SIGNIFICANCE OF FOLLICLE ANATOMY OF APOCYNACEAE

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ABSTRACT

The pericarp structure of *Aganosma*, *Alstonia*, *Catharanthus* sp., *Holarrhena*, *Ichnocarpus*, *Parsonsia*, *Strophanthus*, *Vallaris* and *Wrightia* sp. distinguished into epicarp, mesocarp and endocarp has been used to put forward their taxonomic and phylogenetic importance. Epicarp is single layered in *Catharanthus* sp., *Ichnocarpus*, *Parsonsia* and *Vinca*, while in the rest of the genera it is multilayered. Mesocarp is parenchymatous which embeds vasculature and non-articulated laticifers. Endocarp is multilayered and thick walled. Dehiscence of the follicle is marginicidal. A comparison table of follicular features of *Apocynaceae*, *Asclepiadaceae* and *Periplocaceae* is furnished and their features are discussed. A taxonomic key based on follicular fruit characteristic to indentify the genera and species is appended.

KEY WORDS: *Apocynaceae*, dehiscence, follicle anatomy, phylogeny, taxonomy.

INTRODUCTION

As one of the major organs of the plant, fruit is somewhat neglected for its structural and developmental studies even though such studies have taxonomic and pharmacogonostic value (Dave 1986, Dave and Menon 1986, 1989, Kuriachen and Dave 1989, Wannan and Quinn 1990, Dave and Kuriachen 1991, Kuriachen et al. 1992). Roth (1977) has compiled the available information on fruit anatomy and has used to put forward an evolutionary sequence of different fruit types; among which follicle is considered the most primitive fruit type. Follicular fruits are found to be present in the primitive *Magnoliales* as well as in the advanced *Gentianales* families (Mohana Rao 1986, Kuriachen et al. 1992). The present article incorporates a genus-wise study on the follicles of *Apocynaceae* in order to discuss the taxonomic and evolutionary sequence among the follicles of this family.

MATERIALS AND METHODS

Mature fruits were collected from different locations: *Aganosma*, *Catharanthus* (*C. roseus*), *Ichnocarpus* and *Vallaris* from Sardar Patel University Botanical Garden; *Alstonia* and *Parsonsia* from Thiruvankulam, Kerala; *Strophanthus* from Alleppey, Kerala; *Vinca* from Ooty, Tamil Nadu; and *Wrightia* sp. from Toranmal, Maharashtra. Fruits of *C. pusillus* and *Holarrhena* were collected from the herbarium specimens deposited at the Bioscience Department of Sardar Patel University. Fruit samples were fixed in F.A.A. (Johansen 1940). The materials were dehydrated in a graded series of tertiary butyl alcohol, infiltrated with and embedded in "tissue prep." Serial

transections of 6-8 µm were cut and stained with Safranin-Fast green for general histology. PAS and Ferric chloride (JENSEN 1962) were used to detect carbohydrate and phenolic contents, respectively. Observations and photomicrographs were taken on Carl Zeiss Jena microscope.

RESULTS

Aganosma caryophyllata L.

Its fruits is a pair of constricted follicles (Fig. 1) measuring 12 cm in length and 1.5 cm in diameter. A pair of fruits developing from a single flower are of equal or unequal lengths. Fruit surface shows numerous ridges and furrows (Fig. 2) covered with brown indumentum. Calyx is found to be persistent with colleters at the base of the fruit.

A layer of radially elongated cells constitute the epicarp, covered externally by a thick cuticle with strong intrusions into the epicarpic cells (Figs 3, 4, 5). Epicarp appears multilayered in certain regions due to one or two periclinal divisions of its cells (Fig. 6). Hairs are of multicellular type with a stalk and head; stalk consist of small cells, but the large head consist of a single elongated cell attached to the stalk in the form of an arm of "T". Stomata are present (Fig. 5) throughout the fruit surface and are of anomocytic and paracytic types.

The mesocarp consist of 90-100 layers of parenchymatous cells in the dorsal and ventral sides, whereas it is 45-50 layered thick in the lateral sides. There are 80-100 conjoint, collateral or bicollateral bundles scattered in the mesocarpic

Plate I, Figs. 1-7 *Aganosma caryophyllata*

1. A pair of mature follicles, $\times 0.4$
2. Scanning electron photomicrograph showing hairs and longitudinal ridges, $\times 77$
3. Diagrammatic representation of fruit in transection showing different tissue zones, $\times 72$
4. Transection of pericarp showing epicarp, mesocarp and endocarp, $\times 90$
5. Epicarpic stomata, $\times 266$
6. Multilayered epicarp, $\times 340$
7. Scanning electron photomicrograph of endocarp, $\times 530$

