

A NEW SUBTRIBE IN THE HELIANTHEAE (COMPOSITAE): ESPELETIINAE.

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The genus Espeletia is known as the most representative taxonomic group of the paramo plant life. It is one with a high degree of diversification and endemism, yet growing in an apparently uniform environment. A few of the morphological modifications may be explained by mutation, isolation and ecological adaptation, as the variation in habit. This and other questions will be discussed, along with morphological study of every taxa, arranged according to a new natural classification, in a forthcoming monograph near completion. The purpose of this paper is to offer a summary of the main taxonomic conclusions affecting the present classification and nomenclature of the group, in order to make them available to the interested people before the publication of the whole revision.

The genus Espeletia Mutis was first published by Humboldt and Bonpland in *Plantae Aequinoctiales*, 1808, with three species from the Bogotá area. The floral characterization given was clearly that of the Heliantheae. Bonpland, in his remarks considered the genus close to Silphium from which it can be distinguished by the heavy white-woolly or silvery indumentum, by the phyllaries and by the angulate fruits. Surprisingly no mention was made of the unusual growth form of these plants. Humboldt, 1914, eventually, published a Trixis neriifolia Bonpl. name given to a resiniferous tree called "incienso" growing in the Andean forests of Silla de Caracas. Schultz Bip. transferred this species to the genus Espeletia in Weddell (1856) *Chloris Andina*. Weddell made two groups, one "Frutices" with two species (E. neriifolia, E. banksiaeefolia) and the other "Herbae caespitosae" with nine species. In 1870, Ernst working in Caracas, unaware of the transfer made by Schultz Bipontinus ex Weddell of the Trixis neriifolia, made a new genus for this species, Libanothamnus, which has been regarded as synonym to Espeletia by all subsequent botanist. Standley in 1915 was the first to mention and to publish photographs made by Jahn on the special stipitate rosette growth form of some species of Espeletia; in his key for 17 species he accepted Weddell's main division between trees and other forms. The real scientific treatment of Espeletia, complete at that time, was made by A. C. Smith and M. Koch, 1935, based in gross morphology, floral anatomy and palynology. Smith used largely his field experience in Colombia for the description of the habit and ecologic considerations. Thirty species distributed between Colombia and Venezuela, one extending into Ecuador, were recognized. They were arranged in

a workable key, in which the main division was between trees ("much-branched woody caudices") with 3 species, and Herbs ("caudex simple, subterranean or erect") with the remaining 27 species. Smith & Koch considered in the genus five groups defined on basis of habit: 1) branched caudices, 2) subligneous flowering branches, 3) herbaceous, 4) broad leaves with stout erect caudex, and 5) subterranean caudex with narrow leaves. A thorough comparative study of the groups, using many characters including floral anatomy, was presented. Important phylogenetic considerations were brilliantly exposed. Smith recognized the close connection existing between Espeletia evolution and paramo ecology. He considered that the forebearer of the genus was derived from a woody ancestor similar to Polymnia which, as it migrated to the higher Andes adapted to the new environment; the main evolutionary trend would be from woody to herbaceous habit, a view generally accepted in recent times. Many of the diversification trends singled out by Smith may be sustained. With the considerable amount of information on Espeletia we have today, however, a new evaluation of the characters to be used for a natural classification has been necessary.

Since the classic publication by Smith & Koch in 1935, a flow of new collections from Colombia and Venezuela had been accumulating; this accounts for 61 new binomials totaling 91 validly published species of Espeletia in 1969, the year that I engaged in intensive final work to produce a monograph. This increase in the number of species was already shown in the excellent treatment of the genus by A. Aristeguieta in his vol. 10 of Compositae for the Flora of Venezuela, 1965, in which he recognizes 45 species, 27 more than in the Smith's monograph. Furthermore, since 1970 thirty-three more new species have been described, in great part due to my trips to the paramos and subparamos of Colombia and Venezuela in 1969, 1970 and 1973, with the great help and efficient field activity of my friends and field associates Drs. L. Ruiz-Terán, M. López-Figueiras of Merida, Drs. García Barriga & R. Jaramillo of Bogotá and A. Cleef of Utrecht working in Colombia. The main purpose of my recent trips was, besides the eventual collection of undescribed species, to establish the true vegetative characteristics and type of inflorescences of many species, mainly the Venezuelan, which I had not had the opportunity of seeing "in vivo" before.

On these field trips, I became acquainted with the habit and other vegetative characters of almost all the species, features which can not be seen on the fragmentary herbarium collections with usually poor field annotations. The most important findings were already initiated the first day I collected in Venezuela when I discovered in Páramo del Zumbador that E. jahmii had very showy terminal inflorescences at the center of monocarpic, big rosettes, reminding me of pictures of Argyroxiphium. Similar observation followed near Páramo del Batallón, where I

found specimens of E. atropurpurea with broadly paniculate, profusely branched 2 m tall, terminal inflorescences, and so on. For every species, an attempt was made to find out its growth habit which often is obscured by the degradation of vegetation caused by excessive grazing and fires. The field observation were checked later with dried or preserved specimens at the herbarium, and after thorough study, several growth forms could be defined for Espeletia. These growth forms correlated with other vegetative and inflorescential characters proved to be of sufficient taxonomic importance to draw a new classification at the generic level. Following are listed in short the main types of growth form which prove to be of basic taxonomic significance.

1. Trees. Main erect trunk branched above the middle or at least the fourth of the total height. Branching dichasial or/and pleiochasial, the main stem and main branches monopodial. Alternat leaves. Three types considered:

a) Inflorescences terminal. Distal branchlets growing sympodially. Leaf bases tubular, closed, embracing the stems. Rarely opposite leaves present. Fig.1

b) Inflorescences axillary of the upper leaves crowded at the branchlet-ends. Leaf bases closed, tubular or ring-shaped.

c) Inflorescences terminal. Branchlets growing sympodially. Leaf bases open.

2. Caulirosulae parvae ramosae. Dwarf shrubs or fruticeta, branched near the base, the branches first monopodial, later sympodial, usually decumbent or prostrate, ending each with a large dense rosette. Inflorescence single, terminal to each rosette, this dying after florescence, hence monocarpic.

3. Acauliroslae with tuberose caudex, which might have short branching or lateral buds near the ground. Inflorescence terminal, the main supporting rosette dying after fructification, with further development of lateral buds. Rosettes monocarpic.

