

Floral vascular pattern of the endemic Malagasy genus *Fenerivia* Diels (Annonaceae)

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ABSTRACT

The floral anatomy, especially the receptacle vasculature, of *Fenerivia heteropetala* Diels was studied. The presence of an odd calyx, reduced to a coarsely rectangular flange, is confirmed. The corolla is arranged in three whorls, i.e. the two usual ones in Annonaceae with here three outer ovate petals, and three inner linear petals, and an innermost whorl of six linear petals, not supplied by a perianth cortical vascular system as the previous whorls, and very likely evolved from a petalization of three outer stamen pairs. Moreover the androecium includes *c.* 200 stamens, while *c.* 45 apocarpous carpels comprise the gynoecium. Despite the scarcity of available material, the oddness and the symmetry shown by the floral pattern dismiss any teratological interpretation, and demonstrate that the monotypic genus *Fenerivia* is to be reinstated. The affinity with *Polyalthia* Blume *s.l.*, which was previously suggested, appears unlikely.

KEY WORDS

Annonaceae,
Fenerivia,
Polyalthia,
floral anatomy,
petalization,
stamen pairs,
vascularization.

RÉSUMÉ

Vascularisation florale dans le genre endémique malgache Fenerivia Diels (Annonaceae).

L'anatomie florale de *Fenerivia heteropetala* Diels, notamment la vascularisation du réceptacle, a été étudiée. Elle confirme la présence d'un calice d'un type inhabituel pour les Annonaceae, réduit en un bourrelet à contour grossièrement rectangulaire. La corolle comporte trois verticilles, à savoir les deux cycles trimères classiques dans la famille, avec des pétales externes ovés et internes linéaires, ainsi qu'un cycle additionnel interne formé de six pétales linéaires, non irrigués

MOTS CLÉS

Annonaceae,
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Polyalthia,
 anatomie florale
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 vascularisation.

par un système vasculaire cortical comme les autres pièces périanthaires, et très probablement issus d'une pétalisation des trois paires d'étamines les plus externes. L'androcée est formé d'environ 200 étamines et le gynécée apocarpique d'environ 45 carpelles. Malgré la rareté du matériel disponible, la singularité du diagramme floral, combinée à sa parfaite régularité, permet d'écarter toute interprétation tératologique, et démontre que le genre monospécifique *Fenerivia* Diels doit être rétabli. Sa fusion avec le genre *Polyalthia* Blume s.l., précédemment proposée, ne peut plus être maintenue.

INTRODUCTION

The endemic Malagasy genus *Fenerivia* was described by Diels in 1925 for a very puzzling specimen collected by Perrier de la Bâthie from Fénérive (now Fenoarivo) on the eastern coast of Madagascar. Unfortunately no illustration was provided. Its perianth indeed would exhibit an absolutely unique combination for the Annonaceae family, i.e. a trimerous but very minute calyx, and 12 petals arranged in three whorls, the outer one with three petals much larger than others. Such a pattern was further accepted in the classical monograph of Fries (1959), but was also questioned several times. At first Ghesquière (1939) considered the alleged calyx as an extra-floral nectary, the large "petals" being in fact true ovate sepals enclosing, as is the rule in the Annonaceae, two trimerous – here linear – petals whorls, the innermost being abnormally duplicated in six petals. Consequently *Fenerivia* would be an incorrect genus name for a new *Polyalthia* species, with quite strange, and probably teratological, flowers. A similar view was expressed in the determination key of the floristic treatment by Cavaco & Keraudren (1958: 57). Surprisingly it is not consistent with the full description (p. 61) of *Polyalthia heteropetala* (Diels) Ghesq., which repeats the Diels description by reporting "calice petit, disciforme, aplati, de 6 mm de diamètre" (small, disk-shaped, flattened calyx, 6 mm in diameter). Unfortunately the flowering twig drawn in the figure 14 (p. 59) fails to show any disk. In 1972, Keraudren-Aymonin went back over this problem, and admitted that, due to the scarcity of material, it remained uncertain to de-

cide, but maintaining the genus *Fenerivia* should be wiser, as far as it appeared different from all other known Malagasy *Polyalthia* species, even in its leaf morphology. An opposite conclusion was brought by Schatz & Le Thomas (1990), who interpreted the "calyx" as a mere artefact resulting from the receptacle dehydration. Moreover, after these authors, the teratological meaning of the complex corolla is not to be discarded insofar as its stability cannot be recorded upon a large enough range of specimens. More recently van Heusden (1992: 123) suggested that the flange should even result from a unique (*sic*), connate, and circular sepal.