Figs. 8-11 *Alstonia scholaris*

8. A pair of follicles, $\times 0.3$
9. Diagrammatic representation of fruit in transection showing epicarp, mesocarp, endocarp, seed chamber and dehiscing zone, $\times 110$
10. Transection of pericarp from midcarp region showing different tissue zones, $\times 120$
11. Multilayered sclereified endocarp, $\times 260$

Abbreviations: CU – cuticle; EN – endocarp; ME – mesocarp; DZ – zone of dehiscence; EP – epicarp; H – hair; R – ridge; SC – seed chamber.

tissue, but the main traces are more or less in a ring seen at the middle of the mesocarp. Each bundle has a sclerenchymatous bundle cap. Xylem elements in most of the bundles have very small lumen due to secondary wall deposition. When compared to xylem elements phloem is very little and interrupted by tannin cells (Fig. 4). Tanniniferous cells are present throughout the mesocarp without definite distributional pattern (Fig. 4).

Endocarp is 5-7 layered and sclerenchymatous (Fig. 4) devoid of stomata and hairs; its cells are tangentially elongated, but some of them appear rectangular in transection (Fig. 4) due to their interwoven arrangement. They produce impressions on the adjacent cells (Fig. 7). The placental periphery appears thickened due to the continued layer of endocarp.

On the ventral side of the fruit, two layers of thin walled cells are present, extending from periphery to middle of the placenta. This is the "zone of dehiscence" (Fig. 3). At maturity of the fruit, these cells become empty and elongated favouring the dehiscence of the follicle centrifugally. Seeds are comose on one end and are dispersed by wind.

Alstonia scholaris R. Br.

Its flowers are greenish-white in umbellate cyme. A pair of follicles developing from a single flower shows equal or unequal lengths of the two fruits (Fig. 8).

The radially elongated cells constitute the epicarp layer covered externally with a cuticle (Figs 9, 10). Numerous anomocytic stomata are present on the fruit surface. The mesocarp is made up of 40-45 layered, thick, loosely arranged cells, of which 3-4 layers of cells are radially elongated (Fig. 10). There are 32-34 conjoint, collateral bundles present in the mesocarp. Tanniniferous cells and starch grains are seen in the mesocarpic cells beneath the epicarp. The endocarp is 2-4 layered and sclerenchymatous (Fig. 11).

Dehiscence of the fruit occurs when the fruit dries out. Opening of the fruit is marginicidal, initiating from placenta and proceeding towards the periphery of the fruit through the zone of dehiscence. After dehiscence the pericarp curls spirally and shows longitudinal ridges and furrows extending from base to tip of the fruit. Seeds are oblong or linear, flattened with a fringe of hairs on both the ends, the hairs are longer than the seeds.

Catharanthus pusillus (Murr.) G. Don.

Its follicles (Fig. 39) are produced in the simple opposite leaves. The follicles are erect, diverging and constricted in between two seeds. A mature fruit measures 6 cm in length and 0.15-0.20 cm in diameter. Fruit shows both morphological and anatomical identity with the fruit of *C. roseus*, but differs in the number of layers.

Non-trichomatous epicarp is a stomatic single layer of rectangular or radially elongated cells (Figs 40, 41). Mesocarp is formed of 4-5 layers of loosely arranged cells (Fig. 41). There are 10-12 conjoint and collateral bundles in the mesocarp. Non-articulated laticifers are seen among the mesocarpic cells. Endocarp is wavy and formed of 1-2 layers of thick-walled rectangular cells (Fig. 41). Thin-walled empty cells in the zone of marginicidal dehiscence break to open the fruit. Seeds are black, oval and devoid of coma.

Catharanthus roseus (L.) G. Don.

A pair of equal or unequal follicles develops from bicarpellary pistil of a single flower. They normally measure about 5

cm in length and 3 cm in diameter. Fruit is green in colour when young, but turns yellow at its maturity.

The epicarp is single layered with rectangular cells, interrupted by numerous unicellular hairs and anomocytic stomata (Figs 13, 14). A zone of 7-12 layers of loosely arranged parenchyma cells beneath the epicarp forms the mesocarp embedding the vascular elements and laticifers. There are 16-18 conjoint and collateral bundles in a row. Laticifers are non-articulated as observed in longisections throughout the mesocarp, but are not seen adjacent to the vascular traces. Latex is white in colour. Endocarp is 3-4 layered and lignified (Fig. 13). The entire endocarp appears wavy due to the uneven thickness of the mesocarp (Fig. 13). In surface view endocarpic cells appear elongated and interlocked with each other.

