Fruit Development and Structure in Some Indian Bamboos

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ABSTRACT

Fruit structure and development of seven species belonging to five genera of Indian bamboos are described. The fruit in four species is a caryopsis typical of the family Poaceae. The ovule is bitegmic; the outer surface of the cells of nucellar epidermis becomes cutinized and forms the seed coat. Three species bear a fleshy fruit with a unitegmic ovule. In a mature fruit the endosperm is either completely absorbed by the embryo or is present only in small quantity. The developing embryo comes in direct contact with the fruit wall due to the disintegration of the nucellus and integument. The embryo is covered by a thick brown mat from the disorganized cells of the inner layers of the fruit wall.

Key words: Poaceae, Bambusoideae, *Bambusa*, *Dendrocalamus*, *Melocalamus*, *Ochlandra*, *Pseudostachyum* (fleshy fruits), fruit wall.

INTRODUCTION

The classification of bamboos into subtribes was proposed by Munro in 1868. The subsequent attempts by Bentham (1883), Gamble (1896) and E. G. Camus (1913) to modify Munro's classification have not brought forth any significant changes. Camus (1935) created a new tribe for the bamboos with fused filaments. Holttum's (1946, 1956) scheme of classification of bamboos based on ovary characters is rather unnatural, as species having similar fruit morphology have been placed in different subtribes. The present study was taken up following recent publications by Dransfield (1981) and Hari Gopal and Mohan Ram (1985) to investigate the development and structure of fruit in some representative Indian bamboos and evaluate their systematic significance.

MATERIALS AND METHODS

Development and structure of fruit were studied in *Bambusa tulda* Roxb., *Dendrocalamus hamiltonii* Nees & Arn., *D. longispathus* Kurz, *Melocalamus compactiflorus* Bentham and Hook *Melocalamus sp.nov.*, *Ochlandra travancorica* Bentham and Hook and *Pseudostachyum polymorphum* Munro. Details of sources of collection of these materials for study have been published (Hari Gopal and Mohan Ram, 1985). The young ovaries and fruits at different stages of development were fixed and processed for serial sectioning, following the procedure given by Hari Gopal and Manasi Ram (1981). The new species of *Melocalamus* will be published formally in due course.

RESULTS

The bamboo fruit is indehiscent and the single seed fills the pericarp completely. In external morphology it ranges from a small oval caryopsis to a large spherical or pear-shaped structure (McClure, 1966). For the sake of uniformity, the structure of the fruit wall lying adjacent to the ovule on the opposite side of the placenta has been taken for comparison in each taxon.

Ovule and embryo sac

The ovule is hemianatropus, pseudo crassinucellate, bitegmic in *Bambusa* and *Dendrocalamus* and unitegmic in *Melocalamus* and *Ochlandra* (Fig. 1 A, B). The integuments do not cover the nucellus completely; thus no micropyle is formed. The nucellar epidermis is unilayered except at the micropylar end where two or four cells divide periclinally to form a two- to four-layered tissue in *Bambusa* and *Dendrocalamus* (Fig. 1 A, arrow). However, in *Melocalamus* and *Ochlandra* all the cells of the nucellar epidermis divide periclinally

