



## Pericarp structure in *Protorhus longifolia* (Bernh.) Engl. (Anacardiaceae) and its taxonomic significance

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**Abstract.** The pericarp of *Protorhus longifolia* (Bernh.) Engl. comprises a uniseriate exocarp *sensu stricto*, a typical, resinous anacardiaceous mesocarp and a distinctly layered endocarp *sensu stricto*. The exocarp develops from the outer epidermis of the ovary wall, and is composed of strongly elongated, palisade-like cells with the outer walls impregnated with cutin and covered with a very thick cuticle. The mesocarp is parenchymatous, rich in tanniferous and crystalliferous cells, and contains conspicuous secretory ducts and vascular bundles. In the mature fruit, the initially three-layered endocarp consists mainly of an inner layer of macrosclereids, which have lost their palisade-like shape, and an adjacent layer of brachysclereids. This represents the *Anacardium*-type endocarp which is found in all tribes of the Anacardiaceae except the Spondiadeae. Amongst other evidence, pericarp structure suggests a taxonomic affinity of *Protorhus* Engl. (tribe Rhoëae) with *Semecarpus* L. f. (tribe Semecarpeae).

**Key words:** Anacardiaceae; Flower; Fruit; Pericarp; Phytogeography; *Protorhus*; *Semecarpus*.

### Introduction

Within the large, chiefly tropical and subtropical family Anacardiaceae, the genus *Protorhus* Engl. has been placed in the tribe Rhoëae (Rhoideae) by Engler (1892). Phytogeographically *Protorhus* is centred in the Malagasy Republic, henceforth referred to as Madagascar (15 species according to Perrier de la Bâthie, 1946) with only two species in Africa.

The two African species of *Protorhus* have a disjunct distribution and are morphologically very different from each other. Unpublished observations on *Protorhus namaquensis* Sprague, a species endemic to the lower Orange River valley on the Namibian/South African border (Dyer, 1975; Merxmüller and Schreiber, 1968), raise some doubts as to its current generic placement.

*Protorhus longifolia* (Bernh.) Engl. the other African species and subject of this paper, is of special significance since it is the lectotype of the genus (Farr

*et al.*, 1979). It is largely confined to the forests of the Tongaland-Pondoland Regional Mosaic (White, 1983), with outliers in the afro-montane forests of Swaziland and the eastern and northeastern Transvaal. It is particularly abundant in the subtropical forests of Natal and Kwa Zulu. In the forest these evergreen trees are up to 18 m high with a trunk diameter of about 1 m (Palmer and Pitman, 1972). The shiny foliage is conspicuous and characterized by prominent lateral veins running up to the leaf margin. The occasional presence of a bright red leaf is characteristic of the canopy. Common names include Red Beech and "Rooiboekenhout" (Coates Palgrave, 1981). Although the wood is not very durable, it provides a general purpose timber. Bark and leaves are eaten by Black Rhino, whereas the fruit, despite their strong resinous smell, are eaten by Vervet and Samango Monkeys as well as various birds. Africans have several uses for the milky gum-like bark exudate (Palmer and Pitman, 1972; Watt and Breyer-Brandwijk, 1962).

In addition to the taxonomic treatment of the

genus *Protorhus* by Engler (1881, 1883, 1892, 1921) and Perrier de la Bâthie (1946), *Protorhus longifolia* has subsequently been described only in various popular scientific works on the flora of southern Africa. A paper on the pollen morphology of *Protorhus sericea* Engl. (Rasoarimalala *et al.*, 1982) is about the only other source of information on the genus. The chemical composition of the brown secretion present in the pericarp and other parts of *Protorhus longifolia* is unknown, but it probably contains terpenes or polyphenols. People who have been sensitized after contact with *Smodium argutum* E. Mey. ex Sond., a relative of *Protorhus longifolia*, may also suffer from allergic contact dermatitis when exposed to the secretions of *Protorhus longifolia*.

