# KEY TO THE SPECIES OF *CLIBADIUM* (COMPOSITAE, HELIANTHEAE) WITH NOTES ON SYNONYMY AND MORPHOLOGICAL VARIATION

por

**Jorge E. Arriagada***

## Resumen

**Arriagada, J. E.**: Key to the species of *Clibadium* (Compositae, Heliantheae) with notes on synonymy and morphological variation. Rev. Acad. Colomb. Cienc. 19(74): 453-462, 1995. ISSN 0370-3908.

Se presenta una clave taxonómica para las especies del género *Clibadium* L. (Compositae, Heliantheae). Se proporcionan comentarios adicionales sobre la variación morfológica, sinonimia y distribución de las especies.

**Palabras clave:** *Clibadium*, Asteraceae, Heliantheae, Colombia.

## Abstract

A taxonomic key to the species of *Clibadium* L. (Compositae, Heliantheae) is provided. Additional comments on morphological variation, synonymy, and distribution of the species are included.

**Key words:** *Clibadium*, Asteraceae, Heliantheae, Colombia.

The genus *Clibadium* L. is especially interesting because its broad geographical distribution including many endemic species. *Clibadium* has diversified to a greater extent than the closely related genera *Desmanthodium* Benth., *Ichthyothere* Mart., *Riencourtia* Cass., and *Stachycephalum* Sch. Bip. This genus is distributed from southern Mexico throughout Central America, Caribbean and Lesser Antilles, and northern South America, from sea level to 3,400 m, with high concentration of species in Colombia, Costa Rica, and Ecuador. Few species [e.g., *C. eggersii* Hieron, *C. surinamense* L., and *C. sylvestre* (Aubl.) Baill.] have a broad distribution from Honduras to Ecuador whereas many taxa are restricted to small areas (e.g., *C. divaricatum* S. F. Blake, prov. Tarapoto, Perú; *C. rhytidophyllum* Diels, Volcán Tungurahua, Ecuador; *C. zaruchii* H. Robinson, western slope of Cordillera Occidental, Colombia).

*Clibadium* is defined by a unique combination of characteristics, most of which are individually present in other allopatric closely related genera such as *Desmanthodium, Ichthyothere, Riencourtia,* and *Stachycephalum.* The genus *Clibadium* includes shrubs and small trees with usually loosely aggregated heads, herbaceous phyllaries arranged in 1-5 series, receptacle usually paleaceous throughout, ray corollas 2-4-lobed, disc corollas 4-5-lobed, purple to black anthers, and chromosome number $n = 16$.

Twenty-nine species are here recognized from the more than 80 species previously described.

**Clibadium L.**, Mant. Pl. 161. 1771.

*Baillieria* Aubl., Pl. Gui. 2. 804. t.317. 1775.

*Trixis* Sw., Prod. Veg. Ind. Occ. 815. 1788 (non P.Brown.).

*Oswalda* Cass., in Dict. Sc. Nat. 59. 322. 1829.

*Orsinia* Bertol. ex DC., Prod. 5. 104. 1836.

Shrubs or small trees with a conspicuous single main stem to profusely highly branched at soil level; stem

---

* Department of Plant Biology and Herbarium. The Ohio State University, 1315 Kinnear Road, Columbus Ohio 43212, USA.

rounded or many-angled. striate, glabrous or strigose. Leaves opposite, with blades narrowly lanceolate to broadly ovate, subcoriaceous to coriaceous; 5-50 cm long, 2.5-40 cm wide, at base atenuate, rounded or cordate; at apex acute, obtuse, mucronate; with margin serrate, serrulate, finely irregularly serrate, dentate-serrate, crenate, erose; surfaces pilose, strigose or glabrous, with veins sometimes prominent on abaxial surface. Capitulescences of disciform whitish cymose, thyrsoid or paniculiform arrangement of heads organized in open clusters or dense terminal or axillary glomerules; oppositely branched with subtending bracts decreasing in size near heads. Heads heterogamous, few to 600, sessile or on short peduncles; involucre cupulate or funnelform (occasionally subglobose), of 2-6 imbricate, coriaceous phyllaries; phyllaries ovate or orbicular, at apex acute or mucronate, with margin upper one-third mostly ciliate; 5-12-veined; receptacle with marginal carpellate and fertile florets and withhermaphroditic and sterile central florets; pales subtending carpellate florets, pales often resembling phyllaries, ovate or orbicular, 3-9-veined; pales subtending hermaphroditic florets (sometimes absent) membranaceous, lanceolate, 1-3-veined, with margin upper one-third ciliate. Ray florets 3-40, usually uniseriate or less often multiseriate, fertile; corollas tubular, white or yellow, 2-4 lobed; styles bifid, with strong marginal stigmatic lines; pappus absent, sometimes of tufts of short hairs *(C. anceps)* or two short awns *(C. sylvestre)*; achenes obovoid, compressed, biconvex, brown-black. Disc florets 3-24, with tubular white corollas, 4-5-lobed; anthers purplish or black, saggitate at base; style undivided, longer than the anthers, with a 5- lobed nectary at base; ovaries sterile, linear, pilose at apex; pappus absent. Chromosome number, $n$ = 16 (**Arriagada & Stuessy**, 1993).

1. **Clibadium eggersii** Hieron., Bot. Jahrb. Syst. 28: 598. 1901.

*Clibadium pittieri* Greenm., Proc. Amer. Acad. Arts 39: 98. 1903.

*Clibadium pittieri* Greenm. f. *phrixium* Greenm., Proc. Amer.Acad. Arts 40: 38. 1904.

