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Flower and fruit structure of *Operculicarya decaryi* H. Perrier (Anacardiaceae) from Madagascar

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Abstract. The morphology of unisexual flowers of *Operculicarya decaryi*, a small xerophytic woody species from southern Madagascar, is described for the first time. Pedicels are articulated and have multicellular glandular hairs, which also occur on the bracts, bracteoles and perianth. The receptive surface of the stigma is papillate. The fruit is a typical drupe, containing a mostly unilocular, woody stone which is operculate. The sclerenchymatous operculum originates from the inner epidermis of the ovary wall and adjacent parenchyma, and is demarcated by parenchyma at maturity. The mature pericarp is characterized by a tanniniferous outer epidermis (or exocarp *s.s.*) with a well-developed cuticle as well as an internal cuticular layer on the inner tangential middle lamella of a number of epidermal cells surrounding the stomata. Hypodermal tanniniferous parenchyma layers and prominent secretory cavities and ducts characterize the mesocarp *s.s.* Bundles of fibers, brachysclereids and macrosclereids occur in the woody stone. No fibers occur in the operculum. The inner epidermis (or endocarp *s.s.*) consists of brachysclereids. The genus *Operculicarya*, tribe Spondiadeae, is closely related to the genus *Lannea*. The results suggest that the current separate generic status of *Operculicarya* and *Lannea* deserves further study.

Key words: Drupe; Hairs; Internal cuticular layer; *Lannea*; Operculum; Stigma.

Introduction

The genus *Operculicarya* H. Perrier (Anacardiaceae), comprising only four species (Capuron, 1975; Perrier de la Bâthie, 1946), is endemic to the Malagasy Republic (henceforth referred to as Madagascar). According to the widely accepted intrafamilial classification of the Anacardiaceae by Engler (1892), *Operculicarya* is without doubt a natural member of the tribe Spondiadeae. Other related endemic genera in Madagascar are *Faguetia* March. and *Micronychia* Oliv. (Leroy, 1978). *Operculicarya decaryi* H. Perrier is a deciduous, much branched, thick-stemmed, small, shrub-like tree with small, compound, imparipinnate leaves borne on short shoots (brachyblasts). This growth form is the dominant type among the xerophytic chamaephytes and phanerophytes in Madagascar and represents one of the mechanisms to reduce the transpiration surface under arid conditions (Thomasson, 1989). This species is confined to limestone-derived soils along rocky slopes in the semi-arid southern part of Madagascar.

Except for general morphology presented by Perrier de la Bâthie (1946) as well as for the external pollen morphology (Rasoarimalala *et al.*, 1982), very little is known about this species. Since male and female flowers were not available for the description of the species, the present paper provides the first detailed description of floral morphology as well as ontogeny

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and structure of the pericarp to contribute towards the characterization of this taxon. This investigation forms part of a comprehensive comparative study of the fruit and seed structure of the Anacardiaceae. In the discussion some striking similarities in the flower and drupe of *Operculicarya decaryi* and *Lannea discolor* (Sond.) Engl. will be emphasized. As hitherto conceived, the genus *Lannea* A. Rich. does not occur in Madagascar. It comprises about 40 species and occurs mainly in tropical and southern Africa (Von Teichman, 1987).

Materials and Methods

Female floral buds, flowers and fruits of *Operculicarya decaryi* at different stages of development were collected from a tree growing in the display glass house of the National Botanical Institute, Pretoria (voucher specimen: *Von Teichman 560*, PRU). The second author collected this plant in Madagascar (April, 1969) while it was still very small, the reference number being *Hardy 2773*. He also collected male flowers (preserved in FAA) from a plant in a private nursery in Los Angeles, U.S.A. in September 1987.

Dissected flowers and fruits were studied with a Wild M3 stereomicroscope, and finer detail was observed with a Leitz light microscope; both equipped with a drawing tube. For the anatomical study, either small pieces of fresh material (fixed in 2.5% glutaraldehyde) or pieces of FAA-preserved material which were rinsed in 50% ethanol prior to dehydration, were used.

Material was dehydrated and then infiltrated and embedded in monomer-mixture (containing glycol methacrylate) according to Feder and O'Brien (1968). The monomer mixture is described by Von Teichman (1987).