This paper on the pericarp structure of *Protorhus longifolia*, emanates from a comprehensive comparative morphological study of the fruit and seed of the Anacardiaceae. Its principal aim is to contribute towards a better understanding of the circumscription and taxonomic position of the genus *Protorhus*. Existing descriptions of the genera of the Anacardiaceae contain very little information on fruit and seed structure. It is hoped that this contribution may assist future attempts towards a more natural infrafamilial classification of the family.

Data on the pericarp structure of *Protorhus longifolia* will be related to evidence on other members of the Anacardiaceae previously published by Wannan and Quinn (1990) as well as Von Teichman (1989).

## Materials and Methods

Floral buds, flowers and fruits in various developmental stages were collected from a tree of *Protorhus longifolia* growing in the National Botanical Garden, Pretoria (voucher specimens: *Von Teichman 541 & 556* in PRU). Material from the natural habitat of the species was kindly collected by Mr. A.T.D. Abbott in the Umtamvuma Nature Reserve near Port Edward in southern Natal (voucher specimens: *Abbott 1274 & 1294* in PRU).

For anatomical study, small pieces of fresh material were fixed in 2.5% glutaraldehyde. Air dried fruits were rehydrated before fixation. Material was also preserved in FAA and rinsed in 50% ethanol prior to dehydration. For the glutaraldehyde a 0.1 mol dm<sup>-3</sup> Na<sub>2</sub>PO<sub>4</sub> and NaH<sub>2</sub>PO<sub>4</sub> buffer containing 0.5% caffeine

was used. After fixation the material was dehydrated, infiltrated and embedded in purified glycol methacrylate (GMA) according to the method of Feder and O'Brien (1968), (for the composition of the monomer mixture, see Von Teichman, 1987). Semi-thin sections were treated with the periodic acid-Schiff reaction (PAS) and counterstained with toluidine blue O (Von Teichman, 1987). Some of the sections were treated as follows:

- (a) To test for the presence of fatty substances, especially cutin, sections were placed in a saturated solution of sudan black B in 70% ethanol for 10 min. After rinsing in 70% ethanol, the sections were mounted in liquefied glycerine jelly.
- (b) For the staining of lignified cell walls, sections were mounted in a drop of saturated phloroglucinol in 20% HCl.
- (c) For the detection of calcium oxalate crystals, unstained sections were viewed under crossed polarizing filters.

## Terminology

There is difference of opinion as to the demarcation of the exo-, meso- and endocarp in the Anacardiaceae (Von Teichman, 1989; Wannan and Quinn, 1990). In a comparative study of the pericarp of 29 anacardiaceous genera, Wannan and Quinn (1990) define the mesocarp as the "central zone that includes scattered vascular bundles and resin canals, and often also fibre bundles or zones of sclerenchyma". Their point of departure is that the mesocarp develops from the zone containing the vascular system of the "ancestral fertile leaf".

On the other hand, the present author has initially followed a functional approach, with the exocarp taken as the peel and the endocarp as the stone. This interpretation was applied to members of the tribe Spondiadeae, including species of *Sclerocarya* Hochst. (Von Teichman and Robbertse, 1986b), *Lannea* A. Rich. (Von Teichman, 1987), *Harpephyllum* Bernh. ex Krauss (Von Teichman and Van Wyk, 1988) and *Tapiriva* Aubl. (Von Teichman, 1990), as well as *Rhus* L. of the tribe Rhoeae (Von Teichman and Robbertse, 1986a). Subsequently, an attempt was made to identify specific zones in the ovary wall as the basis for establishing homologous parts of the mature pericarp (Von Teichman, 1989). The latter paper may also be consulted for a more

detailed discussion of the two different approaches, and the use of the terms exo- and endocarp *sensu stricto* (*s. str.*) or *sensu lato* (*s. l.*). In the present contribution the exo- and endocarp of *Protorhus longifolia* are considered in a narrow sense. This implies that the mature exo- and endocarp develop from the cells of the outer (abaxial) and inner (adaxial) epidermis of the ovary wall respectively, or from their derivatives.