*Clibadium polygynum* S. F. Blake, Contr. Gray Herb. 52: 32. 1917.

*Clibadium chocoense* Cuatrec., Rev. Acad. Colomb. Ci. Exact. 9: 236. 1954.

**Distribution.** Belize, Costa Rica, Colombia, Ecuador, Guatemala, Honduras, LesserAntilles, Nicaragua, Panama and Peru; modified wet habitats with secondary vegetation, along roadside; 0-1000 m.

2. **Clibadium leptophyllum** Cuatrec., Rev. Acad. Colomb. Cienc. Exact. 9: 237. 1954.

**Distribution.** Colombia. This species is known only from the Chocó region; tropical rain forest, in secondary vegetation along roadside; 0-500 m.

3. **Clibadium divaricatum** S.F. Blake, Contr. Gray Herb. 52: 7. 1917.

*Clibadium rimachii* H. Robinson, Phytologia 65: 50. 1988.

**Distribution.** Peru, endemic to the Department of Tarapoto; wet montane forest on sandy rocky soil; 800-900 m.

4. **Clibadium terebinthinaceum** (Sw.) DC. Prodr. 5: 506.1836. *Trixis terebinthinacea* Sw., Prodr. 115.1788.

*Clibadium alexandri* Griseb., Flora Brit. W. Ind. 30:368. 1864. Distribution. Endemic to Cuba, Jamaica and Tobago; ridge type vegetation in secondary forests; 200-1500 m.

5. **Clibadium erosum** (Sw.) DC., Prodr. 5: 506. 1836. *Trixis erosa* Sw., Prodr. Veg. Ind. Occ. 115. 1788.

*Clibadium fragiferum* Griseb., Fl. Brit. W. Indian Is. Guadeloupe, Martinique, Monserrat, Nevis, St. Kitts, St. Lucia, St. Vincent), Puerto Rico; secondary rain forest; 700-1500 m.

6. **Clibadium anceps** Greenm., Proc. Amer. Acad. Arts 39: 97. 1903.

*Clibadium pilonicum* Stuessy, Ann. Missouri Bot. Gard. 62: 1073-1074. 1975.

**Distribution.** Costa Rica and Panama; tropical rain forest, mainly in cut-over areas in wet secondary forest along roadside; 700-2200 m.

7. **Clibadium glomeratum** Greenm., Proc. Amer. Acad. Arts 39: 98. 1903. Distribution. Only known from Costa Rica; second growth tropical rain forest, open roadside; from sea level to 500 m.

8. **Clibadium trianae** (Hieron.) S. F. Blake, Contrib. Gray Herb. 52: 6. 1917.

*Clibadium subsessilifolium* Hieron., Bot. Jahrb. Syst. 29: 32. 1900.

*Clibadium sychnocephalum* S. F. Blake, Contrib. U.S. Natl. Herb. 603. 1924.

*Clibadium congestum* Cuatrec., Rev. Acad. Colomb. Cienc. Exact. 9: 237. 1954.

**Distribution.** Colombia, Ecuador and Venezuela, in secondary growth moist tropical forest, mostly in cut areas on roadside (sometimes on rocky slopes); 1000-2200 m.

9. **Clibadium sessile** S. F. Blake, Ann. Missouri Bot. Gard. 28: 475. 1941.

*Clibadium subauriculatum* Stuessy, Ann. Missouri Bot. Gard. 62: 1074. 1975.

**Distribution.** Panamá; rare, only in and around Cerro Horqueta; lower montane rain forest on open hillsides; 1400-1900 m.

10. **Clibadium microcephalum** S. F. Blake, Wash. Acad. Sci. 16: 418. 1926. Distribution. Ecuador; tropical humid forests, mainly in cut-over areas; 900-2800 m.

11. **Clibadium frontinoense** Díaz & Arriagada, Rev. Acad. Colomb. Cienc. 18: 301. 1992.

**Distribution.** Colombia, known only from the type locality in the Frontino region, east slope of the Cordillera Occidental; 1300 m.

12. **Clibadium zaruchii** H. Robinson, Phytologia 65: 51. 1988.

**Distribution.** Known only from Colombia, Municipio de Frontino; wet montane vegetation, disturbed areas along roadside, west slope of Occidental Cordillera;1850-1870 m.

13. **Clibadium rhytidophyllum** Diels, Notizbl. Bot. Gart. Berlin 14: 341. 1939.

*Clibadium harlingii* H. Robinson, Phytologia 44: 282. 1979.

**Distribution.** Ecuador: Carchi and Pichincha provinces; high mountain humid forest; 2000-2600 m.

14. **Clibadium sprucei** S. F. Blake, Contr. Gray Herb. 52: 5. 1917.

**Distribution.** Ecuador, known only in the vicinity of the Tungurahua Volcano and Chimborazo from the slopes of the Páramos de Matanga; tropical evergreen wet forest with secondary vegetation and cultivated areas; 1800-3100 m.

15. **Clibadium grandifolium** S. F. Blake, Contr. U.S. Natl. Herb. 22: 599. 1924.

*Clibadium grande* S. F. Blake, Contr. U.S. Natl. Herb. 22: 601. 1924.

*Clibadium pacificum* Cuatrec., Rev. Colomb. Cienc. Exact. 9:238. 1954.

*Clibadium terebinthinaceum* (Sw.) DC. subsp. *colombiense* Cuatrec., Rev. Colomb. Cienc. Exact. 9: 240. 1954.

**Distribution.** Colombia, Costa Rica, Nicaragua and Panama; tropical moist forest, secondary vegetation, disturbed forests mainly along roadside; 0-2000 m.

