

# Tracing Floral Evolution: A Phylogenetic Insight into the Tribes of Asteraceae

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## ABSTRACT

*This study explores evolutionary patterns and inter-tribal relationships within Asteraceae through floral anatomical and morphological traits. Analyzing 54 species across 47 genera in 13 tribes, results identify Helianthoideae—especially the basal genus Fitchia—as the likely ancestral lineage. Evidence indicates that Cichorieae, Senecioideae, Vernonieae, and Eupatorieae comprise a closely related clade, while Helenieae and Mutisieae form another cohesive group. Arctotideae and Calenduleae likewise cluster together. The tribe Cynaroideae emerges directly from ancestral Helianthoideae but also shares more derived vascular anatomical characteristics with advanced Helianthoideae members. Overall, these findings clarify the structural evolution and phylogenetic pathways shaping Asteraceae diversification.*

**Keywords:** Evolution; Trends; Tribes; Inter-relationship

## INTRODUCTION

The Asteraceae—comprising approximately 1,600 genera and 25,000 species—rank among the largest families of flowering plants (Caligari & Hind, 1996; Hind & Beentje, 1996). Despite its considerable size, the family is dominated by herbaceous species, with few represented by shrubs, climbers, or trees. A hallmark of Asteraceae is the highly specialized capitulum inflorescence and distinctive floret architecture, which remain unmistakable even when detached from the plant (Good, 1956; Leppik, 1960).

Despite their morphological consistency, the phylogenetic relationships among the family's tribes remain controversial. Some researchers have proposed Vernonieae, others Helianthoideae, and still others Mutisieae as the most primitive lineage. Floral anatomy has long been recognized as a powerful tool for mapping evolutionary trajectories and resolving morphological challenges within angiosperms (Eames, 1930–1961; Puri, 1950–1952). Meanwhile, the embryology, cytology, taxonomy, and vegetative anatomy of Asteraceae have been extensively examined (Darlington & Wylie, 1955; Metcalfe & Chalk, 1952; Davis, 1966).

Nevertheless, tribal interrelationships within Asteraceae have remained unresolved. Nearly every major tribe has, at various times, been proposed as ancestral to the rest. This uncertainty stems largely from differing methodologies and criteria applied by various authors. To address this gap in understanding and provide clarity to Asteraceae phylogeny, the present study was undertaken,

focusing on floral anatomical and morphological traits to elucidate evolutionary relationships among its tribes.

## MATERIAL AND METHODS

Floral material representing 54 species from 47 genera across 13 tribes was collected and fixed in FAA (Formalin–Acetic acid–Alcohol; 5:5:90) to preserve tissue integrity. To soften the florets and capitula for sectioning, they were macerated in 2 % hydrofluoric acid for approximately two weeks, then washed under running tap water for 24 hours. Specimens were dehydrated through a graded ethanol series, cleared in xylene, and embedded in paraffin wax following standard histological procedures (Johansen, 1940; Maheshwari, 1939). Serial transverse and longitudinal sections of 10–15 µm thickness were obtained using a rotary microtome. Tissues were double-stained with Crystal Violet and Erythrosin to provide clear differentiation of anatomical structures under light microscopy.

Taxonomic representation included key species such as *Vernonia elaeagnifolia* DC., *Ageratum conyzoides* Linn., *A. houstonianum* Mill., *Bidens biternata* (Lour.) Merr. & Sherff, *Tagetes erecta* Linn., *Cirsium wallichii* DC., *Gerbera jamesonii* Bolus, and *Taraxacum officinale* Wigg., ensuring a broad phylogenetic reference across tribes.

## RESULT AND DISCUSSION

The evolutionary relationships among tribes of the family *Asteraceae* have long been a subject of intense debate and ambiguity. Historically, nearly every major tribe has at some point been regarded as the most primitive and ancestral. This confusion primarily arises from the use of divergent criteria by different authors to determine phylogenetic status.

Broadly, authorities such as Bentham (1873), Bessey (1897, 1915), Hutchinson (1916), Humbert (1927), Stebbins (1939), Cronquist (1955), Benson (1957), and Airy Shaw (1966) have identified the **Helianthoideae** as the most primitive tribe. In contrast, Hooker (1881), Hoffmann (1894), Rendle (1938), and Lawrence (1951) supported **Vernonieae** as the ancestral stock. Others like Leonhardt (1949) and Mastre (1963–64) pointed to **Cynaroideae**, while Prof. James Small (1919) argued for **Senecioideae**, especially *Senecio*, as the most primitive genus.

Carlquist (1976) proposed a more nuanced view, suggesting that discoid (homogamous) and radiate (heterogamous) tribes originated independently from hypothetical discoid ancestors—one line stemming from *Mutisieae*, the other from *Helianthoideae*. According to him, *Senecioideae*, rather than being primitive, likely evolved from *Cynaroideae*.

