but its inclusion there is in doubt.

They show some species of this group: *Vernonia lindheimeri* Gray & Engelm., 1848, *Arctotis stoechadifolia* P.J.Bergius, 1767 and *Malacothrix glabrata* A.Gray, 1884.



*Vernonia lindheimeri* Gray & Engelm., 1848



*Arctotis stoechadifolia* Gray & Engelm., 1848

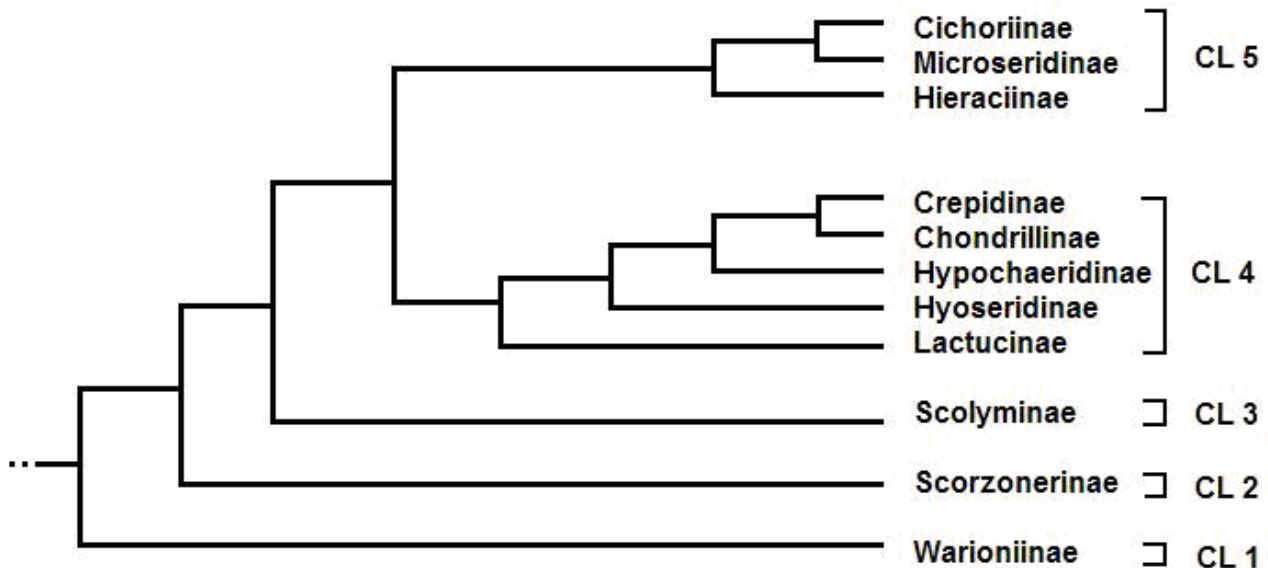


*Malacothrix glabrata* A.Gray, 1884



## *Chicorieae* Lam. & DC., 1806

*Chicorieae* (sometimes *Lactuceae*) is a tribe of plants in the family *Asteraceae* that includes 100 genera and more than 1,600 species. They are found primarily in temperate regions of the Eastern Hemisphere. Well known members include lettuce, chicory, dandelion, and salsify.



## *Chicoriinae* Cass. ex Dumort., 1829

*Chicoriinae* is a group of spermatophytes dicotyledonous plants belonging to the family *Asteraceae* (*Cichorioideae* subfamily, *Chicorieae* tribe).

### Etymology

The name of this group is derived from a kind (*Cichorium* L.), the etymology of which is difficult to define. Probably it is an ancient Arabic name that might sound like “Chikouryeh”. It seems (according to other texts) that derives from an Egyptian name “Kichorion”, or maybe even by the combination of two terms Kio (= I) and chorion (= field). The ancient Greeks called it, for example some plants of this genus kichora; but also *kichòria* or *kichòreia*. Could it be then that the Arabs have taken from the Greeks the name, but it is not certain. The difficulty in finding the origin of the name lies in the fact that these plants were known from the earliest times of human history. We have example of quotations related to plants of this kind in the “Ebers Papyrus” (about 1550 BC) and Pliny himself in his writings cited the species *Cichorium* as known in ancient Egypt; the greek physician Galen advised these plants against diseases of the liver; not to mention all the references in Roman times.