16. **Clibadium cordatum** Cuatrec., Rev. Acad. Colomb. Cienc. Exact. 9: 237. 1954.

**Distribution.** Colombia, mostly restricted to Chocó and Valle; growing in cut-over areas with secondary vegetation; 300-600 m.

17. **Clibadium manabiense** H. Robinson, Phytologia 44: 280. 1979.

**Distribution.** Only known from the provinces of Bolívar and Manabí in Ecuador; secondary vegetation; 100-2000 m.

18. **Clibadium glabrescens** S. F. Blake, J. Wash. Acad. Sci. 27: 381. 1937.

*Clibadium napoense* H. Robinson, Phytologia 73: 152. 1992.

**Distribution.** Colombia, Ecuador and Venezuela, eastern slope of Andes; low humid tropical forest, along wooded stream banks; 500-1000 m.

19. **Clibadium pentaneuron** S. F. Blake, Contr. U.S. Natl. Herb. 22: 598. 1924.

*Clibadium pileorubrum* Cuatrec., Rev. Acad. Colomb. Cienc. Exact. 9: 238. 1954.

*Clibadium sarmentosum* Cuatrec., Rev. Acad. Colomb. Cienc. Exact. 9: 239. 1954.

*Clibadium scandens* Cuatrec., Rev. Acad. Colomb. Cienc. Exact. 9: 239. 1954.

*Clibadium funkiae* H. Robinson, Phytologia 73: 149.1992.

*Clibadium zakii* H. Robinson, Phytologia 73:153. 1992.

**Distribution.** Colombia. Ecuador; cloud forest to subpáramo; (100-), 1400-2800 m.

20. **Clibadium laxum** S. F. Blake, Wash. Acad. Sci. 16: 418. 1926.

*Clibadium alatum* H. Robinson, Phytologia 73: 151-152. 1992.

**Distribution.** Ecuador, broadly distributed in most of the central provinces; tropical wet forest, common along streams; 600-1800 m.

21. **Clibadium sodiroi** Hieron., Bot. Jahrb. Syst. 29:37. 1900.

*Clibadium mexiae* S. F. Blake, Journal Wash. Acad. Sci. 28: 489. 1938.

*Clibadium pallidum* Diels, Notzbl. Bot. Gart. Berlin, 14: 340. 1939.

**Distribution.** Only in Ecuador; tropical low humid forest, on steep slopes and roadsides; 300-1000 m.

22. **Clibadium surinamense** L., Mant. Pl. 294. 1771.

*Trixis aspera* Sw., Prodr. Veg. Ind. Occ. 815. 1788.

*Clibadium asperum* (Aubl.) DC., Prodr. 5: 506. 1836.

*Baillieria aspera* Aubl., Hist. Pl. Guianae 2: 804, *t. 317*. 1775.

*Oswalda baillerioides* Cass., in Dict. Sc. Nat. 59. 322. 1829.

*Clibadium caracasanum* DC., Prodr. 5: 506. 1836.

*Clibadium trinitatis* DC., Prodr. 5:505. 1836.

*Clibadium villosum* Benth., Plant. Hartweg. 2. 205.1845

*Clibadium lehmannianum* O.E. Schulz, Bot. Jahrb. Syst. 46:620. 1912.

*Clibadium lanceolatum* Rusby, Descr. S. Amer. Pl. 150. 1920.

*Clibadium surinamense* var. *macrophyllum* Steyerm., Fieldiana, Bot. 28: 629. 1953.

**Distribution.** Brasil, Colombia, Costa Rica, Cuba, Ecuador, El Salvador, Guatemala, Honduras, Jamaica, Lesser Antilles (Grenada, Martinique, St. Vincent), Nicaragua, Panama, Surinam, and Venezuela (introduced to Borneo, Java, Mauritius, and Sumatra); 0-1000 (-2000) m.

23. **Clibadium peruvianum** Poepp. ex DC., Nov. Gen. Sp. Plant. 3: 1. 1845.

*Clibadium remotiflorum* O. E. Schulz, Bot. Jahrb. Syst. 46: 621. 1912.

*Clibadium heterotrichum* S. F. Blake, Contr. Gray Herb. 52: 3. 1917.

*Clibadium psilogynum* S. F. Blake, J. Wash. Acad. Sci. 21:329-330. 1931.

*Clibadium vargasianum* H. Robinson, Wrightia 6: 46. 1979.

**Distribution.** Argentina, Bolivia and Perú; growing in secondary lowland tropical wet forests, open and grazed selva, riverbanks, and seasonally inundated areas; 100 -600 m (-1200 m).

24. **Clibadium arboreum** Donn. Sm., Bot. Gaz 14: 26. 1889.

*Clibadium donnell-smithii* J. M. Coult., Bot. Gaz. 16: 98. 1891.

*Clibadium pueblanum* S. F. Blake, Contr. U.S. Natl. Herb. 22: 601. 1924.

*Clibadium oligandrum* S. F. Blake, Brittonia 2: 342. 1937.

**Distribution.** Belize, Guatemala, Honduras and Mexico; toward Pacific slopes, humid dense forest in stream-valleys associated with **Carpinus, Magnolia, Podocarpus**, and **Quercus**, damp or wet secondary forest along roadside; sea level to 2,500 m.

25. **Clibadium armanii** (Balb.) Sch. Bip., Linnaea 30:180. 1859. *Eupatorium armani* Balb., Hort. Taurin. Stirp. 1. 27. *t. 6*. 1810.

*Orsinia eupatoria* DC., Prodr. 5. 104. 1836.

*Clibadium rotundifolium* DC., Prodr. 5:505. 1836.

