Synoptic Revision of the genus *Phanerodiscus* Cavaco (Olacaceae) in Madagascar

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SUMMARY
The olacaceous endemic genus *Phanerodiscus* Cavaco is revised for Madagascar. Three species are recognized, including a new one, *Phanerodiscus capuronii* V. Malécot, G.E. Schatz & J. Bosser, named in order to designate the taxon bearing the invalid name *Phanerodiscus louvelii* Capuron. *Phanerodiscus perrieri* var. *orientalis* Cavaco & Keraudren is excluded from the genus, as the type specimen belongs to *Anacolosa pervilleana* Baillon, whereas all the remaining specimens belong to *Phanerodiscus capuronii*. The three recognized species are separated mainly on the basis of fruit appendages and distribution. Identification keys are provided in order to distinguish these three species on the basis of fruits, flowers and leaf morphology.

RÉSUMÉ

Key words: Olacaceae, *Phanerodiscus*, Madagascar, endemism.
INTRODUCTION

Phanerodiscus is a genus of small trees endemic to Madagascar that Cavaco established in 1954 with the single species Phanerodiscus perrieri Cavaco. It belongs to the family Olacaceae and is placed, according to morphological (Cavaco 1954; Malécot & Lobreaux-Callen 1999), anatomical (Baas et al. 1982; van den Oever 1984) and paller-nological (Lobreau-Callen 1980) data near the genus Anacolosa (Blume) Blume and Cathedra Miers in the tribe Anacoloseae.

Phanerodiscus is traditionally defined by its fruit surrounded by an indivisible complex and by its calyx with widely developed sepals. In contrast, the two closest genera of Olacaceae, Anacolosa and Cathedra, have fruits surrounded by an acrescent disk, and a reduced calyx and sepals fused along their entire length. Other diagnostic characters of Phanerodiscus mentioned by Capuron (1968) correspond to characteristics of tribe Anacolosoidae. This is particularly the cupular disk, free from the calyx and ovary, in which petals and stamens are inserted.

Recent phylogenetic studies suggest that Olacaceae are paraphyletic at the base of Santalales and that genus Schoepfia should be excluded (Nickrent et al. 1998; Nickrent & Malecot 2001). Fossil pollen of Olacaceae, known under the name Anacolosidites Cookson & Pike, are mainly attributable to tribe Anacoloseae, which is where Phanerodiscus belongs. These are present from the Maestrichtian (-72 Ma) in both the northern hemisphere and in the southern hemisphere (Muller 1981; Krutsch 1989; Askin 1989), and since the Eocene (-53 Ma) in Africa (Lucas 1994; Kuyl et al. 1955) and India (Thanikaimoni et al. 1984). The members of this tribe probably colonized Madagascar around the same time (Krutsch 1989; Schatz 1996). Anacolosa, represented by two species in Madagascar, belongs to the "Lemurian Stepping-stones" taxa of Schatz (1996), whereas Phanerodiscus is endemic either due to extinction in other regions or following localized evolution in Madagascar.

In the thesis of one of the authors (Malécot 2002), it is apparent that various nomenclatural problems still existed for this genus of Capuron (1968) who considered it composed of three species. A comparative study of Phanerodiscus samples available in major herbaria containing Malagasy material (MO, P, TAN, TEF) led us to follow the taxonomy proposed by Capuron (1968), but mainly to re-examine the nomenclature. This work aims to solve the nomenclatural problems while presenting a detailed study of various species attributable to the genus; a new species is described.

Regarding the exsiccate, collection locations or the collector's name, noted by Capuron (1968) but not mentioned on the herbarium specimens preserved in various institutions, are indicated in braces { }. Square brackets [] are given to the geographic coordinates assigned post facto using the information on place names and malagasy geography found in the "Malagasy gazetteer", available at http://www.mobot.org/MOBOT/research/madagascar/gazetteer/.

TAXONOMIC HISTORY

The genus Phanerodiscus was created in 1954 by Cavaco from material collected in the region of Majunga, north-western Madagascar. At the time, this type had only one species, Phanerodiscus perrieri Cavaco.

