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Illustrated glossary of Compositae

Nádia Roque, David J. Keil and Alfonso Susanna

Abaxial lip

Portion of the corolla limb of a bilabiate or pseudobilabiate corolla that is oriented away from the center of the head (Figs. 1A, 54A); the lamina of a ray corolla (Fig. 2) is homologous with the abaxial lip of a bilabiate or pseudobilabiate corolla. See **Adaxial lip.**

Achene

A single-seeded indehiscent dry fruit with the seed free from the pericarp except at the placenta; the fruit in almost all Compositae. Generally breaks free from the receptacle at maturity and often falls together with pappus elements, which are borne at distal end of the achene (Figs. 3-21, 32-35). Achenes may be pappose (bearing pappus elements; Fig. 3) or epappose (without a pappus) (Figs. 4, 5). Achenes in cross section may be terete (Fig. 6), prismatic (Fig. 7), compressed (laterally flattened; Fig. 8), or obcompressed (dorsiventrally flattened; Fig. 11), and may bear ribs (Fig. 9) or wings (Figs. 8, 10, 11). Longitudinally they range from narrowly cylindrical (Fig. 101) to fusiform (Figs. 12, 13), obovoid (Fig. 14), or globose (Fig. 5), and may be straight to strongly arcuate (e.g., Calendula). Surfaces may be glabrous, papillose, variously hairy (often with twin hairs, sometimes glandular), or may bear tubercles or prickles. Taxonomically important variations include the number of ribs or angles (Figs. 4, 7, 9); presence or absence or degree of development of basal attenuation (Fig. 16) or stipe (Figs. 17, 18) or of apical attenuation (beaked achene; Fig. 19); type of indument; differences in form of the abscission zone or carpopodium (Figs. 20, 21); and presence or absence of apical nectaries or basal elaiosomes. In Eupatorieae, Heliantheae and Tageteae, achenes are usually blackened (carbonized) by phytomelanin deposits (Figs. 32-34); in most Cardueae, some layers accumulate phytomelanins. The achenes of Compositae, derived from inferior ovaries, are often termed cypselas. See Cypsela, Pappus.

Achene complex

Unit of dispersal in which one or more achenes are dispersed together with adherent phyllaries and/or paleas and sometimes with non-fruiting florets. In some Compositae each ray achene falls together with a subtending phyllary. Spine-like appendages (e.g., Acanthospermum; Fig. 15) or glandular trichomes or appendages (e.g., many Madieae) on the phyllary may aid in epizoochory. In Berlandiera the achene complex comprises a ray achene that is dispersed together with a subtending phyllary, two paleas and two staminate disk florets. In *Pectis prostrata* Cav. the basally coherent phyllaries and all the enclosed achenes break free from the receptacle and are dispersed together. In Ambrosia and Xanthium all of the paleas are fused into a spiny, knobby, or winged bur containing one or two achenes. The flattened fruiting head of Delilia biflora (L.) Kuntze (Figs. 50, 51) falls as an anemochorously dispersed unit enclosing a solitary ray achene.

Actinomorphic

See Radial symmetry.

Adaxial lip

Portion of the corolla limb of a bilabiate or pseudobilabiate corolla that is oriented toward the center of the head (Figs. 1B, 54B). See **Abaxial lip.**

Aggregate heads

Heads tightly grouped without losing their individual identities (Fig. 22).

Alveolate receptacle

Receptacle surface more or less deeply pitted, with alveoles (cavities) partially or totally enclosing the achenes.

Androecium

Collective of all the stamens in a flower; the third whorl of parts of a complete flower. In Compositae the androecium comprises (3–)5 stamens alternating with corolla lobes, with their filaments inserted at junction of corolla tube and throat (Fig. 23).

Angled achene

Achene polygonal in cross section (Fig. 7). See **Prismatic** achene, Ribbed achene.

Anthemoid style

Style with a brush-like tuft of sweeping hairs at the tip of each style branch (Fig. 24).

Anther

The pollen-bearing portion of a stamen, borne at the distal tip of a filament. In Compositae each anther comprises four microsporangia that mature as two pollen sacs (thecas) united by a connective with a usually membranous distal appendage. The connective generally extends proximally of the attachment of the anther sacs as a cylindrical anther collar (Fig. 25). Anther bases can be rounded (Fig. 25), truncate, sagittate (Fig. 26) or cordate, or pollen-bearing basal lobes of the anther sacs may extend proximal to the insertion of the anther collar (calcarate anthers; Fig. 26). The bases of the anther sacs may bear tail-like sterile appendages (caudate anthers; Figs. 27, 28). Variations in the form of anther tip appendages and anther base appendages are very important characters in the taxonomy of the family. Compositae anthers are generally accrescent, laterally cohering by their margins (synanthery) into a tube that envelops the style and the stigma (Fig. 23). Anthers are distinct in some wind-pollinated genera (e.g., Ambrosia, Xanthium). In many Heliantheae, anthers are diagnostically darkly pigmented. See Filament, Stamens, Theca.

Anther base appendages

Basal lobes or sterile appendages of the anther thecas. Pollenbearing portions of the anther sac bases often are prolonged as lobes proximal to the insertion of the anther collar (calcarate anthers; Fig. 26) or bear sterile appendages (caudate anthers; Figs. 27, 28). Anther base appendages can be important for the taxonomy of tribes and genera. See Calcarate anther base, Caudate anther base, Ecalcarate anther base, Ecaudate anther base.

Anther collar

A proximal extension of the anther connective in Compositae borne at distal tip of filament (Fig. 25). The collar has abaxial epidermal cells enlarged and lignified and adaxial cells smaller and unlignified. In Mutisieae and Barnadesioideae, this region is imperceptible. Among Eupatorieae, the anther collar shows more variation than in any other tribe. Basal cells are usually short and the uppermost ones are elongated.

Anther tip appendage

More or less membranous sterile appendage that represents a distal prolongation of the anther connective. It can be wider than long, as long as wide, much longer than wide (Fig. 28), toothed (Fig. 26), apiculate (Fig. 27), acute (Fig. 29), retuse (Fig. 25), or obtuse. Anther tip appendages are important for the taxonomy of tribes and genera.

Anther tube

Hollow tube formed by side-to-side connation of anthers (Fig. 30) with introrse dehiscence; not formed in a few genera (e.g., *Ambrosia*). Pollen released into anther tube is generally expressed by elongation of style (Fig. 31).

Apetalous floret

See Naked floret.

Arctotoid style

Style with a ring of sweeping hairs borne on the shaft of the style proximal to the style branches. Differs from the Carduoid style in the swollen articulation below branches of the latter.

Aristate pappus

A pappus composed of one or more awns of variable length and diameter (Figs. 32–34).

Aristate scale

A membranous pappus element bearing a terminal bristle or awn (Fig. 35).

Astylous ray floret

A neuter ray floret without a style (Fig. 36). See **Neuter ray floret**, **Styliferous ray floret**.

Awn

A generally straight, stiff pappus element, varying from stiffly bristle-like to hard and needle-like (e.g., *Bidens*; Figs. 12, 13). Awns may be smooth (Fig. 101), retrorsely (Fig. 32) or antrorsely (Fig. 33, 34) barbed, or plumose (Fig. 7).

Barbellate bristle

A slender, more or less hair-like pappus element with minute, but noticeable lateral projections (Fig. 37).

Beak

A short to elongated, more or less cylindrical, distal seedless part of the achene in some Compositae (Fig. 19). A beak may be erect or more or less bent. Pappus elements are often borne at distal tip of the beak (e.g., *Taraxacum*, *Chaptalia*).

Bi- to multiseriate pappus

Pappus with elements disposed in two or more series (Figs. 38, 39).

Bilabiate corolla

Bilaterally symmetric corolla characterized by a 2-lobed adaxial lip and a 3-lobed abaxial lip (Figs. 1, 68). The abaxial lip may be enlarged, resembling the lamina of a ray floret (e.g., *Acourtia*, *Trixis*) or may be weakly differentiated and erect or nearly so (e.g., central florets of head of *Onoseris*).

Bilateral symmetry

Descriptive of corolla with petals or lobes unequal in size and shape and arranged in such a way that only one line of symmetry can divide the corolla into mirror images. Bilabiate, pseudobilabiate, ray, and ligulate floret corollas are bilateral. See **Radial symmetry**.



Fig. 2. Styliferous pistillate ray floret of Sphagneticola trilobata (L.) Pruski.

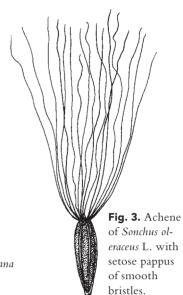


Fig. 1. Bilabiate disk floret of Trixis vauthieri DC. A abaxial lip; B adaxial lip.



Fig. 4. Epappose ribbed achene of *Aphanactis jamesoniana* Wedd.

Fig. 5. Epappose achene of *Smallanthus riparius* (Kunth) H. Rob.



Fig. 6. Ribbed achene of Centratherum punctatum DC. with setose pappus of plumose bristles.



Fig. 7. Four-sided pris-matic achene of *Blainvillea rhomboidea*Cass. with aristate pappus of two short plumose awns.



Fig. 8. Compressed, winged achene of *Verbesina diversifolia* DC. with aristate pappus of two narrow awns.



Fig. 9. Epappose ribbed achene of *Sigesbeckia jorullensis* Kunth.

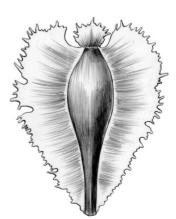


Fig. 10. Winged, obcompressed achene of *Cyathomone sodiroi* S.F. Blake. Pappus of fringed scales.

Biseriate involucre

With phyllaries in two series; phyllaries in the abaxial and adaxial series may be similar or different.

Bisexual floret

See Perfect floret.

Bisexual palea

Receptacular bracts (e.g., in some Gnaphalieae) that individually or collectively subtend central perfect florets within head.

Bracts

Modified leaves associated with flowers or flower clusters. Bracts in Compositae include peduncular bracts (Fig. 40), units of a calyculus (Figs. 41, 42), phyllaries (primary involucral bracts; Figs. 43–45), secondary involucral bracts (Fig. 46), and paleas (receptacular bracts; Figs. 47, 48).

