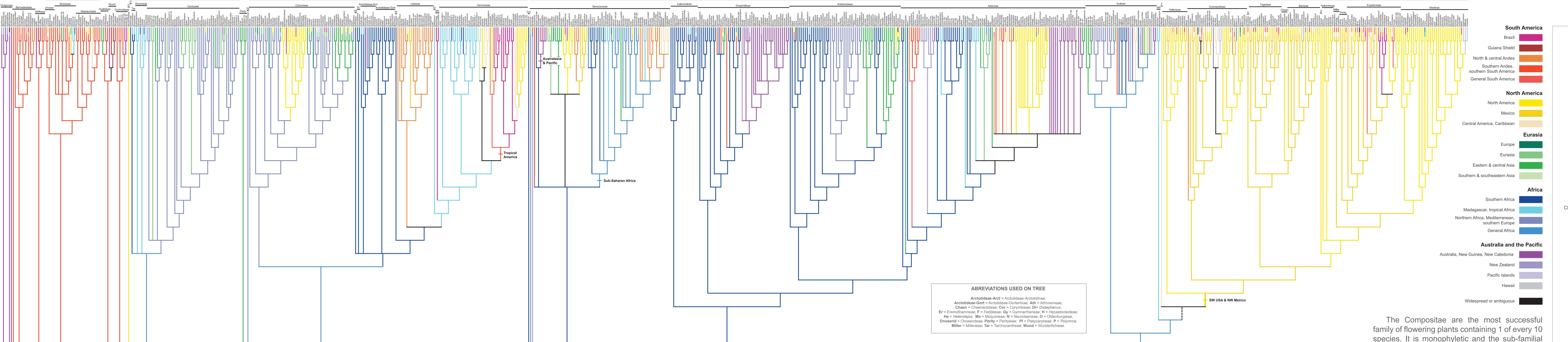
## COMPOSITAE CLASSIFICATION: REVISITED, REEVALUATED, REEVERYTHINGED

**SUMMARY TREE** 

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CALYCERACEAE

endemic to southern South America.

**bution:** Bolivia and Argentina.

Unique or diagnostic features include: annual or perennial herbs, with

the flowers in capitula surrounded by the involcral bracts; calyx not modi-

fied; anthers connate but free; ovules' insertion apical. Distribution:

are endemic to Brazil and one is endemic to French Guiana.

Inique or diagnostic features include: woody plants of south-central

South America with leaves clustered in brachyblasts; heads ligulate. Distri-

Unique or diagnostic features include: woody plants with zygomorphic

or bilabiate corollas; 2-cleft inner lip that is often much coiled and so is

shorter than outer lip; and styles bifid and dorsally smooth. Distribution:

predominantly on the Guiana Shield with one monotypic genus in the Do-

Inique or diagnostic features include: involucral bracts imbricate; corollas often brightly colored; ray corolla bilabiate (rarely absent); disc corollas tubular with 5 lobes equal or unequal in length; anther apical appendage acute or truncate, thecae calcarate and caudate; styles thick, pex rounded, glabrous, rarely papillose; achenes elliptical to turbinate.

glabrous or pubescent; and pappus of 2–4-seriate bristles. **Distribution**: southern South America but also in the Andes.

Unique or diagnostic features include: corollas often brightly colored; marginal corollas usually bilabiate; disc corollas bilabiate or tubular, shallowly lobed, lobes equal to unequal; anther apical appendage not constricted or demarcated; anthers ecalcarate and caudate; and style shallowly bilobed to bifid, rounded at the apex, usually dorsally papillose only above the style bifurcation point, papillae rounded, never acute. Distribution: predominately southern South America with outliers in Africa

Unique or diagnostic features include: all corollas bilabiate; style apex truncate, the only pubescence is on the arms, which have a unique apica crown of sweeping hairs; pollen exine distinctly bilayered, with the ectosexine and the endosexine clearly columellate. **Distribution:** mostly southern

Unique or diagnostic features include: paired axillary spines frequently resent; absence of short, stalked, capitate glands (sesquiterpenes ent, bilabiate; central corollas tubular, deeply lobed; anther apical appendlacking); filaments free or rarely fused; absence of twin hairs on achenes, instead they have "barnadesioid trichomes"; involucral bracts often spineages apiculate; styles glabrous; and pappus of 2- or 3-seriate, scabrid or tipped. Distribution: southern South America, the Andes, and Brazil. ccasionally plumose at the apex capillary bristles with a reduced number outer shorter bristles. **Distribution:** South America and Asia.