Considering the difference of interpretations, all based on the original work of Diels, and in order to establish definitely the flower pattern of this genus, an anatomical study was essential, and was consequently undertaken.

MATERIAL AND METHODS

The species *Fenerivia heteropetala* is known only from a single collection, and even a unique sheet kept at P, which constitutes the holotype (Madagascar, near Fénérive, fl., IX.1912, *Perrier de la Bâthie* 4942). A floral receptacle well past anthesis was selected from the specimen, rehydrated by an aqueous 20% NH₄OH solution at 60°C, postfixed in FAA, then dehydrated in a butanol series (Gerlach 1984) and infiltrated in paraffin (Histomed, melting point: 60°C). Microtome sections were made at a thickness of 20 µm and underwent no staining as far as the strong presence of tannins made this step superfluous,

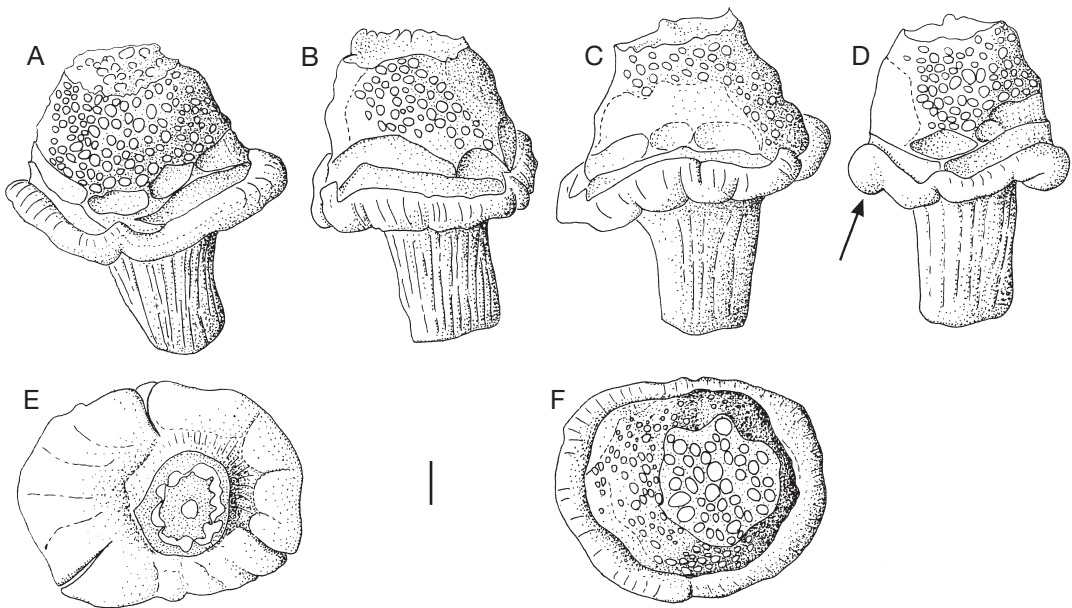


FIG. 1. — Morphology of the studied floral sample of *Fenerivia heteropetala* Diels: **A-D**, side views showing pedicel, calyx, and petal and stamen scars; **E**, under view illustrating the coarsely 3-divided calyx flange; **F**, top view with the obvious carpel scars. Scale bar: 1 mm.

and the sections were mounted directly in Eukitt. Slides are kept in the plant histological collection of the Muséum national d'Histoire naturelle, Paris under the reference *Deroin 167*.

Floral vasculature was reconstituted by drawings of the serial sections using a camera lucida, and then by superimposing tracing papers of them.