**Distribution.** Brasil and Paraguay; gallery forest, disturbed areas, on sandy soil or at edges of wet savanna; 500-1600 m.

26. **Clibadium leiocarpum** Steetz, in Seem. Bot. Voy. Herald 152. 1853.

*Clibadium schultzii* S. F. Blake, Contr. U. S. Nat. Herb. 22:602. 1924.

*Clibadium leiocarpum* Steetz var. **strigosum** S. F. Blake, Jour. Wash. Acad. Sci. 27: 382. 1937.

**Distribution.** Costa Rica, Nicaragua and Panama; secondary wet forest, common along roads and disturbed slopes; 1400-2800 m.

27. **Clibadium sylvestre** (Aubl.) Baill., Hist. Pl. 8: 307. 1886. **Baillieria sylvestris** Aubl., Hist. Pl. Guianae 2: 807. 1775.

*Clibadium havanense* DC., Prodr. 5: 506. 1836.

*Clibadium vargasii* DC., Prodr. 5: 506. 1836.

*Clibadium barbasco* (H.B.K.) DC., Prodr. 5: 507. 1836.

*Bailleria barbasco* H.B.K., Nov. gen. sp. 4: 226. 1818.

*Clibadium badieri* Griseb., Flor. Brit. W. Ind. 368. 1864.

*Clibadium strigillosum* S. F. Blake, Contr. Gray Herb. 52: 4. 1917

*Clibadium latifolium* Rusby, Descr, S. Amer. Pl. 150. 1920.

*Clibadium appressipilum* S. F. Blake, Contr. U.S. Natl. Herb. 22: 600. 1924.

*Clibadium caudatum* S. F. Blake, Contr. U.S. Natl. Herb. 22: 600. 1924.

**Distribution.** Broadly distributed: Brasil, British Guiana, Colombia, Costa Rica, Ecuador, Lesser Antilles, Panama, Peru, Surinam and Venezuela; tropical rain forest, disturbed forest with secondary vegetation, along roadside, also in disturbed soils, commonly cultivated; 200-600 (-1600) m.

28. **Clibadium acuminatum** Benth., Bot. Voy. Sulph. 114. 1844.

*Clibadium parviceps* S. F. Blake, Contr. U. S. Natl. Herb. 22:598. 1924.

*Clibadium sneidernii* Cuatrec., Rev. Acad. Colomb. Cienc. Exact. 9: 240. 1954.

*Clibadium pediculatum* Aristeg., Fl. Venez. (Comp.) 10: 393. 1964.

**Distribution.** Colombia, Costa Rica (Cocos Island), and Venezuela; mostly on edges of secondary tropical wet forest; 300-1300 m.

29. **Clibadium micranthum** O. E. Schulz, Bot. Jahrb. Syst. 46: 625. 1912.

**Distribution.** Bolivia and Peru; secondary vegetation, disturbed areas; 700-1700 m.

## Morphology and Taxonomic Criterea

In *Clibadium* some characters show considerable variation that cause difficulty in delimitation of species. Also, many structures appear to have undergone parallel changes and reversals during evolution of the group. At a practical level, patterns of variation in features need to be clearly presented to facilitate use of keys and descriptions. For these reasons, the understanding of morphology is fundamental for revealing systematic and evolutionary relationships within the genus.

Definitions of qualitative character states follow **Radford** (1986). The term achene is used over cypsela (favored by **Spjut**, 1994) because it represents traditional usage of the term (e.g., **Blake**, 1924; **Cronquist**, 1955). All measurements of quantitative characters were made onherbarium material. Because shrinkage of some parts occurs with dessication, reproductive structures were rehydratated with Aerosol OT (10% aqueous) before measuring.

*Habit.* All species of *Clibadium* exhibit a shrubby or weakly arborescent habit. Most of the species show a highly branched stem (typically represented by *C. surinamense*). Some species have arching branched stems but with one main stem at the base (e.g., *C. anceps, C. glabrescens, C. laxum, C. trianae*), others possess a more or less erect stem (10 cm diam in *C. cordatum* and *C. rhytidophylum*), and still others are arching vines (e.g., *C. pentaneuron*).

*Leaves.* Shape, size, margin, and base of blades are sometimes useful in delimiting species of *Clibadium.* Blades of most taxa are ovate except in *C. leptophyllum* which is easily recognizable by its narrowly lanceolate leaves. *Clibadium rhytidophyllum* and *C. sprucei* are likewise distinctive in their regular lanceolate leaves. The largest leaves (40 x 30 cm) are found in *C. cordatum, C. frontinoense, C. grandifolium,* and *C. zaruchii*, and the smallest leaves (3 x 1.5 cm) in *C. armanii.* Most of the species have blades with a typical serrate margin, but *C. erosum* is distinctly erose. Some species (e.g., *C. armanii, C. cordatum*) have leaves with cordate or truncate bases in contrast to the typical attenuate condition in most other species of the genus. Most species of *Clibadium* have unwinged petioles, but partially or entirely winged petioles are found in *C. laxum* (in mature individuals, e.g., *Harling & Anderson 11525; Jaramillo 6713*). *Clibadium sessile* and *C. leptophyllum* have no or very short petioles, a feature that obviously helps in delimiting these taxa.

*Capitulescence.* The perspectives on capitulescence structure presented here are based in part on Cronquist's (1977) concepts of organization, arrangement of heads and branches, peduncles, etc., for the Compositae. For simplicity of application of terminology, heads are treated as if they represent single flowers. Most members of the family have a basic cymose capitulescence (**Cronquist**, 1977), although solitary heads are also known. The basic cymose capitulescence occurs in two different forms: monochasial and dichasial (**Wyatt**, 1982; **Weberling**, 1989). Monochasial capitulescences have a terminal head that opens first, with the other heads opening in a centrifugal order down the axis. Dichasial capitulescences also mature centrifugally, but they have only three heads arising from the same node in which the central head opens first followed by the two lateral ones shortly thereafter.