Unique or diagnostic features include: heads discoid; pappus showy, whitish, yellowish or reddish with ca. 100 capillary bristles in 4-5 series; Unique or diagnostic features include: woody; leaves clustered near florets actinomorphic, white with corolla lobes rolled; and styles glabrous, stem apex, actinomorphic corollas; styles smooth or slightly asperulous shallowly divided, apex rounded to shortly acute. Distribution: five species at apex, dorsally papillose or dorsally rugulose to papillose much below the bifurcation point. **Distribution:** Guiana Shield and Brazil.

> Unique or diagnostic features include: marginal corollas, when present, pilabiate; disc corollas tubular, deeply lobed; anther apical appendages tates to Argentina and the Caribbean (especially Cuba).

apiculate; and styles glabrous. **Distribution:** America, from southern United Unique or diagnostic features include: stiff holly-like leaves; tricolpate

pollen; heads that are single-flowered and re-aggregated on a secondary

spiny whitish or greenish bract. Distribution: restricted to high elevation

areas (1500–2000 m) in southern Nevada and adjacent California including

receptacle, each group of 1–5 heads being subtended by a relatively large

ranean ones and two different types of achenes; corollas 3-4-lobed; 3-4 anthers; and aerial heads clustered together and with functional male and female florets. Distribution: deserts in northern Africa and the Middle East. Inique or diagnostic features include: almost exclusive presence

Unique or diagnostic features include: woody plants with coriaceous

leaves; large heads; bilabiate corollas; and short rounded style branches.

Unique or diagnostic features include: dioecious trees or shrubs often

omatic with small discoid capitula of ca. 30 florets and heads that are

rranged in generally dense racemes or panicles. Distribution: tropical

Africa (mainly in the eastern part), Madagascar, and southern Africa, and

Unique or diagnostic features include: pungent phyllaries without resin

ducts (or ducts reduced); presence of star-shaped calcium oxalate crystals

in the corollas, anther filaments and styles; anther tails long tapering; pollen

slightly echinate; style branches straight and adjacent; and achenes broadly

tion: tropical and southern Africa, including Madagascar and two species

bconic to cylindrical with twin hairs and without a carpopodium. Distribu-

nique or diagnostic features include: involucral bracts usually in

five rows and spiny-tipped; leaves often spiny; style cylindrical with a

hairs; anthers often with laciniate basal appendages, anther filaments

elaborate mechanism of pollen presentation. Distribution: widespread

in Eurasia, especially diverse in the Mediterranean region where they

constitute an important characteristic of the vegetation; some species

Inique or diagnostic features include: small discoid heads of white,

oink, rose or purple florets; corollas irregularly deeply 5-lobed and there-

ore zygomorphic by having one sinus deeper than the others, appearing

ortly branched, dorsally pilose to shortly pilose. **Distribution:** southeast

pseudo-bilabiate or pseudoligulate; and styles thick, branches bilobed to

Unique or diagnostic features include: ephemeral, dwarf desert annual,

amphicarpic; both chasmogamous aerial heads and cleistogamous subter-

nickened articulation below the branches bearing a short collar of stiff

sually papillose; and stamens often strongly thigmotropic, making up an

one species also present in the Arabian Peninsula

tion: tropical and southern Annea, moreaning and range outward to the Arabian Peninsula, India, and Pakistan.

are cosmopolitan weeds.

Distribution: South Africa.

