Morphology and Development of the Fruit and Seed of Jubaeopsis caffra Becc.

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According to Corner (1966) the majority of palm fruits generally have three common features, viz. they are all fairly large, they are usually one-seeded, and they are indehiscent. However, numerous exceptions occur and *Geonoma* and *Chamaedorea*, for example, have small fruit. Botanically too, various fruit types occur in the different groups of palms. In all cocosoid palms and many of the arecoid palms, drupes are encountered, while in *Phoenix* one-seeded berries occur (Corner, 1966; Murray, 1973). In certain species of *Borassus* the fruits are somewhat more complex, being two- or three-seeded and with each seed enclosed in its own endocarp within a common mesocarp (Corner, 1966). The fruits of the lepidocaryoid palms, e.g. *Raphia*, are botanically of great interest in that they are enveloped by hard scales. Most palm fruits develop a "pulpy" wall at maturity (Corner, 1966). The nature of this wall does, however, vary from the softness of the date to the fibrousness of the coconut.

Considering the extent to which palm fruits are known and used by the peoples of the tropics, it is strange that so little is known about the anatomy and development of the fruits and seeds. According to Murray (1973), these aspects have been studied in only two palm species, viz. *Cocos nucifera* and *Phoenix dactylifera.*

Murray gives three reasons for this general lack of information. Firstly, the long developmental time required by palm fruits; secondly, the geographical inaccessibility of most species, and thirdly, the intractable nature of the fruits themselves.

Until recently, so few data have been available that in the case of drupes it was not known whether the stone was compound and included the three original cavities of the ovary or whether it represented the endocarp of the functional cavity only (Corner, 1966).

Murray (1973), however, has made a major contribution in this regard and has described fruit development, especially with respect to the development of the endocarp, for 17 palm species from four subfamilies, viz. Coryphoideae, Caryotoideae, Arecoideae, and Cocosoideae.

Unfortunately, Murray discussed neither the anatomical nature nor the development of the germination pores that are characteristic of all cocosoid palm fruits. Apart from a very brief description by Juliano (1926) for *Cocos*, no information on this aspect of fruit development is available.

Not only is very little known about the anatomical aspects of fruit development, but there appears to be surprisingly little information available concerning the time required for the development of palm fruits, especially the wild species. In view of the lack of data concerning fruit structure and development in the palms generally and the fact that no information on the development of *Jubaeopsis caffra* fruits is currently avaliable, a study of this aspect was undertaken.

Materials and Methods

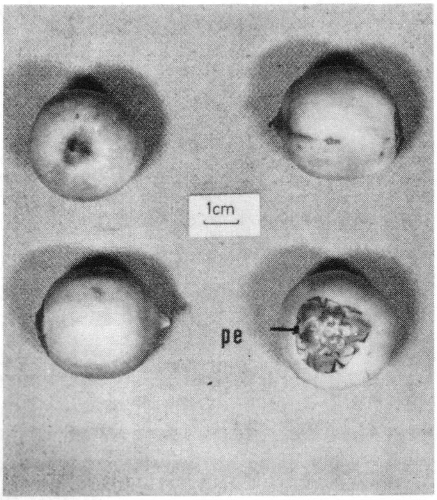
All the plant material used in this study was collected from a cultivated *J. caffra* tree (approximately 43 years old) in St. George's Park, Port Elizabeth. An inflorescence was selected and ten fruits were collected each 14 days from the date on which the inflorescence opened until the fruits reached maturity. These fruits were measured (length and breadth) and fixed in formaldehyde/ethyl alcohol/acetic acid (Sass, 1958).

Dehydration of the material and infiltration with paraffin wax (Carowax; melting point 54–58° C) was achieved by means of graded tertiary butyl alcohol (TBA)/ethyl alcohol and (TBA)/wax series, respectively (Sass, 1958). Ten μm sections were made on a rotary microtome (Brooks, Bradley & Anderson, 1950) and stained in either safranin/fast green (Höltzhausen, 1972) or iron-alum-hematoxylin/safranin (Brooks *et al.*, 1950). Hard, sclerified tissues were softened by soaking the embedded material in 20 ml glacial acetic acid/80 ml 60 percent ethyl alcohol for 24 hours before sectioning.