The variation in these interpretations stems from differing phylogenetic criteria. In this study, we focus on key floral anatomical traits—specifically the vascular system of the flower, pappus, corolla, gynoecium, style, vascular patterns in the inferior ovary, and placentation—to discern

evolutionary trends. Based on these traits, we provide a comparative list of primitive and advanced characteristics (see Tables 1 and 2).

## EVOLUTIONARY TRENDS

Asteraceae flowers show a clear evolutionary trajectory marked by **reduction in vascular traces and organ simplification**, though in some lineages this is accompanied by amplification or structural elaboration. The calyx, corolla, and ovary have all undergone such modifications. Application of these primitive character markers supports the **Helianthoideae**, particularly *Fitchia* (Carlquist, 1957, 1961), as the most primitive extant tribe. This genus exhibits a homogamous capitulum, a pentamerous pappus of sepal-like members with full vascular supply, ten ovary wall traces, well-developed petal midribs, and four stelar bundles—an ancestral combination unmatched by any other tribe.

Within *Helianthoideae*, modern taxa have evolved zygomorphic ray florets via sterilization and modification of peripheral florets. The pappus has undergone varying degrees of reduction and vascular simplification. Transitional forms range from sepal-like pappus with full vascularization to complete suppression in some species (Singh, 2001, 2002; Singh & Kochar, 1999, 2000; Kochar, 1998).

## DERIVED LINEAGES AND RELATIONSHIPS

- **Cynaroideae** likely evolved directly from primitive *Helianthoideae*. *Amberboa ramosa* and *Saussurea candicans* retain ovary vascular patterns similar to *Bidens biternata* and *Galinsoga parviflora* (Singh, 1973). Amplification of the pappus, including multiseriate whorls and loss of vascular supply, is evident in species like *Cirsium wallichii* (Kochar, 2001), which remains homogamous despite these changes.
- **Helenieae** represent a minor divergence from *Helianthoideae*, mainly through loss of the palea. Transitional species such as *Tagetes erecta* maintain a sepal-like, vascularized pappus, while others like *Lasthenia glabrata* show reduced vascular stubs (Singh, 1973).
- **Mutisieae** appear as a specialized offshoot of *Helenieae*, with vascular patterns in *Dicoma tomentosa* and *Gerbera jamesonii* resembling those of *Flaveria repanda*. Amplification and subsequent vascular reduction give rise to multiseriate, setose pappus as seen in *Gerbera*.
- **Asteroideae** and **Inuloideae** branched off early from the Helianthoid line, post ray-floret evolution. The Inuloideae possess tailed anther bases, whereas *Asteroideae* retain blunt bases akin to *Helianthoideae*. Both show varying degrees of pappus reduction or loss.
- **Anthemideae** evolved from *Asteroideae* by further reduction and often complete suppression of the pappus.
- **Arctotideae** and **Calenduleae** are closely allied, both related to *Helianthoideae*. *Calenduleae* shows male disc and female ray florets, while *Arctotideae* features bisexual discs and female rays. Members possess epigynous pappus scales with distinct vascularization.

- **Eupatorieae** likely diverged early from the *Helianthoideae*, before ray floret evolution. In *Ageratum conyzoides* and *A. houstonianum*, the pappus is fully vascularized and calyx-like, resembling *Fitchia*. Setose pappus forms with reduced vascular supply are also observed (Kochar, 2001).
- **Vernonieae** appear derived from *Eupatorieae*, with multiseriate, setose pappus and arrow-shaped anther bases. In *Vernonia elaeagnifolia*, the inner pappus whorl is vascularized and flat, while outer setose whorls lack vascular supply (Kochar, 2001).
- **Senecioideae** evolved from *Vernonieae* by increasing pappus whorls and developing ligulate peripheral florets. Despite earlier assumptions of primitiveness (Small, 1919), *Senecioideae* lacks vascular stubs and dorsal petal bundles, ruling out ancestral status.
- **Cichorieae** likely descended from *Eupatorieae*, with *Taraxacum officinale* showing a reduced ovary vascular pattern nearly identical to *Ageratum*. In *Taraxacum*, vascular traces terminate blindly as stubs, whereas in *Ageratum*, they enter pappus members. Further, species like *Adenostemma lavenia* show deep corolla sinuses, indicating a transition toward the ligulate corolla of *Cichorieae*.

## CONCLUSION

This study reinforces that the **Helianthoideae**—particularly primitive taxa like *Fitchia*—form the ancestral backbone of the *Asteraceae* family. Through comparative floral anatomy and vascular traits, evolutionary links to other tribes such as *Cynaroideae*, *Helenieae*, *Mutisieae*, and *Eupatorieae* are clarified. Tribes like *Senecioideae*, despite morphological diversity, display highly derived characters. The vascular ground plan, pappus development, and corolla modification remain pivotal markers for unraveling tribal relationships within this complex and ecologically dominant family.

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