

**LEUCANTHEMOPSIS (GIROUX) HEYWOOD — A NEW
GENUS OF THE COMPOSITAE — ANTHEMIDEAE**

by

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It is a pleasure to dedicate this paper to Professor S. Rivas Goday under whose patronage my first account of this group of plants was published in 1954.

INTRODUCTION

Several conflicting classifications of the *Chrysanthemum-Leucanthemum-Tanacetum* complex of genera have been proposed (BRIQUET, 1916; HEYWOOD, 1954, 1959; HARLING, 1951; TzVELEV, 1961). Following a series of studies, undertaken during the past twenty years, on the anatomy, morphology, cytology and chemistry of the group a revised classification has been proposed for use in *Flora Europaea* (HEYWOOD, 1975), details of which will be published separately (HEYWOOD, 1975a; HEYWOOD and HUMPHRIES, 1976, 1976a).

One of the most interesting and debatable groups is that comprising the dwarf mountain species *Tanacetum/Chrysanthemum alpinum*, *pallidum*, *pulverulentum*, *radicans* and allies which are concentrated in the Iberian peninsula and N. W. Africa. They have been variously placed in *Pyrethrum*, *Tanacetum*, *Chrysanthemum* and *Leucanthemum* but do not fit comfortably in any of these genera and it is proposed to recognize a new genus for them — *Leucanthemopsis* (Giroux) Heywood, based on *Tanacetum* sect. *Pyrethrum* subsect. *Leucanthemopsis* Giroux.

In a study on the fruit anatomy of Mediterranean members of the Anthemideae-Chrysantheminae, GIROUX (1933) showed that the cypselas of *Tanacetum alpinum* possessed characteristics which separated them from both *Tanacetum* sect. *Pyrethrum* and from *Leucanthemum*

although occupying a somewhat intermediate position between them. On the basis of these features Giroux described a new subsection of *Tanacetum* sect. *Pyrethrum* — subsect. *Leucanthemopsis* Giroux.

Later Maire and Rothmaler included several Spanish-North African taxa such as *Tanacetum pallidum* (Miller) Maire and *T. flaveolum* (Hoffmanns. & Link) Rothmaler in Giroux's subsection. In 1954 Heywood published a revision of the Spanish species of the subsection and reviewed their affinities.

HABIT AND MORPHOLOGY

Habit

All the species of *Leucanthemopsis* are caespitose, scapose perennial, usually dwarf with the flowering stems (scapes) seldom exceeding 20 cm. Some species are long-lived perennials, while *L. pulverulenta* subsp. *pulverulenta* rarely persists more than two or three seasons. This contrasts with the genus *Chrysanthemum* which comprises annual species, with the genus *Tanacetum* which consists of tall, non-caespitose perennials, rarely annuals; and with most European species of the genus *Leucanthemum* which are usually tall, non-caespitose perennials apart from *L. paludosum* (Poiret) Bonnet & Barratte which is an annual of uncertain affinities and *L. arundanum* (Boiss.) Cuatrec., which is a densely caespitose perennial belonging to subgenus *Chrysanthemopsis* and resembling *Leucanthemopsis* species in habit although distinct in other features of flower and fruit. The other North African members of *Leucanthemum* subg. *Chrysanthemopsis* show some resemblance to *Leucanthemopsis* in habit and may deserve recognition as a further genus separate from *Leucanthemum* although similar to it in many features. Further work on this North African group of species is being undertaken at Reading. Some members of the European Alpine *L. vulgare* and *L. atratum* complexes show links with *Leucanthemopsis* in habit, leaf-shape and morphology.

Leaf Indumentum

The leaves of the species of *Leucanthemum* are eglandular. The hairs have been studied by HEYWOOD (1973) and shown to be very

shortly stalked and bifurcate with long flattened arms which are superficially continuous with each other and in one plane giving the appearance of simple, unbranched, appressed hairs. Similar types of hair have been found in *Chrysanthemum coronarium* L. and in *Tanacetum corymbosum* (L.) Schultz.-Bip. but not in other species of *Tanacetum* examined.

CYPSELAR STRUCTURE AND ANATOMY

Since BRIQUET (1916) demonstrated the value of the morphology and anatomy of the cypselas in the classification of the Anthemideae, numerous carpological studies on members of the subtribe Chrysanthemineae have been published. The main features found to be of taxonomic value are:

- (1) Cypselas homo- or heteromorphic.
- (2) Shape and curvature of cypselas.
- (3) Number and prominence of ribs.
- (4) Distribution and type of mucilaginous cells on the epicarp and their behaviour on hydration.
- (5) Thickness (number of cell-layers) of the pericarp.
- (6) Presence or absence of vallecular secretory canals.
- (7) Form and degree of development of the pappus.