Results and Discussion

(a) *General morphology and growth of the fruit.*

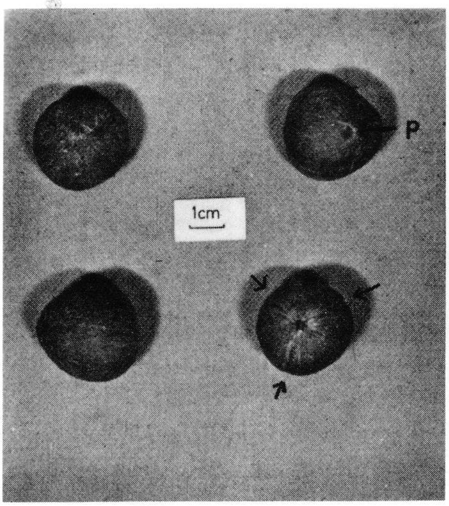
The fruit of *J. caffra* is a drupe consisting of a fleshy exocarp and mesocarp and a lignified or bony endocarp. The size of the ripe fruit varies from tree to tree and from season to season. However, the average fruit size for the tree in St. George's Park is 4.0 cm long and 3.5 cm broad (Fig. 1, 4). The proximal or basal end of the fruit is covered by a persistent perianth comprising two trimerous whorls, viz. the sepals and petals. It would seem that the function of the perianth is to protect the soft, meristematic, basal portion of the ovary.



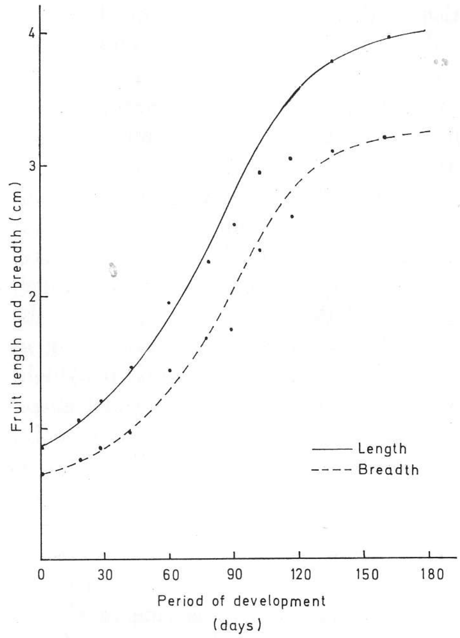
1. Mature fruits of *J. caffra* (pe, perianth).

When the fruit is fully mature, it is abscissed, but the perianth, however, usually remains attached to the rachilla on which the fruit was borne. At this stage the fibrous mesocarp is very loosely attached to the endocarp and usually it starts to split from the basal end of the fruit. The exocarp and mesocarp of the fresh, mature fruit are approximately 3–4 mm thick. When the mesocarp is removed, the fruit has the appearance of a nut in that it consists of a hard, bony, covering structure around a seed (Fig. 2).

The endocarp is divided into three segments by three grooves along which fusion of the carpels took place (Fig. 2). While two of the segments are more or less of equal size, the third is very much larger and constitutes nearly half of the nut's circumference (upper right hand nut in Fig. 2). This latter segment represents the carpel which bore the functional ovule.

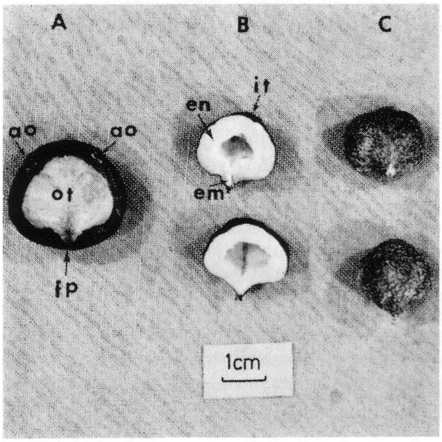


2. "Nuts" or "seeds" after removal of the exocarp and mesocarp (p, germination pore).



