
Studies on Neotropical *Violaceae*: the genus *Fusispermum*

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ABSTRACT

The neotropical genus *Fusispermum* (actinomorphic *Violaceae*) contains two species in northern South America (Peru, Colombia) and a third species *F. laxiflorum* Hekking sp. nov. from Panama. The genus differs from two subfamilies *Violeidae* and *Leonoideae* of the *Violaceae* as distinguished by Melchior, by its convolute aestivation of the petals, its deviating androecium and its capsula containing two different kinds of seeds and is therefore placed in a subfamily of its own, *Fusispermoideae* Hekking subfam. nov. A key to the neotropical actinomorphic genera of *Violaceae* is provided.

I. THE GENUS *Fusispermum* Cuatrecasas.

The neotropical genus *Fusispermum* (actinomorphic *Violaceae*) contains two species in northern South America (Peru, Colombia) and a third species *F. laxiflorum* Hekking sp. nov. from Panama. The three species occur at altitudes varying from 0–1200 m, in primary or secondary rain forests, sometimes extending to submountainous forests. They can be keyed out as follows:

Key to the species of *Fusispermum* (fig. 1 & 2).

1. Inflorescences widely thyrsoid; cymules containing a 1.5–8.0 mm long peduncle; petals longer than 2.0 mm. Colombia, Peru. 1. *F. rubrolignosum* Cuatrecasas
1. Inflorescence narrowly thyrsoid to pseudoracemose; cymules subsessile, containing a peduncle less than 1.5 mm long; petals shorter than 2.0 mm.
 2. Free parts of filaments shorter than 0.5 mm; capsula 3.0–3.25 mm long; branchlets, petioles and inflorescences glabrate; petioles 1.25–1.75 cm long; lateral veins of the costa of the leaves (11–)13–17 (apex excluded). Colombia. 2. *F. minutiflorum* Cuatrecasas

