ANGIOSPERM PHYLOGENY

Flowering Plant Systematics

EARLY ANGIOSPERMS

woody; vessels absent
eustele
sieve tube plastids with starch grains
lvs simple, persistent, entire
flw strobilar, perfect, parts free
P parts varying, often in threes, weakly differentiated
anthers tetrasporangiate
stamen with broad filaments
pollen monosulcate
G apocarpous (style short in most)
compitum (if present) extragynoecial
nectaries absent
siphonogamy
double fertilization > endosperm
embryo very small

ethereal oils in spherical idioblasts (pellucid dots)
tension wood +

benzylisoquinoline alkaloids
embryo sac 8-nucleate
endosperm triploid

ANA GRADE

Characters	No.	Order	Families
woody, vessels lacking; dioecious; flw T5–8, A∞, G5–8, 1 ovule/carpel, embryo sac 9-nucleate; 1 species (New Caledonia)	1/1/1	AMBORELLALES	Amborellaceae
aquatic, herbaceous; cambium absent; aerenchyma; flw T4–12, A1–∞, embryo sac 4-nucleate; seeds operculate with perisperm but endosperm reduced or small; mucilage; alkaloids (no benzylisoquinolines)	3/6/74	NYMPHAEALES	Cabombaceae, Hydatellaceae, Nymphaeaceae
woody, vessels solitary; flw T>10, A∞, G ca.9, embryo sac 4-nucleate; tiglic acid, aromatic terpenoids	3/5/100	AUSTROBAILEYALES	Austrobaileyaceae, Schisandraceae (*incl.* Illiciaceae), Trimeniaceae
lvs opposite, interpetiolar stipules; nodes swollen; flw small T0–3, A1–5, G1, 1 apical ovule/carpel	1/4/75	CHLORANTHALES	Chloranthaceae

MAGNOLIIDS

features as in "Early Angiosperms"

sesquiterpenes; nodes trilacunar

Characters	No.	Order	Families
woody; foliar sclereids, K and C distinct; aromatic terpenoids	2/10/100	CANELLALES	Canellaceae, Winteraceae
± herbaceous; lvs two-ranked, leaf base sheathing; single adaxial prophyll; swollen nodes	4/17/4090	PIPERALES	Aristolochiaceae (*incl.* Hydnoraceae), Piperaceae, Saururaceae
woody; lvs opposite; flw with hypanthium, staminodes frequent; often valvate anthers; carpels with 1 ovule; embryo large	7/91/2858	LAURALES	Calycanthaceae, Gomortegaceae, Hernandiaceae, Lauraceae, Monimiaceae, Siparunaceae
woody; pith septate; lvs two-ranked; ovules with obturator; endosperm ruminate	6/154/2829	MAGNOLIALES	Annonaceae, Degeneriaceae, Eupomatiaceae, Himantandraceae, Magnoliaceae, Myristicaceae

MONOCOTS

extrafloral nectaries

scattered bundles in stem
no secondary thickening
mostly herbaceous
pollen monosulcate
sieve tube plastids with protein crystals
sympodial branching
lvs parallel-veined, entire
no glandular teeth
flw pentacyclic
P 3-merous, A opp. P
filaments narrow
anthers broadly attached
septal nectary
single cotyledon
radicle not persistent
stem-borne roots numerous