A Porter Blum MT-1 ultramicrotome was used for the sectioning. The "Periodic Acid-Schiff's Reaction" (PAS) was carried out according to Feder and O'Brien (1968); the details thereof as well as of the counterstaining in toluidine blue O are given by Von Teichman (1987). Testing for fatty substances, i.e. cutin, was done with sudan black B (Von Teichman, 1987). Unstained sections were viewed under crossed polarizing filters to detect crystals. Maceration of small pieces of the stone (excluding the operculum) and the opercula followed the procedures described in the last mentioned paper.

Results

Morphology of the Flowers

Operculicarya decaryi is dioecious. At anthesis male flowers are creamish yellow, *ca.* 4 mm in diameter, and borne on a very short pedicel. The pedicel is articulated, *ca.* 0.5 mm long and provided with basal bracts. Flowers are mostly pentamerous, although tetramerous ones also occur. Obovate sepals are *ca.* 1.3–1.8 mm long, while obovate petals, slightly recurved at anthesis, are *ca.* 2.1–2.5 mm long. Sepals and petals are free. Anthers, which open introrse and are dorsifixed, are *ca.* 0.7 mm long, with the free filament *ca.* 0.6–0.9 mm long. A prominent, mostly crenate disc and a minute rudimentary gynoecium are present.

Up to four pedicellate female flowers occur together with two or three juvenile leaves at the apex of the short shoot (Fig. 1). Flowers often abscise at the articulation on the pedicel. The pedicel is (3.5–) 5.2 (–6.5) mm long and articulated (0.4–) 0.6 (–0.9) mm from the apex. Pedicels are subtended by minute basal bracts (1.6–) 2.0 (–2.2) mm long. Two minute bracteoles, (1.2–) 1.3 (–1.9) mm long, occur at slightly different levels and more or less opposite to one another, mostly below the articulation on the pedicel. At anthesis the creamish yellow female flowers are (3.0–) 4.1 (–4.8) mm in diameter. They are mostly pentamerous, but *ca.* 23% are hexamerous. Obovate sepals are 1.5–1.9 mm long. Petals as

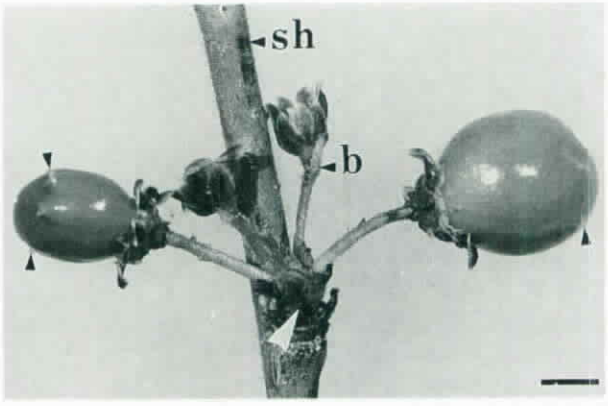

Fig. 1. Female flowers and very young fruit of *Operculicarya decaryi*. b, bracteole on pedicel of flower before anthesis; sh, shoot; white arrow head, short shoot; small black arrow heads, style remnants on very young fruit, which also show remnants of staminodes, the disc and the perianth. Scale bar = 2 mm.

well as sepals are imbricate in bud and mostly 5-segmented. Petals are obovate, *ca.* 1.8–2.3 mm long and slightly recurved at anthesis.

Ten or twelve staminodes, *ca.* 0.7–1.2 mm long, are present on the outside of the yellow, annular 10- or 12-crenate disc. The ovary is unilocular, subglobose, slightly laterally compressed and contains a single, pendulous anatropous ovule. Five or six short free styles terminate in simple to subcapitate stigmas, with the total length *ca.* 0.3–0.5 mm. The receptive surface of the stigma is papillate. These papillae are unicellular.

Male and female flowers are characterized by multicellular glandular hairs on the pedicel, bracts, sepals and petals. Bracts and bracteoles of both types of flowers are covered with numerous, well-developed i.e. often long-stalked, hairs (Fig. 2A). In the male flower five to twelve hairs occur on the sepals, while only one or two are found on the petals. These hairs are not well-developed. In contrast, about 50–60 hairs occur on the sepal margin of the female flower, besides the few on the adaxial surface towards the base. Their overall size is reduced (Fig. 2B & C) when compared to those on the bracts and bracteoles, the head being even reduced to a single cell. Petals of the female flower have only up to six hairs. A light microscopical study of numerous sets of sepals and petals of the female flower also revealed single, unicellular, linear-triangular hairs (Fig. 2D & E), situated on the apex of only (in total) three sepals and three petals. In contrast to the glandular ones, these hairs have secondarily thickened cell walls.