Capuron (1962), in Part V of his contribution to the study of the forest flora of Madagascar, considered that a taxon described by Perrier de la Bâthie (1952) in the genus Diospyros (Ebenaceae) must be placed in the genus Phanerodiscus. He then writes the following lines:

Diospyros sphaerosepala Baker var. calycualata H. Perr., l.c. 141 =
Phanerodiscus diospyroidea
R. Capuron nom. nov.

Cavaco & Keraudren (1963) described a new variety, Phanerodiscus perrieri Cavaco var. orientalis Cavaco & Keraudren. It had as the type specimen RN 8156 present at P. They also mentioned a small number of paratypes.

In 1968, Capuron, as part of his study of the forest flora of Madagascar, wrote a paper titled " Olacées, Opiliacées et Santalacées arbustives ou arborescentes de Madagascar" as a typographic document bearing the letterhead of the Centre Technique Forestier Tropical, Section de Madagascar. In this paper, we find the description of Phanerodiscus perrieri Cavaco, but also that of Phanerodiscus diospyroidea R. Capuron. A third species is also mentioned, Phanerodiscus louveli R. Capuron.

As regards this third taxon, Capuron (1968) notes on page 34: Syn.: Phanerodiscus perrieri var. orientalis Cav. and Ker. (1963) regarding the samples cited excluding the type (cf. Anacolosa pervilleana Baill.), and also mentions in his work (p. 24) Anacolosa pervilleana Baillon (1860-1863); Syn.: Phanerodiscus perrieri var. orientalis Cav. and Ker. (1963) regarding the type and description.

Only a few later studies addressed the genus Phanerodiscus, mainly in palynological or anatomical studies of the family Olacaceae. Thus, Lobreau-Callen (1980), collected pollen from the sample SF 11265, and used the name P. diospyroidea Capuron for the illustrated pollen. The same sample was used by Baas et al. (1982) for the study of leaf anatomy of this genus, using the name P. diospyroidea [diospyroide] Capuron. Lobreau-Callen (1980) also studied the pollen sample SF 6320, P. perrieri Cavaco var. orientalis, and Baas et al. (1982) studied the leaf anatomy of P. perrieri Cavaco based on the sample SF 24226.

From a nomenclatural point of view, three names have been created according to the rules of the International Code of Botanical Nomenclature, Phanerodiscus perrieri Cavaco, P. perrieri var. orientalis Cavaco & Keraudren, and P. diospyroidea Capuron.

Phanerodiscus diospyroidea Capuron is not invalid because it is a substitute name for a name validated by Perrier de la Bâthie published with a different rank.

Phanerodiscus louveli Capuron, is in part invalid because it was published in a document that is not considered an effective publication since the document is typographic (Greuter et al. 2000, Art. 29.1). In this document, dated 1968, among samples assigned to "Phanerodiscus louveli", nothing is mentioned as the type specimen and the name is therefore invalid (Greuter et al. 2000, Art. 37.1). It may be noted that the Louvel 177 specimen present at P is indicated as the type in the hand of Capuron. One should therefore publish a valid taxon corresponding to "Phanerodiscus louveli" Capuron.

From a taxonomic viewpoint, three species are recognized. The type specimen Phanerodiscus perrieri var. orientalis belongs to Anacolosa pervilleana Baillon, while all paratypes belong to Phanerodiscus capuronii.

SYSTEMATIC TREATMENT

PHANERODISCUS Cavaco
Type. - Phanerodiscus perrieri Cavaco

The genus Phanerodiscus, endemic to Madagascar, is composed of three species. They differ mainly in the fruit and especially by the shape of the indvivial investments. The leaves are deciduous at unknown intervals, but probably are annual, falling during the dry season. Flowering usually takes place on leafless branches, two years of age as estimated by Capuron (1968). During the flowering period, some branches may remain leafy and non-flowering. The flowers of different species are very similar morphologically. They have 5 or 6 floral parts per cycle (sepal, petals and stamens). But the number of floral parts is more related to the individual than the species. The floral morphology can hardly be used to distinguish different species. The fruit is a drupe surrounded by an accrescent structure.
or induvium. This structure does not appear to contain a counterpart in the rest of the plant kingdom, since, although placed between the sepals and the “disk” that supports the petals and stamens (Fig. 1C, D), it is completely invisible in the flowers at anthesis (Figs. 1A, B).