Ca oxalate raphides; endosperm nuclear helobial

Characters	No.	Order	Families
infl spadix with spathe; lvs axils with mucilaginous intravaginal squamules; ovules atropous, seeds with epidermal perisperm and copious endosperm; ethereal oils	1/1/2-4	ACORALES	Acoraceae
mostly herbs and aquatics; rhizomatous; hydrophilous; intravaginal squamules; infl ± scapose; flw G apocarpous; placentation often laminar; endosperm helobial; embryo large/green	14/166/4560	ALISMATALES	Alismataceae, Aponogetonaceae, Araceae, Butomaceae, Hydrocharitaceae, Juncaginaceae, Posidoniaceae, Potamogetonaceae, Ruppiaceae, Scheuchzeriaceae, Tofieldiaceae, Zosteraceae
stem with ring of bundles; fr a follicle; East Asia	1/2/4	PETROSAVIALES	Petrosaviaceae
often twining vines; lvs often reticulate; ovary often inferior, style short, branched; steroidal sapogenins/alkaloids	5/21/1037	DIOSCOREALES	Burmanniaceae, Dioscoreaceae, Nartheciaceae, Taccaceae
some woody (with terminally tufted leaves); infl sometimes spathe + spadix	5/36/1345	PANDANALES	Cyclanthaceae, Pandanaceae, Triuridaceae, Velloziaceae
often geophytes (bulbs, tubers, rhizomes); leaf bases often not sheathing; flw tepals sometimes spotted, nectaries on tepals, anthers extrorse; many seeds; phytomelan lacking; fructans in stems, chelidonic acid	10/67/1558	LILIALES	Alstroemeriaceae, Colchicaceae, Corsiaceae, Liliaceae, Melanthiaceae, Petermanniaceae, Philesiaceae, Smilacaceae
often geophytes; capsule or berry; seed coat obliterated or with phytomelan	14/1122/36205	ASPARAGALES	Amaryllidaceae (*incl.* Agapanthaceae, Alliaceae), Asparagaceae (*incl.* Agavaceae, Hyacinthaceae, Ruscaceae), Tecophilaeaceae, Hypoxidaceae, Lanariaceae, Asphodelaceae (*incl.* Xanthorrhoeaceae, Hemerocallidaceae), Iridaceae, Orchidaceae

COMMELINIDS

UV-fluorescing cell walls (ferulic/coumaric acids)
silicic acid in leaves
cuticular waxes often in rodlets aggregated into scallops

Characters	No.	Order	Families
woody, often monopodial; lvs often palmately or pinnately pseudocompound, reduplicate-plicate; intense primary growth, large apical meristem, infl often with spathe; alkaloids	2/192/2585	ARECALES	Arecaceae, Dasypogonaceae
mostly herbaceous; epidermis siliceous; mostly mycorrhiza absent; lvs grassy; flw often anemophilous, minute, chaffy, without nectaries	15/997/18875	POALES	Bromeliaceae, Cyperaceae, Eriocaulaceae, Juncaceae, Poaceae, Rapateaceae, Restionaceae, Typhaceae (*incl.* Sparganiaceae), Xyridaceae
flw monosymmetric or not, few fertile stamens; infl thyrsus of scorpioid cymes; phenylphenalenones	5/68/812	COMMELINALES	Commelinaceae, Philydraceae, Haemodoraceae, Pontederiaceae, Hanguanaceae
rhizomatous, large-leafed herbs; pseudostem common; flw irregular/monosymmetric, septal nectaries; A often strongly modified/reduced, G inferior; seeds often arillate, silicic acid	8/92/2185	ZINGIBERALES	Cannaceae, Costaceae, Heliconiaceae, Lowiaceae, Marantaceae, Musaceae, Strelitziaceae, Zingiberaceae

Characters	No.	Order	Families
aquatic; herbaceous; monoecious; lvs whorled, no pellucid dots; vessels lacking; flw T0 or 9–10*, A1, G1, 1 apical ovule/carpel; pollen inaperturate, pollen tube branched, hydrophilous	1/1/2	CERATOPHYLLALES	Ceratophyllaceae

EUDICOTS

ethereal oils not in idioblasts

pollen tricolpate
protandry common
flw K/C/P opp A
filaments rather narrow
nodes 3:3
stomata anomocytic
microsporogenesis simultaneous

receptacular nectary common; benzylisoquinolines absent

Characters	No.	Order	Families
lvs often divided; flw parts whorled, P single or multiple whorls; G apocarpous/paracarpous, superior; berberines	7/199/4510	RANUNCULALES	Berberidaceae, Circaeasteraceae, Eupteleaceae, Lardizabalaceae, Menispermaceae, Papaveraceae, Ranunculaceae
mostly woody; flw tepals often 4-merous; A epitepalous, connectives sometimes with apical appendage	4/85/1750	PROTEALES	Nelumbonaceae, Platanaceae, Proteaceae, Sabiaceae
woody; vessels lacking; flw tepals missing, A∞; G>5 laterally connate with abaxial nectaries; fr aggregate of follicles	1/2/2	TROCHODENDRALES	Trochodendraceae
mostly woody; mostly monoecious, flw unisexual; lvs evergreen, stomata cyclocytic; flw tepals ± uniform or missing; pregnane pseudoalkaloids	1/7/120	BUXALES	Buxaceae (*incl.* Haptanthaceae)

