MORPHOLOGICAL AND ANATOMICAL INVESTIGATIONS ON ARTOCARPUS FORST.

IV. The Fruit*

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INTRODUCTION

The present communication deals with the fruit of Artocarpus. The plant is important economically and apart from wood, timber and biochemical utility, some species are well known for their fruits. The jack-fruit (A. heterophyllus) and the bread-fruit (A. altilis, the name is associated with the story of voyage of Captain Bligh and the famous mutiny on the Bounty) are now cultivated in different parts of the world. The fruit in A. heterophyllus attains an enormous size and is considered to be the largest fruit in the world (Cowen, 1950). Other species like A. lakoocha ('barhal' or 'monkey-jack') and A. integer ('Champedak'), etc., also yield edible fruits of smaller size.

The material was collected locally and from different places as described earlier (Sharma, 1962). Dissections under binocular, hand sections and microtome sections of variable thickness of the fruit of different ages were obtained and stained by usual customary methods.

OBSERVATIONS

External morphology.—After anthesis, the whole female inflorescence increases and develops into a composite or multiple type of fruit (Fig. 1). The size, shape and quality of the fruit are variable not only in different species but also in different varieties of the same species. A. heterophyllus is a caulifloral species and the female inflorescences produced on the main trunk and stout branches develop into jack-fruits which hang down from the trunk or main branches. This species has two more or less well-defined varieties, 'Barka', a smaller and inferior variety and 'Kapa', a large superior variety

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(Manjunath, 1948). The former is locally called ‘Katahali’ and yields small fruits which are somewhat sour in taste and weigh four to fifteen pounds each. The latter variety locally called ‘Kathal’ yields large fruits weighing nearly up to eighty pounds and at ripening has fleshy sweet perianth. Some fruits may be borne at the ground level or even below.

Bread-fruit (A. altillis) is somewhat similar to jack-fruit but is not caulifloral. Just before anthesis, the inflorescence is small, globular or sub-globular and measures 2.5 to 3.5 cm. Thereafter it grows rapidly and a fully mature fruit measures 20–35 cm. in diameter. The fruit of A. integer, ‘Champedak’, resembles that of A. heterophyllus when young, but remains smaller in old condition. According to Corner (1952), ‘...the Champekak has the strongest and richest smell of any in creation’.

In A. rigidus and A. hirsutus the fruits are globular or sub-globular, small and non-edible. All species described have conical, spiny or horny projections on the fruit surface.

A. lakoocha yields ‘monkey-jack’ commonly known as ‘barhal’ in India. It is very different in appearance from fruits of other species. In this species, even the male inflorescences appear like small orange or yellow coloured ‘fruits’ and are used in culinary. The actual composite fruit when young is globular but becomes irregularly lobed at maturity and measures 6–12 cm. in diameter. The fruit is eaten after ripening and tastes sweetish sour.

Dissection of several fruits of A. heterophyllus revealed that, on an average, the superior ‘Kapa’ variety (‘Kathal’) has ten thousand to twelve thousand flowers in a composite fruit and that the number of normal seeds produced varies from fifty to two hundred per fruit. Besides, there are about two hundred or more ill-developed seeds intermixed with the normal ones. The inferior variety ‘Barka’ (‘Kathali’) has eight to ten thousand flowers per composite fruit and only twenty to fifty seeds are produced in a fruit. In one rather underdeveloped fruit measuring 12.5×7.5 cm., there were found only four normal and about ten ill-developed seeds, all in the upper half of the fruit. It is interesting to note that the unfertilized or sterile flowers also develop and take part in the formation of composite fruit that is actually a spurious fruit developed chiefly from the perianth.

In a Malayan variety of A. altillis, the composite fruit has 1500–2000 flowers of which about 30 develop normal seeds. In A. lakoocha, the so-called fruit has about 2600 flowers, majority of them are sterile and only twenty to fifty develop seeds.
Anatomy.—In Artocarpus the structure and development of fruit can be conveniently given under the following three heads: (i) The fruit-axis, (ii) The persistent perianth and (iii) The true or real fruit.
(i) The fruit-axis.—It is the modified and mature stage of the inflorescence axis and is somewhat dome-shaped (Figs. 23, 31-33). It is rigid and slightly fleshy. At an earlier stage it measures about 3·5×2 cm. but in a mature fruit, it may enlarge to about 30 cm.×8 cm. or more in *A. heterophyllus*. In young fruits of *A. lakooccha* the axis measures 1·6 cm. in diameter with a fruit of 2·2 cm. diameter but at maturity there is much variation in size because of unequal development of perianth.