## Results

### *Morphology of Female Flowers and Fruits*

*Protorhus longifolia* is essentially dioecious. The small, 4–5 mm in diameter, greenish white to yellow flowers are borne in panicles and display the following:

- (1) Small, unicellular, straight or bent trichomes on the rachis, peduncle, pedicel, bracteoles, calyx and corolla;
- (2) Three bracteoles, the basal one larger (about 1 mm long), often present on the pedicels of some of the flowers towards the apex of the inflorescence;
- (3) A five-lobed calyx and pentamerous, imbricate corolla;
- (4) Five pink staminodes, alternating with the petals and inserted below the rim of the ring-like, orange disc; and
- (5) A gynoeceium, purplish red in buds and purplish black at anthesis. It is tricarpeolate, with the three styles connate at the base and tipped by capitate stigmas. The ovary is ovoid to subglobose and unilocular. A single, pendulous ovule with short funicle is suspended practically from the apex of the ovary wall.

The nearly mature fruits are asymmetrically ovoid, purple and very slightly ridged, the ridges caused by the large secretory ducts in the mesocarp (Fig. 1A). Mature fruits are somewhat fleshy and black, becoming wrinkled when dry, and are up to 12 mm long (Fig. 1B). The single seed (Fig. 1C) is relatively large and consists of a membranous seed-coat and green (chlorophyllous) embryo.

### *Ontogeny and Structure of the Pericarp*

Transverse sections of flower buds (Fig. 2) show the following anatomical features of the ovary wall:

- (1) An outer epidermis of nucleate, radially elongated parenchyma cells, rich in cytoplasm and engaged in anticlinal divisions;