CORE EUDICOTS

ellagic and gallic acids

Characters	No.	Order	Families
dioecious, flw unisexual; lvs toothed, sec. veins palmate; flw tepals small to lacking; ellagic acid	2/2/50	GUNNERALES	Gunneraceae, Myrothamnaceae

PENTAPETALAE

flw 5-merous
parts whorled
K + C free
diplostemonous
pollen tricolporate
G connate
style +
endosperm nuclear

Characters	No.	Order	Families
mostly woody; lvs if veins strong, proceed to apex of teeth; flw mostly K5, persisting, mostly A∞, G mostly slightly connate; seeds often with aril; fr usually follicles	1/10/300	DILLENIALES	Dilleniaceae

SUPERROSIDS

Characters	No.	Order	Families
lvs with glandular teeth; often hypanthium, apically unfused carpels, stigma decurrent; fr mostly dry, dehiscent; myricetin, flavonols	15/112/2500	SAXIFRAGALES	Altingiaceae, Cercidiphyllaceae, Crassulaceae, Cynomoriaceae, Daphniphyllaceae, Grossulariaceae, Haloragaceae, Hamamelidaceae, Iteaceae, Peridiscaceae, Paeoniaceae, Saxifragaceae

ROSIDS

stipules

Characters	No.	Order	Families
often tendrillar vines; lvs often divided and with glandular teeth; A epipetalous, 2 ovules per carpel; raphides, pearl glands; berries	1/14/850	VITALES	Vitaceae

FABIDS

Characters	No.	Order	Families
cork origin deep-seated; endosperm lacking; resinous, lignans/neolignans, harman alkaloids	2/24/345	ZYGOPHYLLALES	Krameriaceae, Zygophyllaceae
infl cymose, flw small; G often 3-merous, nectary often intrastaminal disk; seeds often arillate (red-orange) or winged	2/94/1355	CELASTRALES	Celastraceae (*incl.* Hippocrateaceae, Brexiaceae, Parnassiaceae), Lepidobotryaceae

COM clade

Characters	No.	Order	Families
lvs often compound, pulvini (sleep movement); flw A5 or multiple, branched style common; mucilage cells; oxalates	7/60/1815	OXALIDALES	Brunelliaceae, Cephalotaceae, Connaraceae, Cunoniaceae, Elaeocarpaceae, Huaceae, Oxalidaceae
habits and habitats extremely diverse; lvs margins toothed; flw G often tricarpellate	36/716/16065	MALPIGHIALES	Achariaceae, Chrysobalanaceae, Clusiaceae, Erythroxylaceae, Euphorbiaceae, Hypericaceae, Linaceae, Malpighiaceae, Rafflesiaceae, Passifloraceae, Phyllanthaceae, Picrodendraceae, Ochnaceae, Podostemaceae, Rhizophoraceae, Salicaceae, Violaceae

N fix; embryo large, endosperm scanty

Characters	No.	Order	Families
flw often "papilionaceous": wing, standard, keel, C clawed, mostly G1; mostly A10; fr a pod; symbiosis with root nodule bacteria; diverse alkaloids, NP amino acids, lectins (in Fabaceae)	4/754/20140	FABALES	Fabaceae, Polygalaceae, Quillajaceae, Surianaceae
lvs mostly simple with stipules; flw K valvate (and hypanthium) persisting; carpels with 1 ovule, stigma dry; dihydroflavonols	9/261/7725	ROSALES	Barbeyaceae, Cannabaceae, Dirachmaceae, Elaeagnaceae, Moraceae, Rhamnaceae, Rosaceae, Ulmaceae, Urticaceae (*incl.* Cecropiaceae)
lvs mostly alternate; flw often unisexual, G mostly inferior; parietal placentation; cucurbitacins	7/129/2320	CUCURBITALES	Apodanthaceae, Anisophyllaceae, Begoniaceae, Coriariaceae, Corynocarpaceae, Cucurbitaceae, Datiscaceae, Tetramelaceae
mostly trees; lvs mostly undivided; flw small, unisexual; anemophilous, thus T reduced or lacking, G mostly inferior; infl spikes or catkins; fr 1-seeded, mostly nuts; ectomycorrhiza; tannins, dihydroflavonols	7/33/1055	FAGALES	Betulaceae, Casuarinaceae, Fagaceae, Juglandaceae, Myricaceae, Nothofagaceae, Ticodendraceae