The region of the fruit where the margins are fused is the zone of dehiscence, lined with thin-walled, radially elongated cells. Opening of the fruit initiates from the locule towards outside by slackening the thin-walled parenchyma cells of the zone of dehiscence. Seeds are cylindric, black in colour and prominently 3-5 ribbed. Seeds are devoid of hairs.

Holarrhena antidysenteria (L.) WALL.

Its follicles are long and slender (Fig. 42) measuring 15-18 cm in length and 0.8 cm in diameter. Numerous ridges and furrows extend from base to tip on the fruit surface.

The outermost layer together with 3-5 layered collenchymatous zone constitutes the epicarp (Figs 43, 44). Its collenchyma possess tanniniferous contents. Mesocarp is 28-30 layered, embedding 40-50 vascular bundles and laticifers. Bundles are arranged in a ring with a bundle cap of lignified cells. Development of bundle cap is from parenchyma cells by secondary wall deposition (Fig. 44). Tanniniferous cells are also present in the mesocarp. Endocarp is 3-4 layered and sclerenchymatous. Sclerified cells adjacent to the mesocarp are rectangular in outline, but the cells of the innermost layers are tangentially elongated (Fig. 44).

Dehiscence of the fruit at maturity is through the ventral suture. Seeds are comose at one end and are longer than the seed width.

Ichnocarpus frutescens L.

The fruit pair has slender, cylindric, straight or curved follicles (Fig. 15) covered totally with brown hairs. A mature follicle measures 5 cm in length and 3 cm in diameter.

The outermost single layer of the fruit is the epicarp, consisting of radially elongated cells covered externally with a thick cuticle (Fig. 16). Numerous stomata and hairs are present on the fruit surface. Each hair is differentiated into stalk and head. Stalk is multicellular while head consists of a single elongated cell arm attached at right angle to the stalk to form "T" shape. Mesocarp consists of 12-16 layers of cells. There are 38-40 bundles arranged more or less in a ring. A group of thick-walled cells present above the bundle forms a bundle cap. Laticifers are of non-articulated type and are seen adjacent to the vasculature. Many of the mesocarpic cells are tanniniferous. Endocarp is 2-3 layered and cells are tangentially elongated with spindle-shaped nuclei (Fig. 16). Starch grains are localized both in the mesocarpic and endocarpic cells. At a later stage both radial and tangential walls of endocarpic cells become lignified.

The zone of dehiscence is formed of thin-walled cells, which become empty before dehiscence (Fig. 17). Opening of the fruit is marginicidal which initiates from placental side

Platte II, Figs 12-14 *Catharanthus roseus*

12. A pair of follicles, $\times 1.3$

13. Transection of pericarp showing epicarp, mesocarp and endocarp, $\times 130$

14. Scanning electron photomicrograph of stomata, $\times 350$

Figs 15-16 *Ichnocarpus frutescens*

15. A pair of follicles, $\times 1.5$

16. Pericarp showing epicarp, mesocarp and endocarp, $\times 130$

17. Transection of fruit showing zone of dehiscence (at arrow), $\times 110$

Figs 18-20 *Parsonsia spiralis*

18. A pair of ventrally fused follicles, $\times 0.4$

19. Pericarp showing epicarp, mesocarp and endocarp, $\times 92$

20. Zone of separation and zone of dehiscence, $\times 48$

Abbreviations: DZ – zone of dehiscence;
EP – epicarp;
PL – placenta;

EN – endocarp;
ME – mesocarp;
SZ – zone of separation;

VB – vascular bundle.

Platte III, Figs 21-24. *Vallaris solanace*

21. A pair of ventrally fused follicles, x 6

22. Diagrammatic representation of a pair of fruits (F₁ & F₂) showing epicarp, mesocarp, endocarp, zone of dehiscence and seed chamber, x 4

23. Bicollateral bundle, x 86

24. Multilayered sclerified endocarp, x 149

Figs 25-28. *Vinca majus*

25. A pair of follicles, x 1

26. Pericarp in transection showing epicarp, mesocarp and endocarp, x 1110

27. Sclerified endocarp, x 250

28. Zone of dehiscence (at arrow), x 138

Fig 29. *Wrightia tinctoria*

A pair of follicles, x 6

Abbreviations: DZ – zone of dehiscence;
ME – mesocarp;
TC – thick walled cells;

EN – endocarp;
SC – seed chamber;
VB – vascular bundle.