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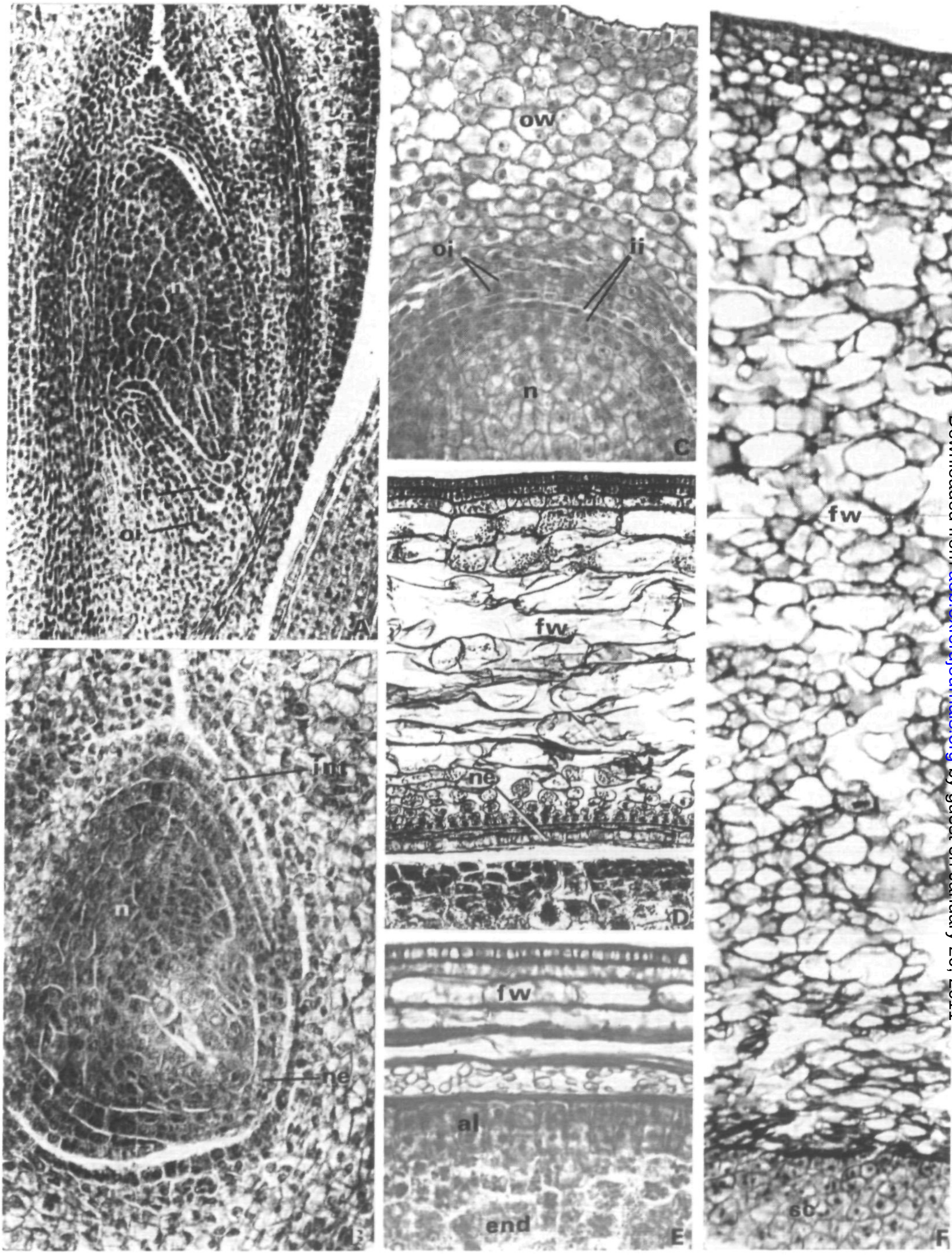

FIG. 1. Ovule and fruit wall in *Bambusa tulda* (A, C–E) and *Melocalamus sp.nov.* (B, F). Abbreviations: al, aleurone layer; end, endosperm; fw, fruit wall; ii, inner integument; int, integument; n, nucellus; ne, nucellar epidermis; oi, outer integument; ow, ovary wall; sc, scutellum. A, L.S. part of ovary showing bitegmic ovule with multi-layered nucellar epidermis at the tip (arrow). × 150. B, L.S. part of ovary showing unitegmic ovule with multi-layered nucellar epidermis. × 250. C, T.S. part of ovary at megaspore tetrad stage. × 300. D, L.S. part ovary at globular embryo stage. The outer radial walls of the cells of nucellar epidermis are cutinized. × 150. E, L.S. part of ovary at the mature embryo stage. × 200. F, Portion of L.S., developing fruit. × 25.

and form a multilayered tissue over the nucellus (Fig. 1B). The embryo sac development is of the Polygonum type. The number of antipodal cells (more than 40) varies in all the plants studied.