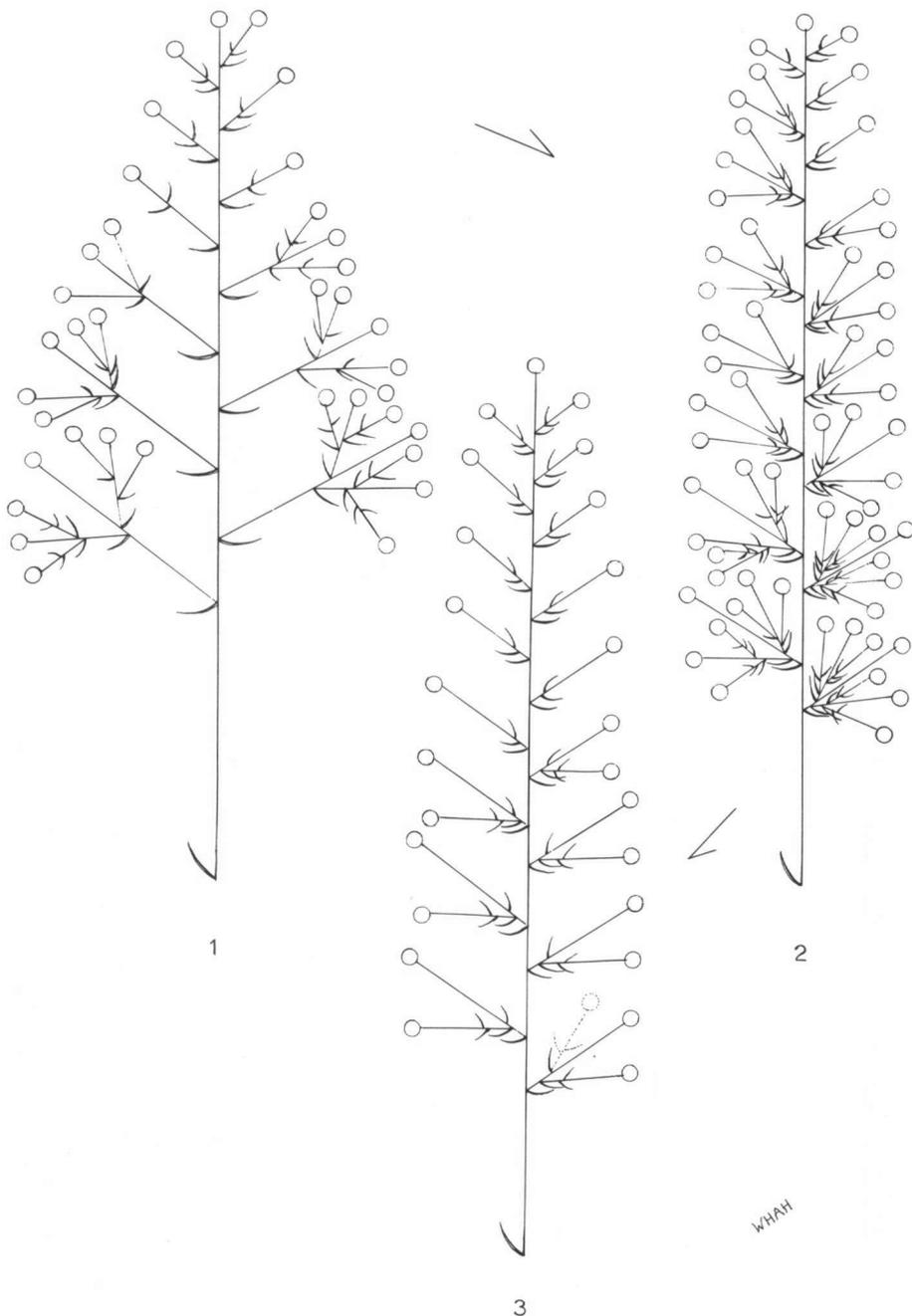


Fig. 1. Reduction of thyrsoid inflorescences in *Fuispermum*

1. *Fuispermum rubrolignosum* Cuatr. Inflorescences widely thyrsoid; cymules with a distinct peduncle and containing 1-7 flowers. 2. - *Fuispermum minutiflorum* Cuatr. Inflorescences narrowly thyrsoid; cymules sessile by reduction of the peduncle; cymules containing 1-7 flowers. - 3. *Fuispermum laxiflorum* Hekking. Inflorescences narrowly thyrsoid to pseudoracemose; cymules sessile by reduction of the peduncle; cymules containing 1-2 (rarely also more ?) flowers.