EP – epicarp;
SZ – zone of separation;

Platte IV, Figs 30-32. *Wrightia tinctoria*

30. Diagrammatic representation of fruit in transection showing different tissue zones, $\times 14$

31. Multilayered sclerified endocarp, $\times 138$

32. Zone of dehiscence, $\times 138$

Figs 33-38. *Wrightia tomentosa*

33. A pair of ventrally fused follicles, $\times 6$

34. Diagrammatic representation of two ventrally fused follicles (F_1 & F_2)

35. Transection of lenticels, $\times 90$

36. Multilayered sclerified endocarp, $\times 85$

37. Zone of dehiscence is at right angle to the zone of separation, $\times 78$

38. Zone of dehiscence, $\times 85$

Abbreviations: DZ – zone of dehiscence;
L – laticifer;
SC – seed chamber;

EN – endocarp;
LC – lenticel;
SZ – zone of dehiscence.

EP – epicarp;
ME – mesocarp;

Figs 39-41. *Catharanthus pusillus*39. A pair of follicles, $\times 1$ 40., 41. Diagrammatic and cellular diagram of pericarp showing tissue zones, $\times 25$; $\times 85$ Figs 42-44. *Holarrhena antidysenterica*42. A pair of follicles, $\times 8$ 43., 44. Diagrammatic and cellular diagram of pericarp showing tissue zones, $\times 20$; $\times 110$ Figs 45-49. *Strophanthus wallichii*45. A pair of diverged follicles, $\times 1$ 46., 47. Diagrammatic and cellular diagram of pericarp showing tissue zones, $\times 4$; $\times 22$ 48. Endocarpic sclereids, $\times 160$ 49. Comose seed, $\times 3$.

Abbreviations: BC – bundle cap;
EN – endocarp;
LC – lignified cell;
SC – seed chamber;

C – calyx;
EP – epicarp;
ME – mesocarp;
VB – vascular bundle;

DZ – dehiscing zone;
L – lenticifer;
pH – phloem;
XY – xylem.

and proceeds towards the periphery. Seeds are oval cylindric with white hair at one end and are dispersed by parachute mechanism.

Parsonsia spiralis WALL.

Follicular fruit is pointed at one end and the other blunt end is with persistent calyx (Fig. 18). A mature follicle measures approximately 6 cm in length and 0.8 cm in diameter. Both the follicles are fused by their ventral sides from base to tip, which is due to a strong postgenital carpel fusion.

The single layered epicarpic cells are rectangular or radially elongated (Fig. 19) interrupted by stomata, unicellular hairs and polygonal in surface view. Mesocarp is 34-36 layered thick. Grouped fibres are present in the mesocarp, adjacent to the epicarp, as broken or continuous band (Fig. 19). There are 50-55 conjoint, collateral or bicollateral bundles, arranged more or less in a ring. Druse crystals are present in the mesocarp. Endocarp is 2-3 layered. Its innermost layer is formed of tangentially elongated cells, while the rest of the cells are rectangular or radially elongated (Fig. 19).

At maturity both the follicles separate from each other and dehisce through the thin-walled empty cells of the zone of dehiscence at ventral sutures which are at right angles to the zone of fruits separation (Fig. 20). Seeds are comose at one end.

Strophanthus wallichii A. DC.

A mature fruit is 12-15 cm long and 3-3.5 cm thick. The two follicles developing from a single flower diverge at 180° (Fig. 45). The follicle is greenish-violet in colour with numerous lenticels on its surface.

The epidermis of radially elongated cells with 3-4 layers of collenchymatous hypodermis constitute the multilayered epicarp (Figs 46, 47). Epicarpic cells are rectangular in shape, interrupted by numerous lenticels. The stomata are totally absent. The Collenchymatous zone of the epicarp possesses starch grains. A thick cuticle is present over the epicarp.

The mesocarp is 300-350 layered and the cells are parenchymatous with intercellular spaces. Patches of thick-walled cells are present throughout the mesocarp and sometimes also above the scattered vascular bundles as bundle caps (Fig. 47). These thick-walled cells are pitted and many of them have reduced cell lumens. Laticifers are found throughout the mesocarp. The endocarp is 4-5 layered and sclerenchymatous; sclereids are heavily thickened with numerous pits (Figs 47, 48).

The fruit opens through the ventral suture. Two rows of thin walled cells on the ventral side of the fruit, extending from periphery to interior, constitute the "zone of dehiscence". Fruit dehisces through this zone by slackening the thin-walled, elongated cells. Thus exposes the comose seeds (Fig. 49) which are attached marginally to the placenta.

Vallaris solanacea (ROTH) O. KTZE.

The fruit is a pair of dark green, pendent and ventrally fused follicles (Fig. 21). A mature follicle measures approximately 12 cm in length and 2.5 in diameter.

The outermost layer together with the collenchymatous zone beneath it form the multilayered epicarp. Numerous anomocytic stomata, ventilating pores and unicellular hairs are present on the fruit surface. On the ventral side, epicarpic cells are smaller in size and are fused with the epicarpic cells of the adjacent fruit.

