TAXONOMIC EVALUATION OF ZINGIBERACEAE

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ABSTRACT

The order Scitaminales is generally accepted as a well-knit assemblage of closely related and highly advanced monocotyledons and forms a natural group. Among the families of the order, the Zingiberaceae are the largest and are best represented in India, there being 21 genera including more than 200 species.

The family is of special interest from the taxonomic stand point. On the basis of morphological differences, Schumann (1904) divided the Zingiberaceae into two subfamilies : the Zingiberoideae with many genera and Costoidae with four genera namely, *Costus* (tropics), *Monocostus* (Peru), *Dimerocostus* (tropical America) and *Tapeinochilus* (Tabutu). The Costoideae differs from the rest of the family in showing vegetative and floral organization that is unique among the flowering plants. Therefore, morphologically, they form a natural group that deserves the status of a subfamily.

It is accepted that taxonomy should be based on evidences from as many disciplines as possible in the final evaluation of its units. But among the Costoideae, only *Costus* has been studied in detail. As the other genera of the Costoideae agree with *Costus* in anatomy, Tomlinson (1956) considers it reasonable to assume that the features that serve to distinguish *Costus* from the Zingiberaceae are equally diagnostic for the Costoidae as a whole. A list of diagnostic characters obtained from various disciplines are given in table I. These evidences also reveal that Costoideae is distinct and forms a natural group deserving the rank of a subfamily.

Certain outstanding feature of the Costoideae are unique not only to the family, but also to the order Scitaminales as a whole. Perhaps, because of these Tomlinson (1956) has suggested that the Costoideae may possibly be given a family rank. However, although Tomlinson's view is really encouraging, it is necessary to study the features of other genera of the Costoideae, with respect to various disciplines, in order to decide such an issue, instead of depending on the results obtained only on *Costus*.

The Zingiberaceae is further subdivided into three tribes Globbeae, Hedychieae and Zingibereae on the basis of the nature of lateral staminodes and the ovary. For the taxonomic consideration of tribes, there are no adequate data. However, it can be said that further research in the divergent fields on many more genera may only help in solving the taxonomic problems.

To a systematist the four families of the Scitaminales show an interesting floral organization, although they form a natural group because of certain morphological features common to all the families. A line of reduction in the number of stamens and ovules can be recognised in this order. The data available from various disciplines are too inadequate to verify the prevailing systematic arrangement of the families of the order. Nevertheless, the available embryological data consolidated in the table II unmistakably speak of a common ancestry of the families and their grouping in the order Scitaminales. At the same time certain distinguishing features of each family are probably suggestive of a family rank for each of them.

The order Scitaminales—also known as Zingiberales or Arillatae—is generally accepted as a well-knit assemblage of closely related and highly advanced monocotyledons. In *Genera Plantarum* Bentham and Hooker considered the order as a whole to be one family included within the second series Epigynae. Subsequently it was elevated to a distinct order by Engler and Prantl in the first edition of Die Naturlichen Pflanzenfamilien and divided into four families: Musaceae, Zingiberaceae, Cannaceae and Marantaceae. Later on the Lawiaceae and Strelitziaceae were separated from the Musaceae by Hutchinson (1934).

Among the families of Scitaminales, the Zingiberaceae consists of about 47 genera and 1400 species, distributed throughout tropics and subtropics, but *Costus* is pantropical in distribution. The family is best represented in India, there being 21 genera including more than 200 species. Its members find wide application in commerce as spices, condiments, dyes, perfumes and medicines. The high starch content of their aromatic rhizomes is a source of food.

MORPHOLOGY

The family comprises perennial rhizomatous herbs. Its fleshy rhizome is branched sympodially, built up from the increments of many years' growth, and bears fibrous roots. Each branch ends in an erect shoot bearing leaves, flowers or generally both. Leaves are sessile or petiolate having a sheath basally. A ligule is present at the junction of blade with petiole or sheath.

The inflorescence is terminal, either on a leafy shoot or on a separate leafless shoot. According to Holttum (1950) the inflorescence consists essentially of an axis bearing spirally arranged primary bracts, each of which subtends a flower-bearing cincinnus. Flowers are trimerous, calyx and corolla being distinct. The members of the androecium whorl are highly modified and are present in two whorls of three each. According to Rendle (1930) the posterior

stamen of the inner whorl is fertile with often a broad connective, while the lateral stamens of the same whorl are united to form a petaloid labellum. The outer whorl is either completely suppressed or only the two lateral stamens of this whorl are present as staminodes. The ovary is inferior, tri-carpellary, trilocular with axile placentation or uni-locular with parietal placentation and the ovules are numerous. The style lies in a channel of the fertile stamen. In most cases, there are two epigynous glands that secrete nectar. The fruit is fleshy and indehiscent or a loculicidal capsule. The seeds are arillate with copious endosperm.