4. Fruit growth of *J. caffra*. Data were obtained by measuring the length and breadth of 20 fruits at regular intervals and calculating the mean values for each day (black dots).

Each segment or carpel has a germination pore, but only the one opposite the micropyle of the functional ovule penetrates the endocarp completely. It is externally somewhat larger than the other two pores and, when pierced, provides access into the seed and the embryo. The remaining two pores are only 1–2 mm deep. All three pores are laterally or equatorially situated.



3. Endocarp and seed of *J. caffra*. A, transverse section through the endocarp shell of the fruit (ao, aborted ovules; fp, functional pore; ot, outer portion of testa); B, transverse section through the seed (em, embryo; en, endosperm; it, inner portion of testa); C, intact seeds.

Removal of the endocarp exposes the kernel (Fig. 3C), which consists of a mass of endosperm covered by a thin brown skin (Fig. 3B). This skin, as will be shown in the subsequent section on the anatomy of the fruit and seed, is actually only a part of the testa and more specifically it is the inner integument. The remaining part of the testa, i.e. the outer integument, is fused to the inner side of the endocarp or shell and can be observed as a cream-colored to light brown lining on the inside of the endocarp. The thickness of the endocarp varies from 3–4 mm.

In a transverse section through the nut (Fig. 3A, 6) the two nonfunctional ovules can be observed in the endocarp.

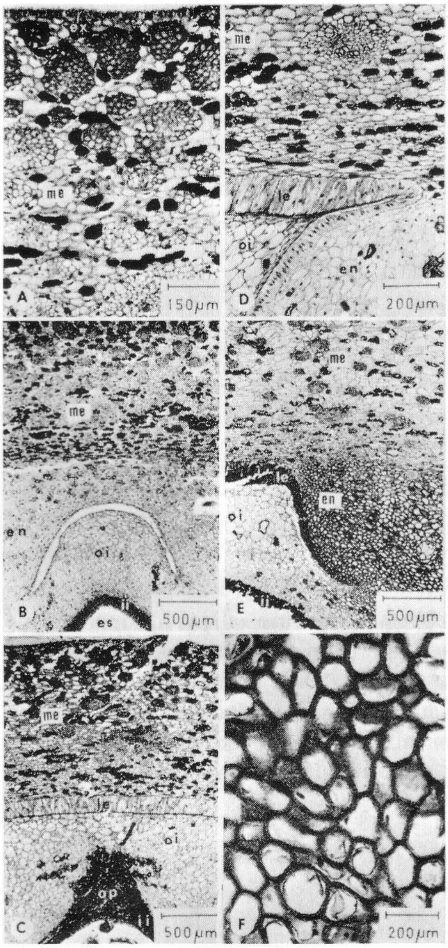
Also evident is the large central cavity in the endosperm (Fig. 3B). This cavity is without liquid endosperm or "milk" in the mature fruit. In the mature seed, the endosperm is approximately 5 mm thick.

Growth of the fruit follows a sigmoidal pattern from the time of appearance of the female flower until the fruit is mature (Fig. 4). During the first 45 days after opening of the inflorescence, growth is relatively slow. This is followed by a second stage, lasting 90 days, in which growth is very rapid. In the last stage of fruit growth, the rate of increase in fruit size slows down dramatically. It is during this final period of fruit development that most of the growth of the embryo takes place (Robertson, 1976a). As shown in Fig. 4, growth takes place at more or less the same rate in all regions of the fruit and the rates of increase in length and breadth of the fruit are essentially the same.

Maturation of the fruit is basipetal, and the basal region of the fruit remains soft and does not differentiate fully until the fruit has newly attained its maximum size.