MALVIDS

Characters	No.	Order	Families
stems sometimes jointed at nodes; lvs with glandular teeth; flw A obdiplostemonous, nectary outside A; fr capsule; ethereal oils, ellagic acid	2(5)/17/836	GERANIALES	Geraniaceae, Francoaceae (*incl.* Ledocarpaceae, Melianthaceae, Vivianiaceae)
lvs opposite, colleters (glandular hair on adaxial surface of petiole base); stipules small (if any), cork deep seated; flw K valvate, persisting, A incurved in bud, ovary inferior, ovules many; endosperm scanty, scaly bark, flavonols, myricetin	9/380/11731	MYRTALES	Combretaceae, Myrtaceae, Penaeaceae (*incl.* Oliniaceae), Lythraceae (*incl.* Punicaceae, Sonneratiaceae, Trapaceae), Melastomataceae (*incl.* Memecylaceae), Onagraceae, Vochysiaceae
woody; stylodia free; hypanthium with nectary	7/12/66	CROSSOSOMATALES	Crossosomataceae, Geissolomataceae, Stachyuraceae, Staphyleaceae, Strasburgeriaceae
trees, dioecious, lvs compound, extrafloral nectaries; staminate flw: A = and opposite C; bark bitter, anthraquinones	1/3/49	PICRAMNIALES	Picramniaceae
mostly woody (silica/silicified); lvs often alternate, odd-pinnately compound; flw often imperfect, intrastaminal disk, ethereal oils	9/471/6700	SAPINDALES	Anacardiaceae, Biebersteiniaceae, Burseraceae, Kirkiaceae, Meliaceae, Nitrariaceae, Rutaceae, Sapindaceae, Simaroubaceae

embryo large; endosperm scanty

Characters	No.	Order	Families
vessel elements with scalariform perforations; mucilage cells; lvs margins toothed, stipules cauline; flw small, A = and opposite K, ovules 1-2/carpel	4/6/24	HUERTEALES	Dipentodontaceae, Gerrardinaceae, Petenaeaceae, Tapisciaceae
bark fibrous; hairs often stellate; flw K often valvate, petals contorted, A often ∞; mucilage; cyclopropenoid fatty acids, flavones	10/338/6000	MALVALES	Bixaceae, Cistaceae, Dipterocarpaceae, Malvaceae (*incl.* Bombacaceae, Sterculiaceae, Tiliaceae), Cytinaceae, Neuradaceae, Muntingiaceae, Sphaerosepalaceae, Sarcolaenaceae, Thymelaeaceae
woody or herbs; flw often 4-merous; often clawed petals, infl racemose; myrosin cells, glucosinolates	18/398/4765	BRASSICALES	Bataceae, Brassicaceae, Capparaceae, Caricaceae, Cleomaceae, Koeberliniaceae, Limnanthaceae, Moringaceae, Resedaceae, Salvadoraceae, Tovariaceae, Tropaeolaceae

SUPERASTERIDS

Characters	No.	Order	Families
woody; lvs stomata cyclocytic; petiole bundles annular; fr indehiscent, more or less fleshy; calcium oxalate as crystals	2/3/4	BERBERIDOPSIDALES	Aextoxicaceae, Berberidopsidaceae
woody; (semi-)parasites; mycorrhiza absent; lvs margins entire; flw A epipetalous; perianth often simple, valvate, persisting; carpels/ovaries/ovules often reduced, placentation free-central; fr drupe, one-seeded; polyacetylenes, triterpene sapogenins, silicic acid	13/151/1992	SANTALALES	Balanophoraceae, Loranthaceae, Misodendraceae, Olacaceae, Opiliaceae, Santalaceae, Schoepfiaceae, Viscaceae
mostly herbaceous; without mycorrhiza; G often unilocular with free-central placentation; pollen colpate, surface spiny; betalains or anthocyanins (latter, e.g., in Caryophyllaceae)	37/749/11600	CARYOPHYLLALES	Aizoaceae, Amaranthaceae (*incl.* Chenopodiaceae), Basellaceae, Cactaceae, Caryophyllaceae, Didiereaceae, Droseraceae, Drosophyllaceae, Frankeniaceae, Molluginaceae, Nepenthaceae, Nyctaginaceae, Phytolaccaceae, Plumbaginaceae, Polygonaceae, Portulacaceae, Simmondsiaceae, Talinaceae, Tamaricaceae

seed exotestal; embryo long

ASTERIDS

mostly sympetalous
C enclosing A and G in bud
G(2)
style single, long
nectary gynoecial
ovules unitegmic
endosperm cellular
iridoids +