Endosperm

The development of endosperm in all the species investigated is free nuclear in the beginning but later becomes cellular. The meristematic activity is restricted to the outermost two to four layers of cells, which by mitotic divisions add to the bulk of the endosperm tissue. In *Bambusa*, *Dendrocalamus* and *Pseudostachyum* the outermost two to four layers of the cellular endosperm are made up of rectangular cells with prominent nuclei and are devoid of starch (Figs. 1E and 2E). This constitutes the aleurone tissue. In *Melocalamus sp.nov.* and *Ochlandra* the endosperm becomes completely cellular when the embryo is at the globular stage. Nevertheless, most of it is absorbed by the embryo during its development and differentiation. Thus, in *O. travancorica* the endosperm at maturity is represented by six to eight layers around the embryo towards the apical part of the fruit whereas in *Melocalamus sp.nov.* it is present in a discontinuous layer around the embryo only in the cavities formed by the scutellar epidermis (Fig. 2B). In *M. compactiflorus* the endosperm formation does not proceed beyond the free nuclear stage and is absorbed rather rapidly. In a mature fruit no trace of endosperm is left around the embryo. Curiously, endosperm cells in *Ochlandra* and *Melocalamus sp.nov.* do not contain any starch grains.

Fruit wall

A species wise account of development of fruit wall is given below:

Bambusa tulda: The ovary wall at the megaspore tetrad stage has an outer epidermis, an inner epidermis and six to ten layers of cells between them (Fig. 1C). The cells along the periphery of the ovary wall are small and have dense cytoplasm. However, the cells towards the stylar base are large and sparsely cytoplasmic. The length of the ovary increases enormously after fertilization.

The outer integument degenerates during megasporogenesis and the inner one during embryo sac development. The degenerating cells become flattened and gradually lose their identity. The nucellar epidermis persists up to the globular embryo stage and its outer surface becomes cutinized but the inner and the radial walls remain thin (Fig. 1D). As the embryo and endosperm increase in size, the cells of the nucellar epidermis become crushed and only the cutinized outer surface persists between the endosperm and the pericarp (Fig. 1E).

During embryo differentiation the cells of the outer epidermis of the pericarp become thick walled. This process is initiated at the base of the style and proceeds towards the base of the fruit. Three or four layers below the epidermis also become thick-walled. The pericarp is thinnest (three to five layers) at the base on the dorsal side covering the embryo and its cells remain thin walled. This part of the fruit wall which becomes wrinkled upon drying is known as embryotegmium.

Dendrocalamus: Development of fruit wall was studied in two species namely, *D. hamiltonii* and *D. longispathus*. In these species the fruit wall development is similar to that in *B. tulda*. In *D. hamiltonii* the embryotegmium is clear, whereas in *D. longispathus* cells of the fruit wall are thick-walled all round and the position of the embryo can not be made out from the surface.

Pseudostachyum polymorphum: Early stages of development could not be studied as insufficient number of young ovaries were available and also because all the parts of the inflorescence became thick and hairy. However, it was possible to study fruit development beyond the globular embryo stage. In such material the integument(s) and the nucellus had already degenerated leaving behind a thick mat of disintegrated cells around the embryo and the endosperm. The pericarp is thicker than that of *Bambusa* and *Dendrocalamus*. The cells of the outer epidermis and two or three layers below it are thick-walled, have prominent nuclei and are devoid of starch grains (Fig. 2C). Two or three layers of cells below this zone are large and have abundant starch. The amount of starch is meagre in the subjacent four to six layers but is abundant in the innermost two to four layers and the inner epidermis (Fig. 2C). All the cell layers on the hilum side have abundant starch grains (Fig. 2D).

During differentiation and maturation of the embryo, those cell layers that have a low amount of starch collapse and leave behind their remnants (Fig. 2E). Consequently the thickness of the fruit wall decreases. Embryo tegmium is not clear in this species.