**TABLE I**

*Showing measurements in centimetres of jack-fruit and its different parts during various stages of development*

<table>
<thead>
<tr>
<th>Sl. No.</th>
<th>Maximum length of fruit</th>
<th>Maximum diameter of fruit</th>
<th>Maximum diameter of fruit axis</th>
<th>Length of perianth</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Total length</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>Length of edible</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Length of fused</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>Length of free</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>tip</td>
</tr>
<tr>
<td>2</td>
<td>4·5</td>
<td>2·5</td>
<td>1·8</td>
<td>0·35</td>
</tr>
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<td>2</td>
<td>7·8</td>
<td>3·6</td>
<td>2·2</td>
<td>0·7</td>
</tr>
<tr>
<td>3</td>
<td>12·5</td>
<td>7·5</td>
<td>2·7</td>
<td>2·4</td>
</tr>
<tr>
<td>4</td>
<td>16·0</td>
<td>10·0</td>
<td>3·8</td>
<td>3·1</td>
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<td>5</td>
<td>26·0</td>
<td>14·0</td>
<td>6·0</td>
<td>4·0</td>
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<td>6</td>
<td>28·0</td>
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<tr>
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<td>35·0</td>
<td>18·5</td>
<td>8·0</td>
<td>5·25</td>
</tr>
<tr>
<td>8</td>
<td>40·0</td>
<td>22·0</td>
<td>9·0</td>
<td>6·5</td>
</tr>
<tr>
<td>9</td>
<td>44·0</td>
<td>25·0</td>
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<td>7·5</td>
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<tr>
<td>10</td>
<td>50·0</td>
<td>34·0</td>
<td>10·0</td>
<td>12·0</td>
</tr>
</tbody>
</table>

The bulk of fruit axis is made of elongated broad parenchymatous cells. The dimension of the axis increases mainly due to actual enlargement of individual cells of the whole ground tissue, although some of the cells also divide and multiply in number. The parenchymatous cells of the central pith region broaden and so do the vascular elements,
In *A. heterophyllus*, sclerenchyma is well developed in the cortical region of the axis but in other species the fibres are uncommon and less developed. The central pith and the peripheral cortical region of the axis have large and numerous laticifers that are specially developed in *A. heterophyllus*. The latex when fresh is milky with thick consistency but becomes yellowish-brown on exposure. Because of the absence of sufficient amount of food (Starch) and of the presence of enormous amount of latex, thick-walled spongy parenchyma and vascular and sclerified fibrous tissue, the axis region of the fruit is rendered non-palatable and useless for edible purposes.

(ii) The persistent perianth.—An important part of the fruit is formed by the persistent perianth which constitutes the major bulk of the fruit (Figs. 2, 23 and 33). This varies considerably in length as well as in extent of fusion in different species. In very young stages, the perianth tubes in *A. heterophyllus* are entirely free from one another but are deeply bilobed at the tip (Figs. 14–19). In course of development, the perianth tubes broaden and begin to fuse among themselves in the middle region leaving the upper and the lower region free in *A. heterophyllus* (Figs. 20–22). This also happens in *A. integer*, *A. rigidus* and *A. hirsutus*, etc. In *A. altilis*, the fusion of perianth gradually extends down but in *A. lakoocha* the fusion goes up to the tips. Thus the perianth in *A. heterophyllus* has three regions (Sharma, 1964): (a) the lower free and fleshy region, (b) the middle fused region and (c) the upper free and horny region (Figs. 3, 4, 20–22). The first one is exclusively fleshy and edible while the second and third regions constitute outer rind of the jack-fruit. Their relative size at different stages of development of fruit is given in Table I.

(a) The lowest free and fleshy region of the perianth of mature fruit in *A. heterophyllus* can be detached easily from the middle fused region. To begin with, it is one-fourth the total length of the perianth but soon it increases and elongates rapidly and in fully mature fruit, it becomes many times longer than the upper two regions put together (Table I and Figs. 3–7). This part of the perianth of a fertile flower is tubular, spindle-shaped and inflated but in sterile flowers, it is narrow and remains flattened or collapsed (Figs. 5–7). It is smooth, white and mealy and is the actual edible part of the fruit having delicious taste both in ripe and unripe conditions. The bulk (length, thickness and girth) and nature of this region determine the quality of the fruit and those having good deal of this region fetch good price.