Characters	No.	Order	Families
mostly woody; lvs mostly undivided, hydathode teeth; flw often 4-merous, K much smaller than C, persisting; intrastaminal disk, G inferior; fr drupaceous; diverse iridoids	6/51/590	CORNALES	Cornaceae, Curtisiaceae, Grubbiaceae, Hydrangeaceae, Hydrostachyaceae, Loasaceae, Nyssaceae
lvs teeth often theoid; nodes unilacunar; flw 5-merous, pentacyclic; nonhydrolyzable tannins, ellagic acid, triterpenoids, hydroquinones	22/346/11545	ERICALES	Actinidiaceae, Balsaminaceae, Clethraceae, Ebenaceae, Ericaceae, Fouquieriaceae, Lecythidaceae, Myrsinaceae, Polemoniaceae, Primulaceae, Roridulaceae, Sapotaceae, Sarraceniaceae, Styracaceae, Theaceae, Theophrastaceae

A=C, polyandry rare; infl cymose, fr a drupe, seed single, ellagic acid lacking

LAMIIDS

late sympetaly

Characters	No.	Order	Families
tropical trees; lvs exstipulate/entire; nodes often unilacunar; pedicels articulated; style short; embryo long; endosperm copious; indole and quinoline alkaloids (camptothecin)	2/24/202	ICACINALES	Oncothecaceae, Icacinaceae
tropical trees; few common features; nodes usu. trilacunar; *Metteniusa*: NE Andes, cloud montane forest; lvs alternate; flw bisexual, fragrant; anthers sagittate; pollen sacs moniliform, dehisce longitudinally; infl axillary cyme; G(5) unilocular	1/1/55	METTENIUSALES	Metteniusaceae
woody; dioecious; flw small, C valvate, G unilocular; fruit indehiscent; iridoids (aucubin), gutta	2/3/18	GARRYALES	Eucommiaceae, Garryaceae (*incl.* Aucubaceae)
lvs spiral, simple; nodes unilacunar; flw petals plicate; K persisting; diverse alkaloids, no iridoids	5/165/4125	SOLANALES	Convolvulaceae (*incl.* Cuscutaceae), Hydroleaceae, Montiniaceae, Solanaceae (*incl.* Nolanaceae), Sphenocleaceae
herbaceous; Africa to India; lvs opposite, glandular-pubescent; flw < 5 mm across, K valvate, G(3) inf, nectary; fr septicidal capsule, K/C/A persistent; seeds minute; iridoids	1/1/8	VAHLIALES	Vahliaceae
lvs opposite, colleters; flw corolla convolute in bud; indole alkaloids; iridoids	5/1118/19840	GENTIANALES	Apocynaceae (*incl.* Asclepiadaceae), Gentianaceae, Gelsemiaceae, Loganiaceae, Rubiaceae
lvs opposite; nodes 1:1; flw mostly monosymmetric; A often 2(+2); gland-headed hairs with radially arranged cells; 6-oxygenated flavones, oligosaccharides cornoside, verbascoside (acetoside)	24/1059/23810	LAMIALES	Acanthaceae, Bignoniaceae, Byblidaceae, Gesneriaceae, Lamiaceae, Lentibulariaceae, Martyniaceae, Oleaceae, Orobanchaceae, Paulowniaceae, Pedaliaceae, Phrymaceae, Plantaginaceae, Scrophulariaceae, Stilbaceae, Verbenaceae
lvs roughly hairy; nodes unilacunar; infl scorpioid; mostly 4 ovules; isokestose, higher inulins, pyrrolizidine alkaloids	6-11/150/3095	BORAGINALES	Boraginaceae, Codonaceae, Coldeniaceae, Cordiaceae, Ehretiaceae (+ Lennoaceae), Heliotropiaceae, Hydrophyllaceae, Namaceae, Wellstediaceae