Branches of the stigma

See Style.

Bristly receptacle

Receptacle bearing soft to stiff hair-like projections or slender, setiform scales that are not homologous with paleas (receptacular bracts; e.g., *Centaurea*, *Cirsium*).

Bur

A unit of dispersal containing one or more achenes, characterized by spine-tipped, knob-like, or winged bracts (e.g., *Ambrosia*, *Arctium*).

Calcarate anther base

Bases of anther thecas with pollen-containing portion prolonged below the insertion of the anther collar as spur-like projections (Fig. 26). See **Ecalcarate anther base**.

Calycle

See Calyculus.

Calyculate involucre

Involucre subtended by a calyculus (Fig. 41, 42).

Calyculus

Structure formed by an outer row of differentiated bracts immediately subtending the true involucral bracts. Sometimes described as an outer involucre. It is frequent and characteristic of some tribes: Senecioneae, Helenieae and Heliantheae (Fig. 41, 42). Synonym: epicalyx. See **Involucral bracts, Involucre, Phyllary.**

Calyx

Collective term for the sepals of a flower; the outermost whorl of parts of a complete flower; sepals in most families are more or less herbaceous and are commonly green or otherwise pigmented. In Compositae the calyx is modified as a pappus of dry scales, bristles, and/or awns; individual units of the pappus correspond very rarely to sepals. See **Pappus**.

Capillary bristle

Very slender, hair-like pappus element. See Pappus bristle.

Capitulescence

Secondary inflorescence in which the floral units are heads; the clustering of heads in Compositae. See **Secondary inflorescence**.

Capitulum

See Head.

Carbonized layer

A hardened, dark brown to black phytomelanin deposit in the pericarp of achenes in some Compositae tribes (Figs. 32–34). See **Phytomelanins.**

Carduoid style

Style with a ring of sweeping hairs borne on the shaft of the style below the style branches. With few exceptions, the style is distinctly swollen proximal to the articulation of the style branches (Fig. 49).

Carpopodium

Basal abscission zone of the fruit, formed by one or more rows of cells generally different from the ones in the achene wall, more or less hardened. The carpopodium is the anchor point of the inferior ovary of the floret to the inflorescence or head. It also constitutes the abscission zone of the achene and can be symmetrical in a ring (Fig. 18), asymmetrical (Fig. 35) or decurrent along the ribs (Fig. 21), among other modifications (see also Figs. 20, 38).

Caudate anther base

Bases of anther thecas flanking anther collar bearing tail-like basal appendages composed of sterile cells. Appendages can be laciniate, plumose (Fig. 27), ciliate, smooth (Fig. 28) or absent. See **Ecaudate anther base**.

Chaff scale

See Paleas.

Chaffy receptacle

See Paleate receptacle, Scaly receptacle.

Collar of the filament

See Anther collar.

Columnar receptacle

See Cylindric receptacle.

Compressed achene

Flattened laterally, parallel to a radius of the head (Fig. 8). See **Obcompressed achene.**

Compressed involucre

Flattened involucre formed by 2–8 foliaceous involucral bracts (Figs. 50, 51).

Concave receptacle

Receptacle shallowly depressed in center.

Conical receptacle

Receptacle narrowing from periphery to center with shape of a cone (e.g., Matricaria prostrata, Rudbeckia hirta) (Fig. 52).

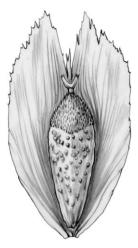
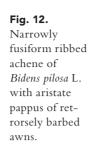


Fig. 11. Winged, obcompressed, tuberculate ray achene of *Rensonia* salvadorica S.F. Blake.



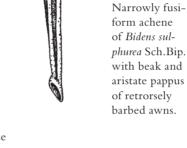


Fig. 13.

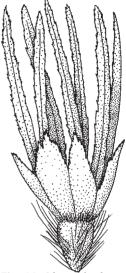


Fig. 14. Obovoid achene of *Stilpnopappus semirianus* R.L. Esteves with biseriate paleaceous pappus of ovate (outer) and linear (inner) scales.

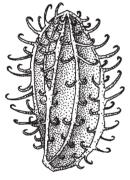


Fig. 15. Epappose ray achene of *Acanthospermum australe* (Loeft.) Kuntze closely enveloped by hardened inner phyllary armed with uncinate prickles.

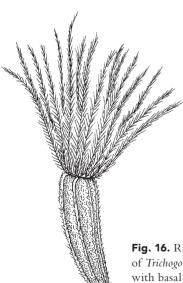


Fig. 16. Ribbed achene of *Trichogonia santosii* with basal attenuation and setose pappus of plumose bristles.

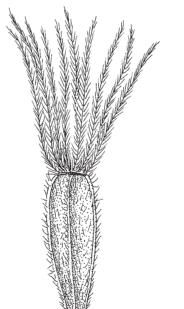


Fig. 18. Ribbed achene of *Trichogonia prancii* G.M. Barroso with proximal stipe and setose pappus of short barbellate bristles.

Fig. 17. Achene of *Trichogonia heringeri* R.M. King & H. Rob. with proximal stipe and setose pappus of short barbellate bristles.

Connective

Portion of the anther axis (filament tip) to which the anther sacs are laterally connected (Figs. 25–30). The anther collar is a proximal extension of the anther connective below the anther sac attachment. The apical anther appendage is a distal membranous prolongation of the connective beyond the anther sacs. See **Anther, Anther collar, Anther tip appendage.**

Convex receptacle

Receptacle elevated in the center forming a smooth curve (Fig. 53).

Cordate anther base

Shallowly notched, ecalcarate or shortly calcarate bases of anther thecas flanking anther collar.

Corolla

Collective term for the petals of a flower; the second whorl of parts of a complete flower. The corolla of a Compositae floret generally comprises five proximally connate petals and has radial (Fig. 48) or bilateral (Fig. 1) symmetry. Number of petals is reduced to four or rarely three in some disk florets, and two corolla lobes corresponding to an adaxial lip are generally wholly suppressed in ray florets (Figs. 2, 36). Corollas in Compositae are generally deciduous from mature achenes, but ray corollas persist and fall with achenes in a few genera (e.g., *Baileya, Zinnia*).

Corolla limb

In a disk floret or ligulate floret the portion of the corolla distal to insertion of anthers, composed of corolla throat and lobes; in a ray floret the more or less expanded distal portion, including the lamina.

Corolla lip

One of the two halves of the limb of a bilaterally symmetric, sympetalous corolla; sinuses separating lips are generally deeper than those separating lobes of a lip though the sinuses between lobes of the adaxial lip may be deeply incised (e.g., Trixis; Figs. 1, 68). Bilabiate florets have a 2-lobed adaxial lip and a 3-lobed abaxial lip (Figs. 1A, 68); pseudobilabiate florets have a 4-lobed lip and a 1-lobed lip (Fig. 54). The lamina of a ray floret (Figs. 2, 36) is usually homologous with the abaxial lip of a bilabiate floret or rarely with the 4-lobed lip of a pseudobilabiate floret.

Corolla lobe

Distal, distinct petal tips of sympetalous corolla. The limb of a disk floret generally has five (less frequently four or three) equal corolla lobes (Figs. 48C, 55A). Lobes vary in shape from shortly triangular to elongated and linear. Bilabiate florets have a 2-lobed adaxial lip and a 3-lobed abaxial lip (Figs. 1, 68); pseudobilabiate florets have a 4-lobed lip and a 1-lobed lip (Fig. 54). The ligule of a ligulate floret is tipped by five lobes (Fig. 56). The lamina of a ray floret most typically has three lobes (Fig. 1) though these may be vestigial or absent in some cases (Fig. 36) or further divided in others. The ray lamina in some Arctoteae is 4-lobed.

Corolla throat

Cylindric to variously dilated portion of disk corolla distal to corolla tube (Figs. 23, 48B) where the anthers are localized.

Corolla tube

Generally cylindric portion of a floret's corolla, in disk (Figs. 23, 48A) and ligulate florets the portion proximal to insertion of filaments. The corolla tube is obsolete in ray florets of some genera.

Coroniform pappus

A pappus composed of very short, distinct or connate elements that collectively form a crown-like ring. Individual elements of a crown may be distinguishable as short bristles or scales, or may be more or less completely connate into a lobed or unlobed crown (Figs. 48, 55).

Corymbiform

A more or less flat-topped simple or compound secondary inflorescence in which the distal, central, most mature heads are borne on shorter peduncles than outer, proximal, less mature heads (Figs. 57, 71).

Corvmb-like

See Corymbiform.

Corymbose

See Corymbiform.

Cylindric receptacle

Elongated receptacle with diameter unchanged from base toward apex (e.g., *Ratibida columnifera*).

Cyme-like

See Cymiform.

Cymiform

A simple or compound secondary inflorescence that develops in the pattern of a simple or compound cyme. Usually restricted in Compositae descriptions to secondary inflorescences that develop in a distinctly cymose pattern, though most Compositae secondary inflorescences are technically cymiform because they are wholly or in part determinate in their pattern of development.

Cymose

See Cymiform.

Cynarioid style

See Carduoid style.

Cypsela

Indehiscent, syncarpic, unilocular and monospermic dry fruit originated from an inferior ovary (Spjut 1994; Stearn 2004). For Marzinek et al. (2008), cypsela is a complex fruit with the pericarp sensu lato formed by the real pericarp (cells from the ovarian wall) and extracarpelar tissues from the receptacle, and hence the fruit of Compositae is a cypsela. In this book, however, we will follow Wagenitz (1976) and Jeffrey (2007) who consider that the more widespread term *achene* is preferable. See **Achene**.

Deciduous paleas

Paleas that break free from the receptacle at maturity of the head. Deciduous paleas sometimes fall together with achenes as part of an achene complex. See **Achene complex**, **Persistent paleas**.

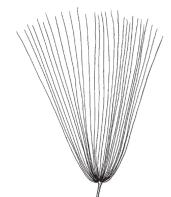


Fig. 19. Narrowly fusiform ribbed achene of Chaptalia integerrima (Vell.) Burkart with slender beak and setose pappus of smooth bristles.