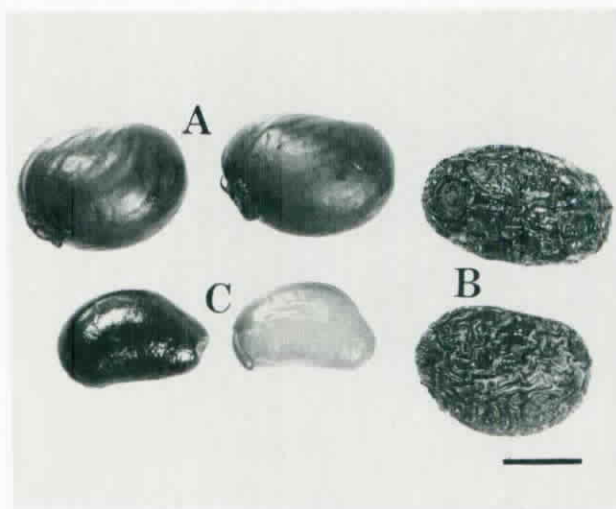


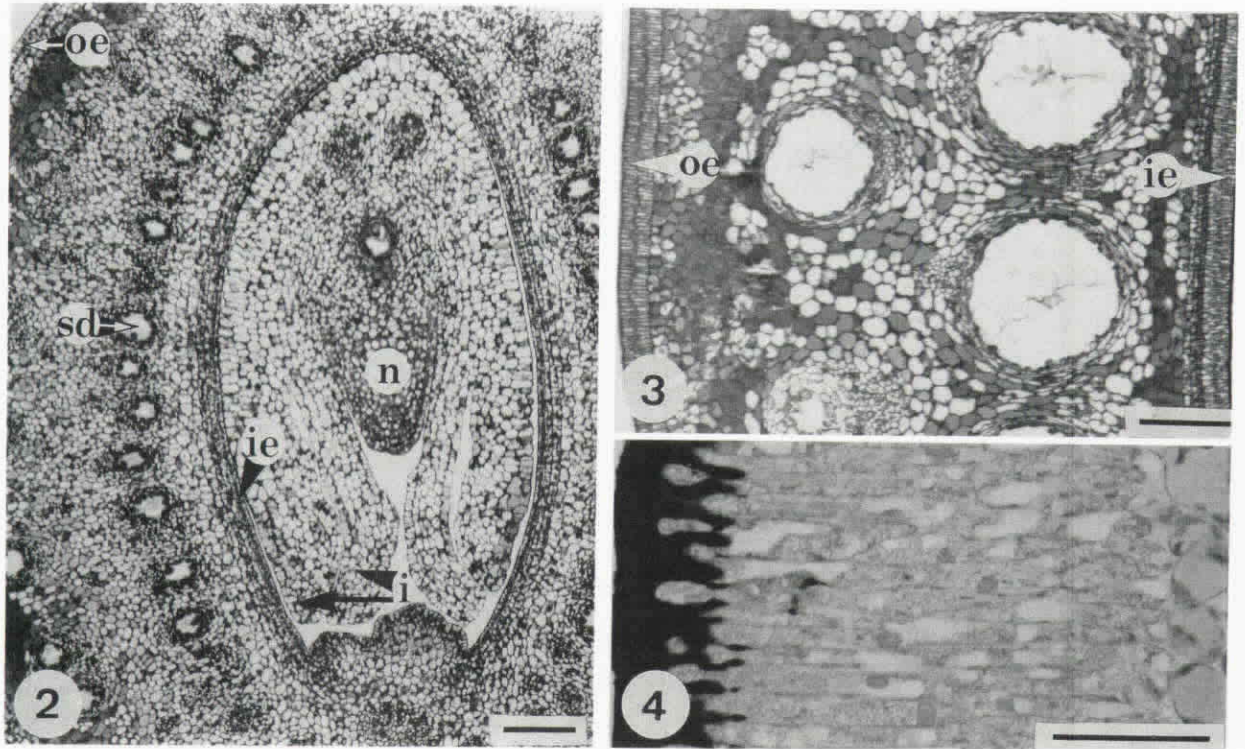
Fig. 1. Mature fruits of *Protorhus longifolia*. A, fresh fruits showing slight ridges; B, dry, wrinkled fruits; C, seed and embryo. Scale bar = 5 mm.

- (2) Hypodermal layers of parenchyma, the cells tanniferous or not;
- (3) A broad, central, parenchymatous zone characterized by secretory ducts arranged in more or less two concentric circles. Vascular bundles occur either in close association with the secretory ducts or in the parenchyma between them;
- (4) A narrow inner zone of parenchyma; and
- (5) The future endocarp, consisting of the three innermost layers of parenchyma cells. In many instances these cells are distinctly radially aligned. Considering the detailed ontogenetic study of the endocarp in *Rhus lancea* L.f. (Von Teichman and Robbertse, 1986a), it is clear that in *Protorhus longifolia* these three layers are derived through periclinal divisions from the inner epidermis of the very young ovary (carpel) wall.