4. Acauliroslae, with simple tuberose caudex and terminal inflorescence. Monocarpic.

5. Acauliroslae with simple tuberose caudex, with axillary inflorescences. Polycarpic rosettes.

6. Acauliroslae with rhizome, or semituberose subterranean caudex. Polycarpic rosettes with axillary inflorescences.

7. Caulirosula. Erect stem terminated with a large and dense rosette of permanent leaves. These are coriaceous and whitish lanate or tomentose. Below the crowded living leaves, often remain the marcescent leaves in the form of a dense cloak covering the whole length of the stem which looks much thick (up to 50 cm. diam) compared to the real width of the trunk (about 6-12 cm. diam). This is the most typical form of "frailejón". The trunk is fundamentally undivided, but eventually may be found with a pleiochasial branching near the base; the few branches in this case all grow erect and undivided, leaving the branching unnoticed, apparently,

without close examination. Accidental destruction of the terminal bud of the very young rosette may cause branching. There are two different types of caulirosula: with

a) Inflorescence single, central, terminal, usually very large. The whole plant dying after fructification. Monocarpic. Fig. 2.

b) Inflorescences numerous, simultaneous, axillary, the caulirosula growing acropetally, indefinitely, along with continued flowering. Polycarpic. Fig. 3.

The biotype of "caulirosula" with short or long stem, is the most characteristic feature of the plant life of the high tropical mountains. It accounts for the physiognomy of the most part of the paramo vegetation. I have called the attention to this growth form since 1934 when I defined it and its collective designation (caulirosuletum). In 1934, I listed caulirosula and caulirosuletum under the heading of nanoarboretum. After many years of experience I consider that caulirosula has to be treated as an independent life-form with its own architecture either simple or branched.

With respect the inflorescences, the different types interesting here for taxonomic purposes are summarized as follows:

1) The thyrsse of definite dichasial panicle with opposite branching and decussate bracts. The primitive basic inflorescence type. Fig. 3.

2) The definite monochasial panicle with alternate branches, branchlets and bracts, usually adopting corymbiform arrangement. Fig. 4 right.

3) The definite racemose, simple or compound disposition, with alternate branching and bracts. Fig. 4 left.

4) The monocephalous scapi with opposite bracts.

5) The monocephalous scapi with alternate bracts. Each type of inflorescence is explained in order to avoid the existing confusion in the use of some technical terms (e.g. thyrsse). It is the general assumption that number 2 is derived from number 1 by the way of abortion of half of the branches (simplification trend). The same explanation, following different mathematical rules, may be used to derive number 3 from number 1, number 4 from 1 or 3, and number 5 from number 2. Of all these types, the more elaborate are the first two, which show a complexity of structure in many cases, with some irregularity about the flowering succession. The explanation must be that these inflorescences are in most cases compound inflorescences on monopodial growing axes until vegetative maturity. For this reason the use of the Troll's concept of synflorescence is here justified. It helps to interpret the variations in the rate of growth of different branches (partial inflorescences) and in the sequence of the anthesis at different levels. Some observations also, indicate the influence of the environment on the eventual asymmetry or other irregularities in the development of inflorescences.

A thorough study of more than one hundred recognizable species, presently known under Espeletia, proves that their differences in habit and inflorescence type are significant enough to base on them seven new basic groups separable at the genus level.

On the other hand, these new established genera have very much in common with respect to floral, fruit, heads and anatomic features which indicates that they compose a major taxonomic unity at the level of subtribe. The main characteristics of this subtribe are: Achenes triangular with at least the adaxial angle very acute, the abaxial side more or less convex and the surface smooth, the epidermis with amorphous traces of black pigment in the cells. Phyllaries at maturity thicker and harder, more or less embracing the achenes especially towards the base, often retaining them for a long time in the marcescent heads. Ray flowers 2-pluriseriate (rarely uniseriate); style branches with two marginal, thickened, stigmatic lines. Disc corollas tubular with broadened limb, 5-dentate. Anther appendices never glandular. Basic chromosome number  $x=19$ . Habit: trees, caulirosettes or acaulirosettes with coriaceous, xeromorphic, usually large leaves, at least abaxially densely hairy. All genera growing in cold and cold-temperate regions of the tropical high Andean mountains (paramos, subparamos, Anden forests near the timber line).

#### References

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ESPELETIINAE Cuatr. subtrib. nov. *Helianthea*rum

Capitula heterogama. Receptaculum paleaceum nudum vel pilosum. Flores numerosi, ei radii feminei 2-pluriseriati, ei disci pseudohermaphroditi masculi fungentes. Corollae radii lamina ligulata alba vel lutea raro rubescens vel purpurea, aut nulla, tubulo fere semper barbato. Rami stylorum radii binis lineis stigmaticis crassiusculis marginalibus. Corollae disci tubulares 5 dentatae, plerumque luteae. Antherae basi breviter sagittatae, cellulis exothelialibus oblongis in parietibus transversis noduliferis, appendicibus apicalibus ovatis mediale carinatis, nunquam glanduliferis. Stylus florū disci distale dense papilloso-pilosulus apice breviter bilobato non stigmatico, basi partiale in discum nectariferum tubulosum immersus. Achaenia exteriora oboviedo-triangulata facie abaxiali plus minusve convexa vel gibbosa, interiora plerumque oblonga quadrangulata; omnia glaberrima, laevia, calva, tantum rarissime pappo 1-3 paleis.

Involucrum pluriseriatum, phyllariis subherbaceis plus minusve inaequalibus, introrsum gradatim minoribus, imbricatis. Phyllaria fertilia maturitate plus minusve indurata, amplectentiuscula, achaenia retinentia. Paleae persistentes rigidulae amplectentes.

Grana pollinis tricolporata, a sphaeroideis prolatis usque sphaeroideis oblates, ora saepe lalongata; exinium spinosum; tectum punctulatum, baculatum; cavum vice infratecti absenti.

Numerus basicus chromosomatum  $x = 19$ .

Arbores, aut frutices inferne ramosi vel caule simplice porrecto plus minusve elevato vel caudice rhizomatoso vel tuberoso, perennifoliati; plerumque polycarpici, aliquot monocarpici. Folia alterna, coriacea, vaginantia, in nodis valde approximatis nascentia, ad extremum caulis vel ramulorum crebra congeste fasciculata vel copiose rosulata, (saepe caulirosula). Lamina foliorum plerumque elongata, xeromorphicā et saltem abaxiale dense trichomatosa. Schyzogeni canales et cellulae resiniferae universales in planta, kauranoide tetracyclici-diterpenoides efferentes.