Fig. 20. Proximal portion of stipitate achene of Trichogonia heringeri R.M. King & H. Rob. with carpopodium.

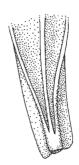
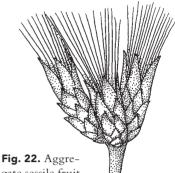


Fig. 21. Proximal portion of achene of Trichogonia cinerea (Gardner) R.M. King & H. Rob. with decurrent carpopodium.



gate sessile fruiting heads of Eremanthus incanus, (Less.) Less. each with a multiseriate involucre of graduated phyllaries.

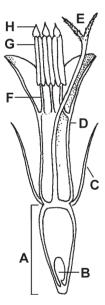


Fig. 23. Diagrammatic longitudinal section of disk floret. A inferior ovary; B basal ovule; C pappus element; D corolla; **E** style, style branches; F filament; ${\bf G}$ connate anthers; ${\bf H}$ anther tip appendage (based on Pruski and Sancho 2004).

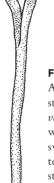


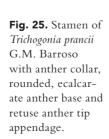
Fig. 24. Anthemoid style of Trixis vauthieri DC. with tufts of sweeping hairs terminating style branches.



Fig. 26. Distal portion of stamen of Dasyphyllum sprengelianum (Gardner) Cabrera with calcarate, sagittate anther base and toothed anther tip appendage.



Fig. 28. Distal portion of stamen of Trixis vauthieri DC. with caudate anther base, and linearoblong anther tip appendage.



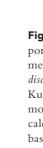


Fig. 27. Distal portion of stamen of Richterago discoidea (Less.) Kuntze with plumose, caudate and calcarate anther base, and narrowly apiculate anther tip appendage.



Fig. 29. Distal portion of stamen of Bidens sulphurea Sch. Bip. with puberulent anther collar, ecalcarate, shortly sagittate anther base, and ovateacute anther tip appendage.

Deciduous phyllaries

Phyllaries that break free from the receptacle at maturity of the head. Deciduous phyllaries sometimes fall together with subtended achenes as part of an achene complex. See **Achene complex**, **Persistent phyllaries**.

Dioecious

A plant in which all flowers are imperfect, and staminate and pistillate flowers are produced on different individuals (e.g., *Baccharis*). See **Monoecious**, **Polygamous**, **Synoecious**.

Disciform head

Type of heterogamous head bearing perfect or functionally staminate disk florets in the center and peripheral filiform florets (e.g., *Pluchea, Pseudognaphalium*; Fig. 58), naked florets (e.g., *Cotula coronopifolia*) or functionally neutral florets with reduced corollas (some *Centaurea*); or a homogamous head consisting solely of filiform florets as in the pistillate head of *Baccharis* or naked florets as in pistillate head of *Ambrosia*. Staminate heads of *Baccharis* and *Ambrosia* are discoid. A disciform head superficially resembles a discoid head in lacking ray florets. See **Discoid head**, **Liguliflorous head**, **Radiant head**, **Radiate head**.

Discoid head

Homogamous head that contains only disk florets (Figs. 59, 60). Corollas may be tubulose, pseudobilabiate, or bilabiate. Ray florets are always absent. In most discoid heads all florets are perfect. In dioecious or monoecious Compositae with separate staminate and pistillate heads (e.g., *Baccharis*, *Ambrosia*) the staminate heads are discoid, composed of staminate disk florets; pistillate heads of these taxa are disciform, composed of filiform florets with tubulose corollas (*Baccharis*) or naked florets (*Ambrosia*). See **Disciform head**, **Liguliflorous head**, **Radiant head**, **Radiate head**.

Disk

The more or less flat-topped to strongly convex aggregate of the disk florets of a radiate or discoid head, or of all the florets of a disciform head. The diameter of the disk is often included in descriptions of heads.

Disk achene

Achene formed by a fertile disk floret.

Disk floret

A perfect, or less commonly functionally staminate, or rarely sterile, floret with a more or less tubulose, (3–4)5-lobed, radial corolla limb (Fig. 48); less commonly the limb is bilabiate (Fig. 1) or pseudobilabate. Disk florets are the only floret types in discoid heads (Fig. 59, 60), and are the centrally located florets in disciform (Fig. 58), radiate (Fig. 61), and radiant heads. Disk florets collectively form the disk of a radiate or discoid head. See Filiform floret, Ligulate floret, Naked floret, Ray floret.

Distal

The portion of a structure farthest from its developmental origin; apical. **See Proximal.**

Double hairs

See Twin hairs.

Double pappus

Pappus with elements in two series that usually are different in length, in texture, or both (Figs. 14, 62, 63).

Drupe

A fleshy, usually one-seeded indehiscent fruit with the pericarp differentiated into an exocarp, a fleshy mesocarp, and a stony endocarp that contains the seed. A rare fruit type in Compositae (e.g., *Chrysanthemoides*, *Tilesia*; Fig. 64).

Ecalcarate anther base

Bases of anther thecas not extending proximal to insertion of anther collar as spur-like projections (Figs. 25, 29). See **Calcarate** anther base.

Ecalyculate involucre

Involucre not subtended by a calyculus (Fig. 44).

Ecaudate anther base

Bases of anther thecas flanking anther collar without tail-like basal appendages composed of sterile cells (Figs. 25, 29). See Caudate anther base.

Endothecial tissue

Inner cell layer of anther theca with cells generally elongated parallel to anther axis. Patterns of thickenings in radial, horizontal, and outer tangential cell walls of endothecial cells are variable within Compositae and may be taxonomically useful microcharacters.

Epaleate receptacle

Receptacle without paleas (receptacular bracts; Fig. 59). See Paleate receptacle.

Epappose achene

Achene without a pappus (Figs. 4, 5, 9). See Pappose achene.

Epicalyx

See Calyculus.

Equal phyllaries

In one or more series of the same length (Fig. 52).

Eupatorioid style

Style branches bearing elongated, cylindrical to flattened, often distally clavate appendages (Fig. 65). Discrete stigmatic lines, often separated by glands, are restricted to the proximal half of the style branches.

Female floret

See Pistillate floret.

Fertile disk floret

A disk floret with an ovary that matures as an achene, the most commonly encountered type of disk floret.

Fertile ray floret

A ray floret with an ovary that matures as an achene, the most commonly encountered type of ray floret (Fig. 2).

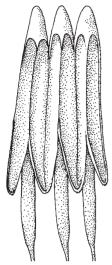
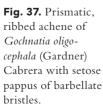


Fig. 30. Stamens of Chresta amplexifolia Dematt., Roque & Miranda Gonç. with distally enlarged filaments, calcarate anther bases, and obtuse anther tip appendages.



Fig. 33. Narrowly winged obcompressed achene of *Calyptocarpus vialis* Less. with aristate pappus of two antrorsely barbed awns. Pericarp carbonized by phytomelanin deposits.



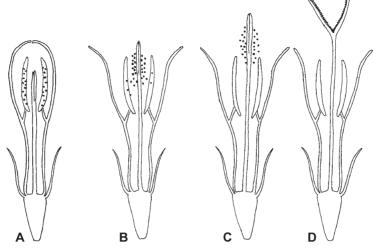
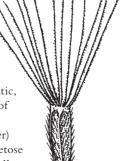
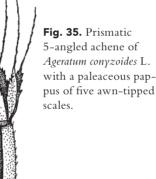


Fig. 31. Pollen presentation in Compositae. **A** Style within anther tube prior to anthesis. **B** Introrse dehiscence of anthers and elongation of style. **C** Continued elongation of style removes pollen from anther tube. **D** Style branches separate, exposing stigmas.







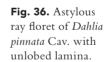




Fig. 32. Obcompressed achene of *Bidens* sp. bearing marginal prickles and aristate pappus of two retrorsely barbed awns.

Pericarp carbonized by phytomelanin deposits.

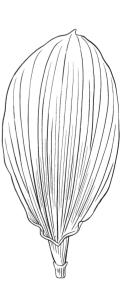


Fig. 38. Prismatic, ribbed achene of *Pseudoclappia arenaria* Rydb. with double pappus, the outer of barbellate bristles, the inner of setiform scales dissected into barbellate, bristle-like segments.

Filament

Stalk-like base of a stamen. In most Compositae the filaments are distinct and individually inserted at the junction of corolla tube and throat (Fig. 23); in a few genera they are connate into a filament tube. In many genera of Cardueae, filaments are contractile in response to touch, resulting in pollen exposure as anthers are pulled back. Except in Barnadesioideae and Mutisieae, the distal end of the filament is separated from the body of the anther by an anther collar. See **Anther**, **Stamen**.

Filament tube

Narrowly tubular structure formed by fusion of filaments of the stamens of a floret (e.g., *Dicoria, Xanthium*); rare in Compositae.

Filiform floret

Pistillate floret characterized by a narrowly tubulose corolla (Fig. 68), sometimes with an unlobed limb or with vestigial lobes (Fig. 66). Filiform florets are located peripheral to central disk florets in disciform heads (e.g., *Pseudognaphalium*) or in separate pistillate heads (e.g., *Baccharis*). Rarely they occur in a head that also contains both disk florets and ray florets (Fig. 67). See **Disk floret**, **Ligulate floret**, **Naked floret**, **Ray floret**.

Flat receptacle

Receptacle planar over surface (Fig. 90).

Floral unit

See Primary inflorescence, Secondary inflorescence.

Floret

The small flower characteristic of Compositae (synonym: floscule; Fig. 23). The highly modified calyx (sometimes much reduced or absent) is a pappus of bristles, scales, and/or awns and is adnate to the distal end of the inferior ovary/fruit. The corolla is (3–)5-merous, sympetalous, diversely tubulose, radial or variously bilateral. The androecium comprises (3–)5 equal stamens with (usually) distinct, epipetalous filaments and (usually) connate anthers forming a tube with introrse dehiscence. The gynoecium comprises 2 connate carpels with a distally 2-branched style and a unilocular inferior ovary containing 1 erect, basal ovule; the ovary matures as an achene. Compositae have several types of florets that differ in corolla symmetry and sexual condition (Fig. 68). Disk, bilabiate, pseudobilabiate and ligulate florets are usually perfect (bisexual). Ray and filiform florets are usually pistillate, less frequently neuter. Heads may contain a single floret type or two or more kinds that may or may not differ in sexual disposition. See Disk floret, Filiform floret, Ligulate floret, Naked floret, Ray floret.