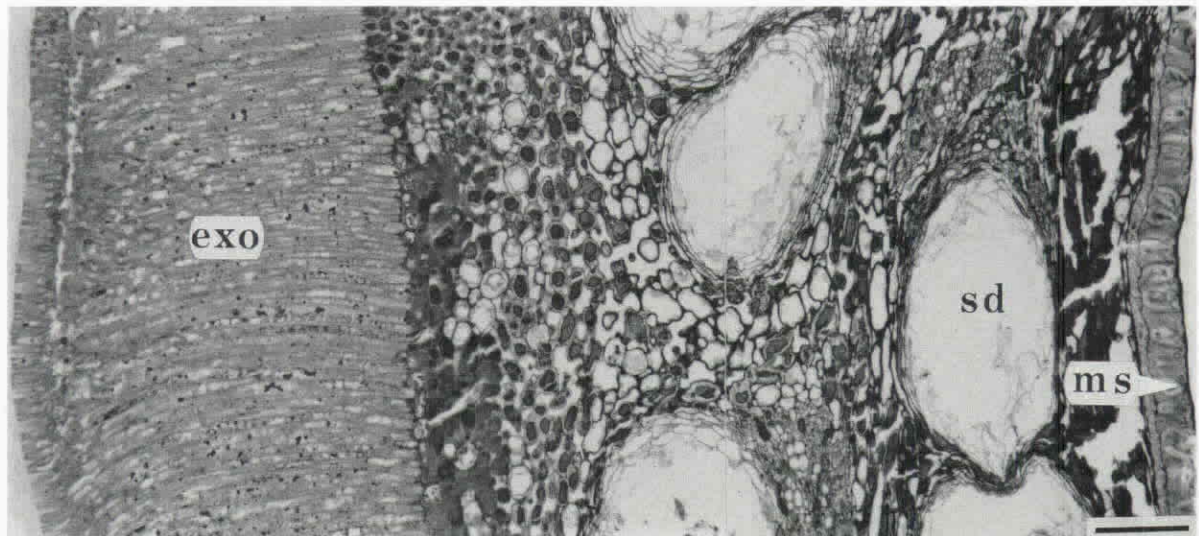
Differentiation during the development towards the mature pericarp affects mainly the outer epidermis, i.e. exocarp, and the three endocarpal layers. The outer epidermal cells divide anticlinally at a very high rate whilst simultaneously undergoing radial elongation (Fig. 3). In the young pericarp the three endocarpal layers are well defined (Fig. 3), with only the innermost layer appearing palisade-like at this stage. These palisade-like parenchyma cells also divide anticlinally.

At 60 and 105 days after anthesis, the older and mature pericarps respectively (Figs. 4 and 5) are char-





- Fig. 2. Transverse section of the ovary with ovule prior to anthesis. i, integuments; ie, inner epidermis of the ovary wall; n, nucellus; sd, secretory ducts, within the parenchyma; oe, outer epidermis of the ovary wall. Scale bar = 100  $\mu$ m.
- Fig. 3. Transverse section of the pericarp about four weeks after anthesis. ie, inner epidermis; oe, palisade-like outer epidermis (exocarp), in which all the nuclei occur centrally in the cells. Scale bar = 100  $\mu$ m.
- Fig. 4. Sudan black B stained transverse section of the pericarp 60 days after anthesis. The palisade-like exocarp with massive cutinization of the outer parts of the cells as well as the outer cell layer of the mesocarp are illustrated. Scale bar = 50  $\mu$ m.



- Fig. 5. Transverse section of the mature pericarp. exo, palisade like exocarp; sd, large secretory ducts within the parenchymatous mesocarp; ms, macrosclereids and adjacent small brachysclereids of the endocarp are illustrated. Scale bar = 100  $\mu$ m.

acterized by a pronounced palisade-like outer epidermis (exocarp). In the mature pericarp these cells are about 380–470  $\mu\text{m}$  long. A very thick cuticle and impregnation with lipids, i.e. cutins, of the outer tangential as well as outer part of the radial cell walls (Fig. 4) also characterize these palisade-like epidermal cells.

Within the mature mesocarp (Fig. 5) the parenchyma is partly tanniferous, while the large secretory ducts are now somewhat compressed. In the endocarp the lignification of the two innermost cell layers begins about 60 days after anthesis. The innermost macrosclereids lose their palisade-like shape through tangential extension (Fig. 5). An adjacent layer of small brachysclereids followed by a layer of more or less squashed parenchyma (cells) can also be distinguished. A thin cuticle covers the tangential cell walls of the innermost layer of macrosclereids, thus lining the fruit locule. Crystals of calcium oxalate are not restricted to a specific layer in the endocarp. Single crystals are present in the layer of small brachysclereids as well as in the mesocarp adjacent to the endocarp. Randomly scattered crystalliferous cells with small prismatic crystals occur abundantly in the mesocarp. Only a few small prismatic crystals were found in the exocarp.

### Discussion and Conclusions

According to existing generic descriptions, the ovary of *Protorhus* is trilocular or through abortion unilocular (Dyer, 1975; Engler, 1881, 1892; Perrier de la Bâthie, 1946). In *Protorhus longifolia* a large number of flowers (ca. 50) from two localities were dissected and the ovary was always unilocular. Since *Protorhus longifolia* is the lectotype of the genus, this observation may suggest an amendment of the existing generic descriptions.