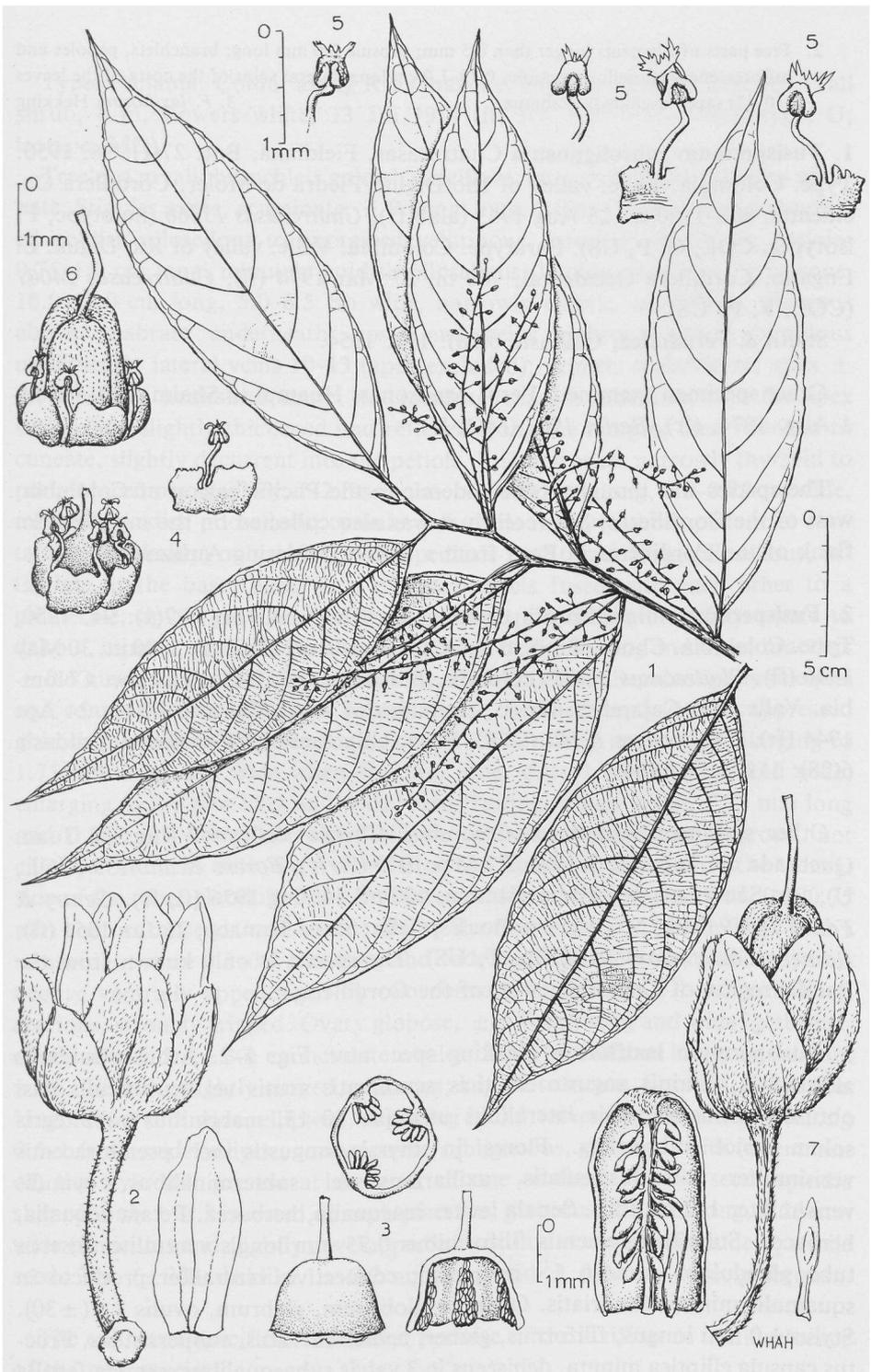


Fig. 2. *Fusispermum laxiflorum* Hekking n. sp. (Foster 2811, holotype, U).

1. Habit - 2. Flower and petal - 3. Ovary and style, longitudinal and cross section showing a placentation $3 \times \infty$ - 4. Ovary surrounded by filamental tube with stamens; part of filamental tube with stamen. - 5. Stamens detailed - Juvenile capsula surrounded by filamental tube with stamens - 7. Adult capsula; one valve containing two different kind of seeds; disklike unfertilized (?) seeds and one spindle shaped fertile seeds containing a well developed embryo.

2. Free parts of filaments longer than 0.5 mm; capsula 2.0 mm long; branchlets, petioles and inflorescences pilosellous; petioles 0.75–1.0 cm long; lateral veins of the costa of the leaves (10–13) (apex excluded). Panama 3. *F. laxiflorum* Hekking

1. ***Fusispermum rubroliginosum*** Cuatrecasas, Fieldiana, Bot. 27(1): 96. 1950. Type. Colombia. Valle: valley of Río Digua: Piedra de Moler. Cordillera Occidental, 900–1180 m, 23 Aug 1943 (alab, fr), *Cuatrecasas 15066* (holotype, F; isotypes, COL, G, P, US). Paratype. Colombia. Valle: valley of Río Digua: El Engaño, Cordillera Occidental, 700 m, 27 Mar 1974 (fl), *Cuatrecasas 24001* (COL, F, P, US).

Smith & Fernández, *Caldasia* 6(28): 112. 1954.