TAXONOMY

The family is of special interest from the taxo-nomic stand point. On the basis of morphological differences, Schumann (1904), and later Loesener (1930) divided the Zingiberaceae into two sub-families: the Zingiberoideae with many genera and Costoideae with four genera; the Costus (tropical), Monocostus (Peru), Dimerocostus (tropical America) and Tapeinochilus (Tabutubka). The members of the Zingiberoideae are aromatic and show a typical monocotyledonous construction being unbranched and composed of a pseudo-stem of closely com-pacted concentric sheaths within which the true stem extends to a variable height. The leaves are distichous with open sheath at the base and have a ligule of various size. Lateral staminodes and nectar glands are usually present. The Costoideae, on the other hand, differ from the Zingiberoideae in showing a vegetative organization that is unique among the flowering plants. The plants are not aromatic; true stem is well developed and the branches break through leaf sheaths; leaves are arranged in a peculiar spiral phyllotaxy; lateral staminodes are absent and septal nectaries are present instead of epigynous glands. Therefore, morphologically, the Costoideae are distinct from the Zingiberoideae and form a natural group that deserves the status of subfamily.

It is an accepted fact that taxonomy should be based on evidences from as many disciplines as possible in a final evaluation of its units. But among the Costoideae, only Costus has been studied in considerable detail. As the other genera of Costoideae agree with Costus in anatomy, Tomlin-son (1956) considers it reasonable to assume that the features that serve to distinguish Costus from Zingiberoideae are equally diagnostic for the Costoideae as a whole. The same view is main-tained at present. A list of diagnostic characters obtained from various disciplines are given in the table I. These evidences also reveal that the Costoi-deae are distinct and form a natural group deserv-ing the rank of a subfamily.

Certain outstanding features of Costoideae are perhaps unique not only in the family, but also to the order Scitaminales as a whole. They are: a peculiar spiral phyllotaxy on a branching stem

(Holttum, 1950); non-vascular plug at the apex of the lamina in the seedling (Boyd, 1932); thick exine resistant to acetolysis (Erdtman, 1950), and some of the embryological features such as uni-layered fibrous endothecium, persistent basal apparatus with hypertophied nuclei, Caryophyllad type of embryo development, cotyledonary mound, occur-rence of cotyledonary sheath in addition to coleoptile, precocious development of secondary primordia, bulbous aril, stony lid and thick hard seed coat developed due to the thickening in the inner epidermis only. These deviating characters seem to have prompted Tomlinson (1956) to suggest that the group Costoideae may possibly be raised to family rank. However, although Tomlinson's view is really encouraging, it is necessary to study the features of the other three genera of Costoideae from various disciplines in order to decide such an issue, instead of depending on the results obtained only from Costus.