Habitus foliorum rosulae vel subrosulae plerumque late comosus, valdeque conspicuus. Capitula parva vel lata in paniculis cymosis thyrsoides, dichasialibus foliis decussatis, vel monochasialibus foliis alternis plerumque corymbiformibus, vel valde simplicibus usque ad singulum capitulum.

Species omnia regiones frigidae vel temperate frigidae Andium tropicorum Americae incola.

Typus: *Espeletia* Mutis ex Humboldt & Bonpland, Pl. Aeq. 2: 10, 1808. Species typica *Espeletia grandiflora* Humboldt & Bonpland, l.c. 2: 11. 1808.

Alia genera sunt: *Libanothamnus*, *Ruizophzia*, *Tamania*, *Carramboa*, *Espeletiopsis* et *Coespeletia*, illa clavis et diagnoses sequuntur.

Clavis genericorum:

1. - Synflorescentiae terminales, floribundae.
2. - Arbores vel raro caulirosulae simplices. Vagina foliorum tubularis. Ligulae albae vel ochroleucae raro luteae. Receptaculum glabrum. Achaenia calva. Libanothamnus.
- 2'. Arbores vel frutices parvi vel caulirosulae simplices. Vagina foliorum aperta.
3. - Achaenia pappo 1-3 paleis instructa. Arbores. Ligulae luteae. Receptaculum parce pilosum. Tamania.
- 3'. Achaenia calva. Caulirosulae erectae et simplices, vel parvae, ramosae; foliis crebris dense rosulatis. Ligulae albae, luteae, aut rubro-purpureae. Receptaculum glabrum vel sparse pilosum. Ruilopezia.
- 1'. Synflorescentiae axillares. Achaenia calva.
4. - Arbores. Vagina foliorum tubularis. Folia ampla viridia. Receptaculum hirtum. Inflorescentiae floribundae ligulis luteis. Carramboa.
- 4'. Caulirosulae, erectae et elevatae vel subsessiles vel sessiles, simplices, interdum e basi paucе ramosae. Vagina foliorum aperta saepe grandis. Inflorescentiae aut floribundae aut modice floriferae vel valde reductae. Ligulae plerumque luteae, interdum albae, aut purpureae.
5. - Synflorescentiae corymboide-paniculatae, ramis ramulis foliis bracteisque alternis. Ligulae plerumque luteae, aut albae. Espeletiopsis.
- 5'. Synflorescentiae dichasiales vel racemiformes. Ligulae luteae.
6. - Synflorescentiae racemi-formes, ramis ramulis bracteisque alternis. Coespeletia.

6'. *Synflorescentiae dichasiales; ramis, ramulis, foliisque saltem proximalibus semper oppositis.*

Espeletia.

LIBANOTHAMNUS Ernst, Vargasia, 7: 186. 1870.

Arbores perennifoliae foliis ad extremos ramulorum saepe glomeratis vel rosulatis raro caulirosula simplice.

Folia alterna, raro aliqua opposita. Vagina foliorum tubularis. Lamina anguste elliptica vel oblongo elliptica, rigide coriacea multiparalleli-nervata nervis patulis (angulo 70-90° ascendentibus) valde approximatis, supra viridis, abaxiale lanata vel tomentosa.

*Synflorescentiae terminales, corymboide paniculatae multicapitulatae, ramis alternis, interdum aliquis oppositis; foliis partis proximalis vegetativae alternis, interdum oppositis.*

Capitula parva vel mediana, radiata vel pseudodiscoidea. Ligulae albae vel eburneae, raro ochroleucae luteae vel obsoletae. Corollae disci limbo subcampanulato, dentato, luteo vel viridi. Receptaculum conicum glabrum. Phyllaria fertilia vel paleae saepe copiosis glandulis obovoideis ad marginibus notatis. Achaenia epapposa.

Species regiones temperate frigidae tropicorum Andium habitant. Venezuela, Colombia.

Typus: Libanothamnus neriifolius (B. ex H.) Ernst. = Trixis neriifolia Bonpland ex Humboldt.

LIBANOTHAMNUS ARBOREUS (Aristeg.) Cuatr. comb. nov.

Espeletia arborea Aristeg. Bol. Soc. Venez. Cienc. Nat. 20: 286. 1959.

LIBANOTHAMNUS BANKSIAEFOLIUS (Sch. Bip. et Ettingsh.) Cuatr. comb. nov.

Espeletia banksiaeefolia Sch. Bip. et Ettingsh. ex Wedd. Chl. And. 1: 67. 1856.

LIBANOTHAMNUS GLOSSOPHYLLUS (Mattfeld) Cuatr. comb. nov.

Espeletia glossophylla Mattfeld Nottizblatt 10: 702. 1929.

LIBANOTHAMNUS GRANATESIANUS (Cuart.) Cuatr. comb. nov.

Espeletia granatesiana Cuatr. Phytologia 27: 44. 1973.

LIBANOTHAMNUS GRIFFINII (Ruiz-Terán & López-Figueiras) Cuatr. comb. nov.

Espeletia griffinii Ruiz-Terán & López-Figueiras, Rev. Fac. Farm. Univ. Andes Merida, 17: 7. 1976.

LIBANOTHAMNUS HUMBERTII (Cuart.) Cuatr. comb. nov.

Espeletia humbertii Cuatr. Not. Syst. Paris 15: 233. 1956.

LIBANOTHAMNUS LISCANOANUS (Cuatr.) Cuatr. comb. nov.

Espeletia liscanoana Cuatr. Phytologia 27: 41. 1973.

LIBANOTHAMNUS LUCIDUS (Aristeg.) Cuatr. comb. nov.

Espeletia lucida Aristeg. Compositae in Fl. Venezuela 10(1): 420. 1964.

LIBANOTHAMNUS OCCULTUS (Blake) Cuatr. comb. nov.

Espeletia occulta Blake, Contr. U. S. Nat. Herb. 20: 537. 1924.

LIBANOTHAMNUS SPECTABILIS (Cuatr.) Cuatr. comb. nov.

Espeletia spectabilis Cuatr. Phytologia 27: 46. 1973.