Other specimen examined: Peru. Amazonas: Huampi to Shaim, 200–575 m, 1 Aug. 1974, (fr), *Berlin 1953* (MO, U).

The species was thought to be endemic to the Pacific region of Colombia, west of the Cordilleras, but recently it was also collected on the northeastern flank of the Cordilleras in Peru from a region bordering Amazonia.

2. ***Fusispermum minutiflorum*** Cuatrecasas, Fieldiana, Bot. 27(1): 94. 1950. Type. Colombia. Chocó: Río San Juan, Quebrada del Taparal, 5–20 m, 30 May 1946 (fl), *Cuatrecasas 21493* (holotype, F; isotypes, F, US). Paratype. Colombia. Valle: Río Cajambre, Barco, riversides of Agua Clara, 5–80 m. 24 Apr 1944 (fr), *Cuatrecasas 17162* (COL, F, G, US). Smith & Fernández, *Caldasia* 6(28): 111. t. 7. 1954.

Other specimens examined: Colombia. Chocó: Valley of Río San Juan, Quebrada del Taparal, 5–10 m, 27 Mar 1979 (fl, fr), *Forero et al. 4139* (COL, U); Río San Juan, just above Istmina, 100 m, 14 Aug 1976 (fl, fr), *Gentry & Fallen 17659* (MO, NY, U); Nariño: Espriella, SE of Tumaco, 21 Jun 1951 (fl), *Romero-Castañeda 2803* (COL, F, US). The species is only known from the Pacific region of Colombia, west of the Cordilleras.

3. ***Fusispermum laxiflorum*** Hekking spec. nov. Fig. 1–2. Arbuscula. Folia alternantia, laminis anguste ellipticis acuminatis acutis vel acutiusculis basi obtuso-rotundatis; venis lateralibus utrinque 10–13, marginibus subintegris solum apice subserratis. Flores in thyrsis angustis vel pseudoracemis verisimiliter 1–2 fasciculatis, axillaribus vel subterminalibus, cymulis verisimiliter 1–2 floribus. Sepala leviter inaequalia, herbacea. Petala aequalia, herbacea. Stamina filamentis filiformibus 0.75 mm longis ventraliter insertis tubo glanduloso carnosio 5×-intersecto; connectivo ventraliter producto in squamulis minutis fimbriatis. Ovarium globosum, glabrum, ovulis 3× (± 30). Stylus 1.0 mm longus, filiformis, glaber, leviter curvatus, subpersistens. Fructus capsula elliptica minuta, dehiscens in 3 valvis subaequalibus; semina fertilia vermicularia vel fusiformia endospermii fere destituta 1.0 mm longa et 0.25 mm lata, sterilia plana et ovata, ± 0.2 mm longa et 0.1 mm lata.

Type: Panama. Colón: along Río Guanche, edge of rocky stream bed. Tall shrub, 4 m, flowers white, 13 Jul 1974 (fl, fr), *Foster 2811* (holotype, U; isotype, MO).