The fruit shape of *Protorhus longifolia* compared with that of the Madagascan species (described and illustrated by Engler, 1881; Perrier de la Bâthie, 1946) shows that two completely different fruit types are involved. While fruits of *Protorhus longifolia* are asymmetrically ovoid, those of the Madagascan species are ellipsoidal and radially symmetrical with a centrally attached stalk. Engler (1881) describes the fruit of *Protorhus* as "fructus drupaceus, oblongus unilocularis". The fruit are unilocular in *Protorhus longifolia* and apparently so in all the Madagascan species. It should

be noted that in four of the fifteen Madagascan species the female flower and/or fruits have not yet been described. Fruit shape of *Protorhus longifolia* therefore supports the view of Bews (1925) that the Madagascan species differ from *Protorhus longifolia*. In this regard a detailed morphological study of fruit in the Madagascan species is particularly desirable and could provide decisive evidence towards a more refined generic demarcation.

A very pronounced palisade-like parenchymatous outer epidermis (exocarp *s. str.*), measuring 380–470  $\mu\text{m}$  in radial extension, characterizes the pericarp of *Protorhus longifolia*. A palisade-like, but strongly lignified outer epidermis occurs in *Semecarpus forstenii* Bl. of the tribe Semecarpeae (Wannan and Quinn, 1990). Weber, in an unpublished dissertation (Weber, D. 1907. 'Beiträge zur Anatomie einiger pharmakognostisch wichtiger Samen und Früchte'. Universität Bern, Druck Budapest.) not quoted by the latter authors, also described a palisade-like outer epidermis of ca. 100  $\mu\text{m}$  radial extension in *Semecarpus anacardium* L. f. Furthermore, this epidermis is covered with a thick layer of wax, and the outer tangential and outer parts of the radial cell walls are thickened. A massive cuticle and cuticular impregnation of the outer parts of the cell walls also characterize the palisade-like exocarp in *Protorhus longifolia*, thus showing a remarkable similarity to the exocarp structure of *Semecarpus* L.f. Weber (*loc. cit.* 1907) also found a slightly palisade-like outer epidermis in *Anacardium occidentale* L. These cells measure about 67.5  $\mu\text{m}$  in radial extension. Wannan and Quinn (1990), however, reported a lignified outer epidermis in *Anacardium occidentale*, but did not mention any radial elongation of this layer. The similarities between the exocarp of *Protorhus longifolia* and *Anacardium* L. are therefore less marked.

The mesocarp in *Protorhus longifolia* is parenchymatous with two concentric circles of large secretory ducts associated with the vascular tissue. The mesocarp of the two species of *Semecarpus* and *Anacardium occidentale* mentioned above is very similar, although only one circle of very large secretory ducts has been reported.

The distinctly layered endocarp of *Protorhus longifolia* represents the *Anacardium*-type endocarp *sensu* Wannan and Quinn (1990). This type of endocarp, found in the tribe Anacardieae, is also well represented in the tribes Rhoeeae, Semecarpeae and Dobineeae (Wannan

and Quinn, 1990). In addition to this type, Wannan and Quinn (1990) distinguish the *Spondias*-type. However, among species with the *Anacardium*-type they recognize three sub-types or groups in the tribe Rhoeeae. Group A of the *Anacardium*-type endocarp is typified by three palisade-like sclereid layers and a fourth crystalliferous one. Although *Protorhus longifolia* has hitherto been considered a member of the tribe Rhoeeae, its endocarp structure does not fit any of the three Rhoeeae endocarpal sub-types or groups. With only two layers of sclereids present, it could be considered a fourth Rhoeeae endocarpal group, i.e. also derived from the group A-type. The inner epidermis of *Schinopsis haenkeana* Engl. (Rhoeeae-endocarp group A) has macrosclereids very similar to those of *Protorhus longifolia* (compare Fig. 28 of Wannan and Quinn, 1990).