Morphology of the Mature Fruit

Mature drupes are purplish black, obliquely subglobose and slightly laterally compressed. They usually occur singly on the short shoots (Fig. 3). Five or six style remnants can be distinguished. The stone is operculate, laterally compressed and slightly ridged with a prominent alveole on one side (Fig. 4A & B). About 92% of the 110 stones examined are unilocular (Fig. 4A–D), while the remainder is bilocular and more triangular (Fig. 4E), or represent the transitional form (Fig. 4D). In the latter, one fruit locule is well-developed, while the second one is only a shallow cavity. Fruit locules are sealed with opercula. These are usually ovate with an acute apex and unipartite (Fig. 4A), or rarely more or less cap-shaped and bipartite, i.e. separating into two parts which are more or less equal (Fig. 4C & D) or unequal in size (Fig. 4E). The funicle of the seed is attached apically in the fruit wall very close to the side of the operculum. A characteristic knob of the

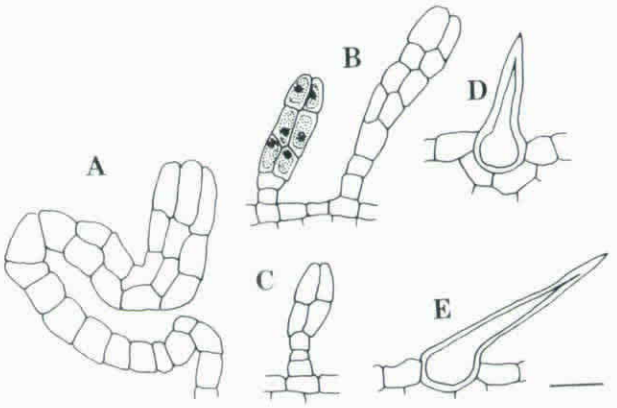

Fig. 2. Glandular hairs from bracts and bracteoles of female flowers (A), similar hairs from their sepals and petals (B & C), and unicellular hairs also on their perianth (D & E). Scale bar = 30 μm.

Fig. 3. Shoot of *Operculicarya decaryi*. Short shoots with leaves and fruit (about six weeks after anthesis). Scale bar = 10 mm.

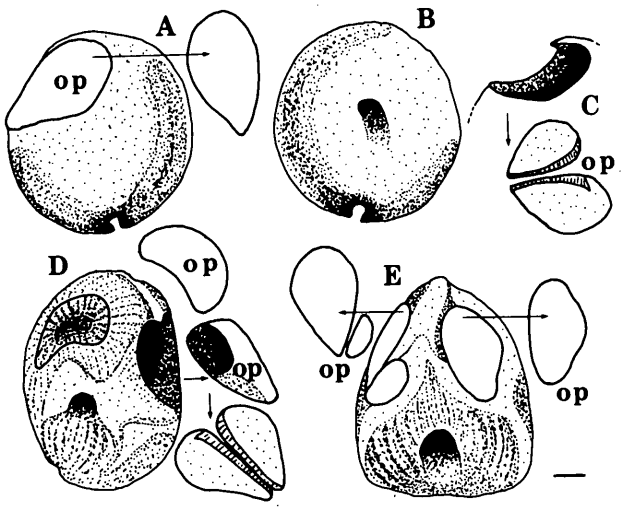

Fig. 4. Mature stones with opercula (op). A & B, two lateral views of the same stone; C, upper portion of a unilocular stone with detached bipartite operculum; D, the transitional form with two detached opercula; E, triangular, bilocular stone with detached bi- and unipartite opercula. Scale bar = 1 mm.

endocarp *s.l.* or woody part of the mesocarp *s.s.* projects deeply into the fruit locule.

Ontogeny and Anatomy of the Pericarp

At anthesis, the ovary wall consists of the five following zones:

(1) An outer epidermis of slightly radially elongated, tanniniferous parenchyma.
(2) An underlying outer zone of tanniniferous parenchyma varying in thickness (three to 15 cell layers thick).
(3) A second outer zone of parenchyma, practically devoid of tanniniferous deposits.
(4) A central parenchymatous zone including secretory cavities and procambium strands.
(5) An inner parenchymatous zone and an inner parenchymatous epidermis. In the region of the future operculum the cells of this inner zone and epidermis appear meristematic since they are rich in cytoplasm and have large nuclei.