Treelet 4 m tall; branchlets goldish strigillose, later on glabrous. Leaves alternate; Stipules ovate, acuminate, ± 9.0 mm long, 2.0 mm wide, densely appressed goldish pilosellous to appressed velutinous, later on deciduous; petioles 0.75–1.0 cm long, minutely goldish pilosellous; lamina papery to coriaceous, 16.0–18.0 cm long, 5.0–6.5 cm wide, narrowly elliptic, acuminate, glabrous above, glabrate underneath; costa and veins glabrous above, hirtellous underneath; lateral veins 10–13 (apex excluded); veinlets scalariform; apex ± 2.5 cm long, acutish to acute, mucronulate; margin subentire, near the apex subserrate, slightly thickened and reflexed along the margin; base rounded to cuneate, slightly decurrent into the petiole. Inflorescences narrowly thyrsoid to pseudoracemose, axillary, 1–2 fasciculate, 6.0–10.0 cm long, 0.5–0.75 cm wide, minutely goldish pilosellous; cymules subsessile nearly without peduncles containing (probably) only 1–2 flowers; pedicels ± 2.0 mm long, pilosellous, articulate at the base; basal part of the pedicels fused with each other to a glomerule; apical part 2.0 mm long, goldish pilosellous; bract(let)s ovate to deltoid, minute, goldish pilosellous; bracts ± 0.25 mm long and wide; bractlets ± 0.1 mm long and 0.075–0.1 mm wide. Flowers white. Sepals slightly unequal and connate at the very base, ovate, obtuse, herbaceous, 3-venose, appressed goldish pilosellous, ciliolate; outer ones 1.25 mm long and wide, enlarging to 1.75 mm long and wide when fruiting; inner ones 1.75 mm long and wide, enlarging to 2.0 mm long and wide when fruiting. Petals white, 1.75 mm long and 0.75 mm wide, (narrowly) elliptic, obtuse, herbaceous, glabrous, not ciliolate. Stamens with the free parts of the filaments inserted on the ventral side of the tube; glandular tube $5 \times$ intersected and irregularly lobed, 0.5–0.75 mm high, carnosely glabrous; free parts of the filaments ± 0.75 mm long, ± 0.1 mm wide; thecae 0.3–0.4 mm long and wide trapezoid, obtuse, glabrous; connective ventrally appendaged by two connate apical slips 0.1–0.2 mm long, scarious, strongly fringed. Ovary globose, ± 1.0 mm long and wide, glabrous, containing $3 \times (\pm 30)$ epunctulate ovules. Style ± 1.0 mm long, ± 0.1 mm wide, filiform, slightly curved, glabrous; stigma truncate. Capsula ± 2.0 mm long, ± 1.5 mm wide, ellipsoid, dehiscent into 3 valves; valves ± 2.0 mm long 0.5–1.0 mm wide, elliptic, coriaceous to subligneous, glabrous, with (a remnant of) the style still present at the apex of one of them. Fertile seeds spindle shaped, only 1 or 2 inserted on each placenta, glabrous, 1.0 mm long, 0.25 mm wide (funiculus and slightly developed carunculus at the apex included); sterile seeds $3 \times (\pm 20)$, disklike, ± 0.2 mm long and ± 0.1 mm wide, glabrous.

The epitheton specificum is chosen because of the laxiflorous inflorescence of the new species.

F. laxiflorum is the first species of *Fusispermum* known from Panama. Earlier this genus seemed to be confined to the Pacific area of Colombia, W.

of the Cordilleras. Its known area of distribution has now been extended to the N.E. flanks of the Cordilleras in Peru by a recent collection of *F. rubrolignosum*, as well as to Panama by the discovery of this new species.

F. laxiflorum can be distinguished from the other species by 1) the apex of the leaves, which tends to be more distinctly acuminate and acute than in *F. rubrolignosum* and *F. minutiflorum*; 2) the lower number of lateral veins; 3) the distance between the lateral veins, which tends to be wider than in *F. rubrolignosum* and *F. minutiflorum* 4) the free parts of the filaments longer than 0.5 mm; 6) the placentation, which is $3 \times (\pm 30)$ (in the other species $3 \times \pm 50$); 7) the capsula, which is shorter than 2.5 mm and 5) the spindle shaped (fertile) seeds, which are only 1.0 mm long (in the other species longer than 2.5 mm).

F. laxiflorum differs furthermore from *F. minutiflorum* by the leaf petioles shorter than 1.25 cm and from *F. rubrolignosum* by shorter petals, which are maximally 2.0 mm long (in *F. rubrolignosum* 2.25–2.5 mm long). Further differences are given in the key.

II. SYSTEMATIC POSITION OF *Fusispermum* Cuatrecasas.

Melchior (1925) made the most recent generic classification for the family *Violaceae*. There are two subfamilies, the *Leonoideae* (monotypic) and the *Violoideae*, which are subdivided into the tribe *Violeae* (flowers zygomorphous) and the tribe *Rinoreeae* (flowers actinomorphaous). The genera *Rinorea* and *Gloeospermum* were arranged in the subtribe *Rinoreinae* and the genera *Amphirrhox* and *Paypayrola* in the subtribe *Paypayrolinae*; both subtribes are

Table 1. Survey of Taxonomic subdivision of actinomorphaous *Violaceae* in the Neotropics, based on Melchior (1925a,b) and completed by Hekking (1983).