LIBANOTHAMNUS SUBNERIIFOLIUS (Cuatr.) Cuatr. comb. nov.

Espeletia subneriifolia Cuatr. Mutisia 16: 3. 1953.

LIBANOTHAMNUS TAMANUS (Cuatr.) Cuatr. comb. nov.

Espeletia tamana Cuatr. Phytologia 27: 171. 1973.

LIBANOTHAMNUS WURDACKII (Ruiz-Terán & López-Figueiras) Cuatr. comb. nov.

Espeletia wurdackii Ruiz-Terán & López-Figueiras, Rev. Fac. Farm. Univ. Andes Merida, 17: 1. 1976.

RUILOPEZIA Cuatr. gen. nov. Heliantheum, subtrib. Espeletiinae.

Caulirosulae simplices monocarpicae, vel paulo et congeste pauciramosae. Caules dense adpressoque cum foliis marcescentibus tecti.

Folia coriacea flexibilia vel rigida crebra congeste rosulata. Vagina foliorum aperta. Lamina foliorum anguste elliptica elongata vel linearis, nervis secundariis angulo acuto vel patulis, abaxiale dense lanata vel sericea.

Synflorescentiae terminales coryboide vel thyrsoidem paniculatae, multicapitatae, ramis alternis, foliis partis proximalis vegetativae alternis, rosula subtendenti monocarpica.

Capitula mediana radiata vel pseudo-discoidea. Ligulae albae, viridulae, eburneae, luteae raro rubescentes vel absentes. Corollae disci limbo subcampanulato dentato luteo, eburneo vel viridi, raro rubescenti. Receptaculum conicum vel convexum glabrum vel parce pilosum. Phyllaria et paleae saepe glanduliferae. Achaenia epapposa.

Species regiones frigidae et temperate frigidae tropicorum Andium incola. Venezuela.

Genus dicatus amici, professores Universitatis Andium Meridensis, Luis Ruiz Terán et Manuel López Figueiras, clari botanici, diligentissimi consociati exploratores Venezuelensis florae, praecipue paramorum, qui plures species Espeletiinarum conjuncte invenerunt.

Typus: Espeletia figureirasi Cuatr.

RUILOPEZIA ATROPURPUREA (A. C. Sm.) Cuatr. comb. nov.

Espeletia atropurpurea A. C. Sm. Brittonia 1: 508. 1935.

RUILOPEZIA BRACTEOSA (Standl.) Cuatr. comb. nov.

Espeletia bracteosa Standl. Am. Journ. Bot. 2: 484. 1915.

RUILOPEZIA BROMELIOIDES (Cuartr.) Cuatr. comb. nov.

Espeletia bromelioides Cuatr. Phytologia 29 (5): 369. 1975.

RUILOPEZIA CARDONAE (Cuartr.) Cuatr. comb. nov.

Espeletia cardonae Cuatr. Rev. Acad. Colomb. Cienc. 5: 20. 1942.

RUILOPEZIA COLORADARUM (Cuartr.) Cuatr. comb. nov.

Espeletia coloradarum Cuatr. Phytologia 29 (5): 372. 1975.

RUILOPEZIA CUATRECASASII (Ruiz T. & López F.) Cuatr. comb. nov.

Espeletia cuatrecasassii Ruiz-Terán & López-Figueiras, Rev. Fac. Farm. Univ. Andes Mérida 14: 5. 1974.

RUILOPEZIA FIGUEIRASII (Cuartr.) Cuatr. comb. nov.

Espeletia fiqueirasi Cuatr. Phytologia 29: 475. 1971.

RUILOPEZIA FLOCCOSA (Standl.) Cuatr. comb. nov.

Espeletia floccosa Standl. Am. Journ. Bot. 2: 481. 1915.

RUILOPEZIA FRAILEJONOTA (Aristeg.) Cuatr. comb. nov.

Espeletia frailejonota Aristeguieta, Compositae in Fl. Venez. 10 (1): 425. 1964.

RUILOPEZIA GRISEA (Standl.) Cuatr. comb. nov.

Espeletia grisea Standl. Am. Journ. Bot. 2: 477. 1915.

RUILOPEZIA HANBURIANA (Cuartr.) Cuatr. comb. nov.

Espeletia hanburiana Cuatr. Soc. Venez. Cienc. Nat. 17: 86. 1956.

RUILOPEZIA JABONENSIS (Cuartr.) Cuatr. comb. nov.

Espeletia jabonensis Cuatr. Phytologia 23: 360. 1972.

RUILOPEZIA JAHNII (Standl.) Cuatr. comb. nov.

Espeletia jahnii Standl. Am. Journ. Bot. 2: 479. 1915.

RUILOPEZIA JOSEPHENSIS (Cuartr.) Cuatr. comb. nov.

Espeletia josephensis Cuatr. Phytologia 29 (5): 374. 1975.

RUILOPEZIA LEUCACTINA (Cuartr.) Cuatr. comb. nov.

Espeletia leucaactina Cuatr. Phytologia 29: 377. 1945.

RUILOPEZIA LINDENII (Sch. Bip. ex Wedd.) Cuatr. comb. nov.

Espeletia lindenii Sch. Bip. ex Wedd. Chl. And. 1: 67.  
1856.

RUILOPEZIA LOPEZ-PALACII (Ruiz-Terán & López-Figueiras.) Cuatr. comb. nov.

Espeletia lopez-palacii Ruiz-Terán & López-Figueiras, Rev. Fac. Farm. Univ. Andes Mérida, 17: 13. 1976.

RUILOPEZIA MARCESCENS (Blake) Cuatr. comb. nov.

Espeletia marcescens Blake, Contr. U. S. Nat. Herb. 20: 536. 1924.

RUILOPEZIA MARGARITA (Castr.) Cuatr. comb. nov.

Espeletia margarita Castr. Phytologia 27: 49. 1973.

RUILOPEZIA PALTONIOIDES (Standl.) Cuatr. comb. nov.

Espeletia paltonioides Standl. Am. Journ. Bot. 2: 482. 1915.

RUILOPEZIA RUIZII (Castr.) Cuatr. comb. nov.

Espeletia ruizii Castr. Phytologia 23: 362. 1972.

RUILOPEZIA VIRIDIS (Aristeg.) Cuatr. comb. nov.

Espeletia viridis Aristeg. Bol. Soc. Venez. Cienc. Nat. 20: 279. 1959.