The Zingiberoideae are further subdivided into three tribes: Globbeae, Hedychieae and Zingibereae on the basis of the nature of lateral staminodes and ovary. Among the first two tribes, the Globbeae are unilocular with parietal placentation, whereas the Hedychieae are trilocular with axile placenta-tion. The last one differs from the rest in not pos-sessing lateral petaloid staminodes which are often absent. But the genus Zingiber differs from the rest of the members of the tribe Zingibereae in having petaloid lateral staminodes. Therefore, Holttum (1950) transferred Zingiber to the tribe Hedychieae and named the remainder as Alpinieae. However, according to the International Code of Botanical Nomenclature (1961) Holttum's tribe Hedychieae should be renamed Zingibereae, since the latter include the type genus Zingiber. Hutchin-son (1934) eliminated the distinction into sub-families and classified the family into four tribes of equal rank.
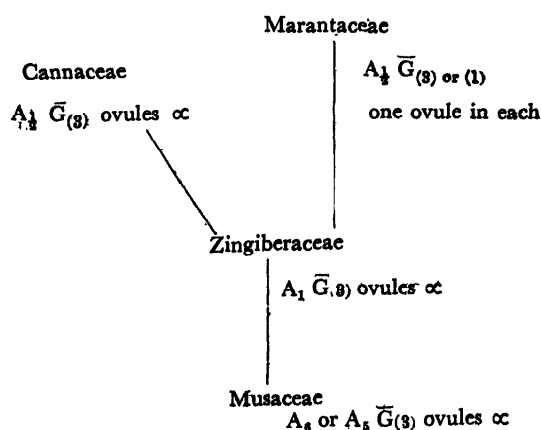
For the taxonomic consideration of the tribes, there are no adequate data. Weisse (1932, 1933) has indicated that the tribes are natural groups based on types of distichy. However, combined evidence from vegetative morphology—median distichy i.e. plane of insertion of leaf being parallel with the direction of rhizome (Weisse, 1932, 1933); floral morphology—occurrence of petaloid lateral stami-nodes (Loesener, 1930) and vegetative anatomy—the absence of silica-bearing cells (Tomlinson, 1956), indicate that the tribe Globbeae has closer affinities with the Hedychieae than with Alpinieae. The last named tribe differs from the rest of the Zingi-beroideae in having transverse distichy—plane of in-sertion of leaf perpendicular to the direction of rhizome-, silica-bearing cells and in the absence of lateral staminodes, but small and never petaloid when present. Tomlinson (1956) states that there are no anatomical features which consistently serve to distinguish the tribes Globbeae, Hedychieae and Alpinieae into which the subfamily is divided and

the distinction based on silica inclusions is not absolute. However, it can be said that further research in the divergent fields on many more genera may help in solving the taxonomic problems.

THE INTERRELATIONSHIP OF THE ZINGIBERACEAE IN THE ORDER SCITAMINALES

To a systematist the four families of the Scitaminales namely, Musaceae, Zingiberaceae, Cannaceae and Marantaceae, form a very natural group as they have common features such as rhizomatous herbaceous habit, imbricate bases of sheathing petioles, sheath being open or nearly close ; calyx and corolla in separate whorls and the inferior nature of the ovary. Hutchinson (1934) considers the order a very advanced group representing the climax of one line of development of the division in which calyx and corolla have remained in separate whorls. He also considers this to be a parallel group to Orchidales, a climax group of the petaloid monocotyledons, with regard to reduction to one stamen in both.

The families of the order show an interesting floral organization. The Musaeeae approach more nearly the common monocotyledonous arrangement in floral features. In the Zingiberaceae, a single stamen is fertile, but in the Cannaceae and Marantaceae only one half-anther is functional, the rest of the stamens being petaloid. The Marantaceae differ from the other families in that the number of ovules is reduced to just one in each chamber, while frequently two of the three chambers abort so that a one-seeded fruit results. The line of reduction in number of stamens and ovules can be represented as follows :

Marantaceae

Cannaceae

$A\frac{1}{2}$ $\overline{G}_{(3)}$ ovules ∞

$A\frac{1}{2}$ $\overline{G}_{(3)}$ or (1)

one ovule in each

Zingiberaceae

A_1 $\overline{G}_{(3)}$ ovules ∞

Musaceae

A_6 or A_5 $\overline{G}_{(3)}$ ovules ∞

The data available are too inadequate to verify the above systematic arrangement of these families. In the field of embryology, the reports of Humphrey (1896), Schachner (1924), Juliano & Alcala (1933), Mauritzon (1936) and Venkataswarlu & Sarojini (1957) are too fragmentary. Nevertheless, out of the data consolidated in the table II, an attempt has been made to draw some tentative conclusions.

It is evident that certain embryological features such as the Polygonum type of embryo sac, nucellar

pad or nucellar cap, perisperm, aril, collar, seed coat from the outer integument only and the chalazal tissue, unmistakably speak of a common ancestry of these families and their grouping in the order Scitaminales. At the same time, the Helobial endosperm of the Zingiberaceae ; reduced structure of aril in the Musaceae ; 3-celled pollen grains and presence of stomata on the seed coat in the Cannaceae and extreme reduction in the number of ovules in the Marantaceae, probably are suggestive of a family rank for each of them.

CONCLUSIONS

The Zingiberaceae, among the families of Scitaminales, is perhaps the only family that has been studied in detail. It is evident from the data collected from various fields that the two subfamilies, Zingiberoideae and Costoideae, are distinct and natural groups. Further considerations of raising the status of the Costoideae to family rank and to verify whether the tribes of the Zingiberoideae are natural groups as stated by Weisse (1932, 1933) or not, depend upon the detailed studies to be made on the members of these categories. However, the genus Costus seems to be very interesting, as it possesses many deviating features among the family. From the taxonomic point of view it is quite necessary to know whether the remaining three genera of the Costoideae also possess the same features as Costus or not. Such results would go a long way in the taxonomic evaluation of the family.