As in the case of the exocarp, the endocarp structure of *Protorhus longifolia* is remarkably similar to that of *Semecarpus forstenii* (Wannan and Quinn, 1990) and *Semecarpus anacardium* (Weber, *loc. cit.* 1907). In *Semecarpus* the radial length of the inner palisade-like macrosclereids is reported as 300–400  $\mu\text{m}$  by Weber (*loc. cit.* 1907), and 90  $\mu\text{m}$  by Wannan and Quinn (1990, *vide* Fig. 43). In *Protorhus longifolia* the radial length of this layer is 40–50  $\mu\text{m}$ , while during their development these macrosclereids in *Protorhus longifolia* were also distinctly palisade-like. Although Weber (*loc. cit.* 1907) described the second endocarp layer (adjacent to the macrosclereids) in *Semecarpus anacardium* to be palisade-like sclereids (30–60  $\mu\text{m}$  in radial extension), this layer in *Semecarpus forstenii* is partially sclerenchymatous (brachysclereids similar to those of *Protorhus longifolia*) and partially parenchymatous. In *Protorhus longifolia*, however, the third layer is very reduced in the mature endocarp compared to that of *Semecarpus*.

The crystalliferous layer present in *Rhus* and some close allies is absent in *Protorhus longifolia* as well as in the two species of *Semecarpus* studied to date.

Pericarp structure of the genus *Protorhus*, as based on *Protorhus longifolia*, does not suggest a close affinity with the genus *Rhus*. The removal of *Protorhus longifolia* (= *Rhus longifolia* Sond.) from *Rhus* is therefore fully justified (Engler, 1881; 1883). The present study would rather indicate an affinity of *Protorhus* with the genus *Semecarpus*.

In *Semecarpus* the extensive lignification in the endocarp provides the main mechanical/protective layer

in the pericarp. *Protorhus* displays an alternative strategy in the remarkable amount of lipids (cutins) deposited in the exocarp, whereas the endocarp is less strongly developed. The genus *Semecarpus* occurs mostly in "primary forest at low and medium altitude" in tropical Malesia and neighbouring countries (Hou, 1978). Its habitat is therefore very similar to that of *Protorhus longifolia* and most species of the genus in Madagascar (Perrier de la Bâthie, 1946; White, 1983). Further similarities between the seed of *Protorhus* and *Semecarpus* will be discussed in a forthcoming paper. The suggested affinity of *Protorhus* with *Semecarpus* supports the observation that taxa of several flowering plant families display fundamental links between Africa–Madagascar on one hand and Southeast Asia on the other (Leroy, 1978; Thorne, 1973).

It would therefore be very informative to study the flowers and fruits of the Madagascan species of *Protorhus*. It is not unlikely that detailed evidence from fruit and seed structure might suggest a revised definition of the genus *Protorhus* with regard to the Madagascan species.

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## 漆樹科 *Protorhus longifolia* (Bernh.) Engl. 的 果皮構造及其分類上的意義

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*Protorhus longifolia* (Bernh.) Engl. 的果皮結構包括：一層單細胞厚的外果皮，一典型漆樹科式具有樹脂的中果皮，及一細胞層狀排列的內果皮。外果皮係由子房外表皮層發育而來，其細胞細長並排列成柵狀，細胞內近外壁的部份浸滿了角質素，外壁上則被覆一層很厚的角皮層。中果皮為薄壁組織，富含單寧細胞及結晶細胞，並具有多數的分泌管及維管束。內果皮原為三層細胞厚，發育成熟時僅含一層桿狀厚壁細胞在內側及一層石細胞在外側。此類內果皮可做為 *Anacardium* 內果皮型的代表，出現在漆樹科所有的族中，除了 *Spondiadeae* 族。果皮構造方面的特徵顯示 *Protorhus* Engl. (*Rhoeae* 族) 與 *Semecarpus* L. f. (*Semecarpeae* 族) 有親密的分類關係。