Capuron (1968) describes this induvium as follows: “The increased lateral tissue gives rise to a more or less hemispherical cupule (called coupe induviale), (thick-walled below, tapering upward until its upper edge is straight truncated or more or less sinuate) and applied to the base of the fruit. On the outside of the induvial cupule arises, either along an almost circular line, or most

Fig. 1. - Phanerodiscus diospyroidea: A, flower, three petals and three stamens removed; B, detail of the base of the flower in longitudinal section; C, very young fruit, two induvial festoons removed, D, very young fruit, in longitudinal section; E, fruit during growth, induvium almost fully developed. (A-B, Forest Service 11265, E-C, Forest Service 27325).
often along a very scalloped line (scallop alternating with the sepals), a large membranous expansion (called the induvial membrane) which in the mature fruit is the most visible and most important of induvia; this expansion, driven by numerous longitudinal ribs (anastomosing with each other by some ramifications) is either full or near its peak deeply divided into as many lobes as there are calyx sepals. The induvial cupule and membranous expansions are finely papillose-puberulous, especially on the inside”.

In other words, the induvium consists of two parts:

-- the induvial cupule, which enircles the base of the fruit, whose upper edge (visible only after dissection) is straight and truncated in Phanerodiscus perrieri and P. capuronii, or sinuous in P. diospyroidea (Figs. 2B, C, E).

-- the induvial membrane, which corresponds to one or more membranous protrusions that insert on the induvial cupule, and are the most visible at maturity. In Phanerodiscus diospyroidea and P. capuronii, this membrane is composed of “festoons”, as many as the petals and alternating with them (Figs. 2C, D). In P. perrieri this induvial membrane is complete, approximately cylindrical in shape, and devoid of “festoons” (Fig. 2A). This induvial membrane always inserts on the induvial cupule in a sinuous line.

During fruit development, the induvial membrane develops first. When the fruit is young, the induvial membrane largely exceeds it, and often presents a significantly different morphology in the mature fruit. Such young fruits, with an atypical induvial membrane are visible in the sample SF 27325 (Fig. 1E), corresponding to Phanerodiscus diospyroidea, or Schatz 3439 shown on the Missouri Botanical Garden website, http://www.mobot.org/MOBOT/Madagascar/Image/638_080I.JPG and belonging to P. capuronii.

The distribution of these three species is clearly disjunct, each is known only from a relatively small geographic area in Madagascar. Phanerodiscus perrieri occurs near Mahajanga in northwest Madagascar. Phanerodiscus diospyroidea was collected only in the Antsiranana province, in the extreme north of Madagascar. Phanerodiscus capuronii is only known from coastal forests south of Toamasina on the east coast of Madagascar (Fig. 3).

**Key to species of Phanerodiscus from the fruit**

1. Indivial membrane sub-cylindrical, not divided into festoons, 2-2.5 cm in height by 2-2.5 cm in diameter; the fruit (without the induvial membrane) measuring 1.5 cm in height by 1.3 to 1.8 cm in diameter; sepals curving or staying late and erected around the base of the induvial cupule, apex of the induvial cupule straight truncated .......................................................... 1. *Phanerodiscus perrieri*

1'. Indivial membrane divided into festoons, as numerous as and alternating with the sepals; fruit (without the induvial membrane) measuring 1.8 to 2.2 cm by 1.5-1.8 cm in diameter, sepals curving quickly, almost always curved and surrounding the stalk of the mature fruit........................................................................................................................................ 2

2. Festoons under 1 cm high, their insertion into the induvial cupule more than 0.5 cm from the insertion of the sepals, induvial membrane measuring 2-2.5 cm. high by 3-3.5 cm. in diameter, apex of the induvial cupule sinuate ........................................................................ 2. *Phanerodiscus diospyroidea*

2'. Festoons over 1 cm high, their insertion on the induvial cupule less than 0.5 cm from sepals, induvial membrane measuring 3.3 to 3.8 cm high by 5-6 cm in diameter, apex of the induvial cupule truncate ........................................................................ 3. *Phanerodiscus capuronii*
**Key to Phanerodiscus species from leaf morphology**

1. Leaves 1.5 to 2 times longer than wide, petiole between 1/15 \(^{th}\) and 1/20 \(^{th}\) of the length of the blade ........................................... 2