Melocalamus: The ovary in this genus is subglobose, has a short, thick style and three feathery stigmas. There are no hairs on the ovary wall. Fruit development was studied in two species (*Melocalamus sp.nov.* and *M. compactiflorus*) of this genus. The ovary wall has an outer epidermis, an inner epidermis and seven to nine cell layers between them.

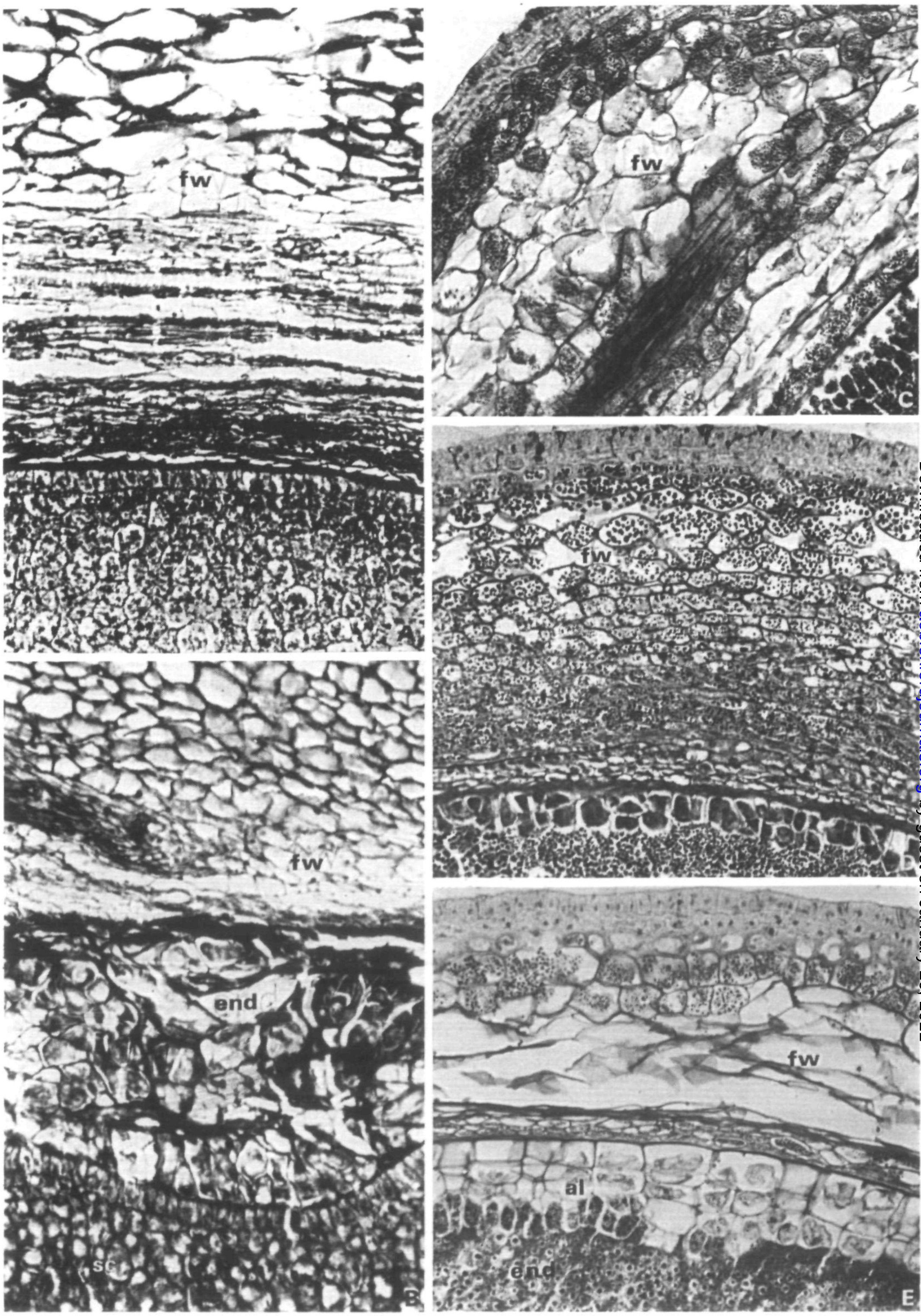

FIG. 2. Fruit wall in *Melocalamus sp.nov.* (A, B) and *Pseudostachyum polymorphum* (C–E). A, Portion of L.S. of fruit showing the collapsing of inner cell layers. ×30. B, Portion of L.S. showing the persistent endosperm in a depression of the scutellum. ×30. C, Part of L.S. of dorsal part of ovary at the globular embryo stage. Note the uneven distribution of starch. ×120. D, Part of hilum side of L.S. of ovary. Note the even distribution of starch. ×90. E, Part of L.S. ovary at mature embryo stage. The middle layers of fruit wall are collapsing. ×100. For abbreviations, see Fig. 1.

The pericarp increases in thickness rapidly after fertilization and reaches its maximum (3–6 mm) by the time the embryo becomes globular. The outer epidermis does not undergo any changes except that the tangential walls become slightly thickened. The tissue immediately below the epidermis is collenchymatous and four to six cells thick. The cells gradually increase in size inwards. The collenchyma gradually passes in to the parenchyma, whose cells are large and have scant cytoplasm (Fig. 1F).

The integument and nucellus degenerate completely soon after fertilization and the developing embryo comes in direct contact with the pericarp. The cells of the inner parenchymatous zone loose their shape and collapse as the embryo becomes large and fills up the entire cavity. The walls of these cells become crushed and form a thick brown layer around the embryo (Fig. 2A). At maturity the pericarp is green, smooth and soft and can be easily separated from the embryo. In a dry fruit the position of the plumule and radicle becomes conspicuous as these push the fruit wall into a hump.