The mesocarp is parenchymatous, formed of 160-180 layers of cells embedding vascular bundles and laticifers. Grouped sclereids are present throughout the mesocarp, and sometimes found as bundle caps (Fig. 23) Laticifers are of non-articulated type with milky latex. Druse crystals are present in the mesocarp.

The endocarp is 10-15 layered and sclerenchymatous, of which the innermost 4-6 layers of cells are tangentially elongated and the remaining endocarpic cells are rectangular or polygonal in shape (Fig. 24). Laticifers are present inbetween the endocarpic cells. Endocarpic sclereids have pitted walls.

Both the follicles fuse ventrally from base to tip due to a strong postgenital carpel fusion. A separation of the two ventrally fused follicles is a must before dehiscence. Thus the zone of separation in transection is found at right angle to the zone of dehiscence (Fig. 22) lined with small thin-walled parenchyma cells. Both the follicles separate while drying and later dehisce through their ventral sutures. Seeds are comose at one end and are compactly arranged in the chamber causing impressions on the inner endocarpic layer.

Vinca major L.

The fruit is a beaked follicle (Fig. 25) constricted at the centre. Two follicles developing from a single flower show equal or unequal lengths. A mature fruit measures approximately 4 cm in length and 0.6 cm in diameter. Calyx is persistent at the fruit base.

The outermost zone of the pericarp is the epicarp, which is single-layered, interrupted by stomata (Fig. 26). A thin cuticle is present on the outer tangential wall of the pericarp. The mesocarp is 12-14 layered, embedding 10-20 vascular bundles and laticifers. Xylem parenchyma and many phloem cells possess starch grains. The endocarp is 1-2 layered with thickened walls (Fig. 26, 27).

Dehiscence of the fruit is marginal. Cells in the zone of dehiscence are smaller in size and empty towards maturity. On either side of the dehiscing zone 2-3 layers of parenchyma cells become thickened (Fig. 28), which initiates from periphery towards centre. Seeds are black, elongated and curved, devoid of hairs.

Wrightia tinctoria (ROXB.) R. BR.

Follicular fruits in pairs show unequal development and are free or attached by their tips (Fig. 29). The fruit is dark green and slender measuring approximately 20 cm in length and 0.6 cm in diameter. The surface of the fruit appears rough due to the presence of numerous lenticels.

Structurally the pericarp can be differentiated into epicarp, mesocarp and endocarp (Fig. 30). The epicarp is multilayered, formed of the outermost layer together with the underlying collenchymatous cells. Stomata and hairs are absent. The mesocarp is 40-45 layered thick. Z zone of 2-3 layers of mesocarp above the endocarp has smaller cells. There are 26-28 conjoint, collateral, bicollateral or concentric bundles arranged in a ring. Each bundle has a bundle cap of thick-walled cells. Laticifers are seen singly and more on either sides of the zone of dehiscence (Fig. 32). Mesocarpic cells possess starch grains. The multilayered endocarp can be differentiated into inner and outer zones. The inner endocarp is formed of 3-4 layers of tangentially elongated cells with highly reduced cell lumens. The outer endocarp consists of 6-8 layers of radially elongated cells (Figs 30, 31).

Dehiscence of the fruit is marginicidal (Fig. 32) at its drying. Seeds are comose at one end and are dispersed by parachute mechanism.

Wrightia tomentosa ROEM and SCHULT

Fruit is a pair of ventrally fused dark green pendent follicles (Fig. 33) measuring 20 cm in length and 0.8 cm in diameter. Numerous lenticels are present throughout the fruit surface.

Histologically the pericarp is differentiated into three zones: epicarp, mesocarp and endocarp (Fig. 34). The outermost pericarpic zone is the epicarp formed of 6-8 layers of collenchyma together with the outermost layer. The epicarp is covered with a thick cuticle. Epicarpic cells are rectangular in surface view interrupted by numerous lenticels (Fig. 35), but stomata are totally absent. The collenchymatous zone possesses starch grains (Fig. 35).

The mesocarp is 60-70 layered. Two rows of vascular bundles are embedded in the mesocarp of which the outer row consist of 34-36 comparatively larger bundles and inner row is formed of 50-55 smaller bundles. The vascular bundles are partially sheathed by sclereified bundle caps. Laticifers are seen singly and are comparatively larger than the surrounding parenchyma cells with deeply stained walls. A zone of 2-4 layers of mesocarpic cells just above the endocarp appears to be made of smaller cells (Fig. 36).