The measurements in Table II indicate clearly that in fertilized and seeded fruits the perianth has maximum girth and thickness while in sterile
TABLE II

Comparative measurements of edible region of perianth in 'Kapa' and 'Barka' varieties in centimeters:

<table>
<thead>
<tr>
<th>Variety</th>
<th>Length of perianth tube</th>
<th>Breadth of perianth tube</th>
<th>Thickness of perianth wall</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fertile seeded</td>
<td>Sterile non-seeded</td>
<td>Fertile seeded</td>
</tr>
<tr>
<td>'Kapa'</td>
<td>7.0-10.0</td>
<td>8.0-11.0</td>
<td>1.0-5.0</td>
</tr>
<tr>
<td>'Barka'</td>
<td>5.0-7.0</td>
<td>6.0-8.0</td>
<td>0.6-3.0</td>
</tr>
</tbody>
</table>

ones, although length of perianth may be even more but its girth and thickness is much less. Hence the varieties of jack-fruit with many seeds are always better and much superior to those of seedless varieties or having limited number of seeds.

Increase in thickness and girth appears to set in just after fertilization. While the number of cell layers increases from about 12 to about 22 at maturity, the cells increase 3 to 5 times their original size (Figs. 9, 10). Besides, they are fully turgid and are rich in food material (starch) which after conversion into sugar adds further to the turgidity at the time of ripening. The starch grains are simple and concentric and vary from 5-10 microns in diameter (Fig. 11). At ripening the cells begin to disorganize and the colour of tissue changes to light yellow. The pulpy mass emits a peculiar somewhat disagreeable odour probably because of fermentation after over-ripening. Another significant change that is noticeable in this region is the absence of laticifers which are common in young perianth. They have obviously been crushed out by cell enlargement. About twenty vascular bundles run through this region. They have poorly developed xylem but phloem with prominent sieve tubes, companion cells and phloem parenchyma is much better developed. Thus anatomically also this region is well suited for eating.

In *A. integer*, *A. hirsutus* and *A. rigidus*, etc., also, there is similar type of free lower region of perianth but in the last two species it does not develop much and does not become fleshy. On the other hand, there is plenty of fibrous and vascular tissue that renders it unsuitable for eating.
In bread-fruit (*A. altillis*), the average length of perianth is about 2.5 cm. and the fusion extends almost up to the base so that there is no lower free region except at the very base (Figs. 24–27). At maturity this region becomes
somewhat fleshy (not to the same extent as in *A. heterophyllus*). The common arm of the two adjacent fused perianth of lower region has 30 or more layers of parenchymatous cells which increase in number. The average parenchymatous cell is 15–32 microns across. Many cells of inner epidermis are produced into long and straight unicellular hairs that remain projected in the tubular cavity of the perianth (Figs. 24–27).

The lower free region of perianth in *A. lakoocha* is about 0.1 cm. in length of a perianth of 0.3 cm., in a young fruit having 2.5 cm. diameter. In a mature fruit of about 5 × 6 cm., the length of perianth in fertile flowers varies from 1.5–2.0 cm. with 1.0–1.5 cm. free lower region, and 0.5 cm. fused upper region. In the same fruit, the perianth of unfertilised or sterile flowers remain only 0.5 cm. in length with 0.2 cm. free and 0.3 cm. fused regions. In some of the well-developed ripe fruits the lower free region of perianth in seeded true fruits is two-thirds or more of the total length. This indicates that as the fruit increases in size, the lower free region also increases faster than the upper fused region and becomes two or three times longer (Fig. 34). On the other hand, unlike that of *A. heterophyllus* the lower region does not grow much in girth (thickness) and accumulates lesser amount of food material. Only a few cell layers are added in thickness though the individual cells increase in size considerably (Fig. 35).

(b) The second region is the fused middle region of the perianth which forms a compact homogeneous mass. It has broad thick-walled cells with little amount of starch in *A. heterophyllus*. As this region broadens, the central cavity of each perianth tube gradually narrows upward. In *A. altilis*, the fusion extends down to the base of perianth but in *A. lakoocha* on the other hand it extends almost up to the tips leaving no conical structures of usual type. In the latter species this region unlike others (jack-fruit, bread-fruit, etc.), also grows vigorously in its girth around the seeded real fruits and forms fleshy tumour-like structure rendering this fruit (Barhal) uneven in shape (Figs. 32–34). It stores large quantity of starch and becomes edible at ripening. The starch grains are more or less angular, concentric and measure 3–10 microns in diameter. The laticifers are present in this region (*A. lakoocha*) but they are more abundant in *A. heterophyllus* and others. In jack-fruit (*A. heterophyllus*), the bundle sheath and vascular supply is much better developed than in bread-fruit (*A. altilis*) and ‘barhal’ (*A. lakoocha*).