Floscule

See Floret.

Foveolate receptacle

Receptacle surface minutely pitted.

Gamopetalous

See Sympetalous.

Glomerules

Small, compact, irregular clusters of heads.

Graduated phyllaries

In several series with the outer shortest, the inner longest, and a gradual transition through series of intermediate length between (Figs. 69, 70).

Gynoecium

Collective term for the carpels of a flower; the centermost whorl of parts of a complete flower. In Compositae the gynoecium comprises two connate carpels with an inferior, 1-loculed compound ovary containing a single erect ovule, a slender style with two distal style branches, and two stigmas borne on the adaxial faces of the style branches (Fig. 23). The ovary in Compositae generally matures as an achene, rarely as a drupe.

Head

A short, dense indeterminate inflorescence of sessile flowers attached to a common receptacle. Heads are the primary inflorescence type characteristic of Compositae (Fig. 47), generally with an involucre of distinct or connate phyllaries, a receptacle with or without paleas, and one to many florets of one or more kinds. Discoid heads (Figs. 40, 41, 43, 59, 60) contain only disk florets. Radiate heads (Figs. 47, 61, 71) contain peripheral ray florets and central disk florets. Disciform heads (Fig. 58) contain peripheral filiform florets and central disk florets or only filiform florets. Liguliflorous heads contain only ligulate florets (Fig. 72). Rarely a head contains three or more floret types (Fig. 67). The sequence of floral initiation and maturation in Compositae heads is indeterminate. Heads may be solitary or in various types of usually determinate secondary inflorescences. The family name Compositae derives from the superficial resemblance of a head to the individual flowers of some other families; the head is a flower-like composite of many smaller flowers (florets). Synonym: capitulum. See Disciform head, Discoid head, Liguliflorous head, Radiant head, Radiate head.

Hermaphroditic floret

See Perfect floret.

Heterocarpous

Condition of a head in which achenes of two or more morphologies are present (e.g., ray achenes of *Leptosyne calliopsidea* are epappose, glabrous, and winged; the disk achenes have a pappus of lanceolate scales, are adaxially hairy, long-ciliate, and wingless).

Heterogamous head

Head that encloses florets with different sexual disposition, usually pistillate and bisexual (Figs. 47, 67). Radiate heads and most disciform heads are heterogamous (Fig. 58, 61). Radiant heads may be homogamous or heterogamous. See **Homogamous head.**

Heteromorphic pappus

Condition in which some florets in a head have a different type of pappus than others. For example: in *Barnadesia caryophylla* (Vell.) S.F. Blake the peripheral ray-like pseudobilabiate florets have a pappus of plumose bristles (Fig. 54), and the disk florets have a pappus of smooth setiform scales (Fig. 73). **See Isomorphic pappus.**

Homogamous head

Head that encloses florets with the same sexual disposition,

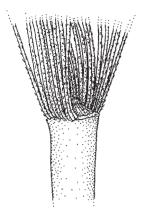


Fig. 39. Distal end of achene of *Gochnatia paniculata* (Less.) Cabrera illustrating biseriate setose pappus with outer and inner series both composed of barbellate bristles.



Fig. 41. Discoid head and distal bractless portion of peduncle of *Erechtites valerianifolius* (Wolf) DC. Uniseriate involucre of distinct phyllaries subtended by calyculus of narrow bracts.



Fig. 40. Discoid head and distal portion of bracted peduncle of *Senecio harleyi* D.J.N. Hind. Uniseriate involucre of distinct phyllaries.



Fig. 42. Radiate head and distal portion of bracted peduncle of *Pseudogynoxys lobata* Pruski. Uniseriate involucre of distinct phyllaries subtended by calyculus of narrow bracts.

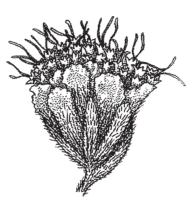


Fig. 43. Discoid head and tip of peduncle of *Scherya bahiensis* R.M. King & H. Rob. Distalmost peduncular bract resembling outer phyllaries of pluriseriate involucre of subequal phyllaries.



Fig. 44. Discoid head and distal tip of bractless peduncle of *Adenostemma brasilianum* (Pers.) Cass. Uniseriate involucre of proximally connate phyllaries.



Fig. 45. Involuce with subequal phyllaries in two series.

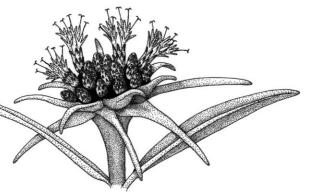


Fig. 46. Peduncled secondary head of Paralychnophora atkinsiae D.J.N. Hind subtended by secondary involucre of subulate bracts. Primary discoid heads each with pluriseriate involucre of graduated phyllaries.

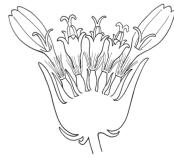


Fig. 47. Diagrammatic longitudinal section of radiate head with calyculus subtending phyllaries, convex paleate receptacle, peripheral ray florets, and central disk florets.

usually all perfect (bisexual) and fertile (Fig. 59). Discoid heads and liguliflorous heads are homogamous (Fig. 60, 72). See **Heterogamous head.**

Honey-combed receptacle

See Alveolate receptacle.

Imbricated phyllaries

Phyllaries of unequal length in several series, overlapping each other like shingles on a roof (Figs. 69, 70).

Imperfect floret

A floret in which the androecium, or gynoecium, or both are nonfunctional (Fig. 68). See **Neuter floret**, **Pistillate floret**, **Staminate disk floret**.

Inflorescence

The grouping of flowers into clusters (primary inflorescences or floral units; e.g., heads in Compositae) or the grouping of floral units into clusters (secondary inflorescence; e.g., clustering of heads in Compositae).

Inner pappus

Collective term for adaxial elements of a double pappus (Figs. 14, 62, 63). See **Outer pappus**.

Introrse dehiscence

Anthers that open on the adaxial side. The connate anthers in Compositae release pollen into the interior of the anther tube where it is brushed or pushed out by sweeping hairs in conjunction with elongation of style or contraction of filaments (Fig. 31).

Involucral bracts

Modified leaves or scales grouped in a ring or cup enclosing or closely subtending an inflorescence, differing from ordinary foliage leaves in size, shape, color or texture. The bracts act functionally as sepals, protecting the young inflorescence during its development. Phyllaries are the involucral bracts of Compositae that surround or enclose individual heads. Syncephalous secondary and tertiary heads found in some Compositae often are enclosed by secondary or tertiary involucral bracts (Figs. 46, 74–76). See **Phyllary**.

Involucre

A disk-like to cup-shaped, ovoid, or cylindric group of bracts in one or more series that collectively subtend or surround the florets of a head (primary involucre; Figs. 40, 45). Involucres are absent in a few genera (e.g., *Psilocarphus*, *Xanthium*), and secondary and tertiary involucres may subtend syncephalous aggregations of heads in other genera (Fig. 46, 74–76). Primary involucres of some Compositae are subtended by a calyculus (Figs. 41, 42) that is sometimes described as an outer involucre. See **Calyculus**, **Involucral bracts**, **Phyllary**.

Isomorphic pappus

All the florets in the head have morphologically similar pappus (Figs. 47, 59). **See Heteromorphic pappus.**

Lamina

The distal, more or less flat, strap-shaped, generally 0-4-lobed

abaxial lip of the corolla of a ray floret (Figs. 2, 36). See **Bilabiate** corolla, **Ligule**.

Ligulate floret

A perfect floret with a proximal tube and a distal, more or less flat, strap-shaped, 5-lobed, bilateral corolla limb (ligule). Ligulate florets are the only floret types in liguliflorous heads (Fig. 56, 68). See **Disk floret**, **Filiform floret**, **Naked floret**, **Ray floret**.

Liqulate head

See Liguliflorous head.

Liqule

The distal, more or less flat, strap-shaped, 5-lobed portion of the corolla limb of a ligulate floret. Used in some references for the lamina of a ray floret (Fig. 56, 68). See **Lamina**.

Liguliflorous head

Type of homogamous head bearing only ligulate florets (e.g., *Taraxacum*, *Lactuca*; Fig. 72). See **Disciform head**, **Discoid head**, **Radiant head**, **Radiate head**.

Male floret

See Staminate disk floret.

Mixed pappus

Pappus composed of two or more types of pappus elements (e.g., an outer series of narrow scales and an inner series of barbellate bristles) (Figs. 14, 62, 63).

Monoecious

A plant in which all flowers are imperfect, and staminate and pistillate flowers are produced on the same individual. Staminate and pistillate flowers may be produced in the same head (e.g., *Blennosperma* and *Delilia* with pistillate ray florets and staminate disk florets; Fig. 51) or in different staminate and pistillate heads (e.g., *Xanthium*). See **Dioecious, Polygamous, Synoecious.**

Multiseriate involucre

Involucral bracts arranged in many series (Figs. 69, 70).

Naked floret

Pistillate floret that lacks a corolla. Naked florets may be located peripheral to central disk florets in disciform heads (e.g., *Dicoria*, some *Cotula*) or in separate pistillate heads (e.g., *Ambrosia*, *Xanthium*) (Fig. 68). See **Disk floret**, **Filiform floret**, **Ligulate floret**, **Ray floret**.

Naked receptacle

See Epaleate receptacle.

Nectary

Secretory structure that produces nectar as pollinator reward, in Compositae borne within corolla as enlarged base of style (stylopodium; Fig. 78).

Neuter disk floret

An unusual type of disk floret that has both non-functional

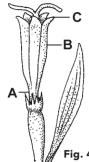


Fig. 49. Distal portion of Carduoid style of Cirsium vulgare (Sav.) Ten. with subterminal swelling bearing sweeping hairs and linear style branches with stigmatic surfaces evenly distributed on the adaxial faces of the branches.