C forming distinct tube; A epipetalous

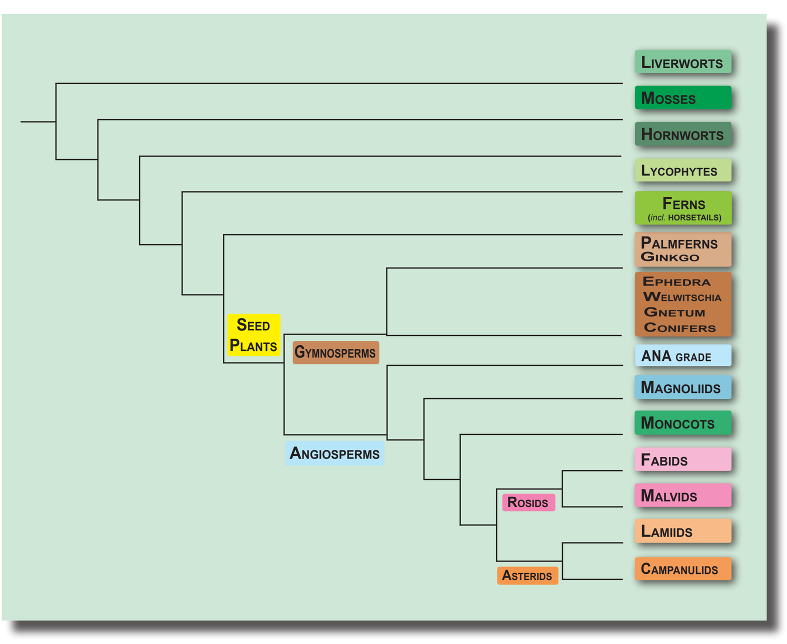
CAMPANULIDS

early sympetaly; flw small; embryo short

Characters	No.	Order	Families
woody; lvs serrate; flw 1-2 ovules/carpel, C± free, K slightly connate; fr usually drupe with broad stigma	5/21/536	AQUIFOLIALES	Aquifoliaceae, Cardiopteridaceae, Stemonuraceae
herbs or shrubs; flw often monosymmetric; plunger sec. pollination device (long style); nodes trilacunar; inulin, sesquiterpenes, secoiridoids	11/1743/26870	ASTERALES	Asteraceae, Calyceraceae, Campanulaceae (*incl.* Lobeliaceae), Goodeniaceae, Menyanthaceae, Pentaphragmataceae, Rousseaceae, Stylidiaceae
mostly woody; infl racemose, C free; anthers basifixed, nectary disc	1/9/130	ESCALLONIALES	Escalloniaceae
woody; evergreen; nodes 1:1; flw polysymmetric, anthers basifixed	2/14/79	BRUNIALES	Bruniaceae, Columelliaceae (*incl.* *Desfontainia*)

G inferior; fr usually 1–few-seeded

Characters	No.	Order	Families
woody (except Apiaceae); lvs often divided; nodes usu. multilacunar; infl mostly umbel; drupe or schizocarp (Apiaceae: mericarp/carpophore)	7/494/5489	APIALES	Apiaceae, Araliaceae, Griseliniaceae, Myodocarpaceae, Pennantiaceae, Pittosporaceae
woody; infl racemose, flw 4-merous; filaments stout; capsule septicidal	1/3/36	PARACRYPHIALES	Paracryphiaceae
lvs opposite, often basally connate; buds with scales; flw often monosymmetric; K persistent in fruit; secoiridoids	2/46/1090	DIPSACALES	Caprifoliaceae (*incl.* Dipsacaceae, Diervillaceae, Linnaeaceae, Morinaceae, Valerianaceae), Adoxaceae



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- hypothetical tree based on molecular phylogenetic data (Dec. 2016)
- phylogeny, classification, and features chiefly follow APweb and APG
- 64 orders and around 420 families currently recognized by APG IV (some minor families excluded here)
- contrary to APG, but in compliance with APweb and other seminal sources, we here recognize several families within Boraginales
- branch lengths deliberate, not expressing actual time scale
- the characters listed do not necessarily apply to all members of the according clade
- position of various characters on the tree uncertain
- for family characteristics see: FGVP, Kubitzki K, ed. (1990 ff)
- orders (and higher ranks) are linked to the according pages on APweb
- numbers set in gray next to orders refer to families, genera, and species

* *Ceratophyllum*: the alleged tepals could be bracts (issue being addressed in ongoing research and debate); ** Rosids: phylogeny within the group controversial

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References: Stevens PF (2017) APweb – www.mobot.org/MOBOT/research/APweb
APG IV (2016); Judd W et al. (2016); Simpson M (2010); Soltis DE et al. (2005/2011/2014); Watson/Dallwitz (2016) delta-intkey.com/

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