TAMANIA Cuatr. gen. nov. Heliantheum subtrib. Espeletinae.

Arbores perennifoliae foliis ad extremos ramulorum  
glomeratis vel rosulatis.

Folia alterna. Vagina foliorum semicircularis, aperta.  
Lamina foliorum coriacea  $\pm$  flexibilis, late oblanceolata vel  
oblance-elliptica, nervis secundariis abaxiale prominulis 2-6 mm  
inter se distantibus, angulo 30-50° ascendentibus, indumento  
dense adpresso sericeo molliterque leporino.

Synflorescentiae terminales corymboide paniculatae multi-  
capitulatae, ramis alternis, foliis partis proximalis vegeta-  
tivae alternis.

Capitula parva, radiata. Ligulae luteae. Corolla disci  
limbo subcampanulato, dentato, luteo. Receptaculum conicum  
parce pilosulum. Phyllaria paleaque eglanduliferae. Achaenia  
pappi 3-1 paleis lanceolatis rigidis, rarissime aliqua calva.  
Flores masculi etiam saepe pappo 1-3 paleis tenuibus linearibus.

Species regiones temperate frigidae tropicorum Andium.  
Páramo de Tama, Colombia, Venezuela.

Typus: Espeletia chardonii A. C. Smith. Synonym:  
Espeletia leporina Castr.

TAMANIA CHARDONII (A. C. Sm.) Cuatr. comb. nov.

Espeletia chardonii A. C. Smith, Bol. Soc. Venez. Cienc.  
Nat. 7: 237. Apr. 1942. Venezuela. Espeletia leporina Castr.

Rev. Acad. Colomb. Cienc. 5: 17, fig. 3-5; 9D, C; pl 2. June 1942. Colombia.

CARRAMBOA Cuatr. gen. nov. *Heliantheum* subtrib. *Espeletiinae*.

Arbores perennifoliae bene vel parum ramosae, foliis latis ad extremos ramulorum glomeratis, seu rosulatis.

Folia alterna. Vagina foliorum tubularis. Lamina foliorum ampla coriacea ovata vel obovata vel elliptica, viridis, nervis secundariis abaxiale prominentibus, inaequalibus, angulo 60-80° ascendentibus, 1-6 cm inter se distantibus, abaxiale moderate villosa lanuginosa vel tomentosa.

Synflorescentiae axillares, corymboide paniculatae multicapitulatae, ramis proximalibus oppositis, alteris plerumque alternis, foliis partis proximalis vegetativae oppositis.

Capitula parva, radiata; ligulae amotis 6-8(-10) mm. Corollae disci limbo subcampanulato dentato luteo. Ligulae luteae. Receptaculum convexo-conicum hirtum. Phyllaria fertilia et paleae disci eglanduliferae, vel glanduliferae Achaenia epapposa.

Species regiones temperate frigidae tropicorum Andium habitant. Venezuela. Nomen incolarum: "carrambo".

Typus: Espeletia pittieri Cuatr.

CARRAMBOA BADILLOI (Cuart.) Cuatr. comb. nov.

Espeletia badilloi Cuatr. Ciencia (Mexico) 6: 261. 1945.

CARRAMBOA PITTIERI (Cuart.) Cuatr. comb. nov.

Espeletia pittieri Cuatr. Ciencia (Mexico) 6: 262. 1945.

CARRAMBOA LITTLEI (Aristeg.) Cuatr. comb. nov.

Espeletia littlei Aristeg. Compositae in Fl. Venez. 10(1): 433. 1964.

CARRAMBOA TRUJILLENSIS (Cuart.) Cuatr. comb. nov.

Espeletia trujillensis Cuatr. Mutisia 16: 5. 1953.

CARRAMBOA RODRIGUEZII (Cuart.) Cuatr. comb. nov.

Espeletia rodriguezii Cuatr. Phytologia 29 (5): 379. 1975.

ESPELETOIPSIS Cuatr. gen. nov. *Heliantheum*, subtrib.

Espeletiinae.

Caulirosulae simplices caule valde elongato erectoque vel brevi, interdum pauciramoso, polycarpicae. Caulis plerumque dense adpresseque cum foliis marcescentibus tectus, vel interdum mox denudatus.

Folia alterna coriacea plerumque rigida vel plus minusve flexibilia crebra congeste rosulata. Vagina aperta plana congeste imbricata. Lamina late vel anguste elliptica vel linearis abaxiale dense lanata vel sericea, nervis secundariis plerumque prominentibus.

Synflorescentiae vel inflorescentiae axillares, cymosomonchasiales corymboide vel subcorymboide paniculatae, multiflorae vel interdum valde reductae, ramis alternis aliquando parcissimis oppositis; foliis partis proximalis vegetativae semper alternis.

Capitula parva vel mediana, radiata vel eradiata; ligulae luteae raro albae; corollae disci limbo tubuloso-campanulato dentato luteo interdum pururascenti. Grana pollinis spinis 3-7 micronis longis. Receptaculum convexum vel conicum, glabrum vel pilosum. Achaenia calva.

Species regiones frigidae vel temperate frigidae, paramorum Andium tropicae Americae incola. Colombia et Venezuela.

Typus: Espeletia jimenez-quesadae Cuatr.

ESPELETOIPSIS ANGUSTIFOLIA (Cuart.) Cuatr. comb. nov.

Espeletia angustifolia Cuatr. Bol. Soc. Venez. Cienc. Nat. 17 (85): 80. 1956.

ESPELETOIPSIS BOGOTENSIS (Cuart.) Cuatr. comb. nov.

Espeletia bogotensis Cuatr. Rev. Acad. Colomb. Cienc. 3: 427. 1940.

ESPELETOIPSIS CALDASII (Cuart.) Cuatr. comb. nov.

Espeletia caldasii Cuatr. Rev. Acad. Colomb. Cienc. 3: 431. 1940.

ESPELETOIPSIS COLOMBIANA (Cuart.) Cuatr. comb. nov.

Espeletia colombiana Cuatr. Rev. Acad. Colomb. Cienc. 3: 249. 1940.

ESPELETOIPSIS CORYMBOSA (Humb. & Bonpl.) Cuatr. comb. nov.

Espeletia corymbosa Humb. & Bonpl. Pl. Aequin. 2: 16. 1808.

ESPELETOIPSIS CRISTALINENSIS (Cuart.) Cuatr. comb. nov.