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*Not seen in original.

TABLE I.

SUMMARY OF DIFFERENCES BETWEEN THE ZINGIBEROIDEAE AND COSTOIDEAE *

	Zingiberoideae	Costoideae
1. Vegetative morphology (Holttum, 1950)	Aerial stem unbranched, pseudostem most conspicuous part of shoot. Leaves distichous. Leaf sheaths long, open	Aerial stem branched, true stem well-developed. Leaves spirally arranged, with divergences, 1/5, 1/6, 1/7, ..., etc. Leaf sheaths short, closed (tubular)
2. Floral morphology (Holttum, 1950)	Lateral staminodes usually present, often small. Stylodes (nectar glands) various, always ± columnar, sometimes absent	Lateral staminodes absent. Stylodes absent, nectar glands embedded below base of flower tube
3. Floral anatomy (Rao, Karnik & Gupte, 1954) Calyx and corolla	Out of the two sets of bundles present beneath the ovary, the outer set supplies to the margin of the sepals, whereas the inner set as dorsal traces of the carpels further run as sepal midribs	Out of the two sets, the outer set supplies traces to the midrib as well as the margins of the sepals, whereas the inner set gives rise to the vascular supply of corolla, androecium, gynoecium and glands
Top of the ovary	A number of separate strands emerge from the anastomosis of the parietal bundles. These supply the corolla, androecium, epigynous glands and style	These strands supply only the corolla and androecium, but placental bundles themselves supply the epigynous glands
Functional stamen	Vascular supply is derivable from three traces. These divide into two tangentially placed xylemopposed bundles	A large number of prominent bundles enter the stamen, of these the median one functions as a midrib
Gynoecium	The dorsal bundles of the carpels function also as sepal midribs above the ovary. The stylar canal is usually V-shaped as the anterior locule is not represented prominently in the style	The sepal midribs are quite distinct from the dorsal bundles of the carpels. The stylar canal is not seen to be V-shaped
4. Vegetative anatomy (Tomlinson, 1956) Leaf Epidermis (surface view)	Cell files and subsidary cells of stomata generally regular. Cells above main veins modified	Cell files and subsidiary cells less precise. Cells above veins not modified
Hypodermis	Generally moderately developed, may be well-developed or absent	Always well-developed either in number of cell layers or cell size. (Proportion of assimilating tissue relatively small)
Vascular bundles (standard level)	At least the largest bundles connected to the epidermis by bundle sheath extensions	Leaf bundles never connected to the epidermis by extensions of bundle sheath
Midrib (standard level)	Main bundle arc towards abaxial surface. Subsidiary arcs, when presnt, one upper or one lower or both, one upper and one lower	Main bundle arc towards adaxial surface. Subsidiary arcs represented by a single median, abaxial bundle
Petiole	Maximum of four bundle arcs, main arc (I) close to abaxial surface. Subsidiary arcs, two above, one below main arc, if present. Bundle sheaths of fibres, collenchymatous development of bundle sheaths very rare	Maximum of four bundle arcs, main arc (I) towards adaxial surface. Subsidiary arcs all below main arc. Bundle sheaths always of collenchyma

* see also Tomlinson (1956).

SUMMARY OF DIFFERENCES BETWEEN THE ZINGIBEROIDEAE AND COSTOIDEAE* (Continued)