The scientific name has been defined for the first time by botanists Barthélemy Charles Joseph Dumortier (Tournai, April 3, 1797-9 June, 1878), botanist, naturalist and Belgian politician and Alexandre Henri Gabriel de Cassini (1781-1832), French botanist and naturalist, in the publication "Analyse des Familles de Plantes: avec l'indication des principaux genres here s'y rattachent. Tournay – 30, 1829" in 1829.

### Description

The species of this subtribe are annuals or perennials with stems branching and foliose or type with scape, in some cases the habit is shrub. Some species are grown for edible leaves (*Cichorium endive*

L. and *Cichorium intybus* L.).

The leaves along the stem are arranged in an alternating manner (but may be almost absent or much reduced); other form a basal rosette. The leaf can be entire, toothed or serrated; the shape is linear, oblanceolate, spatulate, obovate or oblanceolate. In some species the texture is fleshy.

The inflorescence is composed of one or more flower heads (depending on species). The flower heads, only type ligulifloro, are formed by a casing composed of bracts (or scales) arranged on 1-2 (or rarely 3) series within which a receptacle acts as a base to ligulate flowers. The shape of the envelope is campanulate or urceolate; the shape of the scales is lanceolate or linear-lanceolate; the lower part of the outer ones can be fleshy and hardened during flowering or can be connate between them; the edges of the scales in some species are somewhat scariosi. The receptacle is naked ie without wool (in *Rothmaleria* flakes are present and persistent).

The flowers are tetra-cyclic (ie there are 4 whorls: calyx - corolla - androecium - gynoecium) and pentamers (each whorl usually has 5 elements). The flowers are hermaphrodite and zygomorphic generally.

Floral formula: for these plants is shown the following flowering formula:

\* K 0/5, C (5), A (5), G (2), inferus, achene

Calyx: the sepals of the calyx is reduced to a crown of scales.

Corolla: The corolla is mostly blue or yellow and ends with at least 5 apical teeth.

### **Taxonomy**

The family belong to this group (*Asteraceae* or *Compositae, nomen conservandum*) is the largest in the plant world, includes more than 23,000 species spread across 1,535 genera (1,530 genera and 22,750 species according to other sources). The subfamily *Cichorioideae* is one of 12 subfamilies in which it has been divided family *Asteraceae*, while *Cichorieae* is one of the seven tribes of the subfamily. The tribe *Cichorieae* in turn is divided into 11 subtribe (*Cichoriinae* is one of these).

The chromosome number of the species of the subtribe is:  $2n = 18$  In *Tolpis* species can be diploid, tetraploid or hexaploid.

Androecium: stamens with free filaments and 5 are distinct, while the anthers are welded in a sleeve (or tube) surrounding the stylus. The anthers at the base are acute.

Gynoecium: the stylus is wiry, while the stigmas of the stylus are two divergent. The ovary is inferior unilocular consists of 2 carpels. The stigmas are hairy on the underside. In some species the stigmas are short (*Arnoseris*).

The fruits are achenes with pappus. The achenes have a prismatic shape with 3-5 corners, or conical or obovate; the achene can be topped with a short beak. The pappo in some cases is reduced to a crown of teeth (or even zero), while in other cases is composed of a few scales lesiniformi or triangular.

### **Distribution and habitat**

The distribution of this subtribe is quite varied: Europe, Africa (especially in the south), Asia (western part) and North America. In Italy in the wild are the following three kinds: *Arnoseris*, *Cichorium* and *Tolpis*.