Espeletia cristalinensis Cuatr. Phytologia 27: 169. 1973.

ESPELETOIPSIS FUNCKII (Sch. Bip. ex Wedd.) Cuatr. comb. nov.

Espeletia funckii Sch. Bip. ex Wedd. Chl. And. 1: 64. 1855.

ESPELETOIPSIS GARCIAE (Cuart.) Cuatr. comb. nov.

Espeletia garciae Cuatr. Phytologia 23: 358. 1972.

ESPELETOIPSIS GLANDULOSA (Cuart.) Cuatr. comb. nov.

Espeletia glandulosa Cuatr. Rev. Acad. Colomb. Cienc. 3: 434. 1940.

ESPELETOIPSIS GUACHARACA (Diaz) Cuatr. comb. nov.

Espeletia guacharaca Diaz, Caldasia 11: 19. 1975.

ESPELETOIPSIS INSIGNIS (Cuart.) Cuatr. comb. nov.

Espeletia insignis Cuatr. Rev. Acad. Colomb. Cienc. 3: 432. 1940.

ESPELETOIPSIS JAJOENSIS (Aristeg.) Cuatr. comb. nov.

Espeletia jajoensis Aristeg. Comp. in Fl. Venez. 10 (1): 424. 1964.

ESPELETOIPSIS JIMENEZ-QUESADAE (Cuart.) Cuatr. comb. nov.

Espeletia jimenez-quesadae Cuatr. Rev. Acad. Colomb. Cienc. 3: 247. 1940.

ESPELETOIPSIS MERIDENSIS (Cuart.) Cuatr. comb. nov.

Espeletia meridensis Cuatr. Mutisia 16: 4. 1953.

ESPELETOIPSIS MUISKA (Cuart.) Cuatr. comb. nov.

Espeletia muiska Cuatr. Rev. Acad. Colomb. Cienc. 3: 429. 1940.

ESPELETOIPSIS PANNOSA (Standl.) Cuatr. comb. nov.

Espeletia pannosa Standl. Am. Journ. Bot. 2: 480. 1915.

ESPELETOIPSIS PETIOLATA (Cuart.) Cuatr. comb. nov.

Espeletia petiolata Cuatr. Rev. Acad. Colomb. Cienc. 4: 338. 1941.

ESPELETOIPSIS PLEIOCHASIA (Cuart.) Cuatr. comb. nov.

Espeletia pleiochasia Cuatr. Rev. Acad. Colomb. Cienc. 3: 432. 1940.

ESPELETOIPSIS POZOENSIS (Cuart.) Cuatr. comb. nov.

Espeletia pozoensis Cuatr. Ciencia (Mexico), 6: 266. 1945.

ESPELETOIPSIS PURPURASCENS (Cuart.) Cuatr. comb. nov.

Espeletia purpurascens Cuatr. Rev. Acad. Colomb. Cienc. 5: 16. 1942.

ESPELETOIPSIS SANTANDERENSIS (A. C. Smith) Cuatr. comb. nov.

Espeletia santanderensis A. C. Smith, Brittonia 1: 527. 1935.

ESPELETOIPSIS SCLEROHYLLA (Cuart.) Cuatr. comb. nov.

Espeletia sclerophylla Cuatr. Rev. Acad. Colomb. Cienc. 3: 436. 1940.

ESPELETOIPSIS TACHIRENSIS (Aristeg.) Cuatr. comb. nov.

Espeletia tachirensis Aristeg. Comp. in Fl. Venezuela 10 (1): 427. 1964.

ESPELETOIPSIS TRIANAE (Cuart.) Cuatr. comb. nov.

Espeletia trianae Cuatr. Rev. Acad. Colomb. Cienc. 5: 18. 1942.

COESPELETIA Cuatr. gen. nov. Helianthearum, subtrib. Espeletiinae.

Caulirosulae simplices erectae, polycarpicae, raro rosulae

sessili. Caulis infra rosulam crasse densissime adpressissimeque cum foliis marcescentibus undique tectus.

Folia alterna coriacea vel subcoriacea plus minus rigida crebrissime rosulata. Vagina aperta plana congeste imbricata. Lamina anguste elliptica vel linearis crasse denseque lanata vel tomentosa.

Inflorescentiae axillares cymoso-monochasiales stricte racemoides, interdum reductissimae, vel synflorescentiae paniculato-racemoides, axe elongato, ramis semper alternis longitudine uniformi; foliis partis proximalis vegetativae semper alternis.

Capitula mediana vel grandia radiata; corollae radii saepe cum processis dentiformibus vel lingulatis adaxiale munitae; ligulae luteae vel aurantiacae; corollae disci limbo tubuloso dentato luteo. Grana pollinis spinis numerosis usque ad 3 micra longis. Receptaculum planum vel plano-convexum, hirtum. Achaenia calva.

Species omnes regiones frigidae paramorum Andium habitant. Venezuela.

Typus: *Espeletia spicata* Schultz Bip. ex Weddell.

COESPELETIA ALBA (A. C. Smith) Cuatr. comb. nov.

*Espeletia alba* A. C. Smith, Brittonia 1: 512. 1935.

COESPELETIA ELONGATA (A. C. Smith) Cuatr. comb. nov.

*Espeletia elongata* A. C. Smith, Am. Journ. Bot. 27: 546. 1940.

COESPELETIA LUTESCENS (Castr. & Aristeg.) Castr. comb. nov.

*Espeletia lutescens* Castr. & Aristeg. Comp., Fl. Venez. 10 (1): 443. 1964.

COESPELETIA MARCANA (Castr.) Castr. comb. nov.

*Espeletia marcana* Castr. Phytologia 20: 476. 1971.

COESPELETIA MORITZIANA (Sch. Bip. ex Wedd.) Castr. comb. nov.

*Espeletia moritziana* Sch. Bip. ex Wedd. Chl. And. 1: 65. 1856.

COESPELETIA SPICATA (Sch. Bip. ex Wedd.) Castr. comb. nov.

*Espeletia spicata* Sch. Bip. ex Wedd. Chl. And. 1: 65. 1856.

COESPELETIA THYRSIFORMIS (A. C. Smith) Castr. comb. nov.

*Espeletia thyrsiformis* A. C. Smith, Brittonia 1: 513. 1935.

COESPELETIA TIMOTENSIS (Castr.) Castr. comb. nov.