The main groups in the *Chrysanthemum-Leucanthemum* complex are characterized as follows:

	Homo/heteromorphic	Mucilaginous cells	Vallecular canals
<i>Tanacetum</i>	Homo	—	—
<i>Chrysanthemum</i> ..	Hetero	—	—
<i>Leucanthemum</i> ..	Homo	+	+

The *Leucanthemopsis* group have homomorphic cypselas, epicarpic mucilaginous cells thus agreeing with *Leucanthemum* but like *Tanacetum* there are no vallecular secretory canals. Further studies have

shown that the cypselas are not only intermediate in some respects between these latter genera but possess several characteristic features of their own.

The ribs are variable in number, from 3-10 (11) and not prominent, and the surface of the cypselas has one to several rows of elongate mucilage cells on and around each rib. These cells swell up in a few seconds on hydration and in some cases erupt, causing the whole cypselas to be surrounded by a halo of mucilage. The details vary from species to species. In *Leucanthemum* the mucilage cells are restricted to the apex of the rib and are generally less elongate, discontinuous and produce much less mucilage.

The pericarp is 4-8 cells thick at the ribs but very thin, 1- or rarely 2- to 3-celled between the ribs, thus being much less developed than the multi-layered pericarp of *Leucanthemum* and *Tanacetum*. No vallecular secretory canals have been found in any species of the *Leucanthemopsis* group although Giroux (1931) reported possibly secretory lacunae in *T. alpinum*. We have not been able to find such lacunae in any of the many samples of *T. alpinum* sampled. In *Leucanthemum*, on the other hand, all species contain vallecular secretory canals which are visible by simple external inspection because of the coloration caused by the resin content; they are easily dissected out whole after softening of the cypselas by boiling or maceration.

The cypselas of the *Leucanthemopsis* group are, therefore, highly distinctive within the group and are in fact more similar in some respects to some of the small satellite genera such as *Glossopappus*, *Hymenostemma*, *Coleostephus* and *Lepidophorum* although clearly separable from them.

CYTOLOGY AND EVOLUTION

In common with the majority of other members of the tribe Anthemideae the taxa of *Leucanthemopsis* so far examined cytologically have a base number of $x = 9$. Polyploidy is found in several species. Counts so far recorded are given in Table 1.

L. alpina, as indicated in Table 1, shows a great amount of cytological variation with $2n$, $4n$ and $6n$ races. It is too early to draw firm conclusions but it seems that most of the Pyrenean populations

TABLE 1

Chromosome numbers in Leucanthemopsis

	n	2n	AUTHOR**
<i>L. alpina</i>			
subsp. <i>alpina</i>		18	Zulniska in Shalińska et al. (1959); Contandriopoulous & Favarger (1959); Contandriopoulous (1962); Favarger & Kupfer (1968).
		36	Shimotomai (1938); Polatschek (1966); Contandriopoulous & Favarger (1959); Contandriopoulous (1962); Favarger & Kupfer (1968).
		54	Kupfer & Favarger (1967).
subsp. <i>tomentosa</i>	9	36	Contandriopoulous (1962).
subsp. <i>cuneata</i>	27	54	Kupfer (1971).
<i>L. flaveola</i>	18	36*	Kupfer (1971); Wilcox unpublished.
<i>L. pallida</i>		36	Kupfer (1971); Wilcox unpublished.
<i>L. longipectinata</i>		54*	Wilcox, unpublished.
<i>L. pulverulenta</i>		18*	Wilcox, unpublished.
<i>L. radicans</i>	9	18	Kupfer & Favarger (1967); Favarger & Kupfer 1968).

* New count

** References can be obtained from the standard chromosome lists.

are tetraploid with a hexaploid population occupying a very restricted area in the most glaciated regions (Massif de la Maladetta) and a single diploid count reported from Pas de la Casa. In the western Alps most of the samples counted are diploid, surrounded by tetraploid populations in the central and eastern Alps and in the south flank of the western Alps. Populations from the Tatra mountain in Czechoslovakia and Poland are diploid.

KUPFER (1971) regards the absence or near absence of diploids in the Pyrenees as surprising in view of the centre of gravity of the group being in the Iberian Peninsula and the fact that the Corsican endemic race *T. alpina* subsp. *tomentosa* (as well as *T. pallida* and *T. flaveola* in the north and centre of Spain) are tetraploid and the southernmost populations of *L. alpina* are hexaploid (subsp. *cuneata*). He believes

that this pattern supports the thesis that the group penetrated recently into the Pyrenees.