Ochlandra travancorica: Fruit development in this species is as in *Melocalamus* except for the following details. The cells of the parenchymatous zone do not collapse but have a large quantity of starch in them. Thus the thickness of the pericarp remains same except at the base of the fruit where it becomes thin to facilitate the emergence of the plumule and radicle during germination. The style persists as a long beak even at maturity.

DISCUSSION

There is variation in size and number of integuments in bamboos. The ovules are ategmic in *Melocanna bambusoides* (Stapf, 1904; Petrova, 1965) and unitegmic in *Melocalamus* and *Ochlandra*. They are bitegmic in *Bambusa* and *Dendrocalamus* but the integuments fail to cover the nucellus completely and no micropyle is formed. The outer integument in *Phyllostachys nigra* is rudimentary (Gioelli, 1935). In *Arundinaria* and *Maclurolyra* the inner integument forms the micropyle (Yoshida, 1963; Calderon and Soderstrom, 1973). In all the bamboos so far investigated the integuments do not contribute to the formation of the seed coat. In the dry caryopsis type of fruit (*Bambusa*, *Dendrocalamus*) the outer surface of the nucellar epidermis becomes cutinized and forms the 'seed coat' along with the inner cell layers of the fruit wall. In the fleshy-fruited bamboos (*Melocalamus*, *Melocanna*) the inner cell layers of the fruit wall collapse and form a thick brown covering around the embryo. No such covering is seen in *Ochlandra*. In three other genera of the fleshy fruit-bearing bamboos namely *Dinochloa*, *Olmeca* and *Alvimia* fruit development has not been studied. Dransfield (1981) has examined the gross morphology of the fruits in the genus *Dinochloa*. These resemble the fruits of *Melocalamus* in having a fleshy fruit wall and a large embryo, surrounded by a thin layer of endosperm. Among the fleshy fruit bearing taxa, *Dinochloa*, *Melocalamus*, *Melocanna* and *Ochlandra* are either non-endospermic at maturity or contain only a thin layer of endosperm which is devoid of starch or other storage material. Interestingly in these the fruit wall and scutellum (largest part of embryo) contain a large amount of starch and presumably serve the energy needs of the embryonal axis during germination. (Stapf, 1904; Hari Gopal, 1982).