First signs of a differentiation are noticed within the endocarp knob already projecting into the ovary locule. Here bundles of fibre initials, which originated from derivatives of the procambium strands, are present. This differentiation proceeds throughout the central parenchymatous zone. Numerous xylem elements with helical wall thickenings are seen among the fibre initials. However, in a small part, the future operculum, an inner zone of meristematic tissue is present. A number of procambium strands and larger, often tanniniferous parenchyma cells demarcate this zone on the outer periphery.

In the very young fruit the above-mentioned fibre initials differentiate into fibres. A practically solid layer of sclereids and fibre bundles in random orientation is present. Most of the vascular tissue occurs either just to the inside of the prominent secretory cavities or to the inside of the fibre zone. In young fruit, about six weeks after anthesis, the solid zone of sclerenchyma, consisting of brachysclereids and fibres, has extended significantly since adjacent parenchyma cells have differentiated into brachysclereids (Fig. 5A-C). The latter differentiation proceeds also within the inner parenchyma zone and inner epidermis. However, small islands of parenchyma, often including vascular tissue, are still present (Fig. 5). In the outer, tangentially elongated epidermal cells, a fine serration on the outer well-developed tangential cell walls and stomata are also present (Fig. 5B).

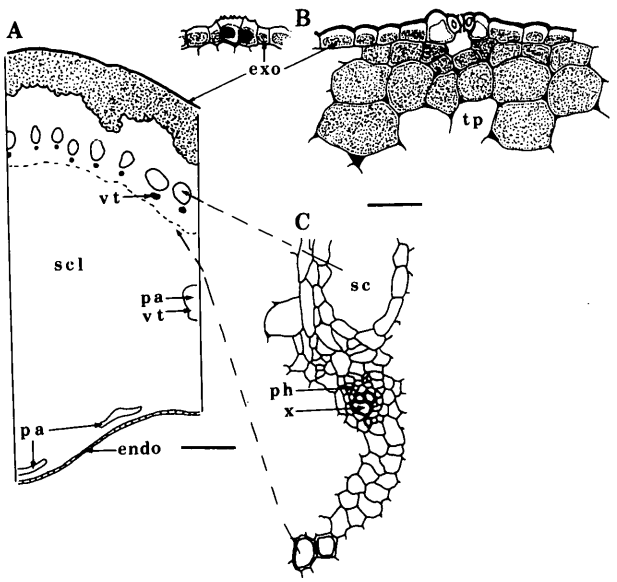

Fig. 5. Transverse section of the pericarp of the young fruit. A, the entire pericarp; B, the exocarp with stoma and outer part of the mesocarp; C, part of the mesocarp with secretory cavity, vascular bundle and two young brachysclereids; endo, endocarp; exo, exocarp; pa, islands of parenchyma; ph, phloem; sc, secretory cavity; scl, sclerenchyma; tp, tanniniferous parenchyma; vt, vascular tissue; x, xylem elements. Scale bar in A = 500 μm, in B & C = 50 μm.

The overall anatomy of the mature pericarp does not differ significantly from that of the young fruit. A tanniniferous outer epidermis (or exocarp *s.s.*) is characterized by a well-developed cuticle proper, *ca.* 2.6 μm thick. This cuticle occurs around the guard and subsidiary cells, thus lining the substomatal chamber. In *Operculicarya decaryi* a remarkable thin extension of the cuticle stretches along the internal surface of three, five or even up to ten adjacent epidermal cells on both sides of the stoma. It appears that the middle lamella bordering the inner tangential cell walls of these epidermal cells is secondarily cutinized. The study of a great number of 4 μm thick serial transverse sections revealed that this internal cuticular layer can be followed for eight sections. This implies that it is rather extensive, stretching for about 32 μm, i.e. radiating from the substomatal chamber to all sides. In sections that include two stomata relatively closely together, this cuticular layer is practically continuous between the stomata. The guard cells are slightly raised (Fig. 5B) or on the same level as the surrounding epidermal cells. Outer and inner cuticular ledges are present, the outer ones well-developed and in some stomata they partially close the stomatal pore.