	Zingiberoideae	Costoideae
Sheath	Main arc not pectinated with subsidiary arc. Abaxial subsidiary arc (II) progressively stronger towards base of sheath. Adaxial subsidiary arcs (III) and (IV) progressively reduced towards base of sheath	Main arc and subsidiary arc pectinated to form a single cylinder, plus single, median abaxial bundle
Air canals	May extend from base of sheath to midrib of lamina	Never extend into petiole, confined to base of sheath
Stem T. S. internode	Cortex generally wide. Fibre cylinder entire, circular in section. Cortical bundles never in contact with fibre cylinder	Cortex narrow. Fibre cylinder undulate in section. Cortical bundles in contact with fibre cylinder
T. S. node (associated with course of bundles in the stem)	No nodal plexus developed. (No branching of the aerial stem)	Nodal plexus developed. (Axillary buds and branching in the aerial stem)
Hairs	Often slightly to markedly sunken. Always unicellular	Never sunken. Frequently multicellular (uniseriate)
Silica	Stegmata : confined to lamina, always dermal. Silica body spherical, surface irregular (granulose)	Stegmata : found in leaf and aerial stem, never dermal. Silica body stellate, druse-shaped, surface smooth
Oil cells	Present in all parts. (Plants aromatic)	Completely absent. (Plants not aromatic)
5. Geographical distribution (Loesener, 1930)	Centre of distribution in Indo-Malaya	Centre of distribution in Central America
6. Seedling development and structure (Boyd, 1932)	Germination hypogeal, cotyledon acts as an haustorium, only ligule well-developed. Two vascular strands in cotyledon	Germination epigeal, cotyledon lamina well-developed. Five vascular strands in cotyledon
7. Pollen structure (Erdtman, 1952)	Non-aperturate. Extine thin, not resistant to acetolysis (requires after-treatment)	Aperturate. Extine thick, resistant to acetolysis (no after-treatment required)
8. Cytology (Raghavan & Venkatasubban, 1943)	Basic number $x = 12$ (Alpinia, Elettaria, Globba, Kaempferia and Phaeomeria) ; $x=11, 12$ (Zingiber) ; $x = 21$ (Curcuma) ; $x = 9, 17, 26$ (Hedychium)	$x=8, 9$. $2n$ values of 16, 18, 36.
9. Embryology (Humphrey, 1896; Schachner, 1924 ; Boehm, 1930 ; Mauritzon, 1936 ; Gregory, 1936 ; Banerji, 1940 ; Raghavan & Venkatasubban, 1941 ; Harling, 1949 and Panchaksharappa, 1961)		
Fibrous layers	2-4 ; also in epidermis	1-layered
Nucellar epidermis at the micropyle.	Multilayered, forms nucellar cap and also contributes to perisperm	Forms uni-layered nucellar pad ; does not contribute to nucellus
Endosperm	Helobial, but basal chamber degenerates quite early at 2-celled stage	Helobial ; basal apparatus is coenocytic and persists even at the time of differentiation of embryo
Storage in endosperm	Aleurone grains and also starch in some cases	Fat only
Embryogeny	Asterad type	Caryophyllad type
Mature embryo	Long, tip tapering in most of the members	Cylindrical
Cotyledonary mound	Absent	Present
Embryonal sheath	Only coleoptile	Both coleoptile and cotyledonary sheath
Cotyledonary strands	Only two	Eight to ten
Secondary root primordia	Only four	Eight to twelve
Storage material in embryo	Absent	Fat bodies present
10. Aril	Thin veil-like, completely covers the seed	Bulbous mound at the micropyle, caruncle
11. Lid	True lid lacking	True lid present.
12. Seed coat (outer integument)	Hardness due to thickening in the outer epidermis or both outer and inner epidermis (Elettaria)	Hardness due to thickening in the inner epidermis only
13. Chalazal tissue	Less developed or absent	Well developed

* see also Tomlinson (1956).