**TARCHONANTHEAE** 

Unique or diagnostic features include: alternate leaves with pinnate venation, often with T-shaped or stellate hairs; heads without rays; corollas mostly blue to reddish or purple; slender tapering style branches, long weeping hairs on outside extending onto upper style shaft; achenes usuhomogamous capitula with 5-dentate, ligulate flowers; and exclusive ally with twin hairs, rarely with phytomelanin in walls, usually with raphids; pollen sublophate or lophate; and anther endothecial cells with thickenings esence of lactiferous canals in both the subterranean and aerial parts. **Distribution:** nearly global with centers of diversity in the Mediterranean on upper and lower ends; rich in sesquiterpene lactones, one group with 5-alkyl-coumarins. **Distribution:** tropical and southern Africa, southeast area and north temperate climates.

Unique or diagnostic features include: ray florets that generally have staminoides and a filiform lobe ventrally in the sinus of the tube; pappus of bristle-like scales which form a pom-pomlike shape in older heads; small achenes covered with dense white twin hairs; and partially connate involucral bracts. **Distribution:** three species endemic to South Africa, mostly in the Cape Floristic Region.

Unique or diagnostic features include: slender style branches bearing relatively long sweeping hairs divided longitudinally into two or three cells; pollen spinulose with larger spines in intercolpi and smaller crowded spines around poles; and involucral bracts multiseriate, gradate, distally papyraceous and usually with apical spine. Distribution: western South

> RCTOTIDEAE - Arctotidinae nique or diagnostic features include: radial anther endothecium, nconspicuous anther collar; apically thickened styles, small, patent and broadly subulate sweeping hairs; and pappus scale cells very long and with abaxially reinforced walls. **Distribution:** mainly southern Africa.

nique or diagnostic features include: latex; connate involucral bracts; eeply alveolate receptacles; 4-lobed, sterile ray florets; and disc corolla obes with sclerified margins. **Distribution:** southern Africa.

> PLATYCARPHEAE Inique or diagnostic features include: complicated secondary head ructures; leaves that are elongate and prostrate; stolons that emanate rom the crown at the base of the secondary head; secondary head and aves lying more or less flat on the ground; anthers purple; styles lavender; and pollen echinate with spines in a regular arrangement or in irregularly arranged ridges surrounding the colpi in a unique bowtie pattern. **Distribution:** three species in southern Africa.

> > Jnique or diagnostic features include: hairs simple; homogamous or

ynodioecious florets; anthers spurred; styles swollen distally with short

scabrae, continuous stigmatic surface inside; achenes without phytomela-

nin; pollen echinate, non-lophate, non-caveate, with non-aligned baculae;

leaf blades elliptical to obovate, with pinnate veins; endothecial cells with

thickenings at upper and lower ends. Distribution: restricted to Brazil.

Asia to Australia and the Pacific, and the Western Hemisphere.

tailed; and achenes small. **Distribution:** centers of diversity in southern Africa, Australia, New Zealand, and South America. Inique or diagnostic features include: leaves usually opposite; latex ANTHEMIDEAE

Unique or diagnostic features include: leaves generally variously dispresent in most taxa; corollas usually yellow; and pollen echinate. **Distribu**ion: tropical America with the vast majority in Peru and Ecuador. sected, rarely entire with characteristic aromatic smell; involucral bracts

with hyaline margin; no tails on anthers; tubular florets hermaphrodite or functionally male, tubular or funnel-shaped; upper part of the filament with cells with thickened walls, forming a split cylindrical or balusterform anther ollar (filament collar); and achenes without a carbonized layer, often with glandular hairs, mucilage cells and resin sacs/ducts. Distribution: mainly in southern Africa, central Asia, and the Mediterranean region.

Unique or diagnostic features include: tufted parallel-veined leaves from

a silky-hairy rhizome; involucres of 2 bracts; single-flowered capitula; and

elongated, densely hirsute ovary. **Distribution:** the area occupied by the

nique or diagnostic features include: uniseriate involucre (although not

universal); di-ester type pyrrolizidine alkaloids and the eremophilane types

achenes, but in ovules; in *Senecio* and many other genera of Senecioninae

of Tussilagininae have a continuous stigmatic surface. Distribution: world-

wide with the most marked center of diversity in South Africa, also with cen-

f sesquiterpene lactones; polyacetylenes lacking; raphids not in walls of

ne stigmatic surface is divided into two parallel bands, but most members

enestrate cavities and a fleshy exocarp. Distribution: mainly Africa with

distinct center in South Africa; only Calendula extending outside Africa

nto Macaronesia, South and Central Europe, and Anatolia eastwards to

naphalioid" pollen, with a 2-layered ectexine comprising an outer colu-

Unique or diagnostic features include: involucral bracts with a papery,

often brightly colored lamina and a cartilaginous basal part (stereome);