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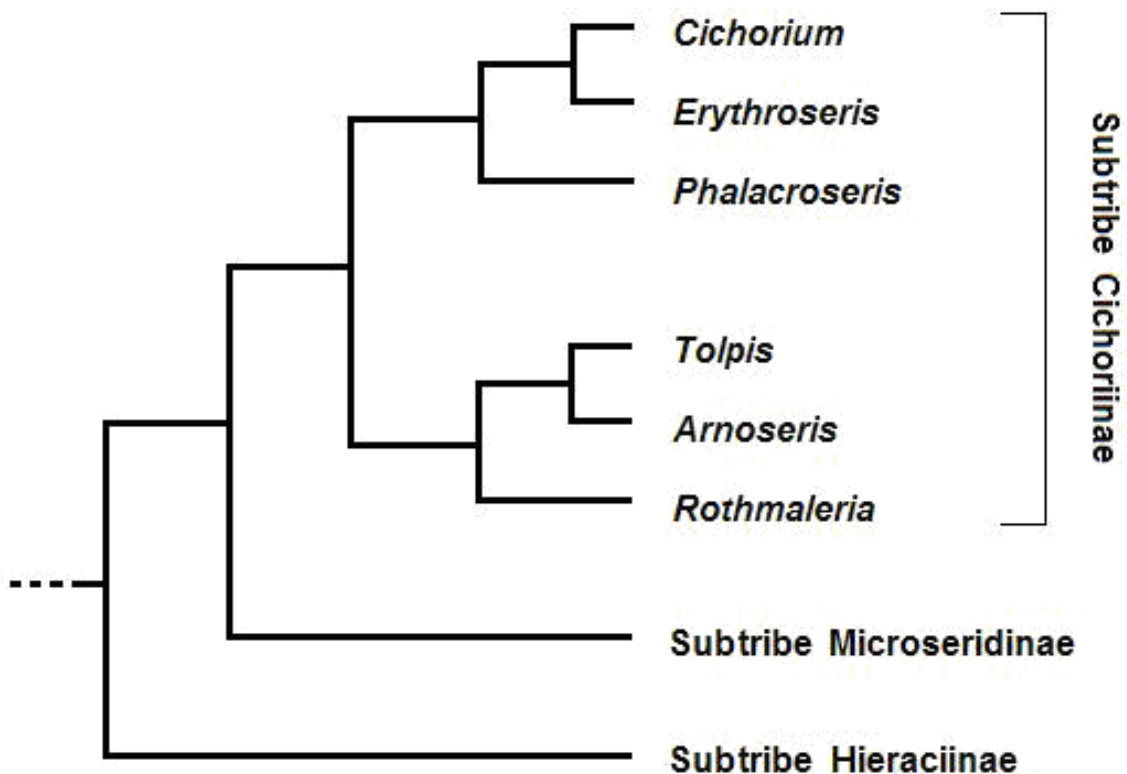
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## Phylogeny

According to recent phylogenetic studies of the subtribe *Cichoriinae* is part of a monophyletic clade ("well-supported") together with the sub-tribe of the *Hieraciinae* and *Microseridinae* s.l. (*sensu lato*) always belong to the tribe of *Cichorieae*.

Four of these genera (*Arnoseris*, *Cichorium*, *Rothmaleria*, and *Tolpis*) were already gathered in a single group in 1953, but not correlated with other genres. In more recent times, but before the recent studies, have been described in various groups: the genus *Arnoseris* in subtribe *Hypochaeridinae*; the genus *Phalacroseris* in subtribe *Microseridinae*; the kind *Rothmaleria* in subtribe *Catananchinae*; the genus *Tolpis* in subtribe *Hieraciinae*. Only recently (2007) were added to the other two genera form the subtribe as currently circumscribed. The six genera are divided into two sub-monophyletic clades supported by results obtained by molecular analysis on chloroplast but also from different morphological type cladistic analysis. Some doubts are raised about the taxonomic position of the genus *Phalacroseris*; position based solely on molecular data that should be reinforced by further studies morphological and phytogeographical.

The shown below cladogram of the subtribe (on the side and from the study cited) shows the phylogenetic relationships of the six genera including the two neighboring subtribe.



This group includes 2 neighboring subtribes, 6 genera and about 25 species:

*Arnoseris* Gaertn., 1791, with the specie *Arnoseris minima* (L.) Schweigger & Koerte;

*Cichorium* L., 1753 with 6 species;

*Erythroseris* N. Kilian & Gemeinholzer, 2007, with 2 species;

*Phalacroseris* A. Gray, 1868, with the specie *Phalacroseris bolanderi* A. Gray;

*Rothmaleria* Font Quer, 1940, with the specie *Rothmaleria granatensis* (Boiss. ex DC.) Font Quer;

*Tolpis* Adans., 1763, with 6 species belonging.