Fig. 48. Palea and disk floret of Sphagneticola trilobata (L.) Pruski with coroniform pappus of connate scales and a radially symmetric, 5-lobed corolla. A corolla tube; **B** corolla throat; C corolla lobe.



Fig. 52. Discoid head and distal portion of bracted peduncle of Isocarpha microcephala S.F. Blake. Biseriate involucre of subequal distinct phyllaries. Florets borne on conic receptacle.

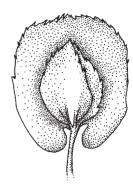


Fig. 50. Flattened involucre of Delilia biflora (L.) Kuntze composed of three unequal phyllaries, the largest much exceeding the others.

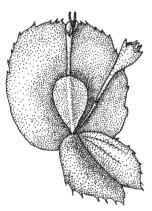
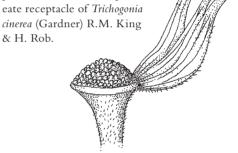


Fig. 51. Flattened involucre of Delilia biflora (L.) Kuntze composed of three unequal phyllaries enclosing a single ray floret with a vestigial lamina and a single staminate disk floret.



Fig. 54. Ray-like pseudobilabiate peripheral floret of Barnadesia caryophylla (Vell.) S.F. Blake with setose pappus of distally plumose bristles. A abaxial lip; B adaxial lip.

Fig. 53. Distal portion of peduncle and convex epal-





floret of Scherya bahiensis R.M. King & H. Rob. with coroniform pappus of connate scales. A corolla lobe.



Fig. 56. Ligulate floret. The ligule is tipped by five lobes.



Fig. 57. Corymbiform secondary inflorescence of radiate heads of Erato costaricensis E. Moran & V.A. Funk.



stamens and a non-functional ovary (e.g., peripheral florets of many *Centaurea*) (Fig. 68).

Neuter floret

A floret in which the gynoecium is non-functional, ranging from vestigial to full-sized, but not producing a functional ovule, and the androecium is absent or non-functional and does not produce pollen grains (Fig. 36, 68). Some ray florets (e.g., *Helianthus*) and the peripheral florets of radiant heads in some genera (e.g., *Centaurea*) are neuter. See **Perfect floret**, **Pistillate floret**, **Staminate disk floret**.

Neuter ray floret

A ray floret in which the gynoecium is non-functional, failing to form an achene (Fig. 68). An ovary is always present though sometimes much reduced. A style may be present (styliferous ray floret) or absent (astylous ray floret, Figs. 36, 68). The lamina of a neuter ray floret is often well developed (Fig. 36), functioning as a pollinator attractant. See **Astylous ray floret**, **Fertile ray floret**, **Styliferous ray floret**.

Obcompressed achene

Dorsiventrally flattened in cross section, perpendicular to a radius of the head (Figs. 10, 11, 33). See **Compressed achene.**

Outer pappus

Collective term for abaxial elements of a double pappus (Figs. 14, 62, 63). See **Inner pappus.**

Ovary

Ovule-containing part of a pistil, attached to the receptacle. In Compositae the ovary is inferior with one locule and one basal ovule (Fig. 23). It matures as an achene in most Compositae, rarely as a drupe. Pappus elements and corolla are inserted on the distal end of the ovary. Ovaries of functionally staminate or neuter florets may be much reduced (Fig. 51) or of normal proportions.

Paleaceous pappus

A pappus composed of one or more flat, more or less membranous scales of variable shape and length (Figs. 79, 80). Scales may be entire, toothed, or variably dissected.

Paleas

Small bracts borne on the receptacle subtending all or some of the florets of a head (Figs. 47, 48); paleas may be similar in size and/or texture to phyllaries or more commonly smaller and of membranous to chartaceous texture. They are a constant character in Heliantheae (with only a few exceptions), in some Anthemideae and Eupatorieae, and in Hypochaeris (Lactuceae). Paleas have been interpreted as rudimentary bracts at the base of each floret or as involucral bracts (Stuessy and Spooner 1988) placed among the florets (Fig. 47). In some genera, each palea is associated with a floret, and if the palea is removed from the head the floret is also removed. In *Ambrosia* and *Xanthium* all of the paleas of pistillate heads are fused into a spiny, knobby, or winged bur containing one or two achenes. Receptacles in some genera, e.g., *Carlina*, *Xeranthemum*, and allies (Cardueae), bear scales that are not homologous with paleas.

Paleate receptacle

Receptacle with paleas subtending some or all of the florets (Fig. 47). See **Epaleate receptacle**.

Panicle-like

See Paniculiform.

Paniculate

See Paniculiform.

Paniculiform

A more or less pyramidal compound secondary inflorescence with a central rachis and shorter side branches; sequence of head initiation and maturation is determinate.

Pappose achene

Achene bearing one or more pappus elements. See **Epappose** achene.

Pappus

Modified calyx consisting of bristles, dry scales, and/or awns, characteristic of Compositae, some Dipsacaceae and some Valerianaceae. Individual units of the pappus may or may not correspond to sepals. The pappus is one of the most important structures in the classification of Compositae. A setose pappus is composed of one or more series of slender, flexible to stiff, bristle-like pappus elements of uniform or variable length and diameter that may be smooth or nearly so (Figs. 3, 81), barbellate (Fig. 37), or plumose (Figs. 16, 82), depending on the divergence and length of the cells that form the bristles. There is a continuum in thickness and stiffness from very fine, hair-like, capillary bristles (Fig. 3) to stiffer, thicker bristles to awns. Bristles may be slender to the base or proximally dilated and may be distinct or proximally connate; bristles grade along a continuum into setiform scales. A paleaceous pappus (Figs. 14, 79, 80) is composed of flat, more or less membranous scales of variable shape and length. Scales may be entire, toothed, or variably dissected into slender lobes or bristle-like segments (e.g., Adenophyllum), the latter sometimes treated as bristles connate in groups. Aristate scales (Fig. 35) taper to or are abruptly tipped by bristles or awns. An aristate pappus is composed of one or more awns of variable length and diameter (Figs. 32-34). Awns may be smooth (Fig. 101), antrorsely (Figs. 33, 34), or retrorsely barbed (Figs. 12, 13, 32), or plumose, and vary from erect to sharply divaricate (Fig. 101). Awn-like structures in some genera traditionally interpreted as pappus elements may be outgrowths of the pericarp. A coroniform pappus (Figs. 2, 55) is composed of very short, distinct or connate pappus elements that collectively form a crown-like ring. Individual elements of a crown may be distinguishable as short bristles, scales, or awns, or may be more or less completely connate into a lobed or unlobed crown. A mixed pappus (Figs. 62, 63) comprises two or more types of pappus elements (e.g., a series of scales and a series of awns or bristles). The pappus may be reduced or entirely absent (Figs. 4, 5, 9). Pappus elements may be diversely deciduous (individually or as a single unit, as in many Cardueae and Wunderlichia mirabilis), persistent, or some elements persistent and others deciduous.

The pappus has a dual function (Stuessy and Garver 1996): it is a defensive structure against predators of the head, blocking the



Fig. 58. Disciform head composed of peripheral filiform florets and central disk florets (in detail).

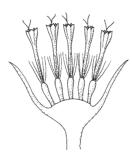


Fig. 59. Diagrammatic longitudinal section of discoid head with convex, epaleate receptacle.



Fig. 60. Discoid head composed of only disk florets (in detail).

Fig. 63. Obconic achene of Lessingianthus santosii (H. Rob.) H. Rob. with biseriate pappus, the outer of narrow scales and the inner of barbellate bristles.



Fig. 61. Radiate head composed of peripheral ray florets and central disk florets (in detail).

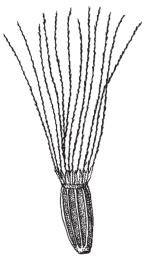


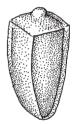
Fig. 62. Ribbed achene of Cyrtocymura harleyi (H. Rob.) H. Rob. with biseriate pappus, the outer of short bristle-like scales and the inner of barbellate bristles.





Fig. 66. Filiform floret of Chaptalia integerrima (Vell.) Burkart. Fusiform, ribbed ovary with slender beak bearing setose pappus of smooth bristles. Corolla narrowly tubulose, unlobed.





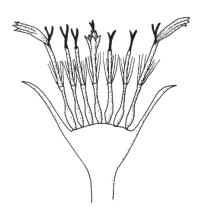


Fig. 67. Diagrammatic longitudinal section of radiate head of Chaptalia with epaleate receptacle bearing peripheral ray florets, intermediate filiform florets, and central, functionally staminate disk floret.



Mikania ternata (Vell.) B.L. Rob. with linearclavate style branches. Marginal stigmatic lines are restricted to proximal adaxial faces of style branches.

space between florets; and it facilitates dispersal of the achenes. Pappus elements may serve in epizoochory through attachment to fur or feathers and in anemochorous dispersal of the achenes by increasing the resistance between the air and the achene and hence prolonging the time of fall. According to Sheldon and Burrows (1973), effectiveness of the pappus in disseminating achenes by anemochory is determined not only by the shape and size of the pappus, but also by the size of the achenes and ecological factors.

Pappus bristle

Flexible to stiff, more or less hair-like pappus element. There is a continuum in thickness and stiffness from very fine, hair-like capillary bristles (Fig. 19) to stiffer, thicker bristles to awns. Bristles may be slender to the base or proximally dilated; bristles grade along a continuum into setiform scales. The surface may be smooth, barbellate, or plumose. See **Capillary bristle**.

Pappus elements

The individual bristles, scales, awns, or other units of the pappus of an achene.

Pauciseriate involucre

Involucral bracts arranged in few series (Figs. 43–45).

Peduncle

The stalk on which a head is borne; it may be weakly to clearly differentiated from vegetative stems (Figs. 40, 71, 83).

Peduncular bract

Bracts borne on the peduncle, separated by long to very short internodes from each other or from the head (Figs. 40, 83).