"gnaphalioid" pollen, with a 2-layered ectexine comprising an outer columellate layer and an irregularly interlaced basal layer; stems generally with fibers in phloem and without resin canals; leaves entire; anthers

genus coincides with the Cape Floristic Region in South Africa.

nique or diagnostic features include: receptacle usually naked; bracts -5 rows and usually imbricate; and style branches pronate, with acute opendage, scabrous or plumose on outer surface, stigmatic lines running up to base of lanceolate to triangular tip. **Distribution:** worldwide with major nters of diversity in Africa, North America, and Australia.

nique or diagnostic features include: heads usually radiate and

yellow-flowered; achenes with elongated crystal in each epidermal cell;

and acute sweeping hairs on style branches. **Distribution:** mainly Medi-

erranean, Saharo-Sindian, but also in East Africa.

Unique or diagnostic features include: combination of epaleate heads; pale or reddish (not blackened) anthers; blackened, striate, usually unflattened achenes; and pappus usually of basally thickened or costate scales or of fascicled or hooked bristles. **Distribution:** mainly southwestern North America (also temperate and montane South America, tropical Africa, and Unique or diagnostic features include: combination of opposite leaves;

uncompressed smooth achenes. **Distribution:** eastern North America. Unique or diagnostic features include: combination of paleate recepacles, with paleae enfolding ovaries; usually blackened anthers; style

apices terminated by tuft of papillae; achenes blackened, flattened; and pappus usually of awns or scales. **Distribution:** mainly warm temperate

paleate receptacles; functionally staminate disc florets; pale anthers; and

Unique or diagnostic features include: combination of usually opposite, often glandular leaves; scarious paleae; usually blackened anther thecae; more or less terete, usually striate, blackened achenes; and radially-arrayed (or absent) pappus scales or bristles. Distribution: mainly Mexico and northern Andes (also Old World tropics, especially Africa).

America (especially California).

Unique or diagnostic features include: combination of often glandular foliage; usually subequal phyllaries (often with one phyllary per ray ovary Unique or diagnostic features include: combination of alternate leaves; and with phyllary at least partially clasping ray ovary); epaleate or often partially paleate receptacle (with paleae limited to periphery of receptacle, etween ray and disc florets); often deeply 3-lobed ray corollas; often dark ourple (not blackened) anther thecae; often flattened ray achenes; and often striate, blackened disc achenes. **Distribution:** mainly western North

Unique or diagnostic features include: outer phyllaries differentiated from inner in color and shape, inner phyllaries with orange-brown striations (resin ducts); paleae with brownish-orange striations; and achenes flat obcompressed to quadrangular. **Distribution:** centered in North and South America. Unique or diagnostic features include: rupicolous herbs and shrubs; glandular foliage; subequal, usually navicular phyllaries; epaleate receptacles; usually 4-lobed disc corollas; pale, ecaudate anthers; smooth, blackened achenes; and pappus (if present) usually of (1-)2 bristles and rudimentary scales. **Distribution:** mainly deserts of southwestern North America (also Andes and Desventuradas Islands of South America).

> Unique or diagnostic features include: combination of alternate, often obed, leaves; discoid heads; epaleate receptacles; pale or reddish (not olackened) anthers; more or less terete (not fl attened), striate achenes; and unribbed and unthickened pappus scales, sometimes deciduous as a unit. Distribution: western and southwestern North America, mainly Cali-

Unique or diagnostic features include: all members of the tribe (with a few exceptions) have mono-ester type pyrrolizidine alkaloids secreted y nectaries; also with pentaynene acetylenes, some monoterpenes and sesquiterpene lactones, an ent-kaurine diterpene glycoside, kolavane devatives, chromenes, benzofurans; raphids in the achenes are completely lacking. Other diagnostic features: mostly opposite leaves; hairs simple; heads discoid; corollas actinomorphic and whitish to reddish or lavender (never yellow); anther appendages hollow or poorly developed; and style branches with enlarged "club shaped" appendages that are often the color of the corolla. Distribution: Western Hemisphere with a few pantropical

lassification and ideas about relationships withir the family remained largely unchanged until the