Holttum (1956) has classified bamboos into four types: Schizostachyum type, Oxytenanthera type, Bambusa–Dendrocalamus type and Arundinaria type, based on the external morphology of ovary and fruit. While proposing this scheme he has emphasized the need for detailed studies involving serial sectioning of fruits at various developmental stages to support or contradict his views. Our investigations on the fleshy fruits of *Melocalamus* and *Ochlandra* have indicated a similarity with the development of the fruits of *Melocanna* (Stapf, 1904) and *Dinochloa* (Dransfield, 1981). The embryo in these four genera shows similar organization in having a large scutellum and a curved embryonal axis (plumule and radicle are juxtaposed) (Stapf, 1904; Dransfield, 1981; Hari Gopal and Mohan Ram, 1985). Holttum (1956) has placed these genera in different groups. While studying the genus *Dinochloa*, Dransfield (1981) has stated that *Melocalamus*, *Melocanna*, *Ochlandra* and *Dinochloa* are related. We support her opinion and propose that these genera be placed in the tribe Melocannae (as *Melocanna* was the first genus studied in detail by Stapf, 1904). The other two fleshy fruit bearing genera (*Alvimia*, *Olmeca*) from the New World (Calderon, 1973; Soderstrom, 1981) may also be placed in this group as the fruits and seedlings resemble those of the above four genera.

The fruits of *Pseudostachyum polymorphum* are endospermic. The fruit wall, scutellum and endosperm contain starch. The embryo is smaller than that of the fleshy fruit bearing bamboos but has a scutellum which is equally developed on either side of the curved embryonal axis (Hari Gopal and Mohan Ram, 1985). In this respect this monotypic genus does not fit into the Melocannae. On the basis of external morphology of ovaries Holttum

(1956) had proposed that the genera *Pseudostachyum*, *Cephalostachyum*, *Schizostachyum* and *Teinostachyum* may be united into a single genus. We have procured a few fruits of *Cephalostachyum* through the courtesy of Dr Soderstrom of the Smithsonian Institution, Washington, DC. These fruits are slightly larger than those of *Pseudostachyum* but have the same morphology. We have not been able to study the internal structure of these fruits. The drawings of fruits in these genera as given in Gamble's atlas of Indian bamboos (Gamble, 1896) indicate the possibility of similarity of form. Further the diagram provided by Reeder (1962) for the embryo of *Cephalostachyum fuchsianum* resembles that of *Pseudostachyum*. As no other mature fruits of bamboos studied so far resemble that of *Pseudostachyum*, we believe that this genus may be placed in the Pseudostachyeae. The other three genera (mentioned above) may also be placed in this group. Nevertheless further investigations are needed to confirm our views.

The structure of the ovule, mature embryo and fruit wall development in *Bambusa* and *Dendrocalamus* are similar (Philip and Haccius, 1976; Hari Gopal and Manasi Ram, 1981; Hari Gopal and Mohan Ram, 1985). Thus, a Bambusa–Dendrocalamus group of bamboos may be recognized.

In external, morphology the bamboo fruit ranges from a caryopsis (measuring 0·4 cm in length and 0·2 cm in diameter) to a large pear-shaped structure (2–8 cm long and 1–15 cm across) (McClure, 1966). Several evolutionary botanists consider large fleshy fruits to be primitive (Holttum, 1956). It has been suggested that the function of a fleshy pericarp is to protect from desiccation and nourish the developing embryo and seedling. An analysis of the distribution of the fleshy fruit bearing taxa of bamboos indicates that these are predominently tropical, where drought stress is not a limiting factor. We believe that the associated changes in the morphology of fruit such as absence of endosperm, large scutellum and fleshy pericarp are products of transference of function of homologous tissue systems found in the conventional fruit of the subfamily Bambusoideae in particular and of the family Poaceae in general. Consequently the fleshy fruits of *Alvimia*, *Dinochloa*, *Melocalamus*, *Melocanna*, *Ochlandra* and *Olmeca* are highly specialized and not primitive. Also, it is unlikely that there is parallel evolution among these genera because there are remarkable differences in vegetative characters and these suggest that the similarity in fruit characters is a case of convergence.

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