All species of *Clibadium* have complex monochasialcapitulescences which, depending on the species, are arranged secondarily into cymes or thyrses. These secondary arrangements are sometimes organized further into compound cymose and thyrsoid aggregations. These categories of capitulescences have also been recognized in other genera of Heliantheae (**Beaman**, 1990; **Strother**, 1991). In all cases the capitulescences are suboppositely branched with subtending bracts decreasing in size near the heads, with heads sessile or on short peduncles and secondarily aggregated into large clusters with up to 600 small, loosely arranged (e.g., *C. grandifolium*) or tightly packed (e.g., *C. zaruchii*) heads. Aggregation of heads is illustrated in one extreme by *C. eggersii* with heads loosely aggregated, moderately aggregated as in *C. surinamense*, or densely aggregated as in *C. glabrescens.* Capitulescences can be very tighly congested (e.g., *C. frontinoense* and *C. zaruchii*). Congested capitulescences also occur in all species of the related genus *Desmanthodium*, in particular *D. congestum* Arriagada & Stuessy. The more loose aggregation typical of *C. eggersii* is also found in many species of *Ichthyothere*, the other close relative of *Clibadium.*

Characterization of the total capitulescence of a taxon is complicated in *Clibadium* because there are many levels of organization. Estimation of the total number of heads is also difficult, particularly because the total number depends on the age of the branch. Many species flower forseveral months, and the capitulescences continue to increase in size and complexity. This is probably one of the reasons why different types of capitulescences have been reported for the same species. For example, *Clibadium sylvestre* when young (e.g., **Nee** *7139*) has a thyrsoidal capitulescence, whereas when older (e.g., Webster *16782*) it may be paniculiform. In *Clibadium armanii*, similarly, thyrsoidal capitulescences are found on young specimens (e.g., *Harley & Castro 11295*) whereas paniculiform ones occur on older ones (e.g., *Irwin et al. 23772*). An even broader range of variation occurs in *C. surinamense.* Here cymose capitulescences are found in young individuals (e.g., *Knapp 1267; Maxon & Valentine 7033*) and panicles are observed in older ones (e.g., *Dwyer 7197; Maxon & Harvey 6505; Stern et al. 720*).

Occasionally an intermediate or slightly different capitulescence arrangement may be observed within a particular species. For example, some individuals of *C. anceps* (e.g., *Dwyer & Correa 8844*) and of *C. glabrescens* (e.g., *Killip & Cuatrecasas 38862*) deviate from the typically capitate panicle to a nearly umbellate one.

Similar morphological variation in capitulescences hasbeen observed in other genera unrelated to *Clibadium* (e.g., *Hieracium* L., **Beaman**, 1990; *Pappobulus* S. F. **Blake**, Panero 1992; *Simsia* Pers., **Spooner**, 1990). Because of the considerable variation in capitulescences of some species of *Clibadium*, and due to the obvious cycles of capitulescences evolution within many of the different taxonomic sections, these characters have not been used in the cladistic analysis. However, *C. frontinoense, C. laxum, C. trianae,* and *C. zaruchii* have very distinctive capitulescences and these features can be diagnostic for specific recognition.

*Heads.* Heads in *Clibadium* are heterogamous with white, tubular corollas, with carpellate and fertile peripheral florets (ray), and hermaphroditic and female-sterile (i.e., functionally male) central disc florets. This is simple monoecy, one of many breeding systems known to occur in the family (**Lowry & Stuessy**, 1982). The number of ray and disc florets is very important in establishing groups of species and for purposes of subsequent identification.

The number of carpellate florets ranges from 3-5 (*C. anceps, C. glomeratum, C. microcephalum, C. sessile,* and *C. trianae*) to 30-40 (*C. divaricatum, C. eggersii, and C. leptophyllum*). The number of disc florets is 3 (*C. microcephalum, C. zaruchii*), 6 (*C. anceps, C. rhytidophyllum*) or 24 (*C. leptophyllum*).

The number of heads per capitulescence varies indifferent taxa as follows: 24-28 heads in *C. eggersii* (*Tyson 3422*), 60-116 in *C. trianae* (*Stuessy & Funk 5623*), 70-170 in *C. surinamense* (*Stuessy & Funk 5510*), 75 heads in *C. sessile* (Allen 4970), 86-119 heads in *C. anceps* (*Dwyer & Correa 8844; Stern et al. 1019*), 94-106 in *C. pentaneuron* (Stuessy & Funk 5595), 98-100 heads in *C. leiocarpum* (*Allen 1341*), 100-130 in *C. glabrescens* (*Stuessy & Funk 5606*), 219 heads in *C. microcephalum* (*Stuessy & Arriagada 12362*), and up to 600 in *C. grandifolium* (*Croat 13372; Lewis et al. 2082*). An unusual number of 245 heads in a cluster was counted in a young individual in *C. trianae* (*Stuessy & Arriagada* 12337), but the basic head and capitulescence organization was the same as observed in other specimens.