Further support comes from the morphological similarity between certain Alpine and Pyrenean tetraploid populations. The additional cytological data presented here complicate the picture in that *L. pulverulenta* subsp. *pulverulenta* from N. and C. Spain and Portugal is reported as diploid like *L. radicans* from Sierra Nevada while *L. longipectinata* from Morocco is found to be hexaploid like *L. alpina* subsp. *cuneata*. *L. alpina* probably belongs to the Mediterranean branch of the Tertiary alpine flora with ancestral diploids persisting in the Tatra, Corsica and in the Maritime and W. Alps. The diploid Iberian populations of *L. pulverulenta* and *L. radicans* may also be relict, especially in the latter case, with the tetraploid and hexaploid taxa of *Leucanthemopsis* in Morocco and in C. and N. Spain being more recent migrations. It would be unwise until further counts are made on all taxa of this complex to attempt to draw detailed conclusions.

GENERIC RELATIONSHIPS

In the light of the evidence reviewed above it does not seem desirable to retain the *Leucanthemopsis* group in *Tanacetum* in view of the differences in habit, indumentum, fruit structure and anatomy. Likewise inclusion of the group in the genus *Leucanthemum*, as has sometimes been proposed for *L. alpina*, would be to ignore a similar series of morphological and anatomical differences. The recognition of *Leucanthemopsis* as a separate genus, in some respects intermediate between *Tanacetum* and *Leucanthemum* but with distinctive characters of its own, seems the best solution. It forms a small, fairly homogeneous genus, with *L. alpina* showing closest links with European *Leucanthemum* on the one hand and *L. longipectinata* on the other hand, suggesting links with the N. African group of *Leucanthemum* which itself may warrant generic separation as already mentioned.

TAXONOMY

Leucanthemopsis (Giroux) Heywood, *stat. nov.*

Syn. *Tanacetum* sect. *Pyrethrum* subsect. *Leucanthemopsis* Giroux in *Bull. Soc. Hist. Nat. Afr. Nord.*, 24: 54 (1933); Heywood in *Anal. Inst. Bot. Cavanilles*, 12 (2): 325 (1954).

Pyrethrum sect. *Leucoglossa* DC., *Prodr.* 6: 53 (1838) pro min. parte.

Tanacetum sect. *Leucoglossa* (DC.) Schultz.-Bip. 3- *Alpina* Schultz.-Bip., *Tanacet.*: 53 (1844).

Pyrethrum sect. *Pyrethrum* Willk. in Willk. & Lange, *Prodr. Fl. Hisp.*, 2: 97 (1865).

Pyrethrum sect. *Leucanthemopsis* (Giroux) Tzvelev in Komarov, *Fl. USSR.*, 26: 227 (1961).

Type species: *Leucanthemopsis alpina* (L.) Heywood.

Dwarf, caespitose, subscapose perennials. Leaves pinnatifid or pinnatilobed to pinnatipartite, the number of lobes sometimes reduced to 3-7; eglandular, subglabrous to hairy (tomentose, sericeous or pubescent), the individual hairs flattened, bifurcate-appressed with a very short stem. Capitula solitary, ligulate. Receptacle convex. Ligulate flowers female, the ligules yellow or white, sometimes becoming pink, or sometimes yellowish at the base. Disc flowers hermaphrodite, tubular-campanulate, yellow. Cypselas homomorphic with 3 to 10 (11) ribs, the rib not prominent; mucilaginous (myxogenic) cells in 1 to several, more or less continuous rows on or around each rib, swelling on hydration to surround the cypselas with a prominent mass of mucilage; pericarp thin, usually 1-celled except at the ribs; vallecular secretory canals absent; pappus short, coroniform, entire or crenate. $2n = 18, 36, 54$.

Distribution: Mountains of Europe, from the Carpathians southwards to S. Spain, C. Appennini and C. Jugoslavia, extending into N. Africa, with a major concentration in the Iberian peninsula.

1. *L. alpina* (L.) Heywood, *comb. nov.*

Syn. *Chrysanthemum alpinum* L., *Sp. Pl.*: 889 (1753).

Leucanthemum alpinum (L.) Lam., *Fl. Fr.*, 2: 138 (1778).

Pyrethrum alpinum (L.) Schrank, *Prim. Fl. Salisburg.*: 215 (1792).

Tanacetum alpinum (L.) Schultz.-Bip., *Tanacet.*: 60 (1844).

(a) Subsp. *alpina*.