   1'. Leaves from 2 to 2.5 times longer than wide, petiole about 1/10 \(^{th}\) of the length of the blade ........................................... 3

2. Leaf base decurrent and apex acuminate ........................................... 2

   2'. Leaf base rounded and apex acute........................................... 1

**Key to Phanerodiscus species from floral morphology**

1. Flower pedicel 1-2 mm long, much shorter than the free part of sepals .............

   ........................................... 3

   1'. Flower pedicel 3-4 mm long, equal or slightly shorter than the free part of sepals .... 2

2. Free part of sepals 2-3 mm long by 1-1.5 mm at its greatest width; style long to 2-3 mm .

   ........................................... 1

   2'. Free part of sepals 3-4 mm long by 1.5-2 mm at its greatest width, style 3-4 mm long .

   ........................................... 2

**1. Phanerodiscus perrieri** Cavaco


Small tree, 6-12 m, all parts of which, when bruised or crushed, with a strong smell of bitter almonds. Bark gray, rhytidome in patches, looking pronouncedly platanoid. Branches glabrous. Leaves [3.5] -4.7 - [6.8] cm long by [1.7] -2 - [2.9] cm wide (between 2 times and 2.5 times as long as wide), base decurrent and apex acuminate, blade color appreciably identical on both sides; petiole 4-5 mm long (about 1 / 10 \(^{th}\) of the blade).

Flowers arranged in clusters or fascicles in the axils of leaf scars on leafless one-year old twigs (very rarely bearing a few old leaves). Floral pedicle 3-4 mm long. Flowers hermaphroditic; calyx externally puberulous, consisting of six sepals united into a hemispherical cup at the base, the free part of which is 2-3 mm long and about 1-1.5 mm at its greatest width, but not persistent (accrescent) and rarely apparent in the mature fruit; disk hemispheric, glabrous; (5-) 6 petals, caducous, inserted on the margin of the disk, alternate with sepals, triangular, 3-4 mm long by 1.5-2 mm wide, externally pubescent, internally bearded with long hairs in the upper half, and shorter, probably glandular hairs in the lower half, placed at the level of the anthers; (5-) 6 caducous stamens, opposite the petals, filament of the same length as the anther, anther basifixed, extrorse, provided with 6-8 pores arranged in a horseshoe shape around the periphery of the anther; ovary superior, glabrous, attenuated into a style 3-4 mm long, shortly pubescent in the upper part. Drupe 1.5 cm to 1.3 high and 1.8 cm in diameter, surrounded by original likely receptacular induvium whose sub-cylindric induvial membrane is not divided into festoons over the fruit; induvial membrane inserted in a sinusoidal line on the induvial cupule where the point closest to the point of attachment of the sepals about 0.5 cm in the latter, whose farthest point, corresponding to the top of the induvial cupule is about 0.7-0.9 cm thereof.

Fig. 2. - Phanerodiscus perrieri: A mature fruit with induvium. B, mature fruit with two lobes of the induvium having been removed, showing the induvial cupule. - Phanerodiscus capuronii: C, mature fruit with an induvial festoon having been removed, showing the induvial cupule. - Phanerodiscus diospyroidea: D, mature fruit with induvium. E, mature fruit of two induvial festoons having been removed, showing the induvial cupule. (A-B, Forest Service 24226; C, Forest Service 17995, D-E, Forest Service 23057).


2. Phanerodiscus diospyroidea Capuron

Small tree, 7-14 m, all parts of which, when bruised or crushed, with a strong smell of bitter almonds. Bark gray, rhytidome in patches, looking pronouncedly platanoid.