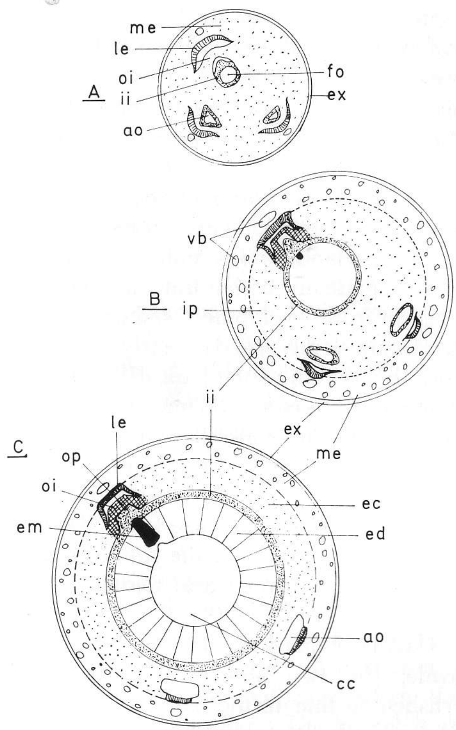
(b) *Anatomy and development of the fruit, germination pores, and testa.*

Like all other drupes, the pericarp of the *Jubaeopsis caffra* fruit consists of an exocarp, mesocarp, and endocarp. The exocarp in this genus is reduced to a single cell layer, viz. the epidermis of the fruit (Fig. 5A), and is covered by a cuticle. The cells of this layer are more or less block-shaped in a transverse section, with thickened outer tangential and radial walls. No significant changes occur in these cells during the course of fruit development.



5. Transverse sections through the pericarp of the fruit at various stages of development. A, exocarp and mesocarp; B, development of the germination pore in a fruit shortly after fertilization; C, mesocarp and germination pore of a fruit approximately 100 days after fertilization; D, mesocarp, germination pore, and endocarp shortly before lignification of the cell walls; E, as D but subsequent to lignification; F, endocarp cells subsequent to lignification or sclerification (en, endocarp; es, embryo sac; ex, exocarp; ii, inner integument; le, locular epidermis; me, mesocarp; oi, outer integument; op, operculum).

The mesocarp, although termed fleshy, is extremely fibrous and is traversed by a large number of vascular bundles and fiber bundles (Fig. 5A–E). In a very young fruit, just after anthesis, the extent of the mesocarp can best be seen opposite the functional ovule where the mesocarp is bounded on the outside by



6. Schematic representation of fruit development, showing transverse sections through the fruit at various stages of growth. A, shortly after anthesis; B, before sclerification of endocarp; C, mature fruit (ao, aborted ovule; cc, central cavity; ec, endocarp; ed, endosperm; em, embryo; ex, exocarp; fo, functional ovule; ii, inner integument; ip, intervening parenchyma; le, locular epidermis; me, mesocarp; oi, outer integument; op, operculum; vb, vascular bundle).

the exocarp and on the inside by the locular epidermis (Fig. 6A).

Cell division and enlargement in the mesocarp is relatively slow and the cells of this region become tangentially elongated as the volume of the fruit increases so that the mesocarp, which is initially not clearly distinguishable from the endocarp, becomes well defined. At this stage, the cells of the endocarp are still more or less isodiametric, thin-walled, and meristematic (Fig. 5B, D), and it is possible to distinguish the limits of all three pericarp components not only in the vicinity of the functional germination pore, but in all regions of the fruit (Fig. 6B).

The vascular bundles in the mesocarp are initially not well differentiated, but as the fruit develops, they become surrounded by thick sclerenchymatous or fibrous sheaths, while fiber bundles not associated with any vascular tissue also differentiate in the mesocarp (Fig. 5A). There is a concentration of sclerenchyma in the peripheral region of the mesocarp and the fibrous sheaths of the vascular bundles in this peripheral zone tend to be thicker and better developed than the more deeply situated vascular bundles. While the number of vascular elements in most of the bundles is relatively small, a large, well-developed, dorsal, carpellary vascular bundle occurs opposite each germination pore (Fig. 5C, 6A–C).

Although only one of the ovules undergoes post-fertilization enlargement and development, all three ovules achieve maturity and contain fully differentiated embryo sacs. *Jubaeopsis caffra* has hemianatropous, crassinucellate, bitegmic ovules embedded in the placental tissues. The outer integument is a massive, dominant structure while the inner integument is only two cell layers thick laterally, with the innermost cell layer forming an endothelium (Robertson 1976b). At the micropyle the inner integument forms an operculum. As the functional ovule enlarges during fruit growth, the endothelial cells divide anticlinally (in relation to the embryo sac) and elongate periclinally, while the cells of the second cell layer in the inner integument divide periclinally, giving rise to approximately six cell layers.