*Involucres.* The number of phyllaries, their arrangement into series, and their shape, texture, and venation are all taxonomically important in *Clibadium*. The phyllaries are herbaceous and spreading and usually reflex during fruiting (clearly seen in *C. manabiense*). The number and length of phyllaries are usually constant, and they are often pubescent over the upper one-third with a ciliate margin. Phyllaries in most species are organized in a single series. A few taxa (*C. anceps, C. glomeratum*, and *C. trianae*), however, have two series. This exceptionalarrangement may be due to a larger number of phyllaries (6) perhaps providing substantive protection as compensation for lack of pales. The most common number of phyllaries in the genus is three, with *C. eggersii* and *C. leptophyllum* with only two (this low number perhaps relating to a larger number of ray florets subtended by pales). Also uncommon is the 4-phyllaried condition in *C. frontinoense* and *C. zaruchii*. The shape of phyllaries ranges from ovate to orbicular with the upper one-third of the margin ciliate, and with apex obtuse (*C. erosum, C. grandifolium, C. pentaneuron, C. sylvestre, C. terebinthinaceum*), acute (*C. anceps, C. eggersii, C. glomeratum, C. laxum*) or mucronate (*C. armanii, C. cordatum, C. manabiense*). Pubescence on the phyllaries is strigose in most species, but a few are glabrous (*C. glomeratum, C. grandifolium, C. leiocarpum, C. microcephalum, C. pentaneuron, C. sessile, C. terebinthinaceum,* and *C. trianae*).

*Pales.* Two different morphological viewpoints exist with regard to bracts subtending ray florets in *Clibadium*. Stuessy, in a broad survey of Heliantheae (1977), has regarded them as inner phyllaries and hence part of the involucre. Funk, in her monograph of *Montanoa* (1982), considered them as pales (i.e., outer row of receptacular bracts; Gleason 1952, **Carter**, 1964, and *Cabrera*, 1978, also holds this viewpoint) because of their similarity of development with bracts substending disc florets. Following **Briquet** (1917), I use the term "pale" for those bracts subtending ray and disc florets, and the term phyllary for those forming the involucre. In *Clibadium*, the female florets are subtended by broad pales often resembling phyllaries but they differ in having fewer veins and less pubescence. In species with more than one series of ray florets, there is a gradual change (reduction in size and pubescence) in pale morphology from outermost to innermost ray florets. Disc florets in some species of *Clibadium* are also subtended by receptacular bracts (pales). Pales subtending the innermost ray florets are similar to those of the disc. Such a transition can be seen clearly in *Clibadium eggersii,* with 5-7 series of ray florets.

*Ray corollas.* The number of lobes of corollas is taxonomically valuable. Ten species are characterized by having 4-lobed corollas. Sixteen species are characterized by having 3-lobed corollas, Three species (*C. rhytidophyllum, C. sessile, and C. sprucei*) have 2-lobed corollas.

*Achenes.* All species have achenes with similar morphology and size proportional to florets and heads. Some species of *Clibadium*, however, possess unusual drupaceous achenes with orangish or greenish juice. This has beenobserved in the field in mature fruits of *C. eggersii* and *C. laxum* which release yellow-green and orange juice, respectively, when squeezed. The drupe-like fruits have an inflated hypodermis with large cells and cell layers in which juice accumulates (*Stuessy & Liu*, 1984). This type of fruit is rare in Compositae, known only in a few other genera, e.g., *Chrysanthemoides* Fabr. (Calenduleae), and *Wulffia* Neck. ex Cass. (Heliantheae).

*Clibadium eggersii, C. erosum, C. divaricatum, C. leptophyllum*, and *C. terebinthinaceum* possess an unusual head superficially resembling an aggregated fruit such as in *Rubus ulmifolius* Schott (Rosaceae). This conspicuous structure is the result of aggregation of 16-40 drupaceous achenes all of which develop fleshy exocarps at maturity. In addition, phyllaries and ray pales also become fleshy at their bases resulting in an inflated structure (even easily observable in dry herbarium specimens). This modified head is used as food by birds (e.g., *C. eggersii* in Costa Rica; *Feinsinger et al. 2182*), which could serve as dispersal agents.

*Vestiture.* Vestiture terminology in this treatment follows **Lawrence** (1951). All species of *Clibadium* have some type of pubescence on leaves (mainly undersurface and along veins of leaves), stems, phyllaries, and achenes. There are two types of trichomes: (1) uniseriate; and (2) biseriate(**Zwillingshaare, Hess**, 1938). Uniseriate trichomes are most common. Their length and density change with position on different structures in different species (e.g., *C. arboreum, C. leiocarpum, C. surinamense, C. trianae*). Biseriate trichomes are restricted to achenes of some species (e.g., *C. armanii, C. leptophy-*

*llum, C. sprucei*). Variation in ray achene pubescence does not correlate subgenerically or sectionally, but it is taxonomically helpful in characterizing individual species. Some taxa are glabrous (*C. anceps, C. leiocarpum, C. micranthum, C. peruvianum, C. rhytidophyllum, C. sessile, C. zaruchii*), and some are hirsute (*Clibadium arboreum, C. armanii,* and *C. leptophyllum*), or pilose (rest of genus).

**Key to species** of *Clibadium*

1. Ray florets multiseriate; number of ray florets always greater than disc florets; all florets subtended by pales; mature heads with drupaceous achenes; phyllaries and pales fleshy (at base) at maturity; capitulescence thyrsoid.

2. Capitulescence with fewer than 25 heads; each with more than 30 ray florets; ray corollas 4-lobed; ray pales 5-veined; Central and South America.