Pellucid glands

Schizogenous cavities formed beneath epidermis of leaves, phyllaries, and sometimes corollas in most genera of Tageteae (Figs. 100, 101). The glandular contents are often highly scented mixtures of monoterpenes and other oil-like substances. Gland contents are non-scented or very weakly scented in some species of *Pectis*. The chemicals apparently serve as deterrents to herbivory.

Perfect floret

Floret with a functional androecium that forms pollen and a functional gynoecium that matures as a seed-bearing fruit (bisexual floret) (Figs. 23, 68, 84). Fertile disk florets and ligulate florets are perfect. Sometimes apparently bisexual florets are functionally staminate, the style being not receptive, and produce only pollen grains. See **Neuter floret**, **Pistillate floret**, **Staminate disk floret**.

Persistent paleas

Paleas that remain attached to the receptacle at maturity of the head. See **Deciduous paleas.**

Persistent phyllaries

Phyllaries that remain attached to the receptacle at maturity of the head. Persistent phyllaries may retain their original position in the head when dry or may spread or reflex in age. See **Deciduous phyllaries.**

Phyllary

One of bracts that forms the primary involucre in Compositae (Fig. 85). The form and arrangement of phyllaries are of great taxonomic value in Compositae. Phyllaries are usually distinct (Fig. 43), but in some groups they are connate. In Adenostemma (Eupatorieae), phyllaries are distinct almost to the base, where they are connate (Fig. 44). Phyllaries are arrayed in one to many series and range from equal (Fig. 77) or subequal in length (Fig. 52, 85) to strongly graduated (Figs. 69, 70). At maturity of the head they may be deciduous or persistent and may spread or reflex when dry. Phyllaries may function in protection (of the ovaries and achenes against predators), may serve a role in dispersal (e.g., by epizoochory as in Arctium and some Madieae), may play a role in pollination (sometimes the bracts are colored increasing the visual appearance of the head as in Carlina or Xeranthemum) and, in some cases, provide protection to achenes during germination (in species in which the whole head constitutes the disseminating unit). See Calyculus, Involucral bract, Involucre.

Phyllary appendage

Distal portion of phyllary that is differentiated from proximal portion in texture, shape, margin, or other features.

Phyllary body

Medial region of a phyllary that is differentiated by texture from phyllary margin and/or apex.

Phyllary lamina

Ascending to widely spreading foliaceous blade of a phyllary.

Phyllary series

A set of phyllaries inserted at the same level around the receptacle (Fig. 85). The involucre may comprise only one or two series (uniseriate or biseriate) or may have several to many series of phyllaries (pluriseriate or multiseriate).

Phytomelanins

Hardened, blackish organic polymers (resinoids) deposited in cell walls and intercellular spaces of the pericarp of achenes in some Compositae (especially Eupatorieae, Heliantheae, Tageteae; Fig. 32–34). Phytomelanins are chemically inert, resistant to both acids and bases, and may serve as a defense against seed predators.

Pistil

Visual unit of the gynoecium (Figs. 23, 78), in Compositae comprising an inferior, one-loculed compound ovary containing a single erect, basal ovule, a slender style with two distal style branches, and two stigmas borne on the adaxial faces of the style branches.

Pistillate floret

An imperfect floret with a functional gynoecium that matures as a seed-bearing fruit. Pistillate florets in Compositae usually lack stamens altogether, but staminodes are sometimes present. Filiform florets (Figs. 66, 68) and many ray florets (Figs. 2, 68) are pistillate. See **Neuter floret**, **Perfect floret**, **Staminate disk floret**.

Pistillate head

A type of homogamous head containing only pistillate florets (e.g., *Baccharis*, *Xanthium*).

Fig. 68. Putative derivation of floret types in Compositae. Radially symmetric fertile disk florets are assumed to be ultimately ancestral to all other types. However the variety of floret types in Barnadesioideae indicates considerable plasticity in corolla form in basal composites. For bilateral florets in this diagram the abaxial lip is to the right and adaxial lip to the left. Pseudobilabiate disk florets in Pectis have the reverse orientation to that presented in the diagram with a one-lobed abaxial lip and a 4-lobed adaxial lip. Intermediate types not shown include ray florets with a vestigial adaxial lip, styliferous neuter ray florets, and ray florets with staminodes. Peripheral sterile florets in some Centaurea heads have reduced corollas. **Top row** (left to right): 4-lobed ray floret; ray-like pseudobilabiate floret; pseudobilabiate disk floret. Middle row (left to right): naked floret; filiform floret; 3-lobed ray floret; bilabiate disk floret; radial disk floret; ligulate floret. Bottom row (left to right): astylous neuter ray floret; staminate disk floret; ray-like neuter disk floret. [Drawing by Michaela Keil.] Fig. 70. Multiseriate involucre of graduated phyllaries of Chresta amplexifolia Dematt., Roque & Miranda Gonç. Fig. 69. Distal portion of peduncle and multiseriate involucre of graduated phyl-

laries of Dasyphyllum brasiliense (Spreng.) Gardner.

Pistillate paleas

Receptacular bracts (e.g., in some Gnaphalieae) that individually subtend pistillate florets within head.

Plumose

Branched like a feather, with a central shaft and slender, hair-like lateral projections (Figs. 16, 82, 86), descriptive of pappus elements (e.g., bristles of *Helminthotheca*, awns of *Tragopogon*, setiform scales of *Cirsium*) and basal appendages of caudate anthers (e.g., *Richterago*; Fig. 27).

Pluriseriate involucre

With phyllaries in several series (Figs. 69, 70).

Polarized endothecial tissue

Characterized by endothecial wall thickenings restricted to horizontal walls.

Pollen grains

Usually tricolporate, porate, regular to large in size, often echinate (spinose), lophate, or psilate. Compositae show an interesting and elaborate secondary pollen presentation mechanism. The style is prolonged within the anther-tube, brushing the pollen grains to the exterior of the tube when the branches are still closed protecting the stigmatic area, making the floret protandrous. The stigmatic areas of the style are always placed on the adaxial faces of the branches and are exposed only after the passage of the style through the anther-tube. The morphology of the style is associated with this pollen presentation mechanism (Fig. 31) and offers some fine examples of coevolution (see Chapter 20).

Polygamous

Plants producing both perfect and imperfect flowers, on the same or different individuals. Plants with radiate heads and disciform heads are generally polygamous. See **Dioecious**, **Monoecious**, **Synoecious**.

Primary inflorescence

Grouping of flowers into clusters or floral units; heads are the primary inflorescences in Compositae. See **Head, Inflorescence.**

Prismatic achene

Achene polygonal in a cross section with three or more longitudinal angles and planar faces (Figs. 7, 35–38). See **Angled achene**.

Proxima

The portion of a structure nearest to its developmental origin; basal. See **Distal.**

Pseudanth

A generic noun for a condensed inflorescence in which many small flowers are grouped in such a way that the cluster simulates a single flower (Weberling 1989). The most frequent are the head (e.g., Compositae), the sycon (Moraceae) and the cyathium (Euphorbiaceae). The family name Compositae derives from the superficial resemblance of a head to the individual flowers of some other families; the head is a flower-like composite of many smaller flowers (florets).

Pseudobilabiate corolla

Bilaterally symmetric corolla characterized by a (3)4-lobed adaxial lip and a 1-lobed abaxial lip (e.g., most *Pectis*) or a 1-lobed adaxial lip and a 4-lobed abaxial lip as in some Barnadesioideae (Figs. 54, 68). See **Bilabiate corolla**.

Raceme-like

See Racemiform.

Racemiform

A more or less cylindrical secondary inflorescence with a central rachis and heads borne on generally unbranched peduncles. Sequence of inflorescence development is usually determinate with distal heads maturing before proximal heads, but in a few Compositae (e.g., some *Ambrosia* species) the sequence appears to be indeterminate.

Racemose

See Racemiform.

Radial endothecial tissue

Characterized by wall thickenings more or less evenly distributed around endothecial cells.

Radial symmetry

Descriptive of corolla with petals or lobes equal in size and shape; the corolla may be divided into mirror images along any radius that bisects a corolla lobe. Corollas of disk florets are usually radial (Fig. 48). See **Bilateral symmetry**.

Radiant head

Type of heterogamous or homogamous head bearing ordinary disk florets in the center and peripheral florets with more or less dilated, radial to strongly bilateral corollas. The peripheral florets may be perfect and fertile (e.g., *Chaenactis*, *Lessingia*), pistillate, or neuter (many *Centaurea*; Fig. 68). See **Disciform head**, **Discoid head**, **Liguliflorous head**, **Radiate head**.

Radiate head

Type of heterogamous head bearing disk florets in the center and peripheral ray florets (e.g., *Leucanthemum*, *Helianthus*; Fig. 61). See **Disciform head**, **Discoid head**, **Liguliflorous head**, **Radiant head**.

Ray

See Lamina, Ray floret.

Ray achene

Achene formed by a ray floret.

Ray floret

Bilaterally symmetric floret with a (2–)3(–4)-lobed (or sometimes unlobed) limb and generally no adaxial lobes. This is the most widespread type of peripheral florets in the family (Figs. 2, 68, 87). Ray florets usually lack an adaxial corolla lip, but an inconspicuous adaxial lip is sometimes present (e.g., *Monolopia*, *Onoseris*, *Sigesbeckia*). Ray florets are usually pistillate or neuter; neuter ray florets have an ovary (sometimes much reduced) and may or may not have a style (Fig. 36). Rarely staminodes or

Fig. 77. Discoid head and distal

portion of bractless peduncle of

coherent, interlocking margins.