A large number of tanniniferous idioblasts are present in most tissues of the fruit, but are especially abundant in the mesocarp and the inner integument. The latter structure, in fact, consists entirely of tanniniferous cells (Fig. 5B, C).

Shortly after anthesis the cells of the locular epidermis become elongated. Those forming the boundary between the mesocarp and the integumentary plug in the pore elongate radially, while those lateral to the integumentary plug become more or less tangentially (in relation to the exocarp) elongated (Fig. 5C, D; 6A–C).

This tissue, i.e. the locular epidermis, which does in fact constitute a portion of the endocarp, will, after lignification of the cell walls, differentiate into macrosclereids (Fig. 5E) and forms the lid and lining of the germination pore (Fig. 6B, C). The outer integument forms a parenchymatous plug which lies just beneath the lid of the germination pore (Fig. 5B–E). This plug remains parenchymatous throughout the lifetime of the fruit. The center of the plug is only five or six cell layers thick where it is penetrated by the tanniniferous operculum of the inner integument (Fig. 5C), and consequently it is easily ruptured by the emerging embryo during seed germination.

Although the inner integument, which eventually consists of four to six layers of tannin cells, remains distinguishable throughout the period of fruit and seed development, the outer integument can only be distinguished as a separate structure in the vicinity of the pore where it forms the plug. This integument is, however, almost entirely fused to the endocarp, the fusion starting at the point where the locular epidermis terminates (Fig. 5B, E; 6A–C). From this point onwards it cannot be distinguished from the endocarp. The endocarp in *J. caffra*, therefore, consists of the locular epidermis, the intervening parenchyma, and part of the outer integument and stretches from the mesocarp on the outside to the inner integument on the inside. It does not include any of the fibrous tissue of the mesocarp (Fig. 6B, C). Lignification of the endocarp cells is initiated when the fruit has reached approximately three-quarters of its maximum size and takes place basipetally. Numerous simple pits occur in the thick lignified walls of these cells (Fig. 5F).

The basal or proximal region of the fruit, i.e. the portion covered by the persistent perianth, does however remain meristematically active until a very late stage in fruit development and only when maximum fruit size is nearly attained does this region of the fruit differentiate into mature tissues. During development of the fruit, the ovules become displaced from their extreme basal position in the ovary at anthesis to a lateral or equatorial position in the mature fruit. This is a further indication of the rapid growth which occurs in the basal region of the fruit.

During expansion of the functional ovule, the two aborted ones become crushed so that in the mature fruit they remain only as two minute cavities or slits in the endocarp of the fruit. Each of these two small cavities has its own pore and lid (Fig. 3, 6C). The structure of these lids is precisely the same as that of the functional pore and consists of a single layer of macrosclereids of locular epidermal origin.

Conclusions

The drupaceous fruit of *J. caffra* is typical of the fruit of all cocosoid palms in that it consists of a fibrous mesocarp and a hard, bony endocarp which has three characteristic pores. The position of the pores, however, varies from genus to genus and is related to the position of the micropyle of ovules. According to Uhl and Moore (1971), the pores are basal in ovaries with anatropous ovules, lateral if the ovules are hemianatropous and above the middle if the ovules are orthotropous. They state further that this feature is, to a large extent, used to separate the three major groups within the subfamily Cocosoideae, viz. the *Cocos*, *Bactris*, and *Elaeis* alliances. In the *Cocos* alliance, which includes *Butia*, *Cocos*, *Jubaea*, and *Jubaeopsis*, the ovules are hemianatropous to anatropous and the pores are consequently near the base of the endocarp (Uhl and Moore, 1971). Although this is true for *Cocos* and *Jubaea*, the pores in the endocarp of *Jubaeopsis caffra* are placed not basally but laterally. In this respect, *J. caffra* is thus similar to the bactroid palms, most of which are distinguished by lateral pores.