Mountains of Europe, from the Carpathians southwards to N. C. Spain, C. Appennines and C. Jugoslavia. $2n = 18, 36, 54$.

(b) Subsp. *tomentosa* (Loisel.) Heywood, *comb. nov.*

Syn. *Chrysanthemum tomentosum* Loisel., *Fl. Gall.*, 2: 253 (1828).

Leucanthemum tomentosum (Loisel.) Gren. & Godr., *Fl. Fr.*, 2: 144 (1850). Mountains of Corsica. $2n = 18$.

(c) Subsp. *cuneata* (Pau) Heywood, *comb. nov.*

Syn. [*Pyrethrum cuneatum* Pau, *Soc. Assoc. Pyr.*, 1905-6].

P. pallidum var. *cuneatum* Pau in *Bull. Inst. Cat. Hist. Nat.*, 11: 93 (1906).

Mountains of N. C. Spain — Sierra de Urbión. $2n = 54$.

2. *L. pallida* (Miller) Heywood, *comb. nov.*

Syn. *Chrysanthemum pallidum* Miller, *Gard. Dict.*, ed. 8 (1768),
Excl. syn. et tab. Barrelieri.

C. aragonense Asso, *Syn. Stirp. Arag.*: 123 (1779).

Pyrethrum hispanicum [Salzm. ex Boiss., *Voy. Bot. Midi Esp.*, 2: 316 (1839)] Willk. in Willk. & Lange, *Prodr. Fl. Hisp.*, 2: 98 (1865).

P. sulphureum Boiss. & Reuter, *Diagn. Pl. Nov. Hisp.*, 17 (1842).

P. hispanicum var. *B. laciniatum* Willk. in Willk. & Lange, *Prodr. Fl. Hisp.*, 2: 98 (1865).

P. pallidum (Miller) Pau in *Bull. Inst. Catalana Hist. Nat.*, 6: 89 (1906).

P. aragonense (Asso) Pau in *Bol. Soc. Iber.*, 23: 102 (1925).
Leucanthemum pallidum (Miller) Sampaio, *Fl. Portug.*, ed. 2,
 577 (1946).

Tanacetum pallidum (Miller) Maire in Emberger & Maire,
Pl. Maroc. Nov., 1: 4 (1929); *Bull. Soc. Maroc*, 100 (1931).

(a) Subsp. *pallida*.

*Mountains of C. Spain, extending north to Sierra de Moncayo, and
 south to Sierra Morena. 2n = 36.*

(i) var. *pallida*.

Syn. *Pyrethrum hispanicum* var. *laciniatum* f. *sulphureum* Willk. in
 Willk. & Lange, *Prodr. Fl. Hisp.*, 2: 98 (1864).

(ii) var. *alpina* (Boiss. & Reuter) Heywood, *comb. nov.*

Syn. *P. sulphureum* var. *alpinum* Boiss. & Reuter, *Diagn. Pl. Nov.
 Hisp.*, 17 (1842).

P. hispanicum var. *laciniatum* f. *versicolor* Willk. *loc. cit.*
 (1864).

(b) Subsp. *virescens* (Pau) Heywood, *comb. nov.*

Syn. *Pyrethrum pallidum* var. *virescens* Pau in *Bull. Inst. Catal.
 Hist. Nat.*, 11: 90 (1906).

Mountains of E. Spain.

(i) var. *virescens*.

Syn. *Pyrethrum pallidum* var. *virescens* f. *xanthoglossum* Pau,
loc. cit. (1906).

(ii) var. *bilbilitanum* (Pau) Heywood, *comb. nov.*

Syn. *Pyrethrum pallidum* var. *virescens* f. *bilbilitanum* Pau et f. *leu-
 coglossum* Pau, *loc. cit.* (1906).

c) Subsp. *spathulifolia* (Gay) Heywood, *comb. nov.*

Syn. *Pyrethrum spathulifolium* Gay in Webb & Heldreich, *Cat. Pl.
 Hisp.... ab Blanco lect.*, Paris (1850), *nomen*; in Webb &
 Heldreich, *Appendix exhib. diagn. Hisp. prov. Gicnn.*
 1849 *detex.* Blanco, Paris (1850) *cum descr.*

P. leucanthemifolium Porta & Rigo in *Atti Accad. Agiati*, 9: 34 (1891); Willk., *Suppl. Prodr. Fl. Hisp.*, 84 (1893).

P. pallidum var. *spathulaefolium* (Gay) Pau, *loc. cit.* (1906).

Tanacetum pallidum subsp. *spathulifolium* (Gay) Font Quer & Rothm., *Fl. Iber. Sel.*, Cent. 1, No. 91 (1934).