RESULTS

A unique sample was selected and removed from the bag linked with the holotype sheet. It consists (Fig. 1A-D) in the axial part of a post-anthesis flower, showing a corrugated pedicel, an irregularly lobed flange (Fig. 1D, arrow) coarsely rectangular in outline (Fig. 1E, F), and a receptacle like a flattened cone, whose lower third is taken up by perianth scars and the rest by stamen scars. The androecial zone, including *c.* 200 stamens, is however not well preserved on one side (Fig. 1C). Rather numerous carpels (*c.* 45) were inserted on the flat top of the receptacle (Fig. 1F).

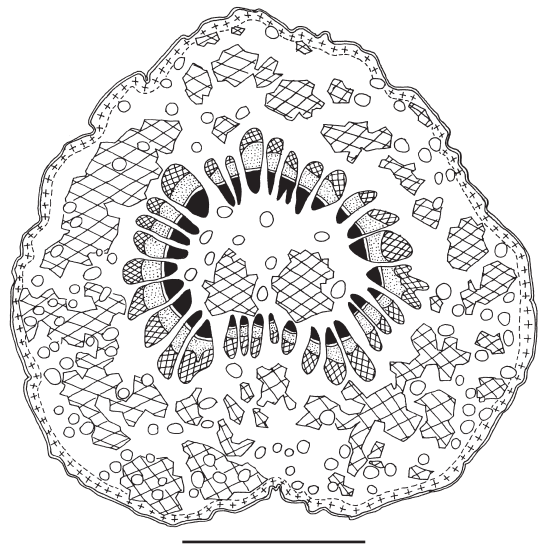


FIG. 2. — Pedicel anatomy of *Fenerivia heteropetala* Diels in a diagrammatic cross-section. Epidermis and cambium delimited by two parallel lines. Small crosses, collenchyma; large cross-hatching, sclerenchyma; close cross-hatching, phloem fibres; rings, secretory cells; stipple, phloem; black, xylem. Ground parenchyma left in white. Scale bar: 1 mm.