(c) The third region is the free uppermost part of the perianth. Except in ‘barhal’ (*A. lakoocha*), whose fruit surface becomes flat, rough and hairy because of fusion up to the tip, this region forms conical, horny or blunt
studs of the rind in jack-fruit (*A. heterophyllus*), bread-fruit (*A. altilis*) and others (Figs. 1-4, 23, 25, 26).

Some tissues of this region undergo considerable structural changes. The epidermis is thickly cuticularized and some of the cells are produced
into unicellular, thick-walled and stiff straight or hooked hairs (Figs. 19–22). The ground tissue has thick-walled cells which enlarge towards inner side. The perianth broadens and the tubular perianth-cavity narrows considerably becoming just sufficient to allow the style to pass through. The hypodermis
is rigid and sclerenchymatous in A. altilis. The most prominent and characteristic is the bundle sheath in A. heterophyllus which consists of highly lignified, deeply stained and thick-walled sclerenchymatous cells radiating outward (Figs. 12, 13). Some of these fibre cells are much elongated measuring 0·1–0·3 mm. in length.

Thus, thick-walled epidermis, stiff hairs, sclerenchymatous hypodermis, thick-walled ground tissue, well-developed vascular elements and fibrous bundle sheath and laticifers make this conical region rigid and strong to protect the internal tissues of the fruit.

(iii) The true or real fruit.—It is of achenial type and constitutes the third internal part of the composite fruit (Figs. 2, 8, 23, 29, 32 and 36). Each carpel is enclosed by perianth and may develop into a small fruit but the majority of the carpels remain sterile. In very young female inflorescence, carpel primordium of a flower develops just after the emergence of the perianth (Figs. 14–16). This is followed by the development of an ovule and after fertilization the entire carpel (ovary) is destined to develop into a true fruit. The pericarp that develops from ovary wall does not become fleshy and undergoes no appreciable changes. It is thicker at the base but remains thin at the middle and upper regions and is indistinguishable into epicarp, mesocarp and endocarp (Fig. 28). In A. lakoocha, however, the wall is distinguishable into outer region with about ten layers of broad and thin-walled loose cells and inner region consisting of 3 to 10 layers of small slightly thick-walled compact cells (Fig. 37). The vascular supply is prominent and laticifers often run irregularly at the base but more commonly so near the vascular supply. The style is persistent and usually remains even up to the fruit condition.

There is developed a single large seed that remains free from the fruit wall and is attached to the pericarp at one point only, i.e., funiculus (Figs. 4, 30 and 34). The seed constitutes major part of the 'achenial fruit'. In the majority of the cases the seeds are either not developed or ill-developed. However, the true fruits are insignificant in the whole bulk of the composite fruit of Artocarpus.

Conclusion

The composite fruit of Artocarpus or syncarp (Jarrett, 1959) appears to be highly specialized in which true fruits are most insignificant units. It is mainly the perianth which after modification forms the bulk of the composite fruit. In this respect, it closely resembles Morus where perianth becomes
fleshy and edible at ripening (Bechtel, 1921), and pine-apple where bract and sepals enlarge considerably into fleshy fruit (Okimoto, 1948).

The perianth in different species shows three more or less distinct conditions. The first condition is quite common and involves the fusion of adjacent perianth at middle region leaving lower and upper parts free from each other. As the fruit develops, the lower free edible region grows vigorously elevating the middle fused and upper free regions in *Artocarpus heterophyllus*. In wild and less edible fruits (*A. hirsutus* and *A. rigidus*, etc.), however, lower edible region grows slowly but the non-edible rind especially upper free region becomes hard and spiny constituting the major portion of the fruits. In the second condition, the fusion of the middle region of perianth extends down to the base (*A. altilis*) and this is edible but the upper region more or less remains free, that forms the rind with somewhat spiny projections as in other species. In the third condition, the lower region is free as in the first condition but the fusion extends almost up to the tips that results the outer region more or less flat, fleshy and edible, more commonly so around fertilised flowers (*A. lakoocha*). It may, therefore, be profitable to try to excite growth in the desired region should that be possible.