*Espeletia timotensis* Castr. Bol. Soc. Venez. Cienc. Nat. 17 (85): 84. 1956.

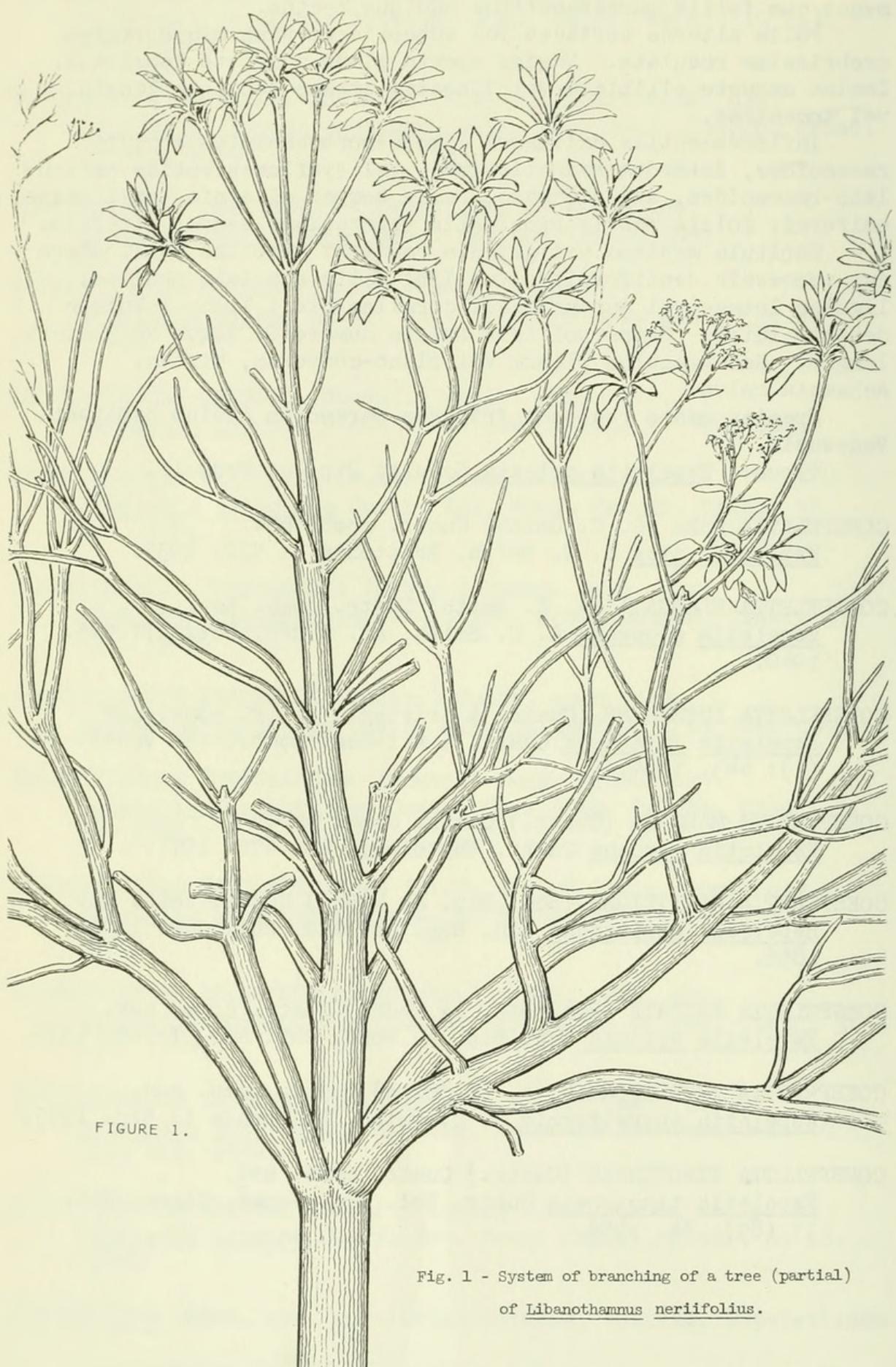


FIGURE 1.

Fig. 1 - System of branching of a tree (partial)  
of Libanothamnus nerifolius.