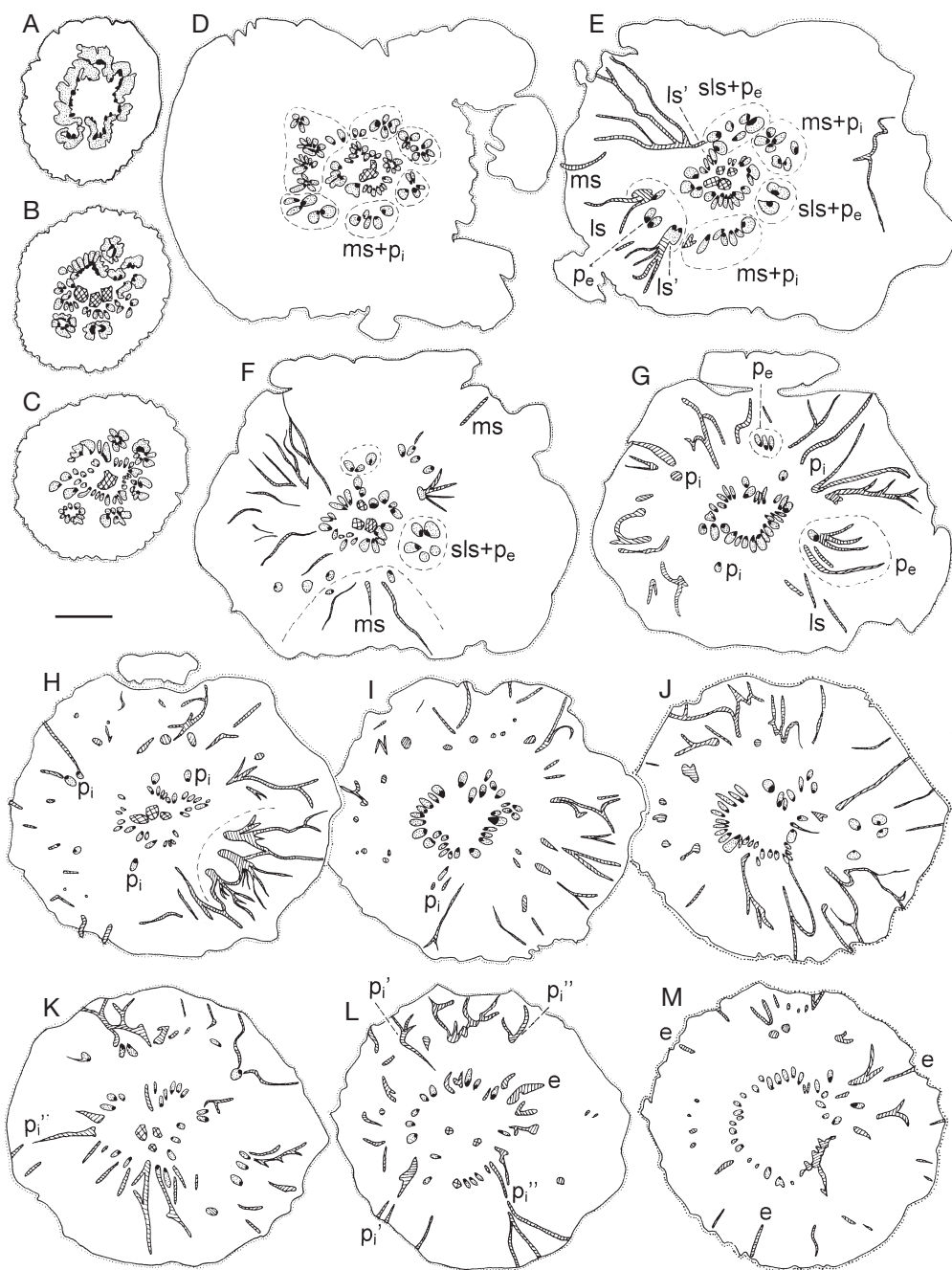


FIG. 3. — Transverse sections of the receptacle showing the floral vasculature of *Fenerivia heteropetala* Diels (see text). Abbreviations: **e**, stamen trace; **ls**, lateral sepal bundle; **ms**, median sepal bundle; **pe**, outer petal trace; **pi**, inner petal trace; **sls**, synlateral sepal bundle. Scale bar: 1 mm.

In cross-section and from the outside, the *Fenerivia* pedicel (c. 2.8 mm in diameter) exhibits the following tissues (Fig. 2): a strongly cutinized epidermis, lined with a 1-layer collenchymatous hypodermis; then 3-6 layers of an annular thin-walled collenchyma showing some intercellular spaces; 20-25 layers of parenchyma in which large brachysclereids clusters and secretory cells (with an orange content) are spread. The stele is made up of narrowly elliptical bundles, separated by 2-4 cell thick rays, and provided with phloem fibres, the phloem with few minute secretory cells (with a rose content), 3 or 4 layers of a cambial zone and c. 32 xylem poles. The pith is very like the cortex as usual, but parenchyma cells and intercellular spaces are larger, brachysclereids moreover fusing at some levels in a nearly complete diaphragm.

At the base of the receptacle, the stele (Fig. 3A-C) emits 6 groups of bundles, of which 5 build above cortical pseudosteles, while one remains as an arch (Fig. 3D, left). Nevertheless all of them are compound and contribute to the supply of the flange, upon the classical pattern previously reported for the calyx vasculature (Deroin 1989). Three of them indeed, in an angular location, and including in this case the abnormal arch bundle, are fused to the median bundle of the sepal and the vasculature of the superposed internal petal (Fig. 3D, ms+pi). The three others are fused to the lateral bundles of adjacent sepals and the vasculature of the alternate external petal (Fig. 3E, E, sls+pe).

Thus each sepal is primarily supplied by 3 traces, while outer and inner petals have unique traces (pe and pi respectively in Fig. 3G, H). The vascularization appears very confused just above the insertion level of the inner corolla (Fig. 3I-M), however the 6 supernumerary inner petals (Fig. 4, P_i' and P_i'') are provided by a unique strand too, as well as the stamens, with the 3 lowest ones (E₁, E₂, E₃) superposed to the 3 inner petals (P_{i1}, P_{i2}, P_{i3}). The gynoecium is wholly supplied by the central stele, whose top is modified into a vascular plexus. Each of the c. 45 carpels is fed by 5 traces, i.e. a separate median, 2 mediolateral and 2 lateral bundles.