3. Heads 4-6 mm tall, with 2 phyllaries; ray florets 30-40; disc florets 8-24.

4. Leaves ovate; disc florets 8-9 .................................................... 1. *C. eggersii*

4. Leaves narrowly lanceolate; disc florets 24; ...................................... 2. *C. leptophyllum*

3. Heads 2-3 mm high, with 5-6 phyllaries; ray florets 24-39; disc florets 6-10 .................................................... 3. *C. divaricatum*

2. Capitulescence with 50-100 heads; each with fewer than 20 ray florets; ray corollas 3-lobed; ray pales 3- veined; Caribbean and Lesser Antilles.

5. Leaves with margin crenate-serrate, at apex acute; disc florets 7; disc corollas 5-lobed; Cuba and Jamaica ...................... 4. *C. terebinthinaceum*

5. Leaves with margin erose, at apex short-acuminate; disc florets 8; disc corolla 4-lobed; Puerto Rico and Lesser Antilles .................................................... 5. *C. erosum*

1. Ray florets uniseriate; number of ray florets same or fewer than disc florets; ray florets subtended by pales only, or heads epaleaceous; mature heads with dry achenes; phyllaries and pales dry (never fleshy) at maturity; capitulescence cymose or paniculiform.

6. Heads arranged in condensed capitulescences.

7. Heads epaleaceous.

8. Capitulescences of flat-topped clusters with 3-6 subsessile heads ............... 6. *C. anceps*

8. Capitulescences of round-topped clusters with 10-30 sessile heads.

9. Leaves pilose on both sides, with margin crenate-serrulate; heads 10-20, 2-3 mm tall; Costa Rica and Panama .................................................... 7. *C. glomeratum*

9. Leaves strigose on both sides, with margin dentate-serrate; heads 20-30, 5 mm tall; Colombia .......... 8. *C. trianae*

7. Heads paleaceous throughout or with pales substending ray florets only.

10. Only ray florets subtended by pales.

11. Leaves sessile; ray florets 5; disc florets 6-8; ray corollas 2-lobed; phyllaries 7-12-veined ........................... 9. *C. sessile*

11. Leaves petiolate; ray florets 3; disc florets 3-4; ray corollas 4-lobed; phyllaries 4-6-veined .................................................... 10. *C. microcephalum*

10. Ray and disc florets subtended by pales.

12. Leaves 20-35 cm long, 15-25 cm wide; heads with 4 phyllaries; Colombia.

13. Heads less than 6 mm tall, in condensed clusters 1.5-2 cm diameter .................................................... 11. *C. frontinoense*

13. Heads 8 mm tall, in condensed clusters 3-4 cm diameter .................................................... 12. *C. zaruchii.*

12. Leaves 7-14 cm long, 2.5-4 cm wide; heads with 3 phyllaries; Ecuador.

14. Leaves ovate to ovate-lanceolate; at apex acute; heads 4 mm tall .................................................... 13. *C. rhytidophyllum*

14. Leaves lanceolate; at apex narrowly acuminate; heads 6 mm tal .................................................... 14. *C. sprucei*

6. Heads arranged in loose cymose or thyrsoid capitulescences.

15. Leaves 30-50 cm long, 10-40 cm wide; capitulescences with 200 or more florets.

16. Leaf bases attenuate, decurrent 1/3 of petiole; 400 or more heads percapitulescence; disc florets epalaceous not subtended by pales .................................................... 15. *C. grandifolium*

16. Leaf base cordate with petiole naked; less than 300 heads per capitulescence; disc florets subtended by pales ............... 16. *C. cordatum*

15. Leaves less than 20 cm long, 10 cm wide; capitulescences with less than 200 florets.

17. Ray florets only subtended by pales.

18. Disc corollas 4-lobed.

19. Leaves at base shortly cuneate, with margin crenate-toothed; heads 100 or more per capitulescence; disc florets 6 or fewer .................................................... .21. *C. sodiroi.*

19. Leaves at base obtuse, with margin serrate to serrate-dentate; heads fewer than 100 per capitulescence; disc florets 10-14 .......................................... 22. *C. surinamense*

18. Disc corollas 5-lobed.

20. Leaves with veins yellowish underneath, at apex acute, at base attenuate, with margin finely irregularly serrate; disc florets 20 or more; phyllaries 3, 7-veined .......................................... 23. *C. peruvianum*

20. Leaves with veins light-green underneath, at apex acuminate, at base rounded, with margin serrate or mucronate-dentate; disc florets fewer than 10; phyllaries 3-4, 5-veined.

21. Leaves membranaceous, 10-20 cm long, pilose, with margin serrate; Mexico, Nicaragua ................................ 24. *C. arboreum*

21. Leaves subcoriceous, rigid, 5-7 cm long, hispidulous, with margin mucronate-dentate; Brasil, Paraguay .......................................... 25. *C. armanii*

17. Ray and disc florets subtended by pales (sometimes 1-2 central disc florets not subtended by pales).

22. Disc corollas 3- or 4-lobed.

23. Disc corollas 3-lobed .......................................... 29. *C. micranthum*

23. Disc corollas 4-lobed.

24. Capitulescence paniculiform; stem many-angled; leaves 14-30 cm long, with blade decurrent on petiole; phyllaries 5-7-veined .......................................... 20. *C. laxum*

24. Capitulescence thyrsoid; stem terete; leaves less than 14 cm long, with petiole naked; phyllaries 8-11-veined.

25. Leaves and stems hirsute; phyllaries dark brown-green, glabrous .................................. 26. *C. leiocarpum*

25. Leaves and stems strigillose; phyllaries light green, strigose .... 27. *C. sylvestre*

22. Disc corollas 5-lobed.

26. Leaves coriaceous, with veins conspicuous on abaxial surface.

27. Phyllaries at apex acuminate, strigose; ray florets 9-13; disc florets 15 ................................ 17. *C. manabiense*