TABLE II

EMBRYOLOGICAL CHARACTERS OF THE FAMILIES IN THE ORDER SCITAMINALES *

	Musaceae	Zingiberaceae	Cannaceae	Marantaceae
1. Stamens	5+1 (staminode), but 6 in *Ravenala madagascarensis*	1+5 (staminodes)	½+5.½ (staminodes)	½+5.½ (staminodes)
2. Anther wall	No Data Available	5-8 layered ; fibrous thickenings in 1-4 layers; tapetum secretory, but plasmodial in *Nicolaia atropurpurea* (Boehm, 1931)	6-layered ; fibrous thickenings in 2 layers ; tapetum secretory	No Data Available
3. Microsporogenesis and male gametophyte.	No Data Available	Sporetetrads isobilateral ; rarely T-shaped and tetrahedral in *Nicolaia atropurpurea* (Boehm, 1931) ; pollen grains 2-celled ; exine spinuliferous or smooth	Sporetetrads isobilateral ; pollen grains 3-celled ; exine structure not known	No Data Available
4. Ovary and ovules	Ovary inferior, tricarpellary, trilocular, syncarpous ; ovules numerous, anatropous, bitegmic and crassinucellate (one in each locule in *Heliconia*) ; placentation axile	Ovary inferior, tricarpellary, trilocular, syncarpous ; ovules numerous, anatropous, bitegmic and crassinucellate ; (unilocular in tribe Globbeae and placentation parietal) placentation axile	Ovary inferior, tricarpellary, trilocular, syncarpous ; ovules numerous, anatropous, bitegmic and crassinucellate ; placentation axile	Ovary inferior, tricarpellary, trilocular, syncarpous ; one or two locules abort and one campylotropous ovule present in each locule
5. Megasporogenesis and female gametophyte.	Spores in linear and T-shaped tetrads; embryo sac Polygonum type	Spores in linear and T-shaped tetrads ; embryo sac Polygonum type ; triads common ; embryo sac Lilium type in *Costus* · (Humphrey, 1896 ; Mauritzon, 1936)	Tetrads only linear ; embryo sac Polygonum type	Tetrads linear ; embryo sac Polygonum type
6. Nucellus	The nucellar epidermis forms nucellar pad, but in *Strelitzia* cells divide periclinally and form nucellar cap and also add to nucellus ; hypostase and epistase present	The nucellar epidermis forms nucellar pad and nucellar cap. The latter adds cells to the nucellus ; hypostase and epistase present	Only nucellar pad present	Only nucellar cap present
7. Endosperm	Nuclear ; reserve food starch	Helobial ; reserve food starch, aleurone grains and fat	Nuclear	Nuclear
8. Embryo	Embryogeny not studied ; mature embryo cylindrical or slightly curved	Embryogeny Caryophyllad type ; but Asterad type in the members of Zingiberoideae ; mature embryo cylindrical or tapering at the cotyledonary tip	Asterad type ; secondary roots and plumule present in mature embryo	Embryogeny not studied ; mature embryo cylindrical or tapering
9. Aril	Multicellular woody fibres in *Strelitzia* ; trichomes in *Musa rosea* ; but absent in *Heliconia pittacorum*	Thin and veil-like ; but bulbous in *Costus speciosus*	Present	Present ; but reduced in *Thalia*
10. Collar	Present ; but absent in *Heliconia* and *Strelitzia*	Present	Present	Present
11. Lid	Present ; the entire tip of the outer integument develops into lid in *Heliconia* ; but only from the inner epidermis and 3-layered in *Strelitzia* ; one-layered in *Musa rosea*	Present in *Costus*, but it develops from the inner epidermis in *Amomum*, *Alpinia* and *Elettaria*	Absent ; but germinal slit is present	Well developed ; 10-20 cells thick in *Thalia* and *Stromanthe lutea*

EMBRYOLOGICAL CHARACTERS OF THE FAMILIES IN THE ORDER SCITAMINALES   (Continued)

	Musaceae	Zingiberaceae	Cannaceae	Marantaceae
12. Seed coat	Formed only from the outer integument ; hard layers are formed from a few hypodermal layers; cells pitted in *Musa rosea*; but in *Heliconia* the endocarp forms a hard coat	Formed only from outer integument ; outer or inner epidermis (in some cases both) forms hard layers. The cells of the latter contain crystals in *Elettaria*, *Amomum* and *Aframomum*	Formed from outer integument ; hard layers are outer epidermis and 4 or 5 layers below ; stomata present	Formed from the outer integument only ; both outer and inner epidermis thickened ; but only inner epidermis in *Calathea pictorata* and *Stomante lutea* ; the cells contain crystals
13. Perisperm	Reduced to a single band of starchy sheath in *Heliconia* and *Strelitzia*	Copious at the micropylar part. Starch present	Copious at the chalazal end	Persists ; cells thick-walled ; starch present
14. Chalazal tissue	Present in *Musa ensete* and *Musa rosea* ; but absent in *Strelitzia reginae*	Present in *Costus* ; but less developed in *Elettaria*	Present ; the tissue occupies half of the ovule	Well developed ; projects into nucellus enclosing perisperm canal ; bilobed in *Thalia* ; but reduced in *Maranta* ; fused into one in *Calathea*

* Previous workers : Humphrey, 1896 ; Schachner, 1924 ; Boehm, 1930 ; Juliano & Alcala, 1933 ; Mauritzon, 1936 ; Gregory, 1936 ; Banerji, 1940 ; Raghavan & Venkatasubban, 1941 ; Harling, 1949 ; Venkateswarlu & Sarojini, 1956 and Panchaksharappa, 1961.