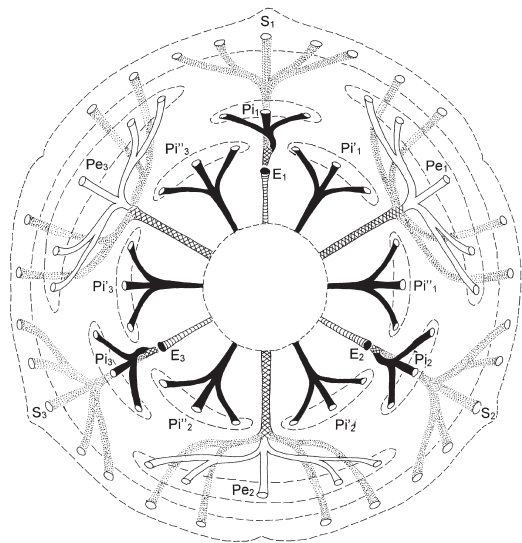


FIG. 4. — Vascular diagram of *Fenerivia heteropetala* Diels: bundles are drawn for perianth and the three first stamens only. Stipple, sepal bundles; white, outer petal bundles; black, inner petal bundles; hatching, stamen bundles; cross-hatching, cortical vascular system (CVS). Abbreviations: E, stamen; Pe, outer petal; Pi, inner petal; S, sepal.

DISCUSSION AND CONCLUSIONS

This brief study establishes several meaningful features about the floral pattern of *Fenerivia* (Fig. 4):

- 1) The "receptacular" disk results in no way from the drying process, as claimed by Schatz & Le Thomas (1990). It is an intact structure, well recognized after restoration, and supplied as expected in an annonaecous calyx (Deroin 1988). A vascular gamosepaly is further demonstrated by the fusion of lateral sepal bundles. Thus the interpretation of Diels (1925), based on external morphology (a rectangular flange, conspicuously 3-splitted below, see Fig. 1, e), is wholly corroborated: the disk is obviously a reduced calyx.
- 2) The corolla is 3-whorled and all petals have a unique trace. The 2 outer whorls (Pe, Pi) are fused with the calyx by their vasculature, building then a complete perianth cortical vascular system (CVS, Deroin 1989). Strikingly the innermost whorl of 6 petals (Pi', Pi'') is supplied by free traces, in the same manner as the stamens. In fact they alternate by pairs with the 3 lower stamens (Fig. 4, E₁, E₂, and E₃). They

cannot be seen as mere supernumerary petals, as in e.g., *Toussaintia hallei* Le Thomas (Deroin 2000); in which the additional petals are supplied by the CVS like normal petals, and their arrangement thus diverges from a strict trimery. Therefore, the innermost petal whorl, so characteristic of *Fenerivia*, results very likely from a petalization of outer stamen pairs, which were recognized as quite frequent in Annonaceae (Ronse Decraene & Smets 1996), instead of a duplication of the usual inner corolla. This regular structure appears homologous with the crown of outer staminodia, already described in *Fusaea* and some Asiatic *Uvaria* species (van Heusden 1992). The most puzzling feature is that the petalized staminodia assume the same shape than inner normal petals.

Because of both its exceedingly reduced calyx and its third petal whorl of androecial origin, the genus *Fenerivia* is wholly characterised and is to be maintained. This morphological specialization coexists with a rich pedicel histology, combined with the high xylem poles number, and the perianth CVS. All these traits indeed are linked with primitive lines (Deroin 1988). Such an odd combination should demonstrate a long evolutive isolation of the clade leading to *Fenerivia*. Consequently, its affinity cannot be clarified at now, but a close affinity with *Polyalthia* s.l. seems unlikely, especially since this large genus was recently shown to be polyphyletic, with at least four locations inside the "Short Branch Clade" (Erkens & Chatrou 2007), i.e. near *Greenwayodendron*; near the group *Haplostichanthus*/ *Trivalvaria*/ *Marsypopetalum*; near *Enicosanthum* and near *Miliusa*, but outer staminodia appear rather spread in the genera of the other half of the cladogram i.e. the "Long Branch Clade". A molecular analysis should be the next step for suggesting us good targets for specifying the most neighbouring extant genera, and thus for steering efficiently the comparative anatomical and palynological studies.

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