Emilia fosbergii Nicolson. Uniseriate

involucre of distinct phyllaries with

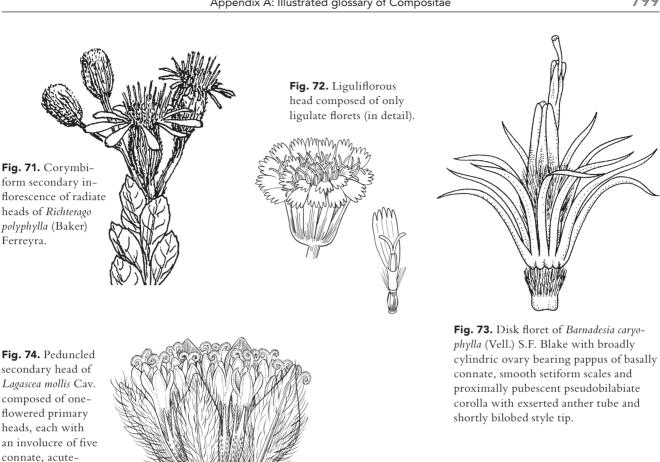
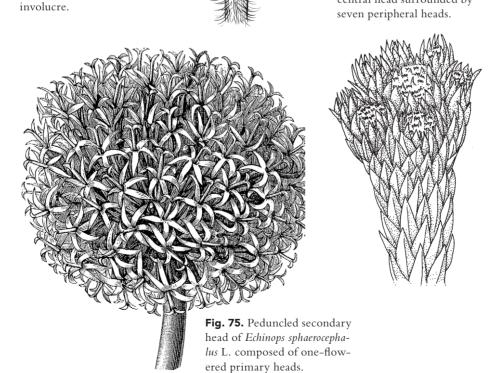


Fig. 76. Secondary head of

Catolesia sp. nov. with one

central head surrounded by



tipped phyllaries. Bracts subtending

the secondary head

compose a secondary

functional stamens are present. Ray florets are located peripheral to central disk florets in radiate heads (Figs. 47, 61). See **Disk floret**, **Filiform floret**, **Ligulate floret**, **Naked floret**.

Receptacle

Basal part of the head onto which are inserted phyllaries, florets, and often paleas (Figs. 53, 88, 90). Receptacle shape varies from weakly concave to flat (Fig. 90), convex (Fig. 53), conical (Fig. 52), or cylindric. The surface may be paleate (e.g., most Heliantheae; Fig. 47) or epaleate (Fig. 59), smooth, foveolate or shallowly to deeply alveolate, glabrous, scaly or variously pubescent (*Lasiolaena*), bristly, or scaly (*Baccharis*; Figs. 88, 89).

Receptacular bract

See Paleas.

Ribbed achene

Bearing raised, longitudinal ridges (Figs. 4, 9, 82).

Rostrum

See Beak.

Rounded anther base

Ecalcarate bases of anther thecas flanking anther collar forming a smooth curve.

Sagittate anther base

Ecalcarate (Fig. 29) or shortly calcarate (Fig. 26) bases of anther thecas flanking anther collar with short, projecting lobes.

Scabrid bristle

See Barbellate bristle.

Scale

A flat, membranous pappus element (Figs. 14, 79) or receptacular appendage (Fig. 89).

Scaly receptacle

Receptacle bearing membranous scales that are not homologous with paleas (Figs. 88, 89).

Scapose head

Solitary head borne at tip of a leafless, essentially naked peduncle that arises directly from a caudex, rhizome, or stolon at or below ground level (e.g., *Taraxacum*, Chaptalia; Fig. 83).

Secondary head

A compact secondary inflorescence in which two or more heads are grouped together onto a common receptacle. Each primary head usually has its own involucre, and the secondary head is often enclosed by a secondary involucre (e.g., *Lagascea*, *Echinops*; Figs. 46, 74–76). See **Syncephaly, Tertiary head.**

Secondary inflorescence

The grouping of floral units into a cluster (synflorescence). The same terminology employed for families in which the basic inflorescence unit is a single flower has often been used for the clustering of the heads in Compositae: e.g., cyme, umbel, spike, corymb, panicle, thyrse, raceme, or head. Some of these primary inflorescences are

indeterminate, others are determinate. With the aim of making the descriptions simpler, Bremer (1994) suggested that the disposition of the heads should be described as "corymbose heads" rather than "heads arranged in corymbs" or even "corymbose capitulescence". Because the sequence of head initiation and maturation in Compositae secondary inflorescences (capitulescences) is almost always determinate, the application of terms such as corymbose, spicate, paniculate, racemose, etc. that apply to indeterminate clusters is inaccurate. Use of descriptors such as corymbiform (Figs. 57, 71), spiciform, paniculiform, and racemiform alludes to the superficial resemblance of the clustering of heads to such inflorescences while acknowledging that they do not follow the same pattern of development. See **Capitulescence**.

Senecioid style

See Anthemoid style.

Sessile

Stalkless

Setiform scale

A long, narrow, flattened pappus element or receptacular appendage that resembles a bristle and may taper to a hair-like tip (e.g., *Cirsium*), sometimes described as a flattened bristle (Figs. 38, 73).

Setose pappus

A pappus composed of one or more smooth (Figs. 3, 81), barbellate (Fig. 37), or plumose (Figs. 6, 82) bristles.

Setose receptacle

See Bristly receptacle.

Simple pappus

A pappus in which the elements are equal (Fig. 82).

Smooth bristle

A slender, hair-like pappus element without evident lateral projections (Fig. 3, 81).

Smooth receptacle

An unappendaged receptacle surface without depressions or with very shallow depressions (Fig. 85).

Solitary head

Head borne in a position on the plant in which it is not clustered with others in a secondary inflorescence (Fig. 83).

Spicate

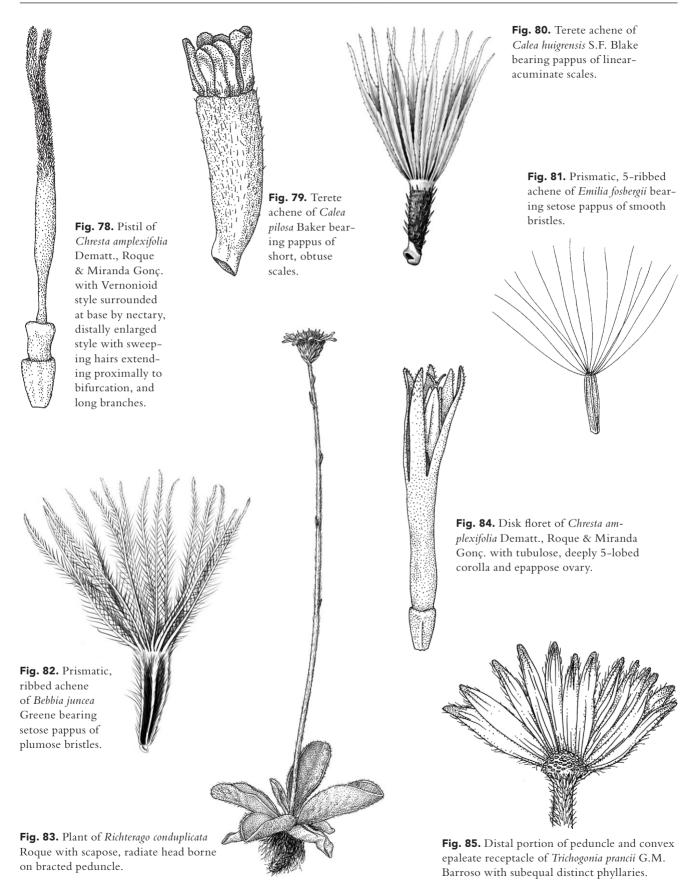
See Spiciform.

Spiciform

A more or less cylindrical secondary inflorescence with a central rachis and sessile or subsessile heads. The sequence of inflorescence development is usually determinate with distal heads maturing before proximal heads (e.g., *Liatris*).

Spike-like

See Spiciform.



Squamella

See Scale.

Stamens

Perfect and functionally staminate Compositae flowers have 5 (rarely 3–4) epipetalous stamens with distinct filaments and introrse anthers that are connate into a tube. The filaments are proximally adnate to the corolla, generally at the junction of the corolla tube and throat (Fig. 23). In some groups (especially in Cardueae) filaments are papillose or bear trichomes in association with a more elaborate pollen presentation mechanism. See **Anther, Filament.**

Staminate disk floret

A disk floret that has functional, pollen-producing anthers and an ovary that fails to mature as an achene (Figs. 51, 68); the ovary may be of normal size or more or less reduced (e.g., *Ambrosia*). Staminate disk florets may be centrally located in the same heads as ray florets (e.g., *Blennosperma*), filiform florets (*Pseudognaphalium*), or apetalous florets (e.g., some *Cotula*), or they may be in separate heads on the same individual (e.g., *Ambrosia*) or different plants (e.g., *Baccharis*). See **Neuter floret, Perfect floret, Pistillate floret.**

Staminate head

A type of homogamous head containing only staminate disk florets (e.g., *Baccharis*, *Xanthium*).

Staminate palea

Receptacular bracts (e.g., in some Gnaphalieae) that individually or collectively subtend central staminate disk florets within a head.

Stereome

Thickened, herbaceous to cartilaginous divided or undivided phyllary body in many Gnaphalieae that is differentiated from hyaline or scarious margin and apex.

Sterile disk floret

See **Neuter disk floret**; sometimes inappropriately used for a staminate disk floret.

Sterile floret

See Neuter floret.

Sterile ray floret

See Neuter ray floret.

Stigma

Pollen-receptive structure of gynoecium (arrays of papillae), usually borne at or near tip of style or style branch; in Compositae presented as stigmatic lines along the adaxial faces of style branches (Fig. 92). Compositae style branches often bear non-stigmatic sterile distal appendages. See **Style**, **Style appendage**, **Style branches**.

Stigmatic line

Linear stigmatic arrays of papillae borne along adaxial faces of style branches (Figs. 65, 91, 92).

Stipe

A short to elongated, more or less cylindrical, stalk-like proximal seedless part of the achene in some Compositae (Fig. 18).