The endocarp is multilayered and sclerenchymatous with two distinct zones. The inner zone is formed of 2-4 layers of radially elongated cells, while the outer zone consists of 8-10 layers of cells (Fig. 36). Cell lumens are highly reduced in the inner endocarpic cells.

The region where the two follicles fused ventrally is the zone of separation and the zone of dehiscence is the region where the margins of the carpel fused (Figs 37, 38). The zone of dehiscence is at right angle to the zone of separation. Margin of the follicle is 60-70 layered and either side of it is lined with sclereified cells as a continuation of the endocarp, extending upto the lower side of the placenta. Prior to dehiscence, the separation of two follicles takes place through the thin-walled cells of the zone of separation. After the separation of the follicles, the fruit dehisces centripetally through the ventral suture. Seeds are comose.

DISCUSSION

In the present investigation it is found that the two follicles of a pair-product of a single flower show their fusion by their ventral sides in *Parsonsia*, *Vallaris* and *Wrightia* (*W. tomentosa*). The fused follicles are the result of a strong postgenital carpel fusion. Endress et al. (1983) have made a survey about the occurrence of post carpel fusion and found that in families like *Rutaceae*, *Sinarubaceae*, *Sterculiaceae*, *Loganiaceae*, *Apocynaceae* and *Asclepiadaceae* the carpel fusion appears to be temporary, i.e. up to anthesis; after that each carpel separates and develops into individual fruit. In *Nerium* also the follicles are fused from base to tip (Thomas and Dave 1991 a). Carpel fusion in *Asclepiadaceae* and *Periplocaceae* is also found to be temporary, hence free follicles are produced (Dave and Kuriachen 1991).

The fused follicular pair, produced as a result of strong carpel fusion, can be considered as an advanced character over the free follicles, a character taken as primitive by Roth (1977).

The follicles in *Apocynaceae* show a more or less identical internal organization of tissues, such as epicarp, mesocarp

and endocarp as in other follicles (Zala et al. 1976, Thomas and Dave 1991 a, b, Dave and Kuriachen 1991, Kuriachen et al. 1991). According to Roth (1977) epicarp is the outermost zone of the pericarp; usually uniseriate and in many fruits represents the main protective layer. Single layered epicarp is observed in the follicles of *Catharanthus* (Zala et al. 1976) and *Asclepias* (Dave and Kuriachen 1990); but multilayered epicarp, formed of the outermost layer together with a hypodermis is noticed in many members of the present study and also in *Nerium* (Thomas and Dave 1991 a) and in several genera of *Asclepiadaceae* e.g. *Tylophora*, *Gymnema*, *Marsdenia*, *Wattakaka*, *Ceropegia* and *Leptadenia* (Kuriachen et al. 1992). The epicarp is covered externally with a thick cuticle showing intrusions into the cells, which may reduce the transpiration rate during summer. In *Parsonsia* and *Strophanthus*, stomata are replaced by lenticels. They are also noticed in *Plumeria* (Thomas and Dave 1991 b) and in many other fruits (see Roth 1977). Tanniniferous contents present in the hypodermis furnish taxonomic clues.

The mesocarp is parenchymatous showing two distinct zones – the outer and inner as in *Wrightia* sp. on the basis of their cell size and shape. Kuriachen et al. (1992) has also observed zonation of mesocarp in the follicles of *Asclepiadaceae*. As in *Asclepiadaceae*, the formation of air chambers in the mesocarp, which is due to the disintegration of its cells towards the maturity of the fruit, does not occur in the follicles of *Apocynaceae* and *Periplocaceae* (Dave and Kuriachen 1991). The formation of air chambers helps in the dehiscence of the follicle and the dispersal of its seeds, hence it is considered as an advanced character. The occurrence of fibrous bundles is noticed in many follicles of *Apocynaceae* and *Asclepiadaceae*. As in *Tylophora* and *Gymnema* of *Asclepiadaceae* here in *Parsonsia* of *Apocynaceae* the fibre bundles are found situated in the peripheral part of the mesocarp, arranged in the form of a ring. Sclerified bundle caps present in the follicle act as tissue of resistance at the time of dehiscence (see Roth 1977).

The endocarp is multilayered and thick walled. The formation of two distinct zones in the endocarp is observed as a characteristic feature of legume (Fahn and Zohary 1955). Such a distinction of the endocarp is noticed in *Plumeria* (Thomas and Dave 1991 b), *Cryptostegia* (Dave and Kuriachen 1991), *Vallaris* and *Wrightia* (Thomas 1989). In *Aganostma* the endocarpic fibres are found elongated in transverse and oblique directions which result in the formation of a parquetry pattern of cell arrangement when seen in surface view. According to Roth (1977) a parquetry pattern develops when the inner epidermal cells may cease with their anticlinal divisional activity, in earlier stages of development than those of outer epidermis and are exposed to tangential stress, and often elongate in longitudinal or tangential or even in different directions. Parquetry pattern of endocarpic tissue is also reported in the follicles of *Asclepiadaceae* (Dave and Kuriachen 1987, Kuriachen et al. 1990).