Branches glabrous. Leaves [2] -4 - [6.8] cm long [1.6] -2 - [3] inches wide (between 2 times and 2.5 times as long as wide), base rounded and apex acute, blade color the same on both sides; petiole 3-4 mm long (about 1/10th of the blade). Flowers arranged in clusters or fascicles in the axils of leaf scars on leafless one-year old twigs (very rarely bearing a few old leaves). Floral pedicels 3-4 mm long. Flowers hermaphroditic; calyx puberulous externally, consisting of six sepals united into hemispherical cup at the base, the free part of which is 3-4 mm long and about 1.5-2 mm at its greatest width, but not persistent (accrescent); disk hemispheric, glabrous, petals 6, deciduous, inserted on the margin of the disk, alternate with sepals, triangular, 3-4 mm long by 1.5-2 mm wide, pubescent outside, bearded inside with long hairs in the upper half and shorter hairs, probably glandular, in the lower half, placed at the level of the anthers; stamens
6, deciduous, opposite the petals, filament the same length as the anther, anther basifixed, extrorse, equipped with 6-8 pores arranged in a horseshoe shape around the periphery of the anther; ovary superior, glabrous, attenuated into a style 3-4 mm long, shortly pubescent in the upper part. Drupes 1.8 to 2.2 cm high and 1.5-1.8 cm in diameter, surrounded by the original receptacular indium whose indivial membrane is divided into festoons reaching two thirds the height of the fruit. Festoons inserted according to a sinusoidal line on the indivial cupule where the closest point of attachment is about 1 cm from the sepalis, and whose furthest point is about 1.5 to 1.6 cm from them.

Common name. - Tsiandalavavy.


Phanerodiscus “louveli” Capuron, Olacacées, Opiliacées et Santalacées arbustives ou arborescentes de Madagascar: 34 (1968), non-men inval.

Species Phanerodiscus perrieri affinis sed fructu magno et foliis differt.

TYPUS. - Louvel 177, Madagascar, prov. Toamasina (Tamatave), coastal forests in the east, 1924, fl. (holo-, P!)

Small tree, 6-15 m, all parts of which, when bruised or crushed, with a strong smell of bitter almonds.. Bark gray, rhytidome in patches, looking pronouncedly platanoid.

Branches glabrous. Leaves from 4 to 5.5 cm long and 2-3.5 cm wide (1.5 to 2 times as long as wide), base rounded and apex slightly acuminate; petioles 2-4 mm (between 1/15th and 1/20th of the blade). Flowers arranged in clusters or fascicles in the axils of leaf scars on leafless one-year old twigs. Pedicels of flowers 1-2 mm long. Flowers hermaphroditic; calyx pubescent outside, composed of five sometimes six sepalis united into a hemispherical cup at the base, the free part of which is 2.5-3 mm long, about 1.5-2 mm at its greatest width, persistent but not accrescent; disk hemispheric, glabrous, the margin is at the point of insertion to the petals, 5 sometimes 6 petals, deciduous, alternate with sepalis, triangular, 3-4 mm long and 2 mm wide, pubescent outside, bearded internally with long hairs in the upper half, and shorter hairs, probably glandular, in the lower half, placed at the level of the anthers; 5 sometimes 6 stamens, deciduous, the filament of the same length as the anther, anther basifixed, extrorse, provided with 6-8 pores arranged in a horseshoe shape around the periphery of the anther; ovary superior, glabrous, attenuated into a style 3-4 mm long, shortly pubescent in the upper part. Drupe 2 cm high and 1.5 cm in diameter, likely surrounded by original receptacular indium whose indivial membrane is divided into festoons, well above the height of the fruit, but indivial cupule inserts at the base of the fruit; the festoons are inserted according to a sinusoidal line, where the point closest to the point of attachment of sepalis is about 1-2 mm from them, whose farthest point, corresponding to one of the top indivial cupule is approximately 6-7 mm from them.

Common name. - Tsilangotongotra.

Paratypes. – Madagascar, Prov. Toamasina: Schatz, Stevens & Rakotomalaza 3439,

Capuron (1968) mentions two other samples: Capuron sn, no date (flowers) and Capuron sn., no date (young fruit in alcohol) that have not been found in the consulted herbaria.

Nomina excludenda

Phanerodiscus perrieri var. orientalis
Cavaco & Keraudren

In 1967, Keraudren attributed the sample to Anacolosa pervilleana (determined from the sample). This new identification was confirmed and revived by Capuron (1968).

Fig. 3. - Distribution of Phanerodiscus in Madagascar. P. perrieri (▲), P. diospyroidea (♦) P. capuronii (★).

Acknowledgments

We wish to thank J. FLORENCE for his comments and advice in preparing the Latin diagnosis, P.H. Raven and his staff for their assistance at the Missouri Botanical Gardens, and P. Morat and his staff for their hospitality at the Laboratoire de Phanérogamie à Paris. The second author benefitted from a grant (DEB-0102727) from the U.S. National Science Foundation.
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