The exocarp is followed by a zone of parenchyma, the vacuoles of the cells of the outer layers filled with fine, granular tanniniferous deposits. In the inner part of this zone, secretory cavities (or ducts) and closely associated vascular bundles are present.

Some of the parenchyma cells are slightly radially elongated. The woody part of the pericarp consists mainly of bundles of thick-walled fibres and brachysclereids. The latter dominate the outer periphery and the innermost cell layers, including the inner epidermis (or endocarp *s.s.*). The thick-walled brachysclereids of the latter form the inner, shiny surface of the stone.

The woody operculum, which originates from the inner epidermis of the ovary wall and the adjacent inner parenchyma, is demarcated by parenchyma which often also contains tanniniferous deposits. Macerated tissue of the operculum consists mainly of monomorphic, thick-walled globoid, spheroidal, as well as vesiculose sclereids (typology of sclereids *sensu* Rao and Bhupal, 1973). The vesiculose sclereids have an uneven outline and narrow cell lumens and usually fit into each other like pieces of a jig-saw puzzle. Variously shaped, thick-walled macrosclereids resembling the fusiform type of Rao and Bhupal (1973) are also present. Besides the sclereids occurring in the operculum, the macerates of the stone (i.e. excluding the operculum) consist of the mentioned bundles of long fibres, as well as vascular elements, especially xylem elements with helical wall thickenings.

Discussion and Conclusion

In the Anacardiaceae, Heslop-Harrison and Shivanna (1977) recorded only a non-papillate receptive surface in the wet stigma of *Cotinus* Miller. In *Operculicarya decaryi* the receptive surface is distinctly papillate. A previous study of the female flower of *Lannea discolor* (Von Teichman, 1987) and the present investigation allow a brief comparison of the floral morphology of these two taxa. In *Lannea* the female flowers are borne in racemes, while in *Operculicarya* up to four flowers occur at the apices of short shoots. While the flowers of *Operculicarya* are mostly pentamerous, tetramerous ones predominate in *Lannea*. However, pentamerous flowers also occur in *Lannea*, whereas ca. 23% of the flowers of *Operculicarya* are hexamerous. The pedicel, bracteoles and sepals of *Lannea* are characterized by fine stellate hairs. On the other hand these floral parts as well as the petals in *Operculicarya* exhibit mostly multicellular glandular hairs, except for the very few unicellular, linear-triangular hairs on the perianth. However, in *Lannea* glandular hairs which are very similar to those described for *Operculicarya* are present on the ovary wall and young exocarp (Von Teichman, 1987; Fig. 8D).

On the whole, floral morphology is very uniform in the Anacardiaceae. This is demonstrated by the following floral characters shared by both taxa under discussion: small, creamish-yellow and pedicellate female flowers; petals imbricate in the bud and recurved at anthesis; a yellow, annular, intrastaminal and crenate disc; staminodes; a syncarpous, subglobose, laterally compressed, usually unilocular ovary mostly with one pendulous and anatropous ovule; and relatively short styles terminating in simple to subcapitate stigmas.

That there is a difference of opinion as to the demarcation of the exo-, meso- and endocarp in the Anacardiaceae, has been discussed previously (Von Teichman, 1991). In members of the Spondiadeae the outer and inner epidermis can be distinguished easily in the mature pericarp; they represent the exo- and endocarp *s.s.* respectively. The mesocarp *s.s.* therefore

comprises the part between these two layers. In the Spondiadeae the stone forms a natural, functional unit and as such represents the endocarp *s.l.*

In *Operculicarya decaryi* the structure of the ovary wall at anthesis, is very similar to that of *Lannea discolor* (Von Teichman, 1987; Fig. 3). Fruit morphology, especially the presence of an operculum in the stone, strongly supports the placement of the genus *Operculicarya* in the tribe Spondiadeae. In *Operculicarya decaryi* the endocarp *s.l.*, consisting of well-developed, irregularly oriented sclerenchyma, conforms with the *Spondias*-type distinguished by Wannan and Quinn (1990). *Operculicarya* may be compared with *Lannea*, also of the tribe Spondiadeae, or more specifically *Operculicarya decaryi* with *Lannea discolor* (Von Teichman, 1987). With regard to flower morphology, only the stellate hairs on the pedicel, bracteoles and sepal bases in *Lannea discolor* present a notable difference.