The type of dehiscence is determined by the outer morphological and the inner anatomical structure of the carpel (Roth 1977). Stopp (1950) distinguishes only two types of dehiscence, ventricidal and septicidal, of which ventricidal is more primitive. According to Roth (1977) the margins of the carpel fuse secondarily during ovary development and the opening is through this region, hence the term "marginicidal" is more appropriate than the "ventricidal".

Roth (1977) reported that the sutures are reformed and predestined regions of dehiscence where the carpel walls develop secondary lines or regions of weakness. The dehiscent zone is

composed of thin-walled, interdigitating cells. The dehiscing zone is evident in the ovary stage of *Nerium*, while in *Catharanthus* it started to appear in the 3rd stage of fruit development. The mechanism of fruit dehiscence is mostly based on active movements brought about by dead or living tissues (Haberlandt 1924, Guttenberg 1971). The thick-walled lignified fibrous endocarp creates a hygroscopic tension in the pericarp by swelling and shrinkage. According to Fahn and Zohary (1955) the fibres show stronger swelling and shrinkage capacity than other cell elements and thus create a hygroscopic tension. The dehiscence under dry conditions termed xerochasy is found in the follicles of *Apocynaceae* except in *Ervatamia*, where the fruit dehisces prior to the drying of the pericarp (Thomas 1989). In the fused follicles, a separation of the two follicles is a must phenomenon before the dehiscence of individual follicles.

Taxonomic significance

It is evident that comparative studies of fruit wall structures will be much more effective taxonomic tool. Different anatomical characters have been taken into consideration to distinguish the fruits of same genera or different genera of the same family; Fahn and Zohary (1955) used the nature of hard layers in the pericarp for the classification of legume types; the "U" shaped thickening of the endocarp in the tribe *Cynoglosseae* is found to be used by Bayer de Kraemer (1970) for distinguishing this group from *Boraginaceae*; Dave (1986), and Dave and Menon (1986) considered various morphohistogenic features of the fruit, like structure of epicarp, mesocarp and endocarp to distinguish the members of *Solanaceae* up to species level. Dave and Menon (1989), Kuriachen and Dave (1989), Dave and Kuriachen (1991, Kuriachen et al. (1992) also have used pericarpic characteristics for taxa identification in *Umbelliferae*, *Oleaceae*, *Periplocaceae* and *Asclepiadaceae*, respectively. According to Roth (1977) families in which the fruit structure is more or less uniform, may be used for the establishment of fruit taxonomy. Follicle anatomy of *Apocynaceae* on gross structure base is more or less the same, even then the genera can be distinguished by morphological and anatomical features of fruits, which have been given below in a tabular form:

1. Follicles fused:

2. Lenticels present:

3. Ridges and furrows absent; epicarpic hairs present; tanniferous cells absent *Parsonia*
3. Ridges and furrows absent; epicarpic hairs absent; tanniferous cells absent *Wrightia* (*W. tomentosa*)

2. Lenticels absent:

4. Ridges and furrows present; epicarpic hairs present; tanniferous cells present *Nerium* (Thomas and Dave 1991 a)

1. Follicles free:

5. Tannin cells present:

6. Fruit ridged; epicarpic hairs present; lenticels absent; endocarp 2-3 layered; seed comose *Aganosma*

6. Fruit ridged; epicarpic hairs present; lenticels absent; endocarp 2-3 layered; seed comose *Ichnocarpus*
6. Fruit ridged; hairs absent; lenticels absent; endocarp 3-4 layered; seed comose *Holarrhena*
6. Fruit non-ridged; epicarpic hairs absent; lenticels present; endocarp 16-20 layered; seed not comose but winged *Plumeria* (Thomas and Dave 1991 b)
6. Fruit non-ridged; epicarpic hairs absent; lenticels present; endocarp 4-5 layered; seed comose *Strophanthus*
5. Tannin cells absent:
 7. Fruit ridged; lenticels absent; endocarp sclereified; seed devoid of coma *Catharanthus*
 7. Fruit not ridged; lenticels present; endocarp sclereified; seed comose *Wrightia* (*W. tinctoria*)
 7. Fruit not ridged; lenticels absent; endocarp not sclereified; seed not comose, but arillate *Ervatamia* (Thomas 1989)
 7. Fruit not ridged; lenticels absent; endocarp sclereified; seed comose *Alstonia*

Key to species:

Catharanthus G. Don

1. Fruit beaked; constricted at the centre; two seeded; pericarp 14-16 layered; endocarp 1-2 layered *C. majus*
1. Fruit not beaked; many constrictions; many seeded:
 2. Pericarp 12-15 layered; endocarp 3-4 layered *C. roseus*
 2. Pericarp 6-8 layered; endocarp 1-2 layered *C. pusillus*

Phylogenetic significance

According to Roth (1977), an evolution of fruit type is mainly based on two criteria: (i) changes of gynoecium types, (ii) distinct differentiation of fruit wall tissues. Phylogenetically the dehiscent fruit is considered as primitive, among which ventricidal (marginicidal) dehiscence is considered as the most primitive. Fused follicles are more advanced than free follicles. In *Apocynaceae*, *Nerium*, *Parsonia*, *Vallaris* and *Wrightia* (*W. tomentosa*) have pairs of fused follicular fruits. In fused follicles, prior to the dehiscence, a separation of the two follicles, is a must.

In an anatomical comparison of the follicles of *Apocynaceae*, *Ervatamia* (Thomas 1989) is more advanced because: (a) the follicle is not much elongated; (b) there is absence of thick walled cells in the pericarp; (c) the fruit dehisces before drying of the pericarp; and (d) there is a less number of seeds. But the character free follicles and arillate seeds of this

plant is primitive (Corner 1976). Follicles of *Catharanthus* and *Vinca* also can be considered as advanced, except that it doesn't have fused follicles. If the reduction of mechanical tissues and development of air chambers can be considered as evolved characters, the follicles of *Asclepiadaceae* are more advanced than *Periplocaceae* and *Apocynaceae*.

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TABLE 1. A comparative account of the follicles of *Apocynaceae*, *Asclepiadaceae* and *Periplocaceae*

Sr. No.	Characters	<i>Apocynaceae</i> (Present study; Thomas Dave 1989)	<i>Asclepiadaceae</i> (Dave and Kuriachen 1989; Kuriachen et al. 1991, 1992)	<i>Periplocaceae</i> (Kuriachen 1989; Dave and Kuriachen 1991)
1	2	3	4	5
1	Fruit type	follicle, berry, capsule, drupe	follicle	follicle
2	Follicle	fused or free	free	free
3	Epicarp	single or multilayered	single or multilayered	multilayered
4	Cuticular ornamentation	absent	present	absent
5	Lenticels	present	absent	absent
6	Hypodermis	collenchymatous or sclerenchymatous (2-8 layered)	colenchymatous (3-8 layered)	collenchymatous or sclerenchymatous (3-10 layered)
7	Mesocarp	4-350 layered	30-140 layered	10-140 layered
8	Aerenchyma	absent	present	absent
9	Tannin content	present	absent	present
10	Vascular cambium	present	absent	absent
11	Endocarp	1-15 layered	2-14 layered	3-20 layered
12	Placenta	Marginal devoid of aerenchyma	Marginal aerenchymatous	Marginal devoid of aerenchyma
13	Seed	comose, winged, arillate or devoid of coma	comose	comose
14	Dry fruit	more or less retains its shape	shrinkage is noticed	more or less retains its shape

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ZNACZENIE BUDOWY ANATOMICZNEJ MIESZKA W RODZINIE APOCYNACEAE

STRESZCZENIE

Badano strukturę perykarpu, z uwzględnieniem epikarpu, mezokarpu i endokarpu, w celu poznania taksonomicznego i filogenetycznego znaczenia następujących rodzajów z rodziny *Apocynaceae*: *Aganosma*, *Catharanthus* sp., *Holarrhena*, *Ichnocarpus*, *Parsonsia*, *Strophanthus*, *Vallaris* i *Wrightia* sp. W rodzajach *Catharanthus*, *Ichnocarpus*, *Parsonsia* i *Vinca* stwierdzono epikarp jednowarstwowy, natomiast w pozostałych rodzajach – wielowarstwowy. Mezokarp ma budowę parenchymatyczną, wnika w obszar wiązkowy i niepołączonych rur mlecznych. Natomiast endokarp ma budowę wielowarstwową i grube ściany komórkowe. Pęknięcie dojrzałych mieszków odbywa się wzdłuż brzegów owocolistka. Przedstawiono porównawczą tabelę cech budowy mieszka *Apocynaceae*, *Asclepiadaceae* i *Periplocaceae*. Dołączono również klucz taksonomiczny oparty na właściwościach budowy mieszka, pozwalający oznaczać rodzaje i gatunki.

SŁOWA KLUCZOWE: *Apocynaceae*, pęknięcie owocu, anatomia mieszka, filogeneza, taksonomia.