The seed coats of palm seeds in general are poorly developed (Corner, 1966) and in this connection *J. caffra* is no exception. According to Esau (1965) both integuments of a bitegmic ovule form the testa. The outer integument of *J. caffra*, however, is fused to the endocarp and is removed with the endocarp when the "nut" is cracked open. The kernel is in fact covered by the inner integument only and consequently the kernel itself does not represent the entire ovule.

With reference to Corner's (1966) statement concerning the composition of the endocarp, i.e. whether tissue around the functional cavity only or all three cavities is involved in construction of the endocarp, it would seem that in *J. caffra* all three cavities are involved, but in a restricted sense only. The locular epidermis of each cavity forms a separate germination pore lid. All three pores are, however, incorporated into the endocarp, and in view of the fact that the locular epidermis represents one of the components of the endocarp, it must be concluded that the locular epidermis of each cavity contributes to the formation of the endocarp and that this latter tissue is consequently a compound structure.

The composition of the endocarp in *J. caffra* is not in accordance with that suggested by Murray (1973) for other cocosoid palms. In *J. caffra* it consists of the sclerified locular epidermis, the intervening parenchyma, which also becomes sclerified, and the outer integument. The Type III (Murray, 1973) described for cocosoid palms provides for an endocarp that includes the sclerified locular epidermis, the sclerified and sometimes confluent sheaths of the inner vascular bundles, and the intervening parenchyma.

The findings of this study in respect to the remains of the aborted ovules, i.e. that they are present and clearly visible in the endocarp of *J. caffra* fruits, are contrary to those of Beccari (1913). In his original description of this species Beccari states that while ovular remnants are present and visible in the endocarp of *Jubaea* fruits, they are not present in that of *Jubaeopsis caffra*.

Acknowledgements

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NEWS OF THE SOCIETY

Biennial Meeting, June 19–22, 1976

There can hardly be a more suitable setting for a meeting of the Palm Society than the campus of Florida Institute of Technology at Melbourne, Florida. Host Dr. Jerome P. Keuper, President of F. I. T. and former Palm Society president, has made the 125-acre campus a veritable palm garden, using these plants almost exclusively for the landscaping. The innumerable large specimens of hardier species with smaller and more tender ones interspersed, met the eye on every side, being used as specimen plants, massed along walls or walks, or silhouetted against buildings. The effect is overwhelming to a palm lover and it still seems incredible that this major palm collection was started just nine years ago. It is impossible to do justice to such a setting in this report of the Biennial Meeting. Those of you who have the April 1975 issue of Principes can look at it again to refresh your memory of what those of us who attended the meeting were privileged to experience.

Upon arriving at F. I. T. on Saturday, June 19, we checked into the commodious and convenient dormitories. For dinner we gathered in a large upstairs room over the cafeteria. The entire north side of the room is of glass and provided a fascinating spectacle as a typical midsummer thunder squall lashed torrents of rain on the palm tree tops in our field of vision.

Next morning, Dr. Oscar Rodriguez, new horticulturist at F. I. T., led groups of members along the Dent Smith Trail where in the shaded dampness the myriad smaller palms are thriving. So many unexpected Palm Society members showed up at the luncheon without reservations that the planned food finally ran out, though adequate substitutions were hastily produced.

There was a turnout of over 100 at the auditorium for the official meeting in the afternoon. After the business meeting (see minutes of the meeting on page 167 of the October issue for this important session.) we heard Dr. Fred Essig tell us about the palms, especially the ptychospermas he had studied while in New Guinea some years ago. Paul Drummond detailed the state of lethal yellowing disease, and noted that new coconut hybrids may hold the key to the replanting of these palms in South Florida, which has lost so much of its tropical appearance due to the death of approximately 500, 000 coconuts and even more *Veitchia merrillii.* Next we were transported to the state of Georgia by Mr. William Manley who showed the beauty of hardy palms on his property. We saw how well many of the plants had recovered after he had had to transplant them when moving into a new home. Dr. Robert Read gave us the highlights of his treatise on the genus *Thrinax*, preparing those who would be going to Jamaica on what to expect to see there.

At the delicious banquet that evening, outgoing President U. A. Young was presented a plaque in recognition of his service as president. Incoming President Myron Kimnach greeted all and thanked those responsible for the most enjoyable