The results of recent broad-scale molecular studies of the tribes (involving > 40 collaborators) were used to produce a meta-tree formed by linking the respective trees together on a known base

By examining the distribution of the terminal taxa a biogeographical pattern emerges. The extant lineages from the basal grade are southern South American in origin followed by a subsequent radiation in Africa that gave rise to most of the tribes we know today. Nested in the African radiation are individual clades in Asia, Eurasia, Australia, The Americas, etc. Highly nested in the base tree there is a North American origin and diversification of the Heliantheae Alliance that involved repeated incursions into Mexico and South America. The South American radiation followed by the African explosion might suggest a Gondwanan origin for the family, but the few data that exist from pollen records and geology seem to indicate a more recent origin for the family. The existence of the monotypic genus Hecastocleis A. Gray inserts a North American taxon in between the South American basal grade and African radiations which might indicate long distance dispersal, or a North American or even Asian presence. The sister group to the western hemisphere clade Heliantheae Alliance is the small tribe Athroismeae, from eastern tropical Africa, leaving an unknown area, possibly Asia, between Africa and western

This global picture of the Compositae provides a framework for studies of characters such as pollen, corolla shape, chromosome number, phytochemestry, and many others. We now have a better picture of the origin and evolution of the Compositae.

Madieae • A-Gorteriinae Heterolepis A-Arctotidineae Platycarpheae • Gymnarrheneae Distephanus 👓 🛑 ( Vernonieae 🔼 Tarchonantheae Hecastocleideae o Cardueae Gochnatieae Stenopadus clade Wunderlichia -Leucomeris clade -Hyalis clade Dinoseris clade Nassauvieae Barnadesieae -

Circle size is indicative of number of species. A white circle indicates less than 100 taxa

The summary tree for the family shows the results of the parsimony mapping of the distributions. In this unrooted connsed tree it is even more evident that the extant Compositae had a South American base with African diversification and radiation into Asia, Eurasia, Europe, Australia, etc. followed by the bursts of diversification in North America. The unrooted diagram here presented provides greater clarity as to the biogeographic patterns of the phylogeny.

National Museum of Natural History



**bution:** confined to Cuba.

tion: mainly Africa and Australia.



Unique or diagnostic features include: stems fistulose and rooting at nodes or not; paleae tightly enfolding achenes in aquatic or marsh-dwelling taxa; receptacle usually paleate; anthers usually blackened; achenes blackened. Distribution: mainly Neotropics (few species in Paleo tropics).

nique or diagnostic features include: heads often purple-flowered

disciform with filiform; tubular florets; achenes without large epidermal

crystal; and style frequently with obtuse sweeping hairs extending below

Unique or diagnostic features include: heads sometimes in pseudoce

Unique or diagnostic features include: leathery entire leaves; heads

phalia, some achenes have phytomelanin; and anthers with tails. Distribu-

discoid, homogamous; involucres multiseriate, and bracts with resiniferous

ducts; florets hermaphroditic, corollas tubular, actinomorphic, white. Distri-

style bifurcation. **Distribution:** warm climate areas worldwide.

Unique or diagnostic features include: epaleate receptacles, most with glandular pockets (dark spots); characteristic smell (monoterpenes); and if glands lacking, then achenes usually strongly 9-15-ribbed. Distribution: warm temperate to tropical New World (1 sp. of Flaveria in Australia), mostly southwestern North America.

Extracted from: Funk, V. A., A. Susanna, T. F. Stuessy & R. J. Bayer. 2009. Systematics, Evolution, and Biogeography of Compositae. International Association for Plant Taxonomy: Vienna.

## **IMAGE CREDITS:** B. Baldwin, J. M. Bonifacino, T. Eriksson, V. A. Funk, C.A. Mannheimer, B. Nordenstam, N. Rogue, I. Ventosa.