S. E. Spain.

3. *L. flaveola* (Hoffmanns. & Link) Heywood, *comb. nov.*

Syn. *Pyrethrum flaveolum* Hoffmanns. & Link, *Fl. Port.*, 2: 341, t. 104 (1834); Willk. in Willk. & Lange, *Prodr. Fl. Hisp.*, 2: 99 (1864).

Chrysanthemum flaveolum (Hoffmanns. & Link) Coutinho, *Fl. Port.*, 633 (1913), ed. 2, 748 (1939).

Tanacetum flaveolum (Hoffmanns. & Link) Rothmaler in *Index Seminum Stat. Agron. Nat. Lusit. 1939*, 3 (1940).

N. W. Spain, Portugal. $2n = 18$.

4. *L. longipectinata* (Font Puer) Heywood, *comb. nov.*

Syn. *Leucanthemum longipectinatum* Font Quer, *Iter. Marocc. 1927*, No. 671 (1927).

Tanacetum longipectinatum (Font Quer) Maire in Sennen & Mauricio, *Cat. Fl. Rif Or.*, 61 (1934).

Tanacetum pallidum subsp. *longipectinatum* (Font Quer) Maire in Emberger & Maire, *Pl. Marocc. Nov.*, 1: 4 (1929).

N. Africa, Morocco. $2n = 54$.

5. *L. pulverulenta* (Lag.) Heywood, *comb. nov.*

Syn. *Pyrethrum pulverulentum* Lag., *Varied. Ciencias*, 40 (1805).

Pyrethrum hispanicum var. *pinnatifidum* forma *pulverulentum* Willk. in Willk. & Lange, *Prodr. Fl. Hisp.*, 2: 98 (1864).

Pyrethrum pallidum subsp. *pulverulentum* (Lag.) C. Vicioso in *Anal. Jard. Bot. Madrid*, 6 (2): 83 (1946).

Leucanthemum pulverulentum (Lag.) Sampaio, *Herb. Portug.*, 132 (1913).

Tanacetum pallidum subsp. *pulverulentum* (Lag.) Font Quer & Rothm., *Fl. Iber. Sel.*, Cent. 1, No. 90 (1934).

(a) Subsp. *pulverulenta*.

N. and C. Spain, Portugal in non-calcareous substrates. $2n = 18$.

(b) Subsp. *pseudopulverulenta* (Heywood) Heywood, *comb. nov.*

Syn. *Tanacetum pulverulentum* subsp. *pseudopulverulentum*. Heywood in *Anal. Inst. Bot. Cavanilles*, 12 (2): 331 (1954).

Mountains of E. and S. E. Spain on calcareous substrate.

6 *L. radicans* (Cav.) Heywood, *comb. nov.*

Syn. *Pyrethrum radicans* Cav., *Descr. Pl. 1801*, 199 (1802); Lag. & Rodr., *An. Ci. Nat.*, 5: 286 (1802).

Pyrethrum hispanicum var. *pinnatifidum* forma *radicans* Willk. in Willk. & Lange, *Prodr. Fl. Hisp.*, 2: 98 (1864).

Tanacetum pallidum subsp. *radicans* (Cav.) Maire in Emberger & Maire, *Pl. Maroc Nov.*, 4 (1929).

Tanacetum radicans (Cav.) Schultz.-Bip., *Tanacet.*, 48 (1884).

S. Spain, Sierra Nevada. Schistose mountain screes above 2500 m, with a disjunct population in the Serranía de Cuenca. $2n = 18$.

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RESUMEN

Se propone un nuevo género *Leucanthemopsis* para el grupo de especies montanas de pequeño porte, centrado en la Península Ibérica y N. O. de Africa, que comprende *Tanacetum/Leucanthemum repenium*, *pallidium* y otros. Estas especies forman un grupo natural distinto del de *Tanacetum* y *Leucanthemum*, aunque se acerca a ambos en algunos rasgos. Se discute su morfología, estructura cypselar, citología y relaciones evolutivas, y se expone un tratamiento formal de su taxonomía.

SUMMARY

A new genus, *Leucanthemopsis* Heywood, is proposed for the group of dwarf mountain species, centred in the Iberian Peninsula and N. W. Africa, comprising *Tanacetum/Chrysanthemum/Leucanthemum repenium*, *pallidium* and allies. These species form a natural group which is distinct from *Tanacetum* and *Leucanthemum* although approaching both of them in some features. Their morphology, cypselar structure and cytology and evolutionary relationships are discussed and a formal treatment of their taxonomy given.

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