Family: *Violaceae* Batsch, Tab. Affin. Regni Veg. 57. May 1802 (‘*Violariae*’), nom. cons.; type genus: *Viola* Linnaeus 1753.

Subfamily: *Violoideae*

Tribus: *Rinoreeae* Reiche & Taubert 1897

Subtribus: *Rinoreinae* Melchior 1925

Rinorea Aublet 1775, type genus, nom. cons. prop.)¹

Rinoreocarpus Ducke 1925)²

Gloeospermum Triana & Planchon 1862

Subtribus: *Paypayrolinae* Melchior 1925

Paypayrola Aublet 1775, type genus

Amphirrhox Sprengel 1827, nom. cons.

Subfamily: *Leonoideae* Melchior 1925

Leonia Ruiz & Pavon 1799, type genus

Subfamily: *Fusispermoideae* Hekking subfam. nov. 1984

Fusispermum Cuatrecasas 1950, type genus

¹ W.H.A. Hekking: (681) Proposal to conserve 5262 *Rinorea* Aublet (1775) against simultaneously published *Conohoria* Aublet (1775) (*Violaceae*) in *Taxon* 31: 754–755. 1982.

² *Rinoreocarpus* is included in the *Rinoreinae* because of its close relationship of *Rinorea*.

sudivisions of the tribe Rinoreeae (see Table 1). The flowers of the Rinoreinae are more distinctly actinomorphic than those of the Paypayrolinae, in which a tendency to zygomorphy is expressed by the different shape of the anterior petal. In the genera of the tribe Violeae the zygomorphy is emphasized by the anterior petal which is also gibbose or calcarate at the base and by the filaments of the anterior stamens which are also gibbose or calcarate on the dorsal side.

The subfamily Leonoideae was created for another actinomorphic genus *Leonia*, which is endemic in the neotropics and which differs mainly from the other genera belonging to the subfamily Violeae by 1) the quincuncial or irregular aestivation of the petals; 2) the filaments as well as the connectives fused to a tube with the thecae arranged nearly horizontally on the upper margin and therefore dehiscing apparently apically; 3) the placentation $3 \times (4-5)$, which stresses the actinomorphic character of the flowers and 4) the closed nutlike fruits with a woody pericarp containing large mucilaginous seeds without caruncle and copious with endosperm (resembling those of *Gloospermum*). Cuatrecasas (1951) described another species *Leonia triandra*, which differs from the former ones by having a trimerous androecium and gynaecium. While a trimerous gynaecium is more common in Violaceae, a reduction of the androecium to three stamens is exceptional in this family.

Comparing *Fusispermum* with other Violaceae, it appears to differ in essential respects from both Violeae and Leonoideae; 1) the thecae of *Fusispermum* are dehiscing laterally and are ventrally appendaged by minute fringed scales, while dorsal connective scales are wanting 2) the thecae are surmounted on free parts of filaments which are attached on the tube 3) the aestivation of the petals of *Fusispermum* is convolute and not imbricate as in all other genera of the Violaceae and 4) the minute capsulas of *Fusispermum* are dehiscing into three (or occasionally also four) valves in which there are two different kinds of seeds present: a. narrow spindle shaped (fertile) seeds, (nearly) without endosperm but provided with a well developed embryo and b. small disklike seeds, which are probably unfertilized. These differing characters support the conclusion to place *Fusispermum* in its own subfamily Fusispermoideae. The main differential characters may be detailed as follows:

1. The aestivation of the petals in *Fusispermum* is convolute, which is unusual in the other genera of the Violaceae. In these other genera they are mostly imbricate i.e. quincuncial or irregularly imbricate in *Leonia* (Leonoideae), and mostly apotact in the Violeae (occasionally also quincuncial as often in *Gloospermum*);
2. The filaments and connectives of *Leonia* are completely fused to a tube, so that the thecae are nearly horizontally arranged on the upper margin of the tube: In *Fusispermum* (free parts of) filaments are still present and are surmounted laterally on a 5 lobed tube (fig. 2: 4, 5 & 6). The thecae of *Fusispermum* are relatively minute in comparison to those of most of the other genera. In the other genera the filaments are free to partly or completely united to a tube.
3. The thecae of *Leonia* and *Fusispermum* are not appendaged by dorsal connective scales as in other genera in the Violaceae; in *Fusispermum* dorsal connective scales are ventrally replaced by two connate fringed scales at the apex of the thecae.
4. The glabrous globose ovary with an erect or slanting style of *Leonia* and *Fusispermum* resemble each other.

5. The placentation in *Leonia* is mostly $(4-5) \times \infty$, in *L. triandra* also reduced to $3 \times \infty$ as normally in the other genera of the Violaceae. The reduction of the gynaecium until 3 is correlated to a reduction of the androecium until 3 (which is unusual in Violaceae). The placentation of *Fusispermum* is $3(-4) \times \infty$ as usually in Violaceae; the androecium consists always of 5 stamens. The number of ovules in *Leonia* and *Fusispermum* is numerous, (in *Fusispermum* $3 \times (30-50)$, in *Gloospermum* $3 \times (7-22)$, in *Rinoreocarpus* $3 \times (6-10)$ and in *Rinorea* only $3 \times (1-4)$).
6. The fruits of *Leonia* remain closed and consist of a nut with a woody pericarp containing large mucilaginous seeds copious with endosperm and without caruncle. The woody fruits resemble those of the (sub)ligneous to coriaceous drupelike fruits of *Gloospermum* containing the same kind of seeds.
The fruits of *Fusispermum* consist of minute loculicidous capsulas dehiscing into 3(-4) valves as mostly in the genera of the subfamily Violoideae. The seeds of *Fusispermum* are completely different from those of the other genera in the Violaceae. They consist of two kind of seeds; minute disklike probably unfertilized seeds and much longer spindle shaped fertile seeds (nearly) without endosperm and containing a well developed erect embryo. The fertile seeds are provided with an elongated funicle and with a carunculous tissue at the apex.
7. The tertiary venation in *Leonia* is reticulate, in *Fusispermum* scalariform. In the other actinomorphic genera this venation may vary from reticulate to scalariform.

Fusispermoideae Hekking subfamilia nova

Flores actinomorphi, petalorum aestivatione convoluta, sepalis liberis vel basi connatis, petalis liberis, filamentis basali parte tubo affixis sed apicali parte liberis, antheris introrsis apice connectivi ventraliter appendiculatis squamis scariosis fimbriatis; capsula dehiscens in 3 vel rarius in 4 valvis; semina fertilia vermicularia vel fusiformia endospermii fere destituta, sterilia plana et ovata.

Flower actinomorphic; aestivation of petals convolute; sepals free or connate at the very base; petals free; basal part of filaments attached to a tube, apical part free; anthers introrse; at the apex of the ventral connective appendaged by fimbriate scarios scales; capsula dehiscent into 3 or rarely into 4 valves; fertile seeds worm- or spindle shaped nearly without endosperm, sterile ones flat and ovate.

Etymology ($\varphi\upsilon\sigma\alpha$, physa = bladder; $\sigma\pi\epsilon\rho\mu\alpha$, sperma = seeds)

type genus: *Fusispermum* Cuatrecasas, Fieldiana, Bot. 27(1): 94. 1950.

type species: *Fusispermum minutiflorum* Cuatrecasas, l.c.

Key to the subfamilies of the Violaceae and to actinomorphic genera occurring in the Neotropics.

1. Aestivation of the petals convolute; free parts of filaments laterally surmounted on the lobes of a glandular tube; dorsal connective scales wanting; thecae ventrally appendaged by two connate fringed scales; fruits capsular dehiscing into 3(4) valves containing two different kind of seeds.

