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**Leaves** – Foliar characters such as size, shape, and indumentum are useful for species distinguishing purposes. The degree of prominence of the venation is also taxonomically informative: secondary and tertiary veins are conspicuous on both surfaces in *Pentacalia floribunda* Cuatrec., whereas in *P. luteynorum* H. Rob. & Cuatrec. only the secondary veins are barely conspicuous.

**Synflorescences** – Two groups of taxa can be easily differentiated according to the position of the synflorescences: (1) species with mostly terminal synflorescences (Fig. 1A → p. 33); (2) species with mostly lateral, axillary synflorescences, where the apical meristem indeterminately elongates (Fig. 1B) (CALVO, 2021). It should be noted that ROBINSON & CUATRECASAS (1993) gave great importance to this character and placed it early in the identification key. Although it certainly has a worthy taxonomic value, it is sometimes difficult to discern on those herbarium specimens not properly or sufficiently collected. *Pentacalia carmelana* H. Rob. & Cuatrec., here treated as a synonym of *P. huilensis* (Cuatrec.) Cuatrec., was originally described as a species with mostly lateral, axillary synflorescences and placed accordingly in Robinson and Cuatrecasas's key. Additional material showed that this species actually displays mostly terminal synflorescences, which is in line with both the description of *P. huilensis* and the key provided in the treatment of the Colombian species (DÍAZ-PIEDRAHITA & CUATRECASAS, 1999). Herein, the author tried to place this character as late as possible in the key.

Three main types of synflorescences are found in *Pentacalia*: (1) corymbiform as in *P. dorrii* H. Rob. & Cuatrec. (Fig. 1C); (2) thyrsoid-paniculiform as in *P. millei* (Greenm.) Cuatrec. (Fig. 1D); (3) racemiform as in *P. hurtadoi* H. Rob. & Cuatrec. (Fig. 1E).

**Capitula** – The type of capitula is very useful for differentiating species: (1) radiate capitula are heterogamous, with peripheral florets pistillate developing a limb (ligule, lamina) and disc florets hermaphroditic and tubular; the peripheral florets can be well-developed and patent (Fig. 1F) or reduced and curved downward (Fig. 1G); (2) disciform capitula are heterogamous, with peripheral florets pistillate and tubular, and disc florets hermaphroditic and tubular; the peripheral florets usually are shorter than the disc florets and (2–)4–5-lobed (Fig. 1H), sometimes with the lobes somewhat atrophied. Such florets are generally thought to be derived by reduction from ray florets, as well as plants with disciform capitula are generally thought to come from ancestors with radiate capitula (BARKLEY et al., 2006); (3) discoid capitula are homogamous, with all florets hermaphroditic and tubular (Fig. 1I).

Except for *Pentacalia celicana* J. Calvo & G. Benítez (described below) and *P. luteynorum* subsp. *luteynorum* that have white ray florets, all species with radiate capita exhibit yellow ray florets, becoming red burgundy as florets mature in a few

species. *Pentacalia carchiensis* (Cuatrec.) Cuatrec., here synonymized with *P. aschersoniana* (Hieron.) Cuatrec., was originally described as having “flores radii feminei circa 4 subtubulosi, corolla angusta 5 mm longa apice lamina subligulari profunde 3-dentata”. Since the peripheral florets sometimes display a vestigial limb or this is absent, it has been described herein as a subradiate capitula although its identification in the key can be achieved both by subradiate capitula or disciform capitula (step 22). The same occurs for *P. disciformis* (Hieron.) Cuatrec., a disciform species with tubular peripheral florets that sometimes develop a very small limb.

**Involucres** – The number and length of involucral bracts are usually regular in each species, and therefore, helpful for separating species. In *Pentacalia palaciosii* H. Rob. & Cuatrec., *P. ruficaulis* (Greenm. & Cuatrec.) Cuatrec., and *P. sevillana* (Cuatrec.) Cuatrec. the number of involucral bracts slightly varies. Characters of the supplementary bracts (calycle) such as the number, length, and shape are also useful.

**Floral microcharacters** – The filament collar is balustriform, which agrees with the placement of the genus *Pentacalia* within the subtribe *Senecioninae* (NORDENSTAM et al., 2009). The anther bases are caudate, sometimes very shortly. In all species examined the style branch apices are truncate with a crown of sweeping hairs. Floral microcharacters are not taxonomically informative at specific rank.

**Achenes** – The achenes of the Ecuadorian *Pentacalia* are homomorphic, cylindrical, ribbed, and glabrous (papillose in a single collection of *P. oronoensis* (DC.) Cuatrec.). The pappus is ordinarily 1-seriate, capillary and composed of barbellate, whitish bristles. Although the genus *Pentacalia* was coined after the 5-ribbed achenes of the type species, *P. arborea*, the number of ribs varies from five to seven (ten) in the species examined. When the achenes are not completely developed, the number of ribs is difficult to determine. Achene's characters have not been used in this work for species identification purposes.