The stones of the two taxa are strikingly similar. However, the opercula in *Lannea discolor* are usually bipartite, although unipartite ones with the same shape as those occurring predominantly in *Operculicarya decaryi* also occur in *Lannea discolor*. An endocarpal knob also projects into the fruit locule in *Lannea discolor*. Pericarp anatomy shows the following similarities between the two species:

(1) An outer tanniniferous, stomatous epidermis, the outer tangential cell walls with fine serration and well-developed cuticle.
(2) Fiber bundles, macrosclereids and brachysclereids characterize the stone.
(3) An inner epidermis consisting of brachysclereids.
(4) An operculum with similar origin and structure.

Even the characteristic forms of the macrosclereids and brachyslereids occurring in the endocarp (as well as the operculum) of *Operculicarya decaryi*, very closely resemble those of *Lannea discolor* described and illustrated by Von Teichman (1987).

The outer zone of tanniniferous parenchyma distinguishes the pericarp of *Operculicarya decaryi*, while in *Lannea discolor* about four cell layers of radially elongated, tanniniferous parenchyma occur on the outside of the stone. In *Lannea discolor* the vascular bundles are not closely associated with the secretory cavities. However, in both taxa the majority of the vascular bundles occur more or less at the same level in the outer parenchymatous pericarp.

Extensions of the cuticle into the substomatal chamber have been referred to as the internal cuticle (Boyer, 1985; Wullschleger and Oosterhuis, 1989). According to Metcalfe and Chalk (1979), in many xerohytic plants the inner periclinal epidermal walls or "even, in extreme xerophytes, the walls of subepidermal layers may also be cutinized." The term "cuticulae interne" was already used by De Lamarliêre in 1906 (Metcalfe and Chalk, 1979). In *Operculicarya decaryi* the exocarp *s.s.* is characterized by the internal cuticular layer on the middle lamella of many inner tangential cell walls. This phenomenon, which was previously reported by Stace (1965), probably represents an adaptation of *Operculicarya decaryi* to the xerophytic habitat. In *Rhus problematodes* Merxm. & Roessl. (Rhoeae - Anacardiaceae), a microphyllous shrublet endemic to the southern desert region of Namibia, a thick cuticle proper, an outer cuticular layer and subepidermal cuticular phlanges distinguish the exocarp *s.s.* (Von Teichman and Van Wyk, 1991). These two species are therefore both macro- and micromorphologically adapted to their extreme xerophytic environment.

Fruit morphology and especially pericarp anatomy in *Operculicarya decaryi* also suggest a closer affinity of *Operculicarya* to the other taxa of the Spondiadeae occurring in southern Africa, e.g. *Sclerocarya birrea* (A. Rich.) Hochst. subsp. *caffra* (Sond.) Kokwaro and *Harpephyllum caffrum* Bernh. ex Krauss, than to *Tapirira guianensis* Aubl. (Spondiadeae) from South America (Von Teichman, 1990).

Capuron (1957) and Kokwaro (1986) have already mentioned the macromorphological resemblance between *Operculicarya* and *Lannea*. Flower as well as fruit morphology show that *Operculicarya* is certainly very closely related to *Lannea*. The main conclusion is that the current separate status of these two genera needs reconsideration.

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馬達加斯加島特有漆樹科 *Operculicarya decaryi* H. Perrier 的花及果實的構造

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Operculicarya decaryi 係產於馬達加斯加島南方的一種矮小的旱生木本植物，其單性花的形態在本文中首次被描述。小花梗具關節並有多細胞的腺毛。這種腺毛亦分佈於小苞片，苞片及花被片上。其柱頭的受粉面爲乳突狀。果實屬典型的核果，木質的核通常一室並具開蓋。此厚壁細胞組成的開蓋起源自子房內表皮及附近的薄壁細胞，在成熟期由薄壁細胞與其他部份界分。成熟果皮的特色之一是外表皮含單寧質及具一層發育良好的角皮層及氣孔四周表皮細胞的弦切面中膠層中含角質層。中果皮的特色是下表皮薄壁細胞含單寧並具明顯的分泌腔或分泌管。在木質的果核中有成束的纖維、石細胞及桿狀厚壁細胞，但在開蓋中不具有纖維。內表皮，即狹義的內果皮，是由石細胞所組成。本研究顯示 Spondiadeae 族的 *Operculicarya* 屬與 *Lannea* 屬具有親密的關係，而兩者目前被處理爲二個獨立的屬似乎有再研究的必要。