Subfamily. **Fusispermoideae**

Fusispermum

1. Aestivation of the petals imbricate; filaments free or fused to a tube; dorsal connective scales present or if absent not replaced by ventral appendages; fruits usually capsular and dehiscing into three valves or closed indehiscing nutlike or drupelike fruits, containing both only one kind of seeds.

2. Aestivation quincuncial or irregularly imbricate; filaments and connectives fused to a tube; thecae nearly horizontal arranged on the upper margin of the tube, dehiscing apically; dorsal connective scales wanting, not replaced by ventral appendages; placentation $(3-5) \times \infty$; fruit indehiscent, nutlike.

Subfamily. **Leonoideae**

Leonia

2. Aestivation usually apotact, sometimes also quincuncial (as sometimes in *Gloeospermum*); filaments free or partly to completely fused to a tube; if filaments and connectives are fused to a tube, then the thecae slanting arranged on the upper margin of the tube and dehiscing laterally; placentation $3 \times (1-\infty)$; fruits usually capsular and dehiscent, sometimes indehiscent and drupelike.

Subfamily. **Violoideae**

3. Flowers strictly zygomorphous i.e. anterior petal gibbose or calcarate at the base and larger and wider than the other ones; dorsal glands of the filaments of the two anterior stamens gibbose or calcarate.

Tribe **Violeae**: *Anchietea*, *Corynostylis*, *Hybanthus*, *Mayanaea Noisetia*, *Orthion*, *Schweiggeria*, *Viola* etc.

3. Flowers varying from actinomorphic to slightly zygomorphous i.e. anterior petals varying from equal to slightly larger than the other ones, never gibbose or calcarate at the base; dorsal glands of filaments never gibbose or calcarate.

Tribe **Rinoreeae**

4. Petals differentiated into a claw and a plate; plate of anterior petal twice-lobbed and wider than those of the other ones; plate of other petals single-lobbed; fruits consisting of loculicidous capsulas

Subtribe **Paypayrolinae**

5. Inflorescences racemoid; filaments and connectives fused to a tube; thecae slanting arranged on the upper margin of the tube; dorsally scarcely or not appendaged. *Paypayrola*

5. Inflorescences cymoid; filaments nearly free; thecae vertically arranged, dorsally appendaged by a long linear connective scale. *Amphirrhox*

4. Petals not differentiated into a claw or a plate; anterior petal equal or sometimes subequal (i.e. slightly longer and wider than the other ones), occasionally exterior petals larger and wider than the ones which are in that case boat shaped (in some sp. of *Gloeospermum*); fruits dehiscent or indehiscent.

Subtribe **Rinoreinae**.

6. Inflorescences cymoid, mono-, di or pleiochasial, compact, common peduncle scarcely visible, only the pedicels of the flowers distinct; petals apotact or quincuncial; placentation $3 \times (7-22)$; fruits globose, indehiscent, drupelike, containing large mucilaginous seeds without caruncle and areola. *Gloeospermum*

Gloeospermum

6. Inflorescences thyrsoid to racemose, sometimes cymoid; petals predominantly apotact; placentation $3 \times (1-9)$; fruits a capsula dehiscing into 3 valves, containing dry seeds usually with caruncle and areola.

7. Inflorescence loosely cymoid with distinct peduncle and pedicels; connective scales minute, subulate or lineary to narrowly deltoid, uncoloured transparent, less than $1/3 \times$ as wide as the thecae; placentation $3 \times (6-9)$; number of ripened seeds usually $3 \times (2-4)$; petals orange reddish.

Rinoreocarpus

7. Inflorescence usually thyrsoïd to racemose, rarely compact cymoid; connective scales conspicuous, deltoid to ovate, coloured, more than $2/3 \times$ as wide as the thecae; placentation $3 \times (1-4)$; number of ripened seeds usually $3 \times (1-2)$; petals whitish, sometimes tinged with green, yellow orange or red.

Rinorea

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