Style

Morphology of the style is critical for the tribal classification of Compositae (Jeffrey 2007). The basal part of the style is often dilated and usually glabrous, with the exception of some Eupatorieae and a few Heliantheae. It is often surrounded or partially surrounded at the base by a nectary (Fig. 78). The style is apically divided into two branches that can be short, as in Cardueae, Mutisieae and Barnadesioideae (Fig. 93) or elongated as in Vernonieae (Fig. 78) and Eupatorieae (Fig. 94). Stigmas or stigmatic areas are borne on the adaxial faces of the style branches and may be evenly distributed on the faces of the branches as in Barnadesioideae, Mutisioideae, Carduoideae and Cichorioideae (Fig. 49) or separated in two parallel marginal lines as in the other subfamilies (Fig. 65). Styles vary according to their thickness, grade of bifurcation, disposition and pattern of trichomes and papillae, organization of papillae within the stigmatic areas and morphology of the base of the branches of the style. All these important characters are observed only in the bisexual florets. Styles of ray florets and filiform florets are less ornamented than those of disk florets of the same species, without sweeping hairs and often with more openly displayed stigmatic surfaces (Fig. 2). The disposition of pollen-collecting trichomes or papillae is also a critical character. The collecting brush can be papillose (Figs. 94, 95) or pilose (Fig. 78). Some styles bear trichomes on the abaxial surfaces of the branches sometimes reaching below the bifurcation, as in Vernonieae (Figs. 78, 96), Cichorieae, Plucheeae, and occasionally in members of other tribes (Figs. 91, 98). In Cardueae, the styles have a ring of collecting trichomes just below the bifurcation of the branches, usually on a more or less marked thickening (Fig. 49). In some cases (many Asteroideae and in Nassauviinae), the penicillate collecting trichomes are concentrated on the apex of the truncate branches of the style (Figs. 24, 92). Some tribes (Eupatorieae, Astereae, many Heliantheae and some Senecioneae) have style branches provided with sterile appendages prolonged above the stigmatic areas (Fig. 91). Style branches in Astereae often cling together at the tip. Style branches of functionally staminate disk flowers often fail to separate at anthesis and are reduced to an undivided tack-shaped structure in Ambrosia. See Stigma, Style appendage, Style branches.

Style appendage

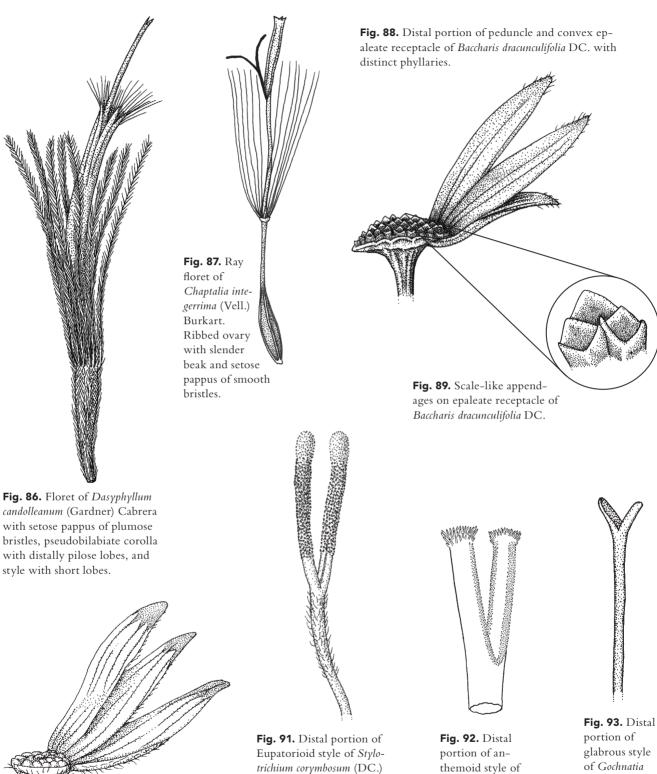
Distal, non-stigmatic tip of style branch of disk floret, sometimes bearing sweeping hairs (Fig. 91), variable in shape and size.

Style branches

The result of incomplete fusion of the distalmost portion of connate carpels of a compound pistil in which the carpel tips are distinct. Compositae styles generally bear two short to elongated branches, each of which is often tipped with an appendage. See **Stigma**, **Style**, **Style** appendage.

Styliferous ray floret

A pistillate or neuter ray floret with a style (Figs. 2, 68). See Astylous ray floret, Fertile ray floret, Neuter ray floret.



Mattf. bearing sweeping hairs

below the bifurcation, and lin-

ear-clavate style branches that

are densely papillose proximal

to the tips. Marginal stigmatic

lines are restricted to proximal

adaxial faces of style branches.

Fig. 90. Distal portion of

peduncle and flat epaleate

receptacle of Trichogonia

villosa (Spreng.) Sch.Bip.

ex Baker with subequal

distinct phyllaries.

of Gochnatia themoid style of paniculata Pentacalia elatoides (Less.) Cabrera (Wedd.) Cuatrec. with marginal with stigmatic stigmatic lines and surfaces covtufts of sweeping ering adaxial faces of short hairs terminating style branches. style branches.

Stylopodium

Structure formed by the basal portion of the style associated with a nectary located at the apex of the ovary (Matzenbacher 1998). The basal part of the style can be totally enclosed in the nectary (Fig. 78), which is then annular (Cardueae, Eupatorieae, Vernonieae), partially inserted (Heliantheae) or placed at the top of the nectary (Astereae and Senecioneae). In Eupatorieae, nectaries have stomas that probably act as secretory pores.

Subequal phyllaries

In two or more series of approximately the same length (Figs. 52, 85).

Sweeping hairs

Hairs borne on distal portion of style and at style tip that brush pollen grains from within anther tube as style elongates or filaments contract (Figs. 24, 78, 95, 96).

Sympetalous

A corolla of connate petals, as in all Compositae corollas.

Synanthery

Anthers laterally connate and introrse, forming a tube that encloses the style and the stigma.

Syncephaly

Combination of several heads into a new morphological entity resembling a single head (Weberling 1989; Figs. 74–76). Individual heads can be free or fused, and they are often subtended by second-order involucral bracts (Figs. 46, 74). See **Secondary head**, **Tertiary head**.

Synflorescence

See Secondary inflorescence, Capitulescence.

Synoecious

Plants in which all flowers are perfect. Compositae with discoid heads and ligulate heads are generally synoecious. See **Dioecious, Monoecious, Polygamous.**

Tailed anther base

See Caudate anther base.

Terete achene

Round in cross section (Fig. 79).

Tertiary head

A congested secondary inflorescence in which sessile small heads are grouped together onto a common receptacle, and these sessile secondary clusters are in turn further clustered (e.g., *Gundelia*); each primary and secondary head may have its own involucre, and the tertiary head may be subtended or enclosed by a tertiary involucre. See **Head, Secondary head, Syncephaly.**

Theca

Pollen sac of an anther (syn. anther sac); each anther has two thecas, separated by their lengthwise attachment to the anther connective (Figs. 25, 26, 28). Variation in the shape and appendages of anther

theca bases can be taxonomically useful. Patterns of cell wall thickenings in the inner cell walls of anther thecae are also useful characters. Thecas of adjacent anthers in a floret are coherent, collectively forming an anther tube and are adaxially dehiscent, releasing pollen into the anther tube. See Calcarate anther base, Caudate anther base, Ecalcarate anther base, Ecaudate anther base, Endothecial tissue, Introrse dehiscence.

Thyrsoid-paniculate

See Paniculiform.

Truncate anther base

Ecalcarate bases of anther thecas squared off on either side of anther collar

Tubular corolla

See Tubulose corolla, Tubulose-filiform corolla.

Tubulose corolla

Generally radially symmetric corolla usually divided into a tube and a limb (Figs. 48, 97), the latter enclosing the anther tube in disk florets. Florets with tubulose corollas are arranged in the center of radiate heads; in disciform and discoid heads, they are distributed throughout the head.

Tubulose-filiform corolla

Tubulose corolla of the pistillate florets of disciform heads (Fig. 58), sometimes with an unlobed limb or with vestigial lobes (Fig. 66). They are usually narrowly cylindrical (Fig. 68), a shape associated with the absence of stamens. See **Filiform floret**.

Twin hairs

Two-celled trichomes characteristic of the achenes of many Compositae.

Unequal phyllaries

Phyllaries in one or more series of differing lengths (Figs. 69, 70).

Uniseriate involucre

Involucral bracts arranged in a single series (Figs. 40, 44, 77).

Uniseriate pappus

Pappus with elements arranged in a single series (Fig. 99)

Unisexual floret

See Pistillate floret, Staminate disk floret.

Vernonioid style

Style with sweeping hairs borne on abaxial surfaces of style branches and extending below the style branches onto the shaft of the style (Figs. 78, 96).

Winged achene

Bearing flattened, longitudinal membranous appendages (Figs. 8, 10, 11).

Zygomorphic

See Bilateral symmetry.

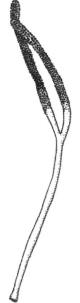


Fig. 94. Distal portion of Eupatorioid style of Scherya bahiensis R.M. King & H. Rob. with linear, distally papillose style branches. Marginal stigmatic lines are restricted to proximal adaxial faces of style branches.

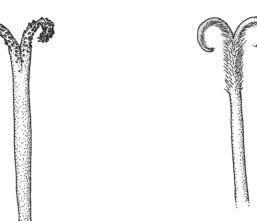


Fig. 95. Style of *Tagetes minuta* L. with papillose style branches.



Fig. 97. Disk floret of *Trichogonia cinerea* (Gardner) R.M. King & H. Rob. with epappose, 5-ribbed, prismatic ovary, tubulose, short-lobed corolla with included stamens, and long-exserted Eupatorioid style.

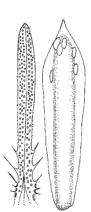
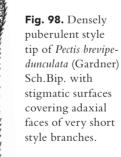


Fig. 100. Abaxial surfaces of leaf and phyllary of *Pectis* ×*floridana* with pellucid glands.



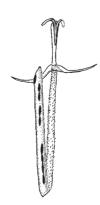


Fig. 96. Distal portion of Vernonioid style of *Centratherum punctatum* DC. with sweeping hairs extending proximally to bifurcation and long branches.

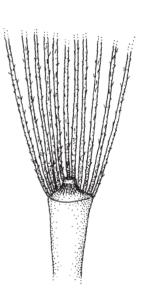


Fig. 99. Distal end of achene of *Richterago discoidea* (Less.) Kuntze illustrating uniseriate setose pappus composed of barbellate bristles.



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