27. Phyllaries at apex obtuse, glabrous; ray florets 5-6; disc florets 5-8 ................................ 19. *C. pentaneuron*

26. Leaves thin-pappery, smooth .... on abaxial surface.

28. Leaf margin serrulate, with teeth entire; phyllaries 5-veined; ray pales 4-veined; disc pales 2-veined .................................. 18. *C. glabrescens*

28. Leaf margin serrate to pauci-serrate, with teeth mucronate; phyllaries 7-veined; ray pales 7-veined; disc pales 3-veined .................. 28. *C. acuminatum*

## Acknowledgments

This paper is based upon a doctoral dissertation submitted to the Graduate School of the Ohio State University. Financial support for this study was provided by National Science Foundation (INT 9017695), The Garden Club of America, and The Ohio State University Janice C. Beatley Award. I thank the curators of the following herbaria who loaned specimens for this study: A, B, BM, CAS, COL, CR, DS, ECON, F, FSU, G, GH, K, LL, LP, MEDEL, MO, NY, P, UC, US, WIS.

## List of References

**Arriagada, J.** 1993. Notas sobre las relaciones genéricas de *Clibadium* L. (Compositae, Heliantheae). Revista Acad. Colomb. Ci. Exact. **18**: 465-468.

________ **& T. F. Stuessy.** 1990. A new species and subgenus of *Desmanthodium* (Compositae, Heliantheae) from southern Mexico. Brittonia **42**: 283-285.

**Blake, S. F.** 1924. New American Asteraceae. Contr.U.S. Natl. Herb. **22**: 587-661.

**Beaman, J. H.** 1990. Revision of *Hieracium* (Asteraceae) in Mexico and Central America. Syst. Bot. Monogr. **29**: 1-77.

**Briquet, J.** 1917. Le critère différentiel des bractées involucrales et paléales dans la calathide des composées. Biblioth. Universelle Geneve, Arch. Sci. Phys. Nat. **43**: 1-5.

**Cabrera, A. L.** 1978. *Flora de la provincia de Jujuy*. Parte 10. Compositae. INTA, Buenos Aires.

**Carter, A.** 1964. The genus *Alvordia* (Compositae) of Baja California, Mexico. Proc. Calif. Acad. Sci. **30**: 157-174.

**Cronquist, A.** 1977. The Compositae revisited. Brittonia **29**: 137-153.

**Cuatrecasas, J.** 1954. Notas a la flora de Colombia. XIII. Revista Acad. Colomb. Ci. Exact. **9**: 233-249.

**Díaz-Piedrahita, S.** 1991. La botánica en Colombia, hechos notables en su desarrollo. Revista Acad. Colomb. Ci. Exact. **6**: 1-125.

________ **& J. Arriagada.** 1992. Una nueva especie de *Clibadium* (Compositae) para Colombia. Revista. Acad. Colomb. Ci. Exact. **18**: 301-303.

**Funk, V. A.** 1982. The systematics of *Montanoa* (Asteraceae, Heliantheae). Mem. New York Bot. Gard. 36: 1-133.

**Hess, R.** 1938. Vergleichende Untersuchungen über die Zwillingsbaare der Compositen. Bot. Jahrb. Syst. **68**: 435-496.

**Jarvis, C. E., F. R. Barrie, D. M. Allan & J. L. Reveal.** 1993. A list of Linnaean generic names and their types. Regnum veg. **127**: 35.

**Koch, M. F.** 1930. Studies in the anatomy and morphology of the Compositae flower II. The corolla of the Heliantheae and Mutisiae. Amer. J. Bot. **17**: 995-1010.

**Lawrence, G. H. M.** 1951. *Taxonomy of Vascular Plants*. New York: The MacMillan Company.

**Lowry, T. K. & T. F. Stuessy.** 1982. The taxonomic and evolutionary significance of female sterility in disc florets of the Compositae. Bot. Soc. Amer. Misc. Publ. **162**: 99. Abstract.

**Panero, J. L.** 1992. Systematics of *Pappobolus* (Asteraceae-Heliantheae. Syst. Bot. Monogr. **36**: 1-195.

**Radford, A. E.** 1986. *Fundamentals of plant systematics.* New York: Harper & Row.

**Sáenz, A. A.** 1981. Anatomía y morfología de frutos de Heliantheae (Asteraceae). Darwiniana **23**: 37-117.

**Schulz, O. E.** 1912. Beitrage zur Kenntnis der Gattung *Clibadium.* Bot. Jahrb. Syst. **46**: 613-628.

**Spjut, R. W.** 1994. *A systematic treatment of fruit types.* Mem. New York Bot. Gard. **70**: 1-182.

**Spooner, D. M.** 1990. Systematics of *Simsia* (Compositae, Heliantheae). Syst. Bot. Monogr. **30**: 1-90.

**Strother, J. L.** 1991. Taxonomy of *Complaya, Elaphandra, Iogeton, Jefea, Wamalchitamia, Wedelia, Zexmenia,* and *Zyzyxia* (Compositae-Heliantheae-Ecliptinae). Syst. Bot. Monogr. **33**: 1-111.

**Stuessy, T. F. & H.-Y. Liu.** 1983. Anatomy of the pericarp of *Clibadium, Desmanthodium* and *Ichthyothere* (Compositae, Heliantheae) and systematic implications. Rhodora **85**: 213-227.

**Weberling, F.** 1989. *Morphology of flowers* and *inflorescences.* London: Cambridge University Press.

**Wyatt, R.** 1982. Inflorescence architecture: how flower number, arrangement, and phenology affect pollination and fruit-set. Amer. J. Bot. **69**: 585-594.