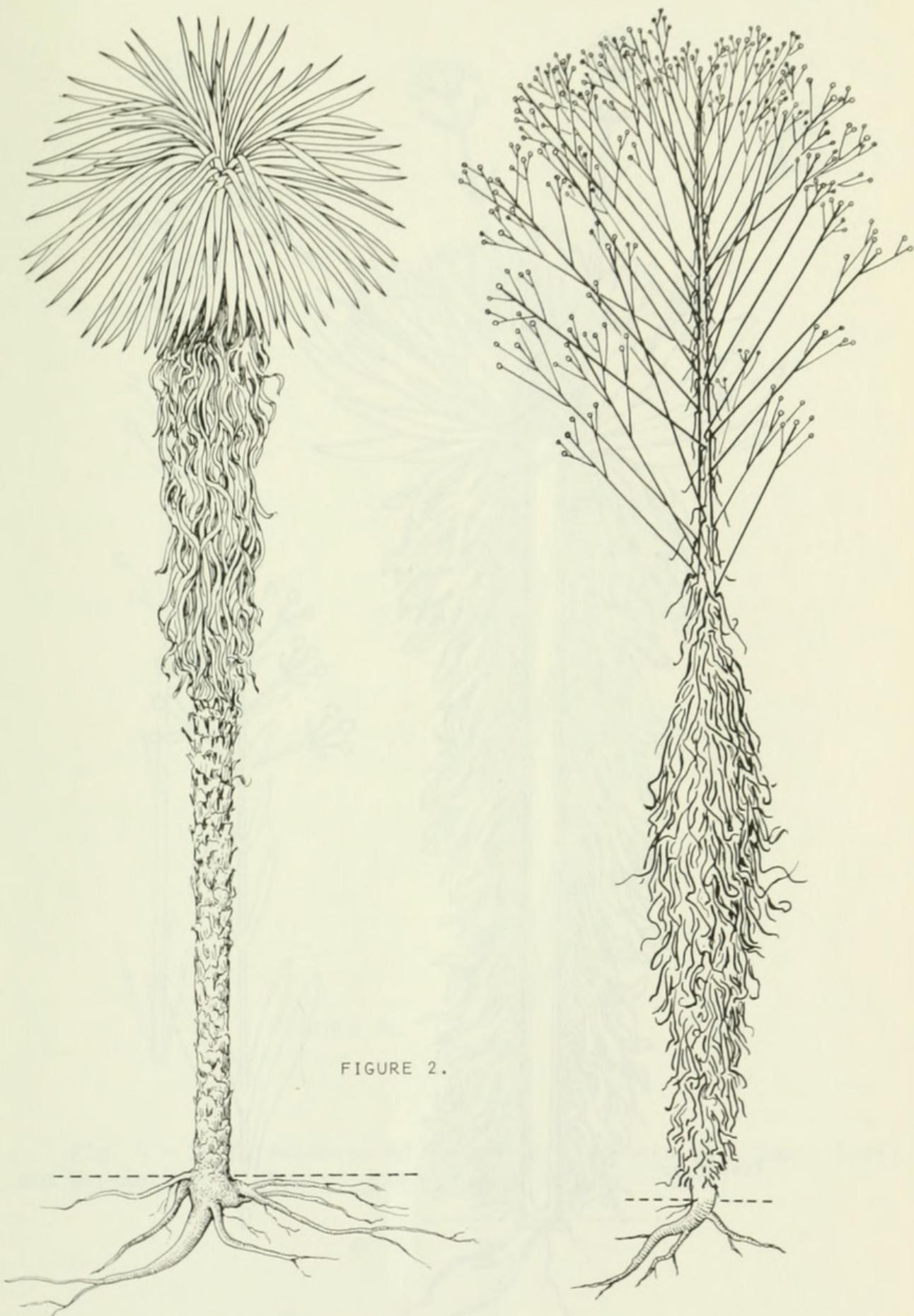


FIGURE 2.

Fig. 2 - *Ruilopezia figueirasi*, typical monocarpic caulirosula: sterile leafy plant (left, about 2 m tall); dying, fructifying individual (right, about 3 m high).

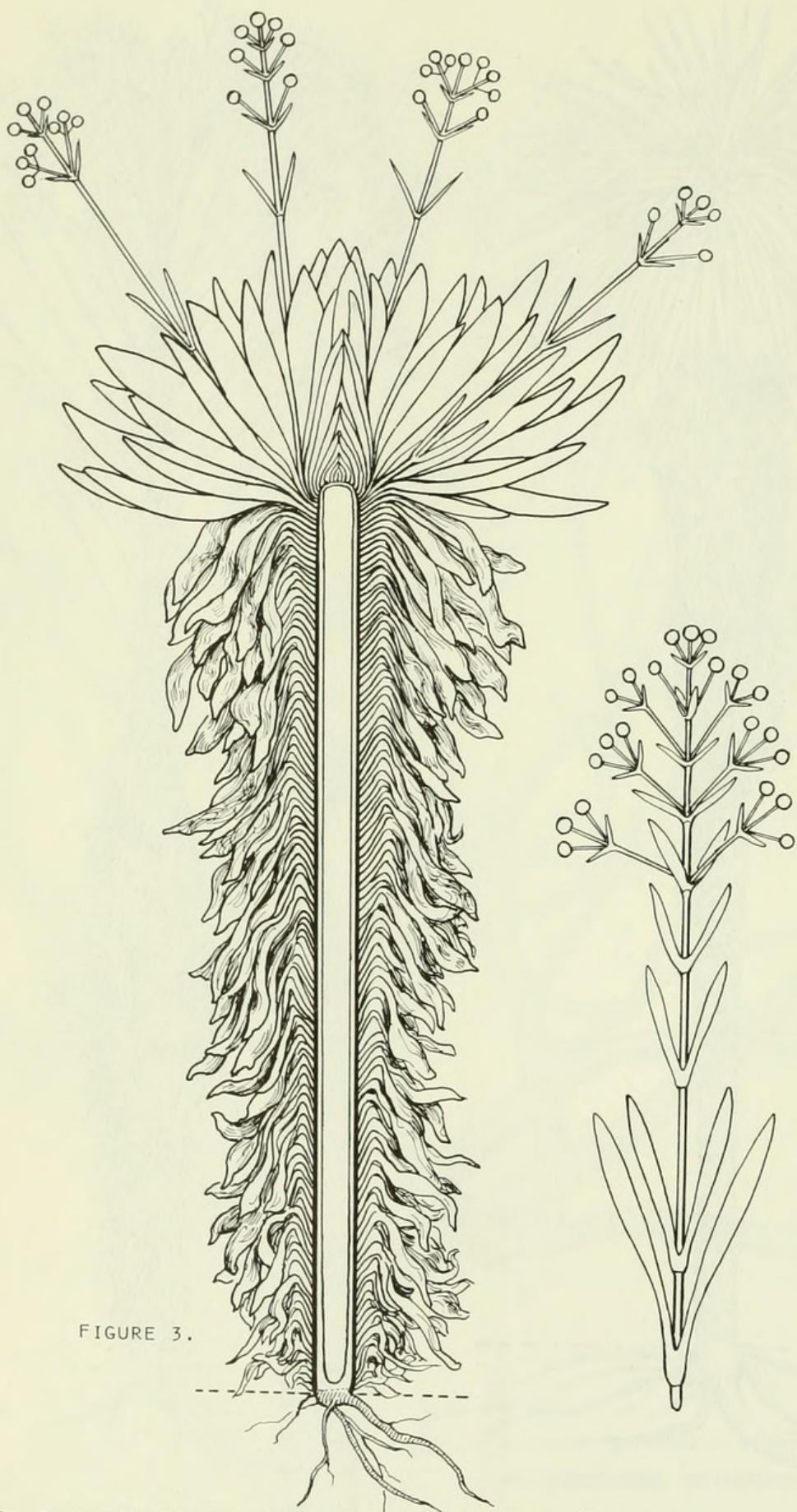


FIGURE 3.

Fig. 3 - Typical polycarpic caulirosula, in section, (about 1.6 m high) and the basic type of inflorescence of E. grandiflora (1 m. nat. size).



FIGURE 4.

Fig. 4 - Inflorescences of Coespeletia spicata (1 m long, left) and Espeletiopsis jimenez-quesadae (80 cm long, right).



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Cuatrecasas, José. 1976. "A new subtribe in the Heliantheae (Compositae): Espeletiinae." *Phytologia* 35, 43–61. <https://doi.org/10.5962/bhl.part.2608>.

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