The true fruit may be considered as a one-seeded ‘achene’. Although the seed is large and the surrounding perianth is fleshy and persistent, the actual pericarp is not especially thick and hard. In the same way the fruits of *Morus* and *Ficus* have been described as a sort of achenes (Cronquist, 1961).

**SUMMARY**

The fruits of *Artocarpus heterophyllus* (jack-fruit), *A. altilis* (bread-fruit) and *A. lakoocha* (barhal), etc., have been studied and described.

The whole female inflorescence increases and develops into a composite or multiple type of fruit. The so-called fruit has three regions: (i) The fruit axis, (ii) The persistent perianth and (iii) The true fruit.

The perianth is the most important part and constitutes the major bulk of the fruit. It has basically three regions (*A. heterophyllus*): (a) The lower free and fleshy edible region, (b) The middle fused region and (c) The upper free and horny non-edible region. In *A. altilis*, the fusion region extends up to the base but in *A. lakoocha* it goes up to the top and this (fusion region) becomes edible.

The true fruit developed from the carpel (ovary) is insignificant and may be considered as similar to one-seeded ‘achene’.
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REFERENCES


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EXPLANATION OF TEXT-FIGURES

Figs. 1-13. Artocarpus heterophyllus. Fig. 1. A young fruit (Y.Fr.). Fig. 2. A part of fruit in L.S. showing fruit axis (Fr.ax.), stelle (st.), perianth (Pr.) and many true fruits (T.Fr.). Figs. 3-4. Young and old fruits in parts showing the main bulk due to the perianth which has (a) lower free edible region, (b) fused middle region (F.pr., fused perianth) and (c) upper free or horny region. Figs. 5-7. Lower free edible region of perianth in sterile, intermediate and fertile cases respectively. Note the maximum girth in fertile perianth (Fig. 7) with true fruit inside (OW., ovary wall, sl., style). Fig. 8. True fruit with a long style. Figs. 9-10. T.S. of young and mature perianth (O.ep., outer epidermis, i.e.p., inner epidermis). Fig. 11. Starch grains in a few cells of perianth. Fig. 12. A part of upper free conical tip of perianth showing the width of perianth with a part of narrow bore through which style passes. Note the thick cuticle (cu.) and well-developed bundle sheath (B.sh.). Fig. 13. A single vascular bundle with bundle sheath enlarged as in Fig. 12 (It., laticifers).

Figs. 14-22. A. heterophyllus. Development of perianth at different stages in L.S. Figs. 14. Young perianth just emerging out of inflorescence axis (inf. ax.). Fig. 15. Perianth emerged but carpel just developing. Figs. 16-17. Perianth is free from adjacent perianth. Carpel (cp.) developing and ovule is initiating. Figs. 18-19. Slightly advanced stages but perianth tubes
still free from adjacent ones. Fig. 20. Adjacent perianth broaden and start fusing at the middle region. Figs. 21–22. Advanced stages of fusion resulting into (a) lower free, (b) middle fused and (c) upper conical free regions (st., stigma, H., hairs). Other abbreviations same as in previous figures.

Figs. 23–30. A. altilis. Fig. 23. A mature fruit in L.S. showing three regions (1) fruit axis, (2) Perianth and (3) True fruit. Fig. 24. A part of young fruit showing lower region of perianth also fused. Figs. 25–26. Young and old fruits in parts showing: (a) very little lower region, (b) well-developed fused middle region extending up to the base and, (c) upper free conical region. Note the well-developed hairs (H) in cavities of perianth. Fig. 27. A part of fused region of perianth with a true fruit. Fig. 28. T.S. ovary. Fig. 29. A true fruit. Fig. 30. A true fruit in L.S. Abbreviations same as in previous figures.

Figs. 31–37. A. lakoocha. Figs. 31–33. Three fruits of different ages in L.S. showing fruit axis, perianth and true fruits. Note the tumour like outgrowth of perianth around fertile ovaries. Fig. 34. A part of mature fruit with a tumour-like structure formed around a fertile ovary having well-developed seed. Note the growth of perianth both in lower free and middle fused regions. The latter, extending up to the tips. No free upper region of perianth tip is left out. Fig. 35. T.S. perianth of lower region. Fig. 36. A true fruit. Fig. 37. T.S. ovary wall. Abbreviations same as in previous figures.