## Phylogenetic relationships

A phylogenetic analysis of the genus *Pentacalia* has not been conducted, however, some insights can be drawn out from the ITS phylogeny of the tribe *Senecioneae* by PELSER et al. (2007). The tree accessions of *Pentacalia* included in the study are nested in the weakly supported *Faujasia*-*Oldfelia* clade: (1) *Pentacalia antioquensis* (Cuatrec.) Cuatrec. based on van der Werff & Giraldo 9736, which corresponds to *P. trianae* (Klatt) Cuatrec. (DÍAZ-PIEDRAHITA & CUATRECASAS, 1999); (2) *Pentacalia arborea* based on Øllgaard & Balslev 8298, identified as *P. theifolia* both here and by Robinson in sched. (AAU); (3) *Pentacalia desiderabilis* (Vell.) Cuatrec. based on Hatschbach & Oliveira 43028. They appear in various parts of the clade

although the support is generally low too. *Pentacalia trianae* from Colombia and *P. arborea* from Colombia and Ecuador are strongly related to each other, and found in a subclade along with species of *Monticalia* and *Scrobicaria* Cass. This latter genus contains three species restricted to Colombia and Venezuela and mainly differs from *Pentacalia* in having opposite leaves. The accession of *P. desiderabilis*, a species endemic to Brazil, is nested among species of *Dendrophorium* and *Graphistylis* B. Nord. also from Brazil. These results, though weakly supported, suggest that *Pentacalia* as currently circumscribed is not monophyletic. Additional studies based on an exhaustive sampling including species of *Pentacalia* that represent the entire distribution area of the genus, as well as species of the aforementioned allied genera, are essential for drawing the evolutionary relationships of these plant groups and, if needed, make the taxonomic adjustments accordingly.

## Material and methods

The present contribution is the result of an exhaustive review of the published bibliography, fieldwork in Ecuador carried out in 2017, 2018, and 2023, and the examination of 369 herbarium specimens (duplicates excluded) kept at the following herbaria: AAU, G, HA, HUTPL, LOJA, MA, P, Q, QAP, QCA, QCNE, QPLS, US, and USM. Additionally, digital images of specimens from B, COL, E, F, GH, HAL, K, LD, LP, MO, MT, NY, P, PR, PRC, S, UC, US, VALLE, and VEN were studied. The loans of specimens received from AAU, MA, P, and US were essential to achieve this revision.

The types of all accepted names and synonyms were studied, except for *Pentacalia pailasensis* H. Rob. & Cuatrec., the holotype of which appears to be lost after having been loaned by F to another institution (K. Hansen, pers. comm.). It is therefore treated as doubtful. The qualitative characters provided in the descriptions were studied, when needed, with the aid of the stereo microscope Leica M60, whereas quantitative characters were recorded using a Mitutoyo digital caliper, CD-15DC. The maps were generated using QGIS 3.16 Hannover. Information concerning the habitat, elevation, and flowering period of each species was obtained from the herbarium specimen labels and the information compiled in the field. Nineteen (19) out of the 27 accepted species were observed in Ecuador during the field trips.

Accepted species are presented in alphabetical order and are listed in Appendix 1. All studied exsiccatae can be found in Appendix 2. An index to all scientific names is provided at the end of this publication. The list of specimens examined given for each species includes only the Ecuadorian material, except for the species that citing the collections from the neighboring countries is relevant for completeness sake. If herbarium specimens from a province were not studied but the presence of the species is expected there, the name of that province is included in the distribution and followed by a question mark.

The leaf descriptions and measurements provided in this treatment correspond to the leaf lamina. General botanical terms largely follow BEENTJE (2012), whereas specific terms concerning the family *Compositae* are in line with those used by ROBINSON & CUATRECASAS (1993).

## Taxonomic treatment

*Pentacalia* Cass. in Cuvier F., Dict. Sci. Nat., ed. 2, 48: 461. 1827.

**Typus:** *Cacalia arborea* Kunth [= *Pentacalia arborea* (Kunth) Cass.].

= *Senecio* sect. *Triana* Cuatrec. in Fieldiana, Bot. 27(2): 71.

1951. = *Pentacalia* Cass. subg. *Pentacalia*.

= *Senecio* sect. *Streptothamni* Greenm. in Bot. Jahrb. Syst.

32: 19. 1902. **Typus:** *Senecio streptothamnus* Greenm. [= *Pentacalia streptothamna* (Greenm.) H. Rob. & Cuatrec.].

*Plants* scandent, woody, with long dangling branches, sometimes rather suberect with branches leaning over adjacent vegetation; stems terete, often furrowed, glabrous or with indumentum, solid or fistulous. *Leaves* alternate (opposite in 3 Peruvian species), simple, petiolate; laminae lanceolate, oblanceolate, elliptic, ovate, or obovate, apex rounded to acuminate, base attenuate to cordate, margin entire to dentate (usually remotely mucronate-denticulate), glabrous to covered by different types of indumentum (trichomes usually simple, multicellular, eglandular, rarely T-shaped in few non-Ecuadorian species), chartaceous, coriaceous, or fleshy, concolorous or slightly discolored, secondary and tertiary veins conspicuous or inconspicuous. *Synflorescences* terminal or lateral (axillary), corymbiform, thyrsoid-paniculiform, or racemiform. *Capitula* radiate, disciform, or discoid, sessile to pedunculate; involucres cylindrical to campanulate, glabrous or covered by indumentum; receptacles epaleaceous, rather flat, smooth or somewhat irregularly alveolate; involucral bracts 1-seriate, usually 8–13, linear-oblong; supplementary bracts (calyculi) (1–)3–5(–7), linear-subulate to ovate. *Ray florets* pistillate; corollas with reduced or well-developed limbs, patent or curved downward, subentire to 3-toothed at apex, yellow or white (becoming red burgundy as florets mature in few species). *Peripheral florets* of disciform capitula pistillate; corollas tubular, usually shorter than disc florets, deeply (2–)4–5-lobed, yellow or whitish. *Disc florets* hermaphroditic; corollas tubular, 5-lobed, yellow or whitish (becoming red burgundy as florets mature in few species); filament collars balustriform; anther bases caudate (sometimes only very shortly caudate), anther appendages 2–3 times longer than wide; style branches truncate with crown of sweeping trichomes. *Achenes* cylindrical, 5–10-ribbed, usually glabrous (pubescent in few non-Ecuadorian species); pappus usually 1-seriate, bristles capillary, barbellate, whitish.